Exact confidence intervals for population growth rate, longevity and generation time

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Abstract

By quantifying key life history parameters in populations, such as growth rate, longevity, and generation time, researchers and administrators can obtain valuable insights into population dynamics. Although point estimates of demographic parameters have been employed since the inception of demography as a scientific discipline, the construction of confidence intervals has typically relied on approximations through series expansions or computationally intensive techniques. This study introduces a novel method for accurately calculating confidence intervals for the aforementioned life history traits when individuals are unidentifiable and data are presented as a life table. These confidence intervals are determined by utilising the statistical properties of known life history trait estimates. The key finding is the accurate estimation of the confidence interval for r, the instantaneous growth rate, which is tested using Monte Carlo simulations with four arbitrary discrete distributions. In comparison to the bootstrap method, the proposed interval construction method proves more efficient, particularly for experiments with a total offspring size below 400. We discuss handling cases where data are organised in extended life tables or as a

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matrix of vital rates.

Keywords: Confidence intervals, Generation time, Population growth rate, Life history traits, Life table, Longevity

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1. Introduction

Estimating life history traits (LHTs), such as growth rate, longevity, and generation time, can provide critical insights into population dynamics. The finite growth rate, λ, is a particularly important parameter, as it measures the number of individuals produced per unit of time per individual. The instantaneous growth rate, r, is a related measure, where $\lambda = e^r$. When $r > 0$, the population is growing. However, estimating the growth rate is usually made by following the life cycle from a sample of individuals, which introduces natural errors into the life history trait estimates, highlighting the importance of calculating confidence intervals. Despite this being a substantial problem, there are currently no specific mathematical expressions for calculating confidence intervals that are functions of the sample size, among other quantities.

Matrix projection models, which include the Leslie matrix for age-classified populations and the Lefkovitch matrix for populations classified into arbitrary life stages, relate the number of individuals in a particular age or stage category at time t, $\mathbf{n}_t$, to that at time $t+1$ as $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$, where $\mathbf{A}$ is the matrix of vital rates. The growth rate, λ, is estimated by finding the largest positive eigenvalue of $\mathbf{A}$ [see 1].

There are two main approaches to constructing confidence intervals for the growth rate, namely the *series expansion* and the *numerical methods*, with the latter mostly based on resampling. [2] was the first to use the theory of series expansions to approximate the variance of functions of random variables, known in statistics as the *delta method*, to derive approximations to the variance of the growth rate λ [see also 3, 4, 5]. Series approaches assume that errors

in estimating the vital rates are small, allowing for straightforward derivation of confidence intervals. The variance estimate for the growth rate, $\hat{\lambda}$, can be obtained through a series expansion involving the estimated vital rates a_{ij}, the elements of $\mathbf{A}$. This method can be extended to estimate other LHTs.

In contrast, computer-intensive methods such as resampling, specifically bootstrap and jackknife, are used to estimate confidence intervals for LHTs [6]. Bootstrap involves resampling from the original sample and analysing the variation in estimates, while jackknife involves excluding observations. [7] showed that jackknife is an approximation to bootstrap. Both methods were once computationally demanding, but advances in computing power now allow for a large number of iterations to be performed quickly on most desktop computers. Bootstrap assumes that sampling with replacement from the original sample of size n mimics taking a sample of size n from a larger population. It has been widely used [see 8] but it may not work well for small samples. Overall, both methods, series expansion and resampling approaches are effective for estimating confidence intervals for LHTs, with each method offering unique advantages and limitations depending on the size and characteristics of the sample.

Monte Carlo simulations are a class of computer-intensive methods used to estimate LHTs in population projection models. These methods assume that the distribution of the estimates is known, allowing for sampling from that distribution to obtain a new dataset that is then analysed to obtain LHTs. For instance, in a matrix model for a stage-classified population, the fraction of individuals moving from stage i to stage j at the next unit of time can be represented as a_{ij}. If there are $\mathbf{n}_t(i)$ individuals in stage i at time t, a Binomial $(\mathbf{n}_t(i), a_{ij})$ distribution can be used to simulate the number of individuals moving from i to j. All events that may occur at the next unit of time, such as transitions between stages, reproduction and deaths must be simulated, and the simulation stops

at a specified time or when the population reaches an equilibrium (that may include extinction). Each simulation produces a series of LHTs, which are then used to infer statistical properties such as the mean, variance, and confidence intervals for these parameters. [see 9]. The Monte Carlo simulation method can be computationally intensive, but it can be useful for situations where other methods are not applicable or practical.

However, the assumption that the vital parameters are known is particularly difficult to fulfil in small samples. In matrix models characterised by stage-classified populations, the matrix $\mathbf{A}$ can be decomposed as $\mathbf{A} = \mathbf{U} + \mathbf{F}$, where $\mathbf{F}$ represents a matrix of fertilities and $\mathbf{U}$ signifies a matrix of stage transitions. The latter can be treated as the transpose of a Markov chain with transient states. [10] derived the variance of certain life history traits using limiting distribution results for passage times, as delineated by [11]. For example, if $\mathbf{N}$ = $(\mathbf{I}$ - $\mathbf{U})^{-1}$, the expected longevity $E[L]$ is provided by the sum of the first column of the elements in the matrix $\mathbf{N}$, and the variance of longevity is given by:

$$V[L] = \mathbf{1}'\mathbf{N}(2\mathbf{N} - \mathbf{I})\mathbf{v}_1 - E[L] * E[L]$$

with $\mathbf{v}_1$ being a vector of zeros with a 1 in the first entry. Nevertheless, this and other expressions assume that the parameters of the transition matrix $\mathbf{U}$ have been estimated without error, a notion that is evident given the absence of n, the sample size, in the mathematical expressions. To illustrate how this becomes a problem, consider X to be the number of attempts required to roll a six on a die, which is $1/p$, with $p = 1/6$ and the variance being $(1-p)/p^2$. However, if p is unknown and must be estimated by rolling the die until the first six is obtained and then repeating this experiment n times, the variance of X, depends not only on p but also on the number of experiments, n. Consequently, the variance is greater than $(1-p)/p^2$. In this scenario, if $\mathbf{U}$ is treated as a

Markov chain, the results on expectation and variances presented in [10] do not differ from those that would be obtained using a Monte Carlo approach, previously described. Recall that the variance of a random variable Y that depends on an estimate of a parameter $\hat{p}$ is

$$V[Y] = E[V(Y|\hat{p})] + V[E(Y|\hat{p})].$$

By assuming $p = \hat{p}$, we are taking $V[Y] = E[V(Y|\hat{p})] = V[Y|p]$ and neglecting the second term. In general, the demographic literature lacks comprehensive discussions on the statistical properties of estimates for the aforementioned life history traits. In the present study, we demonstrate how to derive point and interval estimates of longevity (L), generation time (μ_1), and the instantaneous growth rate (r) using only the statistical properties of these estimates.

