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LIFE HISTORIES OF MAMMALS, REVIVED: A REPLY TO MESSIER

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Messier (1990) argues there are six possible biases in Zammuto's (1987) life table study. I agree that some of the problems he discusses are possible biases of Zammuto (1987) or, for that matter, any life table study (see Caughley 1966, 1977, Millar and Zammuto 1983, Harvey and Zammuto 1985). I disagree, however, with the "evidence" that Messier presents to show these biases exist in Zammuto (1987). In addition, Messier (1990) provides few data or statistical analyses to support his claims. Moreover, Zammuto's (1987) research has been replicated and his conclusions corroborated (Jia and Fox 1990), casting additional doubt on the validity of Messier's criticism.

Messier claims Bronson (1979), Murie et al. (1980), and Boag and Murie (1981) do not provide any indirect support that undisturbed populations of montane ground squirrels may be stationary enough to construct time-specific life tables. Zammuto used the mathematical and verbal definition of a stationary population (l_x and m_x constant, $R_0 = 1$, $r = 0$, no year effects) quoted from Pielou (1974:29) as: "a population of seasonal breeders . . . show[ing] annual fluctuations but . . . show[ing] no trend over a period of several years." Contrary to Messier, I find: (1) Bronson (1979:275; Table 2) clearly showed 0% of the variance in litter size (m_x) was explainable by year effects in ANCOVA, and states: "year of sampling had no effect on any criterion of litter size," in the montane golden-mantled ground squirrel over three years in several populations; (2) Murie et al. (1980:238) report homogenous means for litter size (m_x) among all years and state: "comparisons of [litter size] data within each area between years showed no significant differences, enabling us to combine the [annual] data from [7] different years," in three populations of the montane Columbian ground squirrel; and (3) Boag and Murie (1981:2231, 2236) present minor interyear variation in adult annual survival rates (l_x , 5 of 6 years 0.44–0.56, Table 8) and adult density (5 of 7 years 11.6–12.5 individuals/ha; Table 1) and state: "this . . . relatively small variation . . . in numbers suggest[s] that the density of these ro-

dents may be prevented from fluctuating . . ." again for Columbian ground squirrels. Ironically, Messier writes: "none of these authors suggested that montane ground squirrel populations are characterized by . . . [stable] survival and fecundity rates . . . ; Bronson (1979) did not report on the interyear variability of . . . fecundity rates . . . ; Murie et al. (1980) offered no specific information on the interyear variability of fecundity rates . . . ; (these) ground squirrel populations regularly go through phases of rapid declines and subsequent recoveries, and therefore rarely approach a stationary (state) . . ." In addition, Messier erroneously transposes yearling data from Dobson and Kjelgaard's (1985) tables, mis-cites r values from that study and Boag and Murie's (1981), and exaggerates the importance of the variance of survival rates from four 8–9 yr olds in Sherman and Morton's (1984: Table 2) age-structure of 1246 females (see Conley 1984:117; Zammuto and Sherman 1986:603). The evidence of population stability at (1)–(3) above, and similar litter size and survival patterns from Dobson et al. (1986) and Sherman and Morton (1984), were collected over a total of 30 yr from 15 populations in three montane species. It therefore seems that undisturbed montane ground squirrel populations may be stationary enough to calculate time-specific life tables and that Messier's claims are either unsupported or contradicted.

Messier further criticizes Zammuto (1987) for citing Zammuto and Sherman (1986) as providing additional indirect support for probable stability in fecundity and survival among montane Belding's ground squirrels. Zammuto and Sherman (1986) asked the question: was the Tioga Pass population stationary enough each year to calculate time-specific life tables that were comparable with the known cohort-specific life table of 11 years? The analyses of Zammuto and Sherman indicated fecundity (m_x) and survival (l_x) might be stationary enough to construct life tables because no statistically significant differences were found among 14 time-specific age structures and the cohort age structures for each sex, and no differences in age-specific litter size (m_x) were found among 6 years. Messier argues that is not "proof" of stability. It is obvious to me this is not proof of stability, especially since only the null hypothesis of no differences was supported, but these results are indirectly supportive of the stationary assumption. I agree that Zammuto and Sherman's (1986) sample size for litters of 4–5 yr olds could be too small to detect differences; however, data from younger age classes are most likely numerous enough ($n = 95$; see Conley 1984). There should be more studies to cite like Zammuto and Sherman (1986) for information on the stationary population assumption, but there are not.

