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1   Improved estimation of intrinsic growth r_{max} for long-lived species: integrating matrix models

2   and allometry

3

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21   ABSTRACT

22

23   Intrinsic population growth rate (r_{max}) is an important parameter for many ecological

24   applications, such as population risk assessment and harvest management. However, r_{max} can be

25   a difficult parameter to estimate, particularly for long-lived species, for which appropriate life

26   table data or abundance time-series are typically not obtainable. We describe a method for

27   improving estimates of r_{max} for long-lived species by integrating life-history theory (allometric

28   models) and population-specific demographic data (life table models). Broad allometric

29   relationships, such as those between life history traits and body size, have long been recognized

30   by ecologists. These relationships are useful for deriving theoretical expectations for r_{max}, but

31   r_{max} for real populations may vary from simple allometric estimators for 'archetypical' species of

32   a given taxa or body mass. Meanwhile, life table approaches can provide population-specific

33   estimates of r_{max} from empirical data but these may have poor precision from imprecise and

34   missing vital rate parameter estimates.   Our method borrows strength from both approaches to

35   provide estimates that are consistent with both life-history theory and population-specific

36   empirical data, and are likely to be more robust than estimates provided by either method alone.

37   Our method uses an allometric constant: the product of r_{max} and the associated generation time

38   for a stable-age population growing at this rate. We conducted a meta-analysis to estimate the

39   mean and variance of this allometric constant across well-studied populations from three

40   vertebrate taxa (birds, mammals, and elasmobranchs) and found the mean was approximately 1

41   for each taxon.   We used these as informative Bayesian priors that determine how much to

42   'shrink' imprecise vital rate estimates for a data-limited population toward the allometric

43   expectation. The approach ultimately provides estimates of r_{max} (and other vital rates) that

44   reflect a balance of information from the individual studied population, theoretical expectation,

45   and meta-analysis of other populations. We applied the method specifically to an archetypical

46   petrel (representing the genus *Procellaria*) and to white sharks (*Carcharodon carcharias*) in the

47   context of estimating sustainable fishery bycatch limits.

48

49   Keywords: Population dynamics; integrated population models; demography; intrinsic growth

50   rate

51   INTRODUCTION

52

53   The intrinsic rate of increase is the maximum potential exponential growth rate a population can

54   achieve under optimal resource conditions in its environment (Caughley 1977). It is a key

55   parameter for understanding life-history evolution and population dynamics, and is important in

56   many conservation applications. Intrinsic growth and related terms have been variously defined

57   in the literature (e.g., r_{max}, r_m, $r_{intrinsic}$, $\bar{r}$; Caughley 1977, Niel and Lebreton 2005, Gedamke et al.

58   2007, Fagan et al. 2010). For practical application purposes, our interest is the maximum growth

59   rate that would be possible for a real-world, low-density population (e.g., a small founding

60   group, or one in early stages of recovery from severe depletion) with a stable age distribution in a

61   broadly favourable natural environment, which we refer to as r_{max}. In wildlife and fisheries

62   management, r_{max} may be used for projecting population recovery times, conducting population

63   viability analyses, or estimating exploitation or removal rates that correspond to management

64   targets or thresholds. For example, many species of marine megafauna are impacted by

65   incidental catch (or bycatch) from fisheries (Lewison et al. 2004, Moore et al. 2013). For these

66   data-poor species, the intrinsic growth rate is a fundamental parameter for estimating incidental

67   fishery-catch limits (Moore et al. 2013) and conducting certain types of Ecological Risk

68   Assessments (ERAs) based on the use of Productivity and Susceptibility Analyses (PSAs)

69   (Cortés et al. 2010, Hobday et al. 2011).

70

71   Unfortunately, intrinsic growth rates are difficult to estimate for many species or populations,

72   particularly for many long-lived data-limited species in need of active management. For

73   example, under the U.S. Marine Mammal Protection Act, bycatch mortality to a marine mammal

74   population must be below an estimate of Potential Biological Removal (PBR) or else

75   management procedures to reduce bycatch must be initiated. PBR is calculated as a function of

76   population abundance and intrinsic growth rate estimates (Wade 1998, Taylor et al. 2000). The

77   latter is unknown for most populations, so default values are typically used (0.04 for cetaceans,

78   0.12 for pinnipeds), but the appropriateness of these defaults has not been fully evaluated.

79   Obtaining species- or population-specific estimates of the intrinsic growth rate would therefore

80   improve the PBR management scheme.

81

82   Intrinsic growth rates may be estimated directly or through model-based approaches. Direct

83   estimation requires fairly long time series (relative to generation time) of abundance estimates

84   for fast-growing (e.g., recovering) populations whose growth rates are not yet limited by

85   resource availability and which have age distributions at least close to the stable age distribution.

86   Where these circumstances exist, regression methods for estimating average growth rate as a

87   function of time or population abundance are straightforward to implement (e.g., Eberhardt and

88   Simmons 1992, de Valpine and Hastings 2002, Morris and Doak 2002, Sibly et al. 2005, Clark et

89   al. 2010). However, such data are not usually available, particularly for certain types of species,

90   e.g. the long-lived and late-maturing marine species that motivate our research, whose age as

91   first reproduction can be >10 years and lifespans are decades. Such species are particularly

92   sensitive to human impacts on survival rates (Heppell et al. 1999, 2005). For these species,

93   direct estimates of intrinsic growth generally require decades of data, usually from well-

94   monitored populations recovering from intensive human exploitation after effective conservation

95   measures have been put in place (e.g., Best 1993, Balazs and Chaloupka 2004). Few large

96   marine vertebrate populations fit these criteria. Therefore, despite any limitations from

97   simplifying assumptions (e.g. simplified biology, ignoring density-dependence or senescence),

98   model-based approaches to estimating r_{max} are more common and more practical, at least for

99   these types of species.

100

101   In the wildlife demography literature, there are two general classes of model-based methods for

102   estimating r_{max} or $\lambda_{max} = \exp(r_{max})$ for most populations of long-lived species: analysis of life

103   table methods, and life-history theory and allometric scaling relationships. For purposes of the

104   current analysis, we refer to life table methods in the sense of calculating r_{max} from estimates of

105   annual survival and reproductive rates (in presumably non-limiting resource conditions) using

106   matrix algebra methods (e.g., eigenanalysis or solving the characteristic equation; Caswell 2001)

107   or solving the discrete form of the Euler-Lotka equation (see Skalski et al. 2008, Fagan et al.

