

**Elasticity patterns for sharks, turtles, mammals, and birds: the importance of age at first reproduction, mean age of reproducing females, and survival in the discounted fertilities of the Leslie matrix**

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Running head: Elasticity patterns for sharks, turtles, mammals, and birds

*Abstract.* The elasticity pattern (E-pattern) of an age-structured animal comprising the elasticities  $E(\text{fertility}, m)$ ,  
15  $E(\text{juvenile survival}, S_j)$ , and  $E(\text{adult survival}, S_a)$  is determined by age at first reproduction ( $\bar{A}$ ) and mean age of the  
reproducing females at the stable age distribution ( $\bar{A}$ ). The E-patterns of sharks and marine turtles are characterized  
by  $\bar{A}/\bar{A}$  ratios  $< 2.0$  [ $E(S_a)/E(S_j) < 1$ ] and a proportional change in juvenile survival has the largest effect on  
population growth ( $\bar{A}$ ). Marine mammals and birds generally have  $\bar{A}/\bar{A}$  ratios  $> 2.0$  and adult survival has the  
largest effect on population growth. Terrestrial turtles, mammals, and birds show a large range of  $\bar{A}/\bar{A}$  ratios. The  
20 fast-slow continuum concept is not useful to understand E-patterns of these animals in the context of a prospective  
elasticity analysis with the goal of providing management proposals. It is important to include the survival part in  
the discounted fertilities of the Leslie matrix when calculating the E-pattern, otherwise post- and pre-breeding  
censuses will yield different and biased E-patterns. This bias is largest for animals with  $\bar{A} = 1$  yr. The sum of the E-  
pattern is  $1 + E(m)$  and has to be normalized when graphed in an elasticity triangle for easy interpretation. Assuming  
25 age-independent  $m$  and  $S_a$ , a new 3-term algebraic equation for  $\bar{A}$  facilitates the understanding and interpretation of  
E-patterns.

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## 1. Introduction

Matrix population models have been used extensively for plants and animals to calculate elasticity patterns (E-patterns) based on a prospective analysis with the goal of providing management proposals (Caswell 2001). The elasticity matrix (E-matrix) elements give the proportional change of asymptotic population growth ( $\lambda_1$ ) at the stable age distribution from a proportional change of the corresponding matrix element in the projection A-matrix. For plants an E-pattern based on fertility, growth, and stasis is often used; whereas for age-structured animals an E-pattern based on fertility, juvenile survival, and adult survival is biologically more meaningful (Heppell et al. 2000). The elasticities of chosen stages (e.g. juveniles and adults) are obtained by calculating the elasticities of juvenile and adult stages from a stage-based matrix model or by summing the elasticities in an age-based model (Leslie matrix) over the appropriate age classes. Management proposals based on E-patterns are prospective and identify the vital rates that have the largest effect on population growth, whereas retrospective analyses attempt to understand the E-patterns comprehensively and answers how vital rates varied in the past, are varying now, or might vary in the future. Many studies trying to provide management proposals based on prospective analyses are actually studying life history variation in an evolutionary perspective (Caswell 2001).

There are conflicting statements whether the sum of the E-pattern is 1.0 or  $1.0 + E(m)$ . The sum = 1.0 proponents (de Kroon et al. 1986; Heppell et al. 2000; Caswell 2001, p. 231) are technically correct but they excluded the survival term in the discounted fertilities. When survival in the discounted fertilities is included, the E-pattern sum was  $1 + E(m)$  (Heppell et al. 1996; Rockwell et al. 1997; Mollet and Cailliet 2003). Mollet and Cailliet (2002, 2003) proposed that the E-pattern from a Leslie matrix should yield the same E-pattern as that calculated empirically from the life history table (LHT) from which the Leslie matrix was constructed. This is equivalent to stating that the elasticities of survival alone add up to 1.0 which was first proved by Hamilton (1966). Pfister (1998) recognized the problem that the discounted fertilities incorporate both fertility and survival rates but provided no solution. Morris and Doak (2004) also advocated an alternative analysis based on the underlying vital rates instead of the matrix elements of the projection matrix.

Matrix population models have only been more recently used for elasmobranchs (sharks and rays), turtles, mammals, and birds. The Leslie matrix model was introduced for the lemon shark by Hoenig and Gruber (1990). Stage-based deterministic and stochastic models were used by Brewster-Geisz and Miller 2000 and Cortés 1999,

respectively, for the sandbar shark. Uncertainty in demographic models was incorporated into conservation of shark populations by Cortés (2002). Life history theory and population model analyses were successfully applied to turtle conservation and showed that juvenile survival has the largest effect on population growth ( $\lambda_1$ ) (Crouse et al. 1987; Crowder et al. 1994; Heppell et al. 1996; Heppell 1998). Heppell et al. (2000) developed a stage-based model for mammals where the adults were combined in a single stage. They presented the E-patterns in an elasticity triangle (E-triangle) which indicated that E(adult survival) was largest for most species. Eberhardt (2002) applied a sensitivity analysis based on an age-structured LHT to marine and terrestrial mammals and the spotted owl and concluded that the sensitivity of adult survival was largest for all species. The E-patterns based on a stage-based matrix model for marine and terrestrial birds indicated that adult survival had the largest effect on population growth (Lebreton, and Clobert 1991; Russell 1999; Saether and Bakke 2000).

Mollet and Cailliet (2003) showed that models that exclude survival to age 1 yr and combine adults in a stage (e.g. Heppell et al. 2000; Saether and Bakke 2000) produce biased E-patterns that overestimate the importance of adult survival. They also showed that the E-pattern of stage-based models with few stages should yield the same E-pattern as those obtained from the corresponding Leslie matrices or LHTs. For example, the E-patterns of stage-based models with few stages presented by Mollet and Cailliet (2002) and many publications before them were not correct. All assumed that the elasticities of survival ( $S_i$ ) equals the sum of the elasticities of stasis ( $P_i$ ) and growth ( $G_i$ ) following eq. 9.103 in Caswell (2001) instead of using his eqs. 18.11 or 18.16 or calculating the E-pattern empirically.

Here I first use a hypothetical but realistic example to demonstrate how to construct birth-pulse post- and pre-breeding Leslie matrices from the LHT. The E-pattern is calculated in several ways to show that the results from post- and pre-breeding census models are only identical if the survival part in the discounted fertilities is included. I use an E-triangle graph to demonstrate that the omission of the survival part in the discounted fertilities produces biased E-patterns with largest bias for small age at first reproduction ( $\alpha = 1$  and 2 yr). Assuming age-independent  $m$  and  $S_a$ , a new 3-term algebraic equation for the mean age of the reproducing females at the stable age distribution ( $\bar{A}$ ) is presented which facilitates the calculation, understanding, and interpretation of E-patterns. Finally, I present unbiased deterministic E-patterns for sharks ( $n \sim 66$  populations), marine and terrestrial turtles ( $n \sim 26$ ), mammals

( $n \sim 68$ ), and birds ( $n \sim 79$ ) assuming a stable environment with time-independent vital rates and without density dependence.

## 2. Materials and Methods

### 2.1 Hypothetical but realistic model species

5 I use a hypothetical but realistic model species to demonstrate the derivation of the Leslie matrices for a birth-pulse population using both post- and pre-breeding censuses in Fig. 2. The vital rates are summarized in Table 1. Following Caswell (1989, p.7 footnote), I use the term fertility ( $m$ ) rather than fecundity for the actual reproductive performance (i.e. female offspring per female assuming a 1:1 sex ratio = litter size/2 if the species has one litter per year) and regard these two terms to be synonyms. In this paper it will be more important to distinguish  
10 between fertilities/fecundities that appear in the LHT and discounted fertilities/fecundities that appear in the Leslie matrix. Following Brewster-Geisz and Miller (2000), I use the term ‘discounted’ fertilities for  $F_i$ , to clearly indicate that only a fraction of the mothers at time  $t$  will have offspring at time  $t + 1$  in the post-breeding census and that only a fraction of the offspring born at time  $t$  will survive to time  $t + 1$  in the pre-breeding census. The calculation of the Leslie matrix for birth-pulse post- and pre-breeding censuses from the LHT followed Caswell (2001, eqs. 2.40, 2.42,  
15 and 2.43). The z-transformed life cycle graphs were drawn with PopTools (add-in to Excel) and annotated following Caswell (2001, p. 178). The calculation of the eigenvalues ( $\lambda_1 - \lambda_{\omega}$ ), the eigenvectors ( $w_1$  and  $v_1$ ) of the largest eigenvalue ( $\lambda_1$ ), and the E-matrix were carried out with the help of PopTools. Note that  $\omega$  ( $\lambda_{\omega}$ ) is the last year of reproduction whereas  $w_1$  is the right eigenvector or age-structure vector corresponding to  $\lambda_1$ . The index 1 in  $w_1$  will be dropped henceforth because only eigenvectors for  $\lambda_1$  will be of interest here but the index 1 in  $\lambda_1$  will be retained  
20 to distinguish it clearly from the variable  $\lambda$  in the characteristic function ( $CF$ ). Special attention was paid to the calculation of the E-pattern which is obtained by summing over the appropriate matrix elements of age-classes in the E-matrix. This was carried out seven different ways for both post- and pre-breeding censuses (Fig. 2H, columns 1 - 5 left and right, respectively; duplicate calculations in two columns).

The discounted fertilities in the post- and pre-breeding Leslie matrices are  $F_i = m S_i$  and  $F_i = m S_{i-1}$ ,  
25 respectively (Caswell, 2001, p. 27). To demonstrate better the importance of taking into account the survival rates in the discounted fertilities when calculating the E-pattern, all the possible E-patterns of the hypothetical  $\lambda = 1$  yr species in Fig. 2 were contrasted with the E-patterns of additional hypothetical but realistic model species with  $\lambda =$

2, 5, and 15 yr. I calculated and then graphed the E-pattern using 4 scenarios for each  $\Delta$  in Fig. 3. Scenarios 1 and 2 used post-breeding and pre-breeding censuses assuming that the elasticities add up to  $1.0 + E(m)$  to discover if this would produce identical E-patterns as expected; and scenarios 3 and 4 used post-breeding and pre-breeding censuses assuming elasticities add up to 1.0 (current theory, e.g. de Kroon et al. 1986; Caswell 2001, p. 231) which was expected to produce different E-patterns. The vital rates for these additional hypothetical species are summarized in Table 1 and were chosen based on graphical considerations.

## 2.2 Elasticity triangle (E-triangle)

The E-triangle is a three-way proportional graph for graphing the E-pattern of a species comprising 3 elasticities as a single point (Silvertown et al. 1992; Heppell et al. 2000). Silvertown et al. 1992 used  $E_1 = E(F)$ ,  $E_2 = E(P, \text{stasis})$ , and  $E_3 = E(G, \text{growth})$  suitable for plants. Heppell et al. (2000) modified this to  $E_1 = E(m)$ ,  $E_2 = E(S_j)$ , and  $E_3 = E(S_a)$  which is more meaningful for age-structured animals. The elasticities have to be normalized first if the calculation produces elasticities that do not sum to 1.0. The E-triangle is best understood by considering the elasticity of adult survival  $E(S_a)$  first, which was chosen to be identical with the y-axis following Heppell et al. (2000). The y-axis measures  $E(S_a)$  from the bottom side [ $E(S_a) = 0$ ] to the top corner [ $E(S_a) = 1$ ].  $E(m)$  and  $E(S_j)$  are measured from the right and left sides of the equilateral triangle, respectively, and reach value 1.0 at the opposite corners on the bottom side. For graphing it is easier to calculate  $x$  for each data triplet and it is given by  $x = \{E(S_a) + [E(S_j)/\cos(\pi/3)]\}/\tan(\pi/3)$  using geometry. The E-triangle is half-empty if the E-patterns are unbiased and provides space for hypothetical species with  $\Delta < 1$  yr and an annual reproductive cycle that requires a projection interval of 1 yr. This is not the case in Fig. 3 because this figure includes biased E-pattern but applies to Figs. 4 and 5 which only show unbiased E-patterns.

Three sets of equations that define isometric lines (contours) facilitate the interpretation of the normalized E-pattern. They are obtained by determining the conditions that guarantee that any 2 of the 3 elasticities comprising the E-pattern have the same value. The most useful set of contours is defined by  $\bar{A}/\Delta = \text{constant}$  ('iso- $\bar{A}/\Delta$ 's'). If  $\bar{A}/\Delta = 2.0$ , then  $E_n(S_a) = E_n(S_j)$  ( $E_3 = E_2$ ). If  $\bar{A}/\Delta > 2.0$ , adult survival has a larger effect on population growth than juvenile survival; if  $\bar{A}/\Delta < 2.0$ , then the reverse holds. It is easy to calculate the exact  $E_3/E_2$ -ratio from the  $\bar{A}/\Delta$  value because  $E_3/E_2 = (\bar{A}/\Delta) - 1$  (eq. A2.13.1). The second set of contours is defined by  $E_n(S_j) = \Delta E_n(m)$  ('iso- $\Delta$ 's'). If  $\Delta$  is 1.0 yr, then  $E_n(S_j) = E_n(m)$  ( $E_2 = E_1$ ). As  $\Delta$  increases,  $E_n(S_j)$  becomes  $\Delta$  times as large  $E_n(m)$ . A third set

of contours, defined by  $\bar{A} - \bar{\lambda} = \text{constant}$  ('iso- $(\bar{A} - \bar{\lambda})$ 's'), appears to be less useful. The  $\bar{A} - \bar{\lambda} = 1$  contour defines species for which  $E_n(S_a) = E_n(m)$  ( $E_3 = E_1$ ).

### 2.3 Vital rates used for shark, turtle, mammal, and bird populations

The vital rates used for all shark, turtle, mammal, and bird populations used in this study and their sources are summarized in Appendix 1 which includes the scientific names. For many species, I used a different model for the calculation of population growth, generation times, and E-pattern than that used in the source publication and whenever possible the results based on the same number of species were compared in Table 2. I used a liberal approach for the definition of a population. In most cases it was a species with a particular geographical location but in a few cases a species with different vital rates for demonstration purposes were counted as different populations.

The vital rates of sharks were based on the 41 populations listed in Cortés (2002). Seven of these species had a small, fractional mean  $\bar{\lambda}$  (~1.5, ~2.5, and ~3.5), for which I created two populations each with  $\bar{\lambda}$  rounded up and down to the next integer. The vital rates used and their sources for 16 additional shark and ray populations are given in Appendix 1. I used age-independent fertility and survival rates and the same survival rates for juveniles and adults following Mollet and Cailliet (2002):  $S = \exp(-M)$  with  $M = -\ln(0.01)/\bar{\lambda}$  for the mortality rate ( $M$ ) which leaves ca. 1.0% of the population in the last age class at the stable age distribution if  $\bar{\lambda}_1$  is close to 1.0. Two populations each of scalloped hammerhead and shortfin mako with widely different  $\bar{\lambda}$  were used as demonstration species to explore the effect of  $\bar{\lambda}$  on the E-pattern in Figs. 4 and 5.

The vital rates for 22 marine and terrestrial turtles came from Heppell (1998, Tables 2 and 4) and were supplemented with more recent data for additional populations of marine turtles (see Appendix 1 for vital rates used and their sources). If longevity of a turtle species was not given, I used  $\bar{\lambda} = 6\bar{\lambda}$  yr. Her Table 4 did not include fertility and juvenile survival of 10 terrestrial turtles and they were chosen such that  $\bar{\lambda}_1 = 1.0$ . I followed Heppell (1998) and used 2 populations of painted turtles with 3 sets of vital rates as a demonstration species in Figs. 4 and 5 to show that the  $S_a/\bar{\lambda}$  ratio or the corresponding  $(\bar{\lambda}_1 - S_a)$  difference has a large influence on  $\bar{A}$  and thus the E-pattern. For comparison purposes only, the vital rates used by Tucker (2000) in a 5-stage model for six species of crocodiles were used in a Leslie matrix to calculate the E-pattern.

The vital rates of 50 species of marine and terrestrial mammals came from Heppell et al. (2000, Ecological Archives E081-006) and were supplemented by 16 mammal populations from Eberhardt (2002). Heppell et al.

(2000) used a stage-based model with all the adults in a stage whereas I used a LHT or the corresponding Leslie matrix (Mollet and Cailliet 2002). Eberhardt (2002) used the characteristic equation of the LHT which is equivalent to using an LHT in an Excel spreadsheet or a Leslie matrix in PopTools as I have done. He calculated sensitivities whereas I calculated elasticities (proportional sensitivities) of vital rates. He used survival to age-at-first reproduction ( $l_{\overline{0}}$ ) whereas I used juvenile survival  $S_j$  as a parameter. The sea otter with  $\overline{\Delta} = 3.5$  yr was treated as two populations with  $\overline{\Delta} = 3$  and 4 yr. A third set of killer whale vital rates came from Caswell (2001, p.117) and the killer whale was used as a demonstration species in Figs. 4 and 5 to show the effect of a shorter reproductive period with corresponding larger fertility.

The vital rates of bird populations came from Russell (1999, his Table 2 with 26 marine species) and Saether and Bakke (2000, Ecological Archives E81-005-A1 with 49 marine and terrestrial species). This bird sample included 11 duplicate marine bird species with different vital rates. When  $S_1$  was not available in Saether and Bakke (2000), I used the value given in Russell (1999) or 0.50. The pseudo-stochastic E-patterns (see A2.3 for details) give the E-patterns if  $S_1$  is calculated such that  $\overline{\Delta}_1 = 1.0$  as was done by Saether and Bakke (2000) for these species. Both Russell (1999) and Saether and Bakke (2000) used a stage-based model with a stage for the adults. They used  $P_a = S_a$  for the adult self-loop that produces the diagonal matrix element in the right hand corner of the projection matrix, rather than  $P_a = S_a(1 - \overline{\Delta})$  as given in Caswell (2001, p.160), which implies infinite longevity ( $w$ ) (Heppell et al. 2000). I used  $\overline{\Delta} = 6\overline{\Delta}$  yr as a more reasonable longevity value for birds. However,  $\overline{\Delta} = 100$  yr was used as an approximation for infinite longevity in preliminary calculations and in the final analysis it was used for two bird species to demonstrate the effect of such large longevity values on the E-pattern (golden plover and emperor penguin in Figs. 4 and 5). For the lesser snow goose in Saether and Bakke, (2000, ID #3), I also used data for a population with age-dependent fertility ( $m$ ) from Rockwell et al. (1997) and calculated age-independent  $m = 0.677$  that produces the same  $\overline{\Delta}_1 = 1.021$ , again using  $\overline{\Delta} = 6\overline{\Delta}$  yr rather than  $\overline{\Delta} =$  yr of the model used by Rockwell (1997). Vital rates for an additional spotted owl population came from Eberhardt (2002, ID # 16).

#### 2.4 Demographic calculations

For about 170 out of the 240 populations a LHT was setup in an Excel spreadsheet and solved. The corresponding Leslie matrix and various stage-based models were constructed and solved with the PopTools program (add-in to Excel; Mollet and Cailliet 2002). I used a PopTools version that does not calculate  $\overline{\Delta}$ , only

generation time  $T = \ln(R_0)/\ln(\bar{\lambda}_1)$  ( $R_0$  = net reproductive rate) and  $\bar{\lambda}_1$  (the mean age of the reproducing mothers of a cohort). These preliminary calculations also served as a check on the final results. The final calculations were carried out with GnuOctave (Eaton and Rawlings 2003; <http://www.octave.org/>), a free software package corresponding to MATLAB. GnuPlot (a free graphing program, <http://www.gnuplot.info/>) and AquaTerm (a free graphic terminal, <http://sourceforge.net/projects/aquaterm/>) were used for graphing. The vital rates for all 240 populations were entered into an Octave data file. An Octave script constructed the Leslie matrix  $A = F + T$  of dimension  $(\bar{\lambda} \times \bar{\lambda})$ , largest size 210 x 210) for each species from the vital rates and then the Leslie matrix was solved. Appendix 2.8 gives sample code that includes the calculation of  $\bar{A}$  directly from the Leslie matrix (eq. A2.19). E-patterns calculated from  $\bar{\lambda}_1$  instead of  $\bar{A}$  are termed pseudo-stochastic E-patterns (see Appendix A2.3 for explanation, eqs. (A2.11)).

### 3. Results

#### 3.1 Calculation of the E-pattern and $\bar{A}$ from the characteristic function

Equations for the normalized elasticities  $E_n(m)$ ,  $E_n(S_j)$ ,  $E_n(S_a)$  (the E-pattern), as functions of  $\bar{\lambda}$  and  $\bar{A}$ , were derived from the characteristic function  $\bar{\lambda}(\bar{\lambda})$  (CF) of a life-cycle graph that represents a Leslie matrix derived from an age-structured life history table assuming age-independent  $m$  and  $S_a$  (see Appendix 2 which includes explicit formulas for the elasticities  $E(\bar{\lambda})$ , and  $E(\bar{\lambda})$ ):

$$E_n(m) = E_{n,1} = 1/(\bar{A} + 1) \quad (\text{A2.9.1})$$

$$E_n(S_j) = E_{n,2} = \bar{\lambda}/(\bar{A} + 1) \quad (\text{A2.9.2})$$

$$E_n(S_a) = E_{n,3} = (\bar{A} - \bar{\lambda})/(\bar{A} + 1) \quad (\text{A2.9.3})$$

$$\bar{A} = \bar{\lambda} + \frac{S_a}{(\bar{\lambda} - S_a)} \bar{\lambda} \frac{(\bar{\lambda} - 1)(S_a / \bar{\lambda})^{(\bar{\lambda} - 1)}}{(1 - (S_a / \bar{\lambda})^{(\bar{\lambda} - 1)})} \quad (\text{A2.4})$$

The E-pattern comprising  $E_n(m)$ ,  $E_n(S_j)$ , and  $E_n(S_j)$  in eq. (A2.9), needed for a prospective analysis, is determined by  $\bar{\lambda}$  and  $\bar{A}$  alone, a major simplification because both  $\bar{\lambda}$  and  $\bar{A}$  are well-defined and understood for the animal species in this study. Equations (A2.9) give the exact functional relationship between  $E_n(m)$ ,  $E_n(S_j)$ , or  $E_n(S_j)$  and  $\bar{\lambda}$  &  $\bar{A}$ . Graphs of any component of the E-pattern versus generation time  $\bar{A}$  with  $\bar{\lambda}$  treated as a parameter are best to understand the E-pattern. I suggest that it is not helpful to graph the components of the E-pattern against any vital rate, generation time, or population growth rate for different species and then attempt to establish correlations.



It is often easy to guess estimate if  $\bar{A}$  will increase or decrease in scenarios that change vital rates of a species and therefore the effect on the E-pattern is readily estimated. Given  $\bar{\lambda}$  for a species and an estimate for  $\bar{A}$  already yields an estimate of the complete E-pattern. If  $\bar{A}$  is difficult to estimate without solving the Leslie matrix first,  $\bar{A}$  in eqs. (A2.8) can be replaced with  $\bar{\lambda}$  and a pseudo-stochastic E-pattern is obtained (see Appendix A2.3 eqs. A2.11 for details). A further advantage of these formulas for the E-pattern is that the E-matrix is not needed and fractional  $\bar{\lambda}$  values can be used. It is also easy to estimate the E-pattern appropriate for projection intervals ( $PI$ ) that agree with the reproductive cycle ( $RC$ ) by using estimates of  $\bar{\lambda}$  and  $\bar{A}$  based on units of the  $PI$  (e.g. 5 yr instead of 1 yr) combined with actual instead of annualized fertility.

All three elasticities and  $\bar{A}$  are no longer explicit functions of  $m$  and  $S_a$  and the E-pattern (eqs. A2.9) is not even an explicit function of  $S_a$  and  $\bar{\lambda}$ . However,  $\bar{A}$  is a function of  $\bar{\lambda}$ , which itself is a function of all the vital parameters and  $\bar{A}$  appears in the equations of all three elasticities. This is the reason that elasticities appear to be difficult to predict; but they can in fact be calculated as shown and their interpretation becomes considerably easier by concentrating on the 3-term formula for  $\bar{A}$ , which is exact for species where no age-dependent vital rates are available and age-independent  $m$  and  $S_a$  are assumed as a first approximation. Although (A2.4) is only valid if  $S_a$  and  $m$  are age-independent, the equations for the E-pattern (eqs. A2.9) are exact if  $\bar{A}$  is calculated from the defining equation  $\bar{A} = \sum_x x \bar{\lambda}^x l_x m_x$  (sum over all  $x$  = ages) or from the equivalent equation  $\bar{A} = \langle \mathbf{w}, \mathbf{v} \rangle$  (eq. A2.14) where  $\langle \mathbf{w}, \mathbf{v} \rangle$  is the special scalar product of age-structure vector  $\mathbf{w}$  and reproductive value vector  $\mathbf{v}$  when choosing  $w_1 = v_1 = 1.0$  (see Appendix A2.5 for details, eq. A2.14).

The first term in eq. (A2.4) for  $\bar{A}$  is age at first reproduction ( $\bar{\lambda}$ ). The second term can be written as  $(S_a/\bar{\lambda})/[1 - (S_a/\bar{\lambda})]$  and indicates that the  $S_a/\bar{\lambda}$  ratio, which also appears in the third term, is an important factor in this equation for  $\bar{A}$ . The third term can be called a correction term and is only zero if  $\bar{\lambda} = 1$ . If the formula  $\bar{A} = \bar{\lambda} + S_a/(\bar{\lambda} - S_a)$  (A2.15.1) is used for a stage-based model that was derived from an age-structured LHT or Leslie matrix, then it implies that  $\bar{\lambda} = 1$ . This is not a good approximation for many species because  $\bar{\lambda}$  is finite and the third term cannot be neglected, in particular if  $S_a$  is close to 1.0. The use of a stage-based model with  $S_a$  (instead of  $P_a = S_a (1 - \bar{\lambda})$ ) as a terminating element on the diagonal of the projection matrix instead of the fully age-structured Leslie matrix with  $\bar{\lambda}$  sufficiently large to approximate the  $\bar{\lambda} = 1$  solution does not change this.

Although the third term cannot be neglected if  $\bar{A}$  is finite, in particular if  $S_a/\bar{A} \approx 1$ , the second term and thus  $\bar{A}$  becomes large if  $(\bar{A} - S_a)$  is small. It was sensible to calculate the  $\bar{A}/\bar{A}$  ratio and expect that it would also play an important role in E-patterns and I show below that it is closely related to the  $E_3/E_2$  ratio, the elasticity ratio of adult and juvenile survival.

Equation (A2.4) for  $\bar{A}$  appears to be ill-defined as  $(\bar{A} - S_a) \approx 0$  and/or  $S_a/\bar{A} \approx 1$  because it appears that  $\bar{A} = \bar{A} + \dots$ . However, the critical value exists and is  $(\bar{A} + \bar{A})/2$ . A mathematical proof is given in Appendix 2 (eq. A2.5.2) but my derivation using biological arguments is more illustrative. A viable population ( $\bar{A} \geq 1.0$ ) where ages at first and last reproduction are both  $\bar{A}$  ( $\bar{A}/\bar{A} \approx 1$ ) is a population with only one litter ( $S_a = 0$  and thus  $S_a/\bar{A} = 0$ ). Adult females die after they have had their first and only litter with sufficient offspring to produce  $\bar{A} \geq 1.0$ , and we must have  $\bar{A}_{\text{minimum}} = \bar{A}$  ( $\bar{A}_{\text{minimum}}/\bar{A} = 1$ ). At the other extreme are populations with  $S_a/\bar{A} \approx 1$  ( $\bar{A}/\bar{A} > 1$ ). The adults have constant age structure (same number of adults in each age class between  $\bar{A}$  and  $\bar{A}$ ) and at age  $\bar{A}$  they either become post-reproductive or die. The mean age of the reproducing females in this case must be  $\bar{A} = \bar{A}_{\text{critical}} = (\bar{A} + \bar{A})/2$  (A2.5.1), the critical value of interest. When  $S_a/\bar{A} \approx 1$ , the  $\bar{A}/\bar{A}$  ratio may potentially become very large ( $\approx \dots$ ) but  $\bar{A}$  is finite and is often known. This shows that in addition to the  $S_a/\bar{A}$  ratio, the  $\bar{A}/\bar{A}$  ratio will be important also.

