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ESTIMATING UNCERTAINTY IN POPULATION GROWTH RATES: JACKKNIFE VS. BOOTSTRAP TECHNIQUES[1]

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Abstract. Although per capita rates of increase (r) have been calculated by population biologists for decades, the inability to estimate uncertainty (variance) associated with r values has until recently precluded statistical comparisons of population growth rates. In this study, we used two computer-intensive techniques, Jackknifing and Bootstrapping, to estimate bias, standard errors, and sampling distributions of r for real and hypothetical populations of cladocerans. Results generated using the two techniques, using data on laboratory cohorts of *Daphnia pulex*, were almost identical, as were results for a hypothetical *D. pulex* population whose sampling distribution was approximately normal. However, for another hypothetical population whose sampling distribution was negatively skewed due to high juvenile mortality, Bootstrap and full-sample estimates of r were negatively biased by 3.3 and 1.8%, respectively. A bias adjustment reduced the bias in the Bootstrap estimate and produced estimates of r and SE(r) almost identical to those of the Jackknife technique. In general, our simulations show that the Jackknife will provide more cost-effective point and interval estimates of r for cladoceran populations, except when juvenile mortality is high (at least >25%). Coefficients of variation in the mean of r within laboratory cohorts of *D. pulex* were one-half to one-third the magnitude of the corresponding coefficients of variation in the mean of total reproduction and in the mean day to death (range of values of $\widehat{\text{CV}}[r] = 1.6$ to 3.8%). This suggests that extremes in reproductive output and survival of individuals tend to be dampened at the population level, and that within-cohort variability in r is not explosive. Moreover, between-cohort variability in r can be much greater than within-cohort variability, as indicated by a statistically significant difference of 30% ($P \ll .01$) between the high and low r values that were computed for four cohorts of *D. pulex* born during a 1-mo period from the same laboratory stock population. Based on variability in per capita rates of increase that have been estimated for several cladoceran species, we suggest that the precision for reporting r values should in most cases be limited to two significant figures.

Key words: Bootstrap; Daphnia pulex; *Jackknife; per capita rate of increase; statistical comparisons; temporal variability.*

INTRODUCTION

Ever since Lotka (1907*a*, *b*) published his seminal papers relating birth and death rates to population growth and Fisher (1930) published his landmark book, *The Genetical Theory of Natural Selection,* biologists have been calculating per capita rates of increase (r) for populations. But until recently, no one has attempted to estimate the uncertainty (variance) associated with these calculations (Daley 1979, Lenski and Service 1982, Rago and Dorazio 1984). This has led to two common, yet questionable practices. First, r values based on small subsamples of a population have been assumed to be unbiased estimates of the per capita rate of increase for the entire population. And second, statistical uncertainty about these r values has been ignored because closed-form equations cannot be written to calculate r, thus precluding the development of exact algebraic expressions for estimating the variance of r.

Although the consequences of not being able to infer statistically significant differences between two or more population growth rates have not hindered basic research in population biology, the relatively recent interest in applied population biology has emphasized the need to eliminate this statistical deficiency. Decisions in disciplines such as wildlife management and environmental toxicology require information about potential and realized population-level effects of human activities. Therefore, it is important to develop and test procedures for estimating the uncertainty associated with population growth rates so that levels of confidence can be assigned to observed differences.

In an early attempt to address this problem, Daley (1979) developed algebraic approximations for the bias and variance of r. However, the equations he derived are tedious and are based on unvalidated assumptions, which he used to neglect higher-order terms in several Taylor series expansions. Rago and Dorazio (1984) derived a similar equation for the variance of r, but there have been no other attempts to approximate these values algebraically.

With the advent of high-speed computers, several ad hoc, computer-intensive procedures for estimating variances have become popular (Diaconis and Efron 1983). For example, Keyfitz (1977:354–356) first proposed using the Jackknife of Tukey (1958) for estimating the variance in r. Recently Lenski and Service (1982) and Service and Lenski (1982) used Jackknifing to calculate finite growth rates ($\lambda = e^r$) and their standard errors for aphid populations. Lenski and Service (1982) derived a mathematical proof that the variances

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they calculated using a Jackknife procedure should approximately equal the population variance for repeated subsampling. Yet Efron (1982) concluded that Bootstrapping is generally a more reliable computer technique for estimating variances than is Jackknifing. Despite its reputed superiority, though, Bootstrapping has not previously been applied to population growth rate calculations.

Finally, Rago and Dorazio (1984) recently used a Monte Carlo simulation technique to generate sampling distributions of λ based on smoothed survivorship and fecundity schedules for *Daphnia pulex* cohorts. Since several commonly observed mortality schedules produced distributions of λ that were skewed toward low values in their simulations, Rago and Dorazio (1984) suggested that normal-based statistical procedures for comparing experimental estimates of λ may be misleading (e.g., Lenski and Service 1982). To overcome this difficulty, they proposed a procedure for pairwise comparison of sampling distributions that allowed asymmetrical confidence intervals to be tested for significant differences. They also derived a Taylor series variance estimator similar to the equation derived by Daley (1979), which yielded symmetrical confidence intervals surrounding λ values that were approximately equal to those obtained in their Monte Carlo simulations, and were less conservative than confidence intervals estimated using the Jackknife procedure proposed by Lenski and Service (1982).

But none of these methods has been validated by an appropriate test, wherein a large population is repeatedly subsampled and the reliability of confidence intervals surrounding true population growth rates is tested. Specifically, a critical question is: do 95% confidence intervals estimated using these techniques capture the true population growth rate in 95% of the population subsamples? In this paper, we (1) compare results of Jackknifing and Bootstrapping procedures for estimating the uncertainty in growth rates of laboratory populations of *D. pulex*; (2) evaluate the reliability of Jackknife and Bootstrap 95% confidence intervals by applying these techniques to repeated subsamples from two large, hypothetical populations; and (3) discuss estimation biases when data on survivorship and reproduction in small subsamples of large populations are used to estimate population growth rates.