1.1. Data organisation

In many cases, individuals within a population can be identified, enabling the tracking of age at reproduction, total offspring size per individual, and time until death. However, in certain stage-classified population analyses and models, individuals are not identifiable, allowing researchers only to determine the number of individuals in each stage at time t. Newborns can be counted per time unit, but their mothers cannot be identified, a situation referred to as *anonymous reproduction*. The most limiting scenario arises when only the total number of living individuals and total newborns at each time unit are known. In this study, we address this specific situation where only three data columns are available: time units, number of living individuals, and offspring produced during each time unit. It is important to note that this represents the least informative scenario, as all other data organisation (counts per stage or knowledge of offspring per individual at every unit of time) can be condensed to the data

format utilised here. In other words, the point and interval estimates proposed in this study can be applied to more complex forms of data organisation beyond life tables.

Given these constraints, we are unable to provide variance estimates for R_0, the *basic reproductive number*, which is considered one of the most critical parameters in demography. As we will demonstrate, R_0 is the quotient of two easily observed quantities that measure individuals' reproductive capacity. However, our assumption of anonymous reproduction prevents the assignment of offspring to individuals and, consequently, the acquisition of measures of variation. Considering the close relationship between r and R_0 highlighted in [12], providing intervals for r serves as a means of addressing uncertainty regarding the population's growth rate.

2. Methodology

2.1. Notation

Throughout this study, we employ vector notation, denoting a vector as $\mathbf{x}$, where $x(i)$ represents the i-th element of $\mathbf{x}$. The product $\mathbf{x}'\mathbf{y}$ refers to the cross-product of two vectors, yielding a scalar. The element-by-element multiplication of two vectors is denoted by $\mathbf{x} \circ \mathbf{y}$, which is also known as the Hadamard product and results in a vector.

We assume that our data is organised in a traditional life table format, containing only three columns: a column $\mathbf{t}$ representing the discrete time units at which events were recorded (starting with $t(1) = 1$) and two additional columns $\mathbf{n}$ and $\mathbf{h}$ representing the number of individuals alive and newborns, respectively. Using this initial information, we generate two additional columns: $\mathbf{g}$ and $\mathbf{f}$. First, we define $K = \sum h(i)$ as the total offspring produced during the study period, and N as the initial number of individuals, that is, $n(1)$. The vector

$\mathbf{g}$ is an estimate of the probability mass function of the time to reproduction, obtained by normalising $\mathbf{h}$, that is, $\mathbf{g} = \mathbf{h}/K$. The vector $\mathbf{f}$ contains elements $f(i) = [n(i) - n(i+1)]/N$, representing the number of individuals that died in the i-th interval. Note that $\mathbf{f}$ is one element shorter than $\mathbf{n}$, so we append a 0 at the bottom of $\mathbf{f}$ to maintain compatibility with the other arrays. $\mathbf{f}$ is an estimate of the distribution of deaths.

To construct confidence intervals of size $1 - \alpha$, we will use a value $Z_{1-\alpha}$ representing the $1 - \alpha$ quantile of a standard Normal distribution.

3. Longevity

The life history trait *Longevity* (L) is defined as the expected number of time units that an individual survive. It can be calculated using the fraction of individuals that survive up to time t denoted by $l(t)$, where t represents the time units. Specifically, we have:

$$L = \sum_{t=1} l(t),$$

Note that $l(t) = n(t)/N$, where $n(t)$ is the number of individuals alive at time t, and N is the initial number of individuals. Thus, an estimate of L, denoted by $\hat{L}$, is given by:

$$\hat{L} = \sum_{t=1} l(t) = \sum_{t=1} \frac{n(t)}{N}. \tag{1}$$

To calculate the variance of the estimate $\hat{L}$, we can recalculate equation (1) in an alternative way. Let X be a random variable representing the time to death. Then, we have:

$$L = \sum_{t=1} l(t) = \sum_{t=1} P(X > t) = \sum_{t=1} t\ P(X = t) = E[X],$$

since $P(X = t)$ is estimated with $\mathbf{f}$, we can estimate the mean and variance of the Longevity L using:

$$\hat{\mu}_L = \sum_{t=1} t\ f(t) = \mathbf{t}'\mathbf{f} \tag{2}$$

$$\hat{\sigma}_L^2 = \sum_{t=1} t^2 f(t) - (\hat{\mu}_L)^2 = (\mathbf{t} \circ \mathbf{t})'\mathbf{f} - (\hat{\mu}_L)^2. \tag{3}$$

As we can see from (1), $\hat{L}$ is an average and consequently, it follows a Normal distribution with mean $\hat{\mu}_L$ and variance $\hat{\sigma}_L^2$. A confidence interval of size $1 - \alpha$ for L is:

$$\hat{\mu}_L \ \pm\ Z_{1-\alpha}\ \hat{\sigma}_L/\sqrt{N}. \tag{4}$$

4. $\mathbf{R_0}$, the Basic Reproductive Number

The *Basic reproductive number* (R_0) also known as the *net reproductive net* is a fundamental quantity in population biology that measures the average number of offspring produced by an individual over its lifetime. We can estimate R_0 using equation (5), where $l(t)$ is estimated with $n(t)/N$, representing the fraction that survives up to time t and $m(t)$, the fraction of total offspring produced per individual at time t with $h(t)/n(t)$.

$$R_0 = \sum_{t=1} l(t)\ m(t). \tag{5}$$

R_0 is required to calculate the *Mean generation time*. However, we cannot provide the variance of our estimate of R_0 unless some distributional assumptions (that we do not want to concede here) are made.