The ratio  $E_3/E_2 = E_{n,3}/E_{n,2}$  is related to the  $(\bar{A}/\bar{A})$ -ratio by the following simple equation:

$$E_3/E_2 = E(S_a)/E(S_j) = (\bar{A}/\bar{A}) - 1 \quad (\text{A2.13.1})$$

which using eq. (A2.4) for  $\bar{A}$  gives:

$$E_3/E_2 = (1/\bar{A}) \left[ \frac{(S_a/\bar{A})}{(1 - (S_a/\bar{A}))} - \frac{(\bar{A} - \bar{A} + 1)(S_a/\bar{A})^{(\bar{A} - \bar{A} + 1)}}{(1 - (S_a/\bar{A}))^{(\bar{A} - \bar{A} + 1)}} \right] \quad (\text{A2.13.2})$$

Increasing the mean age of the reproducing females ( $\bar{A}$ ) must increase the importance of the adults on population growth and eq. (A2.13.1) expresses this in the form of a simple linear equation between the  $E_3/E_2$  ratio and  $\bar{A}/\bar{A}$ . Again, I suggest that it not helpful to graph this or any other ratio of elasticities for different species against vital rates, generation times, or population growth rates and then attempt to establish correlations. Instead, more general contour graphs for the function  $E_3/E_2$  will display the crucial features of E-patterns and help to understand how the E-patterns are related to the vital rates. Contour plots for  $E_3/E_2 = (\bar{A}/\bar{A}) - 1$ , while still fairly complicated, are best

suit to demonstrate the importance of the  $S_a/\bar{L}_1$  and  $\bar{L}_1/\bar{L}$  ratios in eq. (A2.13.2) for  $E_3/E_2$  and thus the E-pattern (Figs. 1A, 1B, 1C, and 1D for  $\bar{L}_1/\bar{L} = 3.0, 6.0, 9.0$ , and  $12.0$ , respectively). That is  $\bar{L}_1$  in eq. A2.13.2 is substituted with  $k\bar{L}_1$  ( $k = 3.0, 6.0, 9.0$ , and  $12.0$  or any other value as required) and the  $E_3/E_2$  values are calculated as a function of  $x = S_a/\bar{L}_1$  and  $y = \bar{L}_1/\bar{L}$  and graphed as contours (lines with the same  $E_3/E_2$ -values).

5           The vertical contour lines when  $x = S_a/\bar{L}_1 = 1$  have  $E_3/E_2$  values of 1.0, 2.5, 4.0 and 5.5 in Figs. 1A, 1B, 1C, and 1D, respectively. These value agree with the critical values of  $E_3/E_2$  that can be calculated from (A2.5.1). The first interesting fact is that for  $\bar{L}_1/\bar{L} \leq 3$ ,  $E_3$  can at most be equal to  $E_2$  ( $E_3/E_2 \leq 1$ ) for the populations of most interest which have  $S_a/\bar{L}_1 \leq 1$  (Fig. 1A is for  $\bar{L}_1/\bar{L} = 3$ ). As we shall see, most shark populations have  $\bar{L}_1/\bar{L} < 3$  and therefore elasticity of juvenile survival ( $E_2$ ) must be largest for these populations without any further considerations  
10 if eq. (A2.4) for  $\bar{A}$  is applicable. Second, for given  $y = \bar{L}_1/\bar{L}$  when moving horizontally to the right in any subplot in Fig. 1,  $E_3/E_2$  increases as  $x = S_a/\bar{L}_1$  increases (i.e.  $\bar{L}_1 - S_a$  decreases). Elasticity of adult survival ( $E_3$ ) becomes more important compared to elasticity of juvenile survival ( $E_2$ ) as the difference ( $\bar{L}_1 - S_a$ ) becomes smaller. When  $S_a/\bar{L}_1 = 1$  ( $S_a - \bar{L}_1 = 0$ ) the vertical contour line has been reached (which is valid for any  $\bar{L}_1/\bar{L}$ ). Third, for given  $S_a/\bar{L}_1$  moving vertically in the  $y = \bar{L}_1/\bar{L}$  direction, there are 3 possible results which are determined by opposing  
15 mathematical factors depending on the value of  $S_a/\bar{L}_1$  (see Appendix A2.4 for details).

### 3.2 Calculation of E-patterns for post- and pre-breeding censuses

The E-patterns for post- and pre-breeding censuses are only identical, and therefore unbiased as required, if the survival term in the discounted fertilities is included which is demonstrated step by step in Fig. 2. This hypothetical species with  $\bar{L}_1 = 1$  yr and other vital rates as given in Table 1 has population growth rate  $\bar{L}_1 = 1.59$ , net  
20 reproductive rate  $R_0 = 2.31$ , and ‘generation times’  $\bar{A} = 1.57$  yr (an age),  $T = 1.80$  yr (a time), and  $\bar{L}_1 = 2.08$  yr (an age), with  $\bar{A}/\bar{L}_1 = 1.57$  (Fig. 2A, LHT).

The individuals in the first age-class in the post-breeding census are all 0 yr old and have survival rate  $S_j = 0.5$  during the next projection interval ( $PI$ ), whereas in the pre-breeding census they have just reached age 1 yr and have adult survival rate  $S_a = 0.6$  in the next  $PI$  (Figs. 2B & C, Leslie matrices). However, it is nevertheless the first  
25 year age-class in both censuses. This is best understood if we recall that post- and pre-breeding censuses were ingeniously constructed as limit processes where  $S_i = l(i + p)/l(i - 1 + p)$  with  $p \rightarrow 0$  and  $p \rightarrow 1$  for post- and pre-

breeding censuses, respectively (Caswell 2001 p. 27). In this  $\Delta t = 1$  yr example, the first age-class is also the age-class with the maturing females for both post- and pre-breeding censuses i.e. juveniles that become mature and have their first litter in the next *PI*.

The right eigenvector (age structure) for the post-breeding census corresponding to the largest and real eigenvalue  $\lambda_1$  can be read off the z-transformed life cycle graph (Fig. 2D, left):  $w_1 = 1$ ,  $w_2 = S_1/\lambda_1 = 0.3140$ ,  $w_3 = (S_1/\lambda_1)(S_2/\lambda_1) = 0.1183$  and so forth for  $w_4 - w_5$ . The left eigenvector for the post-breeding census (reproductive values) can be read off the transposed life cycle graph (not shown) with all the arrows reversed:  $v_1 = 1$ ,  $v_5 = mS_5/\lambda_1 = 0.7536$ ,  $v_4 = mS_4/\lambda_1 + (S_4/\lambda_1)(mS_5/\lambda_1) = 1.0375$  and so forth for  $v_3 - v_2$ . The  $F_1/\lambda_1$  self-loop should not be absorbed, as would be the case for a stage-based model with a  $P_1/\lambda_1$  self-loop; therefore, surprisingly,  $F_1 = mS_1$  does not appear in the formulas for  $v_i$ . However, the presence of the  $F_1/\lambda_1$  self-loop (reproduction at age 1.0 yr) produces a larger  $\lambda_1$  and thus affects the values of  $w_2 - w_5$  and  $v_2 - v_5$ , although the formulas for  $v_i$  with and without the  $F_1/\lambda_1$  self-loop are the same. The complete right and left eigenvectors for both post- and pre-breeding censuses were calculated with PopTools in Fig. 2E.

The right and left eigenvectors in the pre-breeding census are different because juvenile survival ( $S_1$ ) differs from adult survival ( $S_2 - S_5$ , all the same in this example) (Fig. 2E, right). Although  $w$  and  $v$  of post- and pre-breeding censuses are different, the product terms ( $w_i v_i$ ) and thus  $\bar{A} = \langle w, v \rangle$  are the same as required (eq. A2.14). Fig. 2E includes the results for  $\bar{A}$  from three different calculations. In this example the result using eq. (A2.4, valid only when  $m$  and  $S_a$  are age-independent) agrees with  $\bar{A} = \langle w, v \rangle$  (eq. A2.14) and  $\bar{A}$  from eq. A2.19, (Octave solution) because  $m$  and  $S_a$  were assumed to be age-independent. The PopTools solution of the Leslie matrices includes net reproductive rate  $R_0$  and the generation time  $\Delta t_1$  that should and do agree with the results from the LHT.

The E-matrices for post- and pre-breeding censuses are identical but the E-patterns are only the same if the survival term in the discounted fertilities is included (Figs. 2F & 2G and 2H). The calculation of the E-pattern ( $E_1$ ,  $E_2$ , and  $E_3$ ) requires that we sum over different matrix elements in the E-matrix for post- and pre-breeding censuses. The E-patterns will not be the same if presently prevalent theory is followed (deKroon et al 1986; Heppell et al. 2000; Caswell 2001, p. 231). In this case, the elasticities of the E-matrix are added over the appropriate age-classes without taking into account of the survival term in the discounted fertilities and the sum is 1.0. This might be considered controversial and I therefore calculated the E-pattern a total of seven ways and summarized the results in

five columns (with duplicate results in 2 columns) for both post- and pre-breeding censuses, first including survival in the discounted fertilities (Fig. 2H, columns 1-3, respectively) and then excluding them (Fig. 2H, columns 4-5, respectively, see figure caption for details).

The difference between post- and pre-breeding census E-patterns are considerable in this hypothetical but realistic  $\bar{\Delta} = 1.0$  yr species. For example, biased  $E_2 = 0.239$  (Fig. 2H, columns 4 or 5 on left) in the post-breeding census and biased  $E_2 = 0$  (Fig. 2H, columns 4 or 5 on right) in the pre-breeding census to be compared with the unbiased normalized  $E_2 = 0.390$  (Fig. 2H, column 3 left or right). The ratio of the results in the fourth and third columns were calculated as an indicator of bias. The biased E-pattern for the  $\bar{\Delta} = 1$  yr example using a post-breeding census overestimates  $E_1$  and underestimates  $E_2$  and  $E_3$  (Fig. 2H, column 4/3 on left). However, in general, the biased E-patterns in a post-breeding census overestimate both  $E_1$  and  $E_2$  and underestimate only  $E_3$  because the bias of  $E_2$  depends on  $\bar{\Delta}$  and changes sign if  $\bar{\Delta} > 1$ . The biased E-pattern of the  $\bar{\Delta} = 1$  yr example using a pre-breeding census overestimates  $E_1$  and  $E_3$  and underestimates  $E_2$  (Fig. 2H, column 4/3 on right). The sign of the  $E_2$ -bias in the pre-breeding census does not depend on  $\bar{\Delta}$  but the  $E_2$ -bias will not be as extreme in general as for this  $\bar{\Delta} = 1$  yr example with ' $4/3$ ' = 0. The  $E_2$ -bias in the pre-breeding census is extreme for  $\bar{\Delta} = 1$  yr because the E-pattern without inclusion of first year survival  $S_1$  (in  $F_1$ ) makes it appear as if survival to age 1 yr has no effect on the E-pattern ( $E_2 = 0$ ).

Finally, the relationships (eqs. A2.12 and A2.13.1) between elasticity ratios and  $\bar{A}$  &  $\bar{A}/\bar{\Delta}$  were applied as checks (Fig. 2H, last two lines, left and right). These relationships are also helpful for the interpretation of E-patterns:  $\bar{A} = E_2/E_1 + E_3/E_1 = 1.5663$  and  $\bar{A}/\bar{\Delta} = 1 + E_3/E_2 = 1.5563$  yielding the same result in this example because  $\bar{\Delta} = 1$ . It is important to point out that the biased E-patterns have different elasticity ratios and they can be calculated from eqs. (A2.20) and (A2.21) for post- and pre-breeding censuses, respectively.

The large biases in the E-pattern of an  $\bar{\Delta} = 1$  yr species, when survival in the discounted fertilities is excluded, is easier to understand if graphed in the E-triangle and compared with the results of identical calculation for species with larger  $\bar{\Delta}$  (Fig. 3). The unbiased E-patterns for the hypothetical  $\bar{\Delta} = 1$  yr species for post- and pre-breeding censuses coincide and fall on the  $\bar{\Delta} = 1$  yr contour whereas the biased E-pattern in the pre-breeding census falls on the meaningless  $\bar{\Delta} = 0$  yr contour (right side of triangle without an  $\bar{\Delta}$ -label) and the biased E-pattern for the post-breeding census is located in-between on the  $\bar{\Delta} \sim 1/2$  yr contour (not shown). Similarly, for the hypothetical  $\bar{\Delta} =$

2 yr species, the unbiased E-patterns coincide and are located on the  $\Delta = 2$  yr contour whereas the biased E-pattern for the pre-breeding census is located on the  $\Delta = 1$  yr contour and the biased E-pattern for the post-breeding census is located in-between on the  $\Delta \sim 1.5$  yr contour (not shown). As  $\Delta$  increases the biases decrease and the four E-patterns begin to coalesce. For the  $\Delta = 5$  yr example, the differences may already be negligible for practical purposes (e.g. management proposals) and the differences are certainly negligible for practical purposes if  $\Delta = 15$  yr.

### 3.3 E-patterns for sharks, turtles, mammals, and birds

The elasticity pattern for sharks, turtles, mammals, and birds show distinct differences (Fig. 4) which remain in the pseudo-stochastic E-patterns (Fig. 5). The E-patterns of sharks and marine turtles are characterized by  $\bar{A}/\Delta$  ratios  $< 2.0$  ( $E_3/E_2 < 1.0$ ) and a proportional change in juvenile survival ( $S_j$ ) has the largest effect on population growth ( $\Delta_1$ ). Marine mammals and birds generally have  $\bar{A}/\Delta$  ratios  $> 2.0$  ( $E_3/E_2 > 1.0$ ) and adult survival ( $S_a$ ) has the largest effect on population growth. Terrestrial turtles, mammals, and birds show a large range of  $\bar{A}/\Delta$  ratios, in particular for mammals and birds with early reproduction at  $\Delta = 1$  yr (Figs. 4 and 5). The contour graphs for  $E_3/E_2$  in Figs. 1 A, B, C, and D for the  $\Delta/\Delta$  ratios 3, 6, 9, and 12, respectively are helpful to better understand the E-patterns, in particular Fig. 1A for  $\Delta/\Delta = 3$ .

The E-patterns of sharks and rays are similar and elasticity of juvenile survival ( $E_2$ ) is largest for all (Fig. 4A). The mean  $\bar{A}/\Delta = 1.31$  ( $n = 66$ ) is much smaller than 2.0 and the coefficient of variation  $CV = 9.9\%$  is small (Table 2, ID #1). The range of  $\bar{A}/\Delta$  is from 1.06 for scalloped hammerhead to 1.75 for sandtiger and even the largest value is less than 2.0. The  $\Delta/\Delta$  ratio of 70% of these shark populations is  $\Delta/\Delta > 3.0$  (mean 2.68,  $CV = 45\%$ , range 1.13 – 5; Table 2, ID #1),  $S_a/\Delta_1$  is less than 1.0 for all sharks and therefore  $E_2$  has to be largest (Fig. 1A, the critical, vertical  $E_3/E_2$  contour has a value of 1.0). The remaining 30% of these sharks with  $\Delta/\Delta > 3.0$  have  $x = S_a/\Delta_1$  sufficiently smaller than 1.0 such that in the appropriate contour plot  $E_3/E_2$  will be less than 1.0 (given  $\Delta/\Delta$  and  $\Delta$ ). The pseudo-stochastic calculation produces similar results (Fig. 5A). However, species with  $\Delta_1 > 1$  have moved closer to or onto the  $\bar{A}/\Delta = 2$  contour which is most noticeable for the Australian sharpnose populations with  $\Delta = 1$  yr and large  $\Delta_1 = 1.68$ . Species with  $\Delta_1 < 1$  have moved further below the  $\bar{A}/\Delta = 2$  contour but this is difficult to see in Fig. 5A because the movement is toward the area with most of the data. Surprisingly at first,  $\Delta$  has little effect on the E-pattern, in particular the  $E_3/E_2$  ratio (Figs. 4A and 5A, special cases). However, as shown in Fig. 1A, if  $\Delta/\Delta \Delta$

3.0 and  $S_a/\bar{\Delta}_1 < 1.0$  then  $E_2$  has to be largest without further considerations (including any value of  $\bar{\Delta}$ ). Large differences for  $\bar{\Delta}$  were reported for different populations of scalloped hammerhead (4 and 15 yr) and shortfin mako (7 and 18 yr) and depend on whether 2 or 1 vertebrae band-pair(s) were used for the length versus age growth curve. All four E-patterns have  $\bar{A}/\bar{\Delta} < 2.0$ , for scalloped hammerhead  $\bar{A}/\bar{\Delta} = 1.21$  and 1.06, respectively ( $E_3/E_2 = 0.21$  and 0.06), for shortfin mako 1.39 and 1.28, respectively ( $E_3/E_2 = 0.39$  and 0.28) (Appendix 1). Obviously, species with larger  $\bar{\Delta}$  have larger  $E_2/E_1$  ratios because  $E_2/E_1 = \bar{\Delta}$  (eq. A2.7).

The mean  $\bar{A}/\bar{\Delta}$  ratio and its coefficient of variation (1.36, CV = 11%,  $n = 7$  only) of marine turtles are smaller than those of terrestrial turtles (2.10, CV = 29%,  $n = 20$ ) (Table 2, IDs #6 & #7). Marine turtles have  $\bar{A}/\bar{\Delta}$  ratios smaller than 2.0 (range 1.257 – 1.61, corresponding to  $E_3/E_2 = 0.257 – 0.61$ ) and the elasticity of juvenile survival ( $E_2$ ) is largest (Table 2, ID #6; Fig. 4B). Again this can be understood in terms of the  $\bar{\Delta}/\bar{\Delta}$  ratio which is less than 3.0 for the three turtle populations for which both  $\bar{\Delta}$  and  $\bar{\Delta}$  were reported. For the other four populations (Loggerhead and Kemps's Ridley for which I used  $\bar{\Delta} = 6\bar{\Delta}$ ),  $x = S_a/\bar{\Delta}_1$  was sufficiently smaller than 1.0 such that  $E_3/E_2$  is less than 1.0 (Fig. 1B, given  $\bar{\Delta}/\bar{\Delta}$  and  $\bar{\Delta}$ ).

For terrestrial turtles, I used  $\bar{\Delta}/\bar{\Delta} = 6$  and Fig. 1B is applicable for all. However, in this case the critical, vertical  $E_3/E_2$  contour in Fig. 1B has a value of 2.5 and therefore Fig. 4B which shows the  $\bar{A}/\bar{\Delta}$  contour of value 2.0 is at first more illustrative. The  $\bar{A}/\bar{\Delta}$  ratio range of terrestrial turtles (1.261 for geometric tortoise to 3.39 for snapping turtle A, corresponding to  $E_3/E_2 = 0.261 – 2.29$ ) is large and the E-pattern for a particular species appears difficult to predict (Table 2, ID #7). Three sets of vital rates for two populations of painted turtles demonstrate that the E-pattern is most effected by the  $\bar{\Delta}_1/S_a$  ratio or the corresponding  $\bar{\Delta}_1 - S_a$  difference. All three painted turtle populations have  $\bar{\Delta}/\bar{\Delta} = 6$  and similar  $\bar{\Delta} = 7$  and 8 yr. Fig. 1B is now helpful to explain why they have such different  $\bar{A}/\bar{\Delta}$  ratios in Figs. 4B and 5B by moving from left to right for  $\bar{\Delta} \sim 7.5$  yr (in Fig. 1B). The smallest  $S_a/\bar{\Delta}_1$  ratio (0.73; largest difference  $\bar{\Delta}_1 - S_a = 0.2822$ ) was based on updated vital rates for a painted turtle population from southeastern Michigan which included smaller  $S_a = 0.76$  (Tinkle et al. 1981) and produced the smallest  $\bar{A}/\bar{\Delta} = 1.38$  ( $E_3/E_2 = 0.38$ ). A proportional change in juvenile survival ( $S_j$ ) has by far the largest effect on population growth. The original painted turtle population from southeastern Michigan with  $S = 0.83$  (Wilbur 1975) gave  $S_a/\bar{\Delta}_1 = 0.83$  ( $\bar{\Delta}_1 - S_a = 0.1712$ ) and produces intermediate  $\bar{A}/\bar{\Delta} = 1.69$  ( $E_3/E_2 = 0.69$ ) but juvenile survival still has the largest effect on

population growth. The largest  $S_a/\bar{\ell}_1$  ratio (0.950; smallest difference  $\bar{\ell}_1 - S_a = 0.0505$ ) was for a population from central Virginia (Mitchell 1988) with large  $S_a = 0.96$  which produced the largest  $\bar{A}/\bar{\ell} = 2.66$  ( $E_3/E_2 = 1.66$ ). A proportional change in adult survival ( $S_a$ ) has by far the largest effect on population growth for this population.

The  $\bar{\ell}/\bar{\ell}$  ratios of marine and terrestrial mammals show large variation (mean 6.49, CV = 46%, range 2.40 – 19.0; Table 2, ID #11) and therefore the contour plots given in Fig. 1 are less useful. The E-patterns shown in Fig. 4C which includes the  $\bar{A}/\bar{\ell} = 2.0$  contour becomes more illustrative. Marine and terrestrial mammals generally have  $\bar{A}/\bar{\ell}$  ratios larger than 2.0 (2.53, CV = 23%,  $n = 17$ ; and 2.34, CV = 32%,  $n = 51$ , respectively) and a change in adult survival has the largest effect on population growth (Table 2, IDs #12 & #13; Fig. 4C). Terrestrial mammals, in particular those with  $\bar{\ell} = 1$  or 2 yr, have a large  $\bar{A}/\bar{\ell}$  range (1.21 for snowshoe hare to 4.96 for little brown bat).

The  $\bar{A}/\bar{\ell}$  range is smaller for marine mammals (1.68 for killer whale to 3.77 for pilot whale) and for many marine mammals  $E_3$  is largest. This is as expected because  $S_a/\bar{\ell}_1$  is close to 1.0. However, large  $E_3$  can be due to overestimating the length of the reproductive period by equating it with longevity with a corresponding underestimate of fertility. The calculations using 3 different sets of orca vital rates demonstrate this in Figs. 4C and 5C. All 3 populations have  $S_a/\bar{\ell}_1$  close to 1.0 (Appendix 1). The results using  $\bar{\ell} = 60$  yr ( $\bar{\ell}/\bar{\ell} = 4.6$ ) and  $m = 0.070$  following Heppell et al. 2000 with  $S_a/\bar{\ell}_1 = 0.967$  ( $\bar{\ell}_1 - S_a = 0.033$ ) produced  $\bar{A}/\bar{\ell} = 2.34$  ( $E_3/E_2 = 1.34$ ). The data from Eberhardt 2002 ( $\bar{\ell} = 50$ ,  $\bar{\ell}/\bar{\ell} = 4.0$  and  $m = 0.11$ ) with  $S_a/\bar{\ell}_1 = 0.959$  ( $\bar{\ell}_1 - S_a = 0.043$ ) already produced  $\bar{A}/\bar{\ell}$  smaller than 2.0 (1.87;  $E_3/E_2 = 0.87$ ). Finally, using the more realistic  $\bar{\ell} = 36$  yr ( $\bar{\ell}/\bar{\ell} = 2.6$ ; reproductive period  $T_3 = 22$  yr) and  $m = 0.12$  from Brault and Caswell (1993) with  $S_a/\bar{\ell}_1 = 0.968$  ( $\bar{\ell}_1 - S_a = 0.034$ ) indicated that  $\bar{A}/\bar{\ell}$  becomes even smaller (1.68;  $E_3/E_2 = 0.68$ ) and now juvenile survival clearly has the largest effect on population growth.

I assumed  $\bar{\ell}/\bar{\ell} = 6$  for all but one marine and terrestrial bird population. However, the contour plots given in Fig. 1B are less useful because the critical, vertical  $E_3/E_2$  contour has value 2.5. The E-pattern graphs in Figs 4D and 5D which include the  $\bar{A}/\bar{\ell} = 2.0$  contour are more illustrative. The mean  $\bar{A}/\bar{\ell}$  ratio of marine birds (2.44, CV = 14%,  $n = 46$ ) has a considerably smaller coefficient of variation (CV) than that of terrestrial birds (2.48 CV = 46%,  $n = 31$ ) (Table 2, IDs #18 & #19; Fig. 4D). Marine birds generally have an  $\bar{A}/\bar{\ell}$  ratio larger than 2.0 but its range (1.71 for great skua to 3.16 for emperor penguin corresponding to  $E_3/E_2 = 0.71 - 2.16$ ) includes a few birds with



$\bar{A}/\bar{\Delta}$  ratio  $< 2.0$ . The  $\bar{A}/\bar{\Delta}$  ratio range of terrestrial birds (1.55 for great tit to 7.80 for spotted owl, corresponding to  $E_3/E_2 = 0.55 - 6.80$ ) is considerably larger because many  $\bar{\Delta} = 1$  yr terrestrial birds have small  $\bar{A}/\bar{\Delta}$  ratios and juvenile survival has the largest effect on population growth. The golden plover and the emperor penguin demonstrate that the  $\bar{A}/\bar{\Delta}$  ratio increases considerably ( $\bar{A}/\bar{\Delta} = 4.0 - 12.9$  and  $3.2 - 4.7$ , respectively) if longevity is increased from  $\bar{\Delta} = 6$  yr to a less reasonable  $\bar{\Delta} = 100$  yr to simulate  $\bar{\Delta} =$  yr in a stage-based model that uses  $P_a = S_a$  for the diagonal matrix element of the adult stage.

#### 4. Discussion

##### 4.1 E-patterns that use $\bar{A}$ and include survival in the discounted fertilities

The use of  $\bar{A}$  simplifies the formulation of E-patterns and the  $\bar{A}/\bar{\Delta}$  and  $E_3/E_2$  ratios ( $E_3/E_2 = \bar{A}/\bar{\Delta} - 1$ ) help in the understanding of E-patterns for age-structured animal populations. The equations (A2.8) for the E-pattern eliminate the need to calculate the E-matrix and yield E-patterns that are the same for post- and pre-breeding Leslie matrix. They also agree with the E-pattern that can be calculated empirically from the corresponding life history table (LHT). Importantly, I have shown that many reported E-patterns are more or less biased because the contributions of the survival terms in the discounted fertilities were omitted. While Caswell (2001) is an outstanding volume covering all aspects of matrix population models, my analysis suggests two improvements for the elasticity analyses of age-structured animal populations. First, a formulation with  $\bar{A}$  simplifies the E-pattern and facilitates interpretation. Second, the calculation of E-patterns requires that the survival rates in the discounted fertilities are included.

First, Caswell (1989, 2001) predominantly dealt with the construction of matrix models for species with complex reproductive cycles (e.g. plants with multiple types of offspring). The mean age of the reproducing females at the stable age distribution ( $\bar{A}$ ) and the mean age of the mothers of a cohort ( $\bar{\Delta}_1$ ) are not well defined for plants (Caswell 2001, p. 130, footnote 9). It is therefore not surprising that they were not used in the formulation of E-patterns for age-structured matrix models for animals.

Caswell (2001) was ambiguous with regard to the second problem which can be phrased in terms of whether the sum of the E-pattern is 1.0 or  $1.0 + E_1$  (i.e.  $E_2 + E_3 = 1.0$ ). I have proved in Appendix 2 (eq. A2.8) that  $E_2 + E_3 = 1.0$  for a Leslie matrix and this was first derived by Hamilton (1966, p.18 his eq. 10 when  $a = 0$ ). Whereas early chapters in Caswell (2001, e. g. p. 231) say that elasticities in the E-matrix add up to 1.0, which is technically

correct, the snow goose example used on p. 635 shows that the sum of the E-pattern is  $1 + E(m)$ . A discussion in terms of upper and lower level elasticities is misleading when using a Leslie matrix. The survival rates appear on the sub-diagonal and thus are upper-level vital rates but they also appear in the discounted fertilities which would make them lower-level vital rates.

5 The snow goose example came from Rockwell et al. (1997) and they were the first to state that “adult survival actually contributes more to the control of  $\bar{\lambda}_1$  than pooling the elasticities of the elements  $P_2, P_3, P_4$  and  $P_5$  indicates”. Mollet and Cailliet (2002, 2003) came to the same conclusion. Note however, that their model used P for survival (S) of their age classes 1 - 4 and  $P_5 = S_5$  for the diagonal stasis element of the adult stage. It is debatable if  $P_2 = S_2$  should not be counted with juvenile survival because  $\Delta = 2$  yr and  $P_5 = S_5$  implies that  $\Delta =$  yr which  
10 overestimates  $\bar{\lambda}_1$ .