108   2010 for good methodological overviews). Allometric methods use empirically verified

109   relationships across species within broad taxonomic groups between demographic rates (e.g.,

110   survival rates, lifespan, age at maturity) and organismal characteristics (namely body size or

111   metabolic rate) to make inference about population growth rate from relatively few input

112   parameters (e.g., Hennemann III 1983, Savage et al. 2004a, Savage et al. 2004b, Niel and

113   Lebreton 2005, Hone et al. 2010). Both approaches have been used to assess risk for long-lived

114   populations. For example, PSAs for sharks have used estimates of λ_{max} derived from matrix

115   models (Cortés 2002, Simpfendorfer et al. 2008, Cortés et al. 2010), while allometric models

116   have been used in developing estimates of Potential Biological Removal (PBR) for birds (Niel

117   and Lebreton 2005, Dillingham and Fletcher 2008, Dillingham 2010, Dillingham and Fletcher

118   2011, Richard and Abraham 2013).

119

120   The two types of model-based approaches have individual advantages but also individual

121   shortcomings. The advantage of using life table methods is that estimates of r_{max} account for age

122   structured demographic rates and these are empirically informed for the population of interest.

123   However, it is difficult to know whether field measures of demographic rates correspond to those

124   that would be observed for a population growing at r_{max} (Gedamke et al. 2007, Fagan et al.

125   2010). Parameterizing a matrix model (or Euler-Lotka equation) may also be hampered by data

126   limitations (error in parameter estimates) and structural uncertainties about the life history

127   schedule (i.e., matrix dimensionality and how many parameters to include) (Heppell et al. 2000,

128   Lynch and Fagan 2009).

129

130   The advantage of using allometric methods is that these require fewer variables than life table or

131   matrix model approaches and fewer data from the particular study population. Rather, r_{max}

132   estimates are informed by well-established evolutionary relationships between, for example,

133   body size and various demographic rates. However, these methods are equally sensitive to input

134   parameter uncertainty and only provide theoretical or expected value estimates of population

135   growth (e.g., given an estimate of body size or age at maturity). As a result, an allometric

136   approach can fail to fully account for population- or species-level variation in demographic

137   complexity given that individual populations are expected to deviate from the 'archetype'

138   (Savage et al. 2006, Ginzburg et al. 2010). For example, Hone et al. (2010) found for mammals

139   a strong relationship between field estimates of population growth rates and age at maturity, but

140   growth rates for individual species could not be predicted precisely from the relationship.

141   Moreover, there remains uncertainty in allometric scaling relationships (Duncan et al. 2007) due

142   at least in part to methodological difficulties or inconsistencies in empirically testing the

143   underlying theories (Fagan et al. 2010).

144

145   We present a general approach that draws on the strengths of both types of model-based methods

146   to provide estimates of r_{max} that are consistent with both allometric theory and population-

147   specific empirical data, and that may therefore be more robust than estimates provided by either

148   method alone.

149

150   METHODS

151

152   **Background**

153

154   For long-lived species in particular, estimates of r_{max} from either life table or allometric methods

155   are strongly influenced by estimates of maximum adult survival. However, the bias in r_{max} (from

156   error in survival estimates) occurs in opposite directions for the two types of methods, a fact that

157   we exploit in our model development. For matrix models, higher survival values lead to higher

158   r_{max} values when other demographic parameters remain constant. Across species, however,

159   many parameters are correlated, and allometric models show that species with higher survival

160   rates generally have lower r_{max} values because of the evolutionary trade-off between survival (s)

161   and reproductive output (Williams 1966, Charnov 2005). For populations that are impacted by

162   anthropogenic mortality (e.g. bycatch in fisheries, hunting), use of empirical estimates of s will

163   either underestimate r_{max} (e.g. matrix models) or overestimate r_{max} (e.g. allometric models)

164   (Dillingham and Fletcher 2008). The differences between the two methods can be striking,

165   highlighting the potential risk from using empirical estimates of adult survival to estimate r_{max}

166   using either method alone. For an example petrel described in Table 1, treating an empirical

167   estimate of survival which incorporates substantial bycatch mortality ($s = 0.89$; Barbraud et al.

168   2008) as if it represented maximum survival would yield estimates of $r_{max} = 0.088$ using a

169   particular allometric model (*DIM*; Niel and Lebreton 2005) and $r_{max} = 0.006$ using a matrix

170   model. For some species (e.g. sharks) little is known about adult survival, and either method

171   would perform poorly. More generally, when there is parameter uncertainty each method can

172   produce estimates of r_{max} discordant with the other: e.g. allometric estimates of r_{max} that require

173   breeding success rates > 1 or similar impossibilities, or matrix model estimates of r_{max} that are

174   strongly inconsistent with ecological allometric theory. The approach we describe in this paper

175   is to analytically identify combinations of demographic parameters that produce matrix model

176   estimates that are also consistent with observed allometric relationships.

177

178   The particular allometric relationship we use is the approximate constancy (invariance) of the

179   product of r_{max} and the associated generation length (in years) for a stable-age population

180   growing at r_{max}. This generation length has previously been termed the "optimal" generation

181   length as generation time depends on conditions but r_{max} occurs when conditions are optimal

182   (Niel and Lebreton 2005); e.g. high survival combined with relatively early age at first

183   reproduction as might occur in resource-replete conditions for a low-density population.

184   Indicative of the general nature of this relationship, we denote optimal generation length using a

185   generic symbol (T_{opt}) not tied to any specific calculation; however, our actual calculations were

186   based on optimal mean generation length ($\overline{T}_{op} = \sum_{i=1}^{\infty} i l_i f_i$, where l_i is the survival probability

187   from birth to age i and f_i is the annual fecundity at age i; Leslie 1966, Niel and Lebreton 2005) as

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188   it is relatively insensitive to senescence (Niel and Lebreton 2005) which is difficult to model for

189   the data-poor populations included in this study. The approximate constancy of $r_{max}T_{opt}$ is based

190   on multiplying distinct allometric relationships for each variable. Allometric relationships are of

191   the form $p = aM^x$, where M is body mass, p is some characteristic, and a and x are constants;

192   these describe broad trends observed across species. Quarter-power exponents are common in

193   allometry (Savage et al. 2004a), and for r_{max} and T_{opt} the exponents are near -0.25 and 0.25,

194   respectively. Multiplying the two allometric relationships leads to the expected relationship

195   previously described (Lebreton 1981, Fowler 1988, Charnov 1993, Niel and Lebreton 2005):

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

197   where $a_{rT} = a_r a_T$ and a_r, a_T are the constants in the allometric equations for intrinsic growth rate

198   and generation time, respectively. The constancy of a_{rT} is assumed to hold within homogenous

199   taxonomic groups independent of body mass, but may vary between taxa. For example, Niel and

200   Lebreton (2005) demonstrated that $r_{max}T_{opt} \approx 1$ for 13 well-studied bird species (from diverse taxa

201   and spanning a large range in body sizes) whose populations were assumed to be growing under

202   non-limiting resource conditions.