We can simplify equation (5) using the fact that $l(t) = n(t)/N$ and $m(t) =$

$h(t)/n(t)$. Thus, we have:

$$R_0 = \sum_{t=1} \frac{n(t)}{N} \frac{h(t)}{n(t)} = \sum_{t=1} \frac{h(t)}{N} \tag{6}$$

$$= \frac{1}{N} \sum_{t=1} h(t) = \frac{K}{N}. \tag{7}$$

Since K is the total offspring produced in the study period and N is the initial number of individuals, R_0 is the total offspring divided by the initial number of individuals. Strictly, since N is the initial number of individuals and these are usually newborns, R_0 is the total number of newborns produced by a newborn. If an individual goes through a series of M stages namely $S_1, S_2, \ldots, S_M$, R_0 is the average number of individuals of stage j produced by an individual of the same stage. Whatever j we choose, the result should be the same, although is easier to start with newborns.

Sometimes it is argued that since only females produce offspring, the analysis of R_0 should be done considering females only. Equation (6) shows that this discussion is irrelevant. Nevertheless, it is preferable to include all individuals, males and females, since larger sample sizes are associated with smaller standard deviations, which is evident in the second term in equation (4). Furthermore, for some species, incorporating sex differentiation may introduce an additional layer of complexity that could potentially burden the analysis.

5. The Generation Time μ_1

The generation time, denoted by μ_1, is defined as the average age of females at the time they bear each offspring, taking into account that a mother can have multiple offspring at different ages. It can be calculated using the following formula:

$$\mu_1 = R_0^{-1} \sum_{t=1} (t - 1 + c)\ l(t)\ m(t). \tag{8}$$

were as previously explained $l(t)$ and $m(t)$ represent the fraction of individuals surviving up to time t and the average number of offspring per individual at time t, respectively, and c is the time within the interval where individuals are born, for instance $c = 0$ if births occur at the beginning and $c = 1$ if births occur at the end [see 13]. In what follows we set $c = 1$.

The estimates for $l(t)$ and $m(t)$ are obtained using $n(t)/N$ and $h(t)/n(t)$, respectively. By substituting $R_0 = K/N$, we can rewrite (8) as:

$$\begin{aligned} \mu_1 &= \frac{N}{K}\sum_{t=1} t\ \frac{n(t)}{N}\frac{h(t)}{n(t)} = \sum_{t=1} t\ \frac{h(t)}{K} \\ &= \sum_{t=1} t\ g(t). \end{aligned} \tag{9}$$

Here, $g(t)$ represents the fraction of eggs laid at time t.

To calculate the mean and variance of the generation time, we can define a random variable T as the age at bearing as:

$$\hat{\mu}_T = \sum_{t=1} t\ g(t) = \mathbf{t}'\mathbf{g} \tag{10}$$

$$\hat{\sigma}_T^2 = \sum_{t=1} t^2 g(t) - (\hat{\mu}_T)^2 = (\mathbf{t} \circ \mathbf{t})'\mathbf{g} - (\hat{\mu}_T)^2. \tag{11}$$

It is important to note that in equation (9), $\sum t\ h(t)$ represents the sum of the mothers' ages at which each of the K offspring was produced. As a result, $\hat{\mu}_T = \sum t\ h(t)/K$ is an average over K observations, and subsequently, it follows a Normal distribution with a mean of $\hat{\mu}_T$ and a variance of $\hat{\sigma}_T^2$. A confidence interval with a size of $1 - \alpha$ for T can be expressed as follows:

$$\hat{\mu}_T \ \pm\ Z_{1-\alpha}\ \hat{\sigma}_T/\sqrt{K} \tag{12}$$

6. The *instantaneous rate of population growth, r*

This is the value such that:

$$\sum_{t=1} e^{-rt}\ l(t)\ m(t) = 1. \tag{13}$$

Recall $l(t)$ is estimated with $n(t)/N$ and $m(t)$ with $h(t)/n(t)$. Since $R_0 = K/N$, we substitute these values in (13):

$$\begin{aligned}
\sum_{t=1} e^{-rt}\ \frac{n(t)}{N}\frac{h(t)}{n(t)} &= 1 \\
\sum_{t=1} e^{-rt}\ \frac{h(t)}{N} &= 1 \\
\frac{K}{N}\sum_{t=1} e^{-rt}\ \frac{h(t)}{K} &= 1
\end{aligned}$$

but $g(t) = h(t)/K$ is the distribution of female age at offspring, and $K/N = R_0$, thus:

$$\sum_{t=1} e^{-rt}\ g(t) = R_0^{-1} \tag{14}$$

[see 12]. The solution for r can be found using numerical methods. From here, λ, the *population growth rate* is $\lambda = e^r$.

6.1. Confidence intervals for r and λ

First we rewrite (14) as:

$$\sum_{t=1} s^t\ g(t) = R_0^{-1} \tag{15}$$

with $s = e^{-r}$. The left side of (15) is the *Probability generating function* (pgf) of $g(t)$, that is, $E[s^t]$, provided that $|s| \leq 1$. Clearly, for $r > 0$ this requirement is fulfilled. The situation $r < 0$ will be discussed later in this section.

The following result regarding probability generating functions is well known: [see 14]:

Let $x_1, x_2, x_3, \ldots, x_n$, be a random sample from a discrete distribution F over $0, 1, 2, \ldots$, with corresponding probabilities $p_i, i = 0, 1, 2, \ldots$. The *empirical probability generating function* (epgf) is defined as:

$$\phi_n(s) = \frac{1}{n} \sum_{i=1}^{n} s^{x_i} \tag{16}$$

for $|s| < 1$. This transform of the empirical distribution function F_n, is an estimator of

$$\phi(s) = E[s^X] = \sum_{i=0}^{\infty} s^k \ p_k \ , \qquad |s| < 1,$$

the pgf associated to F. For each fixed s, $\phi_n(s)$ is an unbiased estimator of $\phi(s)$. Moreover, by the law of large numbers $\phi_n(s)$ is a consistent estimator for $\phi(s)$, and by the central limit theorem

$$n^{1/2}[\phi_n(s) - \phi(s)]$$

converges in distribution to a Gaussian random variable with zero mean and variance $\sigma^2(s) = \phi(s^2) - (\phi(s))^2$. $\square$

We will use the previous results on epgf to derive confidence intervals for r in (14).

