

A comparison of time-specific and cohort-specific life tables for Belding's ground squirrels, *Spermophilus beldingi*

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Eight years of age-specific survival data and 6 years of fecundity data from a free-living population of Belding's ground squirrels (*Spermophilus beldingi*) at Tioga Pass, California, were used to test the hypothesis that time-specific life tables, based on data from individual years, were different from the cohort-specific life table, based on the combined data from all years. The results indicated that neither the age structure of the male nor the female population significantly differed among years (all $P > 0.05$). Furthermore, the means and the variances in the sizes of weaned litters did not differ among years either in the population at large or within individual age-classes (all $P > 0.05$). A 27-day snowstorm that occurred in the spring of 1977 increased mortality and reduced reproduction, but it did not change the ground squirrels' age-specific survival or fecundity patterns. Taken together, our analyses revealed that each time-specific life table provided age-specific survival and fecundity estimates that were statistically indistinguishable ($P > 0.05$) from the composite, cohort-specific life table for each sex, regardless of severe environmental conditions. This is the first demonstration of the equivalence of time- and cohort-specific life tables for a free-living population of mammals.

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L'accumulation de données sur la survie en fonction de l'âge durant 8 ans et de données sur la fécondité durant 6 ans chez une population libre d'écureuils de terre *Spermophilus beldingi* de Tioga Pass en Californie a permis de mettre à l'épreuve l'hypothèse selon laquelle les tables de survie statiques basées sur les données spécifiques à chaque année diffèrent des tables de survie dynamiques telles qu'établies d'après les données combinées de toutes les années. Les résultats indiquent que la structure en fonction de l'âge des populations de mâles ou de femelles ne diffère pas significativement d'une année à l'autre ($P > 0,05$ dans tous les cas). La moyenne et la variance de la taille des portées sevrées ne diffèrent pas non plus d'une année à l'autre, qu'il s'agisse de toute la population ou des classes d'âge considérées individuellement ($P > 0,05$ dans tous les cas). Une tempête de neige d'une durée de 27 jours au printemps de 1977 a augmenté la mortalité et diminué la reproduction, mais n'a pas modifié les taux spécifiques de survie et de fécondité chez les écureuils. Nos analyses démontrent donc que chaque table de survie statique donne des estimations de la fécondité et de la survie en fonction de l'âge qui ne diffèrent pas significativement ($P > 0,05$) des estimations obtenues à partir de la table de survie dynamique globale pour chaque sexe, même dans des conditions particulièrement rigoureuses. C'est la première fois qu'est démontrée l'équivalence des tables de survie statiques et des tables de survie dynamiques chez une population libre de mammifères.

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Introduction

Life tables are valuable tools for investigating evolutionary patterns of reproduction and survival (life histories) in natural populations (Stearns 1976, 1977). Life tables are typically constructed in one of two ways: the time-specific (static, stationary, current, or vertical) method or the cohort-specific (generation, composite, or horizontal) method (see Krebs 1978, p. 155). Time-specific life tables are based on the age structure of a population at an instant in time, whereas cohort-specific life tables are constructed from survival records of entire cohorts. Theoretical arguments suggest that the former are not as accurate as the latter unless three underlying conditions are met for the population at issue: (1) the net reproductive rate, $R_0 = 1$, (2) the intrinsic rate of increase, $r = 0$, and (3) there are no significant differences in survival or reproduction among years or breeding periods (see Pielou 1974, p. 26; Caughley 1977, p. 85).

A recurrent question in field studies of mammalian life histories is how closely the three assumptions underlying the construction of time-specific life tables are approached (Pielou

1974, p. 29). The question arises because the data necessary for constructing cohort-specific life tables are rarely available for long-lived (> 3 years) species. Thus investigators must either assume that conditions 1-3 are met, or else continue their studies long enough to construct cohort-specific life tables. Given the widespread use of time-specific life tables (reviewed in Millar and Zammuto 1983), we decided to directly test their validity, and so to indirectly examine whether or not the assumptions underlying their interpretation were met. The opportunity to conduct such a test was provided by data gathered during a 10-year study of Belding's ground squirrels (*Spermophilus beldingi*) in the central Sierra Nevada of California (Sherman and Morton 1984). We used information on age-specific survival and fecundity from this population to construct both time-specific and cohort-specific life tables and to test for differences among them.

