Note

The Equivocal Mean Age of Parents in a Cohort

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ABSTRACT: The mean age at which parents give birth is an important notion in demography, ecology, and evolution, where it is used as a measure of generation time. A standard way to quantify it is to compute the mean age of the parents of all offspring produced by a cohort, and the resulting measure is thought to represent the mean age at which a typical parent produces offspring. In this note, I explain why this interpretation is problematic. I also introduce a new measure of the mean age at reproduction and show that it can be very different from the mean age of parents of offspring of a cohort. In particular, the mean age of parents of offspring of a cohort systematically overestimates the mean age at reproduction and can even be greater than the expected life span of parents.

Keywords: cohort generation time, age-structured population, mean age at reproduction, mean age of mothers, Crump-Mode-Jagers processes.

Introduction

The mean age at reproduction is a central notion in the study of the evolution of reproductive timing and of the slow-fast continuum. It also plays an important role in demography. However, as with many descriptors of populations, it is not clear how it should be defined—let alone quantified in practice. A standard measure of it is the mean age of parents of offspring produced by a cohort, also frequently referred to as the cohort generation time. To obtain it, consider all offspring produced by a cohort of newborns over its lifetime; for each of these offspring, record the age that their parents (or mother in the case of a female-based model) had when the offspring was born; finally, take the average of these ages.

It is straightforward to compute this quantity from complete census data. In practice, however, it is usually estimated from life tables using the following formula:

$$\mu_1 = \frac{\int_0^{+\infty} t m(t) \ell(t) dt}{\int_0^{+\infty} m(t) \ell(t) dt}. \tag{1}$$

In this expression, the survivorship function ℓ gives the probability that an individual of the chosen cohort reaches age t, and the age-specific fertility m represents its rate of offspring production in such a way that, assuming the individual remains alive between ages a and b, the expected number of offspring it will produce in that interval of time is $\int_a^b m(t) dt$. There is also a discrete-time version of formula (1):

$$\mu_1 = \frac{\sum_{t=1}^{+\infty} t \ell_t m_t}{\sum_{t=1}^{+\infty} \ell_t m_t}, \tag{2}$$

where ℓ_t is the probability that an individual survives to age t and m_t is the expected number of offspring produced at age t by individuals that reach that age.

Formulas (1) and (2) go back a long way and are ubiquitous in the literature. They have been popularized by classic references such as Keyfitz (1968) and Coale (1972) in demography and Charlesworth (1994) and Caswell (2001) in biology. They can also be found in more recent works of reference, including Jørgensen and Fath (2008), Rockwood (2015), and Kliman (2016).

A consensus interpretation of μ_1 is that it represents the mean age at which a typical parent produces offspring. The aim of this note is to show that this interpretation is inaccurate and can be problematic in practice. To do so, I introduce a more direct measure of the mean age at reproduction of a typical parent. Consider a typical parent, and compute the average of the ages at which it gives birth to its offspring. The expected value of this average is what we term the mean age at reproduction. Under standard assumptions, it is given by

$$\tau = \frac{1}{c} \int_0^{+\infty} \frac{\int_0^t s m(s) ds}{\int_0^t m(s) ds} \left(1 - e^{-\int_0^t m(s) ds} \right) f(t) dt, \tag{3}$$

where f denotes the probability density function of the life span of an individual and the constant

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$$c = \int_0^{+\infty} \left(1 - e^{-\int_0^t m(s)ds}\right) f(t)dt \qquad (4)$$

is the fraction of individuals that produce offspring during their lifetime. As with μ_1, there is a discrete-time formula for τ:

$$\tau = \frac{1}{c} \sum_{t \geq 1} \frac{\sum_{s=1}^t s m_s}{\sum_{s=1}^t m_s} \left(1 - \prod_{s=1}^t e^{-m_s}\right) p_t, \qquad (5)$$

where $p_t = \ell_t - \ell_{t+1}$ is the probability mass function of the life spans of individuals and

$$c = \sum_{t \geq 1} \left(1 - \prod_{s=1}^t e^{-m_s}\right) p_t. \qquad (6)$$

Using the expressions of μ_1 and τ, we show that these two quantities can differ greatly, even in the most simple models. We also prove that μ_1 is always greater than τ and that the difference between the two can be arbitrarily large. Finally, comparing the two measures numerically for 3,871 real-world models from the COMPADRE and COMADRE databases, we obtain an average discrepancy of 20.6% and find that in one model out of four they differ by more than 30%.

Interpretation of the Expressions of μ_1 and τ

The detailed derivations of the expressions of μ_1 and τ can be found in appendixes A–C. A brief overview of some of the mathematical notions on which they rely is provided in the supplemental PDF (available online). Here we present the assumptions behind the formulas and explain what the quantities μ_1 and τ correspond to. Note that although they are seldom made explicit, the following mathematical assumptions are essential to the expressions of μ_1 given in the introduction.