Methods

Cladoceran populations

Survivorship and fecundity data for *Daphnia pulex* were taken from a laboratory study on toxic effects of cadmium and copper (Ingersoll and Winner 1982). In that study, tests were started with neonate *D. pulex* females (<24 h old) and were continued for up to 70 d. Animals were maintained in separate beakers in 40 mL of reconstituted lab water at 20°C under a 16:8 L:D photoperiod. Survival and reproduction of 10 females per cadmium or copper exposure concentration (i.e., 10 replicate beakers per exposure level) were monitored daily; new offspring were removed daily from beakers, and adults were transferred to fresh exposure solutions every 3 d. From those data, survival and fecundity of control and exposure cohorts were compared to evaluate chronic effects of exposure to cadmium and copper. (See Ingersoll and Winner 1982 for additional test details and results.) However, population growth rates were not reported by Ingersoll and Winner (1982) because statistical uncertainty surrounding the population growth rates could not be estimated. We reanalyzed Ingersoll and Winner's data for four cohorts of control animals (no toxicant exposure) that came from the same stock population, but were born on different days during June and July 1981. Specifically, we calculated per capita rates of increase and 95% confidence intervals, using two computer-intensive procedures (see Jackknife and Bootstrap Calculations). Then we compare those values to detect significant differences in population growth rate between cohorts.

Since ad hoc procedures for estimating means and standard errors of population growth rates have not yet been validated in the literature for this type of collection, we generated two hypothetical populations of parthenogenically reproducing cladocerans to test the reliability of estimated 95% confidence intervals. Each hypothetical population contained 100 females whose pattern of reproduction was similar to that observed for *D. pulex* controls (Ingersoll and Winner 1982). We randomly assigned daily observations of newborn offspring through Day 28, according to the following rules: (1) no reproduction before Day 7; (2) brood period = 2 or 3 d (50% probability for each, with the brood duration being selected randomly for each brood of each female in the population); (3) brood size was normally distributed about the mean brood size of 10 offspring and was selected randomly for each brood of each female in the population; and (4) coefficient of variation in the mean brood size = 0.25.

Because Ingersoll and Winner (1982) never observed >10% mortality of control adults by Day 28, we imposed no mortality on Hypothetical Population 1. Simulated sampling distributions of per capita rates of increase generated from this first hypothetical population were approximately normal. But Rago and Dorazio (1984) reported that sampling distributions for λ values in *D. pulex* populations are skewed toward low values when juvenile mortality is high and adult reproduction is not substantially changed. To investigate the potential effects of skewness on the validity of estimated 95% confidence intervals, we imposed heavy juvenile mortality on Hypothetical Population 2. In that population all animals survived to Day 5, but then the probability of survival (l_x) decreased linearly in increments of 0.1 from Day 6 ($l_x = 0.9$) to Day 15 ($l_x = 0.0$), when all animals were dead. Approximately 26% of the juve-

TABLE 1. Results of computer simulations of reproduction by the first five females in each of two hypothetical cladoceran populations.*

Age class	Number of offspring produced											
	Hypothetical Population 1						Hypothetical Population 2†					
	Animal	1	2	3	4	5	Animal	1	2	3	4	5
1		0	0	0	0	0		0	0	0	0	0
2		0	0	0	0	0		0	0	0	0	0
3		0	0	0	0	0		0	0	0	0	0
4		0	0	0	0	0		0	0	0	0	0
5		0	0	0	0	0		0	0	0	0	0
6		0	0	0	0	0		0	0	0	0	0
7		0	0	12	8	0		0	0	0	0	0
8		4	0	0	0	0		10	0	0	11	
9		0	0	10	0	12		0		8	0	
10		11	8	0	8	0		0		0	7	
11		0	0	9	0	0		10		0	0	
12		9	0	0	9	7					0	
13		0	11	8	0	0					8	
14		0	0	0	0	0						
15		13	0	9	14	10						
16		0	10	0	0	0						
17		0	0	0	0	6						
18		9	7	16	10	0						
19		0	0	0	0	0						
20		0	0	0	0	11						
21		7	5	8	8	0						
22		0	0	0	0	11						
23		0	0	0	0	0						
24		12	4	9	10	9						
25		0	0	0	0	0						
26		0	0	10	10	11						
27		9	8	0	0	0						
28		0	0	0	10	0						

* For details, see Methods: Cladoceran Populations.
† Underlining indicates the death of the female during the age class.

niles died before reproducing, yet mean brood sizes of the surviving females at each age class in Hypothetical Population 2 were approximately equal to mean brood sizes of females in the same age classes in Hypothetical Population 1 (difference between overall mean brood sizes = 2.2%).

Although the survivorship and reproduction schedules for these hypothetical populations are not typical of all cladoceran populations, they provide a contrast between normal and skewed sampling distributions of r that is useful for testing the reliability of uncertainty estimates. To illustrate this contrast in survival and reproduction schedules, reproduction by the first five animals in each hypothetical population is shown in Table 1. Procedures for calculating 95% confidence intervals surrounding estimates of per capita rate of increase and for testing the reliability of the estimates are described in Confidence Interval Coverage Rates.

Population growth rate calculations

Population growth rates were calculated according to the familiar Euler equation

$$1 = \sum_{x=0}^{\Omega} e^{-r \cdot x} \cdot l_x \cdot m_x, \qquad (1)$$

where r = per capita rate of increase for the population (number per day), x = age class (days; 0, 1, 2, . . . , Ω), Ω = oldest age class in the population, l_x = probability of surviving to age x, and m_x = fecundity at age x. Because this calculation involves a summation over several age classes, r cannot be isolated on one side of the equation to provide a closed-form, algebraic solution. Instead, iterative calculations must be performed in order to determine an r value that satisfies Eq. 1.

For the computations reported in this paper, we used a half-interval iteration algorithm (Arden and Astill 1970) programmed onto a Control Data Corporation Cyber 760 computer. To begin computations for a data set, we approximated the per capita rate of increase using the following equation suggested by Caughley (1977):

$$r \approx \frac{\ln R_0}{T_c} = \frac{\ln \sum_{x=0}^{\Omega} l_x \cdot m_x}{\sum_{x=0}^{\Omega} x \cdot l_x \cdot m_x / \sum_{x=0}^{\Omega} l_x \cdot m_x},$$

where R_0 = net reproductive rate, and T_c = generation time. Given this initial approximation for the value of r, we then proceeded with interval-halving computations and refined our estimate of r until the value of the right-hand side of Eq. 1 was between 0.9999 and 1.0001. Values of r computed under this criterion were

repeatable to within 0.00001 d^{-1} (i.e., repeatable to within ≈0.003% of the r values computed for most data sets used in this study), no matter what initial estimates of r were used to start the iterations.

Jackknife and Bootstrap calculations

We estimated bias, standard errors, and sampling distributions of r using two computer-intensive techniques, Jackknifing and Bootstrapping. Briefly, both procedures are based on (1) recombining the original data, (2) calculating pseudo-values of the parameter of interest for each recombination of the original data, and (3) estimating the mean value and standard error of the parameter of interest from the resulting frequency distribution of pseudo-values. For a more extensive review of theory behind these procedures, see Efron (1982).

