

NOTE

Generation Time Measures the Trade-Off between Survival and Reproduction in a Life Cycle

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ABSTRACT: Survival and fertility are the two most basic components of fitness, and they drive the evolution of a life cycle. A trade-off between them is usually present: when survival increases, fertility decreases—and vice versa. Here we show that at an evolutionary optimum, the generation time is a measure of the strength of the trade-off between overall survival and overall fertility in a life cycle. Our result both helps to explain the known fact that the generation time describes the speed of living in the slow-fast continuum of life cycles and may have implications for the extrapolation from model organisms of longevity to humans.

Keywords: generation time, optimality, slow-fast continuum, longevity, model organisms.

But more often there is a fixed resource budget, so that a greater allocation to survival is to the detriment of reproduction and vice versa. In many species, a trade-off between survival and reproduction is generally believed to exist. This trade-off is perhaps the most fundamental that can be envisaged, and it has been the subject of extensive investigation (see, e.g., Ghalambor and Martin 2001; Partridge et al. 2005; De Paepe and Taddei 2006; Marshall and Sinclair 2009; Dobson and Jouventin 2010), which has largely confirmed its presence in several distinct species. Using matrix population models, we show that the generation time of a life cycle measures the strength of this fundamental trade-off at evolutionary equilibrium.

Introduction

Trade-offs are ubiquitous in life-cycle evolution (Stearns 1992; Roff 1993): traits that directly contribute to fitness usually constrain each other so that the evolutionarily best phenotype is always a compromise. The two key traits in a life cycle are survival and fertility. An organism must survive up to reproductive events—and survival without descent is evolutionarily meaningless. Some theoretical models suggest that in some species of trees and large fish, survival and reproduction may behave in a positively synergistic way (Vaupel et al. 2004). A temporarily risky investment into growth may expand the pool of future resources to allot to survival and reproduction, and an organism that succeeds in progressively increasing in size can both avoid most environmental hazards and produce a larger number of gametes.

Measuring Trade-Offs about a Fitness Optimum

Consider a population of organisms in which individual fitness w depends on individual phenotype $\mathbf{x} = (x_1, x_2)$, which is composed of two traits x_1 and x_2 . Individuals allocate resources between x_1 and x_2 subject to a constraint $h(x_1, x_2) = c$, which is the level curve of scalar value c of $h(x_1, x_2)$. Thus, a change in x_1 has to be accompanied by a change in x_2 . For example, running speed x_1 and size x_2 may be constrained by $x_1 x_2 = 1$ so that an increase in size slows down the organism's running speed. Let B be the intersection between some open subset of the domain of fitness w and the constraint curve $h(x_1, x_2) = c$. Assume that fitness w has a local maximum w^* in B at $\mathbf{x}^* = (x_1^*, x_2^*)$, where the population is assumed to be. To get information about this optimum, we expand on an original argument in Caswell (1982) and Jones and Tuljapurkar (2015) using a Lagrange multipliers approach (see Sundaram 1996). Assume that w and h are differentiable in B and that both $\nabla w(\mathbf{x}^*)$ and $\nabla h(\mathbf{x}^*)$ have a nonzero second component. Then, by the Lagrange multipliers approach, the two gradients are parallel. As gradients are orthogonal to level curves, the tangent at x_1^* to the level curve of optimal fitness defined by $w(\mathbf{x}) = w^*$ is parallel to the tangent at x_1^* to the constraint curve $h(\mathbf{x}) = c$. By the implicit function theorem, there is an open rectangle around \mathbf{x}^* within which $h(\mathbf{x}) = c$ is the

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graph of x_2 as an implicit function of x_1 , and at $x_1 = x_1^*$ this function has slope

$$\left. \frac{dx_2}{dx_1} \right|_{x_1=x_1^*} = - \left. \frac{\partial h}{\partial x_1} \right|_{x=x^*} / \left. \frac{\partial h}{\partial x_2} \right|_{x=x^*}. \tag{1}$$

