

**Elasticity Patterns for Mammals: Age at First Reproduction and Mean Age of  
Reproducing Females are the Determining Parameters**

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## Abstract

Oli and Dobson (2003) reported on the relative importance of life-history variables in mammals and Gaillard et al. (in press) commented that the choice of the ratio between magnitude and onset of reproduction ( $F/\lambda$ ) is not grounded in demographic theory. This was similar to

5 Mollet and Cailliet (2003) who questioned the use of the  $\ln(\text{fertility})/\lambda$  ratio used by Frisk et al. (2001) in a comparative life history study of elasmobranchs. I show that the elasticities calculated by Oli and Dobson (2003) are not correct and that their conclusions from a retrospective analysis using all five elasticities based on nested ANOVAs are therefore questionable. I derive much simpler equations for all five elasticities from the characteristic

10 function of a post-breeding census Leslie matrix that are better suited to understand elasticity patterns of mammals. The E-pattern based on three elasticities needed for a prospective analysis is determined by  $\lambda$  and mean age of the reproducing females at the stable age distribution ( $\bar{A}$ ). The  $\bar{A}/\lambda$  ratio determines the relative importance of adult and juvenile survival. I re-calculated the E-pattern of all 142 mammals from their data, present a prospective analysis, and show that

15 the concept of the ill-defined fast-slow continuum is not helpful to understand the E-patterns of mammals or elasmobranchs.

Gaillard et al. (in press) already commented on Oli and Dobson (2003) and concluded that the choice of the ratio between magnitude and onset of reproduction ( $F/\lambda$ ) is not grounded in demographic theory and that most individual vital rates performed equally well. Their comments were similar to those made by Mollet and Cailliet (2003) regarding Frisk et al. (2001), who used the  $\ln(\text{fertility})/\lambda$  ratio to characterize life histories of elasmobranchs. In addition, the  $F/\lambda$  ratio used by Oli and Dobson (2003) does not characterize the majority of populations (55%) with  $F/\lambda$  ratio between the limit values of 0.60 and 0.15 that they used for classification.

Oli and Dobson (2003) and support papers (Oli and Zinner 2001; Oli 2003a; Oli 2003b) present a tremendous effort to summarize vital rates of 142 mammal populations representing 110 species. Unfortunately, their elasticities are biased because their ratio of elasticity of juvenile survival  $E(S_j)$  to elasticity of fertility  $E(m)$  is not 1 as it should be (see Appendix for proof). In addition, their sample is over-represented by populations with small  $\lambda$  (71 with  $\lambda = 1$ ; 33 with  $\lambda = 2$ ) when the bias is largest. Second, Oli and Dobson (2003) implemented an age-structured post-breeding census model with a Leslie matrix model that uses the same discounted fertility ( $F$ ). This distorts the fertility schedule and produces a biased mean age of the reproducing females at the stable age distribution ( $\bar{A}$ ). Importantly, I will show that  $\bar{A}$  is the major factor determining the E-pattern (comprising  $E(m)$ ,  $E(S_j)$ , and elasticity of adult survival  $E(S_a)$ ) and that the  $\bar{A}/\lambda$  ratio determines the relative importance of adult and juvenile survival.  $\bar{A}$  also plays a major role in the calculation of the elasticities of first and last age of reproduction,  $E(\lambda)$  and  $E(\lambda)$ , respectively. Management proposals derived from a prospective analysis based on biased E-patterns would not be trustworthy. Similarly, a retrospective analysis using all five elasticities in nested ANOVAs, rank correlation analysis, nested ANCOVAs with

log-transformed body mass as covariate, as carried out by Oli and Dobson (2003), will produce biased results and questionable conclusions.

Oli and Dobson (2003) used the term “partial life cycle” for their model and may have been misled by the partial life cycles discussed by Caswell (2001, p. 190) which, I suggest, are only applicable for a pre-breeding census because the same  $F$  appears in all reproduction arcs. The post-breeding Leslie matrix model used by Oli and Dobson (2003) is closer to a standard post-breeding Leslie matrix based on constant fertility, juvenile and adult survival rates (= age-independent  $m$ ,  $S_j$ , and  $S_a$ ). It deviates from a post-breeding Leslie matrix model because they used constant  $F$  instead of constant  $m$ .

I will first show that  $\bar{A}$  and the elasticities of all vital rates of interest can be calculated from the characteristic function ( $CF$ ) for a Leslie matrix and it produces relatively simple formulas. This procedure guarantees that the contribution of the discounted fertilities  $F$  to  $E(S_j)$  and  $E(S_a)$  will be included as they should be (Mollet and Cailliet 2002, 2003) if the correct  $CF$  is used. Second, I will compare my elasticity calculations with the biased elasticities reported by Oli and Dobson (2003) for all 142 species in their fig. 7 and all summary statistics in their table 1. Third, I will present a prospective analysis for mammals, suitable for management proposals, that relies on the three vital rates (fertility, juvenile survival, and adult survival) that we might be able to control and treat age at first and last reproduction as fixed vital rates. I will show that the ill-defined slow-fast continuum as used by Heppell et al. (2000) and Cortés (2002) is not a helpful concept for prospective elasticity analyses. The difference between prospective and retrospective analyses discussed is discussed in Caswell (2001, p. 616).

### Calculation of $\bar{A}$ and elasticities from the characteristic function

Equations for  $\bar{A}$ , normalized elasticities  $E_n(m)$ ,  $E_n(S_j)$ ,  $E_n(S_a)$  (the E-pattern), and elasticities  $E(\square)$ , and  $E(\square)$  are derived from the characteristic function  $\square(\square)$  (CF) of a life-cycle graph that represents a Leslie matrix derived from on an age-structured life history table, as a

5 function of the vital parameters  $\square$ ,  $\square$ ,  $S_j$ ,  $S_a$ , and  $m$  (for details see Appendix):

$$\bar{A} = \square + \frac{S_a}{(\square \square S_a)} \square \frac{(\square \square \square + 1)(S_a / \square)^{(\square \square \square + 1)}}{(1 \square (S_a / \square)^{(\square \square \square + 1)})} \quad (\text{A4})$$

$$E_n(m) = E_{n,1} = 1/(\bar{A} + 1) \quad (\text{A10})$$

$$E_n(S_j) = E_{n,2} = \square/(\bar{A} + 1) \quad (\text{A11})$$

$$E_n(S_a) = E_{n,3} = (\bar{A} - \square)/(\bar{A} + 1) \quad (\text{A12})$$

$$10 \quad E(\square) = (\square / \bar{A}) [\ln(S_j / \square) + \frac{\ln(S_a / \square)(S_a / \square)^{(\square \square \square + 1)}}{(1 \square (S_a / \square)^{(\square \square \square + 1)})}] \quad (\text{A14})$$

$$E(\square) = \square(\square / \bar{A}) \frac{\ln(S_a / \square)(S_a / \square)^{(\square \square \square + 1)}}{(1 \square (S_a / \square)^{(\square \square \square + 1)})} \quad (\text{A15})$$

Note that  $\bar{A}$  and all five elasticities are no longer explicit functions of  $m$  and  $S_j$  and that the E-pattern (A10-A12) is not even an explicit function of  $S_a$  and  $\square$ . However,  $\bar{A}$  is a function of  $\square$ , which itself is a function of all the vital parameters and  $\bar{A}$  appears in the equations of all

15 five 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 is straightforward.

