

Reply

Reply to comments by Miller *et al.* (2003) on Mollet and Cailliet (2002): confronting models with data

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We welcome the chance to reply to the comments made by Miller *et al.* (2003) on our recent paper (Mollet and Cailliet 2002). In most cases we do not feel that their comments have merit, although we acknowledge that certain omissions and errors remained in our published manuscript. Therefore, we will use this opportunity to make those corrections to our paper. We also present a brief, more general discussion of the difficulties of calculating elasticities in stage-based models and point to the problem of choosing the most appropriate projection interval in both stage- and age-based population models when the reproductive cycle is longer than 1 year.

We did not clearly state that our elasticities applied to elasmobranchs with a 1-year gestation period, which was a reasonable approximation for the three shark species, but not for the one ray species we addressed. We also did not mention that it is important to include survival to age one in the elasticity calculations, not only in the post-breeding census that we used, but also in a pre-breeding census. In addition, not all lower-level elasticities were correctly calculated.

More recently, we were able to show that the mean age of reproducing females at the stable age distribution are easily calculated, as are the elasticity patterns (Appendix 1a, b). These new relationships allow us to better explain why stage-based models with few stages have drawbacks for elasmobranchs, which have simple rather than complex life cycles, where individuals of the same age might be in very different demographic states (Caswell 1982). Appendix 1c(i) demonstrates how powerful these relationships are.

It is important first to point out that our paper was strictly a prospective analysis of four carefully selected elasmobranch species that aimed to identify the vital rates (primary demographic parameters such as productivity and survivorship) with the largest proportional effect on population growth (λ) (i.e. the elasticities). These elasticities are best for making recommendations for elasmobranch management (Caswell 2001: section 18.1.3.3, p. 616–619). We never intended our analyses to be an attempt to understand elasmobranch life histories comprehensively, nor especially to answer questions related to how vital rates varied in the past, are varying now, or might vary in the

future (see Caswell 2001: p. 616). This would require a retrospective analysis, also known as life table response experiments (LTRE) decomposition analysis (Caswell 2001: Chapter 10). We accept Caswell's (2001) concepts, recognising the caveats discussed by Frisk *et al.* (2002), who in the end proceeded in a fashion similar to ours.

Frisk *et al.* (2002) used a three-stage model for the barndoor skate *Dipturus laevis* and their own example is most suitable to demonstrate the drawbacks of stage-based models with few stages, as was advocated in our paper. Their paper on the population dynamics of three skates included life history tables (LHTs) for the little skate *Leudoraja erinacea* and the winter skate *L. ocellata*. Had they included a LHT for *D. laevis*, they would have realised that their results for *D. laevis* are of limited value with regard to management proposals. According to their abstract, 'Elasticity analysis indicated that juvenile survival contributed most to population growth in little skate and winter skate, and adult survival contributed the most in barndoor skate'. However, a Leslie matrix or LHT yields $E(\text{juvenile survival})/E(\text{adult survival}) = 2.5\text{--}3.6$, which means that juvenile survival has by far the largest effect on λ (Appendix 1c(ii)). A comparison of their elasticity results for barndoor skate (mean age at first reproduction (α) = 12, maximum age of reproducing females (w) = 50) and winter skate (α = 9, w = 20) (Frisk *et al.* 2002: table 2) already suggested that their elasticity pattern for the barndoor skate was likely to be incorrect. We also point out that the mean age of reproducing females at the stable age distribution in their three-stage model is 9.1 years, which is less than the mean age at first reproduction (assumed to be 12 years) (Appendix 1c(iii)).

