Skewed distributions of LRS: beyond mean and variance

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Abstract

Lifetime measures of reproductive performance are quantified here by the LRS (Lifetime Reproductive Success), the number of offspring an individual produces over its lifespan. General formulas for the mean, variance and higher moments of LRS are given by van Daalen and Caswell (2017). Yet, the complete set of probabilities for LRS are often essential, since empirical studies have consistently revealed that distributions of lifetime reproductive performance measures are often non-normal, zero-inflated and highly skewed. Certainly in the many cases where the distribution is highly skewed or multimodal. We present here a new method for computing the entire probability distribution of LRS for most species described by age+stage models

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(including age-only and stage-only models). We show below by examples that the distribution of LRS contains new and useful biological insights. The first two illustrative examples are age-only models for two human populations: the Hadza, a Tanzanian group of hunter-foragers, and a North American group called the Hutterites. The next example is a stage-only model for the large evergreen tree *Tsuga canadensis*. For these three examples, the data were cited and used by van Daalen and Caswell (2017), who kindly provided the matrices used. The last example, is an age+stage model for Roe deer, *Capreolus capreolus*, based on the data in Plard et al. (2015). In each of the examples we not only produce the full distribution, but we also calculate and discuss the first 3 moments (the same values as the formulas in (van Daalen and Caswell 2017)). Our methods highlight biologically important questions: what factors determine the probability that individuals produce zero offspring during their lifetimes; how skewed the LRS distribution is; what are the effects of skewed LRS distributions on natural selection, effective population size, and life history evolution? We discuss these and other questions, and point towards future work needed in this area.

Introduction

Lifetime measures of reproductive performance describe the number of offspring an individual produces over its lifespan (Clutton-Brock 1988). Many empirical biologists consider such lifetime measures as individual fitness (e.g. Kruuk et al. 1999; Brommer et al. 2004), although, with the exception of truly annual species (Fisher 1930), these measures are correlates of fitness (Grafen 1988). Nonetheless, lifetime reproductive performance is useful as it can provide generational estimators of the opportunity for natural and sexual selection and phenotypic evolution. For instance, many empirical studies have assessed the opportunity for selection using the standardized variance

(I metric, Crow 1958) of reproductive performance and revealed high variation (e.g. from 0.177 in lion, *Panthera leo* to 3.62 in elephant seal, *Mirounga angustirostris* (Cabana and Kramer 1991) for females ; from 0.59 in Atlantic salmon *Salmo salar* to 4.52 in bighorn sheep, *Ovis canadensis*, (Tatarenkov et al. 2008) for males). Comparison of standardized variances of lifetime reproductive performance between sexes within a population is also commonly used for assessing the strength of sexual selection (e.g. Dubuc et al. (2014) on Rhesus macaques, *Macaca mulatta*). These empirical studies have consistently revealed that distributions of lifetime reproductive performance measures are often non-normal, zero-inflated and highly skewed, and this begs the question: what are the demographic causes of these unusually-shaped distributions?

Lifetime Breeding Success (LBS) censuses offspring at birth (e.g. Slate et al. 2000), while Lifetime Reproductive Success (LRS) censuses them at some later stage (e.g. weaning/fledging (Noordwijk and Schaik 1999), one year-old (Newton 1988), two years-old (Clutton-Brock 1988)) that usually corresponds to the end of a critical period for survival. In seasonal breeders this is often defined as being at one year of age. We will analyze discrete-time population models that are formulated in terms of species-appropriate modes of breeding and counting, but for simplicity simply use the term LRS. So the question is: do such models predict LRS distributions that mimic those observed in nature, and why?

In the models here, individuals are distinguished by age and/or stage, and individual life cycles are described by probabilities of survival, stage

transitions, and reproduction. Since transitions such as survival and growth are random events, the LRS is also a random number. Simulations for many species yield a distribution of LRS that is dramatically skewed or multimodal (Tuljapurkar et al. 2009b; Steiner and Tuljapurkar 2012), in accord with the empirical results mentioned above. Hence in any cohort, many individuals have an LRS of 0 so they leave no offspring; a lucky few have an LRS much higher than the average value. This variation is driven purely by chance since all the individuals are governed by the same probability rules; their reproductive success differs only because each one represents a different realization of a stochastic process (Steiner and Tuljapurkar 2012; van Daalen and Caswell 2017) (hereafter we use the abbreviation vDC for the latter reference which we cite often), meaning that "luck" can be more important than "pluck" (Snyder and Ellner 2018).

To quantify such "neutral" variation, Steiner and Tuljapurkar (2012) obtained formulas for the average and variance (and higher moments) using a fixed fertility at every age/stage. In age-only cases, the variance in LRS has also been computed numerically by Waples et al. (2011). But, as emphasized by vDC, offspring only come in integers (0, 1, 2, ...), so offspring production at every age/stage should properly be described by probabilities that an individual has $0, 1, 2, \ldots$ offspring. Using the latter description, vDC derived formulas for the moments – mean, variance, and so on – of LRS for each birth stage (extending Caswell (2011) and Daalen and Caswell (2015)), and showed how these formulas could be used. The analyses by Snyder and Ellner (2018) also examined variance computed in this way as a measure of

dispersion in the LRS.

Yet, we should really have the probability distribution of the LRS and not just the moments. Why? After all, the formulas in vDC easily yield the first three moments (higher order moments don't reveal all the most interesting patterns, including multimodality). But these moments, although valuable, are far from enough. For one thing, our intuitive understanding of these moments is often based on a roughly normal distribution so can be of limited value. For another, a general approach to approximating a distribution by the first few moments, e.g., the Gram-Charlier expansion (Stuart et al. 1994), doesn't work for many (all the ones we've tried) LRS distributions, as we illustrate later in this paper. The complete set of probabilities for LRS are often essential, certainly in the many cases where the distribution is highly skewed or multimodal. We present here a new method for computing the entire probability distribution of LRS for most species. We show below by examples that the distribution of LRS contains new and useful biological insights. Our methods highlight new and biologically important questions: what factors determine the probability that individuals produce zero offspring during their lifetimes; how skewed the LRS distribution is; what are the effects of skewed LRS distributions on natural selection, effective population size, and life history evolution? We discuss these and other questions, and point towards future work needed in this area.

We show how to compute the probability distribution of all possible values of LRS $= 0, 1, 2, \ldots,$ given any birth stage. The main text briefly explains the logic and analysis of our method, focusing on illustrative examples in the

results. Our logic is grounded in three basic points. First, every individual has a particular age of death; second, at each age that an individual is alive, there is a probability distribution for the number of offspring produced at that age; and third, *convolution* of these age-specific probability distributions (weighted appropriately by survivorship and mortality) yields the probability distribution of lifetime reproductive success. We make the assumption that the probability distribution at each age is independent of the probability distribution at all other ages. Computational challenges and details differ among age-only, stage-only and age+stage demographic models. We explain the meaning of "convolution", since it is not familiar to many biologists. *Fourier transforms*, also unfamiliar to biologists, constitute a mathematically convenient tool for calculating high dimensional convolutions. As this is a key to implementing our method for stage-only models, they are presented and employed. The first two illustrative examples are age-only models for two human populations: the Hadza, a Tanzanian group of hunter-foragers, and a North American group called the Hutterites. The next example is a stage-only model for the large evergreen tree *Tsuga canadensis*. For these three examples, the data were cited and used by vDC. We obtained matrices from vDC to ensure that we employ numerically identical examples of vital rates to facilitate comparison of our results to theirs. The last example, and perhaps most general, is an age+stage model for Roe deer, *Capreolus capreolus*, based on the data in Plard et al. (2015). In each of the examples we not only produce the full distribution, but we also calculate and discuss the first 3 moments, noting that our methods yield the same results as the

formulas vDC, as they should.

Methods

Lifetime Reproductive Success can be quantified as a random variable LRS. Our goal is to find the complete probability distribution that corresponds to the different possible values that LRS can take on. We develop methods to compute this distribution for structured populations for which demography is modeled in discrete time; models may be structured only by age, only by stage, or by a combination of age and stage. Mathematical details are in an Appendix and we have written corresponding code (based on R (R Core Team 2019) and the R package FFTW (Fastest Fourier Transform in the West) (Mersmann 2019)). The code is available from the authors. Our results should apply to continuous stages using established methods (Ellner et al. 2016; Snyder and Ellner 2018). We attempt to use notation similar to Caswell (2011) and Caswell et al. (2018). Two other points: higher moments can be computed directly from our distribution or from the vDC formulas.

General Framework

We start by defining basic parameters. *Age* is counted in discrete intervals $a = 1, 2, \ldots, \omega$ and newborns are in the first age interval for all three models (Table 1). *Stage* is defined in discrete categories, $s = 1, 2, \ldots, S$ (indexed as i or j at particular times) for stage-only and age+stage models. *Stage transition probabilities* (conditional on remaining alive) over a single time step are

defined in an $S \times S$ matrix, which is the matrix $\boldsymbol{G}$ for stage-only models and a set of matrices $\boldsymbol{G}_a$ for age+stage models. *One-period survival probabilities* (from one interval of time to the next) are p_a for age-only models, $p(j)$ for stage-only models and $p_a(j)$ for age+stage models (Table 1). Multiplying stage transitions by stage survivals, we obtain an $S \times S$ matrix of *unconditional stage transition probabilities*, $\boldsymbol{U}$ for stage-only models and a set $\boldsymbol{U}_a$ for age+stage models (Table 2).