The same ambiguity appears in Heppell et al. (1996) and Heppell et al. (2000). In their 1996 paper, the E-patterns were calculated empirically (which guarantees an unbiased E-pattern) from a post-breeding 4-stage model that included survival to age 1 yr (hatchlings) and survival of the other stages. Therefore the sum was  $1.0 + E_1$  (e.g. their Fig. 5 for the  $\Delta = 8$  yr scenario for Kemp’s Ridley turtle shows  $E_1 \approx 0.1, E_2 \approx 0.1 + 0.28 + 0.37 \approx 0.75, E_3 \approx$   
15  $0.25$  with sum  $\approx 1.1$ ). The Heppell et al. (2000) pre-breeding model with all adult age-classes in one stage was summarized by Caswell (2001, p. 231) and the biased E-pattern sum is 1.0 because survival to age 1 yr was not included.

An empirical calculation of the E-pattern from a stage-based model is unbiased and therefore an unbiased value for  $\bar{\lambda}_1$  can be calculated from the equation  $E(m) = 1/(\bar{\lambda}_1 + 1)$ . This would prevent the potential problem of  
20 calculating biased elasticities using eq. 9.103 in Caswell (2001) (Mollet and Cailliet 2003). This  $\bar{\lambda}_1$  will be the same as that calculated from the corresponding LHT or Leslie matrix. The stage-based model, although it will yield the same  $\bar{\lambda}_1$  if fixed stage duration is used to calculate the fractions that graduate in each class, will produce biased  $\bar{\lambda}_1$  (Appendix A2.7). In a stage-based model with only the adults in a stage,  $\bar{\lambda}_1$  is always biased high (Mollet and Cailliet 2003, Appendix 1(e)(i)) because the adults are speeding through the adult stage (to the next stage = death)  
25 and their mean age at the stable age distribution becomes larger. If juveniles are put in a stage, the same speeding of juveniles through the juvenile stage occurs but this will now make the adults younger. In principle, these two biases for  $\bar{\lambda}_1$  could offset each other but based on empirical results for a large number of stage-based model, the  $\bar{\lambda}_1$ -bias

from the juveniles is larger and therefore  $\bar{A}$  for a 3-stage model will produce an  $\bar{A}$  that is lower than that of the corresponding LHT or Leslie matrix. (It is best to use a starter age class for the offspring so that  $\langle w, v \rangle = \bar{A}$  and one stage each for juveniles and adults). In short, we cannot use  $\bar{A}$  from stage-based models to calculate E-patterns from eqs. A2.7 or A2.9.

#### 5 4.2 E-patterns for sharks, turtles, mammals, and birds

The use of elasticities to derive management proposal for elasmobranchs is relatively recent (e. g. Brewster-Geisz and Miller 2000; Frisk et al. 2001, 2002; Cortés 2002; Mollet and Cailliet 2002, 2003). Brewster-Geisz and Miller (2000) phrased their E-patterns in terms of fertility, growth, and stasis, terms that are more suitable for plants (Heppell et al. 2000; Mollet and Cailliet 2003). The validity of a comparative life history study by Frisk et al. (2001) was questioned by Mollet and Cailliet (2003) and Cortés (2004). Frisk et al. (2002) used a stage-based model for barndoor skate *Dipterus leaevis* and predicted that adult survival had the most effect on population growth when in fact it is juvenile survival (Mollet and Cailliet 2003; Cortés 2004).

Cortés (2002) reported  $\bar{A}$ , E-pattern, and E-ratios for 41 elasmobranch populations. I suggest that the reported  $E_2/E_1$  and  $E_3/E_1$  ratios (E-ratios 2 and 1, respectively in his Appendix 2) could have been calculated directly from the reported mean  $\bar{A}$  and calculated  $\bar{A}$  and that these ratios are difficult to understand. Cortés (2002) followed Heppell et al. (2000), who did not include survival to age 1 yr, and therefore his  $E_2/E_1$  ratios should be  $\bar{A} - 1$  (ratio of eqs. A2.21.2 and A2.21.2) and the sum of the two ratios  $E_2/E_1 + E_3/E_1$  should be  $\bar{A} - 1$ . The reported  $E_2/E_1$  ratios were on average  $\bar{A} - 0.54$  yr and the sum was on average  $\bar{A} - 0.06$  yr  $\bar{A}$ . It is unlikely that the discrepancies are an effect of the stochastic calculations that were used; I surmise that they arise because the E-patterns were calculated within a LHT which requires that Lotka's equation is made discrete and this should not be attempted (Caswell 2001, p. 197).

Smith et al. (1998) suggested that their intrinsic rebound potential ( $r_{2M}$ ), which was strongly affected by age at first reproduction ( $\bar{A}$ ) but not maximum age ( $\bar{A}$ ), has management implications for sharks. Mollet and Cailliet (2002) showed that their rebound potential could be well represented with a power regression  $r_{2M} = \ln(1.28) \bar{A}^{0.809}$  where 1.28 was interpreted as the effective annual fertility which would be the same for all sharks. Mollet and Cailliet (2002) suggested that population growth rates based on available vital rates will provide more meaningful E-patterns to serve as a basis for elasmobranch management. In this study, I used populations of scalloped

hammerhead and shortfin mako with  $\Delta$  that differed by a factor 3.75 and 2.6, respectively, to show that  $\Delta$  has little effect on the E-pattern. I also showed that the  $\Delta/\Delta$  ratio and thus  $\Delta$  play an important role in the elasticity ratio  $E_3/E_2$ . These are further indications that the intrinsic rebound potential of Smith et al. (1998), which really is a rate constant and not a productivity or yield as claimed, may be a less useful concept to provide management proposals for sharks. Heppell et al. (1996; their Fig. 5) were the first to show that different  $\Delta$ 's of 8, 12, and 16 yr for Kemp's ridley turtle had little effect on the E-patterns and all three E-patterns were characterized by  $E_3/E_2 < 1.0$ .

E-patterns for marine turtles were used extensively to demonstrate the importance of increasing juvenile survival with turtle-excluder devices (TEDs) versus increasing survival of hatchlings with head-start programs (e.g. Heppell et al. 1996; Heppell 1998). Heppell (1998) concluded that most freshwater turtles have similar E-patterns, whereas desert tortoise and sea turtles had different E-patterns and three different life tables for painted turtle produced different E-patterns. The results in Figs. 4B and 5B confirm this. Turtles have relatively large  $\Delta$  (4 – 35 yr) and the E-pattern bias when survival to age 1 yr is excluded becomes small or negligible (Fig. 3). The stage-based model used by Heppell (1998) that assumed  $\Delta =$  produced large  $\bar{A}$  of 116 and 52 yr ( $\bar{A}/\Delta = 6.11$  and 5.21) for snapping turtle A ( $\Delta = 19$  yr) and Australian snake-necked turtle ( $\Delta = 10$  yr) because  $S_a = 0.966$  and 0.98, respectively, were close to 1.0 (Table 4 ID's #8 & #9). I used the painted turtle to demonstrate that the differences in the E-pattern arise because adult survival is different (Fig. 4B). All three turtle populations have the same  $\Delta/\Delta$  ratio and similar  $\Delta$  (7 and 8 yr), and Fig. 1B confirms that the calculated  $E_3/E_2$  ratios from the E-matrix of the Leslie matrix are as predicted from eq. (A2.13.2) with  $\Delta/\Delta = 6$ .

Tucker (2000) reported that “high eigenelasticity was associated with adult survival” for freshwater crocodiles. This is surprising considering that their life histories are similar to those of marine turtles. The reported adult survival rates of crocodiles ( $S_a = 0.85 - 0.90$ ) are within the range of those of marine turtles ( $S_a = 0.74 - 0.95$ , Appendix 1) and elasticity of juvenile survival ( $E_2$ ) is expected to be largest. My calculations for *Crocodilus johnstonii* (QL), *C. johnstonii* (NT), *C. porosus*, *C. acutus*, and *Alligator mississippiensis* produced similar E-patterns ( $\bar{A}/\Delta < 2$ ; 1.59 - 1.88; Table 2, ID #10) to those of marine turtles ( $\bar{A}/\Delta < 2$ ; 1.26-1.61, Table 2 ID # 7) with the exception of *Caiman crocodilus* with  $\bar{A}/\Delta = 2.05$  (Table 2, ID #10). This indicates that  $E_2$  is largest for the first 5 species and almost the same as  $E_3$  for *C. crocodilus*. Tucker (2002) used a 5-stage post-breeding census model with 2 adult-stages without the required  $F_3$ -matrix element (Caswell 2001, eq. 6.150 on p. 173) or a separate age-

class for the maturing juveniles; thus his results apply to  $\bar{l}_{\text{effective}} = \bar{l} + 1$  yr. However, this would underestimate rather than overestimate  $E_3$ . Tucker (2002) based his conclusion on the sum of the elasticity of stasis of the adult stages  $[E(P_4) + E(P_5)]$ , which is indeed largest for all 6 species. However, an E-pattern based on reproduction ( $F$ ), growth ( $G$ ), and stasis ( $P$ ) is more suitable for plants than animals (Heppell et al. 2000; Mollet and Cailliet 2003).

5 Stasis ( $P$ ) cannot be called survival as was done in his Fig. 2 and the reported largest eigenelasticities are not the elasticities of adult survival ( $E_3$ ).

Heppell et al. (2000) modified Grime's triangle used by Silvertown et al. (1992) by replacing the elasticities of fertility, growth, and stasis, suitable for stage-based models of plants, with the elasticities of fertility, juvenile survival, and adult survival more suitable for animals. This produced a most promising tool to investigate E-patterns of mammals because it allowed presentation of the E-pattern of a species as a single data point. They were surprised that the elasticity of adult survival ( $E_3$ ) for 50 mammal species was not significantly correlated with generation time ( $\bar{l}_h$ ) because the exclusion of survival to age 1 yr produced an artificial hump. Correlation analysis is not a suitable tool for elasticity analyses because the explicit and exact functional relationship between normalized  $E_3$  and  $\bar{A}$  is known  $[E_{n,3} = (\bar{A} - \bar{l})/(\bar{A} + 1)]$ , (eq. A2.8.3). The parameter graphs in Fig. 1 are even more general and give the

10  $E_3/E_2$  ratio as a function of  $x = S_a/\bar{l}_h$  and  $y = \bar{l}$  for  $\bar{l}/\bar{l}_h$  ratios from 3.0 to 12.0 and can be extended to any  $\bar{l}/\bar{l}_h$  ratio. Mollet and Cailliet (2003) pointed out that the stage-based model used by Heppell et al. (2000) that used observed  $\bar{l}$  with  $P = S_a (1 - \bar{l})$  for the diagonal matrix element produced biased  $\bar{A}/\bar{l}$  (Table 2, ID's #14 & #15).

Eberhardt (2002) used a LHT and reported sensitivities ( $S$ ) rather than elasticities ( $E$ ) as reported here. He concluded that for all 16 mammals and the spotted owl the sensitivity of adult survival  $S_3 = d(\bar{l})/d(S_a)$  was largest by

20 far with  $S_3/S(l_{\bar{l}})$ -ratios between 12.3 - 1.36. The sensitivity of 'early survival' in his Table 2 is  $S(l_{\bar{l}}) = d(\bar{l}_h)/d(l_{\bar{l}})$  rather than  $S_2 = S(S_j) = d(\bar{l}_h)/d(S_j)$  and the latter would provide a better comparison with  $S_3$ . They are related by the equation  $S(l_{\bar{l}}) = S_2/(\bar{l} S_j^{(\bar{l}-1)})$ . His Fig. 3 suggests that  $S_3$  is largest for all species but my calculation of  $S_2$  indicated that it is larger for 6 out of the 17 mammal species. For 4 out of these 6 species (Grizzly bear B.C., Lysan monk seal, fur seal, and killer whale)  $\bar{A}/\bar{l}$  is  $< 2.0$  and therefore these species also have  $E_3/E_2 < 1.0$  (Table 2, ID #16).

25 Both Russell (1999) and Saether and Bakke (2000) concluded that population growth rates of birds are most sensitive to adult survival. My results support this conclusion in general but suggest that juvenile survival is more important for almost 20% of their bird species, in particular those with  $\bar{l} = 1$  yr and large  $(S_a - \bar{l}_h)$  (Fig. 4D,

Table 2, IDs #20-23). Four marine birds and 11 terrestrial birds (including borderline white stork) have  $\bar{A}/\bar{\Delta} < 2$ .

They did not include survival to age 1 yr, which overestimates the importance of adult survival ( $E_3$ ). In addition, they used a matrix model that assumes  $\bar{\Delta} =$  yr which further overestimates  $E_3$  because  $\bar{A}$  is overestimated, in particular for long-lived species with  $S_a$  close to 1.0. Russell (1999, his Fig. 2) gives a characteristic equation of order  $\bar{\Delta} + 1$  which is different from the one given in Saether and Bakke (2000, their eq. 2). If the maturing juveniles have the same survival rate as adults, then they can be combined with the adult stage in the post-breeding census that was used, but then there are  $\bar{\Delta} - 2$  not  $\bar{\Delta} - 1$  time-steps between ‘immature’ and ‘breeding adult’ stages. Therefore, the results in Russell (1999) apply to  $\bar{\Delta}_{\text{effective}} = \bar{\Delta} + 1$  and his reported  $\bar{\Delta}_h$ ’s are underestimates.

Better longevity estimates for birds are needed to avoid the use of the  $\bar{\Delta} =$  yr approximation. Although some albatross species are long-lived, my longevity estimates of  $w = 6\bar{\Delta}$  yr are probably sufficient. Adelie penguin with  $\bar{\Delta} = 4$  yr has  $\bar{\Delta} = 14$  yr ( $w/\bar{\Delta} = 3.5$ ) and yellow-eyed penguin with  $\bar{\Delta} = 3$  yr has  $\bar{\Delta} < 14$  yr ( $w/\bar{\Delta} \approx 4.7$ ) (H. Nevins, MLML, Moss Landing, CA 95039, USA, personal communication). Nevins and Carter (2003) reported  $\bar{\Delta} = 3$ -5 yr and  $\bar{\Delta} > 10$  yr ( $w/\bar{\Delta} > 2 - 3.3$ ) for the common murre. Eberhardt (2000) used  $\bar{\Delta} = 2$  yr and  $\bar{\Delta} = 25$  yr ( $w/\bar{\Delta} = 12.5$ ) for the spotted owl. For the lesser snow goose my longevity estimate of  $\bar{\Delta} = 6\bar{\Delta} = 12$  yr could be too low, whereas the  $w =$  yr estimate used by Rockwell et al. (1997) is an overestimate. The observed population growth of mid-continent lesser snow geese from 1970 to 1995 was about  $\bar{\Delta}_h = 1.031$  (estimate from the linear regression used by Rockwell et. al. 1997 in his Fig. 1, taking into account footnote 21 on p. 634 in Caswell 2001). This value can be compared with calculated  $\bar{\Delta}_h = 1.013, 1.021, 1.045, 1.051, 1.052, 1.052$  using  $\bar{\Delta} = 10, 12, 18, 30, 40,$  and yr, respectively, which suggests that a longevity between 12 and 18 yr would be best.

#### 4.3 Limitations of deterministic E-patterns based on deterministic $\bar{A}$ formula that assumes age-independent $S_a$ and $m$

The E-patterns presented in this study are deterministic and apply to the populations at their stable age distribution. Several case studies concluded that deterministic elasticities are good indicators of stochastic elasticities whereas the stochastic population growth rate is not well predicted by a deterministic analysis of the mean matrix (Nakaoka 1996; Dixon et al. 1997). E-patterns have been shown to be very robust to even large ( $\pm 50\%$  at least) perturbations of vital rates (Caswell 2001, p. 243). However, the risk of extinction for small populations

increases if stochasticity of vital rates is included (Dixon et al. 1997; Caswell 2001, p. 493). The deterministic results presented here for sharks (mean  $\bar{A}/\bar{L} = 1.30$ , CV = 8.3%, range 1.06-1.60;  $n = 41 + 7$ ; Table 2, ID #2) compare well with the stochastic calculation carried out by Cortés (2002) (mean  $\bar{A}/\bar{L} = 1.46$ , CV = 14%, range 1.11-2.00;  $n = 41$ ; Table 2, ID #4). The pseudo-stochastic E-patterns that assume  $\bar{L}_1 = 1$  for these shark populations provide an ever better approximation (mean  $\bar{A}/\bar{L} = 1.37$ , CV = 16%, range 1.05-2.09;  $n = 41 + 7$ ; Table 2, ID #3) to the stochastic calculation by Cortés (2002). I therefore propose that the pseudo-stochastic E-patterns are good approximations of stochastic calculations for all species in this study of relatively long-lived animals.

The use of age-independent vital rates, in particular  $S_a$  and  $m$ , appears to be a more serious limitation but I will demonstrate that the E-patterns presented here are fairly robust except in extreme cases of size-dependent fertility not found in the animals considered here. Cortés (2002) used a stochastic selection of the survival rates in elasmobranchs and gave most weight to the mass dependent survival rates reported by Peterson and Worblewski (1984) and used wet weight as a proxy for dry weight because it produced more realistic survival rates. While this procedure can be questioned, his results are most suitable for comparison with my pseudo-stochastic calculations because his adult survival rates increase with age whereas mine are age-independent. If older adults have larger survival rates,  $\bar{A}$  and  $\bar{A}/\bar{L}$  are expected to be larger and my calculation might not provide a reasonable approximation for the E-pattern of elasmobranchs. This is not the case based on the results discussed in the previous paragraph.

The data for leopard shark, North Sea haddock, and striped bass with age-dependent fertility presented in Heppell et al. (1999, their Fig. 1) provide excellent cases to explore the effect of age-dependent  $m$  on the E-pattern. The most striking result is for striped bass with surprisingly large  $E_3/E_2$  ( $\approx 0.55/0.34 \approx 1.6$  from their Fig. 1), whereas North Sea haddock and leopard shark had, as expected,  $E_3/E_2$  ratios smaller than 1.0 ( $\approx 0.15$  and  $\approx 0.26$ , respectively). The reported E-pattern for striped bass is in apparent conflict with equation A2.4 which predicts that  $E_3/E_2 (= \bar{A}/\bar{L} - 1)$  should be considerably smaller than 1.0 because  $\bar{L}_1 - S_a = 0.4$  is large. While the reported E-patterns in Heppell et al. (1999) are biased because survival to age 1 yr was not included, the unbiased E-pattern for striped bass with  $E_3/E_2 \sim 0.92$  is still much closer to 1.0 than expected, given that  $\bar{L}_1 - S_a = 0.4$  is very large (Table 3).

In the derivation of eq. (A2.4) for  $\bar{A}$ , fertility ( $m$ ) was assumed to be age-independent and Table 3 illustrates that this approximation is adequate as long as the observed increases in the age-dependent fertilities are small to moderate. This applies to leopard shark and North Sea haddock for which  $m$  increases by a factor of 3.6 and 4.3, respectively (Table 3). The age-independent approximation produces  $\bar{A}$ -biases of only -5% and -8%,  
 5 respectively. When the increase in the age-dependent fertility is large (61, as for striped bass) to extreme (276, as for hypothetical striped bass), the approximation using age-independent fertility is no longer adequate and  $\bar{A}$  has to be calculated more accurately as was done in Table 3 for all three species. For striped bass the age-independent approximation produced  $\bar{A}$ -bias of -29% compared to the calculation with the experimentally observed fertilities.

Berkeley et al. (2004) reported that older rockfish and cod or striped bass produce larvae/infertile eggs with  
 10 higher survival rates. This would require different larval age-classes and would be difficult to incorporate in an age-structured LHT or Leslie matrix. However, such an effect could be simulated with the proposed hypothetical striped bass Leslie matrix model by increasing observed fertility of older fish to reflect that their larvae/eggs will have larger survival to age 1.

Caswell (2001, p. 39) suggested that size-dependent demography is probably the rule rather than the  
 15 exception and his examples included reproductive output that is strongly dependent on adult body size (e.g. turtles according to Gibbons et al. 1982). I suggest that an age-classified Leslie matrix is adequate for turtle populations. In addition, the reported reproductive output for the five turtle species in Gibbons et al. (1982) varies by less than a factor of 5 and even an age-classified model using age-independent  $m$  should provide a good approximation for the true E-patterns.

20 It is often stated that sharks are long-lived and have few offspring (Musick et al. 2000), whereas bony fish more commonly spawn millions of egg and are shorter-lived (Winemiller and Rose 1992). The implication usually is that the E-patterns and thus management are expected to be different. This is not correct unless the number of eggs produced depends strongly on maternal mass as outlined above. If spawning is mass-independent and recruitment does not fluctuate (time-independent), the E-pattern of a spawner is identical to that of a shark producing the same  
 25 number of maturing juveniles ready to “spawn” for the first time. This is best understood from the discounted fertilities in the pre-breeding Leslie matrix, which are  $F_i = m_i S_1$ . A large  $m_i$  with corresponding small  $S_1$  produces the same  $F_i$  as small  $m_i$  with large  $S_1$ . Recruitment of a spawning fish is expected to show large fluctuation but on



average population growth is expected to be around 1.0 and therefore the pseudo-stochastic E-pattern using  $\bar{\lambda}_1$  instead of  $\bar{\lambda}$  should apply in a first approximation.

#### 4.4 Fast-slow continuum and r-K selection

The fast-slow continuum introduced by Read and Harvey (1989) has been used by many to explain the results of prospective elasticity analysis (e. g. Heppell et al. 2000; Saether and Bakke 2000; Cortés 2002). I suggest that the fast-slow continuum is not a useful concept to understand E-patterns of animals in the context of a prospective analysis with the goal of providing management proposals. The “fast” end corresponds to species that start and end reproduction early (small  $\lambda$  and  $\lambda_1$ ), have large fertility ( $m$ ) and low survival rates ( $S_j$  and  $S_a$ ), while the “slow” end corresponds to species with opposite vital parameters. Consider the 44 mammal and bird populations with  $\lambda = 1$  yr in Figs. 4C & D: they would all be expected to be at the fast end because  $\lambda$  (the most important of all the parameters) is small. However, these species have a considerable  $\bar{\lambda}/\lambda$  range of 1.2 - 7.8 ( $= \bar{\lambda}$  because  $\lambda = 1$ ;  $E_3/E_2$  range = 0.20 – 6.8), indicative of a wide range of E-patterns from  $E(S_a)$  much smaller than  $E(S_j)$  to the opposite. The 66 elasmobranch populations have  $\lambda$  between 1-35 (most are between 2-20) and they would be expected to exhibit vastly different E-patterns along a slow-fast continuum because the range of  $\lambda$  is large. This is not the case. Their E-patterns are similar and  $E(S_j)$  is largest for all because  $\bar{\lambda}/\lambda < 2$  (Fig. 4A).

Similarly, r-K selection appears not to be a useful concept either for understanding E-patterns. All 240 populations of birds, mammals, turtles, and mammals studied should be considered K-strategists ( $\lambda_1 = 0.47 - 1.8$ ). The E-matrix and derived E-pattern applies to the stable age-distribution which is often not reached in r-selected species with large  $r_1 = \ln(\lambda_1)$  over the short period of time in a typical growing season (Caswell 2001, p. 99). The E-pattern is determined by  $\bar{\lambda}$  and  $\lambda$  alone and the  $\bar{\lambda}$  formula (A2.4) shows how  $\bar{\lambda}$  depends on vital rates. Nothing else is needed to calculate the E-pattern. I suggest that the formulas presented in this paper are adequate to understand how life histories determine elasticity patterns and that there is no need to calculate second derivatives of eigenvalues, i.e. sensitivities of elasticities as suggested by Caswell (2001, p. 257). If A2.4 is inadequate,  $\bar{\lambda}$  can be calculated more accurately from the LHT or Leslie matrix using age-dependent vital rates to provide more accurate E-patterns. Many studies trying to provide management proposals based on prospective analyses are actually studying life history variation in an evolutionary perspective (Caswell 2001).

#### 4.5. Effect of the reproductive cycle on the E-pattern

The  $\bar{A}/\square$  ratio ( $= E(S_a)/E(S_j) + 1 = E_3/E_2 + 1$ ) perfectly defines the relative importance of adult and juvenile survival and  $\bar{A}/\square = 2$  is equivalent to  $E(S_a) = E(S_j)$ . The relative importance of  $E(S_j)$  and  $E(m)$  with ratio  $E(S_j)/E(m) = \square$  needs to be addressed also. When  $\square = 1.0$  yr, we have  $E(S_j) = E(m)$ . For animals with large  $\square$ ,  $E(S_j)$  becomes large compared to  $E(m)$  and this fact was used in support of management measures that increased juvenile survival because it was far more effective than increasing fertility (e.g. TEDs versus head-start programs for sea turtles (Crouse et al. 1987)). However, while  $E(S_j)$  is certainly much larger than  $E(m)$  when  $\square$  is large, say 15 – 35 yr, the ratio  $E(S_j)/E(m)$  would be 3 - 7 instead of 15 - 35, if a projection interval ( $PI$ ) = 5 yr combined with actual fertility is used instead of  $PI = 1$  yr combined with annualized fertility. Mollet and Cailliet (2003) suggested that this applies to the killer whale and an Australian green turtle population. Many species used in this study have a reproductive cycle  $\geq 2$  yr (e.g. king penguin, several albatrosses, chimpanzee, gorilla, African elephant, hippopotamus, manatee, and several whales). The 66 elasmobranch populations comprised 32 with  $RC = 1$  yr, 29 with  $RC = 2$  yr, and 5 with  $RC = 2.5(2 \text{ or } 3) \text{ to } 3$  yr. In all these cases the observed  $RC$  combined with actual fertility should be used which will increase the importance of fertility because  $E(m)$  becomes larger. In this study I used  $RC = 1$  yr with effective annual fertility for easier comparison with reported results. The E-triangle is suitable for comparison of E-pattern based upon different  $PI$ 's. However, it makes identification of a particular species in the E-triangle more difficult because the  $\square$  contours now have units of the  $PI$  which will be different for different species, rather than 1 yr for all.

#### 4.6 Conclusions

For animals with a simple rather than a complex life history, Mollet and Cailliet (2003) had reservations about the use of stage-based models with few stages because they require great care when calculating the E-pattern. I now suggest the same for the Leslie matrix model. A life history table with an empirical calculation of the E-pattern provides all the information needed for an elasticity analysis, whereas the corresponding Leslie matrix requires attention to the concept of discounted fertilities to obtain the unbiased E-pattern which should be the same for post- and pre-breeding censuses. If a Leslie matrix is used, then results should at least should be compared with those from a life history table. If age-specific fertilities and or survival rates are available, then it would be better to use them rather than average values (Barlow and Boveng 1991) and obtain the best possible  $\bar{A}$  and E-pattern. Matrix models are required for the construction, analysis, and interpretation of species with complex life cycles and

for more advanced topics in population model analyses which are superbly presented in Caswell (2001). Discrete-time, discrete-state matrix models are easier to understand than partial differential equation models (McKendrick-von Foerster equation with boundary condition), delay-differential equation models, or integrodifference equation models (Caswell 2001, p. 205).

5           The E-matrix is a mathematical rather than a biological concept and provides the proportional first derivatives  $[E(a_{ij}) = \partial n(\lambda) / \partial n(a_{ij})]$  of the function  $\lambda = \lambda(a_{ij})$ , where  $a_{ij}$  are vital rates or derived from vital rates. The E-pattern then provides a summary of the E-matrix and like the E-matrix applies to the stable age distribution. I have shown that the E-matrix is not even needed because the E-pattern can be directly calculated from  $\lambda$  and  $\bar{A}$ . It is tempting to suggest that a prospective elasticity analysis might be less useful than previously suggested because E-patterns are so easily estimated. Caswell (2001, p. 109, footnote 7) says: “Solubility is useful to a chemist because it reveals something about the arrangement of electrons in the substance and the solvent, even if the substance never encounters the solvent. Population growth rate is useful to a demographer because it reveals something about the life cycle and the environment, even if the population never encounters constant conditions as  $t \rightarrow \infty$ .” I suggest that the same applies to the E-pattern which describes what would happen (projection) rather than what will happen (forecasting) given certain hypotheses (Caswell 2001, p. 30).

