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Empirical considerations on the stable age distribution

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Abstract. We used 24 years of live-trapping data to investigate four questions about the equivalence of time-specific and cohort life tables in the yellow-bellied marmot (*Marmota flaviventris*). We also reanalyzed parts of the data of Zammuto and Sherman (1986) that claimed equivalence of time-specific and cohort life tables for 8 years of data from Belding´s ground squirrel (*Spermophilus beldingi*). Pulse of births and deaths appeared to move through time for both species. For both marmots and ground squirrels, a k-sample Kruskal-Wallis test showed homogeneity of all time-specific life tables and a χ^2 test showed heterogeneity. Yearly pairwise comparisons from independent samples revealed no differences between years using Kruskal-Wallis and Kolmogorov Smirnov tests, 19% of the 174 χ^2 tests showed heterogeneity of samples. Comparing the 24 time-specific life tables to the cohort life table for marmots, pairwise Kruskal-Wallis and Kolmogorov Smirnov test showed no differences, but χ^2 tests revealed differences for seven of the years. Litter sizes in marmots were not equal among years but were equal among age classes. The yearly crude death rates, gross reproductive rates, and growth rates for marmots were normally distributed without skew or kurtosis, a possible indication of constancy of rates. Kruskal-Wallis and Kolmogorov Smirnov statistics do not seem to have sufficient power for this statistical application, and a χ^2 test must be used. In marmots, time-specific and cohort specific life tables are not equivalent.

Keywords: time-specific and cohort life tables, Marmota flaviventris, stable age distribution

Introduction

A stable age distribution, constant proportions of individuals in each age class through time, is a frequent assumption of theoretical and empirical research. Few natural populations are in a stable age distribution (Charnov 1993, p. 6; Krebs 1985, p. 198), but "moderate" deviations often do not change qualitative predictions (Stearns 1992, p. 25). Empirical investigations of age distributions in long lived species are few because data collection over many years is difficult.

Data for life table analysis of populations may be collected by following births, deaths, and survivorship of individuals over intervals of time (cohort, horizontal) sufficient for their life span, or by methods that only require data from a population survey conducted during a short time period (time-specific, vertical) (Caughley 1977, p. 90-93). Cohort life table methods make no assumption of a stable age distribution or a constant rate of increase (*r*). Time-specific life table methods assume a stable age distribution where *r* is known and constant or where *r* equals zero. Where the birth rate (*b*) and death rate (*d*) and therefore *r* ($r = b - d$) are constant, the population will eventually reach a stable age distribution and the population will be growing geometrically (Krebs 1985, p. 187; Carey 1993, p. 89). Where $b = d$ for some time the equilibrium is called the stationary age distribution (Carey 1993, p. 81; Pianka 1988, p. 137), and there is equivalence of cohort and time-specific age distributions (Caughley 1977, p.88). Constant birth and death rates underlie a stable age distribution, and without constant *b* and *d*, pulses of cohorts would change age classes through time such as that of the aging "baby boomers" in the United States population.

Except for the difficulty of data collection, cohort life tables would be preferred. Data for time-specific life tables are more easily collected, but the constancy of growth rate that is required is frequently unknown. Empirical data sets where both cohort and time-specific life tables can be calculated and compared are necessary to determine similarities and differences of conclusions that might be drawn from the two approaches and if only time-specific sampling with an unknown growth rate might be adequate (Zammuto and Sherman 1986; Zammuto 1990). Zammuto and Sherman (1986) statistically analyzed data from Belding´s ground squirrels (*Spermophilus beldingi*) collected over 8 years and concluded that cohort and time-specific life tables were equivalent for this population. This conclusion was disputed by Menkens and Boyce (1993) because Zammuto and Sherman (1986) did not include the 0 year age class where the most variability might be found and because the statistical tests used had low power due to small sample sizes. Zammuto (1987) claimed a sample of Columbian ground squirrels (*S. columbianus*) collected over a single summer had a stable age distribution, but that conclusion was disputed by Messier (1990) who questioned assumptions and claimed numerous statistical irregularities. Zammuto (1990) and Zammuto and Sherman (1993) provided rebuttals to these criticisms.

To compare their multiyear time-specific life tables and then to compare these to a cohort life table, Zammuto and Sherman (1986) used a statistical test that is a *k*-sample Kruskal-Wallis statistic for right censored data (Lee and Desu 1972). The method was devised for applications such as clinical trials in medicine, where an event occurs (cure, death) or the subject leaves the trial (right censorship) (Gehan 1965; Mantel 1967). The method of Lee and Desu (1972) is not widely available, and although offered as a card deck at the time of publication, now may require original programming. Zammuto and Sherman (1986) also reported that litter sizes were normally distributed within each year and across age classes, that the variances of litter sizes among years and among age classes were equal, and that litter sizes were equal among years and among age classes of reproductive females. Although not specifically stated, these analyses of litter sizes presumably were an attempt to provide some evidence to equate constant litter sizes with constant reproductive rates.