Age at Death is a random variable T. We can determine the complete probability distribution of T from the parameters presented above. Note that even for populations where one-period vital rates depend only upon stage, there is an age at which individuals die. The proportion of a cohort that dies at each age a is given by the probabilities ϕ_a (Table 3). Since every individual in a cohort has to die sometime, we can multiply its probability of still being alive (relative to the others in its cohort) at the beginning of an age interval with its conditional probability of dying during that age interval (given that it was alive at the beginning of it) to obtain ϕ_a. In other words, we multiply one-period survivals p_a (or matrix products of stage transitions $\boldsymbol{U}$, where relevant) together to obtain the *survivorship* of a cohort to each age (the proportion of a cohort that is still alive at each age) l_a for the age-only model and the $S \times S$ matrix $\boldsymbol{L}_a$ that indexes survivors from the initial cohort by starting and ending stage for the stage-only and age+stage models. *One-period mortality probability* (the conditional probability of dying during an interval) is simply $1 - p_a$ for the age-only model, $1 - p(j)$ for the stage only model and $1 - p_a(j)$ for the age+stage model.

Reproduction at each time interval is a random variable; α and β are, respectively, the youngest and oldest ages at which at least one individual in the population may reproduce, for age-only and age+stage models (Table 4). Stage-only models may have non-reproductive stages, but they may occur at any age. The *number of offspring produced by individuals during a single time interval* is a random variable that can take on integer values $k = 0, 1, 2, \ldots, k_m$. *The number of offspring produced by individuals during a lifetime* LRS is a random variable that can take on integer values $k = 0, 1, 2, \ldots, k_u$. We consider that during a single time interval the distribution of reproductive success depends respectively on age $\boldsymbol{\kappa}_a$, stage $\boldsymbol{\kappa}_j$, or age+stage $\boldsymbol{\kappa}_{a,j}$, respectively for the age-only, stage-only and age+stage models (Table 5).

Our calculations assume that, within a single time interval, the event of reproduction precedes the event of death. Thus an individual alive at the beginning of a given time interval will reproduce according to its age and or stage at the beginning of the interval, whether or not it dies during the interval. Other assumptions could be made, but our formulas are easily changed accordingly.

Convolutions of probability distributions are at the core of our approach. As explained in Tables 7, 8, we seek the probability of combinations that result from independent events: the amount of reproduction at each age. There is a probability of making $0, 1, 2, \ldots, k_m$ offspring at each age. The outcome over a lifetime depends upon combining the probabilities across the ages. The idea is familiar to most biologists even though the terminology is

not. For example, a similar approach is used to compute the frequency of each diploid genotype under the assumption of random mating.

Every individual lives until death at some random age T. At each age a before death, this individual produces some (random) number K_a of offspring, and so has an

$$\mathrm{LRS} = K_1 + K_2 + \cdots + K_T.$$

The probability distribution of the possible values of this sum is the repeated convolution

$$\boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2 \star \cdots \star \boldsymbol{\kappa}_T.$$

The total LRS weights such convolutions by the probabilities ϕ_a that individuals born into a particular cohort die at age a. The argument here is similar to one used for the average LRS in Schindler et al. (2012). Thus the average, variance and other moments of the distribution are precisely those in vDC.

The practical flow of decisions about which of the following methods to use is shown in Fig. 1.

Age-only Model

Survival and reproduction during a single time interval depend only upon the age of individuals. The lifetime reproductive success (LRS) is a random variable, so we want the probabilities

$$\Pr[\mathrm{LRS} = k] = \Gamma(k),\ 0 \leq k \leq k_U. \tag{1}$$

These probabilities make a distribution $\boldsymbol{\Gamma} = \{\Gamma(k)\}$. The distribution of offspring is $\boldsymbol{\kappa}_a$ at age a. For the two examples of age-structured human population, we use use a binomial with $k_m = 1$. We break life into segments: individuals who die before reaching age 2, those who live to age 2 but die before 3, and so on.

First, consider individuals who die before reaching age $a = 2$. The probability of such a death is $\phi_1 = l_1 [1 - p_1]$, and reproductive success at age 1 follows the distribution $\boldsymbol{\kappa}_1$, so the LRS for such individuals has the probability distribution

$$\boldsymbol{\gamma}_1 = \phi_1 \, \boldsymbol{\kappa}_1. \tag{2}$$

Next, consider individuals who reach age $a = 2$, reproduce and die before age $a = 3$. Such individuals have had two opportunities to reproduce. If these individuals have LRS = 2, they could have: i) produced 0 offspring at age 1 and 2 offspring at age 2, or ii) produced 1 offspring at age 1 and 1 offspring at age 2, or iii) produced 2 offspring at age 1 and 0 offspring at age 2. In other words, at ages $(1, 2)$, they could have $(2, 0)$, $(1, 1)$ or $(0, 2)$ offspring. Hence the probability of LRS = 2 is

$$\kappa_1(2)\kappa_2(0) + \kappa_1(1)\kappa_2(1) + \kappa_1(0)\kappa_2(2).$$

Each LRS $= k$ is analyzed in this way, and the corresponding probabilities are elements of a *convolution* of the probability distributions at each age, written as

$$\boldsymbol{\delta} = \boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2. \tag{3}$$

There are $(2k_m + 1)$ possible outcomes resulting from the convolution, since an individual could hit the upper limit at either ages 1 or 2 similarly it could produce 0 offspring at both ages.

Since the proportion of a cohort that dies at age 2 is ϕ_2, the LRS for individuals in a cohort who die before reaching age $a = 3$ is distributed according to the probabilities

$$\boldsymbol{\gamma}_2 = \phi_2 \, \boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2. \tag{4}$$

For an individual who lives to age $2 \leq a < \beta$ but dies before reaching $a + 1$, the LRS is distributed as

$$\boldsymbol{\gamma}_a = \phi_a \, \boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2 \cdots \star \boldsymbol{\kappa}_a. \tag{5}$$

Reproduction ends after age β, so survival to later ages does not change the LRS. Consequently, for an individual who lives to age $a \geq \beta$, the LRS has distribution

$$\boldsymbol{\gamma}_\beta = l_\beta \, \boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2 \cdots \star \boldsymbol{\kappa}_\beta. \tag{6}$$

Adding, we have

$$\boldsymbol{\Gamma} = \sum_{a=1}^{a=\beta} \boldsymbol{\gamma}_a. \tag{7}$$

Stage-only Model

For many species, stage (such as size or developmental state) is predictive of vital rates rather than age. (Lefkovitch 1965). Survival, stage-transition,

and reproduction during a single time interval depend only on the stage of individuals. There are S discrete stages, and every individual is in some stage $s = 1, 2, \ldots, S$. Stage transition probabilities from stage j at the beginning of the time interval to stage i at the beginning of the next time interval, conditional on survival (Table 1), are given in the matrix $\mathbf{G}$ with elements

$$G(i, j) = \Pr[i|j, \text{survival}]. \tag{8}$$

Survival rates $p(j)$ are determined by the stage at the beginning of the time interval stage j . So an individual in stage j will be alive and in stage i in the next time period with probabilities given in the matrix $\mathbf{U}$ with elements

$$U(i, j) = p(j)\, G(i, j). \tag{9}$$

(Table 2).

The number of offspring produced during a time interval depends only on stage at the beginning of the time interval, stage j, and is specified by probability distributions $\boldsymbol{\kappa}_j = \{\kappa_j\}$ of producing $k = 0, 1, 2, \ldots$ offspring. These distributions are often taken to be Poisson (vDC), but that is not a requirement of our calculations. They can be of any form.

As for the age-only model, we want the distribution $\boldsymbol{\Gamma}$ whose elements are

$$\Pr[\text{LRS} = k] = \Gamma(k),\ 0 \leq k \leq k_U.$$

Stage-Only Model special challenges

For stage-structure, we can in principle proceed as with age-structure but the need for multiple convolutions quickly makes that procedure computationally unwieldy. This is because, in contrast to an age-structured model where individuals visit a given age class only once in a lifetime, individuals can visit a stage class any number of times before dying. They can also move back and forth between non-reproductive and reproductive stages. So here we need: (a) a fast way of doing repeated convolutions; (b) a way of summing over sums of repeated convolutions.

We have found a solution to both. For (a), we use the mathematical fact that the Fourier transform of a convolution is the product of Fourier transforms, and the numerical fact that the FFTW package (Mersmann 2019) does a fast discrete Fourier transform. For (b), we exploit our earlier work (Steiner and Tuljapurkar 2012) and combine a closed-form generating function with Fourier transforms, then use an inverse FFT. For the details (or if this brief description makes you curious) see the Appendix.

Our analysis establishes a computational method that yields the exact distribution of LRS for any stage-structured model. We can separately, and extremely quickly, compute the probability that the LRS $= 0$. Both analyses are given in the Appendix. The practical flow of decisions is shown in Fig. 1.

Age+Stage Model

Survival, stage transitions and reproduction during a single time interval depend upon the combination of age and stage (*e.g.* Coulson (2012)). Transitions over 1 time interval at each age, conditional on survival, are described by a matrix $\mathbf{G}_a$ of transition probabilities with elements

$$\mathbf{G}_a(i,j) = \Pr[a+1, i | a, j, \text{survival}]. \tag{10}$$

The survival rate from the beginning of age interval a to the beginning of the next age interval $a+1$ is $p_a(j)$. Combining these, an individual in stage j at age a will be alive at age $a+1$ in stage i with probabilities in the matrix $\mathbf{U}_a$ with elements

$$\mathbf{U}_a(i,j) = p_a(j)\,\mathbf{G}_a(i,j). \tag{11}$$

ω is the maximum age, and there are S stages. Then we have $(S \times \omega)$ possible age+stage combinations. From equation (11) we get the elements of a transition matrix $\mathbf{U}$ that has all possible transitions from age+stage at one time to age+stage at the next time (as in Caswell et al. (2018)). In this guise, an age+stage model is simply transformed into a kind of stage-structured model. We can think of the full set of $\mathbf{U}_a$, one for each age a.