Before starting Jackknife and Bootstrap calculations on a given data set, we computed the per capita rate of increase for the original data set (r_{all}, the full-sample estimator) using Eq. 1. Then for the Jackknife procedure, we omitted one of the n replicate animals (the i^{th} animal, $i = 1, 2, \ldots, n$) from the original data set and recomputed a per capita rate of increase ($\hat{r}_i$) using data from the remaining $n - 1$ animals. The Jackknife pseudo-value ($\tilde{r}_i$) was then calculated for this subset of the original data as follows: $\tilde{r}_i = n \cdot r_{all} - (n - 1) \cdot \hat{r}_i$. We repeated this process until pseudo-values were calculated for all n possible omissions of one animal from the original data set. Finally, we computed the mean value (r_J) and the standard error of the n Jackknife pseudo-values as follows:

$$r_J = \frac{1}{n} \cdot \sum_{i=1}^{n} \tilde{r}_i$$

$$\widehat{\mathrm{SE}}(r_J) = \sqrt{s^2_{\tilde{r}}/n},$$

where $s^2_{\tilde{r}}$ = variance of the n Jackknife pseudo-values, $\{\tilde{r}_1, \tilde{r}_2, \ldots, \tilde{r}_n\}$.

In the Bootstrap procedure, we randomly recombined the original data, rather than sequentially omitting one animal as was done in the Jackknife. To initiate a Bootstrap replicate, we placed the original data set of n animals into a pool from which n values were randomly selected with replacement (i.e., each sampled animal was placed back into the data pool before another animal was sampled). Thus, any animal in the original data set could have been represented more than once or not at all in the Bootstrap replicate. (Conceptually, this random sampling of the original data mimicked a hypothetical resampling of the entire population.) We then computed the per capita rate of increase for this random recombination of the original data and designated it r^*_i, the r value estimated for the i^{th} Bootstrap replicate. Random sampling and calculation of r^* were repeated m times (i.e., m Bootstrap replicates were performed), with the value of m depending on the precision desired for the Bootstrap estimates. Finally, to complete the Bootstrap calculation we computed the mean value (r_B) and the standard error of the m Bootstrap r^* values as follows:

$$r_B = \frac{1}{m} \cdot \sum_{i=1}^{m} r^*_i$$

$$\widehat{\mathrm{SE}}(r_B) = \sqrt{s^2_{r^*}},$$

where $s^2_{r^*}$ = variance of the m Bootstrap r^* values, $\{r^*_1, r^*_2, \ldots, r^*_m\}$.

Let r_{pop} denote the per capita rate of increase for the entire population under consideration. If r_{all} is a biased estimate of r_{pop}, then r_B will generally be biased because it estimates r_{all} rather than r_{pop}. The bias of r_{all} is defined as

$$\mathrm{Bias}\,(r_{all}) = r_{all} - r_{pop},$$

which can be estimated by

$$\widehat{\mathrm{Bias}}(r_{all}) = r_B - r_{all}.$$

Therefore, we computed a bias-adjusted Bootstrap estimate of r as follows:

$$r_{B,adj} = 2 \cdot r_{all} - r_B.$$

The precision of a Bootstrap estimate will depend on how many times the original data are randomly recombined (i.e., how many replicates, m, are performed within a Bootstrap calculation), and the Bootstrap estimate will converge on a stable value as m becomes large (by the law of large numbers). Furthermore, repeated Bootstrap calculations performed with the same number of replicates and the same original data will vary somewhat, because a new sequence of random numbers is used to start the m random recombinations performed within each Bootstrap calculation. In order to evaluate consistency of Bootstrap estimates as a function of the number of replicates performed within a Bootstrap calculation, we compared results for one data set (the 9 June cohort of *D. pulex* control animals) using m = 100, 250, 500, and 1000 replicates. This set of calculations was then repeated 12 times using random, nonrepeated starting points for the random number sequences, in order to evaluate variability among repeated Bootstrap calculations. Values reported in this paper for all other *D. pulex* cohorts and for the two hypothetical cladoceran populations were based on 1000 replicates per Bootstrap calculation.

Confidence interval coverage rates

Confidence intervals surrounding Jackknife and Bootstrap estimates of the per capita rate of increase were calculated by two methods. For the first method, we assumed that sampling distributions of r would be approximately normal. Hence the limits of a 95% confidence interval calculated for Jackknife estimates were given by

$$r_J \pm (t_{n-1,0.95}) \cdot [\widehat{\text{SE}}(r_J)], \quad (2)$$

and for bias-adjusted Bootstrap estimates the limits were given by

$$r_{B,adj} \pm (t_{n-1,0.95}) \cdot [\widehat{\text{SE}}(r_B)], \quad (3)$$

where n = number of individuals in the original sample. In this paper, intervals obtained using this method are referred to as "Jackknife normal-based" and "bias-adjusted, Bootstrap normal-based" estimates of 95% confidence intervals.

For the second method, we took advantage of the information contained in the frequency distributions of the 1000 values of r^* that were generated during each Bootstrap calculation. We computed skewness and kurtosis of these distributions according to Sokal and Rohlf (1981) and determined the 2.5th and 97.5th percentile values ($r^*_{2.5\%}$ and $r^*_{97.5\%}$), in order to encompass the central 95% of the Bootstrap distribution. The interval from $r^*_{2.5\%}$ to $r^*_{97.5\%}$ is a candidate for a 95% confidence interval on r (the percentile method of Efron [1982]); however, it was found through computer simulations that this interval is biased when sampling distributions are skewed. We therefore adopted a bias-corrected percentile method for the Bootstrap (Efron 1982) in order to compute the following asymmetrical 95% confidence interval:

$$95\%\ \text{CI}_{(z)} = [r_{B,adj} - (r_B - r^*_{2.5\%});\ r_{B,adj} + (r^*_{97.5\%} - r_B)]. \quad (4)$$

In addition, we computed a bias-corrected, percentile-based 95% confidence interval that is adjusted for small sample size, as follows:

$$95\%\ \text{CI}_{(t)} = [r_{B,adj} - (t_{n-1,0.95}/1.96) \cdot (r_B - r^*_{2.5\%});\ r_{B,adj} + (t_{n-1,0.95}/1.96) \cdot (r^*_{97.5\%} - r_B)], \quad (5)$$

where 1.96 represents the critical t value for a large sample size (i.e., the $z_{0.05}$ value for a normal distribution). Eq. 5 is an ad hoc adjustment of the bias-corrected percentile method that increased coverage rates; however, there is no formal proof that it will always increase them. Analogous to the technique that is used to calculate 95% confidence intervals for normally distributed variables with small sample sizes, the term $t_{n-1,0.95}/1.96$ expands the width of the bias-corrected confidence interval to compensate for small sample sizes. If the Bootstrap distribution is based on a large sample size (n), then Eq. 5 reduces to Eq. 4. In this paper, intervals obtained using these methods are referred to as "bias-adjusted, Bootstrap percentile-based" estimates of 95% confidence intervals.