No recovery times after a catastrophic event were provided, although *D. laevis* was considered to be overfished but not at risk of extinction (Musick *et al.* 2000), vulnerable (Casey and Myers 2000; Dulvy and Reynolds 2002), showing declining population numbers (Stevens *et al.* 2000), near to extinction (Casey and Myers 1998) and endangered as per IUCN criteria (Dulvy 2003). We estimated the recovery time from Frisk *et al.*'s (2002) three-stage-based model to be

unreasonably low (3.4 years), whereas a Leslie matrix predicts a recovery time of 47 years (Appendix 1d). As outlined in Mollet and Cailliet (2002), starting with a state vector of 1,0,0 (i.e. egg cases only), a projection based on the three-stage-based model produces adults after only 3 years and after 4 years the age distribution is already to within 90% of the stable age distribution, which is unreasonable if the mean age at first reproduction is assumed to be 12 years.

Mollet and Cailliet (2002) came to the conclusion that stage-based models with few stages have drawbacks for elasmobranch species, which are basically age-structured over a relatively long lifespan (Brewster-Geisz and Miller 2000). Such models produce the same λ if a fixed-stage duration (Caswell 2001) is used to calculate the fractions graduating from one stage to the next. However, generation and recovery time estimates are different. No data are available that would allow us to test which model is better and we should, therefore, be guided by the plausibility of predicted results (Hilborn and Mangel 1997).

With regard to the comments by Miller *et al.* (2003) on Brewster-Geisz and Miller (2000), after many discussions with the senior author (K. Brewster-Geisz, personal communication), we came to an understanding that: (i) Anderson (1990) and Hoenig and Gruber (1990) meant age-based 'full' Leslie matrices rather than stage-based models to study population dynamics; (ii) a stage-based model produced no real advantage over a Leslie matrix or LHT, with elasticities summed over age-classes; (iii) there was no basis to Miller *et al.*'s (2003) claim that there are problems in application of life-tables to long-lived marine species with the implication that one could construct a stage-based model when it was not possible to construct a LHT; and (iv) there was also no basis to their claim that for long-lived species, such as the sandbar shark, small errors in parameters estimates can become magnified.

We now also suggest that the management proposal for the sandbar shark, *Carcharhinus plumbeus*, (based on their five-stage model) requires scrutiny. The elasticity pattern of their five-stage model was phrased in terms of reproduction, growth, and stasis, terms that are generally more suitable for plants; for animals it might be better to use fertility, juvenile survival and adult survival (Heppell *et al.* 2000).

We were well aware that the immortality in the Brewster-Geisz and Miller (2000) five-stage model is taken care of by total mortality ($Z = M + F$), which makes the contribution of unreasonably old sharks negligibly small. However, this has little to do with correct parameterisation; it simply means that a Leslie matrix or LHT will not produce exactly the same λ . The limiting level of fishing mortality was mentioned by us and is $r = \ln(\lambda)$. Dividing the projection matrix A by λ in the equation $N_{t+1} = A N_t = \lambda N_t$ is equivalent to adding $F = r$ to M (then calculation of new survival rates), and the new λ , with fishing included, will become $\lambda/\lambda = 1$ (stationary population).

We were also well aware of the importance of having both verification and validation in age and growth studies (Cailliet *et al.* 1986; Cailliet 1990). However, we maintain that validated age-specific life history information, although it is nice to have, is not necessary to get a reasonable estimate of potential population growth (e.g. see Cortés 2002). Due to a difference in the interpretation of growth bands in the shortfin mako (*Isurus oxyrinchus*) (Pratt and Casey 1983; Cailliet *et al.* 1983; Campana *et al.* 2002), age at first reproduction for this species could be 7 years, or more likely 14 years, but a demographic analysis would still be better if it were age-based.

We are not convinced by the statement in Miller *et al.* (2003) that tagging studies have contributed a lot to our understanding of elasmobranch population dynamics. However, such tag-recapture studies can provide survival rates for size-based stages. To our knowledge, this has only been done successfully for the lemon shark *Negaprion brevirostris* (Gruber *et al.* 2001), and the sizes of the sharks in their study were converted to age.