In the continuous-time setting, we assume (1) that the lifetimes of individuals are independent copies of a random variable T such that $\mathbb{P}(T \geq t) = \ell(t)$ and (2) that births are punctual random events that occur while individuals are alive (but are independent of everything else) and that there exists a function m such that the expected number of offspring produced by any individual alive between ages a and b is $\int_a^b m(t)dt$—in other words, that the birth events are the points of a point process with intensity m. Such models are known as Crump-Mode-Jagers processes (Crump and Mode 1968, 1969; Jagers 1969) and are also sometimes referred to as generalized branching processes. In the discrete-time setting, formula (2) is replaced by the assumption that at each age $t = 1, 2, \ldots$ at which an individual is alive, it produces a random number of offspring that is independent of everything else and has mean m_t.

Under these hypotheses, if we let N be the random variable corresponding to the number of offspring produced by a typical individual over its lifetime and let S be the sum of the ages at which it produces them, then the quantity μ_1 given in formulas (1) and (2) can be rigorously interpreted as

$$\mu_1 = \frac{\mathbb{E}(S)}{\mathbb{E}(N)}, \qquad (7)$$

where $\mathbb{E}(\cdot)$ denotes the expected value (for details, see app. B). Contrary to what is often claimed, this is neither the average of the ages at which the individual produces offspring, which would be the random variable S/N, nor the expected value of this average, which would be $\mathbb{E}(S/N)$. However, under the assumption that individuals are independent, the average of the ages of the parents of the offspring produced by a cohort goes to μ_1 as the size of the cohort goes to infinity. This justifies the interpretation of μ_1 as the mean age of parents of offspring produced by a cohort.

A natural measure for the mean age at reproduction would be the expected value of S/N, the average age at which an individual produces offspring. However, this average is well defined only when the individual produces some offspring—that is, when $N > 0$. Thus, we define our measure τ to be the conditional expectation

$$\tau = \mathbb{E}(S/N | N > 0). \qquad (8)$$

Equivalently, τ can be defined as follows: consider a typical parent (i.e., sample an individual uniformly at random among all individuals that produce some offspring), and denote by $\tilde{N}$ its number of offspring and by $\tilde{S}$ the sum of the ages at which it produces them. Then,

$$\tau = \mathbb{E}(\tilde{S}/\tilde{N}). \qquad (9)$$

Assuming that birth events form a Poisson point process (or in the discrete-time setting, that individuals produce a Poissonian number of offspring), we prove in appendix C that τ is given by formula (3) (respectively, formula [5] in discrete time). Observe that while the interpretation of μ_1 as an average on a large cohort crucially hinges on the independence of individuals, this hypothesis is not used in the derivation of τ because it is truly a characteristic of individuals, as opposed to μ_1, which is a property of the cohort.

Sometimes, especially when studying evolution, one is interested in the average of a function z of the ages at which a parent produces offspring, rather than in the average of the ages themselves.[1] In that case, letting A be uniformly chosen among the ages at which a typical parent produces offspring, for every function z,

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1. This was pointed out by Mauricio González-Forero.

$$\mathbb{E}(z(A)) = \frac{1}{c} \int_0^{+\infty} \frac{\int_0^t z(s)m(s)ds}{\int_0^t m(s)ds}\left(1 - e^{-\int_0^t m(s)ds}\right)f(t)dt, \tag{10}$$

with the constant c given in equation (4).

Finally, expressions of μ_1 are also available for more general population structures. For instance, in matrix population models, if we let $\mathbf{S}$ be the survival matrix and $\mathbf{F}$ be the fertility matrix (i.e., if we decompose the projection matrix $\mathbf{A}$ into $\mathbf{A} = \mathbf{S} + \mathbf{F}$ to separate survival probabilities from fertilities) and denote by $\mathbf{w}$ the stable distribution of the population (the dominant right eigenvector of $\mathbf{A}$) and $\mathbf{e} = (1, \dots, 1)$ the row vector consisting only of ones, then we can use the following modern version of the classic formula of Cochran and Ellner (1992), which can be found in Ellner (2018):

$$\mu_1 = \frac{\mathbf{eF}(\mathbf{I} - \mathbf{S})^{-2}\mathbf{Fw}}{\mathbf{eF}(\mathbf{I} - \mathbf{S})^{-1}\mathbf{Fw}}. \tag{11}$$

Note that $(\mathbf{I} - \mathbf{S})^{-1} = \sum_{t \geqslant 1}\mathbf{S}^{t-1}$ and that $(\mathbf{I} - \mathbf{S})^{-2} = \sum_{t \geqslant 1} t\mathbf{S}^{t-1}$, so that this expression closely parallels formula (2). The entries of $\mathbf{e}$ represent the weight given to each type of offspring when computing the average age of the parents. Should we wish to give more importance to some offspring type, any vector with positive entries could be used in place of $\mathbf{e}$—in fact, Cochran and Ellner (1992) suggest using the reproductive values as weights. See Steiner et al. (2014) and Ellner (2018) for more on this.

As explained in appendix C, there does not seem to be a simple analogue of equation (11) for τ. Nevertheless, its definition as the mean age at which a typical parent produces offspring still applies in the context of matrix population models, and it can be estimated numerically via individual-based simulations (see sec. S6 of the supplemental PDF).

