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COMMENTS ON ESTIMATING POPULATION RATE OF INCREASE FROM AGE FREQUENCY DATA

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ABSTRACT

Although many papers have described assumptions and calculations of r from different kinds of data, none has compared estimates of r for the same real data set under different assumptions. We used the age distributions of gray foxes collected during six trapping seasons to estimate and compare r and l_x series derived under different assumptions. Because trapped foxes are killed, they are believed by some to represent death history data. We found this treatment underestimates mortality so overestimates survivorship and leads to erroneous conclusions about the population. Use of a projection matrix allowed prediction of population size and thus allowed us to predict "observed" rate of increase. Use of projection matrices also resulted in the most conservative estimated of r .

INTRODUCTION

Since the early 1960's mammalogists have become increasingly interested in population dynamics. Caughley and Birch (1971) pointed out that many of the estimates of rate of increase (r) in papers resulting from this interest were inaccurate because "time-specific" data were used. Construction of time-specific life tables is based on the assumptions that 1) the population has a stable age distribution, 2) there is no bias in the data, and 3) $r = 0$. Estimation of r in time-specific analysis approximates zero because the calculation "retrieves an assumption and disguises it as a conclusion" (Caughley and Birch, 1971). Tait and Bunnell (1980) noted that this statement is not true if age-specific probability of survival from birth (l_x) is estimated from the distribution of ages at death of animals found dead. Still, they concluded that while r was possible to estimate in theory, it is virtually impossible to estimate in practice. Given these usually untenable assumptions, it might seem that there is no point in attempting to estimate rate of increase from life table data. Michod and Anderson (1980) indicated, however, that by calculating r and l_x jointly questions concerning population dynamics, the data, or the validity of the model can be addressed.

Several authors have offered logic for the calculation of population parameters. Leslie (1945; 1948) used matrices to project future age structure and population size. Conley (1978), Downing (1980), Michod and Anderson (1980), Tait and Bunnell (1980), and Lenski and Service (1982) discussed calculation of population parameters from different kinds of data. One approach lacking in these treatments is a comparison of estimates of r calculated for the same real data set under various assumptions. The purposes of this paper are to estimate and compare l_x series and r calculated under different assumptions for trapped samples of gray fox (*Urocyon cinereoargenteus*).

METHODS AND MATERIALS

Skulls of gray foxes were obtained from furbuyers in Arkansas during six December-January trapping seasons from 1977-78 through 1982-83. Age estimates were made using dental criteria (Tumlison and McDaniel, 1984). Accuracy of age estimates affects the calculated values of population parameters, but this was not considered to be a major source of bias because foxes are among the easiest mammals to age (Matson, 1981). Age structure for each sample is given in Table 1.

Three approaches for the development of an l_x series were used with these data. A large sample, obtained during year 2 (1978-79), was used

Table 1. Age structure of samples of gray fox taken during December-January trapping seasons in Arkansas. Year 1 was 1977-78, year 6 was 1982-83.

Age Class	Trapping Season						Total
	1	2	3	4	5	6	
0	31	143	86	22	13	40	335
1	23	50	34	8	2	13	130
2	4	23	10	1	3	8	49
3	2	12	13	0	1	0	28
4	1	6	4	2	2	3	18
5	2	10	2	0	0	0	14
6+	0	4	1	0	0	1	6
	63	248	150	33	21	65	580

to develop a time-specific m_x series in which r is usually assumed to be zero. The approach of Leslie (1945) and Michod and Anderson (1980) does not require an assumption of stability, therefore r was estimated from the single sample using fecundities of the type termed F_x (Leslie, 1945) rather than the usual m_x fecundities.

Because most animal populations are not truly stable, variation in the initial size of the cohorts represented is often reflected in age structure determined from a single sample. Downing (1980) indicated that a composite of several years of census data largely avoids the problem of unequal cohorts. To evaluate the potential difference, another time-specific analysis was made using a composite sample of the 6 years of data. Year 2 contributed significantly to the size of the composite sample, and reduced the differences between l_x schedules. Again, r was estimated as described above.

Finally, a dynamic analysis in which stability is not assumed is possible using data from years 2 and 3. During the analysis, the sample size of year 3 was made equal to that of year 2 and proportioned among age classes. By following age class 0 of year 2 to age class 1 of year 3, survival rate for that cohort during sample year 2 was estimated. Survival

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rates for each cohort in the sample were used to construct an l_x series that did not assume stability.