Some of the vital parameters (in particular, the most important ones, i.e. the survival rates) are poorly known for most elasmobranchs. It is true that an age-structured model suffers shortcomings, but why compound it by using a stage-based model? A stage-based model cannot deal with a logistic fertility function (ogive) unless additional age-classes are used, and one might as well use the full Leslie matrix. We (Mollet and Cailliet 2002) tried to use variable stage duration as per Caswell (2001), but encountered sufficient difficulties and thus decided not to pursue this line of investigation.

Frisk *et al.* (2001) used a surrogate $r' = \ln(f)/T_m$ following Jennings *et al.* (1998), where T_m is said to be an index of cohort generation time ($= \mu_1$), which was replaced by age at maturity (α) without explanation. Figure 3 in Frisk *et al.* (2001) included estimates of mortality, M , and we see no good reason why they did not calculate r from a Leslie matrix or LHT and provide the best possible deterministic potential population growth rates for elasmobranchs, as we did. This would have allowed Frisk *et al.* (2001) to include the appropriate reproductive cycle, rather than assuming a 1 year cycle for all elasmobranchs (Cortés 2002; Mollet *et al.* 2000).

We also suggest that using estimates for survival rates is better than omitting them all together. The definition of generation time is given by $T = \ln(R_0)/r$ (where R_0 = net reproductive rate per generation) and, therefore, $r = \ln(R_0)/T$ (Caswell 2001). Comparison with the equation given for surrogate r' implies that somehow R_0 becomes $m = f/2 =$ female fertility, and it can be shown that this is equivalent to the unreasonable claim that the life expectancy at age at maturity (α) is determined by juvenile survival alone and that adult survival is immaterial.

We agree that alternative models are desirable (Hilborn and Mangel 1997). However, Miller *et al.* (2003) claim that

in data-poor species stage-based models can provide insights into elasmobranch population dynamics. We disagree. Stage-based models with few stages have short-term or transient dynamics that are totally different from age-structured models and the corresponding recovery time estimates are generally not very useful. A better way to cope with data-poor species that have unvalidated age and growth studies is to incorporate uncertainty, as was done by Caswell *et al.* (1998) or Cortés (2002), as suggested by Mollet and Cailliet (2002). In addition, stage-based models with few stages that use fixed-stage duration to calculate the fractions graduating to the next stage require great care when calculating the elasticity pattern of the lower level vital rates of interest (e.g. survival) (Caswell, 2001).

We suggest that some of the difficulties encountered when calculating elasticities of lower level vital parameters arise because Caswell (2001) appears to have conflicting procedures for this. Caswell (2001) used his equation 9.103 on page 203 (elasticity of λ to σ_i is the sum of the elasticities to P_i and G_i) for the desert tortoise example of Doak *et al.* (1994) in which a fixed-stage duration was used to calculate the fractions graduating. However, Caswell (2001) also derived equations for calculating lower-level elasticities of survival (σ_i) for fixed-stage duration models, first for the $\lambda = 1$ approximation (Equation 18.11) and then for iteration of λ (Equation 18.16). These equations were then applied to the loggerhead sea turtle (Crouse *et al.* 1987; Crowder *et al.* 1994). The eight-stage model of Doak *et al.* (1994) used fixed-stage duration and we surmise that Equation 9.103 should not have been used. The elasticity pattern shown in Caswell (2001: fig. 9.3), based on Equation 9.103, is reasonably close to the elasticity pattern obtained from a Leslie matrix because Doak *et al.* (1994) used five juvenile stages of short duration (1, ~3, ~3, ~3, ~3). Had they combined the four juvenile stages with stage duration of ~3 years into one stage of duration 12 years, the resulting elasticity pattern calculated according to Equation 9.103 would have been much different from that based on a Leslie matrix or LHT [e.g. $E(\sigma_2)$ from 5×5 stage-based matrix = $E(P_2) + E(G_2) = 0.20 + 0.06 = 0.26$, compared with $E(\sigma_2) = (14-2) \times 0.0415 = 0.50$ from a 60×60 Leslie matrix ($\alpha = 14$). The latter value agreed with $E(\sigma_2)$ from the 5×5 matrix, when calculated empirically with or without iteration of λ (Crowder *et al.* 1994). In addition, our empirical calculation of the elasticities shown in figs 18.1 and 18.2 in Caswell (2001), based on $E(x) = (\lambda_{x+0.01x} - \lambda_{x-0.01x})/0.02 \lambda_x$ (Crowder *et al.* 1994), indicated that the elasticities without and with iteration, respectively, are the same after normalisation (sum = 1.0). For example, from fig. 18.1 $E(\sigma_1) = \sim 0.055/\sim 1.504 = 0.036$ (as in fig. 18.2) and the same applies to $E(\sigma_2)$, $E(\sigma_3)$, $E(\sigma_4)$, and $E(\sigma_5) + E(\sigma_6) + E(\sigma_7)$.