Examples

Theoretical Examples

Let us start with a simple but fundamental example where individuals reproduce at constant rate m. In that case,

$$\mu_1 = \frac{\mathbb{E}(\int_0^T msds)}{\mathbb{E}(\int_0^T mds)} = \frac{1}{2}\frac{\mathbb{E}(T^2)}{\mathbb{E}(T)} \tag{12}$$

and

$$\tau = \mathbb{E}\left(\frac{\int_0^{\tilde{T}} msds}{\int_0^{\tilde{T}} mds}\right) = \frac{1}{2}\mathbb{E}(\tilde{T}), \tag{13}$$

where T is the life span of individuals and $\tilde{T}$ is the life span of parents. The expression of τ is unsurprising: when birth events are uniformly distributed on the lifetime of individ-

uals, they occur on average in the middle of their life. Also, since

$$\mathbb{E}(\tilde{T}) = \frac{\mathbb{E}(T(1 - e^{-mT}))}{\mathbb{E}(1 - e^{-mT})}, \tag{14}$$

and that for all $t > 0$, $1 - e^{-mt}$ increases to one as m goes to infinity, it follows from the monotone convergence theorem that

$$\mathbb{E}(\tilde{T}) \to \mathbb{E}(T) \quad \text{as } m \to +\infty. \tag{15}$$

By a similar argument (see sec. S3 of the supplemental PDF), we also have

$$\mathbb{E}(\tilde{T}) \to \frac{\mathbb{E}(T^2)}{\mathbb{E}(T)} \quad \text{as } m \to 0. \tag{16}$$

Furthermore, since $\mathbb{E}(\tilde{T})$ is a decreasing function of m, we conclude that when individuals reproduce at a constant rate,

$$\frac{1}{2}\mathbb{E}(T) \leqslant \tau \leqslant \mu_1. \tag{17}$$

In fact, the inequality $\tau \leqslant \mu_1$ holds for general age-specific fertility functions, as shown in section S4 of the supplemental PDF.

To make this example more concrete, let us further assume that individuals die at constant rate η, so that T is an exponential variable and $\ell(t) = e^{-\eta t}$. In that case, we get

$$\mu_1 = \frac{1}{\eta} \quad \text{and} \quad \tau = \frac{1}{2\eta}\left(1 + \frac{1}{1 + m/\eta}\right). \tag{18}$$

Note that here μ_1 is also equal to the expected life span in the population. Interpreting it as the mean age at which parents reproduce would therefore lead to a contradiction, because—in the case where the fertility m is large enough, so that most individuals get to reproduce during their lifetime and the life span of a typical parent is not very different from that of a typical individual—this would imply that the age at which an individual reproduces is on average the same as the age at which it dies. This is absurd, because unless individuals reproduce exactly when they die, the former has to be smaller than the latter.

From formula (18), we also see that for m/η large enough, $\mu_1 \approx 2\tau$. For $m = \eta$, which corresponds to the minimum ratio m/η for a viable population, the difference is already 25% of the value of μ_1. The relative difference between μ_1 and τ as a function of m/η is plotted in figure 1.

Now consider the closely related discrete-time model where individuals survive from one year to the other with probability p and produce Poisson(m) offspring at each age $t \geqslant 1$, so that

$$p_t = (1 - p)p^t \quad \text{and} \quad \ell_t = p^t. \tag{19}$$

After straightforward calculations, we find that the numerator in formula (2), which corresponds to the mean sum of
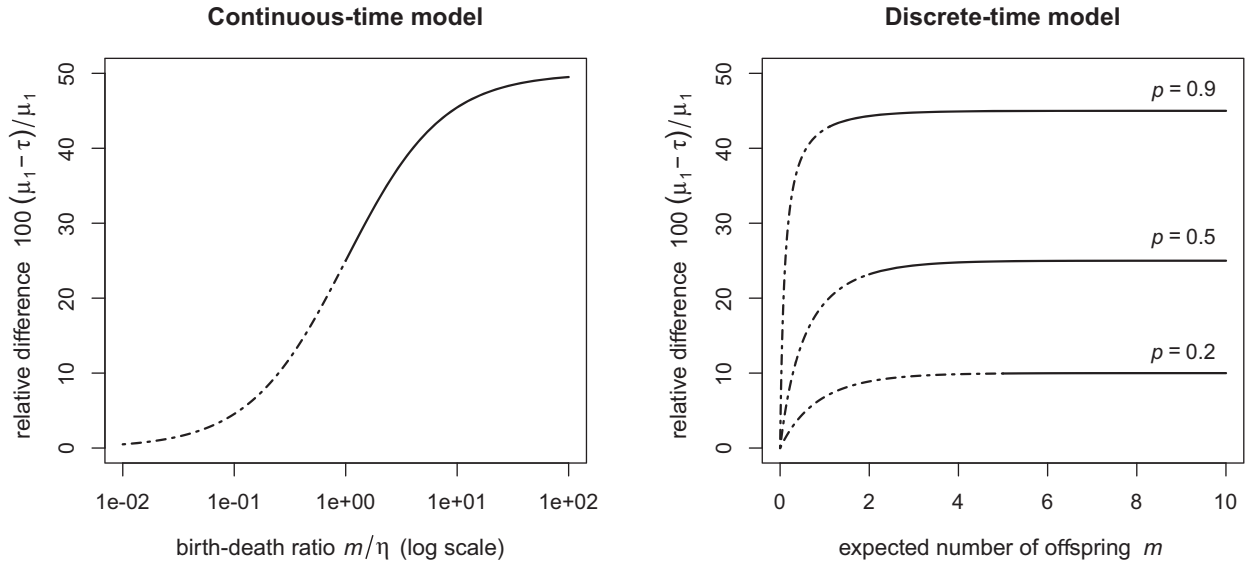
Continuous-time model