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## Table Legends

### Table 1. Vital rates used in hypothetical demonstration species

$\bar{x}$  = age at first reproduction;  $x$  = age at last reproduction;  $S_1$  = survival to age 1 yr;  $S_j$  = juvenile survival;  $S_a$  = adult survival;  $m$  = female fertility.

### 5 Table 2. Summary statistics for $\bar{A}/\bar{x}$ , $\bar{x}/x$ , and $\bar{x}$ for shark, turtle, mammal, and bird populations

$\bar{A}$  = mean age of reproducing females at the stable age distribution;  $\bar{x}$  = age at first reproduction (yr);  $x$  = age at last reproduction (yr);  $\bar{x}$  = population growth; CV = coefficient of variation.

### Table 3. Biased $\bar{A}$ (and E-patterns) for selected species with age-dependent fertility when assuming constant fertility

10 After Heppell et al. (1999, their Table 2) except hypothetical striped bass.  $\bar{x}$  = age at first reproduction (yr);  $x$  = age at last reproduction (yr);  $S_a$  = adult survival;  $m$  = female fertility;  $\bar{x}$  = population growth;  $\bar{A}$  = mean age of reproducing females at the stable age distribution.

## Figure Legends

### Fig. 1. Relative proportional importance of adult and juvenile survival on population growth of animals assuming

15 constant fertility  $m$  and adult survival  $S_a$ . Graphs give  $(E_3/E_2)$ -ratio contours for  $\bar{x}/\bar{x}$  [= w/al] = 3.0 (A), 6.0 (B), 9.0 (C), and 12.0 (D) for  $x = S_a/\bar{x}$  [= Sa/lambda1] and  $y = \bar{x}$  [= alpha]. E.g. for  $\bar{x}/\bar{x} = 6.0$  from eq. (A2.13.2)  $E_3/E_2 = (1/y) \{ [x/(1-x)] - [(5y+1)x^{(5y+1)} / (1-x^{(5y+1)})] \}$ . The  $E_3/E_2 = 1$  contour gives parameter values of  $\bar{x}/\bar{x}$ ,  $S_a/\bar{x}$ , and  $\bar{x}$  for which elasticity of adult survival is the same as elasticity of juvenile survival. (Not all the critical, vertical contours are drawn because of lack of program control.) (Note to editor and reviewers: I am hoping to produce

20 smoother contours, which requires improved 'contours.m' script which in turn requires a newer version of Octave program.)

**Fig. 2.** Life history table (A) and corresponding birth pulse Leslie matrices using post-breeding (B) and pre-breeding (C)) censuses with z-transformed life cycle graphs (D), eigenvalues and eigenvectors (E), elasticity matrices (F&G) and E-patterns (H). The E-matrix for both post- and pre-breeding censuses were used to calculate the E-pattern in 7

25 different ways in 5 columns:

1) Summing over matrix elements of the E-matrix including the contribution of survival in the discounted fertilities;

2) From eqs. (A2.7) or an empirical calculation using  $E(x) = [\lambda(1.001x) - \lambda(0.999x)] / [0.002\lambda(x)]$  (Crowder et al. 1994, their Appendix 2);

3) Calculation of normalized elasticities from the results in 1) or 2) (or using eqs. A2.9);

4) Summing over matrix elements excluding contribution of survival in the discounted fertilities producing biased E-pattern;

5) E-pattern using equations for post- and pre-breeding censuses that exclude survival in the discounted fertilities (equations A2.20 and A2.21, respectively) producing biased E-pattern;

4/3) Calculation of the ratio in columns 4 and 3 as an estimate of the bias when survival in the discounted fertilities is excluded in the calculation of the E-pattern.

**Fig. 3.** Triangle E-patterns as a function of  $\lambda$  for post- and pre-breeding censuses with and without inclusion of survival in the discounted fertilities. Graph shows four E-patterns for each hypothetical species used ( $\lambda = 1$  yr species from Fig. 1 and three additional hypothetical species with  $\lambda = 2, 5$ , and  $15$  yr). Unbiased E-patterns fall on the corresponding  $\lambda$  contour and post- and pre-breeding E-patterns coincide. Biased E-pattern for pre-breeding census (when survival in the discounted fertilities is excluded) fall on the  $\lambda - 1$  contour. Biased E-pattern for post-breeding census (when survival in the discounted fertilities is excluded) fall between the  $\lambda$  and  $\lambda - 1$  contours. As  $\lambda$  increases the bias decreases and the two biased E-pattern approach the unbiased E-pattern.

**Fig. 4.** Triangle elasticity patterns based on  $\bar{A}$ . Contours drawn are for  $\bar{A}/\lambda (= A/\lambda) = 2.0$  and  $\lambda (= \lambda) = 1, 2, 5$ , and  $15$  yr. Duplicate star symbols were used for demonstration species: scalloped hammerhead (Hammerhead) with  $\lambda = 4$  and  $15$  yr (Cortés 2002) and shortfin mako (Sfin mako) with  $\lambda = 7$  (Pratt and Casey, 1983) and  $18$  yr (Natanson et al. in review) (A); painted turtle with 3 sets of different vital rates for 2 populations from Wilbur (1995), Tinkle et al. (1981), and Mitchell (1988) (B); killer whale with 3 sets of different vital rates from Heppell et al. (2000), Eberhardt (2002) and Caswell (2001) (C); golden plover  $\lambda = 1$  yr,  $\lambda = 6$  &  $100$  yr, emperor penguin  $\lambda = 5$  yr,  $\lambda = 30$  &  $100$  yr (D).

**Fig. 5.** Triangle elasticity patterns based on  $\lambda_l$  ( $\lambda_l = 1.0$ ,  $R_0 = 1$  approximation). Contours drawn are for  $\lambda_l/\lambda (= \mu\lambda/\lambda) = 2.0$  and  $\lambda = 1, 2, 5$ , and  $15$  yr. For explanation of symbols see Fig. 4. This is termed a pseudo-stochastic calculation, see text for details.

## Appendix Legends

### Appendix 1. Vital rates and their sources, and demographic results for shark, turtle, mammal, and bird populations.

$\bar{x}$  = age at first reproduction (yr);  $\bar{x}_l$  = age at last reproduction (yr);  $S_1$  = first year survival;  $S_j$  = juvenile survival;  $S_a$  = adult survival;  $m$  = female fertility;  $\lambda$  = population growth;  $R_0$  = net reproductive rate;  $\bar{A}$  = mean age of reproducing females at the stable age distribution;  $\bar{A}_l$  = mean age of reproducing females in a cohort; ID = ID used in reference.

### Appendix 2. Calculation of $\bar{A}$ and E-patterns for age-structured populations

**Table 1. Vital rates used in hypothetical demonstration species**

$\bar{x}$  = age at first reproduction;  $\bar{x}_l$  = age at last reproduction;  
 $S_1$  = survival to age 1 yr;  $S_j$  = juvenile survival;  
 $S_a$  = adult survival;  $m$  = female fertility.

$\bar{x}$	$\bar{x}_l$	$S_1$	$S_j$	$S_a$	$m$	Comments
1	5	0.50	$= S_1$	0.60	2.0	Figs. 1 and 2
2	10	0.70	0.70	0.95	2.0	Fig. 2
5	25	0.87	0.87	0.95	2.0	Fig. 2
15	75	0.90	0.95	0.95	2.0	Fig. 2

**Table 2. Summary statistics for  $\bar{A}/\square$ ,  $\square/\square$ , and  $\square_1$  for shark, turtle, mammal, and bird populations**

$\bar{A}$  = mean age of reproducing females at the stable age distribution;  $\square$  = age at first reproduction (yr);  $\square$  = age at last reproduction (yr);  $\square_1$  = population growth; CV = coefficient of variation.

ID	Reference	n	Mean $\bar{A}/\square$ (CV); Range	Mean $\square/\square$ (CV); Range	$\square_1$ - range	Comments
<b>Sharks and rays (Subclass Elasmobranchii)</b>						
1	This study Fig. 4A	66	1.31 (9.9%); 1.056 - 1.75	2.68 (45%) 1.13 – 7.0 <sup>A</sup>	0.559- 1.79	All sharks and rays in data base; Fig. 5A gives E-patterns for $\square_1 = 1.0$
2	This study using sharks in Cortés (2002)	48 <sup>B</sup>	1.30 (8.3%); 1.056 - 1.56	2.26 (57%) 1.13 – 7.0 <sup>A</sup>	0.559- 1.79	Calculation using constant vital rates for comparison with Cortés (2002, his App. 2)
3	This study using sharks in Cortés (2002)	48 <sup>B</sup>	1.37 (16%); 1.055 - 2.09	2.26 (57%) 1.13 – 7.0 <sup>A</sup>	1.0 for all	Pseudo-stochastic calculation using constant vital-rates for comparison with Cortés (2002, his Appendix 2)
4	Cortés (2002), results in his Appendix 2	41	1.46 (14%); 1.11 - 2.00	2.35 (40%) 1.13 – 5.20	0.847- 1.66	Statistics from stochastic calculation in Cortés (2002, his App. 2;)
<b>Turtles (and crocodiles) (Class Reptilia)</b>						
5	This study Fig. 4B	27	1.91 (32%); 1.26 - 3.39	6.0 for 20 out of 27	0.870- 1.04	All turtles in data base; Fig. 5B gives E-patterns for $\square_1 = 1.0$
6	This study Fig. 4B	7	1.36 (11%); 1.257 - 1.61	4.46 (45%) 1.69 – 6.0	0.952- 1.01	All marine turtles in data base; Fig. 5B gives E-patterns for $\square_1 = 1.0$
7	This study Fig. 4B	20	2.10 (28%); 1.261 - 3.39	6.0 for all	0.870- 1.04	All terrestrial turtles in data base; Fig. 5B gives E-patterns for $\square_1 = 1.0$
8	This study using terrestrial turtles in Heppell (1998)	20	2.10 (29%); 1.26 - 3.39	6.0 for all	0.870- 1.04	$\square = 6\square$ yr approximation
9	This study using terrestrial turtles in Heppell (1998)	20	2.45 (52%); 1.26 - 6.11	for all	0.874- 1.04	Stage-based model with $\square =$ : mean $\bar{A}/\square$ affected by 2 turtles with extremely large $\bar{A}$
10	This study using data for crocodiles in Tucker (2000)	6	1.77 (10%); 1.59 - 2.05	4.09 (30%) 1.23 – 6.25	0.953- 1.15	Added for discussion purposes; expected $E(S_j)$ to be largest i.e. $\bar{A}/\square < 2.0$
<b>Mammals (Class Mammalia)</b>						
11	This study Fig. 4C	68	2.39 (29%); 1.21 - 4.96	6.49 (46%) 2.40 – 19.0	0.835- 1.57	All mammals in data base; Fig. 5C gives E-patterns for $\square_1 = 1.0$
12	This study Fig. 4C	17	2.53 (23%); 1.68 - 3.77	6.48 (49%) 2.57 – 12.5	0.941- 1.06	All marine mammals in data base; Fig. 5C gives E-patterns for $\square_1 = 1.0$
13	This study Fig. 4C	51	2.34 (32%); 1.21 - 4.96	6.50 (45%) 2.40 – 19.0	0.835- 1.57	All terrestrial mammals in data base; Fig. 5C gives E-patterns for $\square_1 = 1.0$
14	This study with mammals in Heppell et al. (2000)	50	2.45 (32%); 1.21 - 4.96	6.98 (44%) 2.40 – 19.0	0.835- 1.57	Leslie matrix with given w was used; $\square_1$ 's are the same as in Heppell et al. (2000)
15	This study with mammals and model in H et al. (2000)	50	2.73 (39%); 1.21 - 6.16	6.98 (44%) 2.40 – 19.0	0.835- 1.57	Stage was used for adults with $P = S_a (1 - \square_1)$ : $\square_1$ 's are the same but $\bar{A}/\square$ biased high
16	This study using mammals in Eberhardt (2002)	17	2.27 (17%); 1.76 - 3.25	5.30 (46%) 3.33 – 12.5	0.978- 1.20	I used E not S; 4 species have $E(S_j)$ largest corresponding to $\bar{A}/\square < 2.0$
<b>Birds (Class Aves)</b>						
17	This study Fig. 4D	77 <sup>C</sup>	2.4765 (32%); 1.55 - 7.80	6.0 for all <sup>C</sup>	0.471- 1.34	All birds in data base; Fig. 5D gives E-patterns for $\square_1 = 1.0$
18	This study Fig. 4D	46 <sup>C</sup>	2.44 (14%); 1.71 – 3.16	6.0 for all <sup>C</sup>	0.928- 1.14	All sea (marine) birds in data base; Fig. 5D gives E-patterns for $\square_1 = 1.0$
19	This study Fig. 4D	31 <sup>C</sup>	2.4756 (46%); 1.55 - 7.80	6.0 for all <sup>C</sup> but one	0.471- 1.34	All terrestrial birds in data base; Fig. 5D gives E-patterns for $\square_1 = 1.0$
20	This study using birds in Saether and Bakke (2002)	49	2.38 (23%); 1.55 - 4.02	6.0 for all	0.471- 1.34	Smaller longevity ( $\square = 6\square$ yr approximation)
21	This study using birds in Saether and Bakke (2002)	49	3.11 (63%); 1.56 - 13.0	for all	0.567- 1.34	Stage-based model, $P_{ad} = S_a$ (i.e. $\square = \infty$ yr)
22	This study using birds in Russell (1999) <sup>D</sup>	26	2.43 (14%); 1.71 - 3.16	6.0 for all	0.949- 1.14	Smaller longevity ( $\square = 6\square$ yr)
23	This study using birds in Russell (1999) <sup>D</sup>	26	2.81 (25%); 1.72 - 4.83	for all	0.950- 1.14	Stage-based model, $P = S_a$ (i.e. $\square = \infty$ yr)

<sup>A</sup>For Australian sharpnose for which I used  $\square = 1.0$  yr for one 'population'. Using mean  $\square = 1.45$  yr would give lower  $\square/\square = 4.83$ .

<sup>B</sup>41 + 7, seven sharks with mean  $\square$   $\square$  1.45 to 3.5 were simulated with two integer  $\square$  values.

<sup>C</sup>Excluding golden plover and emperor penguin populations for which  $\square = 100$  yr was used for demonstration purposes.

<sup>D</sup>Using reported  $\square$ . (Note that Russell (1999) used characteristic equation that yields solution for  $\square_{\text{effective}} = \square + 1$ ).

**Table 3. Biased  $\bar{A}$  (and E-patterns) for selected species with age-dependent fertility when assuming age-independent fertility**

After Heppell et al. (1999, their Table 2) except hypothetical striped bass.  $\bar{\omega}$  = age at first reproduction (yr);  $\omega$  = age at last reproduction (yr);  $S_a$  = adult survival;  $m$  = female fertility;  $\lambda_1$  = population growth;  $\bar{A}$  = mean age of reproducing females at the stable age distribution.

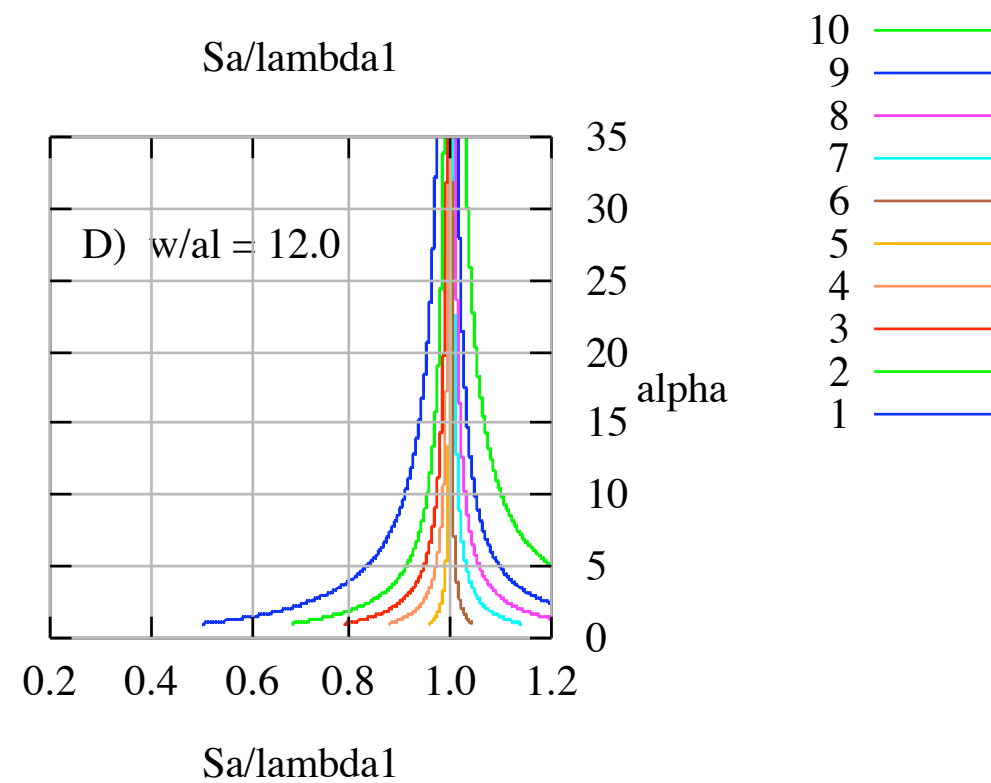
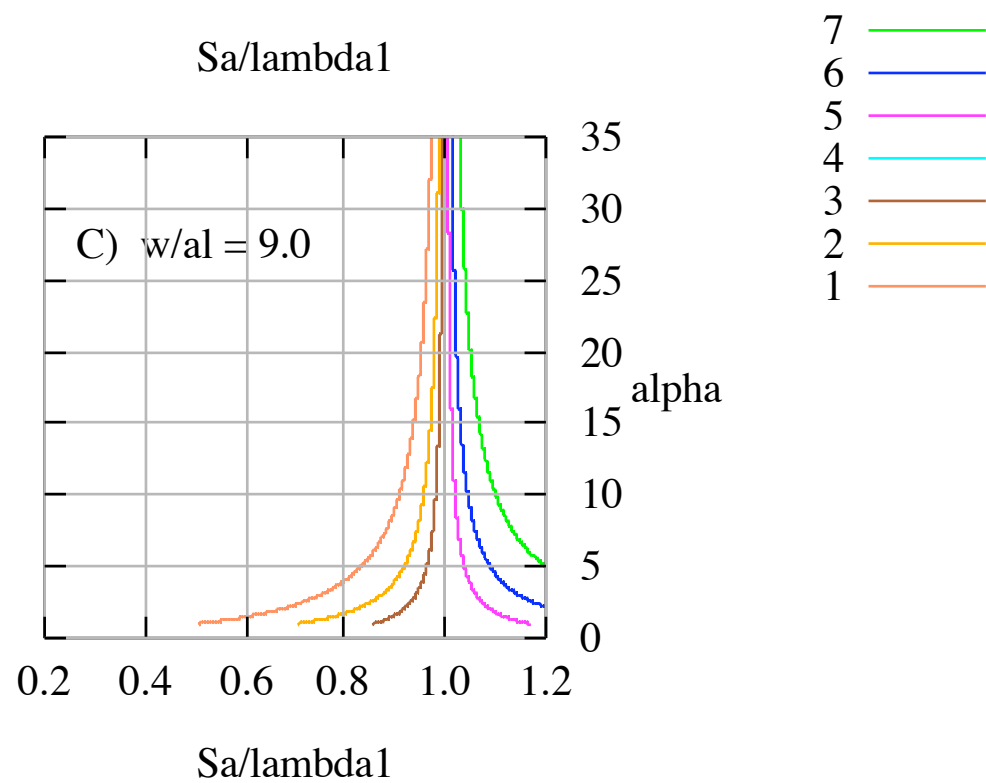
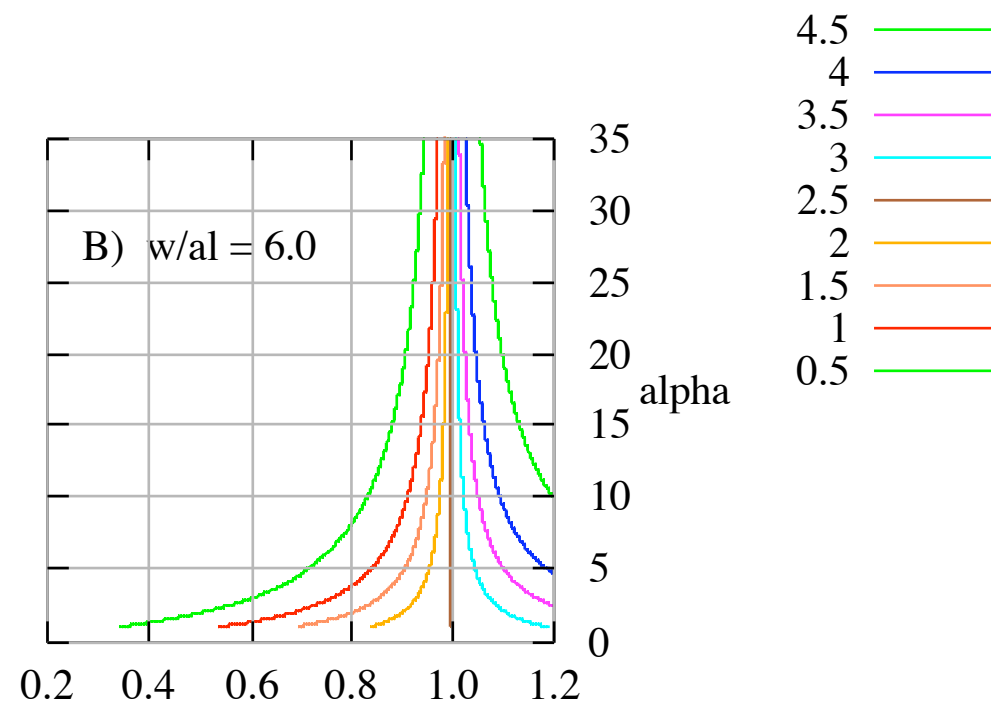
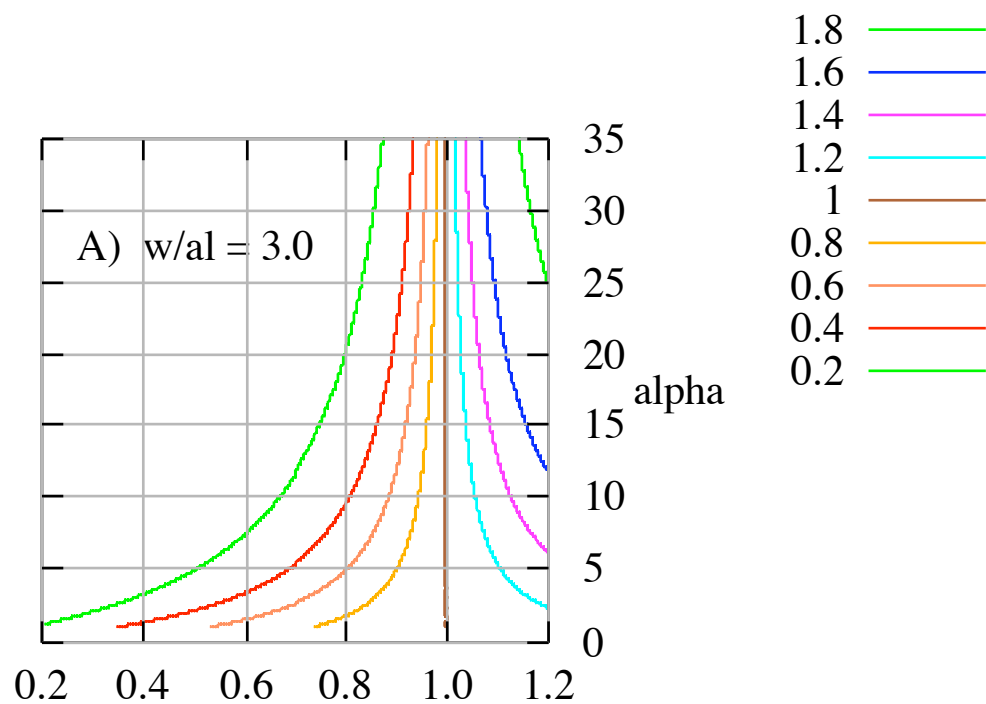
Species	$\bar{\omega}$	$\omega$	$S_a$	$m$	m-Ratio (max/min)	$\lambda_1$	$S_a/\lambda_1$ ( $\lambda_1 - S_a$ )	$\bar{A}$	$\bar{A}$ -bias	$\bar{A}/\bar{\omega}$
Leopard shark	17 <sup>A</sup>	30	0.87	3.13-11.2	3.6	1.07	0.81	21.6		1.27
Triakis semifasciata				observed			(0.20)			
“	17	30	0.87	7.53 <sup>B</sup>	1 <sup>C</sup>	1.07	“	19.5	-4.9%	1.15
North Sea haddock	3	6	0.3	(4.7 10 <sup>4</sup> -	4.3	1.14	0.26	3.64		1.21
Melanogr. aegelfinus				2.0 10 <sup>5</sup> ) obs.			(0.84)			
“	3	6	0.3	(5.25 10 <sup>4</sup> ) <sup>B</sup>	1 <sup>C</sup>	1.14	“	3.34	-8.4%	1.11
Hypothetical striped bass <sup>D</sup>	4	15	0.6	(5.7 10 <sup>4</sup> -	276	1.00	0.60	9.50 <sup>D</sup>		2.37
				1.6 10 <sup>7</sup> ) <sup>D</sup>			(0.40)			
Striped bass	4	15	0.6	(3.3 10 <sup>4</sup> -	61	1.00	0.60	7.69		1.92
Morone saxatilis				2.4 10 <sup>6</sup> ) obs.			(0.40)			
“	4	15	0.6	(2.72 10 <sup>5</sup> ) <sup>B</sup>	1 <sup>C</sup>	1.00	“	5.47	-29%	1.37

<sup>A</sup>Heppell et al. (1999) used larger  $\bar{\omega}$  = 17 yr for leopard shark compared to the values that were used in this study which followed Cailliet (1992) and Cortés (2002) but this is not material here.

<sup>B</sup>Constant female fertility  $m$  was calculated such that  $\lambda_1$  remained the same.

<sup>C</sup>Assuming age-independent female fertility ( $m$ ).

<sup>D</sup>Female fertility  $m$  increases as fast as  $L_x$  decreases, therefore the discrete net reproductive rate function is constant and  $\bar{A}$  approaches the critical value of  $(\bar{\omega} + \omega)/2 = (4 + 15)/2 = 9.50$ . Note that the same critical value is obtained for age-independent  $m$  and  $S_a/\lambda_1 \rightarrow 1$  (eq. A2.5.1).



**Fig. 1.** Relative proportional importance of adult and juvenile survival on population growth of animals assuming constant fertility  $m$  and adult survival  $S_a$ . Graphs give  $(E_3/E_2)$ -ratio contours for  $\square/\square [= w/\alpha] = 3.0$  (A), 6.0 (B), 9.0 (C), and 12.0 (D) for  $x = S_a/\square_1 [= S_a/\lambda_1]$  and  $y = \square [= \alpha]$ . E.g. for  $\square/\square = 6.0$  from eq. (A2.13.2)  $E_3/E_2 = (1/y) \{[x/(1-x)] - [(5y+1)x^{(5y+1)} / (1-x^{(5y+1)})]\}$ . The  $E_3/E_2 = 1$  contour gives parameter values of  $\square/\square$ ,  $S_a/\square_1$ , and  $\square$  for which elasticity of adult survival is the same as elasticity of juvenile survival. (Not all the critical, vertical contours are drawn because of lack of program control.) (Note to editor and reviewers: I am hoping to produce smoother contours, which requires improved 'contours.m' script which in turn requires a newer version of Octave program.)