Methods

Recently, Sherman and Morton (1984) presented detailed analyses of dispersal, mortality, and reproduction in a population of Belding's

TABLE 1. Number of known-age *S. beldingi* at Tioga Pass, California, surviving to each age for each year, based on Sherman and Morton's (1984) study

| Age | 1972 | 1973 | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 |
|---------|------|------|------|------|------|------|------|------|
| Females | | | | | | | | |
| 1 | 8 | 16 | 15 | 25 | 33 | 23 | 21 | 16 |
| 2 | 9 | 2 | 8 | 4 | 10 | 20 | 10 | 9 |
| 3 | 8 | 4 | 2 | 8 | 1 | 5 | 8 | 4 |
| 4 | —* | 2 | 2 | 1 | 3 | 1 | 3 | 5 |
| 5 | — | — | 2 | 1 | 1 | 2 | 0 | 1 |
| 6 | — | — | — | 2 | 0 | 0 | 1 | 0 |
| 7 | — | — | — | — | 1 | 0 | 0 | 1 |
| 8 | — | — | — | — | — | 1 | 0 | 0 |
| Males | | | | | | | | |
| 1 | 14 | 14 | 18 | 24 | 23 | 15 | 16 | 8 |
| 2 | 6 | 6 | 4 | 13 | 11 | 12 | 6 | 6 |
| 3 | 1 | 2 | 0 | 3 | 6 | 5 | 2 | 2 |
| 4 | — | 0 | 0 | 0 | 1 | 4 | 1 | 1 |
| 5 | — | — | 0 | 0 | 0 | 1 | 0 | 0 |

*A dash indicates that the number of animals of that age was unknown because the cohort was born the year preceding the beginning of Sherman and Morton's (1984) study.

ground squirrels located on a subalpine meadow near Tioga Pass, California (119° W, 38° N, elevation 3040 m). Their demographic data comprised yearly recaptures (1969–1979) of animals first ear-tagged or toe-clipped as newly weaned juveniles or as 1-year-olds. Sherman and Morton's (1984) trapping regime was particularly thorough during the middle of the ground squirrels' active season each year, and by early August in 1974–1979, essentially all of the 150–200 yearling and adult ground squirrels inhabiting the study area had been handled previously that year. We obtained Sherman and Morton's (1984) mark–recapture data and reanalyzed them in the present paper. Only data from ground squirrels first captured as juveniles were used to ensure that the ages of animals included in our analyses were accurate.

Time-specific life tables were constructed for males and females that were ≥ 1 year old for every year, as though each year's age structure consisted of a distinct population. Although the marking program at Tioga Pass began in 1969, not until 1972 were enough 1- to 3-year-old ground squirrels alive to permit a quantitative investigation of the population's age structure. Further, because female *S. beldingi* live longer than males (12 years vs. 7 years maximum), more years of data were required to construct life tables for females than for males. Therefore, female life tables could be completed for only 6 years (1974–1979), whereas male life tables were constructed for 8 years (1972–1979). In our analyses, each living animal was considered as a different individual in each year, regardless of how many years it had been in the population. For example, a ground squirrel that lived 3 years was effectively considered as three different animals. Therefore, the exact age of 524 "animals" ≥ 1 year old was known over the 8 years (Table 1); this represented about 80% of all animals ≥ 1 year old in the population during these years (20% of the ground squirrels were "adults" at first capture and therefore of unknown age). Animals that permanently disappeared were presumed to be dead.