Based on the above, we used 24 yr of data from the yellow-bellied marmot, *Marmota flaviventris*, to pose questions about cohort and time-specific life tables and to explore related statistical questions. In doing these analyses we wished to used statistical methods that are in routine use and widely available to researchers. Specifically, we investigated the following: 1) Is it possible to statistically compare multiyear time-specific life tables to find differences among years? 2) Similarly, is it possible to compare time-specific life tables to a cohort life table to claim equivalence? 3) Do analyses of litter sizes support the assumption of a time-specific life table? 4) Do death rates, reproductive rates, and growth rates form a normal distribution that can be use to justify a claim of constant rates for a stable age distribution?

Materials and methods

From 1962 to 1993 the marmots in the East River Valley of Gunnison County, Colorado, were trapped annually and marked with ear tags, and each individual followed through its life by recapture and observation until its disappearance from the population (see Armitage 1962, 1974 for details of field methods). Virtually all marmots in the study population were captured each year. Most individuals were of known age because they were captured and marked at weaning, but some immigrants were aged by their mass class (Armitage *et al.* 1976).

We selected a subset of all these data in the central portion of the study area where there was constant trapping effort over the years. We commenced our analysis with data from 1970 because by then all individuals in the population, except for a few immigrants, were of known age. We used only known age marmots in our analyses. Because there were few individuals in the older age classes, we limited our analyses to females 5 years or younger. We calculated the relative frequencies of females in each yearly age class for each year and for all years combined. We calculated the crude death rates (CDR) for females each year by dividing the number of individuals surviving to the next year (n_{x-1}) by the number alive in this year (n_x). Gross Reproductive Rate (GRR) (Pianka 1988, p. 131), equivalent to Σmx of life tables, was calculated by dividing the number of female young produced by all females in that year. Growth Rate (GR) was calculated as GRR - CDR. Using the intrinsic rate of increase (r_m) and survivorship (l_x) values from life tables (Schwartz, Armitage and Van Vuren (1998), we calculated the overall relative proportions (C_x) expected with a stable age distribution in this population (Krebs 1985, p. 196). All statistical calculations were done using SAS/STAT (1990) software to consider our questions.

1) Multiyear time-specific life table comparisons. A population might be periodically and independently sampled, and it might be useful to know if statistical homogeneity of these time-specific life tables could be used to justify the assumption of a stable-age distribution. To parallel the analysis of Zammuto and Sherman (1986), we used a *k*-sample Kruskal-Wallis test of the absolute frequencies for all time-specific life tables from 1970 to 1993. Although this test was not for right censored data, the frequencies of age classes are not right censored data as described by Gehan (1965) and Mantel (1967). The assumption of independence of a *k*-sample test may be justified since dependence is on the diagonal; an individual in the 0 age class might have little influence on that proportion in the next year. To better define the probability-density function for this application we calculated 174 pairwise Kruskal-Wallis tests of time-specific life tables with years selected 6 years apart so samples would be independent (Neave and Worthington 1988); no animal was alive in each sample. Since there were 174 pairwise comparisons, we set α = 0.005 to reject the null hypothesis of equality of samples. Similarly, we also test the 174 paired samples for heterogeneity with a Kolmogorov-Smirnov test, since it tests for differences in the shape of distributions; this test is sensitive to the entire distributions of two samples and is less sensitive to differences only in location (Sokal and Rohlf 1981, p. 440). A *k*-sample Kolmogorov-Smirnov test is not possible using the SAS/STAT software. Finally, we calculated a χ^2 test of homogeneity using the absolute frequencies on the 24 years of data and then on the 174 pairwise comparisons. We then did these analyses on the published data of Zammuto and Sherman (1986) for k-samples and for the 3 years that could be considered independent samples.

2) Time-specific life tables compared to a cohort life table. We calculated pairwise Kruskal-Wallis, Kolmogorov-Smirnov, and χ^2 tests of each year paired with the cohort life table. Here we set $\alpha = 0.05$ to reject the null hypothesis of equality of samples for the 24 pairwise tests.

3) Analysis of litter sizes. Following Zammuto and Sherman (1986) and after a F_{max} test of the homogeneity of variances (Sokal and Rohlf 1981), we compared mean litter sizes by year and by age class with a one-way analysis of variance.