Offspring may be born into any stage, but here we focus on the number of offspring rather than the type, being concerned with the probability of the number k of offspring born to individuals who are in age a and stage j at

the beginning of a time interval,

$$\boldsymbol{\kappa}_{a,j} = \{\kappa_{a,j}(k)\}, \tag{12}$$

As in the age-only and stage-only models, we want the distribution $\boldsymbol{\Gamma}$ whose elements are

$$\Pr[\text{LRS} = k] = \Gamma(k),\ 0 \leq k \leq k_U.$$

Age+Stage further considerations

Here we can proceed as with the age-structured model. But the computation depends on the "size" of the life cycle, and determines a choice between two options. If all individuals reach a terminal age and die, and if the number of stages is modest, use the age-structured approach. If there are many ages and/or stages, and/or if all individuals reach an "old" age with stages in which they reproduce and remain until death, the age-structured approach is too slow. In that case, use the general stage-structured approach, or a hybrid (see Appendix for further detail).

Results

Age-Only Model: Two examples

We contrast the Hadza, a hunter-forager group thought to be representative of early humans, to the Hutterites who in the 1950s were famous for their

high fertility (vDC). We consider only females with no migration. One-period mortality probabilities by age, p_a, yield survivorship l_a (the probability of surviving until age a.) Reproduction ceases at menopause $\beta \approx 50$ yr, so we do not need later ages. The commonly used fertility rate f_a is the mean number of offspring at each age. Fertility at age a can be 0 or 1 for human populations (vDC), with

$$\begin{aligned} \boldsymbol{\kappa}_a(0) &= \Pr[0 \text{ offspring}|\text{ parent age } a] = \big(1 - f_a\big), \\ \boldsymbol{\kappa}_a(1) &= \Pr[1 \text{ offspring}|\text{ parent age } a] = f_a. \end{aligned} \tag{13}$$

For each age, these numbers constitute a distribution we denote $\boldsymbol{\kappa}_a$. We ignore twinning, which is rare in these populations (but can be included if needed). For other species (e.g., if there are litters with many offspring) we need additional information to create a distribution of offspring at each age.

We used our methods to compute the exact distributions of lifetime reproductive success (LRS), Hadza in Fig. 2(a), Hutterites in Fig. 2(b); the distribution is given by the solid points in the figure. Notable features:

(1) The distribution for the Hadza is dramatically bimodal, with a very high mode at 0 and another at LRS ≈ 6. These locations are very different from the mean LRS of 3.13; the spread in LRS is not described by the standard deviation (= 3.36). The third central moment (= 21.7) does imply the distribution is skewed.

(2) The Hutterites have a low mode at 0 but a high mode at LRS close to

the mean of 7.53. Excluding the mode at 0, the distribution appears to concentrate nicely around the mean value, with a standard deviation ($= 2.93$) that captures the spread of nonzero values. However the third central moment is negative ($= -14.49$), presumably because of the mode at 0. If we didn't have the full distribution on view, this value of the third moment would be hard to understand.

Mode at LRS $= 0$

Is this likely to be a common feature? A female may have 0 offspring if she dies before reproduction begins, or lives on but has 0 offspring at every age. For the Hadza and the Hutterite, reproduction can begin at age 13 yrs. The probabilities of dying by that age are 0.415 for Hadza, 0.043 for Hutterites. The probability of living on but childless is 0.035 for the Hadza and only 0.008 for the high-fertility Hutterites. So the mode at LRS $= 0$ is largely determined by high infant mortality in the Hadza and the much lower infant mortality among Hutterites. Thus in general we should see a mode at LRS $= 0$ unless early mortality is extremely low.

Do 3 moments predict the distribution?

We can compute the LRS distribution from our methods, but can we recover a reasonable approximation from just the first 3 moments? For the Hadza, the answer is emphatically no, as shown by the Gram-Charlier approximation in Fig. 2(a) (the dotted line). For the Hutterites, the approximation works rather well for nonzero LRS but entirely misses the mode at 0, as shown in

Fig. 2(b) (the dotted line); so the answer is still no. We've tried a different method, starting with a Poisson and then using a numerical search for the "best" modification, but the answer is still negative. We have not tried using higher moments, because they do not seem likely to change our results.

Stage-Only Model

An example: An evergreen tree *Tsuga canadensis*

Consider the stage-only model that has been developed for *Tsuga canadensis*, eastern hemlock, an evergreen tree that grows to be 40-75 feet tall in the wild (as cited in vDC). Populations of this tree, as noted by Lamar and McGraw (2005), usually include many saplings, small individuals that may remain in good condition beneath a canopy for hundreds of years. So individuals exhibit considerable stasis. Indeed, long durations of stasis are commonly seen in populations that are stage-structured. This example motivated us to develop a fast and novel method (see Appendix) for such models.

Mode at LRS $= 0$

Noting that individuals may produce 0 offspring even when they are potentially reproductive, we consider that our analysis identifies two related but different probabilities:

(i) One is Pr[LRS $= 0$], which is a high 0.9883 for *T. canadensis*! This number corresponds to the sum of the probability of surviving while in non-reproductive stages plus the probability of producing 0 offspring

while in reproductive stages. We can always compute this probability exactly (see Appendix).

(ii) So does it make sense to ask (as it did in the age-structured case) for

$$\Pr[\text{LRS} = 0 | \text{ die as non-reproductive}]?$$

The answer depends on the life cycle. Suppose we start in a non-reproductive stage. In one special type of stage-structured life cycle, every individual eventually makes an *irreversible* transition to one or more reproducing stages, or dies before it does. For this case, it makes sense to treat the reproducing stages as "absorbing" and then the absorption probability is just what we want (see Appendix). The value of this probability is 0.9878 for *T. canadensis*. But, in life cycles of stage-structured populations that are not of the special case described above, this probability doesn't make sense. In the general stage-structured life cycle, individuals can make any number of transitions back and forth between non-reproductive and reproductive stages and death can occur at any point.

The LRS for *T. canadensis* has an extremely pronounced mode at 0, and the skew of the distribution is so dramatic that we had to plot the logarithms of the probabilities of LRS, as shown in Fig. 3. The average LRS is just 1.42, but the standard deviation of 37.54 is not useful as a measure of spread at either lower or higher values. The third moment is huge, $\approx 25 \times 10^5$, which

certainly means great skew, but does not predict the actual distribution in the figure. We expect a similar skewed distribution for many species (including plants and marine organisms) that produce large numbers of offspring such as seeds or larvae, but few recruits, and even fewer adults. The skew seen in Fig. 3 is relevant to current paradigms about life history evolution and selection, as we discuss further in the final section.

Age+Stage Model

An example: Roe deer *Capreolus capreolus*

In general, an individual is classified by both age $a = 1, 2, \ldots, \omega$ and stage $s = 1, 2, \ldots, S$. We illustrate with an estimated age+stage model for Roe deer *Capreolus capreolus* (Plard et al. 2015). Age is in years, and size in 200 equal body mass intervals from 1 Kg to 40 Kg. There are 4 age groups; in each group, there is one set of transition and survival rates and reproduction probabilities (the age groups are yearlings, adults age 2-7 yr, adults age 8-11 yr, adults over age 11). Age advances in single years.

The "initial stage" is a combination of age (here, yearlings in age class 1) and size. For initial age $a = 1$ there are potentially 200 initial sizes. Yearling sizes actually range from size class 40 to 100, but we provide analyses over the full potential size range (see the Appendix). Fig. 4 plots the LRS distribution for 3 different initial size classes, 1, 75, 200. The distribution shifts from unimodal at LRS = 0 for the smallest yearlings, to unimodal at a nonzero LRS for the largest yearlings, and can be multimodal at intermediate sizes.

Very small offspring have a high mode at 0, and thus the highest probability of leaving no offspring – no surprise. Neither the average LRS nor the standard deviation seem to be useful descriptors of the LRS distribution for the smallest yearlings (plotted in the Appendix). Somewhat bigger yearlings (birth size class 70-84, see Fig. 4, and the plots in the Appendix) have a bimodal distribution of LRS. Larger juveniles (size class 85 upward) have a single nonzero mode but still high odds of leaving 0 offspring. The nonzero mode shifts from an LRS ≈ 3 (for size class 80) to an LRS ≈ 5 (for size class 200) with increasing yearling size, and the distribution of LRS concentrates towards the mode. Very large offspring have a high nonzero mode at LRS ≈ 5, with a normal-like LRS distribution around the mode.

Mode at LRS $= 0$

The height of a mode at an LRS of 0 can be computed using a combination of the age-specific and stage-specific methods described above (see Appendix for plots for the Roe deer). The Pr[LRS $= 0$] declines with increasing birth mass. This is expected, since in this population it pays to be born larger. However the gain from increasing birth weight is strikingly nonlinear, so that the advantage of being born 1 Kg heavier is much greater for small than for large yearlings.

To dissect this effect, we analyzed yearling death probability and the probability of having no offspring if you live to later ages (see the Appendix plots). There is a drop in both as birth mass increases, but the gain in yearling survival reduces faster than the gain in later survival/reproduction.

Discussion

We have presented an analytical method that computes the probabilities of getting every possible lifetime reproductive success, $0, 1, 2, 3, \ldots$. We illustrated our results with examples; two human populations for age-structure, eastern hemlock for stage-structure, and Roe deer for age+stage structure. We showed that the LRS distribution is often multimodal with a mode at LRS $= 0$, and a second mode at nonzero LRS. For several of our examples, the mean, variance and third moment are poor descriptors of the highly skewed and/or multimodal LRS distribution. We hasten to add that these moments are useful descriptors if offspring (often censused as newborns or recruits) have high survival, probably uncommon in nature but common in modern human populations. Even in the latter case, though, we recommend a separate analysis of the probability that LRS $= 0$, using our methods. We find an even greater variability of the LRS than expected from previous work by ourselves and others (Tuljapurkar et al. 2009b; Steiner and Tuljapurkar 2012; Daalen and Caswell 2015; Snyder and Ellner 2018) and vDC. We expect this great variability of LRS to matter in many ecological and evolutionary contexts. Here we discuss extensions and implications of our results, and directions for future work.

Descriptors and Sensitivity analyses

Given the variability that we have found in the LRS, how best should we describe it? And once we decide on a descriptor, what are its sensitivities

to vital rates? In ecology, sensitivities determine how vital rates (or underlying parameters) affect properties of the LRS distribution, whereas in evolution sensitivities capture selection pressures that depend on LRS. A relevant discussion of sensitivity in an age+stage context is in Caswell et al. (2018). Analytical work on the sensitivity of LRS is probably best done using our stage-structured analysis, which applies for stages (or ages) and for age+stage combinations.