203

204   Niel and Lebreton (2005) and Dillingham (2010) combined Eq. 1 with specific population

205   models that allow estimation of r_{max} with limited demographic data for archetypical populations.

206   For example, Niel and Lebreton (2005) use a simple age-based matrix model where adult

207   survival (s) and fecundity (f, female offspring per female per year) are constant from the age at

208   first reproduction (α), referred to as the *constant-fecundity model* (Dillingham 2010). For a

209   matrix of this form, mean generation time (Leslie 1966) reduces to $T = \alpha + s/(\lambda - s)$ (Niel and

210   Lebreton 2005) and, combined with the allometric model, provides the equation for the

211   *demographic invariant method* (*DIM*) (Niel and Lebreton 2005, Dillingham 2010):

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

213   In this context, α should represent the age at first reproduction under non-limiting resource

214   conditions. If a_{rT} is known (e.g., for birds, $a_{rT} \approx 1$; Niel and Lebreton 2005), then intrinsic

215   growth can be calculated, at least approximately, with minimal demographic data using Eq. 2.

216   That is, due to the structure of the matrix model and the requirement that $r_{\max}T_{\mathrm{opt}} = 1$ (for birds),

217   the only demographic parameters required to calculate $r_{\max}$ or $\lambda_{\max}$ are α and s; all other

218   parameters are implied by the model. Dillingham (2010) derived similar equations for a more

219   biologically-realistic model (termed the *varying-fecundity model*) that allows fecundity to

220   increase over a number of age classes but requires some additional information on fecundity.

221   Dillingham (2010) also noted that the varying-fecundity model can be approximated by the

222   constant-fecundity model if α represents a typical (e.g. near the mean or median) age at first

223   reproduction rather than the earliest age that some animals reproduce.

224

225   Our analysis has two parts. First, we develop two new methods to estimate $r_{\max}$ by integrating

226   matrix and allometric (i.e. $r_{\max}T_{\mathrm{opt}}$ invariance) models. Second, we use empirical data to

227   examine the constancy of $r_{\max}T_{\mathrm{opt}}$ for mammals and sharks in an effort to evaluate the taxonomic

228   generality of the relationship that was demonstrated for birds by Niel and Lebreton (2005); the

229   outputs of this meta-analysis are needed to apply the estimation methods to real populations.

230

231   The first $r_{\max}$ estimation method, which we term the *rT-exact* method for an *rT-ideal* population,

232   describes the population growth of an archetypical population. This method assumes the

233   population follows the allometric model exactly. We show how straightforward computational

234   methods allow us to generalise the approaches of Niel and Lebreton (2005) and Dillingham

235   (2010) to allow other matrix population models to be used, estimate the expected value for r_{max}

236   even when a point estimate of optimal (i.e. maximum) adult survival (s_{opt}) is unavailable, and

237   incorporate all available demographic information to inform results. The second method, termed

238   the *rT-adjusted* method, incorporates estimates of process variance (population-level variation)

239   in the $r_{max}T_{opt}$ relationship, appropriate for describing individual rather than archetypical

240   populations. For this method, we use allometric relationships to improve the precision of matrix

241   model results by adjusting estimates towards rT-exact estimates and generating more realistic

242   estimates of uncertainty in r_{max}, but still allow individual populations to vary from the allometric

243   expectation. To demonstrate the applicability and utility of these two new methods, we include a

244   demonstration application of our approach to two case studies regarding management and

245   population viability of an archetypical pelagic seabird (petrels of the genus *Procellaria*) and

246   white sharks (*Carcharodon carcharias*).

247

248   **Model Development**

249

250   The two new r_{max} estimation methods rely on simple variants of Eq. 1. The first method, the rT-

251   exact method, describes r_{max} for an archetypical, or rT-ideal, population, where Eq. 1 is exact.

252   Thus for rT-ideal populations,

253    $$r_{max}T_{opt} = a_{rT} \tag{3}$$

254   While the rT-exact method is useful to describe growth rates for archetypical populations, slight

255   departures from this relationship are expected for individual populations. To allow individual

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256   populations to vary from Eq. 1, we can assume that the variability is normally distributed and

257   model the product of intrinsic growth and optimal generation time as

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

259   where a_{rT} is the allometric constant and σ_{rT} is the population-level standard deviation, which

260   describes the amount of true variation across populations around the theoretical prediction for

261    $r_{\max}T_{\text{opt}}$. While Eq. 4 has advantages of simplicity, it does theoretically allow $r_{\max}T_{\text{opt}} < 0$. For

262   combinations of a_{rT} and σ_{rT} where negative values are a concern (e.g. a_{rT} is less than

263   approximately $2\sigma_{rT}$ from 0), a log-normal or truncated normal distribution could be used in place

264   of Eq. 4.

265

266   *The* rT-exact *method*

267   The rT-exact method combines matrix models with Eq. 3 in order to predict $r_{\max}$ for an

268   archetypical population. Given demographic parameters representative of maximal population

269   growth, matrix model (*MM*) estimates $r_{\max}^{MM}$ and T_{opt}^{MM} are calculated, e.g. using the Euler-Lotka

270   equation and the equation for mean generation time (Dillingham 2010), along with their product

271    $r_{\max}T_{\text{opt}}^{MM}$. If $r_{\max}T_{\text{opt}}^{MM}$ equals a_{rT}, then the population is rT-ideal; otherwise, it is not. Simply,

272   the rT-exact method requires that the matrix model is fully concordant with the allometric model.

273

274   Niel and Lebreton (2005) and Dillingham (2010) both presented special cases of the rT-exact

275   method. For illustration, assume a population that follows the constant-fecundity model where

276   s_{opt} is the only unknown parameter. For both *DIM* and matrix models, $r_{\max}$ is then simply a

277   function of s_{opt}. The relationship between model estimates of s_{opt} and $r_{\max}$ for *DIM* (i.e. Eq. 2)

278   and the matrix model for this illustrative population is shown in Fig. 1a. As s_{opt} increases, $r_{\max}$

279   increases for the matrix model (dashed line), but decreases for *DIM* (solid line). Because s_{opt} is

280   unknown, neither method can calculate r_{max} exactly. However, the point in Fig. 1a where these

281   lines intersect is where the matrix and *DIM* models agree, and is the solution for s_{opt} and r_{max}

282   from the rT-exact method. In short, this new approach finds the values of s_{opt} and r_{max} (using

283   numerical methods) where $r_{max}T_{opt}$ from the matrix model equals the allometric constant a_{rT}.