Discrete-time model

Figure 1: Relative difference between μ_1 and τ as a function of the parameters of the models considered. *Left*, the continuous-time model in which individuals give birth at constant rate m and die at constant rate η. *Right*, the discrete-time model in which they survive from one year to the other with probability P and give birth to Poisson(m) offspring each year. Dashed lines indicate values of the parameters for which the population is not viable in the long term.

the ages at childbirth, is $mp/(1-p)^2$ and the denominator is $mp/(1-p)$. As a result,

$$\mu_1 = \frac{1}{1-p}. \tag{20}$$

Note that this model can also be seen as a 1×1 matrix population model with survival matrix $\mathbf{S} = (p)$ and fertility matrix $\mathbf{F} = (m)$, so formula (11) can also be used and gives the same result.

Because $\mathbb{E}(T) = p/(1-p)$, we see that

$$\mu_1 = \mathbb{E}(T) + 1, \tag{21}$$

which also corresponds to the expected life span of individuals that reach age 1. For the same reason as before, this implies that μ_1 is not credible as an estimate of the mean age at which a typical parent produces offspring.

After standard calculations (see sec. S5 of the supplemental PDF), we find that

$$\tau = \frac{1}{2}\left(\frac{1}{1-p} + \frac{1}{1-pe^{-m}}\right). \tag{22}$$

As previously, $(1/2)\mu_1 \leqslant \tau \leqslant \mu_1$, but the difference between μ_1 and τ can be quite high, even for very reasonable values of p and m: for instance, with $p = .5$ and $m = 2$, both measures differ by 23% of the value of μ_1; for $p = .9$ and $m = 2$, they differ by 44%. Again, this is illustrated in figure 1.

Real-World Examples

The examples of the previous section show that μ_1 and τ can be very different, even in the most simple models. But do they differ significantly in practice? To answer this question, μ_1 and τ were calculated for every model of the COMPADRE Plant Matrix Database (ver. 4.0.1) and COMADRE Animal Matrix Database (ver. 2.0.1; both databases are available at https://www.compadre-db.org) for which this could be done. Because there is no formula for τ in matrix population models, it was estimated numerically in such a way that for each estimated value, the width of the 95% confidence interval was less than 2% of the estimated value itself (for details, see sec. S6 of the supplemental PDF). The code used to perform the simulation is provided as an online enhancement.[2] Figure 2 gives the distribution of the relative difference between the two quantities, computed as $\Delta_\% = 100(\mu_1 - \tau)/\mu_1$, and table 1 lists some statistics of this distribution. These conclusively show that the measures μ_1 and τ differ significantly for most real-world models. In particular, the fact that the median of $(\mu_1 - \tau)/\mu_1$ is of order 20% means that by using μ_1 to quantify the mean age at reproduction, one overestimates its actual value by more than 25% in half of the cases.

For a detailed example of a model in which μ_1 and τ differ greatly, see section S7 of the supplemental PDF. This example is particularly interesting because it illustrates the fact

2. Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.
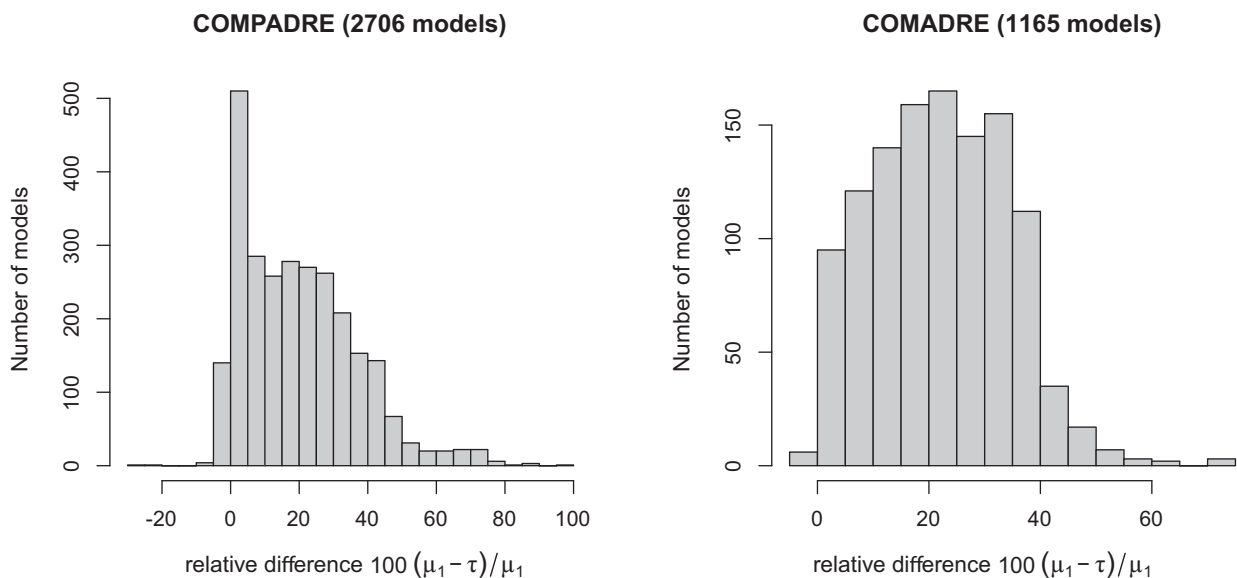
COMPADRE (2706 models)