Let's start with the overall distribution. A biologically meaningful descriptor of the sometimes enormous spread in the LRS is to measure the inequality of LRS by a Gini index (Weiner and Solbrig 1984), which corresponds to the mean of absolute differences in individual lifespan relative to the average lifespan (Shkolnikov et al. 2003) and is bounded between 0 and 1. The Gini index is commonly used in economics and social science to quantify the amount of inequality in wealth but less frequently in ecology and evolution. It has been used to assess individual variation in the distribution of reproductive success of parasites (Dobson 1986), in the mass and fecundity distributions of a cestode infesting pikes (Shostak and Dick 1987), in the strength of forest edge effects (Matlack 1994) and in size hierarchy studies of competitive processes in plants (Weiner and Solbrig 1984). It is also increasingly used to measure the shape of mortality within a population (Archer et al. 2018) and was recently employed to quantify species differences in the distribution of reproductive ages across vertebrates (Healy et al. 2019). We propose that it will be valuable in analyzing variation between sexes or across species in the LRS distribution. To compute the Gini index, find the

cumulative distribution

$$\xi(x) = \sum_{k=1}^{x} \Pr[\text{LRS} = x] = \sum_{k=1}^{x} \mathbf{\Gamma}(x)$$

and plot $\xi(x)$ versus values (x/k_U) of the LRS (remember k_U is the largest possible LRS). This is the Lorenz plot shown for our examples in the panels of Fig.5. Equality means that every individual has the same odds of any LRS and is indicated by the dotted lines. The actual distributions are shown by the solid lines and indicates that a few individuals do most of the reproducing. The Gini index (shown on the plots as GI) is

$$GI = 2\Big(1 - \text{Area between the two curves shown}\Big)$$

Equality means that $GI = 0$ while complete inequality means that $GI = 1$. As we expect from Fig. 2, the Gini is much smaller for Hutteries than the Hadza. And the extreme inequality of LRS for *T. canadensis* is reflected in a very high Gini. Surprisingly (to us) the LRS for a fairly large Roe deer yearling (size class 100) is also quite unequal, with a Gini value halfway between Hazda and Hutterite.

A general approach to the sensitivity of inequality in LRS should be feasible using our results in conjunction with the methods in Raalte and Caswell (2013) and Caswell et al. (2018). More generally, numerical perturbations can be used to examine changes in $\mathbf{\Gamma}$ produced by changes in vital rates, and we can compare distributions using, e.g., the Kullback-Leiber distance

(Cover and Thomas 2012).

A useful measure highlighted by our examples is the probability of having no reproductive success:

$$\Pr[\text{LRS} = 0] = \mathbf{\Gamma}(0)$$

A general expression and computational method for this probability is given in the Appendix (Section A.8). Derivatives of this probability with respect to these parameters should be computable using known approaches, e.g., Caswell et al. (2018) or Steiner et al. (2012).

Another useful measure is the nonzero modal value, call it k^*, of the LRS – if it exists. We found a nonzero mode in several examples, but there is no nonzero mode for the tree (*T. canadensis*). Assuming its existence, a nonzero mode means that

$$\mathbf{\Gamma}(k^* - 1) < \mathbf{\Gamma}(k^*) > \mathbf{\Gamma}(k^* + 1)$$

This modal value may be more meaningful in some populations than the commonly used average LRS. We can use our result to find k^* and the methods in Caswell et al. (2018) should be extendable to compute sensitivities.

Implications

In our age-structured applications each individual is governed by the same set of demographic rates (probabilities). In other words, all individuals have

the same chances of surviving and reproducing at each age. Yet, the distribution of LRS is multimodal; this reveals how much individual heterogeneity can be generated by chance alone. This variation caused Steiner and Tuljapurkar (2012) to conclude that entirely neutral processes could generate the empirically-observed multimodal distributions of LRS so frequently reported.

In our stage and age-stage structured models individuals that start life with different phenotypic trait values can have contrasting distributions of LRS. For each starting phenotypic trait value there is still a large amount of individual heterogeneity in LRS similar to that observed for our age-only models, but when we compare these distributions across individuals with different initial phenotypic trait values we see that distributions do differ. These differences will generate opportunities for selection, and selection, that are not seen in age-only models. Whether such selection would result in evolution will depend upon the extent to which there is a genetic basis for individuals entering the population with different phenotypic trait values.

Stage- and age-stage structured models are astonishingly powerful. They can be constructed for stochastic, density-dependent, and frequency-dependent environments to predict population (Tuljapurkar 1990), life history (Tuljapurkar et al. 2009a; Caswell 2001), and evolutionary dynamics (Coulson et al. 2011, 2017; Childs et al. 2016). A large number of ecological and evolutionarily important statistics can be calculated from these models, with analysis of these models revealing how different values of these statistics arise. By extending the toolkit of structured models to predict entire distributions of LRS we open the door for a number of powerful, new analyses. For exam-

ple, we can ask how different growth trajectories will impact distributions of LRS, we can gain insight into why weak associations between birth weight and LRS are so frequently observed, and the conditions when lifetime measures of reproduction act as a good, or bad, surrogates of fitness. In addition, we could use our approach to generate distributions of other per-generation life-history statistics such as generation times, or life expectancies at a given age.

Previous analyses of LRS distributions in vertebrates relied on the standardized variance and have supported the existence of a link between mating systems and sex differences in LRS distributions, with similar distributions in males and females of monogamous species and much more widespread and skewed distributions in males than in females in highly polygynous species (Andersson 1994). However, our findings demonstrate that only using the first moments such as mean and variance does not allow to capture the main characteristics of an LRS distribution. More comprehensive metric such as the Gini index are much more appropriate and should be used in future comparisons of LRS distributions. Our approach should thus allow accurate comparisons among LRS distributions that are currently accumulating thanks to long-term individual-based monitoring of populations in a broad range of species across the tree of life. Moreover, in addition to sex and species, our approach provides a suitable way to assess how ecological factors (e.g. environmental harshness), life history tactics (e.g. slow vs. fast life cycle, capital vs. income breeding), and population structure (e.g. in terms of age, size) influence LRS distributions within and among populations.

The ability of the discrete-time structured model to gain ecological, life history, and evolutionary understanding is remarkable, and with each year new uses for them are developed. Such utility is not surprising, as these models (Coulson et al. 2011) include the fundamental biological processes of development, inheritance (although not considered in the current paper), survival and reproduction, and these processes can be specified to vary across individuals as a function of age, sex, phenotype, genotype (although not considered in the current paper) and environment. It is consequently unsurprising that analysis of such models has generated so much understanding in recent years. The methods we develop here open up opportunities for yet more biological insight.

Appendix

A.1 Convolutions and Age structure

Consider an age-structured population with only two age classes. Say that an individual of age class 1 has some number of offspring $k_1 = 0, 1, \ldots, k_m$ with probabilities $\boldsymbol{\kappa}_1 = \{\kappa_1(k_1)\}$, and an individual of age class 2 has $k_2 = 0, 1, \ldots, k_m$ offspring with probabilities $\boldsymbol{\kappa}_2 = \{\kappa_2(k_2)\}$. Now consider an individual who may produce offspring at both ages 1 and 2, and call $\delta(n)$ the probability that such an individual produces n offspring, $n = 0, 1, 2, \ldots, 2k_m$. Given any n, some k_1 offspring are produced at age 1 and the rest, $k_2 = (n - k_1)$, must be produced at age 2. The number of ways to obtain a given

n varies with n. For example, there is only one way to obtain $n = 0$ (both $k_1 = 0$ and $k_2 = 0$). Similarly, there is only one way for $n = 2k_m$ (both $k_1 = k_m$ and $k_2 = k_m$). There are only two ways for $n = 1$ (either $k_1 = 1$ and $k_2 = 0$ or $k_1 = 0$ and $k_2 = 1$). In general, we sum over the probabilities of the different ways we could get a particular n

$$\delta(n) = \sum \kappa_1(k_1)\, \kappa_2(n - k_1). \tag{A.1}$$

The number of terms in the summation varies from 1 to a maximum of k_m+1. These probabilities are components of a vector that we write as $\boldsymbol{\delta}$.

We can also describe $\boldsymbol{\kappa}_1$ and $\boldsymbol{\kappa}_2$ by the probability generating functions

$$w_1(x) = \sum_{k_1} \kappa_1(k_1) x^{k_1},\ w_2(x) = \sum_{k_2} \kappa_2(k_2) x^{k_2}, \tag{A.2}$$

where x is a dummy variable. Let the probability generating function for $\boldsymbol{\delta}$ be

$$u(x) = \sum_{k} \delta(k) x^k. \tag{A.3}$$

Setting

$$u(x) = w_1(x)\, w_2(x), \tag{A.4}$$

yields the probabilities in equation (A.1). We say that $\boldsymbol{\delta}$ is the **convolution** of $\boldsymbol{\kappa}_1$ and $\boldsymbol{\kappa}_2$, writing

$$\boldsymbol{\delta} = \boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2. \tag{A.5}$$

The power of this rewriting lies in the fact that convolutions can be

rapidly computed (for discrete and continuous distributions).

For age structured populations, we can use convolutions to compute the LRS distribution as explained in the main text. But this method doesn't work for stage structure so we need a different approach that starts with the property discussed next.