Each of the above approaches treats the data as a sample of the living. Although trapped foxes were killed, they are usually considered to represent a sample from the living population (Caughley, 1966). However, in some exploited furbearer populations trapping may be the major source of mortality. Hence, it might be argued that a trapped sample more accurately reflects a sample of the dying. Each of the 3 l_x series described above was recalculated with this assumption for comparison. Methods for calculation of l_x given life or death assumptions were described by Downing (1980).

To calculate r , both l_x and m_x are required. No m_x values were obtained with the fox age data, so m_x values were estimated. Life tables traditionally are constructed to represent the female portion of the population. Pielou (1977:53) stated that populations with a 1:1 sex ratio and identical age distribution between the sexes do not need to be treated separately. Our data indicated that these assumptions were not violated, therefore the data were pooled and all specimens were treated as females. As a result, calculated m_x values represented the number of female offspring. Wood (1958) provided m_x data on gray foxes which Michod and Anderson (1980) later used. Their m_x values were based on placental scars and embryo counts, and the percentage of foxes not breeding. By using the Leslie matrix, an m_x schedule was developed for our analysis which is proportional to Wood's (1958) data as given by Michod and Anderson (1980) and which made the age structure for the dynamic sample stable (i.e., F_x in the Leslie matrix projected the same future age structure and population size as that obtained in the dynamic sample). The dynamic sample was chosen for stabilization merely because it does not assume stability. Because this treatment to derive the schedule caused the dynamic analysis to indicate stability ($r=0$), the dynamic data may now be used as an heuristic device for comparison of other estimates of r . We expect that all estimates of r should approximate 0 if assumptions of the particular model are not violated.

The discrete time version of the demographic equation (i.e., the characteristic equation of the Leslie matrix) is

$$1 = \sum_{x=1}^{\eta} e^{-\alpha x} l_x m_x \quad \text{Equation (1)}$$

(Murray and Garding, 1984). Michod and Anderson (1980), using harvested animals for analysis, gave the equation

$$1 = \sum_{x=0}^{\eta-1} \lambda^{-(x+1)} \frac{l_x}{l_0} F_x \quad \text{Equation (2)}$$

They incorporated into their equation for the solution of λ the term l_0 , representing average survivorship of newborn to their first harvest season. The number of age 0 individuals could then be treated in the first age class after having accounted for the difference between the number of age 0 individuals sampled and mortality between birth and sampling (i.e., they used F_x data). Their approach allowed simultaneous calculation of λ and l_x without any assumption concerning the growth rate. Note: $r = \ln \lambda$.

RESULTS AND DISCUSSION

The l_x series calculated under each assumption are provided in Table 2. We tested the hypothesis that trapping was the major source of mortality using the G-statistic and a 7x2 contingency test (Sokal and Rohlf, 1969) to compare l_x series developed under both life and death data assumptions. If trapping is the major source of mortality, the age structure must reflect such a reality. Conversely, treatment as a sample of the living incorporates all forms of mortality into population structure.

Comparison of the one-year and dynamic series were each significantly different ($P < 0.005$) while the composite sample was significant only between the 0.25 and 0.10 levels. Comparisons of l_x series may not be meaningful because an error in the frequency of the first age class results in distortion of each r below it in the series (Caughley, 1966). However, values of q_x are independent of frequencies in younger age classes and may serve as more sensitive measures for comparison. In our analyses, all comparisons between q_x series, calculated under life and death base assumptions, were highly significant ($P < 0.005$).

Table 2. The probability of survival from age 0 to age x (l_x series) calculated for each treatment of age data. Life or death base data assumptions are indicated.

Age class	Time Specific				Dynamic	
	Total Sample		Year 2		(Years 2 & 3)	
	Life	Death	Life	Death	Life	Death
0	1.000	1.000	1.000	1.000	1.000	1.000
1	.388	.388	.350	.473	.392	.430
2	.146	.182	.161	.222	.133	.207
3	.084	.104	.084	.129	.119	.131
4	.054	.060	.042	.081	.070	.064
5	.042	.032	.070	.057	.035	.024
6+	.018	.010	.028	.016	.007	.004

Some statistical problems appeared using life-based assumptions with the 1978-79 sample. Unequal cohort size may have been responsible for the larger size of the 5-year class, but this translates mathematically into a negative q_x value; a biological impossibility. For the contingency test, we set the value of q_x for the 5-year class equal to the corresponding value in the contingency table. This procedure removed the contribution of the class to independence and decreased the calculated significance level, but differences were still sufficient for significance. We conclude from these analyses that the trapped sample of foxes does not represent death data, because sources other than harvest mortality affect the population. Harvest data *cannot* represent a sample of the dying.