COMADRE (1165 models)

Figure 2: Distribution of the relative difference between μ_1 and τ for the COMPADRE and COMADRE databases. The difference is given as a percentage of μ_1; for instance, a 30% difference means that $\tau = 0.7\mu_1$.

that μ_1 can be greater than the expected life span conditional on reproduction, which decisively rules out its interpretation as the mean age at reproduction.

Before closing this section, let us comment on the fact that some models (152 out of 3,871) appear to have $\tau < \mu_1$. These are in fact models for which τ is very close to μ_1 but because of the uncertainty in its estimation appears to be slightly smaller than it. Indeed, for most of these models $\mu_1 - \tau$ is very close to zero (only 10 of them have a relative difference $|\Delta_\%| > 1\%$). All things considered, the fact that μ_1 lies below the 95% confidence interval of τ for only 0.46% of all models is consistent with the fact that $\tau \leqslant \mu_1$ (it would have to be more than 2.5% to constitute a contradiction).

Finally, the excess of models for which $\mu_1 \approx \tau$ in COMPADRE compared to COMADRE is due to (mostly 2×2) models with very short generation times, presumably corresponding to annual plants in which the life spans of individuals exhibit little to no variation.

Discussion

The mean age of the parents of the offspring produced by a cohort μ_1 and the mean age at reproduction τ are two genuinely different notions. So why have they not been recognized as such before? Probably because precise definitions of these quantities are seldom given. For instance, in the references given above—which are or have been among the most influential in the field—μ_1 is variously described as the "mean age at childbearing in the stationary population"[3]

3. What Keyfitz calls the stationary population is actually a cohort.

by Keyfitz (1968), the "mean age of childbearing in a cohort" by Coale (1972, eq. [2.10], p. 19), the "mean age at reproduction of a cohort of females" by Charlesworth (1994, eq. [1.47a], p. 30), and the "mean age of the mothers at the time of their daughter's birth" by Rockwood (2015, eq. [4.12], p. 98). Yet these four definitions fail to detail how this "mean" should be computed and could thus be thought to refer to τ.

It is not obvious from the definitions of μ_1 and τ how these two quantities are related—or indeed why they should differ at all. One helpful way to think about it is the following: μ_1 can be seen as an offspring-centric measure of the mean age of parents, whereas τ is a parent-centric measure of it. Indeed, to compute μ_1 we ask each newborn produced by a cohort "how old is your parent?" while for τ we ask a parent "how old are you going to be when you have offspring?" These questions have distinct answers because they correspond to two different ways to sample a parent.

Among other things, this explains why μ_1 is greater than τ: indeed, parents that live longer tend to have more offspring and thus have a higher probability of being sampled via their offspring than when the sampling is done uniformly at random. As a result, they contribute more to μ_1 than to τ. Since these parents with longer life spans are also those that

Table 1: Statistics of the distribution of $(\mu_1 - \tau)/\mu_1$ for the COMPADRE and COMADRE databases

Database	Mean	1st quartile	Median	3rd quartile
COMPADRE	19.97	5.26	17.73	30.49
COMADRE	22.16	12.54	22.60	31.14

Note: All values are percentages.

tend to have a higher mean age at reproduction, this biases μ_1 upward compared to τ.

This also explains why the difference $\mu_1 - \tau$ goes to zero as the fertility becomes vanishingly small (see sec. S3 of the supplemental PDF): in that case, the proportion of parents that give birth to more than one offspring during their lifetime goes to zero, and as a result the two parent-sampling schemes become equivalent.

To close this series of remarks regarding the link between μ_1 and τ, observe that from a purely mathematical point of view the difference between the two can be made arbitrarily large. Indeed, recall that when individuals reproduce at a constant rate m, $\mu_1 = \mathbb{E}(T^2)/\mathbb{E}(T)$ and $\tau \to (1/2)\mathbb{E}(T)$ as $m \to +\infty$. Thus, by choosing an appropriate distribution for the life span T and taking m large enough, we can make μ_1 arbitrarily large and τ arbitrarily small.