A) Life table for hypothetical species with  $\alpha = 1$  yr,  $w = 5$  yr,

$S_{juv} = 0.5$ ,

$S_{adu} = 0.6$ ,

and  $m = 2.0$ .

x	Sx	lx	mx	lx mx	EulerSum	Abar	Mu1
0		1.0000	0	0	0	0	0
1	0.5	0.5000	2.0	1.0000	0.6280	0.628	1.000
2	0.6	0.3000	2.0	0.6000	0.2366	0.473	1.200
3	0.6	0.1800	2.0	0.3600	0.0892	0.267	1.080
4	0.6	0.1080	2.0	0.2160	0.0336	0.134	0.864
5	0.6	0.0648	2.0	0.1296	0.0127	0.063	0.648

Ro= 2.3056 1.0000 1.566 2.078

$\lambda_1 = 1.5924$

Used Solver to set Euler Sum to 1.0

with  $\lambda_1$  as parameter

$T = 1.7955 = \ln(Ro)/\ln(\lambda_1)$

B) Projection matrix A for birth-pulse  
post-breeding census

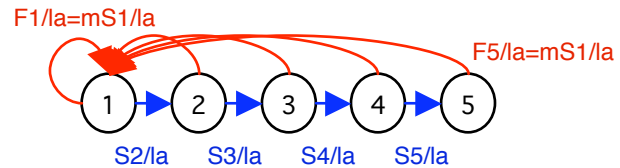
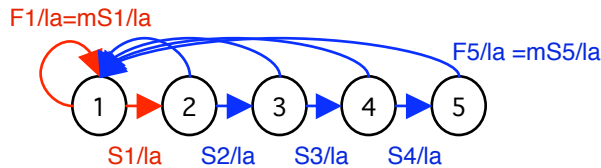
1	F1=1.0	F2=1.2	F3=1.2	F4=1.2	F5=1.2
2	S1=0.5	0	0	0	0
3	0	S2=0.6	0	0	0
4	0	0	S3=0.6	0	0
5	0	0	0	S4=0.6	0

C) Projection matrix A for birth-pulse  
pre-breeding census

1	F1=1.0	F2=1.0	F3=1.0	F4=1.0	F5=1.0
2	S2=0.6	0	0	0	0
3	0	S3=0.6	0	0	0
4	0	0	S4=0.6	0	0
5	0	0	0	S5=0.6	0

$S_5=0.6$  (not part of Leslie matrix, required for calculation of F5)

D) z-transformed life cycle graphs for post- and pre-breeding census ( $\lambda = \lambda_1$ )



E) Eigenvalues and eigenvectors of the stable age distribution for post- and pre-breeding census

	Eigenvalues		Eigenvectors (R&L) for $\lambda_1$			
	Real	Imag	w	v	w(w1=1)	v(v1=1)
$\lambda_1$	1.5924	0	66.9%	19.5%	1.0000	1.0000
$\lambda_2$	0.133	0.533	21.0%	23.1%	0.3140	1.1848
$\lambda_3$	0.133	-0.533	7.9%	22.4%	0.1183	1.1445
$\lambda_4$	-0.429	0.293	3.0%	20.3%	0.0446	1.0375
$\lambda_5$	-0.429	-0.293	1.1%	14.7%	0.0168	0.7536
r	0.4652					
Ro	2.3056		Abar=<w,v>		1.5663	
T	1.7955		Abar (eq. A2.19)		1.5663	
Mu1	2.0784		Abar (eq. A2.4)		1.5663	

	Eigenvalues		Eigenvectors (R&L) for $\lambda_1$			
	Real	Imag	w	v	w(w1=1)	v(v1=1)
$\lambda_1$	1.5924	0	62.8%	22.6%	1.0000	1.0000
$\lambda_2$	0.133	0.533	23.7%	22.3%	0.3768	0.9873
$\lambda_3$	0.133	-0.533	8.9%	21.5%	0.1420	0.9538
$\lambda_4$	-0.429	0.293	3.4%	19.5%	0.0535	0.8646
$\lambda_5$	-0.429	-0.293	1.3%	14.2%	0.0202	0.6280
r	0.4652					
Ro	2.3056		Abar=<w,v>		1.5663	
T	1.7955		Abar (eq. A2.19)		1.5663	
Mu1	2.0784		Abar (eq. A2.4)		1.5663	

F) E-matrix for post-breeding census

0.4009	0.1511	0.0569	0.0214	0.0081
0.2375				
	0.0864			
		0.0295		
			0.0081	

Sums

0.638
0.2375
0.0864
0.0295
0.0081
1.000

G) E-matrix for pre-breeding census

0.4009	0.1511	0.0569	0.0214	0.0081
0.2375				
	0.0864			
		0.0295		
			0.0081	

Sums

0.638
0.2375
0.0864
0.0295
0.0081

H) E-pattern for post-and pre-breeding census (see caption for details)

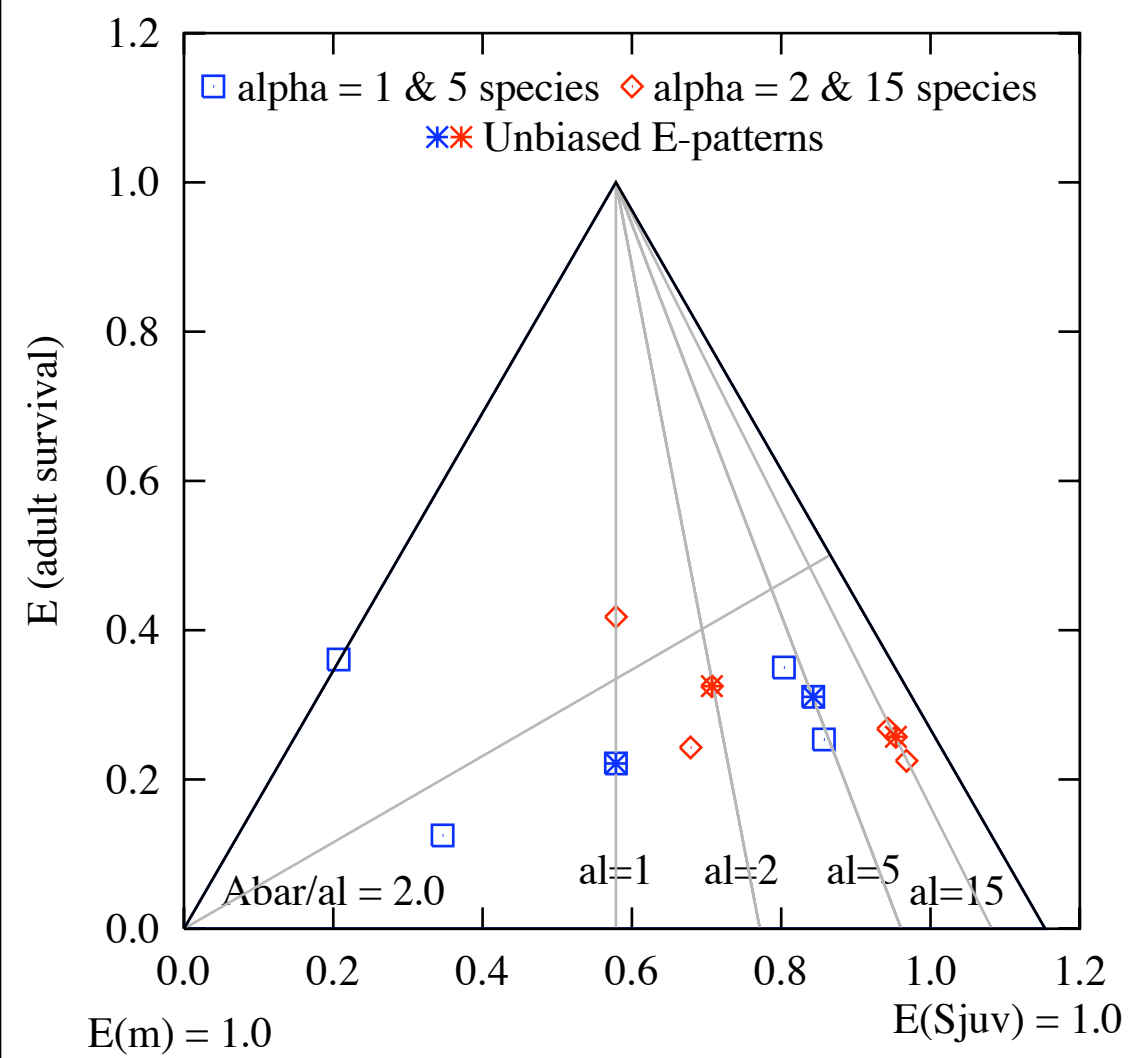
	Col 1	Col 2	Col 3	Col 4	Col 5	Cols 4/3
E1	0.638	0.638	0.390	0.638	0.638	1.638 + bias
E2	0.638	0.638	0.390	0.238	0.238	0.610 - bias
E3	0.362	0.362	0.221	0.124	0.124	0.562 - bias
Sums	1.6384	1.6384	1.000	1.000	1.000	
	1.5663 Abar = E2/E1 + E3/E1, as check					
	1.5663 Abar/alpha = 1 + E3/E2 (= Abar if alpha =1), check					

	Col 1	Col 2	Col 3	Col 4	Col 5	Cols 4/3
E1	0.638	0.6384	0.390	0.638	0.638	1.638, +
E2	0.638	0.6384	0.390	0	0	0, --
E3	0.362	0.3616	0.221	0.362	0.362	1.638, +
Sums	1.6384	1.6384	1.000	1.000	1.000	
	1.5663 Abar = E2/E1 + E3/E1, as check					
	1.5663 Abar/alpha = 1 + E3/E2 (= Abar if alpha =1)					

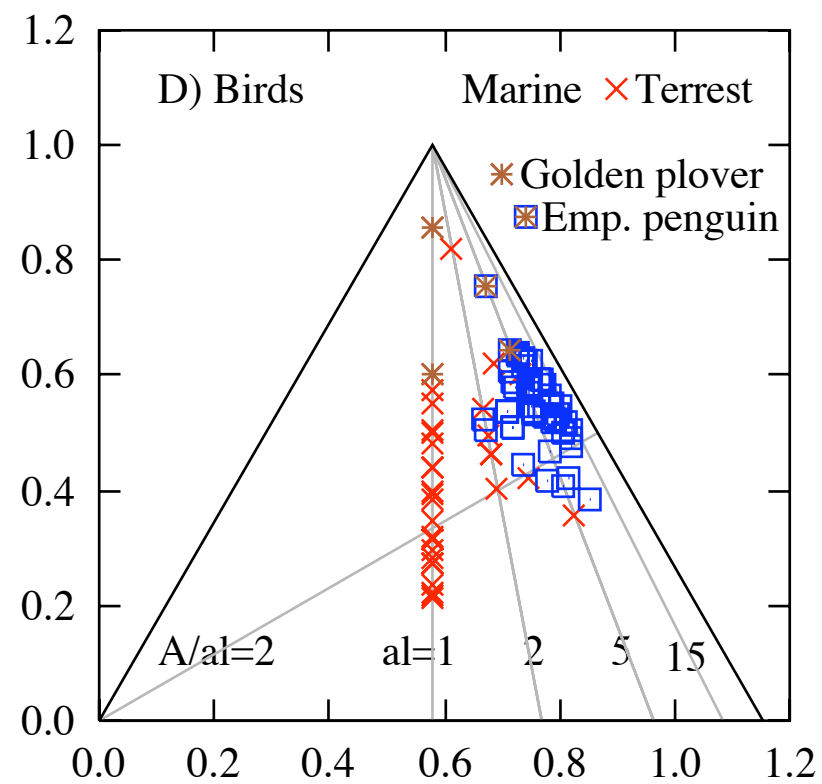
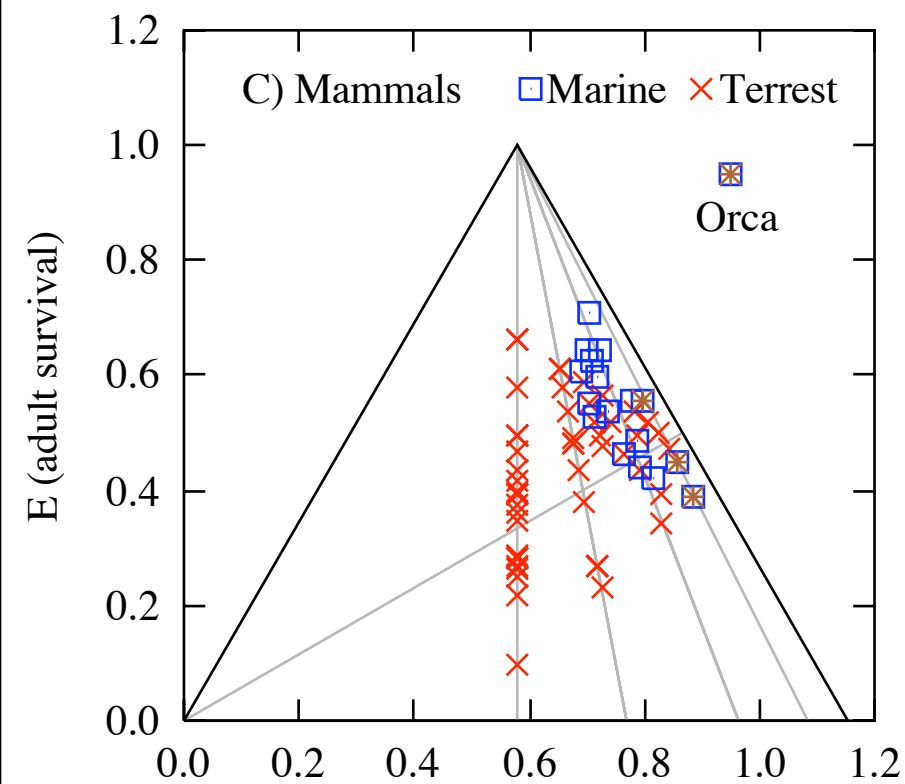
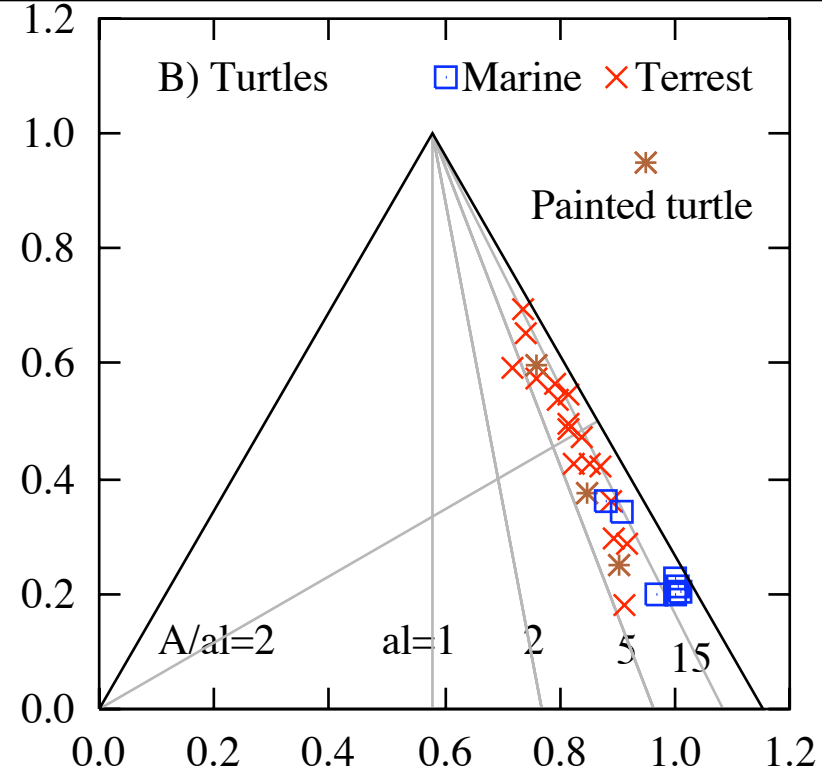
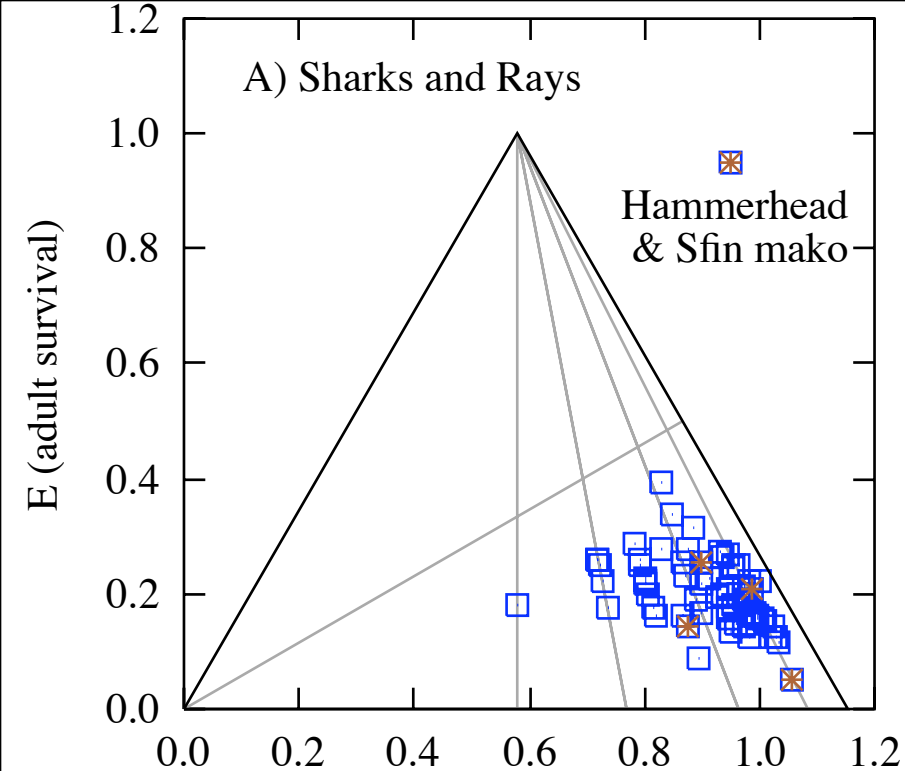


**Fig. 2.** Life history table (A) and corresponding birth pulse Leslie matrices using post-breeding (B) and pre-breeding (C)) censuses with z-transformed life cycle graphs (D), eigenvalues and eigenvectors (E), elasticity matrices (F&G) and E-patterns (H). The E-matrix for both post- and pre-breeding censuses were used to calculate the E-pattern in 7 different ways in 5 columns:

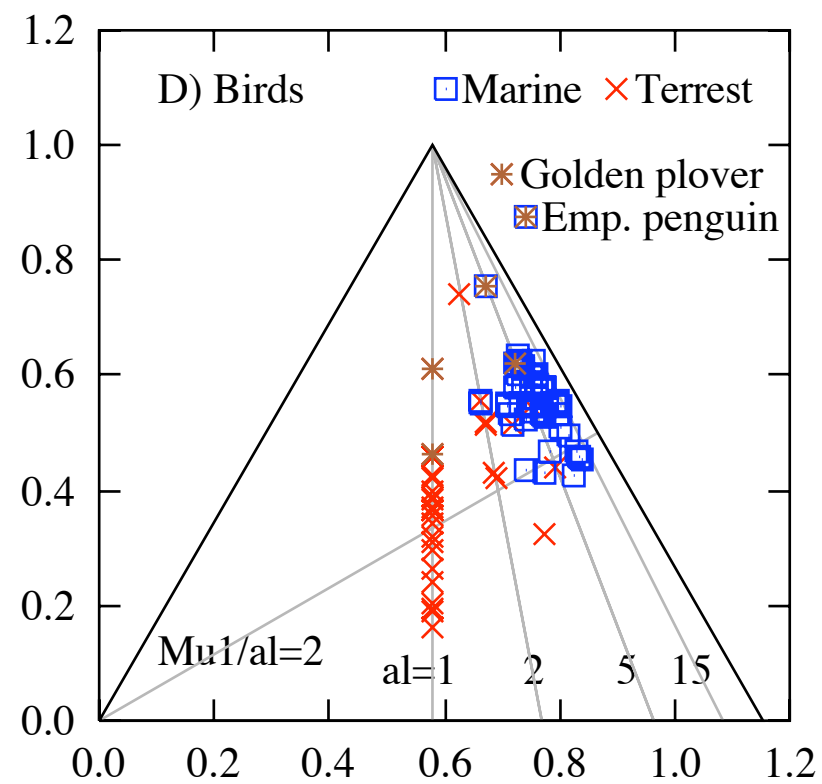
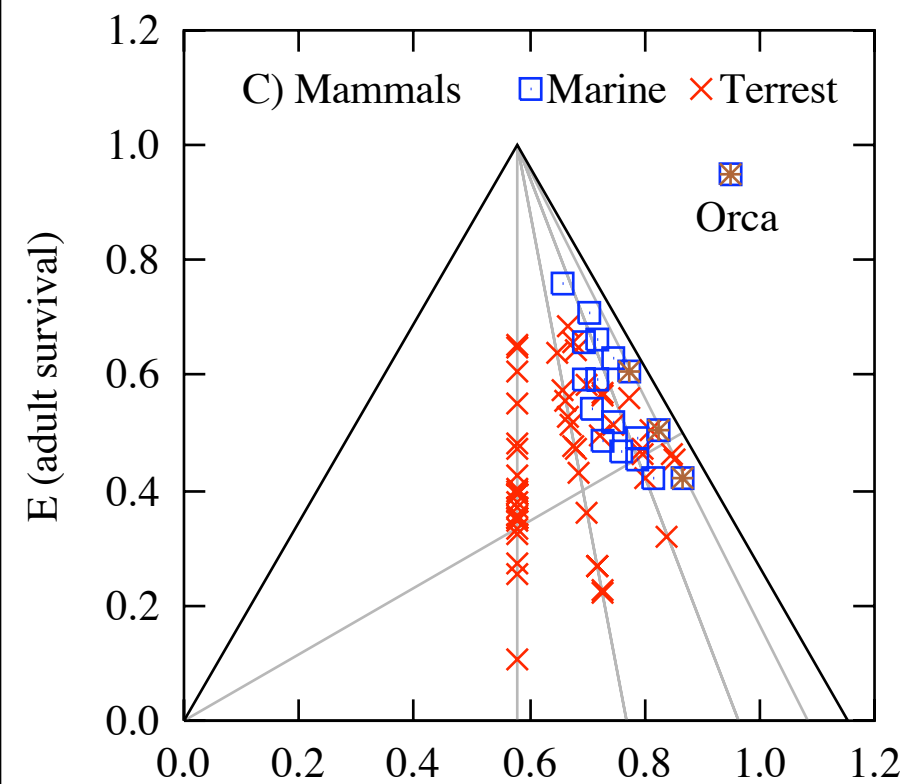
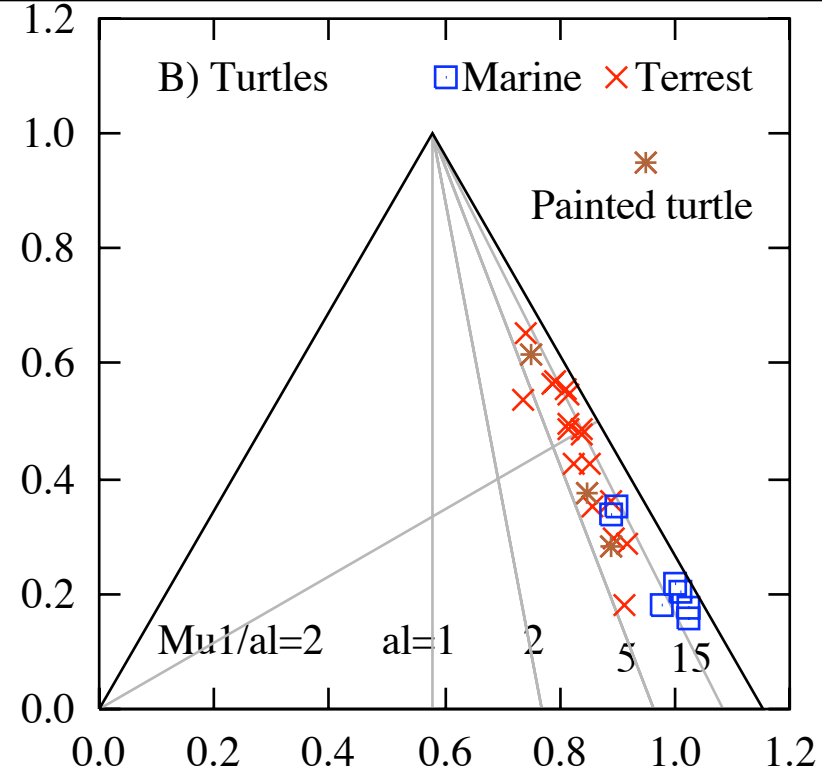
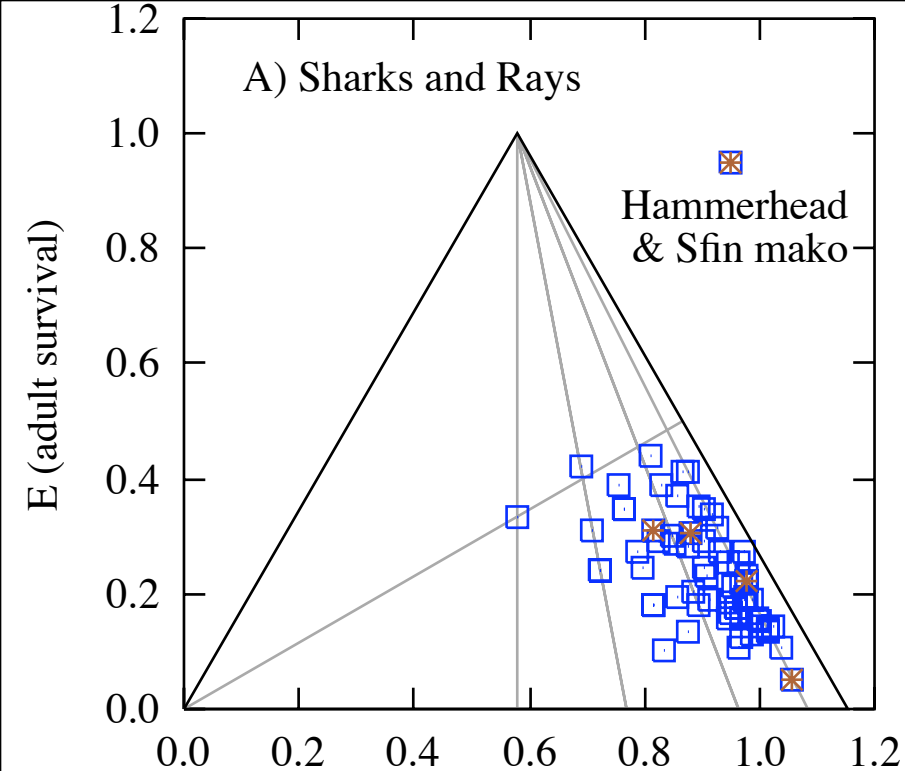
- 1) Summing over matrix elements of the E-matrix including the contribution of survival in the discounted fertilities;
- 2) From eqs. (A2.7) or an empirical calculation using  $E(x) = [\lambda(1.001x) - \lambda(0.999x)] / [0.002\lambda(x)]$  (Crowder et al. 1994, their Appendix 2);
- 3) Calculation of normalized elasticities from the results in 1) or 2) (or using eqs. A2.9);
- 4) Summing over matrix elements excluding contribution of survival in the discounted fertilities producing biased E-pattern;
- 5) E-pattern using equations for post- and pre-breeding censuses that exclude survival in the discounted fertilities (equations A2.20 and A2.21, respectively) producing biased E-pattern;
- 4/3) Calculation of the ratio in columns 4 and 3 as an estimate of the bias when survival in the discounted fertilities is excluded in the calculation of the E-pattern.



**Fig. 3.** Triangle E-patterns as a function of  $\lambda$  for post- and pre-breeding censuses with and without inclusion of survival in the discounted fertilities. Graph shows four E-patterns for each hypothetical species used ( $\lambda = 1$  yr species from Fig. 1 and three additional hypothetical species with  $\lambda = 2, 5$ , and 15 yr). Unbiased E-patterns fall on the corresponding  $\lambda$  contour and post- and pre-breeding E-patterns coincide. Biased E-pattern for pre-breeding census (when survival in the discounted fertilities is excluded) fall on the  $\lambda - 1$  contour. Biased E-pattern for post-breeding census (when survival in the discounted fertilities is excluded) fall between the  $\lambda$  and  $\lambda - 1$  contours. As  $\lambda$  increases the bias decreases and the two biased E-pattern approach the unbiased E-pattern.