Suppose that p_k is known, and that the solution of s in $\sum_{t=1} s^t \ g(t) = R_0^{-1}$ is θ, then let:

$$\mu = R_0^{-1} = \sum_{t=1} \theta^t \ g(t) \tag{17}$$

$$\sigma^2 = \sum_{t=1} \theta^{2t} \ g(t) - \mu^2 \tag{18}$$

then

$$n^{1/2}[\phi_n(\theta) - R_0^{-1}]/\sigma$$

follows a $N(0,1)$ distribution. In other words, for our fixed θ-value, the epgf $g_n(\theta)$ follows a Normal distribution with mean R_0^{-1} and variance σ^2/n, with σ^2 as in (18).

Let $\mathbf{x} = \{x_1, x_2, x_3, \ldots, x_n\}$, be a random sample from X. If θ were known, then, by the distribution properties of $\phi_n(\theta)$, evaluating the epgf at θ in this sample would yield:

$$\phi_n(\theta) = R_0^{-1} + W$$

were W follows a $N(0, \sigma/\sqrt{K})$ distribution. We could use this expression to estimate θ by solving for θ above, but W is not observable. Nevertheless, the distributional properties of $\phi_n(\theta)$ guarantees there are two values L and U such that

$$P(L < \phi_n(\theta) < U) = 1 - \alpha$$

which are clearly $R_0^{-1} \pm Z_{1-\alpha}\sigma/\sqrt{K}$. Therefore, *the solution* for s in $g_n(s) = 1/R_0$ will range between (θ_L, θ_U) with probability $1 - \alpha$ if θ_L and θ_U are the solutions of:

$$\begin{aligned} \sum_{t=1} \theta_L^t \; g(t) &= R_0^{-1} - Z_{1-\alpha}\sigma/\sqrt{K} \\ \sum_{t=1} \theta_U^t \; g(t) &= R_0^{-1} + Z_{1-\alpha}\sigma/\sqrt{K} \end{aligned}$$

recall that the sample size for this parameter is K, the total offspring.

6.2. Implementation of the epgf method

In practice, we use $\exp(-r)$ instead of θ, and the observed vector $\mathbf{g}$ as an estimate of $g(t)$. We obtain R_0 from the data, then we estimate r with $\hat{r}$, the

solution for s in:

$$\exp(-s\ \mathbf{t}')\ \mathbf{g} = \mu, \tag{19}$$

with $\mu = 1/R_0$. Then use this r-value in (18) to estimate σ^2 with:

$$\hat{\sigma}^2 = \exp(-2\ r\ \mathbf{t}')\ \mathbf{g} - \mu^2 \tag{20}$$

and derive confidence intervals as the solutions of r_L and r_U in:

$$\exp(-r_L\ \mathbf{t}')\ \mathbf{g} = R_0^{-1} + Z_{1-\alpha}\hat{\sigma}_T/\sqrt{K} \tag{21}$$

$$\exp(-r_U\ \mathbf{t}')\ \mathbf{g} = R_0^{-1} - Z_{1-\alpha}\hat{\sigma}_T/\sqrt{K} \tag{22}$$

Similarly, point an interval estimates of the same size for λ are:

$$\begin{aligned} \lambda &= e^r \\ (\lambda_L, \lambda_U) &= (e^{r_L}, e^{r_U}). \end{aligned} \tag{23}$$

We develop a full exercise in the Appendix applying these formulae, but first, we will test the accuracy of the interval proposed with Monte Carlo simulations.

6.3. A cautionary note

It is important to note that the theory presented earlier, concerning epgf's, is strictly valid only when $r > 0$, implying that it seems to be functional exclusively when the instantaneous growth rate r is greater than 0. The condition $r > 0$ has been established to ensure that the sum in equation (15) converges to a finite value, as we must remember that function $g(t)$ is defined for $t = 1, 2, 3, \ldots, \infty$. However, in real-life experiments, we utilise a function $g(t)$ defined for a shorter set of t-values, thus the sum converges for a broader range of r-values, including negative values. The advice is simple: if a numerical solution for r exists in

equation (15) (which could be negative), then the sum has converged, and that solution serves as our estimate of r.

Another crucial consideration pertains to the assumption of independence between samples. To establish confidence intervals for the population growth rate r, we utilise the distribution $\mathbf{g}$, which represents the age distribution of mothers at birth. Although the time of birth for two individuals from different mothers is independent, the time of birth for those from the same mother is not. To visualise this more clearly, imagine that we could collect the data in a matrix wherein each row contains the ages of a single mother at the time of each of her offspring's births; data between rows are independent, but data within rows are not. The larger the rows, the more significant the violation of independence required to utilise the theory of epgfs. That is, the larger R_0, the less independence in the whole dataset, unless N is even larger. Generally, the closer the value of $|s|$, the solution of equation (15) is to 1, the better the approximation to the Normal distribution of the empf. However, as seen in (15), this depends strongly on the size of R_0. Thus, the closer R_0 is to 1, the better the approximation of the epgf.

6.4. Simulations

The primary objective of these simulations is to assess the accuracy of expressions (21) and (22) by applying them to four arbitrarily selected discrete distributions that are described below. For each distribution, we calculate point and interval estimates of r using Sec. 6.2 where $\mathbf{g}$ is the known distribution. Then we conduct 10^5 simulations, with each simulation j executed as follows:

1. Sample n values from the target distribution and obtain $x_1, x_2, x_3, \ldots, x_n$.
2. Compute $g_n^{(j)}(\theta)$ using (16) for this sample.
3. Determine the solution for s in (19) for this sample and denote it as $s(j)$.
4. Estimate the growth r for this sample as $r(j) = -\log(s(j))$.

The mean and variance of $g_n^{(\cdot)}(\theta)$ should be equivalent to μ and σ^2/n, respectively. Finally, we calculate the fraction of the $r(j)$'s that fall within the theoretical CI for r provided in (21) and (22).