Now that we have seen that μ_1 and τ are two different concepts that differ significantly in practice and so we better understand the link between them, one important question remains: which of μ_1 or τ should be favored in which context? From a practical point of view, the expressions of τ are admittedly more complex than those of μ_1. This, of course, is not a problem for real-world applications, where they are going to be evaluated numerically; for theoretical applications, however, this does make exact calculations harder, if possible at all.

Another important difference between both measures is their slightly different domain of validity. While the interpretation of μ_1 hinges on the assumption that there are no interactions between individuals, the expression of τ relies on that of Poissonian births. One might cynically argue that this is hardly a problem, because both hypotheses are often used jointly in theoretical models and never met in real-world applications. Nevertheless, there is a real difference here that should be taken into account when deciding which measure to choose.

Last, τ has the advantage of having a more direct interpretation than μ_1. Judging from the phrasing used by several authors, it seems that it is sometimes τ they have in mind, even when working with μ_1. Moreover, the interpretation of μ_1 might not be as intuitive as we usually assume; notably, the fact that it can be greater not only than the expected life span but also than the expected life span conditional on reproduction (as illustrated by the "medium density" scenario for *Astrocaryum mexicanum* in sec. S7 of the supplemental PDF) is likely to come as a surprise to many researchers.

Acknowledgments

APPENDIX A

An Explicit Model for the Population

Here we recall and further detail the assumptions on which the expressions of μ_1 and τ and their interpretations rely, and we introduce some notation. The setting that we use is that of a Crump-Mode-Jagers process (Crump and Mode 1968, 1969; Jagers 1969), where the population consists of a discrete set of individuals such that (i) each individual i has a random life span T_i with distribution ν and that is independent of everything else and (ii) individual i produces a new offspring at age t for every point of P_i at t such that $t \leqslant T_i$, where P_i is a point process with intensity m on $[0, +\infty[$ that is independent of everything else. Note that the point processes P_i are not homogeneous (m is a function of the age of individuals) and that they do not have to be simple (an individual can give birth to several offspring simultaneously). For mathematical tractability, however, it is often convenient to work with Poisson point processes. As explained in section S1 of the supplemental PDF, where a few useful results about Poisson point processes can also be found, these allow one to formalize the familiar idea that events "occur at rate m." While the assumption that P_i are Poisson point processes is not needed in the study of μ_1, it will be required to derive explicit formulas for τ.

In this setting, the definition and interpretation of the survivorship function and the age-specific fertility are straightforward. The survivorship is defined by[4]

$$\ell(t) = \mathbb{P}(T_i \geqslant t) = \nu([t, +\infty[). \qquad (A1)$$

Working with the measure ν is convenient because it makes it possible to treat the case where T_i is a continuous random variable and the case where it is a discrete random variable simultaneously. However, in many applications T_i will have a density f. Thus, we will do most of our calculations with ν but express our final results in terms of f or ℓ, as in formulas (1) and (3). Note that this essentially consists in replacing $d\nu(t)$ by $f(t)dt$ in integrals and that either of f and ℓ

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4. In probability theory and statistics, the survival function almost invariably refers to the complementary cumulative distribution function of T_i, $t \mapsto \mathbb{P}(T_i > t)$. Here, however, we will stick to the convention used in biology.

can be deduced from the other, since $\ell(t) = 1 - \int_0^t f(s)ds$ and $f(t) = -\ell'(t)$.

The age-specific fertility is the function m. If we denote by $M_i(a, b)$ the integer-valued random variable corresponding to the number of offspring produced by i between ages a and b, then assuming that $b \leqslant T_i$ we have, as expected,

$$\mathbb{E}(M_i(a, b)) = \int_a^b m(t)dt. \tag{A2}$$

Obviously, the framework of Crump-Mode-Jagers processes is not meant to take into account all phenomena that shape the structure and dynamics of real-world populations. For instance, it assumes that individuals are independent and thus excludes any kind of density dependence. Similarly, the (optional) assumption that individuals reproduce at rate m is constraining and in particular implies that they cannot produce several offspring simultaneously. Nevertheless, this framework is close to the minimal setting containing all the ingredients needed to define most descriptors of populations, while being simple enough to remain tractable and make it possible to derive explicit formulas for these descriptors. Moreover, the hypotheses above correspond quite well to the assumptions that are made (typically implicitly) to obtain the classic expressions of many descriptors of populations.

Finally, to obtain discrete-time equivalents of formulas (1) and (3), we will need to consider the following version of the model, which allows simultaneous births: we keep assumption (i) under the extra hypothesis that the life span T_i is an integer-valued random variable, and we replace (ii) by the assumption that at each age $t = 1, \dots, T_i$, individual i gives birth to $M_t^{(i)}$ new individuals. Again, this corresponds quite well to the usual hypotheses on which many classic formulas rely.