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Messier claims "again, small sample sizes should have warned the author . . . total sample size was (only) 506 . . ." to detect differences between age structures of the sexes. Table 7 of Zammuto (1987:1356) uses exactly the same (standing age structure) data Messier claims are too few, and significant ($P < .05$) differences existed between age structures for $> 50\%$ of the 15 comparisons between populations. Four of these analyses were $P < .001$, with a total sample size of only 198 animals. In addition, the age structure for population 6 differed from three other age structures with a sample size of only 29 animals, a sample size smaller than all but one of the seven comparisons between the sexes. These results show that, contrary to Messier, sample sizes of Zammuto (1987) were large enough to detect differences between the sexes' age structures if they existed.

Messier contends the smoothing method used by Zammuto (1987) to calculate life tables was an "unusual manipulation" and cites Caughley (1966:912) as the correct method. However, Caughley (1966, 1977) is followed exactly in Zammuto (1987). The change in l_0 values Messier criticizes is automatically caused by the smoothing procedure and is the same adjustment made to all age classes so that all age classes fit one polynomial equation. Simple mathematics ($\Sigma l_x m_x$) demonstrate that R_0 would artificially deviate from 1 without this "adjustment."

Messier argues "one thing cannot be done . . ." the sexes cannot be combined for a life table using only female m_x . To the contrary, the results in Table 7 and the statistics depicting insignificant differences between the sexes' age structures allowed Zammuto (1987) to combine the sexes to increase sample size (Caughley 1977). That this method causes "all other parameters . . . [to be] erroneously derived" is easily contradicted by simple multiplication. No life table parameter is changed when males are treated as though they were females to increase sample size when m_x is one-half the litter size and the age/sex structure of males equals that of females (see Charlesworth 1980:11).

Messier claims substantial "biases," "many irregularities," and nonpositive correlations "due to rounding effects" in Zammuto's (1987) q_x values. Contrary to Messier's claim, Zammuto (1987:1354) reported that q_x increased with age at $P < .001$ among populations and within 5 of his 6 populations at $P \leq .06$. The rounding biases in q_x Messier claims exist are therefore not systematic and are statistically contradicted in Zammuto (1987).

Messier insists Zammuto's (1987) use of Pianka's (1978) method to calculate e_x instead of Krebs' (1985) method is biased. He insists Pianka (1978) and Zammuto (1987) overestimate e_x by 0.5 yr so "all" Zam-

muto's (1987) "regression analyses . . . give spurious results." First, Zammuto (1987) calculates only *correlations* not *regressions*. Second, subtracting or adding 0.5 (or any constant) to values of any variable and recalculating a correlation coefficient always provides the same coefficient (Zar 1984). Therefore, contrary to Messier, calculating correlations between life table parameters and e_x using Krebs (1985) or Pianka (1978) would change *nothing*, and all correlations Zammuto (1987) reports between e_x and other parameters are exactly the same using Krebs' or Pianka's method.

Messier continuously attacks Zammuto (1987) for improper "verification of critical assumptions" for stationary populations. However, no researcher presenting time-specific life tables of mammals in the scientific literature ever verified these "critical assumptions" and Zammuto and Sherman (1986) treated them with the most detail to date. In addition, Messier seems unaware that Charlesworth (1980) and Michod and Anderson (1980) found that some of these assumptions (i.e., $r = 0$) may be unnecessary to construct life tables. For example, Zammuto and Sherman (1986) found no differences among annual, time-specific life tables for Belding's ground squirrels even though Sherman and Morton (1984) calculated an r of 0.13 for the 11-yr cohort life table. Thus, it is likely that an r as high as 0.13 is statistically equal to 0 in practice.

Most of the theoretical predictions examined by Zammuto (1987) were statistically supported from his data and from data of a subsequent study (Jia and Fox 1990). These results suggest either that time-specific life tables have more to offer than Messier believes or the predictions supported by them may be wrong since (allegedly) faulty life tables supported the predictions. In conclusion, the six objections Messier claims "might affect the validity of conclusions" by Zammuto (1987) have little basis.

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