284

285   A more generic computational approach for rT-ideal populations is to (1) put prior distributions

286   on all parameters, (2) simulate a large number of matrix models, and (3) then calculate the

287   product of growth and generation time ($r_{max}T_{opt}^{MM}$) for each; and finally, (4) keep those iterations

288   that satisfy the allometric theory constraint of $r_{max}T_{opt}^{MM} = a_{rT}$ (within an allowed numerical

289   tolerance, i.e. $\left| r_{max}T_{opt}^{MM} - a_{rT} \right| \leq \delta$ for some small δ) and form the posterior distribution for

290    $r_{max}T_{opt}$. For data-rich populations, there may be relatively little uncertainty in $r_{max}T_{opt}^{MM}$, while

291   for data-poor populations the uncertainty would be large. Thus, uncertainty about r_{max} will

292   reflect uncertainty in demographic rates but parameters will be constrained by asserting that the

293   population must be rT-ideal. For the illustrative population shown in Fig. 1, if there was

294   uncertainty in parameters in addition to s_{opt}, matrix model methods would produce a range of

295   possible growth rates for each value of s. Equation 3 would be satisfied for all parameter sets

296   that produce combinations of α, s_{opt}, and λ_{max} that also satisfy Eq. 2. Figure 1b shows

297   realisations of 1000 simulated matrix models that are rT-exact (within $\delta = 0.05$).

298

299   *The* rT-adjusted *method*

300   The rT-adjusted method estimates population growth for individual populations by combining

301   matrix models with Eq. 4. This method relaxes the rT-ideal constraint and only assumes that

302    $r_{\max}T_{\text{opt}}$ is near a_{rT}, allowing for population-level variation from the ideal. The first three steps of

303   the computational approach are the same as for the rT-exact method (i.e. simulating and

304   calculating values for the matrix models). For the rT-adjusted method, step (4) is to simulate

305    $r_{\max}T_{\text{opt}}{}^{A}$ from the allometric model (A) (e.g. Eq. 4). Equation 4 is appropriate for the allometric

306   model as long as $r_{\max}T_{\text{opt}}{}^{A} > 0$ for the vast majority of iterations; otherwise, a log-normal or

307   truncated-normal model could be used instead. In step (5), those iterations where $r_{\max}T_{\text{opt}}{}^{MM}$ is

308   near $r_{\max}T_{\text{opt}}{}^{A}$ (i.e. $\left| r_{\max}T_{\text{opt}}{}^{MM} - r_{\max}T_{\text{opt}}{}^{A} \right| \leq \delta$) are kept and others discarded. For the constant-

309   fecundity population described in Fig. 1, matrix model estimates that fall near Eq. 2 are kept with

310   increasing probability (Fig. 1c), but no longer must lie on Eq. 2. In Supplement 1,

311   implementation of the rT-exact and rT-adjusted methods is described for the illustrative

312   population in Fig. 1.

313

314   The tolerance, δ, sets the allowable numerical error, where smaller values equate to higher

315   precision but increased computational time. Based on $a_{rT} \approx 1$ for birds (Niel and Lebreton

316   2005), $\delta \leq 0.05$ provides a reasonable balance between speed and precision (e.g. for a

317   population with generation time $T_{\text{opt}} = 10$ years, this corresponds to error of ± 0.005 in $r_{\max}$ for

318   any individual iteration, with overall error reduced by the total number of iterations) while

319    $\delta \leq 0.01$ is appropriate for high-precision applications or populations with lower generation

320   times. The resulting, integrated estimates (I) of intrinsic growth, generation time, and their

321   product ($r_{\max}^{I}$, T_{opt}^{I}, and $r_{\max}T_{\text{opt}}{}^{I}$) are derived from posterior intervals of the simulation, while the

322   integrated distribution for maximum annual growth (λ_{max}^{I}) is calculated by transforming

323   quantiles of r_{max}^{I}. As a diagnostic, we also examine the distributions of $r_{max} T_{opt}^{MM}$ and $r_{max} T_{opt}^{A}$,

324   where limited overlap could be used as a model diagnostic, potentially indicating flawed model

325   assumptions, data errors, or an unusual population.

326

327   **Estimating allometric parameters for birds, mammals and sharks**

328

329   We gathered data for birds, mammals, and sharks to estimate allometric parameters for each

330   group. Niel and Lebreton (2005) noted that Eq. 1 could be re-written as

331     $\log r_{max} = -\log T_{opt} + \log a_{rT}$. They therefore modelled the data as

332     $E(\log r_{max}) = \beta \log T_{opt} + \log a_{rT}$ and ran a regression to test the assumption of $\beta = -1$. The

333   authors then estimated a_{rT} by back-transforming the intercept in a revised model with the slope

334   forced to -1. Equation 4 is a similar but simpler model and is a natural extension of Eq. 1.

335   Further, it eliminates potentially difficult choices about which regression method to use (e.g.

336   ordinary least squares (OLS), major axis, or standardised major axis, see Warton et al. (2006)

337   and O'Connor et al. (2007) for discussion). However, the log-log regression provides an easy

338   way to examine relationships not evident from Eq. 4. For example, in an allometric analysis of

339   basal metabolic rate and mass, Kolokotrones et al. (2010) were able to find previously

340   undetected curvature and a body temperature effect by using regression methods within a log-log

341   regression.

342

343   We therefore modelled data using both the log-log regression and the simpler method based on

344   Eq. 4. The log-log regression was designed to examine general linearity and whether the slope

16

345   was near -1, and Eq. 4 was used to actually estimate a_{rT} and σ_{rT}. Since the first method was

346   used for basic diagnostics only, rather than adjusting the degrees of freedom or otherwise

347   modelling phylogenetic dependence, we simply note that the standard error of the slope from

348   OLS estimates may be underestimated if the dependence is strong, but other values (e.g. the

349   estimated slope and R^2) are appropriate for estimating r_{max} conditional on T_{opt} (O'Connor et al.

350   2007). We also note that the corresponding estimate of σ_{rT} from Eq. 4 will include the intrinsic

351   population-level variability (i.e. process error) that we are interested in, but also includes

352   measurement error and possible sources of model-based bias. Therefore, the actual population-

353   level variability is likely $< \hat{\sigma}_{rT}$.