Conley (1984, p. 117) demonstrated that survival rates of the small number of animals belonging to advanced age-classes have little influence on the overall accuracy of most life tables. Therefore, females older than 5 years (2.0% of the 299 female "animals") and males older than 3 (3.6% of the 225 male "animals") were excluded from our analyses to provide a larger number of years with comparable life tables (i.e., the same number of age-classes for each sex in each year). The age structures of the male and female population were compared among years using Lee and Desu (1972) *D*-statistics, with and without the cohort-specific life table (Table 1 in Sherman and Morton 1984) treated as an additional year.

TABLE 2. Statistics derived from comparing *S. beldingi* time-specific life tables among years with and without the cohort-specific life table considered as a distinct population (year)

| | Without cohort-specific life table | With cohort-specific life table |
|---------------------|------------------------------------|---------------------------------|
| Males (1972–1979) | | |
| <i>D</i> | 8.90 | 9.57 |
| df | 7.00 | 8.00 |
| <i>P</i> | 0.26 | 0.30 |
| Females (1974–1979) | | |
| <i>D</i> | 7.31 | 8.41 |
| df | 5.00 | 6.00 |
| <i>P</i> | 0.20 | 0.21 |

Fecundity estimates, which Sherman and Morton (1984) based on the litter sizes of known-age females when pups emerged from the natal burrow, were available for 115 females over 6 years (1974–1979). The litter size distribution was tested for normality within each year and across each age using Kolmogorov–Smirnov one-sample tests (Hull and Nie 1981). The variances in litter sizes among years were tested for homogeneity with Bartlett's (1937) *F*-tests (see Zammuto 1984). Differences among mean litter sizes within and among age-classes were examined among years using one-way ANOVA (Nie et al. 1975).

Results

The age structure of the male and female population differed in 1974, the first year the sexes could be statistically compared ($D = 5.9$, $df = 1$, $P < 0.05$; also Sherman and Morton 1984). Therefore, males and females were treated separately for every year. The age structure of the Tioga Pass population did not differ among years for either sex, with or without the cohort-specific life table considered as a unique population (i.e., year; see Table 2).

Litter size distributions did not deviate from normality (all $P > 0.05$) within any year or across any age. Mean litter size ($F = 1.6$, $df = 114$, $P = 0.17$, ANOVA) and the variance of litter sizes ($F = 1.8$, $P = 0.12$, Bartlett's *F*) did not vary among years (Table 3). Further, age-specific litter sizes and their variances did not differ among years for females 1 to 5 years old (all $P > 0.20$, ANOVA).

Discussion

Our analyses indicate that time-specific and cohort-specific life tables were statistically indistinguishable for Tioga Pass *S. beldingi* during the study years. The equivalence of time- and cohort-specific life tables for *S. beldingi* at Tioga Pass implies that reliable demographic information might have been gathered in a 1-year study if Sherman and Morton's (1984) long-term investigation had not been feasible. The two types of life tables yielded equivalent results in all years analyzed, despite considerable interannual fluctuations in the length and severity of the winter and in resulting mortality rates. Theoretically, a researcher could have collected a random sample of ≥ 50 ground squirrels (the minimum number of males plus females we analyzed per year), determined their ages using some destructive but accurate technique (e.g., growth rings in periosteal bone; see Costain and Verts 1982), and then constructed a valid time-specific life table for each sex using standing age and fecundity estimates. "Smoothing" the age structure data

TABLE 3. Mean litter sizes (\pm SD) of known-age female *S. beldingi* at Tioga Pass for each year