**Fig. 4.** Triangle elasticity patterns based on  $\bar{A}$ . Contours drawn are for  $\bar{A}/\bar{\lambda}$  ( $= A/al$ ) = 2.0 and  $\bar{\lambda}$  ( $= al$ ) = 1, 2, 5, and 15 yr. Duplicate star symbols were used for demonstration species: scalloped hammerhead (Hammerhead) with  $\bar{\lambda}$  = 4 and 15 yr (Cortés 2002) and shortfin mako (Sfin mako) with  $\bar{\lambda}$  = 7 (Pratt and Casey, 1983) and 18 yr (Natanson et al. in review) (A); painted turtle with 3 sets of different vital rates for 2 populations from Wilbur (1995), Tinkle et al. (1981), and Mitchell (1988) (B); killer whale with 3 sets of different vital rates from Heppell et al. (2000), Eberhardt (2002) and Caswell (2001) (C); golden plover  $\bar{\lambda}$  = 1 yr,  $\bar{\lambda}$  = 6 & 100 yr, emperor penguin  $\bar{\lambda}$  = 5 yr,  $\bar{\lambda}$  = 30 & 100 yr (D).



**Fig. 5.** Triangle elasticity patterns based on  $\bar{\mu}_I$  ( $\bar{\mu}_I = 1.0$ ,  $R_0 = 1$  approximation). Contours drawn are for  $\bar{\mu}_I/\bar{\mu}$  ( $= \mu_1/\mu$ )  $= 2.0$  and  $\bar{\mu} = 1, 2, 5$ , and  $15$  yr. For explanation of symbols see Fig. 4. This is termed a pseudo-stochastic calculation, see text for details.

# Appendix 1. Vital rates and their sources, and demographic results for shark, turtle, mammal, and bird populations.

$\bar{x}$  = age at first reproduction (yr);  $\bar{x}_l$  = age at last reproduction (yr);  $S_1$  = first year survival;  $S_j$  = juvenile survival;  $S_a$  = adult survival;  $m$  = female fertility;  $\lambda$  = population growth;  $R_0$  = net reproductive rate;  $\bar{A}$  = mean age of reproducing females at the stable age distribution;  $\bar{A}_l$  = mean age of reproducing females in a cohort; ID = ID used in reference.

Sharks and rays (Subclass Elasmobranchii)													Reference	ID
Common name	Scientific name	$\bar{x}$	$\bar{x}_l$	$S_1$	$S_j$	$S_a$	$m$	$\bar{x}$	$R_0$	$\bar{A}$	$\bar{A}_l$	$\bar{A}/\bar{x}$		
Australian sharpnose	<i>Rhizoprionodon taylori</i>	1	7	0.5179	0.5179	0.5179	2.25	1.6830	2.3934	1.44	2.00	1.44	Cortés (2002)	9a
Australian sharpnose	<i>Rhizoprionodon taylori</i>	2	7	0.5179	0.5179	0.5179	2.25	1.0733	1.2280	2.86	2.96	1.43	Cortés (2002)	9b
Blacknose shark	<i>Carcharhinus acronotus</i>	3	5	0.3981	0.3981	0.3981	1.25	0.5593	0.1228	3.78	3.46	1.26	Cortés (2002)	1
Bonnethead	<i>Sphyrna tiburo</i>	2	7	0.5179	0.5179	0.5179	3.75	1.2929	2.0466	2.64	2.96	1.32	Cortés (2002)	23a
Bonnethead	<i>Sphyrna tiburo</i>	3	7	0.5179	0.5179	0.5179	3.75	1.0103	1.0406	3.87	3.88	1.29	Cortés (2002)	23b
Atlantic sharpnose	<i>Rhizoprionodon terranenovae</i>	3	7	0.5179	0.5179	0.5179	2.5	0.9114	0.6938	4.00	3.88	1.33	Cortés (2002)	20a
Atlantic sharpnose	<i>Rhizoprionodon terranenovae</i>	4	7	0.5179	0.5179	0.5179	2.5	0.8.043	0.3464	4.98	4.76	1.24	Cortés (2002)	20b
Spot-tail shark	<i>Carcharhinus sorrah</i>	2	7	0.5179	0.5179	0.5179	1.55	0.9458	0.8459	3.04	2.96	1.52	Cortés (2002)	14a
Spot-tail shark	<i>Carcharhinus sorrah</i>	3	7	0.5179	0.5179	0.5179	1.55	0.8107	0.4301	4.17	3.88	1.39	Cortés (2002)	14b
Brown smooth-hound	<i>Mustelus californicus</i>	2	9	0.5995	0.5995	0.5995	1.75	1.1455	1.5441	3.05	3.36	1.53	Cortés (2002)	26a
Brown smooth-hound	<i>Mustelus californicus</i>	3	9	0.5995	0.5995	0.5995	1.75	0.9797	0.9152	4.34	4.30	1.45	Cortés (2002)	26b
Pelagic stingray	<i>Dasyatis violacea</i>	3	10	0.6310	0.6310	0.6310	3.0	1.1740	1.9907	4.11	4.50	1.37	Mollet and Cailliet (2002)	1
Grey smooth-hound	<i>Mustelus henlei</i>	2	13	0.7017	0.7017	0.7017	2.0	1.4033	3.2543	3.00	4.18	1.50	Cortés (2002)	27a
Grey smooth-hound	<i>Mustelus henlei</i>	3	13	0.7017	0.7017	0.7017	2.0	1.1890	2.2695	4.41	5.12	1.47	Cortés (2002)	27b
Pacific lesser electric ray	<i>Narcine entemedor</i>	3	15	0.7356	0.7356	0.7356	3.0	1.3709	4.4343	4.15	5.54	1.38	C. Villavicencio (p. c.) <sup>A</sup>	1
Lesser spotted dogfish	<i>Scyliorhinus canicula</i>	4	9	0.5995	0.5995	0.5995	52.75	1.7886	16.221	4.50	5.20	1.12	Cortés (2002)	30
Australian blacktip	<i>Carcharhinus tilstoni</i>	3	13	0.7017	0.7017	0.7017	1.5	1.1156	1.7021	4.63	5.12	1.54	Cortés (2002)	15a
Australian blacktip	<i>Carcharhinus tilstoni</i>	4	13	0.7017	0.7017	0.7017	1.5	1.0286	1.1839	5.92	6.05	1.48	Cortés (2002)	15b
Starspotted smooth-hound	<i>Mustelus manazo</i>	5	10	0.6310	0.6310	0.6310	3.0	0.9580	0.7616	6.40	6.31	1.28	Cortés (2002)	28
Oceanic whitetip	<i>Carcharhinus longimanus</i>	5	11	0.6579	0.6579	0.6579	1.55	0.9088	0.5288	6.81	6.53	1.36	Cortés (2002)	10
Common thresher	<i>Alopius vulpinus</i>	5	15	0.7356	0.7356	0.7356	2.0	1.0649	1.5743	7.04	7.39	1.41	Cortés (2002)	36
Blue shark	<i>Prionaca glauca</i>	5	16	0.7499	0.7499	0.7499	9.25	1.3708	8.4930	6.20	7.61	1.24	Cortés (2002)	18
Smalltail shark	<i>Carcharhinus porosus</i>	6	12	0.6813	0.6813	0.6813	1.5	0.8996	0.4386	7.95	7.63	1.33	Cortés (2002)	13
Sandtiger shark	<i>Carcharias taurus</i>	6	17	0.7627	0.7627	0.7627	0.5	0.9043	0.3987	9.60	8.73	1.60	Cortés (2002)	37
Sandtiger shark	<i>Carcharias taurus</i>	6	25	0.8318	0.8318	0.8318	0.5	0.9961	0.9594	10.50	10.43	1.75	Mollet and Cailliet (2002)	2
Bat ray	<i>Myliobatis californica</i>	6	30	0.8577	0.8577	0.8577	1.75	1.1723	4.7903	8.72	11.48	1.45	Martin and Cailliet (1988)	1
Blacktip shark	<i>Carcharhinus limbatus</i>	7	10	0.6310	0.6310	0.6310	1.23	0.7631	0.1117	8.26	7.96	1.18	Cortés (2002)	9
Grey reef shark	<i>Carcharhinus amblyrhynchus</i>	7	12	0.6813	0.6813	0.6813	1.03	0.8302	0.1982	8.94	8.47	1.28	Cortés (2002)	2
Gummy shark	<i>Mustelus antarcticus</i>	7	16	0.7499	0.7499	0.7499	13.0	1.2351	6.5416	8.48	9.40	1.21	Cortés (2002)	25
Shortfin mako	<i>Isurus oxyrinchus</i>	7	17	0.7627	0.7627	0.7627	2.54	1.0455	1.5253	9.34	9.63	1.33	Cortés (2002)	32
Spinner shark	<i>Carcharhinus brevipinna</i>	8	12	0.6813	0.6813	0.6813	1.75	0.8505	0.2175	9.57	9.28	1.20	Cortés (2002)	4
Silky shark (NWGM)	<i>Carcharhinus falciformes</i>	8	14	0.7197	0.7197	0.7197	2.75	0.9551	0.6354	9.94	9.79	1.24	Cortés (2002)	6
Galapagos shark	<i>Carcharhinus galapagensis</i>	8	15	0.7356	0.7356	0.7356	2.18	0.9578	0.6466	10.21	10.03	1.28	Cortés (2002)	7
Pelagic thresher	<i>Alopias pelagicos</i>	8	30	0.8577	0.8577	0.8577	1.0	1.0560	1.9978	12.13	13.33	1.52	Mollet and Cailliet (2002)	4
Barndoor skate	<i>Dipturus laevis</i>	9	15	0.7356	0.7356	0.7356	23.5	1.1624	4.9549	10.43	10.86	1.16	Mollet and Cailliet (2003)	1



## Sharks and rays cont.

Common name	Scientific name	$\bar{L}$	$\bar{W}$	$S_1$	$S_f$	$S_a$	$m$	$\bar{L}$	$R_o$	$\bar{A}$	$\bar{L}_1$	$\bar{A}/\bar{L}$	Reference	ID
Tiger shark	<i>Galeocerdo cuvier</i>	9	16	0.7499	0.7499	0.7499	13.75	1.1281	3.7104	10.67	11.11	1.19	Cortés (2002)	16
Pelagic thresher	<i>Alopius pelagicus</i>	9	16	0.7499	0.7499	0.7499	1.0	0.8911	0.2699	11.62	11.11	1.29	Cortés (2002)	34
Pacific electric ray	<i>Torpedo californica</i>	9	25	0.8318	0.8318	0.8318	8.5	1.2022	9.2069	11.21	13.17	1.25	Neer and Cailliet (2001)	1
White shark	<i>Carcharodon carcharias</i>	10	15	0.7356	0.7356	0.7356	2.25	0.9107	0.3324	11.89	11.65	1.19	Cortés (2002)	31
Angel shark	<i>Squatina californica</i>	11	22	0.8111	0.8111	0.8111	3.0	1.0271	1.4596	14.01	14.24	1.27	Cortés (2002)	41
Silky shark (SGM)	<i>Carcharhinus falciformes</i>	12	22	0.8111	0.8111	0.8111	2.55	0.9990	0.9856	15.08	15.07	1.26	Cortés (2002)	5
Bigeye thresher	<i>Alopius superciliosus</i>	12	30	0.8577	0.8577	0.8577	1.0	1.0031	1.0535	16.88	16.94	1.41	Chen et al. (1997)	1
Spiny dogfish (NWA)	<i>Squalus acanthia</i> (NWA)	12	40	0.8913	0.8913	0.8913	1.65	1.0759	3.6760	16.70	19.13	1.39	Cortés (2002)	39
Bigeye thresher	<i>Alopius superciliosus</i>	13	20	0.7943	0.7943	0.7943	1.0	0.9034	0.2051	15.84	15.36	1.22	Cortés (2002)	35
Lemon shark	<i>Negaprion brevirostris</i>	13	21	0.8031	0.8031	0.8031	2.7	0.9759	0.6824	15.76	15.63	1.21	Cortés (2002)	17
Leopard shark	<i>Triakis semifasciata</i>	13	24	0.8254	0.8254	0.8254	10.75	1.0998	4.5739	15.61	16.39	1.20	Cortés (2002)	29
Leopard shark	<i>Triakis semifasciata</i>	13	30	0.8577	0.8577	0.8577	6.0	1.1040	5.3699	16.29	17.82	1.25	Cailliet (1992)	1
Soupfin shark	<i>Galeorhinus galeus</i>	13	53	0.9168	0.9168	0.9168	5.68	1.1769	21.431	16.52	22.82	1.27	Cortés (2002)	25
Porbeagle	<i>Lamna nasus</i>	14	22	0.8111	0.8111	0.8111	2.0	0.9572	0.4792	16.94	16.68	1.21	Cortés (2002)	33
Longfin mako	<i>Isurus paucus</i>	14	28	0.8483	0.8483	0.8483	0.67	0.9524	0.4043	18.94	18.20	1.35	Mollet unpublished	1
Porbeagle	<i>Lamna nasus</i>	14	45	0.9027	0.9027	0.9027	2.0	1.0793	4.7213	19.01	22.02	1.36	Natanson et al. (2002)	1
Scalloped hh (NWGM2)	<i>Spyrna lewini</i>	15	22	0.8111	0.8111	0.8111	8.75	1.0285	1.6297	17.32	17.45	1.15	Cortés (2002)	22
Shortspine spurdog	<i>Squalus mitsukurii</i>	15	27	0.8432	0.8432	0.8432	0.90	0.9526	0.3960	19.36	18.79	1.29	Cortés (2002)	40
White shark	<i>Carcharodon carcharias</i>	15	60	0.9261	0.9261	0.9261	1.48	1.0818	6.1492	20.91	26.15	1.39	Mollet and Cailliet (2002)	5
Sandbar shark	<i>Carcharhinus plumbeus</i>	16	24	0.8254	0.8254	0.8254	2.1	0.9596	0.4590	19.03	18.78	1.19	Cortés (2002)	12
Sevengill shark	<i>Notorynchus cepedianus</i>	16	45	0.9027	0.9027	0.9027	20.0	1.1898	38.131	19.14	23.82	1.20	VanD and Mollet (2002)	1
Bull shark	<i>Carcharhinus leucas</i>	18	24	0.8254	0.8254	0.8254	2.0	0.9374	0.2677	20.50	20.26	1.14	Cortés (2002)	8
Basking shark	<i>Cetorhinus maximus</i>	18	40	0.8913	0.8913	0.8913	1.0	1.0030	1.0757	24.35	24.44	1.35	Mollet unpublished	2
Whale shark	<i>Rhincodon typus</i>	18	55	0.9197	0.9197	0.9197	75.0	1.2575	198.28	20.72	27.80	1.15	Mollet unpublished	3
Dusky shark	<i>Carcharhinus obscurus</i>	19	39	0.8886	0.8886	0.8886	1.54	1.0119	1.3439	24.74	25.06	1.30	Cortés (2002)	11
Copper shark	<i>Carcharhinus brachyurus</i>	20	30	0.8577	0.8577	0.8577	3.75	0.9999	0.9971	23.53	23.53	1.18	Cortés (2002)	3
Spiny dogfish (NEP)	<i>Squalus acanthias</i> (NEP)	35	81	0.9447	0.9447	0.9447	1.78	1.0306	4.0987	45.20	48.60	1.29	Cortés (2002)	38
Scalloped hhead (WP) <sup>B</sup>	<i>Spyrna lewini</i> (WP)	4	14	0.7197	0.7197	0.7197	13.0	1.5889	12.108	4.83	6.26	1.21	Cortés (2002)	22 <sup>B</sup>
Scall. hhead (NWGM) <sup>B</sup>	<i>Spyrna lewini</i> (NWGM)	15	17	0.7627	0.7627	0.7627	17.5	0.9782	0.7053	15.84	15.82	1.06	Cortés (2002)	21 <sup>B</sup>
Shortfin mako <sup>B</sup>	<i>Isurus oxyrinchus</i>	7	21	0.8031	0.8031	0.8031	2.08	1.0809	2.1909	9.71	10.50	1.39	Pratt and Casey (1983)	1 <sup>B</sup>
Shortfin mako <sup>B</sup>	<i>Isurus oxyrinchus</i>	18	36	0.8799	0.8799	0.8799	2.08	1.0198	1.5798	23.06	23.50	1.28	Natanson et al. (in review)	1 <sup>B</sup>
Turtles (Order Testudines)														
Common mud turtle	<i>Kinosternon subrubrum</i>	4	24	0.261	0.6720	0.879	0.96	0.9504	0.5865	11.26	9.77	2.81	Heppell (1998)	1
Slider turtle	<i>Trachemys scripta</i>	7	42	0.105	0.7646	0.814	1.28	0.8702	0.1443	17.90	11.35	2.56	Heppell (1998)	2
Yellow mud turtle	<i>Kinosternon flavescens</i>	11	66	0.191	0.8206	0.95	2.55	1.0094	1.2727	25.06	26.64	2.28	Heppell (1998)	6
Blanding's turtle	<i>Emydoidea blandingii</i>	14	84	0.261	0.783	0.96	4.0	1.0008	1.0255	33.64	33.86	2.40	Heppell (1998)	7
Snapping turtle A	<i>Chelydra serpentina</i>	19	114	0.064	0.754	0.966	16.18	0.9686	0.1821	64.46	43.81	3.39	Heppell (1998)	8
Snapping turtle B	<i>Chelydra serpentina</i>	13	78	0.23	0.7397	0.93	12.0	1.0019	1.0491	25.45	25.73	1.96	Heppell (1998)	9
Desert turtle	<i>Gopherus agassizi</i>	15	90	0.47	0.8152	0.941	4.0	1.0211	1.8053	26.59	30.19	1.77	Heppell (1998)	10

Turtles cont.														
Common name	Scientific name	$\bar{L}$	$\bar{W}$	$S_1$	$S_f$	$S_a$	$m$	$\bar{L}$	$R_o$	$\bar{A}$	$\bar{L}_1$	$\bar{A}/\bar{L}$	Reference	ID
Llanos sideneck turtle	<i>Podocnemis voglii</i>	10	60	0.6179 <sup>C</sup>	0.6179 <sup>C</sup>	0.92	10.0 <sup>C</sup>	1.0000	1.0000	20.76	20.76	2.08	Heppell (1998)	11
Australian snake-necked t.	<i>Chelodina longicollis</i>	10	60	0.6517 <sup>C</sup>	0.6517 <sup>C</sup>	0.98	2.25 <sup>C</sup>	1.0000	1.0000	30.70	30.70	3.07	Heppell (1998)	12
Sonoran mud turtle	<i>Kinosternon sonoriense</i>	7	42	0.6539 <sup>C</sup>	0.6539 <sup>C</sup>	0.86	2.75 <sup>C</sup>	1.0000	1.0000	12.98	12.98	1.85	Heppell (1998)	13
Ornate box turtle	<i>Terrapene ornata</i>	11	66	0.7832 <sup>C</sup>	0.7832 <sup>C</sup>	0.83	2.50 <sup>C</sup>	1.0000	1.0000	15.88	15.88	1.44	Heppell (1998)	14
Ornate box	<i>Terrapene ornata</i>	9	54	0.6922 <sup>C</sup>	0.6922 <sup>C</sup>	0.91	2.50 <sup>C</sup>	1.0000	1.0000	18.50	18.50	2.06	Heppell (1998)	15
Spanish Terrapin	<i>Mauremys leprosa</i>	8	48	0.7250 <sup>C</sup>	0.7250 <sup>C</sup>	0.79	2.75 <sup>C</sup>	1.0000	1.0000	11.76	11.76	1.47	Heppell (1998)	16
Gopher tortoise	<i>Gopherus polyphemus</i>	11	66	0.7465 <sup>C</sup>	0.7465 <sup>C</sup>	0.9	2.50 <sup>C</sup>	1.0000	1.0000	19.85	19.85	1.80	Heppell (1998)	17
Giant tortoise	<i>Geochelone gigantea</i>	23	138	0.7778 <sup>C</sup>	0.7778 <sup>C</sup>	0.97	10.0 <sup>C</sup>	1.0000	0.9999	51.84	51.84	2.25	Heppell (1998)	18
Greek tortoise	<i>Testudo graeca</i>	12	72	0.7765 <sup>C</sup>	0.7765 <sup>C</sup>	0.88	2.50 <sup>C</sup>	1.0000	1.0000	19.31	19.31	1.61	Heppell (1998)	19
Geometric tortoise	<i>Psammobatis geometricus</i>	6	36	0.5823 <sup>C</sup>	0.5823 <sup>C</sup>	0.61	10.0 <sup>C</sup>	1.0000	1.0000	7.56	7.56	1.26	Heppell (1998)	20
Painted turtle <sup>B</sup>	<i>Chrysemys picta</i>	7	42	0.08	0.83	0.83	6.6	1.0012	1.0142	11.81	11.84	1.69	Heppell (1998)	3 <sup>B</sup>
Painted turtle <sup>B</sup>	<i>Chrysemys picta</i>	7	42	0.67	0.76	0.76	2.8	1.0422	1.5062	9.69	10.16	1.38	Heppell (1998)	4 <sup>B</sup>
Painted turtle <sup>B</sup>	<i>Chrysemys picta</i>	8	48	0.193	0.7673	0.96	2.05	1.0105	1.2582	21.30	22.54	2.66	Heppell (1998)	5 <sup>B</sup>
Loggerhead (U.S.)	<i>Caretta caretta</i>	22	132	0.675	0.7190	0.809	76.5	0.9518	0.2651	27.66	26.24	1.26	Heppell (1998)	21
Loggerhead (Australia)	<i>Caretta caretta</i>	35	210	0.827	0.8408	0.91	32.54	0.9957	0.8238	45.61	45.11	1.30	Heppell (1998)	22
Kemp's Ridley	<i>Lepidochelys kempi</i>	12	72	0.1625	0.6551 <sup>D</sup>	0.7425	105	0.9700	0.6320	15.26	14.88	1.27	Heppell et al. (1996)	23
Kemp's Ridley	<i>Lepidochelys kempi</i>	10	60	0.31	0.6509 <sup>D</sup>	0.85	18.75	0.9870	0.8125	16.18	15.65	1.62	Heppell NCEAS (p. c.) <sup>E</sup>	24
Loggerhead (U.S.)	<i>Caretta caretta</i>	34	66	0.37	0.8222	0.893	63.65	0.9745	0.3356	43.00	41.54	1.26	Melissa Snower (p. c.) <sup>F</sup>	25
Green turtle	<i>Chelonia mydas</i>	35	59	0.4394	0.8308	0.9482	60.0	0.9915	0.6844	44.72	44.31	1.28	Chaloupka (2002)	26
Hawksbill turtle	<i>Eretmochelys imbricata</i>	14	50	0.01	0.9	0.9	47.29	1.0075	1.1777	21.80	22.23	1.56	Heppell and Crowder (1996)	27
Mammals	(Class Mammalia)													
Dall's sheep	<i>Ovis dalli</i>	2	12	0.50	0.50	0.88	0.50	0.9604	0.7864	6.14	5.76	3.07	Heppell et al. (2000)	1
Thar	<i>Hemitragus jemlahicus</i>	1	12	0.47	0.47	0.85	0.33	0.9753	0.8869	4.93	4.68	4.93	Heppell et al. (2000)	2
Waterbuck	<i>Kobus defassa</i>	2	12	0.70	0.70	0.82	0.34	0.9636	0.8212	5.47	5.16	2.73	Heppell et al. (2000)	3
Wildebeest	<i>Connochaetes taurinus</i>	2	16	0.5831	0.5831	0.84	0.38	0.9557	0.7485	6.73	6.07	3.37	Heppell et al. (2000)	4
Black-tailed deer A	<i>Odocoileus hemionus</i>	1	9	0.63	0.63	0.87	0.36	1.0577	1.2465	3.76	4.10	3.76	Heppell et al. (2000)	5
Black-tailed deer B	<i>Odocoileus hemionus</i>	1	9	0.47	0.47	0.78	0.74	1.1137	1.4120	2.96	3.47	2.96	Heppell et al. (2000)	6
Red deer	<i>Cervus elaphus</i>	2	15	0.8832	0.8832	0.80	0.34	1.0474	1.2678	4.90	5.36	2.45	Heppell et al. (2000)	7
Reindeer	<i>Rangifer tarandus</i>	2	11	0.70	0.70	0.79	0.45	0.9894	0.9506	4.78	4.72	2.39	Heppell et al. (2000)	8
Warthog	<i>Phacochoerus aethiopicus</i>	2	12	0.40	0.40	0.77	1.40	0.9824	0.9190	4.82	4.69	2.41	Heppell et al. (2000)	9
Hippopotamus	<i>Hippopotamus amphibius</i>	10	45	0.8977	0.8977	0.94	0.17	0.9930	0.8592	21.93	21.32	2.19	Heppell et al. (2000)	10
Zebra	<i>Equus burchelli</i>	3	20	0.8750	0.8750	0.89	0.24	1.0306	1.2822	7.95	8.57	2.65	Heppell et al. (2000)	11
African elephant	<i>Loxodonta africana</i>	14	60	0.9606	0.9606	0.94	0.10	0.9960	0.8976	27.47	26.95	1.96	Heppell et al. (2000)	12
Red fox	<i>Vulpes vulpes</i>	1	8	0.44	0.44	0.51	1.41	1.1293	1.2603	1.81	2.00	1.81	Heppell et al. (2000)	13
Lion	<i>Panthera leo</i>	2	17	0.6325	0.6325	0.90	0.39	1.0346	1.2711	6.76	7.36	3.38	Heppell et al. (2000)	14
Lynx	<i>Lynx rufus</i>	1	9	0.88	0.88	0.56	1.15	1.5719	2.2875	1.55	2.22	1.55	Heppell et al. (2000)	15
Black bear	<i>Ursus americanus</i>	5	19	0.7752	0.7752	0.86	0.48	0.9843	0.8599	9.64	9.40	1.93	Heppell et al. (2000)	16
Badger	<i>Taxidea taxus</i>	1	11	0.45	0.45	0.53	0.81	0.8933	0.7748	2.42	2.12	2.42	Heppell et al. (2000)	17
Black-footed ferret	<i>Mustela nigripes</i>	1	8	0.28	0.28	0.60	1.54	1.0253	1.0599	2.30	2.36	2.30	Heppell et al. (2000)	18