To test the reliability of these approximate 95% confidence intervals, we subsampled 10 animals (n = 10) 1000 times from the two hypothetical cladoceran populations described above, computed Jackknife and Bootstrap standard errors and Bootstrap sampling distributions for each population subsample, and calculated how often the resulting 1000 Jackknife and bias-adjusted Bootstrap confidence intervals captured the true r value of the hypothetical population. Observed coverage rates were then compared to the expected coverage rate (950 out of 1000) by a chi-square test with one degree of freedom. Larger population subsamples (n > 10) might have improved precision and accuracy of Bootstrap and Jackknife estimates. However, we chose this sample size for our computer simulations because 10 animals are usually tested in applied cohort studies (e.g., cladoceran chronic toxicity tests).

Estimation biases

Besides testing the reliability of 95% confidence intervals, we compared the 1000 paired Jackknife and bias-adjusted Bootstrap r values that were calculated for each hypothetical population subsample (1) with each other, (2) with the full-sample estimate of r for each population subsample, and (3) with the true population r value to determine whether r_J and $r_{B,adj}$ were biased estimators. We also compared the 1000 paired Jackknife and Bootstrap estimates of SE(r) to determine whether $\widehat{\text{SE}}(r_B) = \widehat{\text{SE}}(r_J)$. Finally, we computed the following mean square error values (MSE) as indexes for overall comparisons of the estimates of r and SE(r):

$$\text{MSE}(r_J) = \frac{1}{1000} \cdot \sum_{i=1}^{1000} (r_{J,i} - r_{pop})^2 = \left[\frac{1}{1000} \cdot \sum_{i=1}^{1000} (r_{J,i} - \bar{r}_J)^2\right] + [(\bar{r}_J - r_{pop})^2] \quad (6)$$

$$\text{MSE}(r_B) = \frac{1}{1000} \cdot \sum_{i=1}^{1000} (r_{B,i} - r_{pop})^2 = \left[\frac{1}{1000} \cdot \sum_{i=1}^{1000} (r_{B,i} - \bar{r}_B)^2\right] + [(\bar{r}_B - r_{pop})^2] \quad (7)$$

$$\text{MSE}[\widehat{\text{SE}}(r_J)] = \frac{1}{1000} \cdot \sum_{i=1}^{1000} [\widehat{\text{SE}}(r_{J,i}) - \text{SE}(r_{all})]^2 \quad (8)$$

$$\text{MSE}[\widehat{\text{SE}}(r_B)] = \frac{1}{1000} \cdot \sum_{i=1}^{1000} [\widehat{\text{SE}}(r_{B,i}) - \text{SE}(r_{all})]^2, \quad (9)$$

where $r_{J,i}$ = Jackknife estimate of r for the ith population subsample; $r_{B,i}$ = Bootstrap estimate of r for the ith population subsample; r_{pop} = true r value of the hypothetical population; $\bar{r}_J = \sum_{i=1}^{1000} r_{J,i}/1000$; $\bar{r}_B = \sum_{i=1}^{1000} r_{B,i}/1000$; $\widehat{\text{SE}}(r_{J,i})$ = Jackknife estimate of SE(r) for the ith

TABLE 2. Per capita rates of increase, with 95% confidence intervals in parentheses, for four laboratory cohorts of *Daphnia pulex*. Calculations* were based on data for 10 individuals per cohort reported by Ingersoll and Winner (1982).

Date cohort born	Per capita rate of increase (d^{-1})			
	Full sample estimate (r_{all})†	Normal-based estimates‡		Percentile-based estimate ($r_{B,adj}$)§
		r_J	$r_{B,adj}$	
9 June	0.327	0.327 (0.307–0.347)	0.326 (0.307–0.346)	0.326 (0.306–0.345)
21 June	0.427	0.427 (0.403–0.450)	0.427 (0.404–0.449)	0.427 (0.404–0.448)
1 July	0.325	0.325 (0.314–0.337)	0.326 (0.314–0.337)	0.326 (0.313–0.337)
9 July	0.350	0.350 (0.319–0.382)	0.350 (0.320–0.381)	0.350 (0.323–0.382)

* For details, see Methods: Jackknife and Bootstrap Calculations.

† r_{all} = per capita rate of increase calculated from the original cohort data.

‡ r_J and $r_{B,adj}$ are the Jackknife and bias-adjusted Bootstrap estimates of the per capita rate of increase, respectively, with 95% confidence limits calculated by Eq. 2 and Eq. 3, respectively.

§ $r_{B,adj}$ = bias-adjusted Bootstrap estimate of the per capita rate of increase, with 95% confidence limits calculated by Eq. 5.

population subsample; $\widehat{\text{SE}}(r_{B,i})$ = Bootstrap estimate of SE(r) for the i^{th} population subsample; and SE(r_{all}) = standard error of the 1000 r_{all} values. On the right-hand side of Eq. 6 and of Eq. 7, the first term inside brackets is the variance of the estimator, and the second term inside brackets is the square of the bias of the estimator.

RESULTS

Daphnia pulex *cohorts*

Per capita rates of increase estimated for the four control cohorts of *D. pulex* are shown in Table 2. Jackknife and bias-adjusted Bootstrap values (r_J and $r_{B,adj}$) rounded to three significant figures differed by no more than 0.001 d^{-1} (≈0.2–0.3%). Furthermore, each value differed from its respective full-sample estimate of r by no more than 0.001 d^{-1}. Confidence intervals estimated by the Jackknife normal-based procedure (Eq. 2); the bias-adjusted, Bootstrap normal-based procedure (Eq. 3); and the bias-adjusted, Bootstrap percentile-based procedure (Eq. 5) were similar. In all cases, corresponding values of upper or lower confidence limits differed by 1.3% or less. Among the four cohorts, though, per capita rates of increase ranged from 0.325 to 0.427 d^{-1}, with the value for the 21 June cohort significantly greater than that for any of the other cohorts ($P \ll .01$; Tukey Method for Pairwise Comparisons [Neter et al. 1985]). There was no apparent temporal trend toward increasing or decreasing r values.