4) Normality of reproductive rate, death rate, and growth rate. If these rates are independent samples and normally distributed, it might justify the assumption of a constant growth rate for a time-specific life table, thus showing "moderate" deviations from a stable-age distribution (Stearns 1992). These marmot populations are extrinsically regulated by predation and aspects of weather (Schwartz, Armitage and Van Vuren (1998). With extrinsic population regulation, yearly death rates may be independent since a death in one year might not affect an individual in the next. Similarly for reproductive rates, a female may or may not reproduce in consecutive years, but that would be mostly dependent on body condition that would mostly be a function of the quality of the previous and current growing seasons. Thus birth, death, and growth rates in consecutive years may be regarded as independent estimates. For CDR, GRR, and GR we calculated a *W* statistic (SAS/Stat 1990) to test normality of distribution, the g_1 statistic for skew, and the g_2 statistic for kurtosis. We test g_1 and g_2 for significance with a t-test (Dixon 1988, p. 135). We calculated the same statistics for arcsine transformed data, but because our conclusions were the same, we do not report the results.

Results

There is considerable variation in the proportions in each age class (Table 1). For example, the proportions in the 0 age class ranged from 10.6 to 49.4 %. As early as age 2 there were no individuals in an age class in a year. The expected frequencies in a stable age distribution (C_x) are close to those of the 24 yr average (cohort, Table 1).

1) Multiyear time-specific life table comparisons. There was no significant heterogeneity among the frequencies of the 24 yearly samples with the Kruskal-Wallis test ($H = 20.5$, df = 23, $p = 0.667$). None of the 174 pairwise samples differed significantly with all $P > 0.01$; this smallest P was for the 1970-91 pairwise comparison. Similar to the finding of Zammuto and Sherman (1986), our reanalysis of their Belding's ground squirrel data using the *k*-sample Kruskal-Wallis statistic showed no significant differences among samples ($H = 1.41$, df = 7, $P = 0.98$). For the three paired comparisons, the Kruskal-Wallis test ($P > 0.55$) detected no significant differences in Belding's ground squirrels.

None of the 174 pairwise samples differed significantly with the Kolmogorov-Smirnov statistic with all $P > 0.03$; the smallest P value was for the 1970-91 pair of years. In Belding's ground squirrels the Kolmogorov-Smirnov test detected no significant differences between samples for the 3 years used ($P > 0.51$).

The chi-square statistic was the only one to demonstrate heterogeneity among age classes in the 6 by 24 matrix tested ($\chi^2 = 290.4$, df = 115, $P < 0.0001$). In paired comparisons, 19% of the 174 tests differed significantly ($P < 0.005$, df = 5) between years. The smallest P ($P < 0.0001$) was for the 1983-93 years. For the 1970-91 pair, the most different in the other two tests, P was 0.64 in the χ^2 test. The 5 by 8 matrix for Belding's ground squirrels showed significant heterogeneity ($\chi^2 = 48.1$, df = 28, $P = 0.011$). The three paired comparisons of Belding's ground squirrel showed no significant heterogeneity ($P > 0.07$).

2) Time-specific life tables compared to a cohort life table. The Kruskal-Wallis and Kolmogorov-Smirnoff tests for marmots revealed no significant differences ($P > 0.05$). Significance differences were found by χ^2 for 7 of the 24 comparisons ($P < 0.05$). The differences were for the years 1973, '82, '83, '84, '85, '90, and '93.

3) Analysis of litter sizes. Variances were homogeneous for litter sizes by year ($F_{max} = 8.07$, df = 24,3, $P > 0.05$) and by age class ($F_{max} = 2.56$, df = 9,3, $P > 0.05$). Litter sizes were not equal among years ($F = 2.22$, df = 23, 214, $P = 0.0017$) (Fig. 1), but were equal among age classes ($F = 1.51$, df = 8,256 , $P = 0.16$).

4) Normality of reproductive rate, death rate, and growth rate. The CDR (Fig. 1, X = 32.4, SE = 2.45, n = 24) is normally distributed ($W = 0.96$, df = 23, $P = 0.43$) and there is no significant skew ($g_1 = -0.28$, $t_{23} = 0.56$, $P = 0.59$) or kurtosis ($g_2 = -0.89$, $t_{23} = 0.89$, $P = 0.19$). The GRR (Fig. 1, X = 31.3, SE = 1.86, n = 24) is normally distributed ($W = 0.98$, df = 23, $P = 0.9$) and there is no significant skew ($g_1 = -0.10$, $t_{23} = 0.20$, $P = 0.42$) or kurtosis ($g_2 = -0.42$, $t_{23} = 0.42$, $P = 0.34$). Likewise, The GR (Fig. 1, X = -0.35, SE = 2.79, n = 24) is normally distributed ($W = 0.94$, df = 23, $P = 0.25$) and there is no significant skew ($g_1 = -0.24$, $t_{23} = 0.20$, $P = 0.42$) or kurtosis ($g_2 = -1.10$, $t_{23} = 1.10$, $P = 0.14$).