A.2 Fourier transforms

Fourier transforms require complex numbers. Denote

$$\mathbf{i} = \sqrt{-1}. \tag{A.6}$$

For an integer N, define the frequencies

$$\theta(z) = \exp\Big[\frac{-2\pi z\mathbf{i}}{N}\Big], z = 0, 1, \ldots, N-1. \tag{A.7}$$

Then for the discrete function $\boldsymbol{\kappa} = \{\kappa(0), \kappa(1), \kappa(2), \ldots, \kappa(q)\}$, define the Fourier transform for each frequency,

$$\widehat{\kappa}(\theta(z)) = \sum_{b=0}^{q} \kappa(b)\, \theta(z)^b. \tag{A.8}$$

Now suppose that $\boldsymbol{\psi}$ is another series of numbers, $\boldsymbol{\psi} = \{\psi(0), \psi(1), \ldots, \psi(q)\}$. For any frequency $\theta(z)$, equation (A.8) defines the Fourier transform

$\widehat{\psi}(\theta(z))$. It is well known that (James 2002)

$$\boxed{\text{the Fourier transform of } \{\boldsymbol{\kappa} \star \boldsymbol{\psi}\} \text{ is the product } \widehat{\kappa}\,\widehat{\psi}}$$

In consequence: for any integer $m \geq 0$,

$$\widehat{\left(\kappa^m\right)}(\theta(z)) = \left(\widehat{\kappa}(\theta(z))\right)^m, \tag{A.9}$$

and for any non-negative integers m_a, m_b

$$\left(\widehat{\kappa^{m_a} \star \psi^{m_b}}\right)(\theta(z)) = \widehat{\kappa}(\theta(z))^{m_a}\, \widehat{\psi}(\theta(z))^{m_b}. \tag{A.10}$$

A.3 Generating Function

We consider a general age+stage model following Steiner and Tuljapurkar (2012). Age and stage together define a state. Let there be S living states, with transitions between them by rates as defined in text equation (11). Form the matrix $\mathbf{U}$, write $\mathbf{U}^T = \mathbf{Q}$. Starting in a particular state i let τ_j be the (random) time spent in state j before death. (In the main text we use the subscript j for the starting state and subscript i for the ending state to match the convention in matrix population models, but here, to match convention in stochastic process models, we reverse that usage).

Consider the outcome $\tau_j = m_j$, conditional on starting in state i, and

write

$$P[m_1, m_2, \ldots, m_S] = \Pr[\tau_1 = m_1, \tau_2 = m_2, \ldots, \tau_S = m_S | \text{ starting state } i]. \tag{A.11}$$

Let $w_i, i = 1, \ldots, S$ be a set of (dummy) variables, and form the diagonal matrix

$$\mathbf{W} = \text{diag } \{w_i\}, i = 1, \ldots, S. \tag{A.12}$$

Define the vector function

$$\mathbf{V} = \mathbf{W} \left(\mathbf{I} - \mathbf{Q}\,\mathbf{W}\right)^{-1} \mathbf{d}, \tag{A.13}$$

where $\mathbf{I}$ is the identity matrix and the death rates for states 1 to S are components of the vector

$$\mathbf{d} = \left(\mathbf{I} - \mathbf{Q}\right) \mathbf{e}. \tag{A.14}$$

Then $\mathbf{V}$ from equation (A.13) is the generating function

$$\mathbf{V} = \sum_{m_1, m_2, \ldots, m_S} P[m_1, m_2, \ldots, m_S]\, w_1^{m_1} w_2^{m_2} \ldots w_S^{m_S}. \tag{A.15}$$

for the probabilities defined in equation (A.11). This equation is derived by the same logic used in the age-structured case, as in the main text.

A.4 From Generating Function to LRS

Start by choosing a number N that is the largest possible number of offspring. This may be approximated by a product like $k_U \leq (\omega \times k_m)$ with ω being an estimated maximum age, and k_m being the maximum number of offspring per time period. Or a biological upper limit can be used. Either way, we can test the adequacy of our choice by computing $\mathbf{\Gamma}$ and then its sum, which should be very close to 1.

Given N, for every state i we pad each offspring probability distribution $\boldsymbol{\kappa}_i$ by adding zeros so that the padded distribution has N elements. For any frequency θ, let the Fourier transforms of the padded distributions $\boldsymbol{\kappa}_i$ be $\widehat{\boldsymbol{\kappa}}_i$, so for example

$$\widehat{\boldsymbol{\kappa}}_i(\theta) = \sum_{k=0}^{N-1} \kappa_i(k)\, \theta^k. \tag{A.16}$$

For any non-reproducing state i we have $\kappa_i = \{1, 0, \dots\}$, and so

$$\widehat{\boldsymbol{\kappa}}_i(\theta(k)) = 1, \text{ for all } \theta(k) \text{ for non-reproducing states.} \tag{A.17}$$

Now refer to the previous subsection, and assume that for states $j = 1, 2, \dots,$ that we spend time τ_j in state j before death. The total offspring numbers that result have the distribution

$$\boldsymbol{\kappa}_1^{m_1} \star \boldsymbol{\kappa}_2^{m_2} \star \cdots \star \boldsymbol{\kappa}_S^{m_S} = \boldsymbol{\delta}, \tag{A.18}$$

say. So in this case

$$\Pr[\text{number of offspring is } k]$$

is given by the kth element of the convolution δ in equation (A.18)

The lifetime probability of having k offspring is the kth element of

$$\mathbf{\Gamma} = \sum_{m_1, m_2, \ldots, m_S} P[m_1, m_2, \ldots, m_S]\, \boldsymbol{\kappa}_1^{m_1} \star \boldsymbol{\kappa}_2^{m_2} \star \cdots \star \boldsymbol{\kappa}_S^{m_S}. \tag{A.19}$$

Using the facts about Fourier transforms and equation (A.19) we conclude that

$$\widehat{\mathbf{\Gamma}}(\theta) = \sum_{m_1, m_2, \ldots, m_S} P[m_1, m_2, \ldots, m_S]\, \widehat{\boldsymbol{\kappa}_1}(\theta)^{m_1} \ldots \widehat{\boldsymbol{\kappa}_S}(\theta)^{m_S}. \tag{A.20}$$

The sum here can be exactly computed using the generating function equation (A.15).

A.5 Method for Stages

Start with choosing a large number N, fix the starting stage i, then find the frequencies as in equation (A.7). For each frequency $\theta(k)$, make the Fourier transforms $\widehat{\Gamma_1}$, and then make a matrix

$$\mathbf{W} = \begin{pmatrix} \widehat{\Gamma_1}(\theta(k)) & 0 & 0 & \ldots \\ 0 & \widehat{\Gamma_2}(\theta(k)) & 0 & \ldots \\ \vdots & \vdots & \vdots & \vdots \end{pmatrix}. \tag{A.21}$$

Remembering the generating function, compute the vector

$$\mathbf{V} = \Big(\mathbf{I} - \mathbf{Q}\,\mathbf{W}\Big)^{-1}\,\mathbf{d}. \tag{A.22}$$

Then use equation (A.20) to find

$$\widehat{\mathbf{\Gamma}}(\theta(k)) = \text{Component } k\text{th of } \mathbf{W}\,\mathbf{V}. \tag{A.23}$$

Repeat for all frequencies.

Final step: use the Inverse FFT to find $\mathbf{\Gamma}$.

Note: since every age+stage model can be cast as a stage-only model, this method can also be used for age-only or age+stage models. But the age-structured analysis in the main text explains the basic logic that the general method does not. The age-based method is often computationally useless for stage based or age+stage models when we have a large number of stages, or when individuals can stay in a stage for a long time. In such cases, the method here is essential.

A.6 Hybrid method for age+stage

An age+stage model has ages $a = 1, 2, \ldots, \omega$, stages $s = 1, 2, \ldots, S$. We call the probability distribution for the number of offspring produced during a time interval "the reproduction distribution." An age+stage combination is written a, s. In some cases, the general method of the preceding section may be computationally lengthy and the hybrid method described here is faster.

There is a certain age A that partitions the life cycle. After age A onward the vital rates are the same at every age, and so depend only on stage. For ages $a < A$, vital rates depend upon both age and stage. Individuals may be in different stages when they reach age A. First, we track the reproduction distribution for individuals who die before age A, $\boldsymbol{\gamma}_{A-}$; second, we track the reproduction distribution of individuals who are still alive at age A, but are in different stages at that age (see the R code).

Then, we consider that for ages $a \geq A$ we have a stage-structured model, a stage transition matrix $\mathbf{U}_A$ that does not change with age, and stage-specific reproduction distributions given by the rows of $\widetilde{\boldsymbol{\kappa}}_A = (\boldsymbol{\kappa}_{A,1}, \boldsymbol{\kappa}_{A,2}, \ldots, \boldsymbol{\kappa}_{A,S})$. So we can use the methods detailed above for stage-structured models, and compute a distribution of LRS for each of the stages that entered age A. Now we convolute the reproduction distributions of $a < A$ ending at a given stage and the reproduction distributions of $a \geq A$ starting at the same stage. Summing all the convoluted distributions across stage gives the reproduction distribution for individuals who die after or at age A, $\boldsymbol{\gamma}_{A+}$. (See the R code.)

Finally we have the LRS

$$\boldsymbol{\Gamma} = \boldsymbol{\gamma}_{A-} + \boldsymbol{\gamma}_{A+}. \tag{A.24}$$

A.7 Special probabilities: Ages only

To compute Pr[LRS = 0], observe that an individual has 0 offspring if it either (a) dies before reaching reproductive age α or (b) survives through

the pre-reproductive period, but has 0 offspring thereafter. At reproductive age a the probability of having 0 offspring is $\kappa_a(0)$. Assuming survival, the cumulative probability of having had no offspring by age a is

$$p'_a = \kappa_1(0)\,\kappa_2(0)\ldots\kappa_a(0). \tag{A.25}$$

Thus,

$$\begin{aligned}\Pr[\mathrm{LRS}=0] = \big(1-l_\alpha\big)&+\\ &+\sum_{a\geq\alpha}^{\beta-1}\phi_a\,p'_a+\\ &+l_\beta\,p'_\beta.\end{aligned} \tag{A.26}$$

The first line gives us (a) above, the second line adds in reproduction at intermediate ages weighted by the odds of death, and the third line gives us the final contribution to childlessness.