6.5. Distributions used.

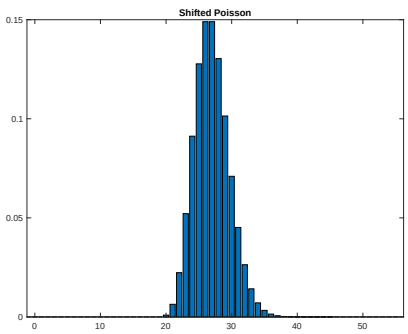
The following four distributions were used in the simulations:

1. Distribution 1. A Shifted Poisson distribution where $P(Y = y) = P(X = y - 20)$, with X being a Poisson random variable with a parameter of 7. In this case, $Y = 20, 21, 22, \ldots$, (Fig. 1a).
2. Distribution 2. Poisson mixture. Two Poisson random variables X and Y were generated with respective parameters of 30 and 60. The resulting distribution is bimodal, and the random variable W is defined such that $P(W = k) = (P(X = k) + P(Y = k))/2$, (Fig. 1b).
3. Distribution 3. Discretized Beta. For $t = 0, 1, 2, \ldots, 200$, we calculated the probability mass function (pmf) of the random variable Y as $P(Y = t) = P(X = t/200)/c$, where X is a Beta $(1/2, 1/2)$ distribution and $c = \sum_{t=1}^{200} P(X = t/200)$, (Fig. 1c).
4. Distribution 4. Similar to the previous distribution, but with X being a Beta $(2, 2)$ distribution, (Fig. 1d).

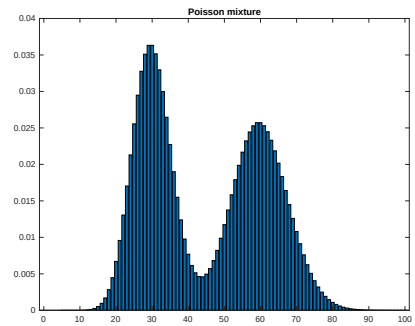
In all distributions, the value of R_0 in equation (15) is arbitrarily selected as a constant for testing purposes.

7. Results

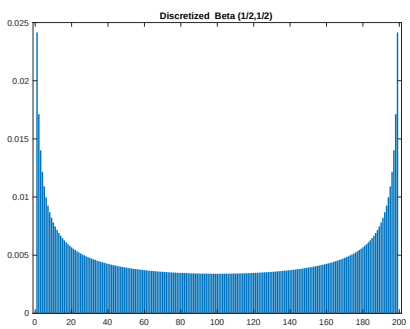
In this study, Monte Carlo simulations were not employed to evaluate the confidence intervals for longevity and mean generation time provided in (4) and (12) because of the robust and unambiguous statistical foundations underlying the distribution of the sample mean. Instead, due to the less familiar nature of



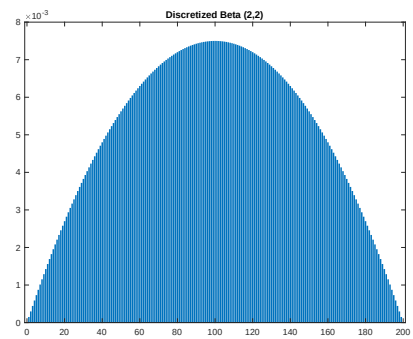
(a) A Shifted Poisson distribution.



(b) A mixture of two Poisson.



(c) Discretized Beta $(1/2, 1/2)$



(d) Discretized Beta $(2, 2)$

Figure 1: Distributions used in the Monte Carlo simulations described in Sec. 6.2.

the empirical probability generating function $\phi_n(\theta)$, we focused our efforts on testing the confidence intervals for the growth rate.

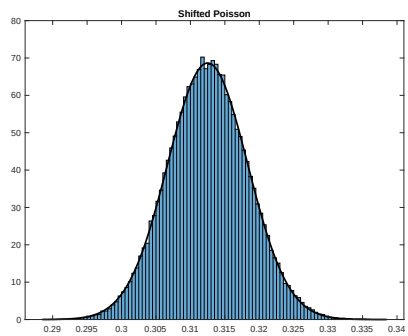
The distributions employed for the age of mothers at reproduction in our simulations may be questionable, particularly distributions 2 and 3, but our objective was to test the estimates in situations that include distributions far from bell-shaped. From Table (1) and Figs (2a -2d), it can be observed that the distribution of the epgf $g_n(t)$ closely aligns with a Normal distribution, with parameters as predicted. It is worth noting that we did not use large sample sizes in all cases, which could have increased the similarity between observed and expected distributions. Table (2) demonstrates that the fraction of the 10^5 simulations falling inside the confidence interval closely matches the expected

outcome across all tested distributions.

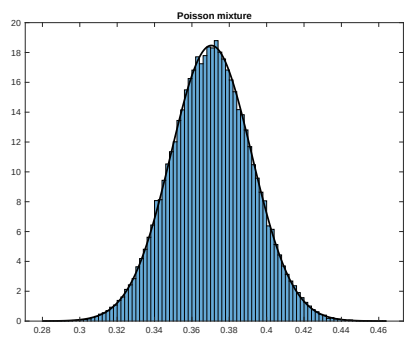
Table 1: Comparison of first two moments of the theoretical and empirical distributions for $g_n(\theta)$

Distribution	n	R_0	μ^*	$\hat{\mu}^\dagger$	$\sigma^\star/\sqrt{n}$	$\hat{\sigma}^\ddagger$
1	40	3.2	0.3125	0.3125	0.0056	0.0056
2	40	2.7	0.3704	0.3703	0.0216	0.0216
3	50	2.5	0.4000	0.4002	0.0432	0.0432
4	50	5.0	0.2000	0.2001	0.0250	0.0251

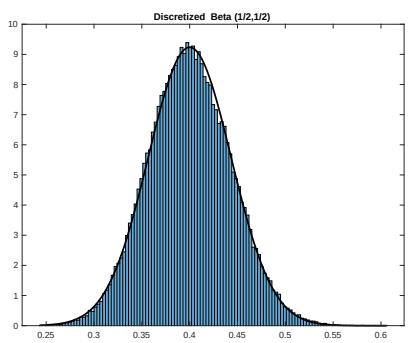
* Using (17). * Using σ obtained in (20).
† The average of $g_n^{(\cdot)}(\theta)$. ‡ The s.d. of $g_n^{(\cdot)}(\theta)$.



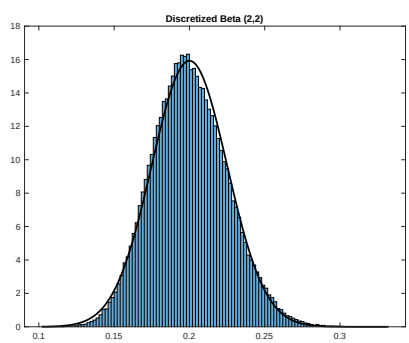
(a) Histogram of $g_n(\theta)$ for dist. 1.



(b) Histogram of $g_n(\theta)$ for dist. 2.