354

355   For birds, we used the data from Niel and Lebreton (2005). For mammals, we used empirical

356   r_{max} estimates from count data for fast-growing populations for 41 out of 64 species compiled by

357   Duncan et al. (2007), including 10 orders of mammals and ranging in size from rodents and

358   lagomorphs to elephants and baleen whales. Data for the other 23 species did not satisfy

359   inclusion measures for our analysis (briefly, $r_{max} < 2$, $\alpha > 0.5$, and $s < 1$ when calculated by the

360   characteristic equation; see Appendix A for details). We compiled female age at first

361   reproduction and fecundity estimates from other published databases for the mammals (Ernest

362   2003, Jones et al. 2009, Tacutu et al. 2013), with the merged data available in Supplement 2 for

363   the 41 included species. To calculate generation time, survival estimates are also required.

364   However, age- or stage-specific survival estimates were not available, so we assumed a single

365   annual survival rate through life and found this rate by solving the characteristic equation for s:

366    $\lambda^{\alpha} - s\lambda^{\alpha-1} - fl_{\alpha} = 0$, where $\lambda = \exp(r)$ and $l_{\alpha} = s^{\alpha}$. The simplifying assumption of a single

367   survival rate is a suitable proxy for age-structured survivorship for purposes of estimating r and

368   allometric relationships (Lynch and Fagan 2009).   We then estimated optimal generation time

369   as $T_{\mathrm{opt}} = \alpha + s/(\lambda - s)$ (assuming α, s, were estimated for optimal or near-optimal conditions)

370   using the mean generation length (Leslie 1966) and an assumption of constant fecundity from

371   age at first reproduction (Niel and Lebreton 2005, Dillingham 2010), and performed a log-log

372   analysis *sensu* Niel and Lebreton (2005) to estimate the regression slope and confirm it was close

373   to −1. We then used the simpler Eq. 4 to estimate the allometric parameters.

374

375   For sharks, we used estimates of growth and generation time from matrix models presented by

376   Cortés (2002). Developing matrix models for sharks is challenging due to the lack of empirical

377   survival estimates for this taxon. In their place, Cortés (2002) used indirect estimators developed

378   primarily using data for teleosts, whose application to elasmobranchs has not been empirically

379   justified (Kenchington 2013). Cortés (2002) combined several different estimators and used the

380   differences between them as one approach to estimating uncertainty in survival. Therefore, the

381   estimates for sharks have greater measurement error and potential sources of bias than the

382   estimates for birds or mammals. While the values from Cortés (2002) may be broadly

383   interpreted as estimates of intrinsic growth, we recognise their limitations. For example, some

384   estimates of intrinsic growth were < 0, and estimates of uncertainty were conditional on the

385   assumed models for survival. We thus analysed the data to look for general consistency with the

386   log-log analysis and Eq. 4 and general similarities in parameter estimates between sharks, birds,

387   and mammals. Using only those populations where the estimate of $r_{\mathrm{max}} > 0$ led to 32 of 41

388   populations in Cortés (2002) for inclusion in the log-log analysis. Because Cortés (2002)

389   provided uncertainty estimates for population growth rates, we were able to perform an

18

390   additional analysis to estimate mean a_{rT} and the population-level variation in this parameter (σ_{rT})

391   by adjusting for measurement error in r_{max} (see Appendix A for details).

392

393   **Case studies**

394

395   *The* rT-exact *method for petrels*

396   Many petrel species (Family Procelliidae) are listed as threatened by the International Union for

397   Conservation of Nature (IUCN) due to incidental capture (bycatch) in fishing gear (BirdLife

398   International 2013). Because of these impacts, empirical estimates of survival, where available,

399   incorporate anthropogenic mortality and therefore do not represent potential maximum survival.

400   For example, recent survival estimates for the white-chinned petrel (*Procellaria aequinoctialis*)

401   are very low (<0.90) compared to similar, less impacted species (Barbraud et al. 2008). One

402   solution is to use survival estimates from congeneric species at lower risk from bycatch (e.g.

403   Barbraud et al. 2009, Dillingham and Fletcher 2011) to estimate r_{max} or λ_{max}, and recognise that

404   the estimates may be biased as a result or treated as an approximation. As an alternative

405   approach, we demonstrate the rT-exact method for an archetypical *Procellaria* species.

406

407   In this example, we compare estimates of λ_{max} from matrix, *DIM* (i.e. Eq. 2), and rT-exact

408   methods (λ_{max}^{MM} , λ_{max}^{DIM} , and λ_{max}^{rTe}), and also estimate optimal survival using the rT-exact method (

409   s_{opt}^{rTe}). Our purpose is to compare the sensitivities of λ_{max} to a_{rT} and the demographic parameters

410   among the three models to identify those parameters that, for a given level of error, most

411   influence point estimates of λ_{max}. By combining knowledge of sensitivities with estimates of

412   parameter uncertainty, this type of analysis can help a researcher determine which model is most

413   appropriate for their data; for example, models that are sensitive to parameters which have large

414   associated uncertainties would be expected to perform poorly.

415

416   We first built a matrix population model for a generic *Procellaria* species. We then selected

417   parameter values by examining relevant species-specific estimates available from primary or

418   secondary sources (Brooke 2004, Barbraud et al. 2008, Fletcher et al. 2008, Dillingham et al.

419   2012, ACAP 2013, BirdLife International 2013), with specific details described in Appendix A.

420   The resulting matrix was then used to estimate s_{opt} and λ_{max} using the rT-exact method, assuming

421    $a_{rT} = 1$ based on the estimate from Niel and Lebreton (2005). The rT-exact estimate of s_{opt} was

422   used for the matrix model and *DIM* approaches to estimate λ_{max}. Sensitivities of λ_{max} to model

423   parameters were then calculated using numerical derivatives.

424

425   *The* rT-adjusted *method for white sharks*

426   To demonstrate the rT-adjusted method, we built a matrix population model for the eastern north

427   Pacific population of white shark. In 2012, this population was petitioned for listing under the

428   U.S. Endangered Species Act. The National Oceanic and Atmospheric Administration (NOAA)

429   convened a Biological Review Team (BRT) of government scientists to evaluate relevant

430   scientific information and provide an assessment report (Dewar et al. 2014) that the Agency used

431   to determine whether the white shark should be listed as a threatened or endangered species (the

432   decision was to not list the species; 78 Federal Register 40104-40127). The population viability

433   analysis for the BRT assessment was partially based on estimates of r_{max}, derived using our

434   methods as presented here. We began by building a demographic matrix model for the white

435   shark, but parameter uncertainty meant that matrix model results, by themselves, were

436   unsatisfactorily imprecise. Therefore, in combination with the matrix model, we used the

437   estimates of allometric parameters (a_{rT}, σ_{rT}) for sharks (i.e. based on our analysis of the data

438   from Cortés (2002)), informed by estimates from the other taxa which had higher data-quality, to

439   provide rT-adjusted estimates of intrinsic growth.