The E-pattern comprising  $E_n(m)$ ,  $E_n(S_j)$ , and  $E_n(S_j)$  in (A10)-(A12), needed for a prospective analysis is determined by  $\square$  and  $\bar{A}$  alone, a major simplification, whereas  $E(\square)$  and  $E(\square)$  are more complicated but are both inversely proportional to  $\bar{A}$ . The advantage of these

20 formulas for the E-pattern is that the E-matrix is not needed and fractional  $\square$ -values present no problem. It is also easy to estimate the E-pattern appropriate for different projection intervals

(*PI*) by using estimates of  $\bar{\lambda}$  and  $\bar{A}$  based on different units of the *PI* (e.g. 5 yr instead of 1 yr).

The calculation of  $\bar{A}$  requires that the characteristic equation (*CE*, defined by  $\lambda(\lambda) = 1$ ) is solved first but should  $\lambda_l$  be reasonably close to 1, the mean age of reproducing females in a cohort ( $\lambda_l$ ) can be substituted for  $\bar{A}$  to obtain an approximate E-pattern without having to solve the *CE*.

Three sets of contour equations facilitate the interpretation of the E-pattern. They are obtained by determining the conditions that guarantee that any two of the three elasticities comprising the E-pattern have the same value. The most useful set of contours is defined by  $\bar{A}/\lambda = \text{constant}$ . If  $\bar{A}/\lambda = 2$ , then  $E_n(S_j) = E_n(S_a)$ . If  $\bar{A}/\lambda > 2$ , adult survival has a larger effect on population growth than juvenile survival; if  $\bar{A}/\lambda < 2$ , then the reverse holds. The second set of contours is defined by  $E_n(S_j) = \lambda E_n(m)$ . If the constant  $\lambda$  is 1, then  $E_n(m) = E_n(S_j)$ . As  $\lambda$  increases,  $E_n(S_j)$  becomes  $\lambda$  times as large  $E_n(m)$ . A third set of contours, defined by  $\bar{A} - \lambda = \text{constant}$ , appears to be less useful. The  $\bar{A} - \lambda = 1$  contour defines species with  $E(S_a) = E(m)$ .

As  $\lambda_l$  approaches  $S_a$ ,  $\lambda_l - S_a \rightarrow 0$  and  $\lambda_l/S_a \rightarrow 1$ ,  $\bar{A} = \lambda + \lambda_l - S_a$  appears to be ill-defined. However, the limit-value exists and is  $(\lambda + \lambda_l)/2$ . A mathematical proof is given in the Appendix (A5) but my derivation using biological arguments is more illustrative. A viable population ( $\lambda_l \geq 1$ ) where ages at first and last reproduction are both  $\lambda$  is a population with only one litter ( $S_a = 0$ ), adults die after they had their first and only litter with sufficient offspring, and we must have  $\bar{A} = \lambda$  ( $\bar{A}/\lambda = 1$ ). At the other extreme, we have a population with  $S_a/\lambda = 1$ ; the adults have constant age structure (same number of adults in each age class between  $\lambda$  and  $\lambda_l$ , and at age  $\lambda$  they either become post-reproductive or die), for which the maximum possible  $\bar{A}$  is  $\bar{A}_{\max} = (\lambda + \lambda_l)/2$ , the limit-value of interest. The maximum  $\bar{A}/\lambda$  ratio is  $(\bar{A}/\lambda)_{\max} = (\lambda + \lambda_l)/2\lambda$ . Based on empirical calculations without mathematical proof, I found that the second term in (A4) is

always larger than the third. This will prove useful to understand that hypothetical or natural populations with large  $\bar{A}$  or  $\bar{A}/\lambda_1$  must have  $\lambda_1$  close to  $S_a$ . Conversely, populations with small  $\bar{A}$  or  $\bar{A}/\lambda_1$  have  $\lambda_1 \gg S_a$ .

Gaillard et al. (in press) used  $T_b \equiv \bar{A} = \lambda_1 + S_a/(\lambda_1 - S_a)$  in their eq. (2); however, the comparison with (A4) shows that this is only correct if  $\lambda_1 \gg S_a$  for species with  $S_a/\lambda_1 < 1$ , when the third term in (A4) becomes zero. All but two species in the mammal sample have  $S_a/\lambda_1 < 1$  and therefore their  $\bar{A}$  has positive bias for most species. In addition, if  $S_a/\lambda_1 > 1$ , their equation will produce negative  $\bar{A}$ . For *Kobus ellipsirpymnus* (a waterbuck population with  $\lambda_1 = 2$ ,  $\lambda_2 = 11$ ,  $S_a = 0.833$ ,  $\lambda_1 = 0.772$ ), their equation would give  $\bar{A} = 2.0 - 13.7 = -11.7$  yr, whereas (A4) yields  $\bar{A} = 2.0 - 13.7 + 18.8 = 7.1$  yr,  $\bar{A}/\lambda_1 = 3.55$ . Note that this not a viable population and would become extinct if the observed vital rates persisted. Therefore, the calculated  $\bar{A}$  (7.1 yr) is larger than  $\bar{A}_{\max}$  (6.5 yr) introduced in the previous paragraph because the age-structure at the hypothetical stable age-distribution is U-shaped

### Comparison of reported biased elasticities in Oli and Dobson (2003)

#### with proposed correct elasticities

There are large differences between the reported elasticities and those calculated here (fig. 1, table 1). The differences are particularly apparent for  $E(S_j)$  and  $E(S_a)$  of species with population growth rates ( $\lambda_1$ ) larger than 1.5. For example, for the species with the largest  $\lambda_1 = 2.619$  (*Tamias striatus*, the eastern chipmunk,  $\lambda_1 = 1$ ,  $\lambda_2 = 7$ ), the reported E-pattern is  $E(F) \sim 0.70$ ,  $E(S_j) \sim 0.23$ , and  $E(S_a) \sim 0.07$ . It implies that  $E(F)$  is about three times as large as  $E(S_j)$ , which is not possible. The ratio should be one for an  $\lambda_1 = 1$  species (see Appendix A10 and A11). The proposed correct E-pattern has  $E(m) = E(F) = 0.77$  (44%),  $E(S_j) = 0.77$  (44%), and  $E(S_a) = 0.23$  (13%).