| Age (years) | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | All populations pooled |
|-----------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|------------------------|
| 1 | 2.5 \pm 1.3 (4)* | 4.2 \pm 1.2 (9) | 2.8 \pm 2.0 (8) | 3.0 \pm 1.2 (10) | 3.5 \pm 3.5 (2) | 4.3 \pm 1.6 (6) | 3.4 \pm 1.7 (39) |
| 2 | 5.0 \pm 1.4 (2) | 6.3 \pm 0.6 (3) | 4.7 \pm 2.4 (10) | 4.1 \pm 2.7 (9) | 2.4 \pm 1.3 (5) | 4.4 \pm 1.5 (8) | 4.3 \pm 2.2 (37) |
| 3 | 6.0 \pm 0.0 (1) | 4.5 \pm 1.3 (4) | 6.0 \pm 0.0 (1) | 4.8 \pm 2.6 (4) | 4.0 \pm 2.3 (5) | 5.8 \pm 2.2 (4) | 4.8 \pm 2.0 (19) |
| 4 | 5.5 \pm 0.7 (2) | 5.0 \pm 0.0 (1) | 7.0 \pm 2.0 (3) | 8.0 \pm 0.0 (1) | 4.0 \pm 4.2 (2) | 6.2 \pm 1.9 (5) | 6.0 \pm 2.1 (14) |
| 5 | 3.0 \pm 0.0 (1) | 5.0 \pm 0.0 (1) | 5.0 \pm 0.0 (1) | 3.5 \pm 0.7 (2) | — | 5.0 \pm 0.0 (1) | 4.2 \pm 1.0 (6) |
| All ages pooled | 4.0 \pm 1.8 (10) | 4.7 \pm 1.3 (18) | 4.4 \pm 2.5 (23) | 3.9 \pm 2.2 (26) | 3.4 \pm 2.3 (14) | 5.0 \pm 1.8 (24) | 4.3 \pm 2.1 (115) |

*Sample size is in parentheses.

(Caughley 1977, p. 96) would produce even greater similarity between this time-specific life table and the real age structure of the population.

The equivalence of time- and cohort-specific life tables was maintained despite fluctuations in survival and fecundity at Tioga Pass. For example, in 1977 a 27-day-long snowstorm occurred at the start of the mating season in April (Morton and Sherman 1978). This severe storm deposited 2–20 cm of snow daily, covering burrow entrances and food sources. As a result, emergence from hibernation was delayed and mating activity was curtailed. Eventually about half the adult females either aborted their litters or suffered a reduction in litter size. Additionally, the storm increased adult mortality by at least 12% over previous years through starvation, freezing, predation, and cannibalism. Nonetheless, despite this serious perturbation, both the 1977 (prestorm) and 1978 (poststorm) time-specific life tables provided survival and fecundity estimates that were homogeneous ($P > 0.05$) with those from other years and homogeneous ($P > 0.05$) with the cohort-specific life tables.

Our results imply that assumptions 1–3 for constructing and interpreting time-specific life tables were probably met for the Tioga Pass population during 1972–1979. Whether or not these conditions apply to other populations is unknown. In the only similar study of which we are aware, Murphy and Whitten (1976) reported considerable interyear variability in survival, fecundity, and population size among the Mt. McKinley Dall sheep (*Ovis dalli*) that they and Murie (1944) studied. These variations led to an apparent lack of equivalence between time- and cohort-specific life tables. However, Murphy and Whitten (1976) pointed out that uncontrolled biases might have existed in their own and Murie's (1944) techniques for aging the sheep (see also Geist 1971, p. 61; Hoefs and König 1984) and for estimating population size. Therefore Murphy and Whitten's (1976) results may not constitute a robust rejection of the hypothesis that time- and cohort-specific life tables for *O. dalli* are equivalent.

We hope that our reanalysis of the Tioga Pass *S. beldingi* data will stimulate direct comparisons between time- and cohort-specific life tables for other species. Such analyses are desirable for three reasons. First, they would further test for the reliability

of time-specific life tables. Second, such comparisons would clarify the sampling protocols necessary to obtain accurate time-specific life tables. Heretofore, large numbers of animals or even entire populations were sacrificed to construct time-specific life tables (e.g., see Millar and Zammuto 1983 for references on mammals). Results presented in the present paper suggest that such drastic sampling regimes may be unnecessary. Finally, direct comparisons between time- and cohort-specific life tables would elucidate how interyear variations in survival and fecundity affect the overall age structures and fecundity schedules of natural populations.

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