APPENDIX B

Mean Age of the Parents of the Offspring Produced by a Cohort

We now give a rigorous interpretation of the quantity μ_1 given by formulas (1) and (2). As we will see, this interpretation is more subtle than what is usually assumed. This is because μ_1 does not correspond to the expected value of the average of the ages of the parents of the offspring produced by a cohort but only to the limit of this average when the size of this cohort goes to infinity.

Let $\mathcal{C}$ denote a cohort, that is, a set of n individuals considered from the time of their birth to the time of their death. Let T_i be the life span of individual i and P_i be the set of ages at which it produces offspring. Note that in our setting, conditional on T_i, P_i is a point process with intensity m on $[0, T_i]$.

The average of the ages of the parents of the offspring produced by the cohort over its lifetime is

$$Z_{\mathcal{C}} = \frac{\sum_{i \in \mathcal{C}} \sum_{t \in P_i} t}{\sum_{i \in \mathcal{C}} \sum_{t \in P_i} 1} = \frac{\sum_{i \in \mathcal{C}} S_i}{\sum_{i \in \mathcal{C}} N_i}, \tag{B1}$$

where $N_i = \sum_{t \in P_i} 1$ is the number of offspring produced by individual i and $S_i = \sum_{t \in P_i} t$ is the sum of the ages at which it produces them. Note that $Z_{\mathcal{C}}$ is well defined only when $\sum_{i \in \mathcal{C}} N_i > 0$ but that this happens with probability arbitrarily close to one for a large enough cohort.

As we have already seen, the expected number of offspring produced by an individual i whose life span is $T_i = t$ is

$$\int_0^t m(s)ds. \tag{B2}$$

This quantity can be thought of as $\mathbb{E}(N_i | T_i = t)$, even though this interpretation is subject to some caution. At any rate, it follows that

$$\mathbb{E}(N_i) = \int_0^{+\infty} \left(\int_0^t m(s)ds \right) d\nu(t). \tag{B3}$$

Moreover, using Fubini's theorem,

$$\int_0^{+\infty} \left(\int_0^t m(s)ds \right) d\nu(t) = \int_0^{+\infty} m(s) \left(\int_s^{+\infty} d\nu(t) \right) ds. \tag{B4}$$

Using the fact that $\int_s^{+\infty} d\nu(t) = \ell(s)$, we get the well-known expression for R_0, the mean number of offspring produced by an individual during its lifetime:

$$R_0 = \mathbb{E}(N_i) = \int_0^{+\infty} m(t)\ell(t)dt. \tag{B5}$$

Using Campbell's formula (eq. [S1.1] in the supplemental PDF) and the exact same reasoning, we can express the mean sum of the ages at which an individual produces offspring as

$$\mathbb{E}(S_i) = \int_0^{+\infty} tm(t)\ell(t)dt. \tag{B6}$$

Let N (respectively, S) denote a random variable that has the common distribution of the variables N_i (respectively, S_i). Then, as pointed out in most sources presenting the measure μ_1, we have

$$\mu_1 = \frac{\mathbb{E}(S)}{\mathbb{E}(N)}. \tag{B7}$$

This does not, however, establish a link between μ_1 and $Z_{\mathcal{C}}$, the average age of the parents of offspring produced by the cohort. To see how these two quantities are related, observe that since the variables N_i (respectively, S_i) are independent, if we denote by $n = \text{Card}(\mathcal{C})$ the size of the cohort, then by the law of large numbers, as $n \to +\infty$,

$$\frac{1}{n}\sum_{i\in\mathcal{C}}N_i \to \mathbb{E}(N) \quad \text{and} \quad \frac{1}{n}\sum_{i\in\mathcal{C}}S_i \to \mathbb{E}(S). \qquad (B8)$$

As a result,

$$Z_{\mathcal{C}} = \frac{(1/n)\sum_{i\in\mathcal{C}}S_i}{(1/n)\sum_{i\in\mathcal{C}}N_i} \xrightarrow[n\to+\infty]{} \mu_1, \qquad (B9)$$

where the convergence is almost sure (i.e., happens with probability 1).

Importantly, note that μ_1 is not the expected value of S_i/N_i or of $Z_{\mathcal{C}}$. In fact, the expected value of S_i/N_i (conditional on this variable being well defined) is precisely what we have termed the mean age at reproduction. We explain how to compute it in the next section.

APPENDIX C

Mean Age at Reproduction τ

Recall that we have defined the mean age at reproduction to be the expected value of the average of the ages at which a typical parent produces offspring. Formally, assuming that individual i has some offspring, the average age at which it produces them is

$$\bar{X}_i = \frac{1}{N_i}\sum_{t\in P_i}t, \qquad (C1)$$

where, as before, N_i is the total number of offspring produced by i and P_i is the set of ages at which it produces them. The mean age at reproduction is thus

$$\tau = \mathbb{E}(\bar{X}_i|N_i > 0), \qquad (C2)$$

which, given our assumptions, does not depend on i or the composition of the population.