Mollet and Cailliet (2002) did not fully understand why a three-stage model was so successfully used for the killer whale *Orcinus orca*, based on a geometric distribution

(Caswell 2001). The use of a geometric distribution to calculate the fraction graduating to the next stage implies that the age-structure within a stage is constant, corresponding to a survival of 1.0, which is a reasonable first approximation for a species with high juvenile and adult survival (note that the projection matrix A is based on the actual survival rates). However, elasmobranchs have much lower survival rates than *O. orca* and we cannot use a geometric distribution in this situation (Mollet and Cailliet 2002). Therefore, we feel that our reservations about stage-based models for elasmobranchs are fully justified. We now also suggest that the elasticity pattern in Brault and Caswell (1993) is different from that calculated with the corresponding Leslie matrix, which we presume to be better. Using the elasticities of lower level parameters displayed in table 1 of Brault and Caswell (1993), we calculated $\sigma_2/\sigma_3 = 0.3785/0.5585 = 0.68$ (i.e. adult survival has the largest effect on λ by far). In contrast, our Leslie matrix produced $\sigma_2/\sigma_3 = 0.5353/0.4236 = 1.26$ (i.e. juvenile survival has the largest effect on λ (Appendix 1c(iv)).

Stage-based models are difficult to set up correctly because one has to understand post-breeding versus pre-breeding census, birth-pulse versus birth-flow, the calculation of discounted fertilities (F_i 's), and the calculation of the fractions graduating from one stage to the next. In addition, iteration of λ is required to solve the projection matrix because the matrix elements are functions of λ if the fixed stage duration is used to calculate the fractions graduating, which is the most suitable stage-duration distribution for elasmobranchs. Therefore, elasticities of the lower level vital rates of interest, as they appear in a Leslie matrix or in a LHT, are not easily calculated and require empirical calculations or a good knowledge of differentiation (Caswell 2001).

We now feel even more strongly that Mollet and Cailliet's (2002) reservations about stage-based models with few stages are fully justified. Elasmobranchs have a relatively simple life cycle, rather than a complex one, and we suggest that there is no need to consider stage-based models with few stages. Although Heppell *et al.* (2000) combined only the adult age classes of mammals into one stage with promising results, we feel that it is still better to use the full Leslie matrix or a LHT because even their model yields a distorted elasticity pattern. The mean age of reproducing females at the stable age distribution (\bar{A}) of their model is always a little higher than that of the corresponding Leslie matrix or LHT (Appendix 1e(i),(ii)). Because $E(\text{fertility}) = 1/\bar{A}$, $E(\text{fertility})$ is underestimated, and this leads to an underestimate of $E(\text{juvenile survival})$ with a corresponding overestimate of $E(\text{adult survival})$. In a few cases the distortion of the elasticity pattern is considerable because \bar{A} (stage-based model) is unreasonably large (Appendix 1e(iii)).