Coefficients of variation in the mean of r ($\widehat{\text{CV}}[r] = \widehat{\text{SE}}[r]/r$) for the control cohorts of *D. pulex* ranged from 1.6 to 3.8%. Coefficients of variation in the mean of brood size ($\widehat{\text{CV}}$[mean brood size] = $\widehat{\text{SE}}$[brood size]/[mean brood size]) for these same cohorts ranged from 5.4 to 9.0%, and coefficients of variation in the mean of total reproduction ($\widehat{\text{CV}}$[mean total reproduction] = $\widehat{\text{SE}}$[total reproduction]/[mean total reproduction]) ranged from 3.2 to 11.5%. In addition, coefficients of variation in mean day to death ($\widehat{\text{CV}}$[mean day to death] = $\widehat{\text{SE}}$[day to death]/[mean day to death]) ranged from 2.6 to 8.2%, where $\widehat{\text{CV}}$[mean day to death] is a measure of variability in survivorship. Therefore, coefficients of variation in the mean of r ranged from approximately one-half to one-third the magnitude of coefficients of variation in the means of the data on reproduction and survival from which the r values had been calculated.

To evaluate between-run variability of the Bootstrap procedure, we repeated Bootstrap calculations 12 times for the 9 June data set. Each time, Bootstrap values were estimated using 100, 250, 500, and 1000 Bootstrap replicates (m) per run. Means of the 12 r_B values calculated using the same number of Bootstrap replicates per run were similar. Specifically, the mean values ranged from 0.32690 (m = 250) to 0.32731 d^{-1} (m = 500), and the standard deviations computed for each set of 12 r_B values ranged from 0.00026 (m = 1000) to 0.00058 d^{-1} (m = 500). Thus, r_B values were consistent to within ≈0.001 d^{-1} (i.e., 2 × SD[r_B]), which is why we rounded all other r values to three significant figures. Means of the 12 standard error values ($\widehat{\text{SE}}[r_B]$) estimated by the Bootstrap procedure (using the same number of Bootstrap replicates per run) also were similar. Specifically, mean $\widehat{\text{SE}}(r_B)$ values ranged from 0.00844 (m = 500) to 0.00877 d^{-1} (m = 100). However, the standard deviation computed for each set of 12 $\widehat{\text{SE}}(r_B)$ values decreased monotonically from 0.00075 (m = 100) to 0.00016 d^{-1} (m = 1000) as the number of Bootstrap replicates increased. Thus, $\widehat{\text{SE}}(r_B)$ values computed using 100 replicates per run were approximately five times as variable as those computed using 1000 replicates per run.

Hypothetical cladoceran population 1

Average Jackknife and bias-adjusted Bootstrap estimates of r based on 1000 subsamples (n = 10) drawn from Hypothetical Population 1 agreed well between

TABLE 3. Jackknife and Bootstrap estimates* of per capita rate of increase (r), based on 1000 subsamples of the hypothetical cladoceran populations.

	Hypothetical Population 1			Hypothetical Population 2		
	True population value	Jackknife estimates	Bias-adjusted Bootstrap estimates†	True population value	Jackknife estimates	Bias-adjusted Bootstrap estimates†
Mean r (d^{-1})	0.374	0.374	0.374	0.313	0.311	0.311
$\widehat{SE}(r)$ (d^{-1})		0.0129	0.0122		0.0329	0.0335
Coverage rate‡						
Using normal-based 95% confidence intervals§		0.944 ($X^2 = 0.758$)	0.934 ($X^2 = 5.389$)		0.965 ($X^2 = 4.737$)	0.964 ($X^2 = 4.126$)
Using percentile-based 95% confidence intervals‖			0.932 ($X^2 = 6.821$)			0.960 ($X^2 = 2.105$)

* Jackknife and bias-adjusted Bootstrap estimates are based on 1000 subsamples of 10 animals each that were randomly drawn from the hypothetical population. For details, see Methods: Jackknife and Bootstrap Calculations.

† 1000 Bootstrap replicates were run within each Bootstrap calculation for each of the 1000 population subsamples.

‡ Coverage rates are expressed as the fraction of times that the 1000 95% confidence intervals captured the true population r value. Chi-square method used to test for significant differences from the expected coverage rate of 0.950 (950 out of 1000). Critical values are: $\chi^2_{1,0.95} = 3.841$, $\chi^2_{1,0.99} = 6.635$.

§ Based on Eqs. 2 and 3.

‖ Based on Eq. 5.

themselves and with the true r value of the population (Table 3). For this hypothetical population, the unadjusted Bootstrap estimate and these three r values were all equal. However, the average Jackknife estimate of SE(r) was 5.7% greater than the average Bootstrap estimate of SE(r). Confidence intervals calculated assuming normal-based distributions (Eqs. 2 and 3) captured the true population r value in 94.4% of the 1000 population subsamples using the Jackknife procedure and in 93.4% of the same 1000 population subsamples using the bias-adjusted Bootstrap procedure (Table 3). Furthermore, 95% confidence intervals calculated using the bias-adjusted, Bootstrap percentile-based method adjusted for small sample size (Eq. 5) captured the true population r value in 93.2% of the 1000 population subsamples. The higher rate of capturing the true population r value using the Jackknife procedure reflects the larger Jackknife $\widehat{SE}(r)$ value relative to the Bootstrap $\widehat{SE}(r)$ value and indicates that the Bootstrap sampling distributions may have been too narrow. Indeed, the Jackknife confidence interval coverage rate did not differ significantly from the expected value of 95% ($P > .05$; Table 3), whereas coverage rates for the Bootstrap normal-based and percentile-based methods were significantly less than 95% ($P < .05$ and $P < .01$, respectively; Table 3). For comparison, Jackknife and Bootstrap confidence intervals captured the true population r value in only 91.3 and 90.0% of the 1000 population subsamples, respectively, when $\widehat{SE}(r)$ was multiplied by the critical z value (1.960) instead of by the critical t value (i.e., when confidence intervals were not adjusted for small sample size). Similarly, the bias-adjusted Bootstrap percentile-based method not adjusted for small samples (Eq. 4) proposed by Efron (1982) captured the true population r value only 89.4% of the time.

