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TIME-SPECIFIC AND COHORT LIFE TABLES FOR BELDING'S GROUND SQUIRRELS

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Zammuto and Sherman (1986) and Menkens and Boyce (1993) analyzed different data sets. The former considered 1–5 yr old female and 1–3 yr old male *Spermophilus beldingi,* whereas the latter considered 0–2 yr olds of both sexes. The reasons for these discrepancies are illuminating.

Menkens and Boyce (1993) inferred that Zammuto and Sherman excluded the 0-yr age class from their analyses because they "lacked confidence that the estimated litter size, based upon counts following initial emergence from the natal burrow, was unbiased." More pups were undoubtedly born than survived to weaning (≈3 wk) every year. But there is an additional reason why Zammuto and Sherman (1986) omitted 0-yr-old animals: the original capture data (from Sherman and Morton 1984) did not accurately quantify the total number of juveniles in each year's birth pulse. This was because Sherman, Morton, and their field assistants were unable to capture every litter and pup that appeared aboveground yearly on the large, heterogeneous Tioga Pass Meadow (≈5×10^5 m^2), especially since the available person-power and the intensity with which pups were sampled differed among years. In addition, some of the weaned juveniles that were captured each year undoubtedly immigrated from outside the study area (especially males; see Holekamp 1984), and so should not figure into the population's birth statistics.

These problems create a dilemma for comparative life table analyses. One could either *estimate* the size of each year's 0-yr age class from the available data, or *omit* the 0-yr age class from consideration. The first approach increases statistical power but potentially at the expense of accuracy, and the second approach does the reverse. Menkens and Boyce (1993) opted for the former, Zammuto and Sherman (1986) the latter.

To estimate the number of neonates in each year's birth pulse Menkens and Boyce used a reasonable procedure, but the validity of three of their four assumptions is questionable. First, they assumed an "equal sex ratio among age-0 individuals"—but sex ratios of emerging pups were not equal in any year of the study and, in fact, differed significantly from 50:50 in 3 of the 6 yr under consideration (P. W. Sherman, *unpublished data*). Second, Menkens and Boyce assumed that the proportion of females breeding in each age class was the same every year, and that this proportion was adequately quantified by "summary values presented by Sherman and Morton (1984)." The summary values for different age classes are averages, however, and the proportion of females that bred varied among years (see Morton and Sherman 1978), especially for 1-yr-olds, the age class comprising the preponderance of females. Third, Menkens and Boyce assumed that the

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number of young born equalled the number of pups captured at first emergence (weaning), despite their cautionary arguments and the caveat quoted above.

The data set analyzed by Menkens and Boyce (1993) also differed from Zammuto and Sherman's (1986) in that fewer adult age classes were considered. Zammuto and Sherman used all Sherman and Morton's (1984) original data on reproductive age animals; they excluded only the few females ($n = 5$) that were >5 yr old and males ($n = 8$) >3 yr old. Menkens and Boyce (1993:Table 1) also subsampled the original data, but they omitted all males ($n = 26$) and females ($n = 55$) >2 yr old. Why they omitted multiple adult age classes and how this procedure affected their results are unknown.

The strength of Menkens and Boyce's conclusions depend on this, as well as on how closely their yearly estimates of natality correspond to reality. Since neither can be determined directly, it seems inappropriate to reject Zammuto and Sherman's assessment that time-specific and cohort life tables did not differ for the Tioga Pass population in 1974–1979. We continue to "hope that our reanalyses of the Tioga Pass *S. beldingi* data will stimulate direct comparisons between time- and cohort-specific life tables for other species" (Zammuto and Sherman 1986:604).

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