Discussion

There appears to us to be a number of birth or death pulses in cohorts moving from upper left to lower right through the 24 time-specific life tables. For example, poor reproduction in 1982 resulted in few one-year-olds in 1983 and no two-year-olds in 1984 (Table 1). Inspection of the Belding's ground squirrel data (Table 1, Zammuto and Sherman 1986) suggested age-class pulses moving through the population similar to those for the yellow-bellied marmot. Qualitatively it appeared that there were not constant proportions in each age class.

The Kruskal-Wallis and Kolmogorov-Smirnoff

	SAMPLE SIZE																									
	21	28	28	31	26	31	38	42	36	58	87	88	47	59	59	67	74	81	96	95	89	77	74	53	518	
	YEAR																									
	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	Cohort	(C_x)
	PROPORTION IN AGE CLASS																									
AGE																										
0	38.1	35.7	21.4	22.6	26.9	25.8	47.4	28.6	36.1	48.3	49.4	35.2	10.6	49.2	35.6	43.3	43.2	48.1	42.7	46.3	23.6	29.9	45.9	17.0	37.4	35.9
1	14.3	21.4	39.3	9.7	15.4	19.4	13.2	23.8	19.4	15.5	23.0	31.8	23.4	3.4	30.5	17.9	18.9	21.0	25.0	16.8	38.2	18.2	10.8	35.8	21.7	21.3
2	19.0	10.7	14.3	38.7	3.8	12.9	5.3	11.9	11.1	10.3	9.2	11.4	36.2	11.9		16.4	10.8	4.9	11.5	16.8	6.7	22.1	6.8	7.5	12.2	11.4
3	14.3	14.3	3.6	12.9	26.9	9.7	5.3	7.1	2.8	6.9	6.9	8.0	10.6	18.6	8.5		10.9	6.2	3.1	7.4	14.6	5.2	18.9	5.7	8.9	8.3
4	14.3	7.1	7.1	3.2	15.4	16.1	7.9	4.8	5.6	1.7	4.6	4.5	6.4	5.1	16.9	4.5		8.6	5.2	1.1	6.7	13.0	4.1	20.8	6.9	6.9
5		10.7	3.6	3.2	3.8	9.7	7.9	7.1	5.6	1.7	1.1	3.4	4.3	5.1		13.4	4.1		6.3	4.2	1.1	5.2	6.8	3.8	4.4	4.7
6			10.7	3.2	3.8	3.2	7.9	4.8	5.6	3.4	1.1	1.1	4.3	1.7	3.4		8.1	1.2		5.3	3.4	1.3	1.4	5.7	3.0	3.4
7				6.5		3.2	2.6	7.1	2.8	3.4	1.1	1.1		1.7	1.7	1.5		6.2	1.0		5.6	1.3	1.4	1.9	2.1	2.6
8					3.8		2.6	2.4	8.3	1.7	1.1	1.1	2.1		1.7	1.5	1.4		4.2	1.1		3.9	1.4		1.6	2.0
9								2.4		5.2	1.1		2.1				1.4	1.2		1.1			2.7		0.8	1.2
10									2.8		1.1	1.1		1.7				1.2						1.9	0.4	0.7
11										1.7		1.1			1.7										0.2	0.4
12													*			1.5									0.1	0.3
13														1.7			1.4								0.1	0.3
14																		1.2							0.1	0.3
15																			1.0						0.1__	

* One animal not captured

Table 1. Relative frequencies of the ages of female yellow-bellied marmots from selected sites in the East River Valley of Colorado.