There are also difficulties in the interpretation of the elasticity pattern for both stage-based and Leslie matrix or

LHT models when the projection interval is different from the reproductive cycle. Assume that a 1-year projection interval is used for a species with a 5-year reproductive cycle and that the calculation produced $\bar{A} = 25$ years and therefore $E(\text{fertility}) = 1/26 = 3.85\%$. The use of a 5-year projection interval suggests that \bar{A} will be $\sim 25/5 = 5$ (5-year units) in a first approximation and therefore $E(\text{fertility}) = 1/(\sim 5 + 1) = \sim 16.7\%$, which is approximately five times larger. This illustrates that the use of different projection intervals can produce large changes in the elasticity pattern, in particular for $E(\text{fertility})$ and the corresponding ratios (see Appendix 1f for a more detailed example).

Indeed, the reproductive cycles of the killer whale (Olesiuk *et al.* 1990) and the Australian population of the green turtle *Chelonia mydas* (Chaloupka 2002) both are approximately 5 years and a 5-year projection interval might be best to calculate population growth and elasticity pattern. Many elasmobranchs have a reproductive cycle of 2 years (Cortés 2002) and a few have a reproductive cycle of 3 years (Mollet *et al.* 2000; Cortés 2002), for which projection intervals of 2 and 3 years, respectively, should be used rather than the standard 1 year. This suggests that elasticity patterns and resulting management proposals have to be interpreted cautiously when the reproductive cycle does not agree with the projection interval used.

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Appendix 1. Calculation procedure for estimating the mean age of reproductive females and elasticity patterns in a population with a stable age distribution with applications

(a) Proof that $\bar{A} \langle w, v \rangle = 1/E(\text{fertility}) = 1/E_1$

Proof that $\langle w, v \rangle = \bar{A}$ for a 4×4 Leslie matrix with terms $F_2, F_3, F_4, P_1, P_2, P_3$:

Age-structure: $w_1 = 1, w_2 = P_1 \lambda^{-1}, w_3 = P_1 P_2 \lambda^{-2}, w_4 = P_1 P_2 P_3 \lambda^{-3}$;
 Reproductive values: $v_1 = 1, v_2 = F_2 \lambda^{-1} + P_2 F_3 \lambda^{-2} + P_2 P_3 F_4 \lambda^{-3}, v_3 = F_3 \lambda^{-1} + P_3 F_4 \lambda^{-2}, v_4 = F_4 \lambda^{-1}$;

$\langle w, v \rangle = \text{scalar product} = 1 + P_1 F_2 \lambda^{-2} + 5 \text{ more terms};$

Replace 1 with characteristic equation, which is:

$1 = P_1 F_2 \lambda^{-2} + P_1 P_2 F_3 \lambda^{-3} + P_1 P_2 P_3 F_4 \lambda^{-4}$;

Collect terms and compare with equation for \bar{A} , which is:

$\bar{A} = 2 \lambda^{-2} P_1 F_2 + 3 \lambda^{-3} P_1 P_2 F_3 + 4 \lambda^{-4} P_1 P_2 P_3 F_4$;

It shows that $\langle w, v \rangle = \bar{A}$. This can be generalised for any Leslie matrix and it applies to stage-based models as long as the first stage is an age class (observation based on empirical checks of a large number of stage-based matrices).

For the second part, that is, $\langle w, v \rangle = 1/E(\text{fertility})$, see Caswell (2001, p. 232, Equation 9.96). It is correct that this equation was derived for the stage-based matrix model of Heppell *et al.* (2000); however, empirical calculations ($n > 200$) showed that it applies also to a Leslie matrix.