Each of the 3 life-based l_x series were tested in all combinations for independence. Comparison of the 6-year composite and 1-year samples showed significant differences ($P < 0.05$). This observation indicates that yearly fluctuations in Arkansas gray fox populations reduce the predictive usefulness of single samples. The l_x series of the composite and dynamic samples were also different ($P < 0.05$). While the dynamic treatment does not assume stability, it is based on relatively static data (2 years). A comparison of the 1-year and dynamic series was highly significant ($P < 0.005$). The greater significance level is probably due to variation from each of these latter series being absorbed in the composite sample, making comparison with the composite series relatively less significant. All comparisons of corresponding q_x series were highly significant ($P < 0.05$).

As mentioned earlier, the dynamic l_x series was used to develop a m_x series that would stabilize that age structure, thus we expect $r=0$. Rate of increase was calculated by Eq. 1 to be 0.002. Our treatment to develop a l_x series necessarily set $l_0=1$, thus rate of increase estimated by Eq. 2 was 0.005.

The Leslie matrix projects future population characteristics assuming constant survivorship and fecundity schedules. By projecting next year's population size based on our sample and observing differences between this estimate and our sample size, an estimate of r (in this case, observed rate of increase) can be obtained. For our "stabilized dynamic" sample this value was 0.003. We have shown that, given some rounding error, $r=0$ for the dynamic data using our derived fecundity schedule.

Equation 1 cannot be applied to the composite or one-year samples because the l_x series for these samples are based on the assumption of stability. Equation 2 or Leslie matrices may be used, however. Rate of increase estimated by Eq. 2 for the composite sample indicated a decline ($r = -0.029$), as did the one-year sample ($r = -0.020$). Observed r estimated by projecting the population for next year via the Leslie matrix also predicted declines ($r = -0.017$ and -0.012 , respectively). Estimates of r by Eq. 2 compared to those derived from Leslie projections were appreciably different. We used the age structure represented by the l_x series as the column vector multiplicand of the Leslie matrix. Solution of Eq. 2 or calculation of the first position in the projected age structure estimates the agreement between recruitment and the

characteristic value of the first age class of the l_x series (i.e., 1.000). For example, if there are 1000 individuals in the first age class at time t , Eq. 2 predicts the number expected to be present at time $t+1$. If $\lambda = 0.971$ ($r = -0.029$), recruitment is 971 individuals, which does not replace the age class. The value of r indicates a loss of 29 individuals from the age class at $t+1$. Notice that this is a change of 29 per 1000. Since observed rate of increase is based on change in numbers between t and $t+1$, we sum both the sample and projected l_x series to simulate our "population" sizes. For the above example the sums at t and $t+1$ were 1732 and 1703, respectively. This still represents a loss of 29 individuals, but it is now 29 per 1732. Now, $\lambda = 0.983$ and $r = -0.017$.

The hypothesis that the data represent death history was refuted earlier. To examine the effect of erroneously accepting that hypothesis, r was estimated by Eq. 2 and by the change in the projected population size. These estimates were, respectively: 0.133, 0.076 (dynamic); 0.030, 0.017 (composite), and 0.213, 0.123 (one-year). Because treatment of the data as death history underestimates mortality, survivorship (l_x) is overestimated; consequently, r appears more favorable. This type of treatment would lead to a more positive, but invalid, conclusion about the population.

CONCLUSIONS

The method one uses to estimate r depends on the kinds of data available for analysis. Although Eqs. 1 and 2 are mathematically identical, the data required for solution are different. Equation 1 can be used only if an l_x series can be obtained that does not assume stability. Since many data sets are based on single samples and Eq. 2 makes no assumptions concerning the growth rate, it has greater utility. Further, it allows the simultaneous calculation of r and an l_x series that accounts for population changes. However, it requires extra effort to obtain l_0 . As Michod and Anderson (1980) point out, "... it may be more reasonable to assume some value for l_0 rather than assume $\lambda = 1$, or $r = 0$, as is often done." Investigators should note, if they choose to use Eq. 2, that r deals with changes in recruitment into the first age class, whereas observed r deals with changes in recruitment into the population. Because of larger sample size, observed r is the more conservative estimate. If we continue to use the l_x series to represent the age structure of the population, "observed" r based on matrix projections will always provide the more conservative estimate of r .

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