To compute τ, let I be a "typical parent"—that is, be uniformly sampled among the individuals that produce offspring during their lifetime. We then have

$$\mathbb{E}(\bar{X}_i|N_i > 0) = \mathbb{E}(\bar{X}_I). \qquad (C3)$$

Moreover, letting $\tilde{T}$ denote the life span of I, $\bar{X}_I$ is the average of a point process with intensity m on $[0, \tilde{T}]$. As explained in section S1 of the supplemental PDF, in the case of a Poisson point process, the expected value of this average is simply the expected value of a random point of $[0, \tilde{T}]$ with density $t \mapsto m(t)/\int_0^{\tilde{T}}m(s)ds$. The remarkable fact that it does not depend on the value of N_i is a consequence of the absence of internal structure of Poisson point processes. From this, we get

$$\mathbb{E}(\bar{X}_I|\tilde{T}) = \frac{\int_0^{\tilde{T}}sm(s)ds}{\int_0^{\tilde{T}}m(s)ds}. \qquad (C4)$$

As a result,

$$\tau = \int_0^{+\infty}\frac{\int_0^t sm(s)ds}{\int_0^t m(s)ds}\,d\tilde{\nu}(t), \qquad (C5)$$

where $\tilde{\nu}$ is the law of the life span $\tilde{T}$ of I. Note that it is different from ν, the life span of a fixed individual, because conditioning on the fact that an individual produces offspring biases its life span (e.g., if there exists an age α such that $m(t) = 0$ for $t < \alpha$, as is frequently the case in real applications, then individuals that produce offspring all live longer than α, whereas it is not necessarily the case for other individuals).

The last thing that we need to do to get an explicit formula for τ is thus to determine $\tilde{\nu}$. For this, note that

$$\begin{aligned}\mathbb{P}(\tilde{T} \leqslant t) &= \mathbb{P}(T_i \leqslant t|N_i > 0) \\ &= \frac{\mathbb{P}(T_i \leqslant t, N_i > 0)}{\mathbb{P}(N_i > 0)}.\end{aligned} \qquad (C6)$$

Conditioning on T_i, using the void probabilities of Poisson point processes (see eq. [S1.1] in the supplemental PDF) for the probability that an individual with lifetime s produces some offspring, and finally integrating against ν, we get

$$\mathbb{P}(T_i \leqslant t, N_i > 0) = \int_0^t\left(1 - e^{-\int_0^s m(r)dr}\right)d\nu(s). \qquad (C7)$$

As a result,

$$d\tilde{\nu}(t) = \frac{1}{c}\left(1 - e^{-\int_0^t m(s)ds}\right)d\nu(t), \qquad (C8)$$

where the constant $c = \mathbb{P}(N_i > 0)$ is given by

$$c = \int_0^{+\infty}\left(1 - e^{-\int_0^t m(s)ds}\right)d\nu(t). \qquad (C9)$$

Note that by integrating by parts and using $\ell(t) \to 0$ as $t \to +\infty$, we can also express c directly in terms of ℓ and m as

$$c = \int_0^{+\infty}e^{-\int_0^t m(s)ds}m(t)\ell(t)dt. \qquad (C10)$$

Putting the pieces together in the case where T_i has a density f, we get formula (3):

$$\tau = \frac{1}{c}\int_0^{+\infty}\frac{\int_0^t sm(s)ds}{\int_0^t m(s)ds}\left(1 - e^{-\int_0^t m(s)ds}\right)f(t)dt. \qquad (C11)$$

Note that neither the biological interpretation of τ nor the derivation of its expression depends on the assumption that individuals are independent.

Formula (10) for the average of a function z of the ages at which a parent produces offspring is obtained similarly, except that we have to work with

$$\bar{W}_i = \frac{1}{N_i} \sum_{t \in P_i} z(t) \tag{C12}$$

instead of $\bar{X}_i$ and use equation (S1.10) instead of equation (S1.6) to get

$$\mathbb{E}(\bar{W}_I | \tilde{T}) = \frac{\int_0^{\bar{T}} z(s)m(s)ds}{\int_0^{\bar{T}} m(s)ds}. \tag{C13}$$

The justification of the expression of τ for discrete age structures can be found in section S2 of the supplemental PDF. It essentially consists of approaching the discrete-time model with the continuous-time model by choosing appropriate age-specific fertilities and relies on the assumption that the number of offspring produced each year by each individual follows a Poisson distribution. It should also be pointed out that because in the discrete-time setting individuals can produce several offspring simultaneously, there are two possibilities to define the average age at offspring production: counting all births equally or weighting them by the number of offspring produced. Formula (5) is obtained by weighting the ages by the number of offspring produced when averaging them.

Finally, to obtain an equivalent of formula (5) for more general population structures, such as those allowed by matrix population models, one would need to (1) find the law of the conditional trajectory of an individual in the life cycle given that it produces offspring and (2) integrate the average of the ages at which it produces offspring against this law. While the first of these steps is feasible,[5] it is unclear whether the resulting expression—if it can be obtained— would be simple enough to be useful.

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5. This was explained to me by Stephen Ellner—see, e.g., ch. 3 of Ellner et al. (2016).