(c) Histogram of $g_n(\theta)$ for dist. 3.



(d) Histogram of $g_n(\theta)$ for dist. 4.

Figure 2: The histograms illustrate the observed distribution of $g_n(\theta)$ for each distribution, employing θ as the solution for s in (16). The superimposed distribution represents the theoretical (Normal) distribution, with mean and variance specified in (17) and (18). A comparison of the first two moments for the theoretical and empirical distributions of $g_n(\theta)$ is presented in Table 1.

Table 2: Theoretical (r) and empirical ($\hat{r}$) values of the growth rate. The Table shows the $\mathrm{CI}_{1-\alpha}$ and the fraction of samples where the estimated r was inside the predicted interval for $\alpha = 0.1, 0.05$ and 0.01. Results of 10^5 simulations as described in Sec. 6.4.

Distribution	n	r^*	$\hat{r}^\dagger$	$1-\alpha$	$r_L^\star$	$r_U^\star$	$p \in (r_L, r_U)^\ddagger$
1	40	0.0433	0.0433	0.90	0.0422	0.0444	0.8997
2	60	0.0237	0.0237	0.90	0.0214	0.0263	0.9002
3	40	0.0125	0.0129	0.90	0.0095	0.0169	0.9029
4	50	0.0198	0.0199	0.90	0.0170	0.0236	0.9029
1	40	0.0433	0.0433	0.95	0.0420	0.0446	0.9499
2	60	0.0237	0.0237	0.95	0.0209	0.0268	0.9512
3	40	0.0125	0.0129	0.95	0.0091	0.0181	0.9522
4	50	0.0198	0.0199	0.95	0.0165	0.0245	0.9520
1	40	0.0433	0.0433	0.99	0.0416	0.0451	0.9893
2	60	0.0237	0.0237	0.99	0.0201	0.0279	0.9906
3	40	0.0125	0.0129	0.99	0.0082	0.0206	0.9899
4	50	0.0198	0.0200	0.99	0.0157	0.0264	0.9916

* Using $-\log(\theta)$ with θ the solution of s in (19).
† The average of $r(j)$'s as described in step 4 of simulations.
* Obtained using (22).
‡ The fraction of the $r(j)$'s that falls within the CI.

We also analysed how confidence intervals (CI) obtained with bootstrap methods compare with the method introduced here. For this, we perform another set of simulations: for each distribution described in Sec. 6.4, we took $n_1 = 10^4$ samples of size n, then each sample was resampled $n_2 = 10^3$ times to calculate the empirical $\mathrm{CI}_{0.95}$, and then recorded the fraction of the n_1 intervals that contained the known value of r, which was recorded as $p(i, n)$ since it is a function of the distribution used ($i = 1, 2, 3, 4$) and the value of n, for $n = (10, 20, 30, 40, 50, 100, 200, 300)$.

Figure 3 illustrates the fraction p_n as a function of sample size, averaging across all four distributions. The performance of bootstrap methods improves when the sample size n increases and is efficient for moderate n; however, it is less effective for small sample sizes. In contrast, the empirical probability mass function (empf), despite being founded on asymptotic properties of the sample,

demonstrates greater efficiency for small sample sizes. The empf commences slightly above the threshold and exhibits more rapid improvement than the bootstrap method, approaching the anticipated 95

It is important to note that in this context, n pertains to the total number of available observations, which is equivalent to K, the total offspring size. Recall that distribution $\mathbf{g}$, initially outlined in Section 2.1, represents the offspring distribution, constructed using K observations. This observation is crucial for subsequent discussions concerning the compared efficiency of the bootstrap method.

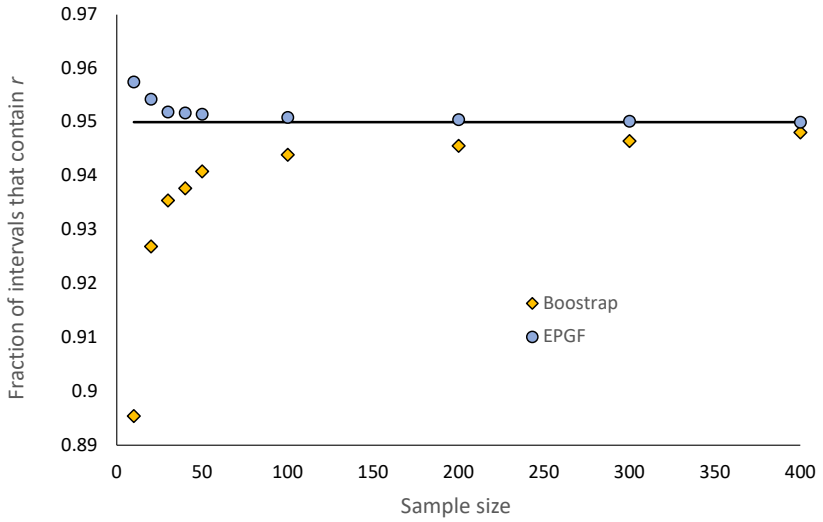


Figure 3: Comparsion with Boostrap. The plot shows the fraction of the intervals that contained the true growth rate r at different sample sizes for the Boostrap method (diamonds) and the epgf method (circles) proposed here. The horizontal line is the 0.95 target value. Convergence of Bootrsap is much slower. Details are shown in Sec. 7.

8. Discussion

Whilst the confidence intervals for longevity and generation time were derived using known properties of sample means, it is interesting how the distribution of empirical probability generating functions (epgf) was absent from

the construction of confidence intervals for r, despite the clear relationship between pgf's and R_0 given in equation (14). The confidence intervals provided in (22) are easily calculated from data organised as a life table and possess a solid theoretical framework.

Although the distribution of $g_n(\theta)$ is known for fixed θ, the distribution of the solution for x in:

$$\phi_n(x) = R_0^{-1} + W$$

for $W \sim N(0, \sigma^2/n)$ is not derived here and remains an open problem. This would have allowed for the determination of the distribution of $r = -\log(x)$, but at the very least, confidence intervals of any size can be derived.

Constructing confidence intervals for R_0 cannot be achieved without making assumptions that we are not willing to concede in this study. Nonetheless, given the close relationship between R_0 and r demonstrated in equation (14), the uncertainty regarding population growth is addressed through the confidence intervals for r or λ.