(b) Calculation of normalised elasticities

The following equations can be used to calculate the normalised elasticities of interest from the Leslie matrix (i.e. summed fertility elasticities, summed juvenile survival elasticities including survival to age one, summed adult survival elasticities and all three elasticities divided by the sum of the elasticities). Note that the elasticities in Mollet and Cailliet (2002) were not normalised and their sum was $1 + E_1$ and that $GP = \text{gestation period}$:

$$(1) E_1 = E(\text{fertility}) = 1/(\bar{A} + 1);$$

$$(2) E_2 = E(\text{juveniles survival}) = (\alpha - GP)/(\bar{A} + 1);$$

$$(3) E_3 = E(\text{adult survival}) = (\bar{A} - \alpha + GP)/(\bar{A} + 1);$$

$$(4) E_2/E_1 = \alpha - GP;$$

$$(5) E_3/E_1 = \bar{A} - \alpha + GP;$$

$$(6) E_2/E_3 = (\alpha - GP)/(\bar{A} - \alpha + GP)$$

The (\bar{A}/α) -ratio is promising for quick evaluation of the elasticity pattern. If we assume that $GP = 0$, then $\bar{A}/\alpha = 2$ produces $E_2/E_3 = 1$. For species with $\bar{A}/\alpha < 2$ (corresponding to relatively low adult survival and high fertility) $E(\text{juvenile survival})$ is larger than $E(\text{adult survival})$; for species with $\bar{A}/\alpha > 2$ (corresponding to relatively high adult survival and low fertility) the reverse holds.

(c) Applications

(i) Relationship between adult survival and generation time (Heppell *et al.* 2000: fig. 3)

Heppell *et al.* (2000) reported a hump-shaped correlation between adult survival and generation time (μ_1) in their fig. 3. We suggest that the hump it is an artifact of excluding survival to age one in their elasticity calculations, which leads to an overestimate of adult survival, in particular for the $\alpha = 1$ and 2 species. If survival to age one is included and if adult survival is graphed against \bar{A} instead of μ_1 , then the relationship is as expected and follows our Equation 3 in Appendix 1b with $GP = 0$: $E(\text{adult survival}) = (\bar{A} - \alpha)/(\bar{A} + 1)$ with α used as parameter between 1 and 14 years. It is an indication of how powerful our theoretical calculation of normalised elasticities in terms of α, \bar{A} , and GP are.

(ii) Calculation of normalised elasticities from 50×50 Leslie matrix for *Dipturus laevis*

From 50×50 elasticity matrix after normalisation or using Appendix 1b with $\alpha = 12$ years and $\bar{A} = 15.018$ years ($\bar{A}/\alpha = 1.25$):

$$E(\text{fertility}) = E_1 = 0.06243;$$

$$E(\text{egg case survival}) = 0.06243 (=E_1);$$

$$E(\text{juvenile survival}) = E_2 = 11 \times 0.06243 = 0.6867;$$

$$E(\text{adult survival}) = E_3 = 0.1884; \text{ and}$$

$$E_2/E_3 = 3.64.$$

If we assume that maturing juveniles have adult survival, as was done by Frisk *et al.* (2002), then $E_2/E_3 = (0.6867 - 0.06243)/(0.1884 + 0.06243) = 2.49$.

(iii) Calculation of $\bar{A} = \langle w, v \rangle$ for *Dipturus laevis* from data in Table 2 of Frisk *et al.* (2002)

Note that we have to use w with $w_1 = 1.0$:

$$\bar{A} = w_1v_1 + w_2v_2 + w_3v_3 = (0.50/0.50) 1.0 + (0.47/0.50) 4.08 + (0.03/0.50) 71.01 = 9.1 \text{ years, which ought to be compared with } \alpha = 12 \text{ years, i.e. the mean age of reproducing females is smaller than the mean age at first reproduction.}$$

(iv) Calculation of σ^2/σ^3 for *Orcinus orca* from 36×36 Leslie matrix or LHT

$$\alpha = 15 \text{ years, } \bar{A} = 24.29 \text{ years } (\bar{A}/\alpha = 1.62) \text{ and we use } GP = 1 \text{ year because maturing juveniles are pregnant adults. From our Appendix 1b:}$$

$$E(\text{fertility}) = E_1 = 0.03954 (=E(\text{calf survival}));$$

$$E(\text{juvenile survival}) = E_2 = 14 \times 0.03954 = 0.5536;$$

$$\sigma_2 = E_2 - E_1 = 0.5140;$$

(subtracting the elasticity of calf survival from the elasticity of juvenile survival to be able to compare with σ_2 given by Braut and Caswell (1993))

$$E(\text{adult survival}) = E_3 = \sigma_3 = 0.4069; \text{ and}$$

$$\sigma_2/\sigma_3 = 0.5140/0.4069 = 1.26.$$

(d) Estimation of recovery time after a catastrophic event for *Dipturus laevis* based on three-stage model by Frisk *et al.* (2001) following Caswell (2001)