The discrepancy arises because Oli and Dobson (2003) assumed that the sum of the matrix elements of the E-matrix of an age-structured Leslie matrix is one (e.g. de Kroon et al. (1986); Caswell 2001, p. 230). While technically correct, this overlooks the fact that the discounted fertilities ( $F$ ) consist of a fertility term ( $m$ ) and a discount term ( $S_j$  and  $S_a$  when using a post-breeding census;  $S_j$  = survival to age one when using a pre-breeding census). The “discount” has to be included when calculating the E-pattern from the E-matrix of a Leslie matrix because otherwise elasticities calculated empirically from a life history table, which only consists of fertilities and survival rates but no discounted fertilities, would not agree with those calculated from the corresponding Leslie matrix. The sum of  $E(S_j)$  and  $E(S_a)$  alone adds up to 1.0 (Caswell 2001, p. 237; Mollet and Cailliet 2003; see Appendix in this paper for a more general proof). Accordingly, the sum of  $E(m)$ ,  $E(S_j)$  and  $E(S_a)$  is  $1.0 + E(m)$ , rather than 1.0.

In the pre-breeding census the discounted fertilities are  $F = m S_j$ . If the discount is neglected, it appears as if a species with  $\lambda = 1$  has zero elasticity to juvenile survival and these species are incorrectly located on the left side of the equilateral elasticity triangle (Heppell et al. 2000, their fig. 1). As  $\lambda$  increases, the error becomes progressively smaller (see Mollet and Cailliet 2003, Appendix (c) discussing Heppell et al. 2000, their fig. 3). If survival to age one is omitted, the correct E-pattern is easily calculated by adding  $E(m)$  to  $E(S_j)$ , leaving  $E(S_a)$  as is, and re-normalizing if desired.

In the post-breeding census used by Oli and Dobson (2003), it is more complicated to correct the E-pattern and it was easier to re-calculate the E-pattern for all 142 species (see Appendix for details). However, there is a further complication when trying to correct the reported E-patterns because Oli and Dobson used a post-breeding census with an ill-advised constant  $F$ . In the *T. striatus* example, this is the source of the difference for  $E(F)$  (reported



biased 0.70 vs. suggested 0.77) because their post-breeding Leslie matrix based on constant  $F$  produces a different  $\bar{A} = 1.42$  yr (thus  $1/1.42 = 0.70$ ) vs. correct  $\bar{A} = 1.30$  yr based on constant  $m$  (thus  $1/1.30 = 0.77$ ), although the  $\lambda_i$ 's are the same. The  $\lambda_i$ 's are the same by design because my  $m$  was calculated such that it produced the same  $\lambda_i$ . Note that Oli and Dobson (2003) did not  
5 calculate  $\bar{A}$  and therefore did not realize that their post-breeding Leslie matrix produced a more or less biased  $\bar{A}$  for all species but one (*Tayassu tajacu*, collared peccary, with  $S_j = S_a$ ).

This is best understood by calculating the fertility schedule that corresponds to a constant- $F$  post-breeding Leslie matrix. For *Ochotona princeps* (pika or rock rabbit,  $\lambda = 1$ ,  $\lambda = 6$  with  $S_j = 0.111 < S_a = 0.661$ ), it produces an unrealistic fertility schedule with  $m_1 =$   
10  $0.771/0.111 = 6.95$  and  $m_{2-6} = 0.771/0.661 = 1.17$ . This fertility schedule with  $m_1$  much larger than subsequent  $m$ 's will lower  $\bar{A}$  to 1.50 yr compared to  $\bar{A} = 2.42$  yr for the correctly implemented post-breeding matrix with constant  $m = 3.28$ , which agrees with the reported  $m = 3.25$  that did not vary with age (Smith 1974). The majority of mammal populations used by Oli and Dobson (2003) have  $S_j < S_a$ , which is as expected, unlike the *T. striatus* example used  
15 previously with  $S_j = 0.960 > S_a = 0.602$  that produced biased  $\bar{A} = 1.4 >$  correct  $\bar{A} = 1.3$  yr. The use of a constant- $F$  post-breeding Leslie matrix misrepresents the fertility schedule for the majority of species, including the ones for which age-specific fertilities were reported.

*O. princeps* produced the largest relative difference for  $\bar{A}$  (-37.8%) which has a large effect on the E-pattern. The difference for  $\bar{A}$  of about 1 yr is perhaps large enough that it might  
20 be possible to determine the correct  $\bar{A}$  experimentally from a population near the stable age distribution. The bias due to an incorrect  $\bar{A}$  can add or partially cancel the bias in the calculation of the E-pattern without the contribution from the discounted fertilities ( $F$ ) which complicates the analysis of the combined bias in the E-patterns reported by Oli and Dobson

(2003). In addition, both  $E(\square)$  (A12) and  $E(\square)$  (A13) are inversely proportional to  $\bar{A}$  and accordingly a biased  $\bar{A}$  will affect both.

My summary statistics for  $E(m)$ ,  $(S_j)$ , and  $E(S_a)$  of 142 mammals are significantly different ( $p \leq 0.003$  for re-normalized elasticities) from those reported by Oli and Dobson (2003) which indicates that there is a difference for most species, not just a few outlier species (table 1). Oli and Dobson (2003) reported that the mean absolute value of  $E(\square) = 0.40$  was largest, followed by mean  $E(m) = 0.35$ , whereas I found that mean  $E(S_a) = 0.54$  was largest followed by mean  $E(S_j) = 0.46$ , mean  $E(\square) = 0.36$ , and mean  $E(m) = 0.32$ . If the elasticities reported by Oli and Dobson (2003) show large bias, then the results and conclusions of a retrospective elasticity analysis using nested ANOVAs, rank correlation analysis, and nested ANCOVAs with log-transformed body mass as a covariate are of questionable value. The same would apply to a prospective elasticity analysis based on  $E(m)$ ,  $E(S_j)$ , and  $E(S_a)$ .