When the data is organised in a Leftkovitch matrix containing vital rates, including transition and fertility rates, which can be decomposed as: $\mathbf{U} + \mathbf{F}$, we must recall that matrix $\mathbf{U}$ was obtained by estimating the likelihood of individual transitions from stage i to stage j at the next unit of time [see 15]. If the original data that allowed the construction of $\mathbf{U}$ is available, the results derived here can be applied after collapsing the number of individuals alive at time t in all stages into a single column.

It is feasible to apply the proposed calculations to a life table containing the traditional columns t, $l(t)$, and $m(t)$, as previously described if N or K is known. To begin, we can calculate R_0 using equation (5), then, we obtain the

columns **g** and **f** using the following equations:

$$\begin{aligned} g(i) &= m(i)\ l(i)\ R_0^{-1}. \\ f(i) &= l(i) - l(i+1) \end{aligned}$$

Furthermore, constructing confidence intervals requires the knowledge of both N and K, the total offspring size, to be incorporated into equations (4), (12), (21) and (22). Since $R_0 = K/N$, knowing any of N and K will enable the calculation of the other.

The comparison with the bootstrap method suggests that for most entomological or fish data, which usually record hundreds or thousands of eggs, the bootstrap method will perform very well, although in some mammals or birds, with limited offspring, they would have limited use. Still, expressions (21- 23) are more accurate since they involve the sample size. The method proposed here, based on properties of epgf's, seems to perform very well for $K \geq 20$, but in the simulations $p_{(i,n)}$ never was below the 0.95 threshold even for $K = 10$.

As previously mentioned, the larger the R_0 value, the greater the violation of sample independence. However, for moderate R_0 values (less than or equal to five), the violation is not severe. It is evident that in many laboratory studies, the recorded R_0 is quite high, but this may be attributable to unusually protective conditions that do not accurately replicate the field conditions to which individuals are exposed. Remember that R_0 represents the number of times a population grows per generation; therefore, real-life R_0 values should be close to 1.

9. Conclusions

The proposed methodology for constructing confidence intervals has demonstrated efficacy, obviating the need for approximations through series expan-

sion or reliance on computationally demanding techniques. While the method is specifically designed for data structured as life tables, it can be effortlessly adapted to extended life tables where the number of individuals at each stage is documented, or to data presented as a Leftkovitch matrix. It is worth mentioning that when the total offspring size (K) gathered in the experiment is below 400, the epgf approach demonstrates superior performance in comparison to the bootstrap method.

10. Software availability

We have developed software in R, Python and Matlab® to derive point and interval estimates for longevity, mean generation time, and growth rate. Files are available at the GitHub site:

`https://github.com/car-git/Confidence-Intervals-LHT`

11. Acknowledgements

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12. Conflicts of interest

The author declares no conflicts of interest to disclose regarding the development of this research.

13. Data availability

The data used as a sample calculation in this research is included in the Appendix section.

14. Bibliography

[1] Caswell H. Matrix population models. Sinauer Associates Sunderland, MA, USA; 2001.

[2] Lande R. Demographic models of the northern spotted owl (Strix occidentalis caurina). Oecologia. 1988;75:601-7.

[3] Alvarez-Buylla ER, Slatkin M. Finding confidence-limits on population-growth rates. Trends In Ecology & Evolution. 1991;6(7):221-4.

[4] Alvarez-Buylla ER, Slatkin M. Finding confidence-limits on population-growth rates - three real examples revised. Ecology. 1994;75(1):255-60.

[5] Sibly R, Hansen F, Forbes V. Confidence intervals for population growth rate of organisms with two-stage life histories. Oikos. 2000;88(2):335-40.

[6] Efron B, Tibshirani R. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Statistical Science. 1986:54-75.

[7] Tibshirani RJ, Efron B. An introduction to the bootstrap. Monographs on statistics and applied probability. 1993;57(1).

[8] Meyer JS, Ingersoll CG, McDonald LL, Boyce MS. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. Ecology. 1986;67(5):1156-66.

[9] Alvarez-Buylla ER, Slatkin M. Finding confidence-limits on population-growth rates – Monte-Carlo test of a simple analytic method. Oikos. 1993;68(2):273-82.

[10] Caswell H. Stage, age and individual stochasticity in demography. Oikos. 2009;12(118):1763-82.

[11] Iosifescu M. Finite Markov processes and their applications. Dover Publications Inc., New York, USA; 1980.

[12] Wallinga J, Lipsitch M. How generation intervals shape the relationship between growth rates and reproductive numbers. Proceedings of the Royal Society B: Biological Sciences. 2007;274(1609):599-604.

[13] Hernandez-Suarez CM. A note on the generation time. Oikos. 2011;120(1):159.

[14] Nakagawa M, Perez-Abreu V. Empirical probability generating function - an overview. Insurance Mathematics & Economics. 1993 JUN;12(3):287-95.

[15] Hernandez-Suarez C, Medone P, Castillo-Chavez C, Rabinovich J. Building matrix population models when individuals are non-identifiable. Journal of Theoretical Biology. 2019;460:13-7.

[16] Mermer S, Maslen EA, Dalton DT, Nielsen AL, Rucker A, Lowenstein D, et al. Temperature-Dependent Life Table Parameters of Brown Marmorated Stink Bug, Halyomorpha halys (Stål ring) (Hemiptera: Pentatomidae) in the United States. Insects. 2023;14(3):248. Available from: https://www.mdpi.com/2075-4450/14/3/248.

15. Appendix

This is an example of calculating point and confidence intervals for longevity (L), generation time (μ_1), and growth rate (r and λ) using data from the study in [16].

The Brown marmorated stink bug, *Halyomorpha halys* (Ståal) (Hemiptera: Pentatomidae), is an invasive pest of over 300 plant species in North America, Asia, and Europe. It was first recorded in the US in 1996 and is a destructive agricultural and nuisance pest. It has high reproductive and dispersal capabilities and feeds on plant tissues, causing necrosis and scarring. The impact of temperature on its development, fecundity, survival, and mortality has been studied to determine its invasive potential and seasonal risk. Age-specific fecundity and survival data related to temperature extremes are needed to estimate reproduction, survival, and population dynamics. This is part of the data set corresponding to the study in Oregon at $25°C$. The data is shown in Table A1.