440

441   Few vital rates are known precisely for white sharks, but variously informative priors can be

442   placed on all key parameters (see Appendix A for details). Drawing parameters from these

443   distributions provides a prior distribution for matrix model parameters $r_{max}T_{opt}^{MM}$ that does not

444   take the allometric model into account. To incorporate the allometric model, we matched each

445   matrix model draw with one from the allometric model ($r_{max}T_{opt}^{A}$), but used a log-normal

446   distribution in place of Eq. 4 so that $r_{max}T_{opt} > 0$. Similarly, we accounted for uncertainty in σ_{rT}

447   by sampling from a log-normal distribution with a CV based on our analysis of the Cortés shark

448   data (Cortés 2002). Those iterations where the allometric and matrix models agreed formed the

449   integrated, rT-adjusted posterior distribution.

450

451   Analyses were performed using R 3.0.1 (R Development Core Team 2013). For the Bayesian

452   analysis of the Cortés (2002) shark data, the OpenBUGS variant (version 3.2.2; Thomas et al.

453   2006) of BUGS (Lunn et al. 2000) was linked to R using the R2WinBUGS library (Sturtz et al.

454   2005), with estimates based on 4 chains of 260,000 iterations with the first 10,000 iterations

455   discarded and thinning set to 100, with good convergence diagnostics and low Monte Carlo

456   error.

457

458   RESULTS

459

460   *Estimating allometric parameters for birds, mammals and sharks*

461   All three taxonomic groups showed strong relationships between r_{max} and T_{opt} (Fig. 2), with R^2

462   from the log-log regression equal to 0.96, 0.91 and 0.72 for birds, mammals, and sharks,

463   respectively. In each case, the estimated slope was close to -1, with estimated slopes ($\pm$ 95%

464   confidence interval) equal to -0.93 $\pm$ 0.12 (birds), -0.99 $\pm$ 0.10 (mammals), and -0.96 $\pm$ 0.46

465   (sharks). Both R^2 and precision were lowest for sharks, which was expected given the

466   uncertainties in the matrix model estimates of r_{max} for them.

467

468   The allometric constants were similar for all three taxa, with $a_{rT} \approx 1$. Estimates of a_{rT} from Eq.

469   4 were 1.07 $\pm$ 0.09 (birds), 1.17 $\pm$ 0.09 (mammals), and 0.97 $\pm$ 0.25 (sharks). The associated

470   standard deviations, σ_{rT}, were estimated as 0.15 (birds), 0.30 (mammals), and 0.69 (sharks),

471   accounting for all sources of noise (i.e. population-level variability and measurement error, as

472   well as any model-based bias). When using the Bayesian model to adjust for measurement error

473   for sharks, $\hat{a}_{rT} = 0.84$ (95% credible interval 0.65 to 1.05) and the remaining error reduces to

474   $\hat{\sigma}_{rT} = 0.41$ (0.23 to 0.61). For an animal with a generation time of 10 years or more, this

475   suggests that variation in r_{max} among populations is likely < 0.04 for any of these taxa.

476

477   *Case Study 1: Petrels*

478   For the rT-ideal population based on the demography of *Procellaria* petrels, we treated s_{opt} as

479   unknown and other parameters as known, and calculated rT-exact estimates of population growth

480   (λ_{max}^{rTe}) and optimal survival (s_{opt}^{rTe}). Using s_{opt}^{rTe} in a matrix model and *DIM* (Eq. 2) allowed us to

481   compare sensitivities of three point estimators ($\lambda_{\max}^{rTe}$, $\lambda_{\max}^{MM}$, $\lambda_{\max}^{DIM}$) to demographic parameters to

482   analyse approximate model performance. The rT-exact estimate of the maximum growth rate

483   when $a_{rT} = 1$ is $\lambda_{\max}^{rTe} = 1.070$ (or $r_{\max}^{rTe} = 0.068$) and the corresponding estimate of optimal survival

484   is $s_{opt}^{rTe} = 0.947$. The estimates of $\lambda_{\max}$ and s_{opt} are very similar to those presented by Dillingham

485   and Fletcher (2011), who estimated $s_{opt} \approx 0.94$ using empirical data from a number of petrel

486   species and $\lambda_{\max} \approx 1.074$ using *DIM*.

487

488   For the rT-exact method where s_{opt} is unknown, intrinsic growth was most sensitive to a_{rT} and

489   the proportion breeding (k), and least sensitive to age at maturity, α (Table 1). Sensitivities were

490   always smaller when using the rT-exact method compared to the matrix model or *DIM* for shared

491   parameters. Hence, relative model performance depends on sensitivities and uncertainties for

492   those parameters not in common. Compared to the matrix model, the impact on $\lambda_{\max}$ of error in

493   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

494   method, if the other parameters were known without error. Compared to *DIM* estimates, the rT-

495   exact method has three additional parameters (c_1, c_2, which are the ratios of younger age-class

496   survival rates to adult survival, and k; see Appendix A) not used by *DIM*, while *DIM* has one

497   parameter (s_{opt}) not used by the rT-exact method. Because the rT-exact method is insensitive to

498   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

499   case where all errors are in the same direction) has the equivalent impact of error of 0.016 in s_{opt}.

500   From a management perspective, this means that the rT-exact method would be expected to

501   outperform *DIM* in most settings. The exceptions would be where c_1, c_2, and k are highly

502   uncertain or where s_{opt} is measured with high precision.

503

504   *Case Study 2: white sharks*

505   Distributions for $\lambda_{\max}$ from the matrix model only, allometric model only, and the rT-adjusted

506   method that integrates both models are in Fig. 3. For this example, we set $a_{rT} = 1$ and sampled

507   from a log-normal distribution with average population-level variation $\sigma_{rT} = 0.4$ (see Appendix

508   A for details). The value $a_{rT} = 1$ is consistent with the estimate from either Eq. 4 or the

509   Bayesian model that adjusted for measurement error for sharks (see Appendix A), as well as the

510   value for the other taxa with higher quality data. The rT-adjusted distribution reflects

511   uncertainty in matrix model parameters, but constrains the uncertainty so that Eq. 4 is satisfied.