### **E-patterns for mammals with summary E-triangle**

My normalized elasticities of the 142 mammal populations in Oli and Dobson (2003) show simple patterns when graphed against  $\bar{A}$  with  $\square$  treated as a parameter (fig. 2).  $E(m)$  decreases as  $\bar{A}$  increases independently of  $\square$  and no  $\square = \text{constant}$  contours are needed (fig. 2A).  $E(S_j)$  has a similar pattern as  $E(m)$  but shows the effect of  $\square$  and the results falls on the  $\square = \text{constant}$  contours ( $\square = 1, 5, 10$ , and  $15$  are shown) (fig. 2B).  $E(S_a)$  shows the reverse pattern of  $E(S_j)$  and the value of the  $\square = \text{constant}$  contours can be read off the  $\bar{A}$ -axis (fig. 2C). The  $\square = 15$  contour, for example, applies to only one species, the elephant, *Loxodonta africana*.

These elasticities are summarized in a ‘Triangle’ graph (three-way proportional graph after Silvertown et al. 1993; Heppell et al. 2000)(fig. 2D). The E-Triangle shows again the  $\square = 1, 5, 10, 15$  contours but also one  $\bar{A}/\square = \text{constant}$  contour ( $= 2$ ). The E-patterns of mammals on

average have  $\bar{A}/\square > 2$  (mean 2.37, median 2.19, CV = 31.1%, range 1.3-4.9), indicating that adult survival has the largest effect on population growth for the majority of populations. This is similar to the 50 mammal populations presented by Heppell et al. (2000) with mean  $\bar{A}/\square = 2.44$ , CV = 33.5%, range 1.2-5.0 (Mollet and Cailliet 2003, our Appendix (e)(ii)).

5           The E-triangle is best understood by considering  $E(S_a)$  first, which is identical with the y-axis and 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 at the opposite corners on the bottom side. For graphing it is easiest to calculate  $x = (E(S_a) + (E(S_j)/\cos(\square/3))) / \tan(\square/3)$ . Note that the triangle appears to be half-empty and provides  
10   space for hypothetical species with  $\square < 1$  yr and an annual reproductive cycle requiring a projection interval of 1 yr.

A more detailed analysis based on mammal orders shows that  $\bar{A}/\square > 2$  for Artiodactyla except *Odocoileus virginianus* ( $\bar{A}/\square = 1.45$ , a white-tailed deer population introduced into a fenced reserve with large  $\square_l = 2.065$ , Jenson 1995; thus large  $\square_l - S_a$ ); Perissodactyla (no figure,  $n$   
15   = 6 only); Pinnipeds; and Primates (except *Macaca thibetana* with  $\bar{A}/\square = 1.43$  because this macaque monkey is short-lived with maximum possible  $\bar{A}/\square = 1.67 ((3+7)/2/3)$ , whereas only about half the populations of Carnivora and Rodentia have  $\bar{A}/\square > 2$  (figs. 3A-3E). Conversely, all 60 elasmobranch populations have  $\bar{A}/\square < 2$  (mean 1.31, CV = 9.3%, range 1.1-1.8, unpublished)(fig 3F). The majority of Carnivora and Rodentia with  $\bar{A}/\square < 2$  have  $\square = 1$  and are  
20   relatively short-lived with large  $(\square_l - S_a)$ , which produces small  $\bar{A}$  according to (A4) and therefore small  $\bar{A}/\square$ .

E-patterns of species with different reproductive cycles ( $RC$ ) can be compared in the same graphs if we take into account that  $\bar{A}$  is measured in units of the projection interval ( $PI$ )

rather than 1 yr. Oli and Dobson (2003) correctly used the observed  $RC$  as the choice for the  $PI$ . They used  $RC = PI = 1$  yr for most species in their sample but included 11 species with  $RC \sim 1$  month (using  $PI = 1$  mo) and 4 species with  $RC = 2$  year (using  $PI = 2$  yr). Gaillard et al. (in press) excluded species with  $PI \sim 1$  mo because species with a short  $RC$  may require a seasonal matrix model. I included all 142 species in my analysis because it did not appear to distort the E-patterns.

The  $\bar{A}/\square$  ratio perfectly defines the relative importance of juvenile and adult survival and  $\bar{A}/\square = 2$  is equivalent to  $E(S_j) = E(S_a)$ . The relative importance of  $E(S_j)$  and  $E(m)$  with ratio  $ER_2 = \square$  needs to be addressed also. When  $\square = 1$ , 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. turtle excluder devices (TED) vs. 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  $ER_2$  would be 3-7 instead of 15-35, if  $PI = 5$  yr combined with actual fertility is used instead of  $PI = 1$  with annualized fertility. Mollet and Cailliet (2003) suggested that this applies to the killer whale, *Orcinus orca*, and an Australian green turtle *Chelonia mydas* population. Oli and Dobson (2003) used  $PI = 1$  yr for chimpanzee, *Pan troglodytes*; weeper capuchin, *Cebus orivaceus*; manatee, *Trichechus manatus*; and elephant for which  $PI = 3$  and 5 yr, respectively, might have been more appropriate. However, my calculations used the same  $PI$ 's as those used by Oli and Dobson (2003). It should also be incorporated for elasmobranchs where many species have  $RC = 2$  yr and a few have  $RC = 3$  yr but instead annualized fertilities are used (e.g. Cortés 2002). My sample of 60 elasmobranch populations comprised 26 with  $RC = 1$  yr, 29 with  $RC = 2$  yr, and 5 with  $RC = 2.5(2 \text{ or } 3) - 3$  yr and this was accounted for in my calculations (fig.

3F, unpublished). However, the use of different  $PI$ 's for different species makes identification of a particular species in the E-triangle more difficult.