A.8 Special probabilities: Stages

To compute Pr[LRS = 0] here, we need a different method. Each stage i has a corresponding probability that an individual in that stage produces 0 offspring. This probability is 1 for non-reproducing stages, and $\kappa_i(0)$ for all

other stages. Define $\mathbf{W}_2$ to be a diagonal matrix whose elements are

$$\begin{aligned} W_2(i,i) &= 1, \text{ non-reproductive stage } i, \\ W_2(i,i) &= \kappa_i(0), \text{ reproductive stage } i. \end{aligned} \tag{A.27}$$

Then use the definitions of the preceding section and compute

$$\mathbf{V}_2 = \mathbf{W}_2 \left(\mathbf{I} - \mathbf{Q}\,\mathbf{W}_2\right)^{-1} \mathbf{d}. \tag{A.28}$$

Then the ith component of $\mathbf{V}_2$ is

$$\Pr[\text{LRS} = 0 | \text{ initial stage } i].$$

Since every age+stage model can be cast as a stage-only model, this answer can also be used for age-only or age+stage models.

For some life cycles we can also compute

$$\Pr[\text{LRS} = 0 | \text{ die as non-reproductive}]$$

Suppose we start in a non-reproductive stage. In suitable lifecycles, every individual eventually makes an irreversible transition to one or more reproducing stages, or dies. Here it makes sense to treat the reproducing stages as "absorbing" and then the absorption probability is just what we want. See Caswell (2001) or Kemeny and Snell (1976) for details on how to do this.

A.9 Special distributions

A.9.1 Poisson

Here the average fertility is f_i for stage i, and $\boldsymbol{\kappa}_i$ is a Poisson distribution. So $\boldsymbol{\kappa}_i$ has the probability generating function

$$\kappa_i(k) = \exp\big[f_i\,(k-1)\big]. \tag{A.29}$$

So for stage j, and any frequency $\theta(k)$ as defined in equation (A.7), the Fourier transform is

$$\widehat{\kappa_j}(\theta(k)) = \exp\big[f_j\,(\theta(k)-1)\big]. \tag{A.30}$$

A.9.2 Binomial

Here the average fertility is f_i for stage i, and $\boldsymbol{\kappa}_i$ is a Binomial (with 1 trial, also known as a Bernoulli) distribution. So $\boldsymbol{\kappa}_i$ has the probability generating function

$$\kappa_i(k) = \kappa_i(0) + (1-\kappa_i(0))k, \tag{A.31}$$

where $\kappa_i(0)$ is the probability that an individual in stage i has 0 offspring.

So for stage i, and any frequency $\theta(k)$ as defined in equation (A.7), the Fourier transform is

$$\widehat{\kappa_i}(\theta(k)) = \kappa_i(0) + (1-\kappa_i(0))\theta(k). \tag{A.32}$$

A.10 Roe deer plots

Small offspring have a high mode at 0, and thus the highest probability of leaving no offspring. Neither the average LRS nor the standard deviation seem to be useful descriptors of the LRS distribution for the smallest yearlings (plotted in the Appendix, Fig. A.1). For the full spectrum of size class, Fig. A.2 shows 41 initial stages spread over size class 1 to 200. Between size class 5 to 200, there are 5 size class interval between each curve. Fig. A.3 shows the $\Pr[\mathrm{LRS} = 0]$ declines with increasing birth mass.

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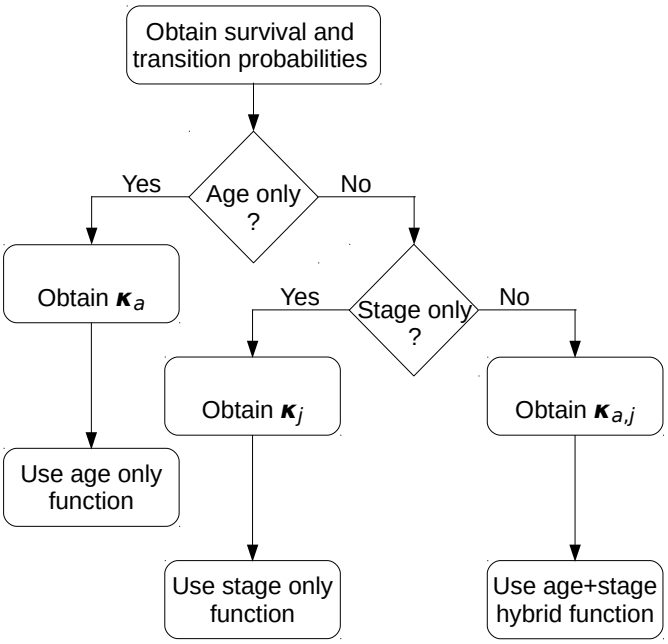

Figure 1: The flow chart of decisions. Survival probabilities (Table 1) and/or survival-transition matrices (Table 2); Reproduction distributions $\boldsymbol{\kappa_a}$, $\boldsymbol{\kappa_j}$, $\boldsymbol{\kappa_{a,j}}$ (Table 5).

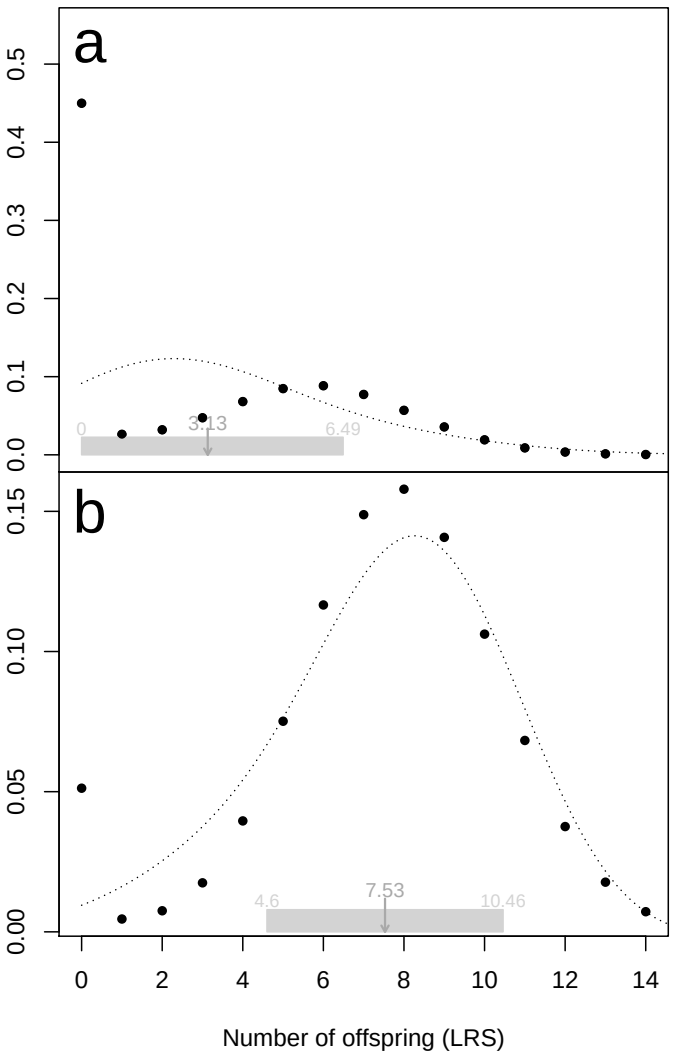

Figure 2: The LRS distribution of Hadza (a) and Hutterites (b) [solid points], and a Gram-Charlier approximation based on the first three moments [dotted lines].

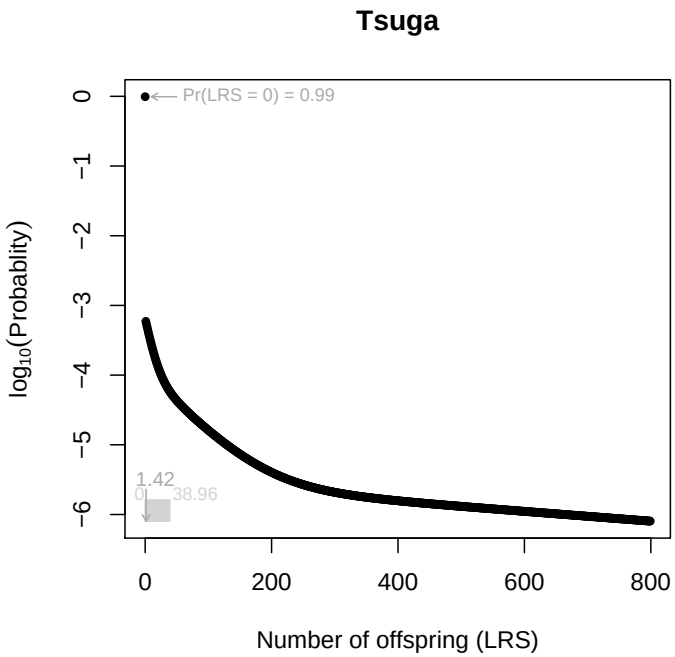

Figure 3: The LRS distribution of *Tsuga canadensis*, eastern hemlock.

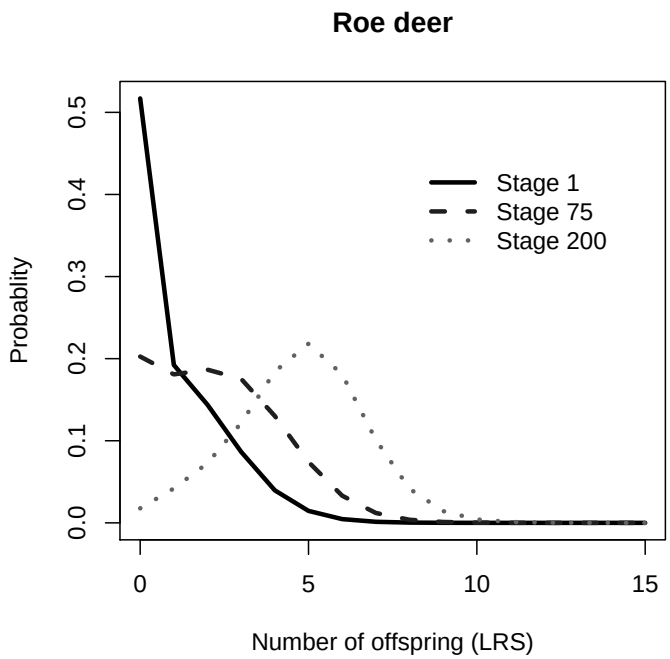

Figure 4: The LRS distribution of yearlings of Roe deer *Capreolus capreolus* for different initial size classes of 1, 75 or 200.