Mammals cont.														
Common name	Scientific name	$\bar{L}$	$\bar{W}$	$S_1$	$S_f$	$S_a$	$m$	$\bar{L}_1$	$R_o$	$\bar{A}$	$\bar{L}_1$	$\bar{A}/\bar{L}$	Reference	ID
Vervet monkey	<i>Cercopithecus aethiops</i>	5	12	0.7696	0.7696	0.88	0.43	0.9418	0.6195	8.15	7.84	1.63	Heppell et al. (2000)	28
Chimpanzee	<i>Pan troglodytes</i>	14	50	0.9218	0.9218	0.95	0.09	0.9746	0.4894	29.13	26.48	2.08	Heppell et al. (2000)	29
Gorilla	<i>Gorilla gorilla</i>	8	40	0.9512	0.9512	0.95	0.12	1.0144	1.3124	18.47	19.56	2.31	Heppell et al. (2000)	30
Short-tailed fruit bat	<i>Carollia perspicillata</i>	1	10	0.54	0.54	0.66	0.65	1.0058	1.0162	2.76	2.78	2.76	Heppell et al. (2000)	31
Little brown bat	<i>Myotis lucifugus</i>	1	12	0.31	0.31	0.86	0.50	0.9843	0.9259	4.96	4.79	4.96	Heppell et al. (2000)	32
Beaver	<i>Castor canadensis</i>	1	19	0.46	0.46	0.65	0.71	0.9765	0.9329	2.98	2.85	2.98	Heppell et al. (2000)	33
Coypu	<i>Myocastor coypus</i>	2	6	0.4123	0.4123	0.52	2.81	0.9851	0.9573	2.90	2.89	1.45	Heppell et al. (2000)	34
Jumping mouse	<i>Zapus princeps</i>	1	6	0.31	0.31	0.59	1.33	0.9830	0.9632	2.21	2.17	2.21	Heppell et al. (2000)	35
Yellow-bellied marmot	<i>Marmota flaviventris</i>	2	7	0.4690	0.4690	0.75	1.14	0.9501	0.8245	3.83	3.70	1.92	Heppell et al. (2000)	36
Belding's ground squirrel	<i>Spermophilus beldingi</i>	1	9	0.39	0.39	0.52	1.70	1.1826	1.3774	1.78	2.06	1.78	Heppell et al. (2000)	37
Daurian ground squirrel	<i>Spermophilus dauricus</i>	1	7	0.33	0.33	0.54	1.42	1.0024	1.0051	2.07	2.08	2.07	Heppell et al. (2000)	38
Golden-mantled g. squirrel	<i>Spermophilus lateralis</i>	1	6	0.21	0.21	0.69	1.56	0.9769	0.9427	2.55	2.50	2.55	Heppell et al. (2000)	39
Columbian g. squirrel A	<i>Spermophilus columbianus</i>	1	5	0.30	0.30	0.46	1.86	1.0069	1.0121	1.74	1.75	1.74	Heppell et al. (2000)	40
Columbian g. squirrel B	<i>Spermophilus columbianus</i>	1	7	0.40	0.40	0.61	1.01	1.0014	1.0033	2.33	2.34	2.33	Heppell et al. (2000)	41
Columbian g. squirrel C	<i>Spermophilus columbianus</i>	2	7	0.6633	0.6633	0.57	1.03	1.0057	1.0177	3.10	3.11	1.55	Heppell et al. (2000)	42
Columbian g. squirrel D	<i>Spermophilus columbianus</i>	1	7	0.36	0.36	0.60	1.13	0.9950	0.9885	2.31	2.30	2.31	Heppell et al. (2000)	43
Columbian g. squirrel E	<i>Spermophilus columbianus</i>	2	5	0.4690	0.4690	0.72	1.74	0.9999	0.9996	3.10	3.10	1.55	Heppell et al. (2000)	44
Uinta ground squirrel A	<i>Spermophilu armatus</i>	1	5	0.33	0.33	0.43	1.62	0.9547	0.9241	1.73	1.68	1.73	Heppell et al. (2000)	45
Uinta ground squirrel B	<i>Spermophilu armatus</i>	1	7	0.40	0.40	0.54	1.99	1.3346	1.7073	1.67	2.08	1.67	Heppell et al. (2000)	46
Gray squirrel	<i>Sciurus carolinensis</i>	1	7	0.25	0.25	0.60	1.94	1.0769	1.1786	2.14	2.30	2.14	Heppell et al. (2000)	47
Red squirrel	<i>Tamiasciurus hudsonicus</i>	1	6	0.33	0.33	0.52	1.90	1.1414	1.2804	1.78	1.96	1.78	Heppell et al. (2000)	48
European hare	<i>Lepus europaeus</i>	2	6	0.1732	0.1732	0.51	9.90	0.8354	0.5852	3.10	2.86	1.55	Heppell et al. (2000)	49
Snowshoe hare	<i>Lepus americanus</i>	1	4	0.10	0.10	0.20	9.30	1.1291	1.1606	1.21	1.24	1.21	Heppell et al. (2000)	50
Grizzly bear Yellowstone	<i>Ursus arctos</i>	4	20	0.8144	0.8144	0.94	0.35	1.0527	1.6698	9.44	10.54	2.36	Eberhardt (2002)	2
Grizzly bear Brit. Col.	<i>Ursus arctos</i>	6	20	0.9209	0.9209	0.95	0.42	1.0939	2.7498	10.55	12.05	1.76	Eberhardt (2002)	3
Grizzly bear Swan Mount.	<i>Ursus arctos</i>	6	25	0.8313	0.8313	0.90	0.26	0.9777	0.7537	12.86	12.23	2.14	Eberhardt (2002)	4
Feral horse	<i>Equus caballus</i>	3	20	0.9726	0.9726	0.97	0.29	1.1603	3.7536	7.35	10.68	2.45	Eberhardt (2002)	6
Elk Yellowstone	<i>Cervus elaphus</i>	3	18	0.8707	0.8707	0.99	0.48	1.1999	4.7065	6.94	10.29	2.31	Eberhardt (2002)	8
Moose	<i>Alces alces</i>	3	25	0.6768	0.6768	0.95	0.56	1.0899	2.4050	8.77	11.79	2.92	Eberhardt (2002)	10
Caribou	<i>Rangifer tarandus</i>	3	16	0.7990	0.7990	0.84	0.40	1.0227	1.1642	6.65	6.91	2.22	Eberhardt (2002)	11
Red deer	<i>Cervus elaphus</i>	4	16	0.8532	0.8532	0.95	0.37	1.0762	1.9084	8.33	9.29	2.08	Eberhardt (2002)	12
White-tailed deer	<i>Odocoileus virginianus</i>	2	16	0.6403	0.6403	0.70	0.71	0.9919	0.9657	4.32	4.26	2.16	Eberhardt (2002)	13
Giant panda	<i>Ailuropoda melanoleuca</i>	4	18	0.8050	0.8050	0.98	0.20	1.0089	1.0978	10.46	10.62	2.61	Eberhardt (2002)	14
Northern fur seal	<i>Callorhinus ursinus</i>	3	20	0.6768	0.6768	0.90	0.33	0.9846	0.8695	9.18	8.82	3.06	Heppell et al. (2000)	19
Northern sea lion	<i>Eumetopias jubatus</i>	4	26	0.8144	0.8144	0.86	0.28	0.9836	0.8524	9.86	9.40	2.47	Heppell et al. (2000)	20
Harbor seal	<i>Phoca vitulina</i>	4	35	0.7208	0.7208	0.89	0.41	0.9984	0.9820	11.38	11.30	2.85	Heppell et al. (2000)	21
Southern elephant seal	<i>Mirounga leonina</i>	3	23	0.7047	0.7047	0.80	0.37	0.9413	0.6415	7.95	6.80	2.65	Heppell et al. (2000)	22
Manatee	<i>Trichechus manatus</i>	4	50	0.8727	0.8727	0.91	0.19	1.0148	1.2100	12.40	13.55	3.10	Heppell et al. (2000)	23

Mammals cont.														
Common name	Scientific name	$\bar{L}$	$\bar{W}$	$S_1$	$S_2$	$S_a$	$m$	$\bar{L}_1$	$R_o$	$\bar{A}$	$\bar{L}_1$	$\bar{A}/\bar{L}$	Reference	ID
Sei whale	<i>Balaenoptera borealis</i>	6	60	0.9331	0.9331	0.94	0.11	1.0082	1.1698	18.59	19.77	3.10	Heppell et al. (2000)	24
Gray whale	<i>Eschrichtius robustus</i>	8	60	0.8999	0.8999	0.95	0.23	1.0295	1.8479	19.19	23.26	2.40	Heppell et al. (2000)	25
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	7	60	0.9340	0.9340	0.97	0.06	1.0000	1.0007	26.41	26.41	3.77	Heppell et al. (2000)	27
Lysan monk seal	<i>Monachus schauinslandi</i>	6	20	0.8721	0.8721	0.90	0.28	0.9980	0.9782	11.14	11.11	1.86	Eberhardt (2002)	1
Manatee Blue Spring	<i>Trichechus manatus</i>	4	50	0.9516	0.9516	0.96	0.15	1.0618	2.6236	13.01	19.91	3.25	Eberhardt (2002)	5
Sea otter California	<i>Enhydra lutris</i>	3	15	0.8573	0.8573	0.91	0.23	1.0171	1.1377	7.49	7.71	2.50	Eberhardt (2002)	7a
Sea otter California	<i>Enhydra lutris</i>	4	15	0.8909	0.8909	0.91	0.23	1.0105	1.0908	8.28	8.40	2.07	Eberhardt (2002)	7b
Weddell seal	<i>Leptonychotes weddelli</i>	6	20	0.8039	0.8039	0.99	0.30	1.0099	1.1331	12.63	12.81	2.10	Eberhardt (2002)	9
Fur seal	<i>Callorhinus ursinus</i>	5	18	0.8011	0.8011	0.91	0.45	1.0194	1.2092	9.73	10.01	1.95	Eberhardt (2002)	14
Killer whale <sup>B</sup>	<i>Orcinus orca</i>	13	60	0.9820	0.9820	0.99	0.07	1.0234	2.1155	30.39	34.58	2.34	Heppell et al. (2000)	26 <sup>B</sup>
Killer whale <sup>B</sup>	<i>Orcinus orca</i>	15	50	0.9836	0.9836	0.99	0.11	1.0327	2.6059	28.11	31.42	1.87	Eberhardt (2002)	17 <sup>B</sup>
Killer whale <sup>B</sup>	<i>Orcinus orca</i>	14	36	0.9775	0.9847	0.9986	0.1186	1.0321	2.1489	23.56	24.94	1.68	Caswell (2001)	1 <sup>B</sup>
Birds (Class Aves)														
Sparrow hawk	<i>Accipiter nisus</i>	1	6	0.49	0.59	0.59	0.99	1.0607	1.1333	2.07	2.17	2.07	Saether and Bakke (2000)	1
Common kingfisher	<i>Alcedo atthis</i>	1	6	0.22	0.28	0.28	1.62	0.6338	0.4948	1.75	1.39	1.75	Saether and Bakke (2000)	2
Snow goose	<i>Anser caerulescens</i>	2	12	0.42	0.82	0.82	1.31	1.1923	2.2240	4.02	5.16	2.01	Saether and Bakke (2000)	3
Meadow pipit	<i>Anthus pratensis</i>	1	6	0.28	0.34	0.34	2.13	0.9350	0.9022	1.56	1.51	1.56	Saether and Bakke (2000)	4
Scrub jay	<i>Aphelocoma coerulescens</i>	2	12	0.35	0.83	0.83	1.03	1.0907	1.5334	4.61	5.26	2.31	Saether and Bakke (2000)	5
Temmink's stint	<i>Calidris temminckii</i>	1	6	0.21	0.75	0.75	0.61	0.7553	0.4212	3.48	2.70	3.48	Saether and Bakke (2000)	7
Hermit thrush	<i>Catharus mustelinus</i>	1	6	0.31	0.61	0.61	0.92	0.8585	0.6936	2.57	2.24	2.57	Saether and Bakke (2000)	9
White stork	<i>Ciconia ciconia</i>	3	18	0.30	0.66	0.66	1.24	0.8711	0.4760	5.94	4.92	1.98	Saether and Bakke (2000)	10
Mute swan	<i>Cygnus olor</i>	5	30	0.55	0.83	0.83	1.30	1.0796	1.9803	8.30	9.68	1.66	Saether and Bakke (2000)	11
House martin	<i>Delichon urbica</i>	1	6	0.17	0.33	0.33	2.43	0.7399	0.6158	1.76	1.48	1.76	Saether and Bakke (2000)	12
Prairie warbler	<i>Dendroica discolor</i>	1	6	0.39	0.68	0.68	1.06	1.0655	1.1642	2.33	2.47	2.33	Saether and Bakke (2000)	13
Lesser kestrel	<i>Falco naumanni</i>	2	12	0.34	0.71	0.71	0.93	0.9381	0.7563	4.57	4.19	2.29	Saether and Bakke (2000)	16
Pied flycatcher	<i>Ficedula hypoleuca</i>	1	6	0.14	0.32	0.32	2.52	0.6686	0.5183	1.85	1.46	1.85	Saether and Bakke (2000)	17
Large cactus finch	<i>Geospiza cornirostris</i>	1	6	0.11	0.50	0.50	0.61	0.4707	0.1321	3.68	1.90	3.68	Saether and Bakke (2000)	20
Ground finch	<i>Geospiza fortis</i>	1	6	0.74	0.69	0.69	0.32	0.8664	0.6814	2.86	2.50	2.86	Saether and Bakke (2000)	21
Pinyon jay	<i>Gymnorhinus cyanocephalus</i>	2	12	0.41	0.72	0.72	0.61	0.9029	0.6258	4.94	4.27	2.47	Saether and Bakke (2000)	22
Oyster catcher	<i>Haematopus ostralegus</i>	5	30	0.45	0.90	0.90	0.21	0.9593	0.5800	14.07	12.20	2.81	Saether and Bakke (2000)	23
Acorn woodpecker	<i>Melanerpes formicivorus</i>	1	6	0.39	0.58	0.58	1.00	0.9498	0.8932	2.24	2.14	2.24	Saether and Bakke (2000)	25
Song sparrow	<i>Melospiza melodia</i>	1	6	0.33	0.62	0.62	1.87	1.2268	1.5317	1.92	2.27	1.92	Saether and Bakke (2000)	26
Eastern screech owl	<i>Otus asio</i>	1	6	0.36	0.75	0.75	1.30	1.1884	1.5388	2.31	2.70	2.31	Saether and Bakke (2000)	28
Blue tit	<i>Parus caeruleus</i>	1	6	0.16	0.40	0.40	4.23	1.0750	1.1234	1.58	1.64	1.58	Saether and Bakke (2000)	30
Great tit	<i>Parus major</i>	1	6	0.22	0.48	0.48	3.90	1.3362	1.6298	1.55	1.85	1.55	Saether and Bakke (2000)	31
Willow tit	<i>Parus montanus</i>	1	6	0.50 <sup>G</sup>	0.51	0.51	1.22	1.1144	1.2230	1.79	1.93	1.79	Saether and Bakke (2000)	32
Cliff swallow	<i>Pterichlidon pyrrhonata</i>	1	6	0.18	0.57	0.57	0.92	0.6762	0.3719	3.01	2.11	3.01	Saether and Bakke (2000)	35
Eastern bluebird	<i>Sialia sialis</i>	1	6	0.50 <sup>G</sup>	0.43	0.43	1.36	1.1077	1.1854	1.61	1.72	1.61	Saether and Bakke (2000)	40
Spotted owl	<i>Strix occidentalis</i>	3	18	0.26	0.84	0.84	0.31	0.8766	0.3336	9.60	7.20	3.20	Saether and Bakke (2000)	44

Birds cont.														
Common name	Scientific name	$\bar{L}$	$\bar{W}$	$S_1$	$S_2$	$S_a$	$m$	$\bar{L}_1$	$R_o$	$\bar{A}$	$\bar{L}_1$	$\bar{A}/\bar{L}$	Reference	ID
Common sandpiper	<i>Tringa hypoleucos</i>	1	6	0.57	0.64	0.64	0.32	0.7544	0.4719	3.03	2.34	3.03	Saether and Bakke (2000)	46
Spotted sandpiper	<i>Tringa macularia</i>	1	6	0.21	0.58	0.58	1.28	0.8135	0.6156	2.58	2.14	2.58	Saether and Bakke (2000)	47
White-crowned sparrow	<i>Zonotrichia leucophrys</i>	1	6	0.48	0.55	0.55	1.12	1.0781	1.1616	1.93	2.05	1.93	Saether and Bakke (2000)	49
Golden plover <sup>B</sup>	<i>Pluvialis apricaria</i>	1	6	0.58	0.76	0.76	0.11	0.6334	0.2146	4.02	2.73	4.02	Saether and Bakke (2000)	34 <sup>B</sup>
Golden plover <sup>B</sup>	<i>Pluvialis apricaria</i>	1	100	0.58	0.76	0.76	0.11	0.8238	0.2658	12.88	4.17	12.88	Saether and Bakke (2000)	34 <sup>B</sup>
Lesser snow geese	<i>Anser caerulescens caerul.</i>	2	12	0.30	0.88	0.88	0.677 <sup>H</sup>	1.0210	1.1249	5.58	5.76	2.79	Rockwell et al. (1997)	1
Spotted owl	<i>Strix occidentalis caurina</i>	2	25	0.2828	0.2828	0.94	0.24	0.8989	0.2475	15.60	10.64	7.80	Eberhardt (2002)	17
King penguin	<i>Aptenodytes patagonica</i>	6	36	0.47	0.92	0.92	0.13	0.9546	0.4654	18.11	14.97	3.02	Saether and Bakke (2000)	6
South polar skua	<i>Catharacta maccormickii</i>	6	36	0.44	0.93	0.93	0.13	0.9610	0.5085	18.42	15.63	3.07	Saether and Bakke (2000)	8
Wandering albatross	<i>Diomedea exulans</i>	10	60	0.40 <sup>G</sup>	0.92	0.92	0.45	1.0022	1.0473	20.53	20.76	2.05	Saether and Bakke (2000)	14
Black-browed albatross	<i>Diomedea melanophris</i>	10	60	0.52 <sup>G</sup>	0.91	0.91	0.20	0.9673	0.4905	23.50	19.69	2.35	Saether and Bakke (2000)	15
Atlantic puffin	<i>Fratercula arctica</i>	5	30	0.78	0.94	0.94	0.41	1.1050	3.3286	10.30	14.16	2.06	Saether and Bakke (2000)	18
Northern fulmar	<i>Fulmarus glacialis</i>	8	48	0.88	0.94	0.94	0.18	1.0243	1.5765	17.90	20.14	2.24	Saether and Bakke (2000)	19
Yellow-eyed penguin	<i>Megadyptes antipodes</i>	3	18	0.31	0.84	0.84	0.81	1.0054	1.0393	7.12	7.20	2.37	Saether and Bakke (2000)	24
Northern gannet	<i>Morus bassanus</i>	5	30	0.35	0.90	0.90	0.38	0.9839	0.8162	12.88	12.20	2.58	Saether and Bakke (2000)	27
Snow petrel	<i>Pagodroma nivea</i>	10	60	0.50 <sup>G</sup>	0.94	0.94	0.16	0.9872	0.7314	25.34	23.40	2.53	Saether and Bakke (2000)	29
Shag	<i>Phalacrocorax aristotelis</i>	2	12	0.44	0.87	0.87	0.55	1.0446	1.2695	5.28	5.66	2.64	Saether and Bakke (2000)	33
Cory's shearwater	<i>Puffinus diomedea</i>	9	54	0.29	0.92	0.92	0.18	0.9514	0.3277	25.81	19.49	2.87	Saether and Bakke (2000)	36
Short-tailed shearwater	<i>Puffinus tenuirostris</i>	6	36	0.50 <sup>G</sup>	0.90	0.90	0.22	0.9684	0.6248	15.59	13.77	2.60	Saether and Bakke (2000)	37
Adelie penguin	<i>Pygoscelis adeliae</i>	4	24	0.37	0.89	0.89	0.35	0.9739	0.7581	10.88	10.10	2.72	Saether and Bakke (2000)	38
Black-legged kittiwake	<i>Rissa tridactyla</i>	5	30	0.79	0.85	0.85	0.60	1.0516	1.6254	9.11	10.28	1.82	Saether and Bakke (2000)	39
Parasitic jaeger	<i>Stercorarius parasiticus</i>	4	24	0.72	0.80	0.80	0.61	1.0141	1.1140	7.59	7.80	1.90	Saether and Bakke (2000)	41
Least tern	<i>Sterna antillarum</i>	2	12	0.50 <sup>G</sup>	0.88	0.88	0.56	1.0844	1.5501	5.08	5.76	2.54	Saether and Bakke (2000)	42
Arctic tern	<i>Sterna paradisaea</i>	4	24	0.50 <sup>G</sup>	0.87	0.87	0.19	0.9281	0.4554	11.70	9.50	2.92	Saether and Bakke (2000)	43
Ancient murrelet	<i>Synthliboramphus antiquus</i>	3	18	0.50 <sup>G</sup>	0.77	0.77	0.75	0.9920	0.9519	6.19	6.10	2.06	Saether and Bakke (2000)	45
Common murre	<i>Uria aalge</i>	6	36	0.47	0.95	0.95	0.39	1.0545	2.2583	13.82	17.06	2.30	Saether and Bakke (2000)	48
King penguin	<i>Aptenodytes patagonica</i>	6	36	0.49	0.952	0.952	0.155	0.9981	0.9680	17.34	17.21	2.89	Russell (1999)	1
Adelie penguin	<i>Pygoscelis adeliae</i>	5	30	0.51	0.894	0.894	0.316	0.9930	0.9185	12.22	11.94	2.44	Russell (1999)	3
Royal penguin	<i>Eudyptes schlegeli</i>	7	42	0.67	0.86	0.86	0.245	0.9485	0.4723	15.63	12.98	2.23	Russell (1999)	4
Yellow-eyed penguin	<i>Megadyptes antipodes</i>	3	18	0.34	0.871	0.871	0.59	1.0064	1.0503	7.67	7.78	2.56	Russell (1999)	5
Little penguin	<i>Eudyptula minor</i>	3	18	0.47	0.858	0.858	0.42	0.9912	0.9351	7.68	7.53	2.56	Russell (1999)	6
Wandering albatross	<i>Diomedea exulans</i>	10	60	0.40	0.968	0.968	0.185	1.0124	1.3971	26.04	28.26	2.60	Russell (1999)	7
Royal albatross	<i>Diomedea epomophora</i>	9	54	0.87	0.946	0.946	0.25	1.0439	2.3824	18.16	22.64	2.02	Russell (1999)	8
Waved albatross	<i>Diomedea irrorata</i>	6	36	0.88	0.959	0.959	0.50	1.1420	6.3273	11.10	17.74	1.85	Russell (1999)	9
Laysan albatross	<i>Diomedea immutabilis</i>	9	54	0.76	0.946	0.946	0.235	1.0329	1.9563	19.07	22.64	2.12	Russell (1999)	10
Black-browed albatross	<i>Diomedea melanophris</i>	10	60	0.52	0.934	0.934	0.245	1.0005	1.0120	22.47	22.53	2.25	Russell (1999)	11
Grey-headed albatross	<i>Diomedea chrysostoma</i>	12	72	0.73	0.947	0.947	0.195	1.0134	1.4222	25.26	27.58	2.11	Russell (1999)	12
Sooty albatross	<i>Phoebastria fusca</i>	12	72	0.77	0.95	0.95	0.13	1.0031	1.0889	27.61	28.21	2.30	Russell (1999)	13
Northern giant petrel	<i>Macronectes halli</i>	10	60	0.52	0.906	0.906	0.172	0.9572	0.3888	24.40	19.30	2.44	Russell (1999)	14

Birds cont.														
Common name	Scientific name	$\bar{L}$	$\bar{L}_1$	$S_1$	$S_j$	$S_a$	$m$	$\bar{L}_1$	$R_0$	$\bar{A}$	$\bar{L}_1$	$\bar{A}/\bar{L}$	Reference	ID
Southern giant petrel	<i>Macronectes giganteus</i>	11	66	0.52	0.912	0.912	0.25	0.9763	0.5847	23.92	21.04	2.17	Russell (1999)	15
Bulwer's petrel	<i>Bulweria bulwerii</i>	7	42	0.27	0.947	0.947	0.22	0.9818	0.6946	20.71	18.97	2.96	Russell (1999)	16
Cory's shearwater	<i>Puffinus puffinus</i>	9	54	0.288	0.956	0.956	0.267	1.0027	1.0654	23.71	24.08	2.63	Russell (1999)	17
Manx shearwater	<i>Puffinus diomedea</i>	6	36	0.41	0.905	0.905	0.25	0.9691	0.6253	15.90	14.06	2.65	Russell (1999)	18
Northern gannet	<i>Sula bassanus</i>	5	30	0.35	0.901	0.901	0.50	1.0070	1.0875	11.98	12.25	2.40	Russell (1999)	19
Masked booby	<i>Sula dactylatra</i>	4	24	0.37	0.914	0.914	0.33	0.9925	0.9200	11.12	10.88	2.78	Russell (1999)	20
Shag	<i>Phalacrocorax aristotelis</i>	3	18	0.398	0.878	0.878	0.65	1.0488	1.4308	7.15	7.92	2.38	Russell (1999)	21
Great skua	<i>Catharacta maccormickii</i>	8	48	0.81	0.93	0.93	0.62	1.0925	4.0965	13.67	19.08	1.71	Russell (1999)	22
South Polar skua	<i>Catharacta skua</i>	7	42	0.38	0.938	0.938	0.17	0.9769	0.6388	20.26	18.14	2.89	Russell (1999)	23
Thick-billed murre	<i>Uria lomvia</i>	5	30	0.64	0.90	0.90	0.28	1.0079	1.0998	11.90	12.20	2.38	Russell (1999)	24
Common murre	<i>Uria aalge</i>	5	30	0.47	0.93	0.93	0.395	1.0418	1.6833	11.89	13.64	2.38	Russell (1999)	25
Atlantic puffin	<i>Fratercula arctica</i>	6	36	0.47	0.963	0.963	0.335	1.0565	2.4291	14.44	18.05	2.41	Russell (1999)	26
Emperor penguin <sup>B</sup>	<i>Aptenodytes forsteri</i>	5	30	0.19	0.951	0.951	0.32	0.9805	0.7401	15.80	14.75	3.16	Russell (1999)	2 <sup>B</sup>
Emperor penguin <sup>B</sup>	<i>Aptenodytes forsteri</i>	5	100	0.19	0.951	0.951	0.32	1.0003	1.0068	23.54	23.63	4.71	Russell (1999)	2 <sup>B</sup>

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<sup>B</sup>Species that were used as demonstration species with special symbol in Figs. 4 and 5.

<sup>C</sup>Heppell (1998, her Table 4) did not include fertility and juvenile survival of 10 terrestrial turtles and they were chosen such that  $\bar{L}_1 = 1.0$ .

<sup>D</sup>Age-independent  $S_j$  was calculated from the reported juvenile survival rates using  $(\prod_i S_i)^{1/(\bar{L}-1)}$  (product for i from 2 to  $\bar{L}$ ).

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<sup>G</sup>When  $S_1$  was not available in Saether and Bakke (2000), I used the value given in Russell (1999) or 0.50. My pseudo-stochastic E-patterns in Fig. 5 give the E-pattern for  $S_1$  that gives  $\bar{L}_1 = 1.0$  for these species as used by Saether and Bakke (2000) (and all other species, see text).

<sup>H</sup>Constant fertility m was determined such that  $\bar{L}_1$  remained the same but I used  $\bar{L} = 12$  yr instead of  $\bar{L} =$  yr.