The only data required are columns t, $n(t)$ and $h(t)$, the rest is calculated as:

$$\begin{aligned} g(t) &= h(t)/K \\ f(t) &= (n(t) - n(t+1))/N \end{aligned}$$

with $K = 2430$, the total egg production and $N = 50$, the initial number of individuals. A zero must be appended to the end of $\mathbf{f}$ to match the required length.

For this data $N = 50$, $K = 2430$.

Table A1: Surving individuals **n** and number of eggs laid **h** by day **t**. Columns **g** and **f**, containing the relative frequency of eggs laid per day and mortality at time **t** are obtained as described in text.

t	**n**	**h**	**g**	**f**	**t**	**n**	**h**	**g**	**f**
1	50	0	0.0353	0.0000	38	14	77	0.0676	0.0200
2	50	0	0.0366	0.0000	39	13	82	0.0674	0.0200
3	50	0	0.0380	0.0200	40	12	4	0.0667	0.0400
4	49	0	0.0387	0.0000	41	10	61	0.0595	0.0200
5	49	0	0.0402	0.0000	42	9	0	0.0570	0.0000
6	49	0	0.0419	0.0000	43	9	0	0.0604	0.0000
7	49	0	0.0438	0.0200	44	9	29	0.0643	0.0000
8	48	0	0.0448	0.0400	45	9	27	0.0687	0.0000
9	46	0	0.0450	0.0400	46	9	20	0.0738	0.0000
10	44	28	0.0450	0.0000	47	9	58	0.0796	0.0400
11	44	28	0.0472	0.0000	48	7	3	0.0673	0.0200
12	44	10	0.0495	0.0200	49	6	0	0.0619	0.0000
13	43	118	0.0509	0.0400	50	6	28	0.0659	0.0000
14	41	111	0.0511	0.0000	51	6	0	0.0706	0.0000
15	41	136	0.0539	0.0400	52	6	0	0.0759	0.0200
16	39	162	0.0542	0.0400	53	5	0	0.0685	0.0000
17	37	110	0.0543	0.0400	54	5	0	0.0735	0.0000
18	35	49	0.0543	0.0400	55	5	0	0.0794	0.0200
19	33	231	0.0542	0.0400	56	4	0	0.0690	0.0000
20	31	0	0.0538	0.0600	57	4	3	0.0741	0.0000
21	28	0	0.0514	0.0200	58	4	22	0.0800	0.0000
22	27	61	0.0522	0.0600	59	4	28	0.0870	0.0000
23	24	155	0.0490	0.0000	60	4	0	0.0952	0.0200
24	24	60	0.0515	0.0000	61	3	0	0.0789	0.0000
25	24	36	0.0543	0.0200	62	3	0	0.0857	0.0000
26	23	72	0.0550	0.0400	63	3	14	0.0938	0.0000
27	21	42	0.0532	0.0200	64	3	0	0.1034	0.0000
28	20	57	0.0535	0.0000	65	3	0	0.1154	0.0000
29	20	94	0.0565	0.0400	66	3	0	0.1304	0.0000
30	18	71	0.0539	0.0200	67	3	0	0.1500	0.0000
31	17	77	0.0538	0.0000	68	3	0	0.1765	0.0000
32	17	25	0.0569	0.0000	69	3	0	0.2143	0.0000
33	17	30	0.0603	0.0200	70	3	0	0.2727	0.0000
34	16	0	0.0604	0.0400	71	3	0	0.3750	0.0000
35	14	76	0.0562	0.0000	72	3	20	0.6000	0.0200
36	14	68	0.0596	0.0000	73	2	4	1.0000	0.0400
37	14	43	0.0633	0.0000	74	0	0	0.0000	0.0000

15.1. Longevity

Using (2) and (3):

$$\begin{aligned} \hat{\mu}_L &= \mathbf{t}'\mathbf{f} = 28.34 \\ \hat{\sigma}_L^2 &= (\mathbf{t} \circ \mathbf{t})'\mathbf{f} - (\hat{\mu}_L)^2 = 302.06 \end{aligned}$$

And the 95% confidence interval for L given in (4) are:

$$CI_{0.95} = (23.52,\ 33.15)$$

15.2. R_0

Using (7) we have:

$$R_0 = K/N = 2430/50 = 48.6$$

15.3. Generation Time μ_1

Using (10) and (11):

$$\begin{aligned} \hat{\mu}_T &= \mathbf{t}'\mathbf{g} = 26.88 \\ \hat{\sigma}_T^2 &= (\mathbf{t} \circ \mathbf{t})'\mathbf{g} - (\hat{\mu}_T)^2 = 151.77 \end{aligned}$$

And the 95% confidence interval for T given in (12) are:

$$CI_{0.95} = (26.39,\ 27.37)$$

15.4. The instantaneous rate of population growth, r.

We need to solve for r in equation (19):

$$\exp(-r\ \mathbf{t}')\ \mathbf{g} = R_0^{-1}$$

which yields $r = 0.2021$. To derive the lower limit of a 95% CI for r, we first use (20) to calculate $\hat{\sigma}^2$, which is 7.1149×10^{-4}, from here, $\hat{\sigma} = 0.0266 \times 10^{-4}$

To derive the lower limit for r, we use equation (21) and solve numerically for r_L in:

$$\exp(-r_L\ \mathbf{t}')\ \mathbf{g} = R_0^{-1} + Z_{1-\alpha}\hat{\sigma}/\sqrt{K}$$

and the upper limit for r is found using equation (22) with the solution for r_L in:

$$\exp(-r_U\ \mathbf{t}')\ \mathbf{g} = R_0^{-1} - Z_{1-\alpha}\hat{\sigma}/\sqrt{K}$$

Thus the 95% confidence interval for r is $(0.1988, 0.2055)$.

For λ we use $\hat{\lambda} = \exp(r) = 1.224$ and the interval is $(1.220, 1.228)$ is found as described in equation (23).

We also compare the confidence interval obtained using boostrap. For these, we sample from the distribution $\mathbf{g}$ in Table A1 a total of $K = 2,430$ eggs 10^6 times, and recorded the $q_{0.025}$ and $q_{0.975}$ quantiles (to achieve $\alpha = 0.05$). The comparison is shown in Table A2. Since number of eggs is high, there is no noticeable improvement of epgn over bootstrap.

Table A2: Comparison of epgn method vs bootstrap for the data in [16].

	r		λ	
	Low	Upper	Low	Upper
epgn	0.199	0.206	1.220	1.228
Boostrap	0.199	0.205	1.220	1.228