Assuming $x_2^* \neq 0$, we can multiply through this equation by x_1^*/x_2^* and then use the rules from calculus for a scalar function z of scalar variable y that is differentiable at $y = y_0$:

$$\left. \frac{1}{z(y_0)} \frac{dz}{dy} \right|_{y=y_0} = \left. \frac{d \ln z}{dy} \right|_{y=y_0}, \quad \text{with } z(y_0) \neq 0,$$

and

$$y_0 \left. \frac{dz}{dy} \right|_{y=y_0} = \left. \frac{dz}{d \ln y} \right|_{\ln y = \ln y_0}, \quad \text{with } y_0 > 0,$$

to obtain

$$\left. \frac{d \ln x_2}{d \ln x_1} \right|_{\ln x_1 = \ln x_1^*} = -x_1^* \left. \frac{\partial h}{\partial x_1} \right|_{x=x^*} / x_2^* \left. \frac{\partial h}{\partial x_2} \right|_{x=x^*}, \tag{2}$$

which is the slope of the curve $h(\mathbf{x}) = c$ at the optimum in logarithmic coordinates. This slope measures the local strength of the trade-off between traits x_1 and x_2 (Charnov 1997; Jones and Tuljapurkar 2015), for it is the x_1 -elasticity of x_2 at the optimum: the percentage change in x_2 that is required in response to a percentage change in x_1 so that the organism still has approximately optimal fitness. In practice, the constraint h is often unknown, and therefore the slope in equation (2) may not be directly accessible. But this slope equals the slope of the level curve $w(\mathbf{x}) = w^*$ at x_1^* , which is, by analogous reasoning,

$$\left. \frac{d \ln x_2}{d \ln x_1} \right|_{\ln x_1 = \ln x_1^*} = -x_1^* \left. \frac{\partial w}{\partial x_1} \right|_{x=x^*} / x_2^* \left. \frac{\partial w}{\partial x_2} \right|_{x=x^*}. \tag{3}$$

Hence, if the fitness function is known, then the trade-off between x_1 and x_2 is indirectly measurable at the optimum via combining equation (2) with equation (3), even if h remains unknown.

Survival and Fertility in a Life Cycle

Organisms typically go through a number of stages (e.g., age classes, sizes, developmental stages, or physiological conditions) throughout their life. To capture this generalized (as opposed to purely age-based) demography, we use the matrix population modeling approach, which is a deterministic approach to population dynamics (for a broad introduction, see Caswell 2001). Accordingly, a life cycle comprising k stages

is represented by a $k \times k$ matrix $\mathbf{A} = [a_{ij}]$, where a_{ij} gives the expected number of individuals in stage i in the next time step per individual in j now. Let $\mathbf{n}(t)$ with components $n_i(t)$, $1 \leq i \leq k$, be the column vector of stage-specific abundances, which gets updated by $\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t)$. If \mathbf{A} is primitive, then it has a real positive eigenvalue λ strictly greater in modulus than all other eigenvalues. As $t \rightarrow \infty$, the population becomes demographically stable: \mathbf{n} becomes proportional to any eigenvector corresponding to λ , and this eigenvalue measures population growth.

Following Cochran and Ellner (1992), we distinguish survival events from fertility events in the matrix model. Each nonzero entry can be regarded either as a fertility entry or as a survival entry. Fertility entries indicate new individuals that enter the population in the next time step. Survival entries give the fraction of already-existing individuals that persist in the population and possibly move from their present stage to some other stage. With this distinction, the matrix model is decomposed as

$$\mathbf{A} = \mathbf{U} + \mathbf{F}, \tag{4}$$

where \mathbf{U} collects survival entries and \mathbf{F} collects fertility entries. Take, for example, an age-classified population. In the corresponding (Leslie) matrix model, \mathbf{U} is nonzero only in the subdiagonal, and $u_{j+1,j}$ is the fraction surviving from age class j to age class $j + 1$; \mathbf{F} has nonzero entries exclusively in the first row, where $f_{1,j}$ is fertility in age class j .

Life-Cycle Parametrization and Fitness

We exploit equation (4) to parametrize the life cycle in terms of two scalar traits: survival s and fertility f , which are assumed to be under selection and subject to $h(s, f) = c$. A phenotype is then $\mathbf{x} = (s, f)$. The demography of a large population that is monomorphic for \mathbf{x} is governed by the matrix

$$\mathbf{A}(s, f) = s\mathbf{U} + f\mathbf{F}, \tag{5}$$

where \mathbf{U} and \mathbf{F} are constant, and thus s and f affect all stages equally. When the population is demographically stable, has dynamics that are independent of density and frequency, selection is weak, and the environment is constant, $r = \ln \lambda$ is both the average population fitness (Barfield et al. 2011) and the maximand of selection (Metz et al. 2008). Under these conditions, we assume that there is a phenotype $\mathbf{x}^* = (s^*, f^*)$ and, therefore, a life cycle captured by $\mathbf{A}^* = \mathbf{A}(s^*, f^*)$ at which r has a constrained local maximum. Any phenotype slightly deviating from \mathbf{x}^* is selected against and the population is at evolutionary equilibrium. Nonzero entries of $s^*\mathbf{U}$ are assumed to be smaller than 1 to ensure that any increment in s preserves their nature as probabilities (a different parametrization that applies to age-specific trade-offs between survival and fertility is discussed in the appendix).