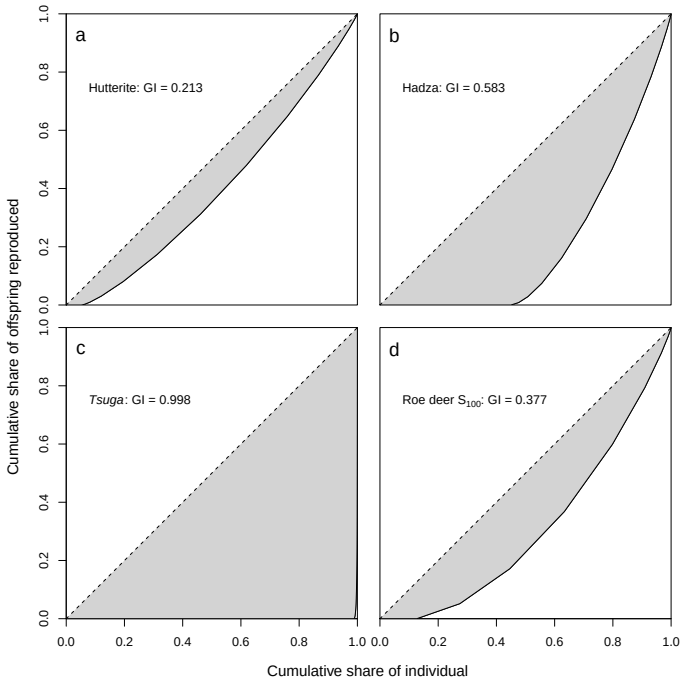

Figure 5: The Lorenz plots for Hutterite, Hadza, *T. canadensis*, and Roe deer (with initial stage 100).

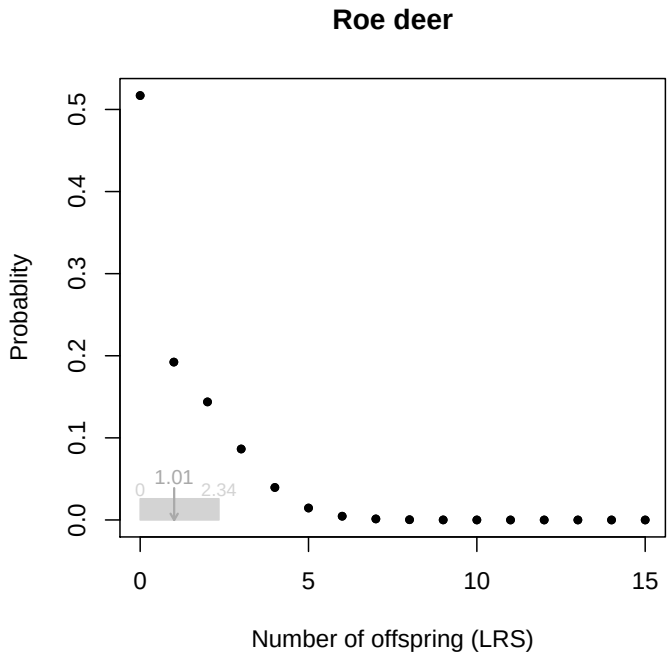

Figure A.1: The LRS distribution of Roe deer *Capreolus capreolus*. Mean LRS = 1.01 and the standard deviation is 1.34.

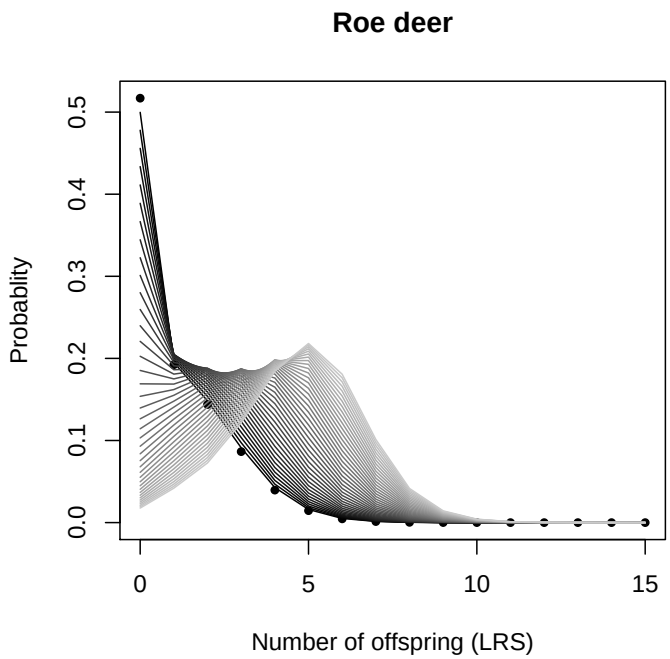

Figure A.2: The LRS distribution of Roe deer *Capreolus capreolus*. There are 41 initial stages. Solid points are for yearlings in size class 1. The gradient gray lines are the distribution spread over size class 5 to 200 with interval 5.

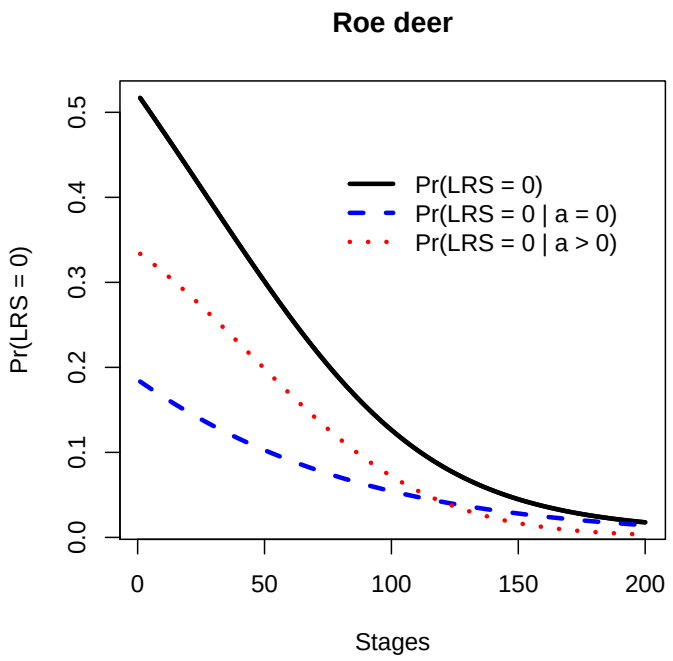

Figure A.3: The probability that LRS = 0 for different initial size classes for yearlings of Roe deer *Capreolus capreolus*. The blue dashed line shows the yearling death probability. The red dotted line shows the probability of having no offspring if you live to later ages.

Table 1: Age, Stage, Transitions and One Period Survival

Parameter	Meaning	Notes
$a = 1, 2, \ldots, \omega$	Age, discrete intervals	Newborns are in the first age interval $a = 1$, ω is the maximum age
$s = 1, 2, \ldots, S$	Stage, discrete categories	S is the total number of stages
$\mathbf{G}$, $0 \leq \mathbf{G}(i,j) \leq 1$, $i = 1, 2, \ldots, S$, $j = 1, 2, \ldots, S$	Stage transition matrix (stage only), probability an individual in stage j at the beginning of one time interval will be in stage i at the beginning of the next time interval, conditional on its survival	$S \times S$ matrix, column stochastic Markov chain
$\mathbf{G}_a$, $0 \leq \mathbf{G}_a(i,j) \leq 1$, $i = 1, 2, \ldots, S$, $j = 1, 2, \ldots, S$	Stage transition matrix for each age a (age + stage), probability an individual in stage j at the beginning of age interval a will be in stage i at the beginning of age interval $a + 1$, conditional on its survival	$S \times S$ matrix, column stochastic Markov chain
p_a, $0 \leq p_a \leq 1$	One period survival (age only), Probability an individual survives from the beginning of age interval a to the beginning of age interval $a + 1$	$p_\omega = 0$
$\mathbf{P}$	A vector of one-period survivals (age only), the elements are p_a	$1 \times \omega$ vector
$p(j)$, $0 \leq p(j) \leq 1$, $j = 1, 2, \ldots, S$	One period survival (stage only), Probability an individual in stage j survives from the beginning of one time interval to the beginning of the next time interval	
$p_a(j)$, $0 \leq p_a(j) \leq 1$, $j = 1, 2, \ldots, S$	One period survival (age+stage), Probability an individual age a and stage j at the beginning of one time interval survives to the beginning of the next time interval	$p_\omega(j) = 0$ for all j
$\widetilde{\mathbf{P}}_a$	A diagonal matrix, where the diagonal is $p_a(j)$	$S \times S$ matrix

Table 2: Unconditional Stage Transitions, Cohort Projection Matrices

Parameter	Meaning	Notes
$\mathbf{U}$, $0 \leq \mathbf{U}(i,j) \leq p(j)$, $i = 1,2,\ldots,S$, $j = 1,2,\ldots,S$, $\mathbf{U}(i,j) = \mathbf{G}(i,j)\ p(j)$	Cohort projection matrix (stage only), probability an individual in stage j at the beginning of one time interval will be alive and in stage i at the beginning of the next time interval	$S \times S$ cohort projection matrix, does not change with age
$\mathbf{U}_a$, $0 \leq \mathbf{U}_a(i,j) \leq p_a(j)$, $i = 1,2,\ldots,S$, $j = 1,2,\ldots,S$, $\mathbf{U}_a(i,j) = \mathbf{G}_a(i,j)\ p_a(j)$	Cohort projection matrix for each age a (age + stage), probability an individual in stage j at the beginning of age interval a will be alive and in stage i at the beginning of age interval $a+1$	$S \times S$ cohort projection matrix, may change with age