The damping ratio $\rho = \lambda_1/|\lambda_2|$ is 3.90, versus 1.05 for the Leslie matrix. The time required for the contribution of λ_1 to become 10 times as great as that of λ_2 is given by $t_{10} = \ln(10)/\ln(\rho) = 1.7$, versus 47 years for the Leslie matrix. Because $|\lambda_2| = |\lambda_3|$ (complex conjugate solutions), we expect a better t_{10} estimate to be $\sim 2 \times 1.7$ years = 3.4 years, which was confirmed by a projection matrix analysis.

(e) Calculation of ratio \bar{A} (stage-based model; Heppell *et al.* 2000) / \bar{A} (Leslie matrix)

(i) Proof that \bar{A} (stage-based model; Heppell *et al.* 2000) is greater than \bar{A} (Leslie matrix)

$$\bar{A} \text{ (stage)} = \sum w_i v_i \quad (i = 1 \text{ to } \alpha)$$

$$= w_1 v_1 + w_2 v_2 + w_3 v_3 + \dots + w_\alpha v_\alpha$$

$$= \alpha - 1 + w_\alpha v_\alpha$$

$$\bar{A} \text{ (Leslie matrix)} = \sum w_i v_i \quad (i = 1 \text{ to } w)$$

$$= w_1 v_1 + w_2 v_2 + w_3 v_3 + \dots + w_\alpha v_\alpha + \dots + w_w v_w$$

$$= \alpha - 1 + w_\alpha v_\alpha + \dots + w_w v_w$$

$$= \alpha - 1 + \sum w_i v_i \quad (i = \alpha \text{ to } w)$$

We have (using S for stage and L for Leslie):

$$(A) w_\alpha(S) = \sum w_i(L) \quad (i = \alpha \text{ to } w),$$

proportional number in adult stage of Heppell-matrix equals the sum of the proportional numbers in all adult age classes of the Leslie-matrix; and

$$(B) v_\alpha(S) = v_\alpha(L) > v_{\alpha+1}(L) > \dots > v_w(L),$$

the reproductive value of the adult stage in the Heppell-model equals the reproductive value of the first adult age-class in the Leslie matrix and is larger than all subsequent reproductive values of adult age-classes.

Therefore $w_\alpha v_\alpha(S) > w_\alpha v_\alpha(L) + \dots + w_w v_w(L) = \sum w_i v_i(L) \quad (i = \alpha \text{ to } w)$,

$$\text{and } \bar{A}(S) = \alpha - 1 + w_\alpha v_\alpha(S) > \bar{A}(L) = \alpha - 1 + \sum w_i v_i \quad (i = \alpha \text{ to } w).$$

(ii) Empirical calculation of the mean ratio (stage-based model; Heppell *et al.* 2000) / (Leslie matrix)

We calculated \bar{A} (stage-based model; Heppell *et al.* 2000) and \bar{A} (Leslie matrix) for all 50 mammals given in Appendix A of Heppell *et al.* (2000), ESA's Electronic Data Archive: Ecological Archives E081-006. The mean ratio \bar{A} (with adult stage) / \bar{A} (Leslie matrix) was 1.10, CV = 8.3%, range 1.002 (Lynx) – 1.36 (Dall's sheep), $n = 50$.