The ill-defined fast-slow continuum has been used by many for a prospective elasticity analysis (e. g. Heppell et al. 2000; Cortés 2002) and retrospective elasticity analysis (e. g. Oli and Dobson 2003; Gaillard et al. in press). I suggest that the fast-slow continuum is not useful 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  $\Delta$  and  $\Delta$ ), have large fecundity ( $m$ ) and low survival rates ( $S_j$  and  $S_a$ ) while the “slow” end corresponds to species with opposite vital parameters (large  $\Delta$  and  $\Delta$ , small  $m$ , high  $S_j$  and  $S_a$ ) (Gaillard et al. in press). They showed that the first axis (PC1) of a PCA analysis corresponded to the fast-slow continuum and that  $\bar{A}$  was highly correlated with PC1. Small  $\bar{A}$  must be associated with small  $\Delta$  and therefore with the fast end of the continuum and the reverse would hold for large  $\bar{A}$ . Consider mammal species with  $\Delta = 1$  in fig. 2D: they would all be expected to be at the fast end because  $\Delta$  is small. However, these species have a considerable  $\bar{A}/\Delta$  range of 1.3-4.9 ( $= \bar{A}$  because  $\Delta = 1$ ), indicative of a wide range of E-patterns from  $E(S_j)$  much larger than  $E(S_a)$  to the opposite. The 60 populations of elasmobranchs have  $\Delta$  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  $\Delta$  is large. This is not the case. Their E-patterns are similar and  $E(S_j)$  is largest for all because  $\bar{A}/\Delta < 2$  (fig. 3F).

Oli and Dobson (2003) collated a large amount of information on life-histories for 142 mammals. It provided an incentive to produce the best possible E-pattern for a prospective analysis. My elasticity formulas also should be useful for improved retrospective analyses of mammals. Gaillard et al. (in press) pointed out that  $\bar{A}$  is based on a deterministic model of a

population at the stable age distribution. Based on two case studies, Dixon et al. (1999) concluded that deterministic elasticities are good indicators of stochastic elasticities. However, the risk of extinction for small populations increases if stochasticity of vital rates is included (Doak et al. 2004; Nakaoka 1996; Caswell 2001, p. 493). E-patterns have been shown to be very robust to even large ( $\pm 50\%$  at least) perturbations (Caswell 2001, p. 243).

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. I now suggest the same for the Leslie matrix model. A standard life history table 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 correct E-pattern. Matrix formulations and calculations have advantages but the results 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. I am concerned that management recommendations based on a prospective elasticity analysis might be less useful than previously suggested because E-patterns are so easily estimated based on  $\bar{A}$  and  $\bar{p}_i$  alone, do not require the E-matrix at all, and  $\bar{p}_i$  can serve as first approximation to  $\bar{A}$ , thus eliminating the need to solve the characteristic equation.

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## Appendix. Calculation of $\bar{A}$ and elasticities from the characteristic function

I assume that a life history table of a species is characterized by age at first ( $\square$ ) and last ( $\square$ ) reproduction, juvenile survival up to age  $\square$  ( $S_j$ ), adult survival ( $S_a$ ) for age  $\geq \square$ , and step-like female fertility ( $m$ ) for age  $\geq \square$ . I assume that  $S_j$  is constant to simplify the notation but it is not required, whereas it will be essential to assume that  $S_a$  and  $m$  are constant (independent of age). The maturing juveniles that have their first litter at age  $\square$  are assumed to have  $S_j$  from age  $\square - 1$  to age  $\square$ . Accordingly, the first discounted fertility in the corresponding post-breeding census Leslie matrix is  $F_{\square} = m S_j$  and all subsequent discounted fertilities are  $F_i = m S_a$  ( $i = \square + 1$  to  $\square$ ). This assumption is not quite appropriate for species with a long a gestation period because these animals are pregnant adults. However, it is appropriate for many mammal species used by Oli and Dobson (2003), it was the assumption used by them, and it yields simpler formulas that do not include gestation period (Mollet and Cailliet 2003, Appendix 1b provide equations including gestation time).

The characteristic function  $\square(\square)$  ( $CF$ ) for an age-structured life history table or the corresponding Leslie matrix can be written down by inspection of the z-transformed life cycle graph (Caswell 2001, p. 178):

$$\square(\square) = m(S_j / \square)^{\square} (S_a / \square)^0 + m(S_j / \square)^{\square} (S_a / \square)^1 + \dots + m(S_j / \square)^{\square} (S_a / \square)^{(\square - \square + 1)} \quad (A1)$$

Note that the same  $CF$  applies to a pre-breeding Leslie matrix with discounted fertilities  $F = m S_j$  because it is merely a pair of survival rates within each term that are arranged differently in the life cycle graph. The  $(\square - \square + 1)$  terms of this  $CF$  form a finite geometrical series because I assume that  $m$  and  $S_a$  are constant and the sum formula yields:

$$\square(\square) = \frac{[m(S_j / \square)^{\square}][1 - (S_a / \square)^{(\square - \square + 1)}]}{[1 - (S_a / \square)]} \quad (A2)$$

The mean age of the reproducing females at the stable age distribution ( $\bar{A}$ ) can be calculated from the *CF* (Cochran and Ellner 1992):

$$\bar{A} = \sum_{i=1}^{\infty} i \left( \frac{\lambda^i}{\sum_{j=1}^{\infty} \lambda^j} \right) \quad (A3)$$

The *CF* (A2) comprises three terms, each in a square bracket (two numerator and one

5 denominator term), 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 as  $\lambda(\lambda) = 1$ , which will be used to determine the eigenvalues including the largest, real eigenvalue of interest here, namely  $\lambda_1$ :

$$\bar{A} = \lambda + \frac{S_a}{(\lambda_1 S_a)} \lambda \frac{(\lambda \lambda_1 + 1)(S_a / \lambda_1)^{(\lambda \lambda_1 + 1)}}{(1 \lambda (S_a / \lambda_1)^{(\lambda \lambda_1 + 1)})} \quad (A4)$$

10 The limit-value of  $\bar{A}$  for  $(\lambda_1 - S_a) \rightarrow 0$  and  $(S_a / \lambda_1) \rightarrow 1$  is  $(\lambda + \lambda)/2$ . I use biological reasoning in the text to derive the result. For the mathematical proof, I simplified using  $y = \bar{A} \lambda$ ,  $x = S_a / \lambda_1$ , and  $c = \lambda - \lambda + 1$ , then converted the  $(\infty - \infty)$  limit problem to a  $(0/0)$  limit problem and used L'Hôpital's rule twice to obtain the limit value.

$$\lim_{x \rightarrow 1} y = \frac{x}{(1 \lambda x)} \lambda \frac{c x^c}{(1 \lambda x^c)} = \frac{c \lambda 1}{2} \quad (A5)$$

