

real relationship. The presence of environmental effects could lead to a false-positive association between reproduction and longevity. On the other hand, management decisions, such as exporting or euthanizing animals that have already bred successfully, along with under-recording of births to animals born a long time ago could lead to a false-negative relationship.

We also suggest that the threshold analysis is a weak test of life-history trade-offs. As the age cut-off is set somewhat arbitrarily (e.g. when 50% of offspring recorded in the data set are born), it is unlikely to reflect individual variation in early reproductive investment. A stronger test would be to analyse annual survival as a function of reproduction over a previous time step, as it is typically done in analyses of individuals in wild populations. This would also allow tests of the recent and cumulative cost of reproduction. These analyses can be done using mixed effect models where zoo identity, year of sampling and repeated observations can be taken in account. This should also reduce problems associated with estimating longevity in long-lived zoo animals (Wiese & Willis 2004). However, although zoo life-history records remain under-used and could shed light on very important aspects of animal life-histories – especially for endangered species – we remain unconvinced that zoo data are ideal to investigate life-history trade-offs.

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#### REJOINER TO RICKLEFS & CADENA (2007): RESPONSE TO MACE & PELLETIER

Mace and Pelletier raise important concerns about the quality and size of the ISIS database, and its suitability for answering questions concerning life history trade-offs. While we agree that the ISIS data have limitations, they also provide unique opportunities for analysis. Mace and Pelletier comment on (1a) the accuracy and completeness of zoo records, (1b) sample size issues and risk of type II error, (2) management of reproduction by zoo personnel, (3) zoo effects, and (4) design of the analysis. We address these issues here.

1a. In our original analysis, we cleaned the ISIS data for each species by removing individuals with missing or ambiguous information. We agree that these data ideally should be checked against original zoo records. However,

while this can be performed in preparing studbooks for individual species, especially endangered species represented by few individuals in captivity, it was clearly beyond the scope of our study. The important issue is not that some records are incomplete or otherwise unsuitable for analysis, but that complete records are available and lack bias. Mace and Pelletier correctly point out that long life spans cannot be recorded for individuals born recently. We neglected to point out in the original manuscript that we avoided this obvious source of bias by considering only individuals that could have attained the maximum life span recorded for a species within the period of data collection.

1b. Because we used a conservative approach in accepting data, sample sizes for individual species were small (maximum  $n = 82$ ). However, while our statistical analyses had limited power to reject the null hypothesis of no association between reproduction and life span, several tests

can be applied to the combined data set. We mentioned, for example, that 22 of 49 regression coefficients for the mammal data were negative, which has a binomial probability of 0.28 based on a random probability ( $P = 0.5$ ) of obtaining a negative slope. Among the slopes for the 50% cutoff samples in our Table 1, seven of 18 were negative, which also does not differ from random. The average slope for the 18 regressions based on a total of 735 individuals was  $0.03 \pm 0.17$  SE. Accordingly, the actual mean of the aggregate slope could be negative, and as large as  $-0.30$  with a probability of 0.05. Cutting life span by 0.3 years for each additional offspring produced would represent a substantial trade-off, of course, but the odds, based on the data, favour the absence of a trade-off.

2. Mace and Pelletier point out that zoo management and breeding programmes override individual life-history decisions of captive animals, but this unintentional 'experimental' treatment is a positive aspect of the zoo data. As a result, reproduction in zoo animals is independent, to some degree, of aspects of individual quality that might also influence life span. Thus, one can examine the direct effects of reproductive events on life span 'controlling' for individual quality. Variations in the quality of individuals or of husbandry that might cause positive correlations between the two are reduced or eliminated by management of reproduction.

3. Variation among zoos in conditions affecting life span is a major concern in the ISIS database. As Mace and Pelletier point out, a large part of the variation in age at death is associated with zoo identity. Unlike their analysis of Sumatran tigers (*Panthera tigris sumatrae* Pocock), we did not include births to individuals that could not have attained the maximum species life span in the dataset, and so our data lack the decrease in longevity with birth year evident in Mace and Pelletier's figure. Relatively few of the data in ISIS for the species that we analyzed pertain to individuals born prior to 1960, and so most of the records are 'modern.' We have conducted new ANOVAs on age at death as a function of year of birth (covariate used to identify trends) and the zoo in which an individual died. Sample sizes were larger than in our analysis of reproduction and subsequent survival because we included both males and females and individuals that died before our 50% cutoff point. Of 17 species of mammal (records for the cotton-top tamarin *Saguinus oedipus* L. were not included), four exhibited significant year effects ( $P < 0.05$ ) accounting for 1–6% of the variance in life span. The zoo effect (8–156 institutions;

an average of  $5.4 \pm 1.5$  individuals of each species per zoo; all  $P < 0.0001$ ) accounted for 30–60% of the variance. When zoo identity was entered as a main effect in ANCOVAs relating life span to number of young produced up to the 50% cutoff point for each mammal species, only four of 17 slopes were negative; one slope differed significantly from 0, and it was positive (*Macropus rufus* Desmarest,  $0.49 \pm 0.22$ ,  $P = 0.034$ ). This analysis, with zoo identity included, reemphasizes our original observation that trade-off between reproduction and longevity is not evident in zoo populations.

4. Mace and Pelletier object to our use of an age cutoff, comparing prior reproduction with subsequent survival as a function of the previous annual history of reproduction. This would be a potentially useful approach for very large samples, however, it is limited by the reality that each individual dies only once and therefore contributes only a single useful datum. With samples of 15–82 individuals for the mammal species that we considered, birth year, age and zoo identity could not be factored into such analyses. Furthermore, our interest was in the influence of reproductive events on subsequent longevity. To ask whether reproduction up to a certain age influences survival beyond that age seems straightforward and useful. The ISIS data clearly are not suited for more sophisticated analyses because of sample size and issues of data quality. Nonetheless, we were able to demonstrate that the act of reproduction itself has little influence (or perhaps none) on female life span under zoo conditions.

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