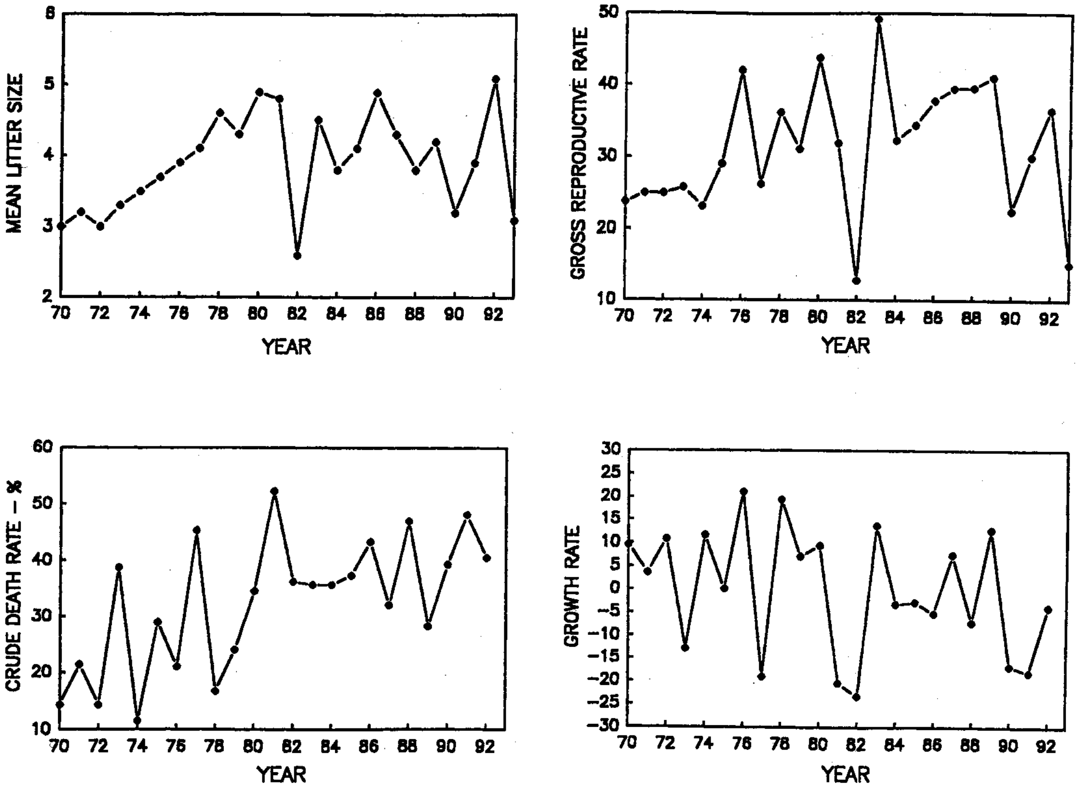

Fig. 1. Annual variation of mean litter size, gross reproductive rate (%), crude death rate (%), and growth rate (%) for yellow-bellied marmots.

tests revealed no differences in *k*-sample or in pairwise tests for marmots or Belding's ground squirrels, even in years with widely different proportions in each age class. Likely these statistics are not of sufficient power to be of use in showing heterogeneity among time-specific life tables. The chi-square statistics for marmots and Belding's ground squirrels suggested that there was heterogeneity among the yearly samples. Such an analysis of repeated, independent samples to justify use of a time-specific life table would depend on the dynamics of the study population during the period of study.

In comparing time-specific life tables to the cohort life table, the Kruskal-Wallis and Kolmogorov-Smirnov revealed no differences, but 7 of 24 χ^2 tests differed. The latter result demonstrates that there is no equivalency of time-specific and cohort-specific life tables for marmots.

For marmots there was heterogeneity in litter sizes among years that was likely due to extrinsic factors (Schwartz, Armitage and Van Vuren 1998), but litter size is only a correlate of growth rates and is likely irrelevant to the requirement for a constant reproductive rate. Rather, the maternity component of a stable age distribution needs to be determined as a rate. By years for marmots, sample size ranged from 3 to 18 litters and by age class sample sizes ranged from 4 (age 10) to 56 (age 4), so these statistical tests may also be criticized for having low power due to small sample sizes (Menkens and Boyce 1993).

Although birth rates, death rates, and growth rates are normally distributed without skew or kurtosis, their range is wide and there are pulses due to variation in these rates that can be seen moving through the yearly samples. Thus, demonstration of statistical homogeneity in rate measures may not show the biological reality of the population processes. The stable age distribution from the cohort life table (C_x) may be calculated, but it says nothing about the range of variations that produce it.

The weight of the evidence would lead us to conclude that for marmots there was no equivalence of time-specific and cohort specific life tables. This conclusion agreed with those of Stearns(1992), Krebs (1985), and Charnov (1993) that stable age distributions seldom are found in nature. The constant normality of rates in this paper may allow theoreticians to conclude that deviations from the stable-age distribution are "moderate". The frequent assumptions by modelers of a stable age distribution and its rarity in nature suggest the need to clarify the goals when integrating empirical and theoretical work. Our extensive data set may be used to better develop statistical tests to address questions about time-specific and cohort specific life tables.

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