512   While still allowing for population-level variability, Fig. 3 shows the constrained distribution

513   that results from incorporating allometric trends with the matrix model. The rT-adjusted

514   posterior distribution for $\lambda_{\max}$ for white sharks has a mean of 1.050, SD = 0.017, and 95%

515   credible interval of 1.022 to 1.091. By comparison, the distribution of $\lambda_{\max}$ for the matrix model

516   alone had a mean of 1.059, SD = 0.028, included negative values, and had a substantially wider

517   95% credible interval (1.008 to 1.114) that included unrealistically small values. The variance

518   for the rT-adjusted distribution was only 37% that of the variance for the matrix model (i.e.,

519    $0.017^2 / 0.028^2 = 0.37$), contains no negative values, and the credible interval represents a more

520   plausible range, showing the benefits of the rT-adjusted model compared to a matrix model for

521   this Case Study.

522

523   DISCUSSION

524

525   Generating robust estimates for demographic parameters and $r_{\max}$, in particular, for long-lived

526   species is a priority for both ecological research and conservation applications. Estimating

24

527   intrinsic growth from matrix models provides population-specific estimates, but precision can be

528   unsatisfactory when important demographic parameters such as survival are unavailable or

529   measured with low precision. Here, we have presented two new methods that combine

530   demographic information used for matrix models with broader ecological understanding

531   garnered from empirical allometric relationships to generate improved estimates of intrinsic

532   growth rates. The first (rT-exact) method provides estimates of intrinsic growth for what we call

533   an rT-ideal population (e.g., the expected growth rate for an archetypical population with a

534   particular combination of adult survival and maturation age). The second (rT-adjusted) method

535   acknowledges that species may vary from some theoretical expectation and thus incorporates

536   process error in the allometric constant (a_{rT}) to generate distributions for intrinsic growth that

537   reflect this natural variability. These methods can be applied generally, but are especially

538   applicable for data-poor populations, for which neither matrix models nor allometric models are

539   fully satisfactory. As our case studies demonstrate, our methods provide biologically meaningful

540   inferences about species life history parameters, and can inform conservation and management.

541

542   As with all models, our approach depends on empirically validating the theoretical prediction

543   with data; i.e. that the product $r_{max}T_{opt}$ is approximately invariant. Our meta-analysis of data for

544   birds, mammals, and sharks indicates that the theory is well-supported across several taxa with

545   expected $r_{max}T_{opt} \approx 1$ across the full range of generation lengths included in the datasets. Data

546   types and the amount of data used to evaluate this taxonomic generality varied by taxon. For

547   birds, r_{max} estimates were generated from matrix models for rapidly growing populations for

548   which high-quality demographic data were available, and a broad suite of taxa were represented

549   (Niel and Lebreton 2005). Estimates for r_{max} for mammals were based on count data for dozens

550   of rapidly increasing populations, although the dataset was taxonomically biased toward certain

551   orders with relatively high growth rates (e.g., many ungulate and carnivore species, few bats or

552   primates). For sharks, r_{max} was calculated from matrix models that relied on multiple indirect

553   survival estimators derived for teleosts (Cortés 2002). These differences suggest that estimates

554   of the allometric constants are most reliable for birds and least reliable for the data-poor sharks.

555   For the rT-adjusted method, quantifying population-level variation σ_{rT} and accounting for that

556   variation in predictive models is also required. For birds and mammals, relatively high-quality

557   data suggests that estimates of σ_{rT} primarily reflect the population-level variation that we are

558   interested in, but still incorporate some amount of measurement error. For sharks, we were able

559   to separate some of the measurement error from population-level variation by adding an

560   additional component to our model, but overall data quality was lowest for this taxon.

561

562   Given available data and the limited number of taxa studied, it is unknown whether $a_{rT} \approx 1$ is

563   general across all animal taxa or whether the similarities between values for these taxa were

564   coincidental or only apply to relatively long-lived species (noting that taxa characterized by truly

565   rapid growth potential such as teleosts or insects were not included in the analysis, nor were

566   mammals that mature younger than 1 year and have multiple litters per year). It is also unclear

567   whether the larger estimate of σ_{rT} for sharks was a result of model-based bias and uncertainty,

568   or possibly represents additional variation caused by greater phylogenetic diversity or

569   poikilothermy in that taxon. This suggests two areas of future research: (1) examining additional

570   taxonomic groups to better explore the generality of our findings, and (2) determining the effect

571   of model-based assumptions (e.g. from the use of indirect survival estimates) on the estimates of

572   the allometric parameters for sharks.

573

574   The rT-exact method, designed to estimate intrinsic growth for a typical population by

575   combining all available demographic data with knowledge of allometric patterns, was found to

576   yield robust estimates of r_{max} for a long-lived seabird even when important demographic

577   parameters (e.g. survival) are poorly known. In fact, while our focus is on estimating r_{max}, we

578   note that this method also can be used to estimate optimal survival and other demographic

579   parameters. Compared to methods such as *DIM* or matrix models that rely heavily on estimates

580   of adult survival for long-lived populations, the rT-exact method is relatively insensitive to its

581   parameter inputs and therefore error in any one has limited impact on the estimate of r_{max}. We

582   primarily focus on the effect of survival due to its importance in *DIM* and matrix models, but

583   estimation of other demographic parameters can be challenging for long-lived species (e.g. age at

584   first reproduction). In settings where survival is estimated well and other parameters poorly, the

585   rT-exact method would yield essentially the same estimates as *DIM* when using the constant-

586   fecundity model. For data-poor populations that have reproductive information available, and

587   where estimates of survival are poor or impacted by unquantified anthropogenic mortality, the

588   rT-exact method would perform especially well compared to the others. *DIM* and matrix

589   methods risk large bias in r_{max} when s_{opt} is measured poorly, while the rT-exact method reduces

590   this risk by taking advantage of the opposite directions of those biases. This is especially

591   important in conservation settings that use reference point (e.g., mortality limit) estimators based

592   on r_{max}. For example, PBR, which has also been adapted for seabirds and sea turtles (Dillingham

593   and Fletcher 2008, 2011, Curtis and Moore 2013, Richard and Abraham 2013), includes the

594   parameter $R_{max} = \exp(r_{max}) - 1$, and is <0.10 for many of the long-lived marine megafauna to

595   which it is applied (Moore et al. 2013). Small errors in R_{max} translate to large proportional errors

596   in the PBR, and therefore can have large management impacts (Dillingham 2010).