## Appendix 2. Calculation of $\bar{A}$ and E-patterns for age-structured populations

### A2.1 Calculation of $\bar{A}$ and E-pattern from the characteristic function of a LHT or corresponding Leslie matrix

I assume that a life history table (LHT) of a species is characterized by age at first ( $\ell$ ) and last ( $L$ ) reproduction, juvenile survival ( $S_j$ ) up to age  $\ell$ , adult survival ( $S_a$ ) for ages  $\geq \ell$  yr, and step-like female fertility ( $m$ ) for ages  $\geq \ell$  yr. I

5 assume that  $S_j$  is age-independent to simplify the notation but it is not required, whereas it will be essential to assume that  $S_a$  and  $m$  are age-independent. The characteristic function  $\lambda(\lambda)$  (CF) for a LHT or the corresponding Leslie matrix for a post-breeding census can be written down by inspection of the z-transformed life cycle graph (Caswell 2001, p. 178):

$$\lambda(\lambda) = m(S_j/\lambda)^\ell (S_a/\lambda)^0 + m(S_j/\lambda)^\ell (S_a/\lambda)^1 + \dots + m(S_j/\lambda)^\ell (S_a/\lambda)^{(L-\ell)} \quad (\text{A2.1})$$

The same CF applies to a pre-breeding Leslie matrix with discounted fertilities  $F = mS_\ell$  because it is merely a pair of

10 survival rates within each term that are arranged differently in the life cycle graph. The  $(\ell - \ell + 1)$  terms of this CF form a finite geometrical series if  $m$  and  $S_a$  are assumed to be age-independent and the sum formula yields:

$$\lambda(\lambda) = \frac{[m(S_j/\lambda)^\ell][1 - (S_a/\lambda)^{(L-\ell+1)}]}{[1 - (S_a/\lambda)]} \quad (\text{A2.2})$$

The mean age of the reproducing females at the stable age distribution ( $\bar{A}$ ) can be calculated from the first derivative of the CF with respect to  $\lambda$  at  $\lambda = \lambda_1$  (Cochran and Ellner 1992):

$$15 \quad \bar{A} = \lambda_1 \left( \frac{\lambda(\lambda)}{\lambda(\lambda_1)} \right)_{\lambda=\lambda_1} \quad (\text{A2.3})$$

The CF (eq. A2.2) comprises three terms, each in a square bracket, and the partial derivative with respect to  $\lambda$  will produce three additive terms. Each term can be simplified with the help of the characteristic equation (CE) defined by  $\lambda(\lambda) = 1$ :

$$\bar{A} = \ell + \frac{S_a}{(\lambda_1 - S_a)} \lambda_1 \frac{(\ell - \ell + 1)(S_a/\lambda_1)^{(\ell - \ell + 1)}}{(1 - (S_a/\lambda_1)^{(\ell - \ell + 1)})} \quad (\text{A2.4})$$

The second term can be written as  $(S_a/\lambda_1)/[1 - (S_a/\lambda_1)]$  i.e. in terms of the  $S_a/\lambda_1$  ratio that appears in the third term. The

20 critical value of  $\bar{A}$  if  $(\lambda_1 - S_a) \rightarrow 0$  and  $(S_a/\lambda_1) \rightarrow 1$  is:

$$\bar{A}_{\text{critical value}} = (\ell + \ell)/2 \quad (\text{A2.5.1})$$

I use biological reasoning in the text to derive the result. For the mathematical proof, I simplified using  $y = \bar{A} - \ell$ ,

$x = S_a/\lambda_1$ , and  $c = \ell - \ell + 1$ , then converted the  $(\infty - \infty)$  limit problem to a  $(0/0)$  limit problem and used L'Hôpital's rule twice to obtain the critical value:

$$\lim_{x \rightarrow 1} y = \frac{x}{(1-x)} \cdot \frac{c x^c}{(1-x^c)} = \frac{c}{2} \quad (\text{A2.5.2})$$

The elasticity of vital rate  $x$  (where  $x = m, S_j, S_a, \bar{\lambda}, \bar{\lambda}_1$ ) is defined as  $E(x) = \frac{\partial \ln(\bar{\lambda})}{\partial \ln(x)} = (x/\bar{\lambda}) \frac{\partial \bar{\lambda}}{\partial x}$ . The derivative  $\partial \bar{\lambda} / \partial x$  can be calculated from the implicit function  $\bar{\lambda}(\bar{\lambda})$ , using  $\partial \bar{\lambda} / \partial x = - (\partial \bar{\lambda} / \partial x) / (\partial \bar{\lambda} / \partial \bar{\lambda})$ . From eq. (A2.3), it follows that  $(\partial \bar{\lambda} / \partial \bar{\lambda})_{\bar{\lambda}=\bar{\lambda}} = - \bar{\lambda} / \bar{\lambda}_1$  and therefore:

$$E(x) = (x/\bar{\lambda}) (\partial \bar{\lambda} / \partial x) \quad (\text{A2.6})$$

which can be calculated for each vital rate and simplified for several. Of most interest for a prospective analysis are the elasticities of  $m, S_j$ , and  $S_a$ :

$$E(m) = E_1 = 1/\bar{\lambda} \quad (\text{A2.7.1})$$

$$E(S_j) = E_2 = \bar{\lambda} / \bar{\lambda} \quad (\text{A2.7.2})$$

$$E(S_a) = E_3 = (\bar{\lambda} - \bar{\lambda}_1) / \bar{\lambda} \quad (\text{A2.7.3})$$

The derivation also proves that

$$E(S_a) = (1/\bar{\lambda}) [S_a / (\bar{\lambda}_1 - S_a)] \cdot \frac{(1 - (S_a / \bar{\lambda}_1)^{(\bar{\lambda} / \bar{\lambda}_1 + 1)})}{(1 - (S_a / \bar{\lambda}_1))} = (1/\bar{\lambda}) [\bar{\lambda} - \bar{\lambda}_1] = 1 - \bar{\lambda}_1 / \bar{\lambda} = 1 - E(S_j), \text{ i.e.}$$

$$E(S_j) + E(S_a) = 1 \quad (\text{A2.8})$$

This result corresponds to Hamilton (1966, p. 18 his eq. 10 when  $a = 0$ ) and Caswell (2001, p. 237) for a homogenous function of degree 1 to the survival rates  $S_j$  and  $S_a$ .

The sum of these three elasticities is  $(1 + \bar{\lambda})/\bar{\lambda} = 1 + 1/\bar{\lambda} = 1 + E(m)$  and the normalized elasticities are:

$$E_n(m) = E_{n,1} = 1/(\bar{\lambda} + 1) \quad (\text{A2.9.1})$$

$$E_n(S_j) = E_{n,2} = \bar{\lambda} / (\bar{\lambda} + 1) \quad (\text{A2.9.2})$$

$$E_n(S_a) = E_{n,3} = (\bar{\lambda} - \bar{\lambda}_1) / (\bar{\lambda} + 1) \quad (\text{A2.9.3})$$

The normalized elasticities (what I call the E-pattern) simply have denominator  $(\bar{\lambda} + 1)$  instead of  $\bar{\lambda}$ . I suggest that it is not helpful to graph the components of the E-patterns of different species against any vital rate, generation time, or population growth rates and then attempt to establish correlations. Equations (A2.9) give the exact functional relationship between  $E_n(m)$ ,  $E_n(S_j)$ , or  $E_n(S_a)$  and  $\bar{\lambda}$  &  $\bar{\lambda}_1$ . Graphs of any component of the E-patterns versus generation time  $\bar{\lambda}$  with  $\bar{\lambda}_1$  treated as a parameter are best to understand the E-patterns.

While I assumed that  $m$  and  $S_a$  are age-independent, which produces a new 3-term formula for  $\bar{\lambda}$ , the derived formulas for the E-pattern (eqs. A2.7 or A2.9) are exact and can be used for species with age-dependent  $m$  and  $S_a$  if  $\bar{\lambda}$  is



calculated from the definition  $\bar{A} = \sum_x (x \bar{l}_x m_x)$  (sum over all  $x$  = ages) or from  $\bar{A} = \langle w, v \rangle$  with  $w_1 = 1$  and  $v_1 = 1$  (see eq. A2.14 below). The equation  $E(m) = 1/\bar{A}$  (A2.7.1) holds for any discrete Leslie matrix (Hamilton 1966, p. 42 his eq. 25; Charlesworth 1994, p. 192 his eq. 5.2) and is also applicable for a continuous model based on Lotka's renewal equation (Keyfitz 1985, p. 161 his eq. A.5).

## 5 A2.2 Elasticities of first and last age of reproduction

Starting with eq. (A2.6), the elasticities of first ( $\square$ ) and last ( $\square$ ) age of reproduction are obtained after lengthy mathematical manipulations including use of the *CE*:

$$E(\square) = (\square / \bar{A}) [\ln(S_j / \square_1) + \frac{\ln(S_a / \square_1)(S_a / \square_1)^{(\square \square \square + 1)}}{(1 - (S_a / \square_1)^{(\square \square \square + 1)})}] \quad (\text{A2.10.1})$$

$$E(\square) = \square (\square / \bar{A}) \frac{\ln(S_a / \square_1)(S_a / \square_1)^{(\square \square \square + 1)}}{(1 - (S_a / \square_1)^{(\square \square \square + 1)})} \quad (\text{A2.10.2})$$

10 Both  $E(\square)$  and  $E(\square)$  are inversely proportional to  $\bar{A}$ , as are  $E(m)$  and  $E(S_j)$ .  $E(\square)$  and  $E(\square)$  should be useful in the study of life history variations in an evolutionary perspective.

## A2.3 Pseudo-stochastic E-patterns

The vital rates for many species are not well known and accordingly the resulting population growth rates ( $\square_1$ ) are approximate estimates only. A population with  $\square_1 \gg 1$  likely cannot maintain a large  $\square_1$ -value for a long time and a  
 15 population with  $\square_1 < 1$  would become extinct if the declining population growth rate persisted. Over an extended time period of many generations,  $\square_1$  is expected to average out to 1.0 and a stochastic calculation using fluctuating vital rates would be more appropriate. If the basic vital rates are estimates only and not entirely satisfactory for a deterministic calculation, a stochastic calculation would be questionable. I suggest that the E-pattern corresponding to  $\square_1 = 1.0$  is easily estimated by replacing  $\bar{A}$  with  $\square_1$  in eqs. A2.9 and I name this a pseudo-stochastic (*PS*) E-pattern ( $n$  = normalized):

$$20 \quad E_{n,PS}(m) = E_{n,1} = 1/(\square_1 + 1) \quad (\text{A2.11.1})$$

$$E_{n,PS}(S_j) = E_{n,2} = \square/(\square_1 + 1) \quad (\text{A2.11.2})$$

$$E_{n,PS}(S_a) = E_{n,3} = (\square_1 - \square)/(\square_1 + 1) \quad (\text{A2.11.3})$$

This can be justified as follows: Based on given vital rates for a species and calculated  $\square_1$  (say  $> 1.0$  and therefore  $\bar{A} < T < \square_1$ ), the E-pattern is determined by the intersection of the  $\square$  and  $\bar{A}/\square$  contours in Fig. 4. If  $m$  remains age-  
 25 independent (it does not have to be the same value) and  $S_a$  keeps the same value,  $\square_1 = \sum_x (x l_x m_x) / \sum_x (l_x m_x) = \sum_x (x l_x) / \sum_x (l_x)$  (sum over all  $x$  = ages) will not change. I now assume that  $S_j$  is decreased to produce  $\square_1 = 1.0$  and we now have

$\bar{A} = T = \bar{\lambda}_1$ . The new value for  $\bar{A}/\bar{\lambda}_1 = \bar{\lambda}_1/\bar{\lambda}_1$  will be larger and the new E-pattern corresponding to  $\bar{\lambda}_1 = 1.0$  will have moved up on the  $\bar{\lambda}_1$  contour. Conversely, if  $\bar{\lambda}_1 < 1.0$  and therefore  $\bar{A} > T > \bar{\lambda}_1$ , the new E-pattern will be located farther down on the  $\bar{\lambda}_1$  contour because the new  $\bar{A}/\bar{\lambda}_1 = \bar{\lambda}_1/\bar{\lambda}_1$  will be smaller. The calculations are easily carried out for a large number of species with a few extra code lines in an Octave script. First the E-patterns are calculated and drawn using  $\bar{A}$ , as was done in Fig. 4, and then the pseudo-stochastic E-patterns are calculated and drawn using  $\bar{\lambda}_1$ , as was done in Fig. 5.

#### A2.4 Elasticity ratios

The sum of the elasticity ratios  $E_2/E_1 = E_{n,2}/E_{n,1}$  and  $E_3/E_1 = E_{n,3}/E_{n,1}$  is  $\bar{A}$ :

$$E_2/E_1 + E_3/E_1 = \bar{\lambda}_1 + (\bar{A} - \bar{\lambda}_1) = \bar{A} \quad (\text{A2.12})$$

The ratio  $E_3/E_2 = E_{n,3}/E_{n,2}$  is related to the  $(\bar{A}/\bar{\lambda}_1)$ -ratio by the following simple equation:

$$E_3/E_2 = E(S_a)/E(S_j) = (\bar{A}/\bar{\lambda}_1) - 1 \quad (\text{A2.13.1})$$

which using A2.4 for  $\bar{A}$  gives:

$$E_3/E_2 = (1/\bar{\lambda}_1) \left[ \frac{(S_a/\bar{\lambda}_1)}{(1 - (S_a/\bar{\lambda}_1))} - \frac{(\bar{\lambda}_1 \bar{\lambda}_1 + 1)(S_a/\bar{\lambda}_1)^{(\bar{\lambda}_1 \bar{\lambda}_1 + 1)}}{(1 - (S_a/\bar{\lambda}_1))^{(\bar{\lambda}_1 \bar{\lambda}_1 + 1)}} \right] \quad (\text{A2.13.2})$$

Contour plots of  $E_3/E_2$  using parameter values for  $\bar{\lambda}_1/\bar{\lambda}_1$  of 3, 6, 9, and 12 (i.e.  $\bar{\lambda}_1 = k\bar{\lambda}_1$ ,  $k = 3, 6, 9$ , and 12) are shown in Figs. 1A, B, C, and D, respectively. The range of  $x = S_a/\bar{\lambda}_1$  is from 0.2 to 1.2 and the range of  $y = \bar{\lambda}_1$  is from 1 to 35 yr.

The vertical contour lines when  $x = S_a/\bar{\lambda}_1 \leq 1$  have  $E_3/E_2$  values of 1.0, 2.5, 4.0 and 5.5 in Figs. 1A, 1B, 1C, and 1D, respectively. These value agree with the critical values of  $E_3/E_2$  that can be calculated from eq. (A2.5.1) i.e.

$(E_3/E_2)_{\text{critical}} = (\bar{A}_{\text{critical}}/\bar{\lambda}_1) - 1 = [(\bar{\lambda}_1 + \bar{\lambda}_1)/2\bar{\lambda}_1] - 1 = [(\bar{\lambda}_1 + x\bar{\lambda}_1)/2\bar{\lambda}_1] - 1 = [(1 + x)/2] - 1 = 1, 2.5, 4.0$ , and 5.5 for  $x = 3, 6, 9$ , and 12, respectively. The first interesting fact is that for  $\bar{\lambda}_1/\bar{\lambda}_1 \leq 3$   $E_3$  can at most be equal to  $E_2$  ( $E_3/E_2 \leq 1$ ) for the

populations of most interest which have  $S_a/\bar{\lambda}_1 \leq 1$  (Fig. 1A is for  $\bar{\lambda}_1/\bar{\lambda}_1 = 3$ ). For  $\bar{\lambda}_1/\bar{\lambda}_1 \leq 2$  (no figure is shown),  $E_3/E_2$  is  $\leq 1$

for any population including declining populations with  $S_a/\bar{\lambda}_1 > 1$  ( $S_a > \bar{\lambda}_1$ , thus  $\bar{\lambda}_1 < 1.0$ ).

Second, for given  $\bar{\lambda}_1$  when moving horizontally to the right in any subplot in Fig. 1,  $E_3/E_2$  increases as  $x = S_a/\bar{\lambda}_1$  increases (i.e.  $\bar{\lambda}_1 - S_a$  decreases). The elasticity of adult survival ( $E_3$ ) becomes more important compared to the elasticity of juvenile survival ( $E_2$ ) as the difference  $(\bar{\lambda}_1 - S_a)$  becomes smaller. When  $S_a/\bar{\lambda}_1 \leq 1$  ( $S_a - \bar{\lambda}_1 \leq 0$ ) the vertical contour line has been reached (which is valid for any  $\bar{\lambda}_1$ ). If we move further to the right horizontally for given  $\bar{\lambda}_1$ ,  $E_3/E_2$  increases even more but such populations are of less interest because  $S_a/\bar{\lambda}_1 > 1$  and thus  $\bar{\lambda}_1$  now must be  $< 1.0$ . We have a declining population where the fraction of adults in each age class increases with age at the stable age distribution, i.e. the reproducing females have piled up in the older age classes.

Third, for given  $S_a/\lambda_1$  moving vertically in the  $y = \lambda$  direction, there are 3 possible results which are determined by opposing mathematical factors depending on the value of  $S_a/\lambda_1$ . The two factors offset each other exactly if  $S_a/\lambda_1 = 1.0$  and  $E_3/E_2$  becomes independent of  $\lambda$  which produces a vertical contour line. The results of most interest are for populations with  $S_a/\lambda_1 < 1$  and  $E_3/E_2$  decreases if  $y = \lambda$  increases. In these cases,  $\bar{A}$  increases for increasing  $\lambda$ , but  $E(m) = 1/(\bar{A} + 1)$  remains large enough that when multiplied by  $\lambda$ , it will produce relatively larger  $E_2$  compared to  $E_3$  and thus  $E_3/E_2$  decreases. Of less interest are the results for populations with  $S_a/\lambda_1 > 1$  and therefore  $\lambda_1 < 1$ . In these cases,  $\bar{A}$  increases so much (due to the pile-up of adults) that it will produce very small  $E(m) = 1/(\bar{A} + 1)$ . When multiplied by  $\lambda$  the resulting  $E_2$  will become relatively smaller and  $E_3/E_2$  increases.

#### A2.5 Comparison of results for post- and pre-breeding censuses

Post-breeding and pre-breeding censuses must yield the same population growth rate ( $\lambda_1$ ), same net reproductive rate ( $R_0$ ), and same generation times ( $\bar{A}$ ,  $T$ , and  $\lambda_1$ ) because a population of a species does not know anything about our census models. Alternatively, I can argue that since the  $CF$ 's are identical, the values of  $\lambda$  when  $CF = 1$  (i.e.  $\lambda_1$ ) are the same; the values of the  $CF$  at  $\lambda = 1$  are the same, which is the net reproductive rate  $R_0$ . The derivatives must be also identical including the derivative at  $\lambda = \lambda_1$  which is  $-\bar{A}/\lambda_1$  and the derivative at  $\lambda = 1$  which is  $-\lambda_1 R_0/1.0$ .

The  $CF$ 's of post- and pre-breeding censuses are identical and they have the same  $\bar{A}$  as outlined in previous paragraph. We also have

$$\bar{A} = \langle \mathbf{w}, \mathbf{v} \rangle \quad (\text{A2.14})$$

if we chose  $w_l = 1$  and  $v_l = 1$  for the calculation of the scalar product (Mollet and Cailliet 2003). However, the age structure ( $\mathbf{w}$ -vector) and the reproductive values ( $\mathbf{v}$ -vector) at the stable age distribution are different unless  $S_j = S_a$ .

Therefore, each  $v_l w_l$  product-term in the scalar product  $\langle \mathbf{w}, \mathbf{v} \rangle$  must be the same for post- and pre-breeding census.

It is indeed much easier to calculate  $\bar{A}$  as the special scalar product with  $w_l = 1$  and  $v_l = 1$  compared to using eq. (A2.4) because right and left eigenvectors corresponding to  $\lambda_1$  are standard output of matrix programs like PopTools or GNU Octave. However, for the interpretation of  $\bar{A}$ , equation (A2.4) is superior because it comprises only three terms including two simple ones.

#### A2.6 Limit values of $\bar{A}$ for a Leslie matrix model

For comparison with  $\bar{A}$  of stage-based model, the following limit values (LV) for  $\bar{A}$  in eq. (A2.4) are of interest. If  $S_a/\lambda_1 < 1.0$  ( $\lambda_1 > S_a$ ), the third term in (A2.4) will become zero if  $\lambda \rightarrow \lambda_1$  :

$$\bar{A}_{LV1} (\lambda \rightarrow \lambda_1) = \lambda_1 + S_a/(\lambda_1 - S_a) \quad (\text{A2.15.1})$$

If  $S_a/\lambda_1 = 1.0$  ( $\lambda_1 = S_a$ ), then the critical value in eq. (A2.5.1) applies (valid for any  $\lambda$ ):

$$\bar{A}_{LV2}(\lambda/\lambda_1) = (\lambda + \lambda_1)/2 \quad (\text{A2.5.1}) = (\text{A2.15.2})$$

If  $S_a/\lambda_1 > 1.0$  ( $\lambda_1 < S_a$ , thus  $\lambda_1 < 1.0$ ), the limit value of (A2.4) does not exist if  $\lambda/\lambda_1$  but the following approximation for  $S_a/\lambda_1 > 1.05$  and large  $\lambda$  applies:

$$\bar{A}_{LV3}(\lambda/\lambda_1) \approx \lambda - S_a/(S_a - \lambda_1) + \lambda_1 + 1 \quad (\text{A2.15.3})$$

#### A2.7 Comparison of results from Leslie matrix with those from stage-based model with fixed stage duration

The fully age-structured Leslie matrix and any derived stage-based models using fixed stage duration all have different  $CF$ 's but the  $\lambda_1$ 's are the same, while  $\bar{A}$ ,  $R_0$ , and  $\lambda_1$  are all different. The stage-based models comprise i) the pre-breeding stage-based model with the adult age-classes in one stage (Heppell et al. 2000 model), ii) the post-breeding stage-based model with the adult age-classes in one stage, which requires a separate age class for the maturing females, iii) various post- and pre-breeding stage-based models with few stages (e.g. 3-stage and 2-stage models). An outline of the proof comparing the Leslie matrix and the 2-stage pre-breeding matrix follows and empirical calculations showed that it is correct for all the models mentioned. All these models have different  $CF$ 's but the same dominant eigenvalue  $\lambda_1$  and therefore the  $CF$ 's intersect at  $\lambda = \lambda_1$  where  $CF(\lambda) = 1$ . Therefore, since the  $CF$ 's are not identical and they are all continuously decreasing functions of  $\lambda$ , the derivatives are different, including the derivatives at  $\lambda = \lambda_1$  which is  $-\bar{A}/\lambda_1$ . As the  $CF$ 's are continuously decreasing functions in the region of interest, they can only cross once and they must have different values for all values of  $\lambda$  other than  $\lambda = \lambda_1$  which includes the value when  $\lambda = 1$ , which is  $R_0$ . The derivatives at  $\lambda = 1.0$  (which are  $-\lambda_1 R_0/1.0$ ) are different also and thus the  $\lambda_1$ 's are different.

The  $CF$  of the Leslie matrix was given in eq. (A2.2). The  $CF$  of a 2-stage model with pre-breeding census can be read off the life cycle graph after reduction by adsorption of the  $P_1$  and  $P_2$  self-loops:

$$\lambda(\lambda) = [F_2/(\lambda - P_1)] [G_1/(\lambda - P_2)] \quad (\text{A2.16})$$

where  $F_2 = m S_1$ ,  $G_1 = S_2 \lambda$ ,  $P_1 = S_2 (1 - \lambda)$ , and  $P_2 = S_a (1 - \lambda)$ . For fixed state distribution the fractions graduating from juvenile stage (1) to adult stage (2) and from adult stage to the next stage (death in this case) are given by eq. 6.103 in Caswell (2001, p. 161):

$$\lambda_i = \frac{(S_i/\lambda)^{T_i} \lambda (S_i/\lambda)^{T_i} \lambda_1}{(S_i/\lambda)^{T_i} \lambda_1} \quad (\text{A2.17})$$

where  $i = 1$  for the juvenile stage,  $i = 2$  for the adult stage,  $T_1 = \lambda - 1$ , and  $T_2 = \lambda - \lambda + 1$ . The maturing juveniles are in the adult stage in the pre-breeding census and  $S_1$  appears in  $F_2 = m S_1$ .

We have to show that the two  $CE$ 's corresponding to the two  $CF$ 's (A2.2) and (A2.16) have the same solution  $\lambda = \lambda_1$ . The term  $1/(\lambda - P_2)$  in eq. (A2.16) is the only term that involves  $S_a$ . Inserting  $P_2$  and using several algebraic manipulations produces the two terms involving only  $S_a$  in eq. (A2.2) apart from a factor  $1/\lambda$ . Next  $F_2$  and  $G_1$  are inserted into (A2.16) and after several steps the proof is complete if it can be shown that:

$$\frac{\lambda^1 (S_j / \lambda)}{[\lambda^2 (1 - (S_j / \lambda)^{\lambda^1}) (\lambda - P_1)]} = 1? \quad (A2.18)$$

First simplifying and then inserting  $1/(\lambda - P_1)$  shows that all the terms on the left cancel and produce 1. Since (A2.18) has the form of a characteristic function, the equality of (A2.2) and (A2.16) only holds for  $\lambda = \lambda_1$ .

For stage-based models with post-breeding census, a subtle step in the construction is important to obtain the same  $\lambda_1$  as that from the Leslie matrix from which it was derived. The discounted fertility in a stage-based model with all the adults in one stage is simply  $F_\lambda = m S_1$  when using a pre-breeding census. The corresponding discounted fertility in the post-breeding census is sometimes given as  $F_\lambda = m P_a$  (e.g. Caswell 2001, p.173, last stage in 6.150) but it should be  $F_\lambda = m S_a = m (P_a + G_a)$ . For the proof I assume that the maturing females in both post- and pre-breeding model have adult survival ( $S_\lambda = S_{adult}$ ) so that post- and pre-breeding matrices have exactly the same size and form. The pre-breeding matrix has  $S_2$  to  $S_\lambda (= S_{adult})$  on the subdiagonal,  $P_a$  on the diagonal, and the discounted fertility is  $F_\lambda = m S_1$ . The post-breeding matrix has  $S_1$  to  $S_{a-1}$  on the subdiagonal,  $P_a$  on the diagonal, and the discounted fertility matrix element has to be  $F_\lambda = m S_a$ , otherwise, post- and pre-breeding matrix would not produce the same characteristic equation and the same results.

#### A2.8 Octave script for the calculation of $\bar{A}$

```
% 1. Calculation of dominant eigenvalue  $\lambda_1$  of projection matrix  $A = F + T$ 

lambda1 = max(eig(A));

% 2. Calculation of Generation Time (GT) and  $\lambda_1$  from the fundamental matrix  $N$ 

% Note that here 'T' is used for Transition Matrix  $T$  and Generation Time is abbreviated with  $GT$ 

N = inv(eye(length(T))-T); %  $N = (I - T)^{-1}$  (Caswell 2001, p. 118)

R = F*N; % Caswell (2001, p. 126, eq. 5.64)

R0 = max(eig(R)) %  $R_0$  is dominant eigenvalue of R-matrix

GenerationTime = log(R0)/log(lambda1) %  $GT = \ln(R_0)/\ln(\lambda_1) = \ln(R_0)/r$ 

MulMatrix = F*N^2./R0; % After (Cochran and Ellner 1992, Table 2);

% Note that * and ^ implies matrix multiplication, whereas ./ is used for element by element division
```

```

Mu1 = Mu1Matrix(1,1) %  $\bar{\mu}_1$  is the (1,1) element of the  $\bar{\mu}$ -matrix
% 3. Calculation of  $\bar{A}$  from new matrices  $F^*$  and  $N^*$ 
Fstar = lambda1*F; %  $F^* = \bar{\mu}_1 F$ , this study
Nstar = inv(lambda1*eye(length(T))-T); %  $N^* = (\bar{\mu}_1 I - T)^{-1}$ , this study
5 AbarMatrix = Fstar*Nstar^2; % This study
Abar = AbarMatrix(1,1) %  $\bar{A}$  is the (1,1) element of the  $\bar{A}$ -matrix (A2.19)

```

#### A2.9 Biased E-patterns for post- and pre-breeding censuses

The biased E-pattern for a post-breeding census if adult survival in the discounted fertilities is excluded is (needed in Fig. 2H (D-column on left):

$$10 \quad E(m) = 1/\bar{A} \quad (A2.20.1)$$

$$E_b(S_j) = (\bar{\mu}_j/\bar{A}) - e_{1,\bar{\mu}_j} \quad (A2.20.2)$$

$$\begin{aligned}
E_b(S_a) &= 1 - E(m) - E_b(S_j) = 1 - (1/\bar{A}) - (\bar{\mu}_j/\bar{A}) + e_{1,\bar{\mu}_j} \\
&= 1 - (\bar{\mu}_j/\bar{A}) - [(1/\bar{A}) - e_{1,\bar{\mu}_j}] \quad (A2.20.3)
\end{aligned}$$

where  $e_{1,\bar{\mu}_j}$  is the  $\bar{\mu}_j^{\text{th}}$  element in the 1<sup>st</sup> row of the E-matrix and is given by  $e_{1,\bar{\mu}_j} = (F_{\bar{\mu}_j}/\bar{\mu}_j)(v_1 w_{\bar{\mu}_j}/\langle w, v \rangle) = (m$

15  $S_{\bar{\mu}_j}/\bar{\mu}_j)(1/\bar{A})(S_{\bar{\mu}_j}/\bar{\mu}_j)^{(\bar{\mu}_j-1)}$ .  $E(S_a)$  was then calculated assuming that the sum of all three elasticities is 1.0, rather than the correct  $1 + E(m)$ . The term  $[(1/\bar{A}) - e_{1,\bar{\mu}_j}]$  is a short-cut to calculate  $\bar{\mu}_j e_{1,j}$  ( $j = \bar{\mu}_j + 1$  to  $\bar{\mu}_j$ ). These biased elasticities sum to 1.0 and do not require normalization.

The biased E-pattern for the pre-breeding census, if survival to age 1 yr in the discounted fertilities is not included, is more easily calculated because it is only  $E(S_j)$  that is underestimated by the elasticity of survival to age 1 yr.

20 These biased elasticities sum to 1.0 and do not require normalization (needed in Fig. 2H, D-column on right):

$$E(m) = E_1 = 1/\bar{A}; \quad (A2.21.1)$$

$$E(S_j) = E_2 = (\bar{\mu}_j - 1)/\bar{A}; \quad (A2.21.2)$$

$$E(S_a) = E_3 = (\bar{A} - \bar{\mu}_j)/\bar{A} \quad (A2.21.3)$$