Bootstrap estimates of SE(r) for Population 1 were consistently less than or equal to the corresponding Jackknife estimates of SE(r) (Table 4). Yet mean square error for the 1000 Bootstrap estimates of r was only 0.4% less than mean square error for the 1000 Jackknife estimates of r (MSE[r_B] = 0.0001763 and MSE[r_J] = 0.0001770). In addition, MSE($\widehat{SE}[r_B]$) was only 4.2% less than MSE($\widehat{SE}[r_J]$). The 1000 Jackknife and Bootstrap estimates were approximately evenly distributed about the true population r value and were unbiased (Tables 3 and 4). Full-sample estimates of r values for the 1000 population subsamples were also evenly distributed about the true population r value and were unbiased (Tables 3 and 4). Mean skewness (0.025) and kurtosis (−0.082) of the Bootstrap distributions generated for the 1000 subsamples of Hypothetical Population 1 were not significantly different from zero ($P > .5$, Test of Significance of a Statistic; Sokal and Rohlf 1981).

Hypothetical cladoceran population 2

The average unadjusted Bootstrap estimate of r based on 1000 subsamples ($n = 10$) drawn from Hypothetical Population 2 was 2.6% less than the average Jackknife estimate of r, and 3.3% less than the true r value of the population. However, the average bias-adjusted Bootstrap estimate of r equalled the average Jackknife estimate of r (Table 3). The average Jackknife estimate of SE(r) was 1.8% less than the average Bootstrap estimate of SE(r) (Table 3). Confidence intervals calculated assuming normal-based distributions (Eqs. 2 and 3) captured the true population r value in 96.5% of the 1000 population subsamples using the Jackknife procedure, and in 96.4% of the same 1000 population subsamples using the bias-adjusted Bootstrap procedure; 95% confidence intervals calculated using the bias-adjusted, Bootstrap percentile-based method adjusted

for small sample size (Eq. 5) captured the true population r value in 96.0% of the 1000 population subsamples (Table 3). Confidence interval coverage rates for the Jackknife and Bootstrap normal-based methods were significantly greater than the expected value of 95% ($P < .05$; Table 3), whereas the coverage rate for the Bootstrap percentile-based method did not differ significantly from 95% ($P < .05$).

Bootstrap estimates of SE(r) for Population 2 were often greater than or equal to the corresponding Jackknife estimates (Table 4), but mean square error for the 1000 Bootstrap estimates was only 1.9% greater than the mean square error for the 1000 Jackknife estimates (MSE[r_B] = 0.0009642 and MSE[r_J] = 0.0009460). Since the 1000 Jackknife and bias-adjusted Bootstrap estimates were approximately evenly distributed about the true population r value (Table 4), the approximately fivefold increases in MSE(r) values for Hypothetical Population 2 compared to Hypothetical Population 1 were predominantly caused by increased variance in r_B and r_J. Values of mean square errors of $\widehat{\text{SE}}(r)$ were similar in the hypothetical populations; but in Hypothetical Population 2, MSE[$\widehat{\text{SE}}(r_B)$] was 9.1% greater than MSE[$\widehat{\text{SE}}(r_J)$]. Full-sample estimates of r for the 1000 population subsamples tended to be less than the true population r value ($\overline{r_{all}} = 0.307$ d^{-1}, whereas $r_{pop} = 0.313$ d^{-1}; see also Table 4). Mean skewness (−0.774) and kurtosis (1.574) of the Bootstrap distributions generated for the 1000 subsamples of Hypothetical Population 2 were significantly different from zero ($P < .001$, Test of Significance of a Statistic; Sokal and Rohlf 1981).

TABLE 4. Results of comparisons of per capita rates of increase (r) and standard errors estimated by Jackknife and Bootstrap procedures for Hypothetical Cladoceran Populations 1 and 2.

Outcome*	Frequency of occurrence†	
	Hypothetical Population 1	Hypothetical Population 2
$r_{B,adj} < r_J$	0.172	0.366
$r_{B,adj} = r_J$	0.673	0.351
$r_{B,adj} > r_J$	0.155	0.283
$r_{B,adj} < r_{pop}$	0.493	0.488
$r_{B,adj} = r_{pop}$	0.027	0.016
$r_{B,adj} > r_{pop}$	0.480	0.496
$r_J < r_{pop}$	0.489	0.482
$r_J = r_{pop}$	0.036	0.018
$r_J > r_{pop}$	0.475	0.500
$r_{all} < r_{pop}$	0.498	0.539
$r_{all} = r_{pop}$	0.034	0.013
$r_{all} > r_{pop}$	0.468	0.448
$\widehat{\text{SE}}(r_B) < \widehat{\text{SE}}(r_J)$	0.638	0.242
$\widehat{\text{SE}}(r_B) = \widehat{\text{SE}}(r_J)$	0.362	0.288
$\widehat{\text{SE}}(r_B) > \widehat{\text{SE}}(r_J)$	0.000	0.470

* $r_{B,adj}$ = bias-adjusted Bootstrap estimate of per capita rate of increase, based on 1000 replicates per Bootstrap calculation; r_J = Jackknife estimate of per capita rate of increase; r_{pop} = true per capita rate of increase for the hypothetical population; r_{all} = full-sample estimate of per capita rate of increase, calculated from the original data for each population subsample; $\widehat{\text{SE}}(r_B)$ = Bootstrap estimate of SE(r), and $\widehat{\text{SE}}(r_J)$ = Jackknife estimate of SE(r).

† Based on 1000 subsamples of 10 animals each that were randomly drawn from each hypothetical population. For details, see Methods: Estimation Biases.

DISCUSSION

The Bootstrap and Jackknife are two ad hoc, computer-intensive techniques that have become popular for estimating variances of variables when closed-form variance formulas do not exist. Although the theoretical advantages of the Bootstrap procedure over the Jackknife have been touted recently (e.g., Efron 1982), our analyses of *D. pulex* population growth rates showed that the two techniques produce similar results. For these control cohorts (no pollutant exposure) taken from laboratory populations of *D. pulex*, it appeared that normal-based statistical comparisons (e.g., t tests) were valid and that estimation biases were relatively small (<0.3%).

However, comparing results for small cohorts of *D. pulex* that yielded approximatley normal sampling distributions of r does not necessarily validate the procedures. A more appropriate test would be to sample repeatedly from a large population whose true per capita rate of increase is known and whose sampling distribution of r is nonnormal. In this study we created two hypothetical cladoceran populations each containing 1000 parthenogenic females; survival and reproduction schedules for Hypothetical Population 1 yielded approximately normal sampling distributions of Bootstrap r values, whereas Hypothetical Population 2 yielded skewed and kurtotic sampling distributions. For each hypothetical population, we compared 95% confidence intervals that were estimated by assuming (1) normal sampling distributions of r, and (2) skewed sampling distributions of r.