597

598   The second method we present, the rT-adjusted method, extends the first by focusing on

599   individual rather than archetypical populations. While the rT-exact method is useful for

600   predicting how we expect an archetype to behave and may be sufficient for many applications,

601   these predictions may not be sufficiently accurate for individual populations that differ from the

602   expectation, in which case population-level variation in r_{max} with respect to $r_{max}T_{opt}$ must be

603   accounted for. For these settings, the rT-adjusted method uses allometric patterns to adjust

604   matrix model estimates of population growth towards the allometric ideal, but still allows for

605   variation from it. The amount of adjustment depends on the distance between matrix model

606   estimates of $r_{max}T_{opt}$ and the allometric constant, the precision of matrix model estimates, and the

607   normal level of variation from the ideal expected within a taxon. While our analyses provide

608   initial estimates for σ_{rT} for three taxa, these estimates include sampling variance and thus over-

609   estimate population-level variance. Future research that improves the precision of these

610   estimates would make these methods even more useful.

611

612   Like any method, these methods should be used with care. While the primary purpose of the rT-

613   adjusted method is to improve precision of r_{max} estimates by using all available data, it also

614   naturally removes inconsistencies between allometric and matrix models. However,

615   inconsistencies could highlight data or model errors, or an interesting population that does not

616   follow the allometric trend. For example, inconsistencies between allometric and matrix models

617   could be a relatively simple way to identify whether the survival estimate used is potentially sub-

618   optimal. We therefore recommend that estimates from matrix and allometric models be

619   compared to each other and to the integrated estimates from the rT-adjusted method (as shown in

620   Fig. 3 for white sharks) as part of a quality control process.

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784

785 **Supplemental material**

786

787 **Appendix**

788   Appendix A: Data analysis to estimate allometric parameters for mammals and sharks, and

789   parameterising models for case studies

790

791   **Supplement**

792   Supplement 1: Worked example for the rT-exact and rT-adjusted methods

793   Supplement 2: Intrinsic growth (r_{max}) and vital rate estimates for 41 mammal species

794

795   Table 1. Sensitivity of $\lambda_{\max}$ to the allometric constant (a_{rT}), adult survival (s), the ratios of

796   breeding success and juvenile survival to adult survival (c_1, c_2), age at first reproduction (α), and

797   the proportion of adults breeding (k) for an archetypical *Procellaria sp.* petrel for matrix,

798   demographic invariant method (*DIM*), and rT-exact models. Sensitivities were calculated based

799   on the values $a_{rT} = 1$, $s = 0.947$, $c_1 = 0.8$, $c_2 = 0.9$, $\alpha = 7$, and $k = 0.75$.

		Model-type	
Parameter	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

800

801   FIGURE LEGENDS

802

803   Figure 1. The inverted relationship between optimal adult survival (s_{opt}) and intrinsic growth

804   (r_{max}) for matrix and allometric models can be used to predict r_{max}. The allometric model states

805   the product of intrinsic growth and optimal generation time ($r_{max}T_{opt}$) is approximately a constant

806   (a_{rT}). When $r_{max}T_{opt} = a_{rT}$ (Eq. 3) (a,b), we term this an rT-ideal population and consider it to

807   represent an archetypical population. In (a), s_{opt} is the only unknown, while in (b, c) there is

808   uncertainty in multiple parameters. In (a), the rT-exact solution (●) occurs where the matrix

809   model solution (- -) intersects the allometric solution (*DIM*, Niel and Lebreton 2005). In (b),

810   multiple demographic-parameter combinations from the matrix model within a small tolerance (δ

811   = 0.05) of *DIM* are rT-exact (●) while others (○) are not. In (c), the rT-adjusted method allows

812   individual species to deviate from being rT-ideal ($r_{max}T_{opt} \sim N(\mu, \sigma^2)$; Eq. 4), with iterations near

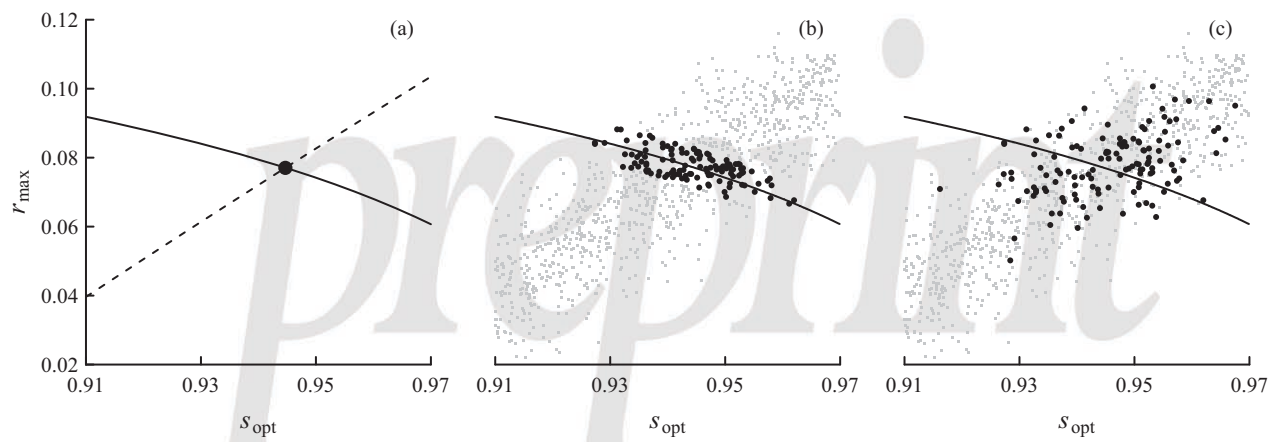813   *DIM* more likely to be accepted (●) than not (○), but populations are not required to be rT-ideal.

814

815   Figure 2. Log-log regressions of optimal generation time (T_{opt}) versus maximum growth rate

816   (r_{max}) for (a) birds (▲), (b) mammals (♦), and (c) sharks (●). The regression slopes were set to

817   −1 as predicted by Equation 1, and the regression fit only the intercepts.

818

819   Figure 3. Distributions for λ_{max} for white sharks using matrix model (black), *DIM* (clear), and rT-

820   adjusted (grey) methods. Distribution of matrix model estimates solely reflects measurement

821   uncertainty in matrix model parameters. Expected λ_{max} from the allometric-based *DIM* are

822   calculated using the estimator of Niel and Lebreton (2005) and incorporate population variability

823   from the allometric constant ($a_{rT} = 1$, $\sigma_{rT} = 0.4$, $CV(\sigma_{rT}) = 0.35$, generated from a log-normal

824   distribution) as well as uncertainty in age at first reproduction (α) and optimal adult survival

825   (s_{opt}). The distribution from the rT-adjusted method accounts for uncertainty in all demographic

826   parameters adjusting for allometric patterns and population variability.