15 The elasticity of vital rate  $x$  (where  $x = m, S_j, S_a, \lambda, \lambda_1$ ) is defined as  $E(x) = \lambda n(\lambda) / \lambda n(x) = (x / \lambda) (\lambda n / \lambda x)$  and  $\lambda n / \lambda x$  can be calculated from the implicit function  $\lambda(\lambda)$ , using  $\lambda n / \lambda x = - (\lambda n / \lambda x) / (\lambda n / \lambda \lambda)$ . From (A3), it follows that  $(\lambda n / \lambda \lambda) = - \bar{A} / \lambda$  and therefore  $E(x) = (x / \bar{A}) (\lambda n / \lambda x)$ , which can be calculated for each vital parameter and simplified for several. Of most interest for a prospective analysis are the elasticities of  $m, S_j$ , and  $S_a$ :

$$20 \quad E(m) = E_1 = 1 / \bar{A} \quad (A6)$$

$$E(S_j) = E_2 = \lambda / \bar{A} \quad (A7)$$

$$E(S_a) = E_3 = (\bar{A} - \lambda) / \bar{A} \quad (A8)$$



The derivation also proves that

$$E(S_a) = (1/\bar{A})[S_a/(\bar{A} - S_a) - \frac{(1 - (S_a/\bar{A}))^{(\bar{A}+1)}}{(1 - (S_a/\bar{A}))}] = (1/\bar{A})[\bar{A} - 1] = 1 - 1/\bar{A} = 1 - E(S_j)$$

that is:

$$E(S_j) + E(S_a) = 1 \quad (\text{A9})$$

as it should be for a homogenous function of degree 1 to the survival rates  $S_j$  and  $S_a$  (Caswell

5 2001, p. 237).

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

$$E_n(m) = E_{n,1} = 1/(\bar{A} + 1) \quad (\text{A10})$$

$$E_n(S_j) = E_{n,2} = 1/(\bar{A} + 1) \quad (\text{A11})$$

$$10 \quad E_n(S_a) = E_{n,3} = (\bar{A} - 1)/(\bar{A} + 1) \quad (\text{A12})$$

Note that the normalized elasticities (what I call the E-pattern) simply have denominator  $(\bar{A} + 1)$  instead of  $\bar{A}$ . The sum of the elasticity ratios  $ER_2 = E_2/E_1 = E_{n,2}/E_{n,1}$  and  $ER_3 = E_3/E_1 = E_{n,3}/E_{n,1}$  is  $\bar{A}$ :

$$ER_2 + ER_3 = 1 + (\bar{A} - 1) = \bar{A} \quad (\text{A13})$$

15 The elasticities of  $\bar{A}$  and  $\bar{A}$  are:

$$E(\bar{A}) = (\bar{A}/\bar{A})[\ln(S_j/\bar{A}) + \frac{\ln(S_a/\bar{A})(S_a/\bar{A})^{(\bar{A}+1)}}{(1 - (S_a/\bar{A}))^{(\bar{A}+1)}}] \quad (\text{A14})$$

$$E(\bar{A}) = 1(\bar{A}/\bar{A}) \frac{\ln(S_a/\bar{A})(S_a/\bar{A})^{(\bar{A}+1)}}{(1 - (S_a/\bar{A}))^{(\bar{A}+1)}} \quad (\text{A15})$$

Note that both are inversely proportional to  $\bar{A}$ , as are  $E(m)$  and  $E(S_j)$ . I suggest that these equations, much simplified by the use of the well-defined  $\bar{A}$ , are better suited for the analysis of

20 elasticities compared to the complicated formulas with 10-16 terms derived by Oli and Zinner

(2001, their Appendix B). In addition, the correct  $CF$  should yield  $E(m) = E(S_j)$  when  $\square = 1$ , and  $E(S_j) + E(S_a) = 1$  as I have proved (A7 and A9).

As stated, the  $CF$ 's of post- and pre-breeding censuses are identical. However, the age structure ( $w_i$ ) and the reproductive values ( $v_i$ ) at the stable age distribution are different unless  $S_j = S_a$ . Importantly, the product terms  $v_i w_i$  in the scalar product  $\langle \mathbf{w}, \mathbf{v} \rangle$  are again the same and therefore also the scalar product  $\langle \mathbf{w}, \mathbf{v} \rangle$ , as it must be because  $\bar{A} = \langle \mathbf{w}, \mathbf{v} \rangle$  if we chose  $w_i = 1$  and  $v_i = 1$  for the calculation of the scalar product (Mollet and Cailliet 2003). It is indeed much easier to calculate  $\bar{A}$  as the special scalar product with  $w_i = 1$  and  $v_i = 1$  compared to using (A4) because right and left eigenvectors corresponding to  $\square_i$  are standard output of matrix programs like PopTools or GNU Octave and are also easily calculated for a life history table in an Excel spreadsheet. However, for the interpretation of  $\bar{A}$  equation (A4) is far superior.

Post-breeding and pre-breeding censuses must yield the same population growth rate ( $\square_i$ ), same net reproductive rate ( $R_0$ ), and the same generation times ( $\bar{A}$ ,  $T$ , and  $\square_i$ ) 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 the  $CF$  at  $\square = 1$  are the same, which is the net reproductive rate  $R_0$ . The derivatives must be also identical including the derivative at  $\square = \square_i$  which is  $-\bar{A}/\square_i$ .

My calculations that duplicated the biased results for  $E(m)$ ,  $E(S_j)$ , and  $E(S_a)$  reported by Oli and Dobson (2003) did not use the complicated equations given in Oli and Zinner (2001, their Appendix B). Instead, I converted my equations (A6)–(A8) so they would produce biased (b) results based on information provided by Madan Oli (personal communication):  $E(m) = 1/\bar{A}$  (result will not be the same if biased  $\bar{A}$  is used);  $E_b(S_j) = \square/\bar{A} - e_{1,\square}$ , where  $e_{1,\square}$  is  $\square^{\text{th}}$  element in the 1<sup>st</sup> row of the E-matrix; and  $E(S_a)$  was then calculated assuming that the sum of all three

elasticities was 1, rather than the correct  $1 + E(m)$ :  $E_b(S_a) = 1 - E(m) - E_b(S_j) = 1 - 1/\bar{A} - \lambda/\bar{A} + e_{1,\lambda} = 1 - \lambda/\bar{A} - (1/\bar{A} - e_{1,\lambda})$ . The term  $(1/\bar{A} - e_{1,\lambda})$  is a short-cut to calculate  $\sum_{\lambda+1}^{\lambda} e_{1,j}$ .