Under the first assumption, confidence intervals were calculated by multiplying the standard error of r times the critical t value at $n - 1$ degrees of freedom (Eqs. 2 and 3). Mosteller and Tukey (1977) recommended this procedure for estimating Jackknife confidence intervals, and our results support their ad hoc recommendation. However, no guidance has previously been proposed in the literature regarding what multiplier should be used to estimate Bootstrap confidence intervals for a normally distributed parameter. In this study, even though data sets were randomly recombined 1000 times within each Bootstrap calculation, the statistical uncertainty in r appeared to be limited by the sample size of the original data ($n = 10$). Confidence intervals calculated using the z value (i.e., the critical t value for infinite sample size) did not capture the true population r values as well as corresponding confidence intervals calculated using the critical t value at $n - 1$ degrees of freedom. Therefore, for populations

whose sampling distributions of r are approximately normal, we recommend that the Bootstrap standard error should likewise be multiplied by the critical t value at $n - 1$ degrees of freedom to estimate a confidence interval on r, where n = sample size of the original data set.

Jackknife and bias-adjusted, Bootstrap normal-based estimates of 95% confidence intervals (Eqs. 2 and 3) tended to be liberal for the population with a normal sampling distribution of r (i.e., they yielded slightly narrower confidence intervals than necessary to capture the true population r value 95% of the time), whereas the confidence intervals tended to be slightly conservative for the population with a skewed sampling distribution of r. However, coverage rates were approximately the same as those attained by selecting the 2.5th and 97.5th percentile values of the skewed, bias-adjusted Bootstrap distributions as interval limits, and then expanding the interval to account for the small sample size of the original data set (Eq. 5).

Our results for normal sampling distributions of r agree with Efron's (1982) conclusion that the Jackknife appears to be a more conservative estimator of 95% confidence intervals than the Bootstrap. But because Bootstrap confidence intervals were slightly larger than Jackknife confidence intervals for skewed sampling distributions of r, it appears that Efron's analysis is not robust. More important, (1) Jackknife estimates of r were as accurate as Bootstrap estimates of r, (2) relative errors in estimating r, as measured by MSE[r], were approximately equal for both methods, and (3) relative errors in estimating SE(r), as measured by MSE($\widehat{\text{SE}}$[r]), did not differ considerably. Therefore, since Jackknife calculations for a data set of 10 replicate animals required only 1% as much computation time as a corresponding Bootstrap calculation incorporating 1000 replicates per run, Jackknifing will usually be more cost-effective when computer time or capacity is limited (e.g., with desk-top computers), and when survivorship and fecundity in a population are similar to those reported in this study.

We have not yet compared Jackknife and Bootstrap techniques using survivorship and fecundity schedules typical of other invertebrate or vertebrate populations. But it appears that the Bootstrap will be superior to the Jackknife only when sample sizes are large, or extremely skewed sampling distributions of r can be expected, such as when juvenile mortality is high (Rago and Dorazio 1984). Even then, the Jackknife may be acceptable if actual 95% confidence interval coverage rates ranging from $\approx$93 to 97% can be tolerated.

Our results do not support Lenski and Service's (1982) conclusions concerning Jackknife estimation procedures. Although they used a Jackknife procedure to estimate λ and Var(λ), their calculations of finite growth rates were based on the premise that individual lives with deterministic survival and reproduction are randomly selected from a population, rather than the premise that survival and reproduction within a given life are independent stochastic events. Based on that analysis, Lenski and Service (1982) discarded the traditional Jackknife procedure that we used in our calculations because they believed that it underestimated Var(λ). Instead, they proposed several modified Jackknife procedures to estimate Var(λ) (their $\widehat{\text{var}}[F'_i]$ and $\widehat{\text{var}}[F''_i]$). But our results show that the traditional Jackknife procedure provides reliable estimates of 95% confidence intervals. Therefore Lenski and Service's (1982) modified Jackknife procedures are extremely conservative, because their results yielded much larger variance estimates than the traditional Jackknife procedure. Rago and Dorazio (1984) extensively critiqued one of those modified Jackknife estimators and demonstrated that it yielded estimates of Var(λ) that were two to three orders of magnitude too large for experimental cohorts of *D. pulex*. Yet Rago and Dorazio's (1984) analysis must also be interpreted with caution. They tested the validity of estimated 95% confidence intervals by asking the question: What percentage of the distribution generated in one Monte Carlo simulation for a cohort of 20 animals was captured by the estimated 95% confidence interval? This criterion only defined a "tolerance interval" for their sampling distributions (Bury 1975), which itself was based on data for only a small subset of the original *D. pulex* population. A more appropriate test would be to subsample repeatedly a large population and determine how often the estimated 95% confidence intervals capture the true population growth rate, thus defining "confidence" in the uncertainty estimates rather than "tolerance" within a given sampling distribution.

If the Bootstrap procedure is used to estimate confidence intervals surrounding per capita rates of increase, we recommend that between 500 and 1000 replicates be run within each Bootstrap calculation for two reasons. First, although the mean r value can be estimated consistently using as few as 100 Bootstrap replicates per run, variability in the standard error of r decreases considerably as the number of Bootstrap replicates increases (e.g., coefficients of variation for 12 standard error values decreased steadily from 8.6% at 100 replicates per calculation to 1.9% at 1000 replicates per calculation, based on the same original data set; see Results: *Daphnia pulex* Cohorts). And second, if the sampling distribution is skewed and Eq. 5 is used to compute a 95% confidence interval, the 2.5th and 97.5th percentile r^* values in a Bootstrap distribution are more consistent when they are selected from a large sampling population. Therefore, between-run variability in 95% confidence intervals will tend to be minimized using 500–1000 Bootstrap replicates per run, whether a normal or skewed distribution of r^* values exists.