(iii) Example when \bar{A} (stage-based model) is unreasonably large

For chimpanzees (*Pan troglodytes*) \bar{A} (stage-based model) was 37.2 years (\bar{A} (stage)/ $\alpha = 2.66$), which ought to be compared with the maximum possible $\bar{A} = (\alpha + w)/2 = (14 + 50)/2 = 32$ years (as $\lambda = 0.97 > \sigma$ (adult) = 0.95). The Leslie matrix or LHT produced a more reasonable $\bar{A} = 29.1$ years (\bar{A} (LHT)/ $\alpha = 2.08$, \bar{A} (stage)/ \bar{A} (LHT) = 1.20). This produces a distortion of the elasticity pattern because \bar{A} (stage) is unreasonably large. The stage-based model has $E(\text{fertility}) = 1/38.2 = 2.62\%$ and $E(\text{juvenile survival})/E(\text{adult survival}) = 0.61$, whereas the LHT yields $E(\text{fertility}) = 1/30.1 = 3.32\%$ and $E(\text{juvenile survival})/E(\text{adult survival}) = 0.93$.

(f) Effect of the projection interval on the elasticity pattern of the green turtle (*Chelonia mydas*)

The usual calculations of population growth and elasticity pattern for marine turtles use a projection interval (PI) of 1 year in combination with an effective annual fertility. Using the vital rates (including $\alpha = 35$ years and $w = 59$ years) from Chaloupka (2002) in a 59×59 Leslie matrix with $PI = 1$ yielded $\bar{A} = 46.06$ years ($\bar{A}/\alpha = 1.32$; $R_0 = 0.6966$, $\lambda = 0.9922$). Our Appendix 1b produced the following elasticity pattern (using $GP = 0$, which is a reasonable approximation for sea turtles):

$$E(\text{fertility}) = E_1 = 2.125\%, E(\text{juvenile survival}) = E_2 = 74.35\%,$$

$$E(\text{adult survival}) = E_3 = 23.50\%, E_2/E_1 = 35.0, E_3/E_1 = 11.6,$$

$$E_2/E_3 = 3.16.$$

This green turtle population has a remigration interval (= reproductive cycle) of ~ 5 years (Chaloupka 2002) and we suggest $PI = 5$ years is more appropriate to calculate population growth and elasticity pattern. We now have $\alpha = 7$ (5-year units) and in a first approximation $\bar{A} = 46.06/5 = 9.21$ (5-year units). Appendix 1b now yields:

$$E_1 = 9.79\%, E_2 = 68.54\%, E_3 = 21.66\%, E_2/E_1 = 7.0, E_3/E_1 = 2.21,$$

$$E_2/E_3 = 3.16.$$

E_1 and related ratios change by approximately a factor of five, whereas E_2/E_3 remains constant. In this example, where $\alpha = 35$ years is a multiple of five and $w = 59$ years is close to a multiple of five, we can easily calculate the new \bar{A} from a 11×11 Leslie matrix instead of using an approximation. As expected (Mollet and Cailliet 2002), the calculated \bar{A} of 8.81 (5-year units) = 44.05 years ($\bar{A}/\alpha = 1.26$) is a little smaller because λ increases slightly ($R_0 = 0.7626$, $\lambda = 0.9711^{(1/5)} = 0.9941$). Appendix 1b yields:

$$E_1 = 10.19\%, E_2 = 71.33\%, E_3 = 18.48\%, E_2/E_1 = 7.0, E_3/E_1 = 1.81,$$

$$E_2/E_3 = 3.86.$$

E_1 and related ratios change by a factor of five (approximately), whereas E_2/E_3 remains reasonably constant. It is also straight forward to calculate elasticity patterns with juveniles divided into pelagic juveniles, benthic juveniles, and sub-adults, and adults divided into maturing adults and adults (the age-classes used by Chaloupka (2002)). All three deterministic calculations presented here indicate that juvenile survival has by far the largest effect on population growth, whereas the stochastic simulation model by Chaloupka (2002) indicated that fertility and adult survival had the largest effect, which we find difficult to understand.