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Table 1: Summary statistics for vital rates, population growth rates ( $\lambda_t$ ), elasticities, mean age of reproducing females at the stable age distribution ( $\bar{A}$ ) and  $\bar{A}/\lambda$ . Comparison of means reported by Oli and Dobson (2003) with results reported here (N = 142).

Variable	O&D (2003) Mean (SE)	My Results Mean (SE)	LSD Means Test F-ratio (P)
Mass (kg)	74.869 (20.963)	74.869 (20.964)	
$\lambda$	2.056 (0.143)	2.056 (0.143)	
$\lambda_t$	13.176 (0.786)	13.176 (0.786)	
$S_j$	0.561 (0.019)	0.561 (0.020)	
$S_a$	0.714 (0.014)	0.714 (0.014)	
$m$	NR	1.064 (0.074)	
$F$	0.542 (0.026)	0.542 (0.026)	
$\lambda_t$	1.055 (0.020)	1.055 (0.020)	
$E(m)$	0.349 (0.018) 34.9%	0.321 (0.016) 22.8%(a)	1.38 (0.24) NS 36.4 (<10 <sup>-6</sup> )
$E(S_j)$	0.311 (0.010) 31.1%	0.459 (0.011) 34.7%(a)	105 (<10 <sup>-6</sup> ) 9.16 (0.003)
$E(S_a)$	0.340 (0.013) 34.0%	0.541 (0.011) 42.6%(a)	137 (<10 <sup>-6</sup> ) 23.5 (2 10 <sup>-6</sup> )
$E(\lambda)$	-0.400 (0.030)	-0.358 (0.025)	1.31 (0.25) NS
$E(\lambda_t)$	0.049 (0.005) 0.060 (0.006)(b)	0.054 (0.006)	0.450 (0.50) NS
$\bar{A}$	NR	4.89 (0.31)	
$\bar{A}/\lambda$	NR	2.37 (0.06)	

5

Note: Life-history variables (vital rates) are as follows:  $\lambda$  = age at first reproduction;  $\lambda_t$  = age at last reproduction;  $S_j$  = juvenile survival;  $S_a$  = adult survival;  $m$  = fertility;  $F$  = discounted fertility;  $\lambda_t$  = population growth rate;  $E(x)$  = elasticity of  $\lambda$  to changes in vital rate  $x$ ; LSD = Fisher's least significant difference; NR = not reported; NS = not significant (P>0.05)

10

- a) The sum of  $E(m)$ ,  $E(S_j)$ , and  $E(S_a)$  in my calculation is not 1.0 and for comparison of the E-patterns comprising these three elasticities, normalized elasticities should be compared.
- b) My calculations using (A13) with biased  $\bar{A}$  produced a different mean for  $E(\lambda)$ .

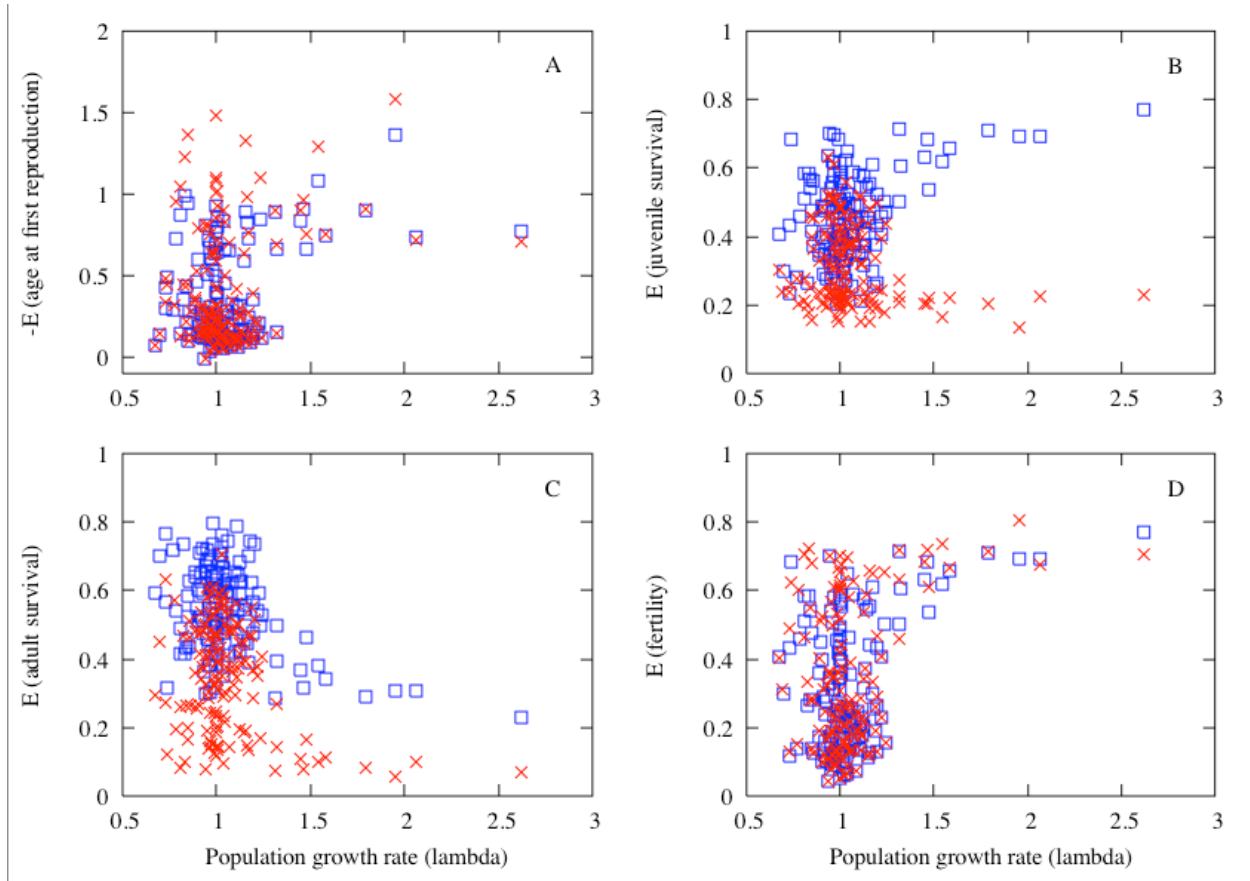
## Figure legends

**Figure 1:** Comparison of biased elasticity patterns of 142 mammal species reported by Oli and Dobson (2003) (| |) with elasticity pattern reported here ( $\square$ ). Relationship between population growth rates ( $\lambda_t$ ) and elasticity of  $\lambda_t$  to changes in (A) age at first reproduction; (B) juvenile survival; (C) adult survival; and (D) fertility.