Coefficients of variation in per capita rates of increase for *D. pulex* ($\approx$2–4% in this study) were one-half to one-third the magnitude of coefficients of vari-

ation in the mean of reproduction, a variable from which r values are calculated. This trend has also been observed with two other cladoceran species tested in our laboratory at the University of Wyoming, *Daphnia magna* ($\widehat{CV}[r]$ = 0.9% and $\widehat{CV}$[mean total reproduction] = 1.7%; A. Boelter, *personal communication*) and *Ceriodaphnia affinis/dubia* ($\widehat{CV}[r]$ = 1.5–4.8% and $\widehat{CV}$[mean total reproduction] = 3.7–13.5%; D. Brookshire, *personal communication*). This result is surprising, since variability in per capita rates of increase might be expected to be greater than variability in the parameters used to calculate r values (i.e., survival and reproduction). Instead it appears that variability in brood size is poorly correlated among individuals in a population, and that extremes in reproductive output and survival of individuals tend to be dampened at the population level. These results also suggest that if the absolute values of the per capita rate of increase and average total reproduction are equally sensitive to perturbations such as pollutant stress, then the per capita rate of increase should be a more sensitive indicator of population responses to perturbation because variability in estimates of r is lower than variability in estimates of total reproduction.

Temporal variability in r values is also important to consider. For example, we identified a significant difference ($P \ll .01$) in per capita rates of increase among four *D. pulex* cohorts born from the same laboratory stock population during a 1-mo period (Table 2). This result could have been caused by (1) fortuitous sampling; (2) genetic differences between lineages within the stock population; (3) environmentally induced physiological differences between individuals in different cohorts; or (4) differences in nutritional quality of algae fed to the test animals. Although we cannot reject any of these hypotheses, it is obvious that experimental estimates of r values for a stock population of *D. pulex* can change drastically over a short time interval. Supporting this conclusion, Parkhurst et al. (1981) reported significantly different reproduction among four cohorts of control *D. magna* born from a laboratory stock population over a 1-yr period. In their study, the average number of young produced per control female in a 28-d test was ≈50% greater than the average number of young produced per control female in an identical test conducted 3 mo later. Furthermore, average reproduction in the presence of a toxicant, acridine, varied by up to 300% throughout the year. Those results suggest that per capita rates of increase repeatedly estimated for the same laboratory population of cladocerans may vary considerably more than the 30% differences in r values that we calculated for cohorts of control animals born during a 1-mo period in Ingersoll and Winner's (1982) study.

Finally, the Jackknife and Bootstrap are generally accepted as reliable techniques for estimating parameter bias that is introduced by randomly subsampling large populations (see Efron 1982). Although we found that the full-sample estimate of r calculated for a small population subsample can be a biased estimator of the true per capita rate of increase, the relative bias was only a 0.13% overestimate of the true population r value for an approximately normal sampling distribution of r, and a 1.9% underestimate of the true population r value for a negatively skewed sampling distribution of r. Jackknife and Bootstrap estimates of r were also close to the true population r value for the normal sampling distribution of r (0.2% overestimation bias). Moreover, Jackknife and bias-adjusted Bootstrap estimates of r were closer to the true population r value for the negatively skewed sampling distribution of r (0.6% underestimation bias) than were full-sample estimates of r, illustrating that Jackknife and Bootstrap estimates can reduce sampling bias. For normal sampling distributions of r, this bias is small relative to $\widehat{CV}(r)$. But for nonnormal sampling distributions of r, the bias is more important. Lenski and Service (1982) and Rago and Dorazio (1984) demonstrated that sampling bias can be decreased by increasing the size (n) of population subsamples.

In summary, we conclude that the Jackknife technique is often as good as the Bootstrap for estimating 95% confidence intervals surrounding per capita rates of increase for *D. pulex* populations. Given the uncertainty surrounding population growth rates of several cladoceran species reported here, we believe that population biologists should suppress their penchant for reporting per capita rates of increase to more than three significant figures and begin questioning the reliability of r values reported to even two significant figures. Instead of ignoring variability, population modelers should adopt stochastic techniques recently developed by O'Neill et al. (1982) for estimating uncertainty in ecosystem models. And applied population biologists attempting to predict the potential effects of human activities on populations, communities, and ecosystems should appreciate the many potential sources of uncertainty associated with estimating per capita rates of increase from laboratory and field data.

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LITERATURE CITED

Arden, B. W., and K. N. Astill. 1970. Numerical algorithms: origins and applications. Addison-Wesley, Reading, Massachusetts, USA.

Bury, K. V. 1975. Statistical models in applied science. John Wiley and Sons, New York, New York, USA.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, Chichester, England.

Daley, D. J. 1979. Bias in estimating the Malthusian parameter for Leslie matrices. Theoretical Population Biology **15**:257–263.

Diaconis, P., and B. Efron. 1983. Computer-intensive methods in statistics. Scientific American **248**:116–130.

Efron, B. 1982. The Jackknife, the Bootstrap and other resampling plans. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania, USA.

Fisher, R. A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford, England.

Ingersoll, C. G., and R. W. Winner. 1982. Effect on *Daphnia pulex* (DeGeer) of daily pulse exposures to copper or cadmium. Environmental Toxicology and Chemistry **1**:321–327.

Keyfitz, N. 1977. Introduction to the mathematics of populations (with revisions). Addison-Wesley, Reading, Massachusetts, USA.

Lenski, R. E., and P. M. Service. 1982. The statistical analysis of population growth rates calculated from schedules of survivorship and fecundity. Ecology **63**:655–662.

Lotka, A. J. 1907*a*. Studies on the mode of growth of material aggregates. American Journal of Science **24**:199–216.

———. 1907*b*. Relation between birth rates and death rates. Science **26**:21–22.

Mosteller, F., and J. W. Tukey. 1977. Data analysis and regression. Addison-Wesley, Reading, Massachusetts, USA.

Neter, J., W. Wasserman, and M. H. Kutner. 1985. Applied linear statistical models. Second edition. Richard D. Irwin, Homewood, Illinois, USA.

O'Neill, R. V., R. H. Gardner, L. W. Barnthouse, G. W. Suter II, C. W. Gehrs, and S. G. Hildebrand. 1982. Ecosystem risk analysis: a new methodology. Environmental Toxicology and Chemistry **1**:167–177.

Parkhurst, B. R., J. L. Forte, and G. P. Wright. 1981. Reproducibility of a life-cycle toxicity text with *Daphnia magna*. Bulletin of Environmental Contamination and Toxicology **26**:1–8.

Rago, P. J., and R. M. Dorazio. 1984. Statistical inference in life-table experiments: the finite rate of increase. Canadian Journal of Fisheries and Aquatic Sciences **41**:1361–1374.

Service, P. M., and R. E. Lenski. 1982. Aphid genotypes, plant phenotypes, and genetic diversity: a demographic analysis of experimental data. Evolution **36**:1276–1282.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman, San Francisco, California, USA.

Tukey, J. 1958. Bias and confidence in not quite large samples. Annals of Mathematical Statistics **29**:614.