Table 3: Survivorship, One period Mortality and Age at Death

Parameter	Meaning	Notes
l_a, $0 \leq l_a \leq 1$	Survivorship to age a, Probability of being alive at the beginning of age interval a for those born into a particular cohort $a-1$ years ago	$l_1 = 1$, $l_2 = p_1\ l_1$, $l_3 = p_2\ l_2$, $\ldots$, $l_{\omega+1} = 0$
$\boldsymbol{L}_a$, $0 \leq \boldsymbol{L}_a(i,j) \leq 1$, $i = 1, 2, \ldots, S$, $j = 1, 2, \ldots, S$, $a = 1, 2, \ldots, \omega$	Survivorship to age a by stage, probability of being alive and in stage i at the beginning of age interval a for those born into stage j in a particular cohort $a-1$ years ago	$S \times S$ matrix, changes with age in both the stage-only and the age+stage models, but computation differs (see text)
$1 - p_a$	One period mortality (age only), Probability an individual in stage a alive at the beginning of age interval a dies before the beginning of the next time interval $a+1$	
$1 - p_j$	One period mortality (stage only), Probability an individual in stage j alive at the beginning of one time interval dies before the beginning of the next time interval	
$1 - p_a(j)$	One period mortality (age + stage), Probability an individual age a and stage j alive at the beginning of one time interval dies before the beginning of the next time interval	
ϕ_a, $0 \leq \phi_a \leq 1$, $a = 1, 2, \ldots, \omega$, $\sum_a \phi_a = 1$	Probability of age at death, the proportion of a cohort that dies at each age a	$\phi_a = l_a\ (1 - p_a)$ for age-only model, details differ for stage-only and age+stage models (see text)
T with density ϕ_a	Age at death, random variable	Mean, Variance of T denoted by μ_T, σ_T^2

Table 4: Age of reproduction and possible number of offpsring

Parameter	Meaning	Notes
α	Age at First Reproduction, youngest age interval during which reproduction occurs	
β	Age at Last Reproduction, oldest age interval during which reproduction occurs	
$k = 0, 1, 2, \ldots, k_m$	Number of offspring that could be produced by an individual during a single age interval	k_m is the maximum number of offspring that could be produced by an individual during a single interval
$k = 0, 1, 2, \ldots, k_U$; $k_U = k_m\,(\beta - \alpha)$; or $k_U = k_m\,\omega$	Number of offspring that could be produced by an individual during the entire life time	k_U is the maximum number of offspring that could be produced by an individual during the entire life time

Table 5: Single time-step distributions of reproductive success

Parameter	Meaning	Notes
$\boldsymbol{\kappa}_a(k)$, $0 \leq \boldsymbol{\kappa}_a(k) \leq 1$, $\sum_k \boldsymbol{\kappa}_a(k) = 1$, $a = 1, 2, \ldots, \omega$	Probability an individual in age interval a produces k offspring before the beginning of age interval $a+1$	ω is the maximum age attained, $\boldsymbol{\kappa}$ is defined even for ages that do not reproduce
$\boldsymbol{\kappa}_a$, components are $\boldsymbol{\kappa}_a(0)$, $\boldsymbol{\kappa}_a(1)$, $\boldsymbol{\kappa}_a(2)$, $\ldots$, $\boldsymbol{\kappa}_a(k_m)$	Vector of probabilities that an individual of age a produces $0, 1, 2, \ldots, k_m$ offspring during a single time interval	the probability of each outcome varies with age
$\boldsymbol{\kappa}_j(k)$, $0 \leq \boldsymbol{\kappa}_j(k) \leq 1$, $\sum_k \boldsymbol{\kappa}_j(k) = 1$, $j = 1, 2, \ldots, S$	Probability an individual in stage j at the beginning of a time interval produces k offspring before the beginning of the next time interval	$\boldsymbol{\kappa}$ is defined even for stages that do not reproduce
$\boldsymbol{\kappa}_j$, components are $\boldsymbol{\kappa}_j(0)$, $\boldsymbol{\kappa}_j(1)$, $\boldsymbol{\kappa}_j(2)$, $\ldots$, $\boldsymbol{\kappa}_j(k_m)$	Vector of probabilities that an individual in stage j produces $0, 1, 2, \ldots, k_m$ offspring during a single time interval	the probability of each outcome varies with stage
$\boldsymbol{\kappa}_{a,j}(k)$, $0 \leq \boldsymbol{\kappa}_{a,j}(k) \leq 1$, for each a,j, sum over k, $\sum_k \boldsymbol{\kappa}_{a,j}(k) = 1$, $a = 1, 2, \ldots, \omega$	Probability an individual in age interval a that is in stage j at the beginning of the interval produces k offspring before the beginning of age interval $a+1$	ω is the maximum age attained, $\boldsymbol{\kappa}$ is defined even for ages that do not reproduce
$\boldsymbol{\kappa}_{a,j}$, components for each age are $\boldsymbol{\kappa}_{a,j}(0)$, $\boldsymbol{\kappa}_{a,j}(1)$, $\boldsymbol{\kappa}_{a,j}(2)$, $\ldots$, $\boldsymbol{\kappa}_{a,j}(k_m)$	For each age, an $S \times k_m$ matrix of probabilities (each row is for a stage j) that an individual in stage j produces $0, 1, 2, \ldots, k_m$ offspring during a single time interval	the probability of each stage-specific outcome varies with age

Table 6: Fertility and LRS

Parameter	Meaning	Notes
f_a, $0 \leq f_a \leq k_m$	Mean number offspring produced by individuals who are in age interval a	$f_a = \sum_k k\, \boldsymbol{\kappa}_a(k)$, $f_a = 0$ for $\alpha \leq a < \beta$
f_j, $0 \leq f_j \leq k_m$	Mean number offspring produced during one time interval by individuals who are in stage j	$f_a = \sum_k k\, \boldsymbol{\kappa}_j(k)$, $f_j = 0$ for non-reproductive stages
$\boldsymbol{\Gamma}(k)$, $0 \leq \boldsymbol{\Gamma}(k) \leq 1$, $\sum_k \boldsymbol{\Gamma}(k) = 1$	Probability an individual produces k offspring during its lifetime	
$\boldsymbol{\Gamma}$, components are $\boldsymbol{\Gamma}(0)$, $\boldsymbol{\Gamma}(1)$, $\boldsymbol{\Gamma}(2)$, $\ldots$, $\boldsymbol{\Gamma}(k_U)$	Vector of probabilities that an individual produces $0, 1, 2, \ldots, k_U$ offspring during its lifetime	k_U = maximum possible number of offspring
LRS	Lifetime Reproductive Success, random variable	Mean, Variance of LRS denoted by $\mu_{\text{LRS}}, \sigma^2_{\text{LRS}}$
$R_0 = \sum_a l_a\, f_a$, $a = 1, 2, \ldots, \omega$	Net Reproductive Rate	Mean Life Time Reproductive Success

Table 7: Convolutions of age-specific distributions of reproductive success for two ages

Parameter	Meaning	Notes
k_m	Maximum number of offspring that can be produced by an individual during one time interval	
$k_m + 1$	Number of elements in a vector where each element references one possible number of offspring produced by an individual during one time interval	
$2k_m + 1$	Number of elements in a vector representing number of offspring produced cumulatively during two time intervals	
$\boldsymbol{\kappa}_1$, components are $\boldsymbol{\kappa}_1(0)$, $\boldsymbol{\kappa}_1(1)$, $\boldsymbol{\kappa}_1(2)$, $\ldots$, $\boldsymbol{\kappa}_1(k_m)$, $\boldsymbol{\kappa}_1(k) \geq 0$	Vector of probabilities that an individual produces k offspring at a given age	k is a particular number of offspring produced
$\boldsymbol{\kappa}_2$, components are $\boldsymbol{\kappa}_2(0)$, $\boldsymbol{\kappa}_2(1)$, $\boldsymbol{\kappa}_2(2)$, $\ldots$, $\boldsymbol{\kappa}_2(k_m)$, $\boldsymbol{\kappa}_2(k) \geq 0$	Vector of probabilities that an individual produces k offspring at a different age	k is a particular number of offspring produced
$\boldsymbol{\delta}$, components are $\boldsymbol{\delta}(0)$, $\boldsymbol{\delta}(1)$, $\boldsymbol{\delta}(2)$, $\ldots$, $\boldsymbol{\delta}(2k_m - 1)$, $\boldsymbol{\delta}(k) \geq 0$	Vector of probabilities than an individual produces a total of k offspring after reproducing at 2 different ages, conditional on being alive at each of these ages	k is a particular number of offspring produced
$\boldsymbol{\delta} = \boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2$	Convolution of $\boldsymbol{\kappa}_1$ and $\boldsymbol{\kappa}_2$	see text for computation

Table 8: Convolutions of age-specific distributions of reproductive success for all ages

Parameter	Meaning	Notes
$\boldsymbol{\gamma}_a = \phi_a \ \boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2 \star \boldsymbol{\kappa}_3, \cdots \star \boldsymbol{\kappa}_a$	Vector of probabilities of LRS for individuals who live to age a but die before $a+1$ for $a < \beta$	
$\boldsymbol{\gamma}_a = l(\beta) \ \boldsymbol{\kappa}_1 \star \boldsymbol{\kappa}_2 \star \boldsymbol{\kappa}_3, \cdots \star \boldsymbol{\kappa}_\beta$	Vector of probabilities of LRS for individuals who live to age a but die before $a+1$ for $a \geq \beta$	
$\boldsymbol{\Gamma} = \sum_{a=1}^{a=\beta} \boldsymbol{\gamma}_a$	Vector of probabilities of LRS for entire lifetime, from summing across contributions by each age, up to and including the last reproductive age	same as $\boldsymbol{\Gamma}$ above