**Figure 2:** Normalized elasticity patterns for 142 mammals based on vital rates reported in Oli and Dobson (2003) except discounted fertility  $F$ . Relationship between  $\bar{A}$  and elasticity of  $\lambda$  to changes in (A) fertility; (B) juvenile survival; (C) adult survival. (D) Elasticity triangle showing all three elasticities. Contour lines for  $\lambda = 1, 5, 10$ , and  $15$  (in units of the projection interval; 1 yr for 127 out of 142 species) are shown in sub-plots (B)-(D). The triangle plot (D) shows an additional contour line for  $\bar{A}/\lambda = 2$ , which bisects the triangle from left corner to mid-opposite side. Species above this line have  $E(S_a) > E(S_j)$ , for species below the reverse holds.

**Figure 3:** Triangle elasticity patterns for 5 orders of mammals and the subclass Elasmobranchii. (A) Artiodactyla ( $n = 29$ ); (B) Carnivora ( $n = 26$ ); (C) Pinnipedia ( $n = 10$ ); (D) Primates ( $n = 13$ ); (E) Rodentia ( $n = 41$ ); (F) Elasmobranchii ( $n = 60$ ).

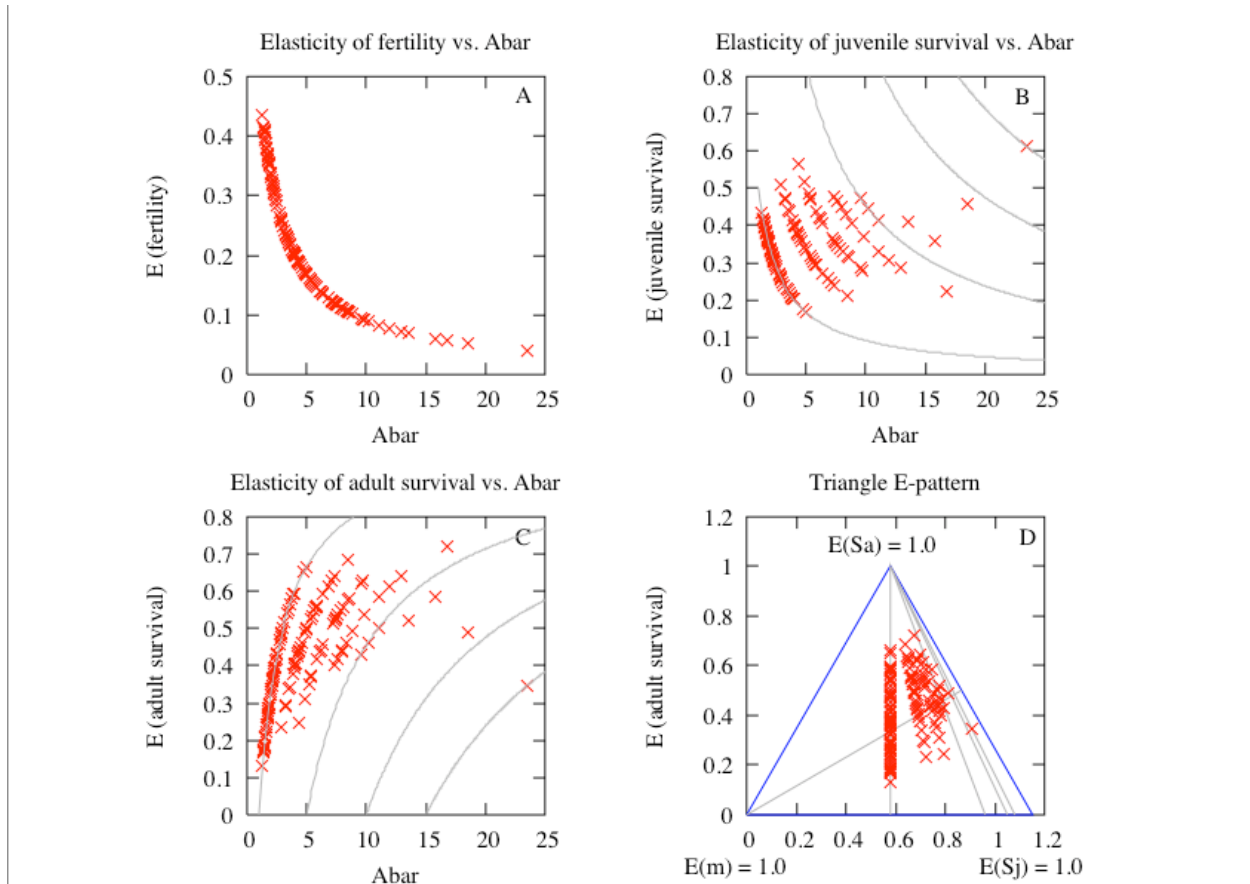
**Figure 1:** Comparison of biased elasticity patterns of 142 mammal species reported by Oli and Dobson (2003) (x) with elasticity pattern reported here ( $\square$ ). Relationship between population growth rates ( $\lambda_t$ ) and elasticity of  $\lambda_t$  to changes in (A) age at first reproduction; (B) juvenile survival; (C) adult survival; and (D) fertility.



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**Figure 2:** Normalized elasticity patterns for 142 mammals based on vital rates reported in Oli and Dobson (2003) except discounted fertility  $F$ . Relationship between  $\bar{A}$  and elasticity of  $\lambda$  to changes in (A) fertility; (B) juvenile survival; (C) adult survival. (D) Elasticity triangle showing all three elasticities. Contour lines for  $\lambda = 1, 5, 10$ , and  $15$  (in units of the projection interval; 1 yr for 127 out of 142 species) are shown in sub-plots (B)-(D). The triangle plot (D) shows an additional contour line for  $\bar{A}/\lambda = 2$ , which bisects the triangle from left corner to mid-opposite side. Species above this line have  $E(S_a) > E(S_j)$ , for species below the reverse holds.



**Figure 3:** Triangle elasticity patterns for 5 orders of mammals and the subclass Elasmobranchii.

(A) Artiodactyla ( $n = 29$ ); (B) Carnivora ( $n = 26$ ); (C) Pinnipedia ( $n = 10$ ); (D) Primates ( $n = 13$ );  
(E) Rodentia ( $n = 41$ ); (F) Elasmobranchii ( $n = 60$ ).