Trade-Off between Survival and Fertility in Structured Populations

Using the strategy outlined at the beginning, we study the survival-fertility trade-off at x^* by substituting s for x_1 , f for x_2 , and r for w in equation (3) to get

$$\frac{d \ln f}{d \ln s} \Big|_{\ln s = \ln s^*} = -s^* \frac{\partial r}{\partial s} \Big|_{x=x^*} / f^* \frac{\partial r}{\partial f} \Big|_{x=x^*}. \quad (6)$$

At first sight, we are still a long way from getting our hands on this quantity. However, Bienvenu and Legendre (2015) derived exactly the expressions on the right-hand side of equation (6). Here we briefly (and somewhat heuristically) review their work. They followed backward in time the route of a gene through the ancestry of a haploid, demographically stable, and selectively neutral stage-structured population. According to their results, the a_{ij} -elasticity of λ coincides with the asymptotic frequency at which a gene passes from stage i to stage j up the lineage along which the gene has persisted in the population (Bienvenu and Legendre 2015). The passage can occur either because the gene follows a backward transition of its current carrier from stage i at t to stage j at $t - 1$ or because the carrier in i at t was generated at $t - 1$ by an individual in j with that gene. Taking the generation time T to be the expected time that a gene spends in the body of an organism (i.e., from birth of the organism to transmission of a gene copy to offspring), only those entries of \mathbf{A} that refer to the generation of new individuals are relevant—the fertility entries collected in \mathbf{F} . Let Φ be the set of ordered pairs (i, j) that correspond to the nonzero entries of \mathbf{F} . By the definition of T and the fact that the expected time of an event is the inverse of the event frequency, one has that

$$T = \left(\sum_{(i,j) \in \Phi} a_{ij} \frac{\partial r}{\partial a_{ij}} \right)^{-1} \quad (7)$$

(Bienvenu and Legendre 2015). Using the parametrization in equation (5), Bienvenu and Legendre (2015) rewrote and rearranged the expression in equation (7) as

$$f \frac{\partial r}{\partial f} = \frac{1}{T}. \quad (8)$$

Since λ is homogeneous of degree 1 in \mathbf{A} in virtue of the usual eigenvector equation $\mathbf{A}u = \lambda u$, the sum of all of the a_{ij} -elasticities of λ is 1 (de Kroon et al. 1986), by Euler's homogeneous function theorem (Mesterton-Gibbons 1993). Therefore, from equation (8) and the parametrization in equation (5), one gets

$$s \frac{\partial r}{\partial s} = 1 - \frac{1}{T} \quad (9)$$

(Bienvenu and Legendre 2015). We can, therefore, substitute equations (8) and (9) into equation (6) to obtain our main result:

$$\frac{d \ln f}{d \ln s} \Big|_{\ln s = \ln s^*} = 1 - T^*. \quad (10)$$

This means that the generation time T^* of the optimal life cycle measures the local strength of the trade-off between log survival and log fertility at evolutionary equilibrium (fig. 1). In matrix models, reproduction always occurs over at least one time step. Hence, $T \geq 1$ and the trade-off between survival and fertility is negative, as it should be.

Discussion

Several mutations enhance longevity in model organisms (Kenyon 2010). But a related fitness cost on reproduction is often apparent (Partridge et al. 2005). Model organisms— for example, the mouse or the nematode—generally have much shorter generation times than humans. Our result suggests that because of this discrepancy, the fertility cost that model organisms with increased life spans have to bear may be an (even dramatic) underestimate of the fertility cost that a proportionally equivalent increase in survival may entail for humans. However, mutations can impact longevity in many different ways (which may also be species specific; Hughes and Hekimi 2016) that depart from our simplifying assumption of uniform multiplicative changes in survival. Moreover, how to compare life cycles that are measured on different timescales—for example, days for a worm and 5-year intervals for human demography—is an open problem (Wrycza and Baudisch 2014).

Life cycles are sometimes hypothesized to form a slow-fast continuum from cycles with low mortality and low fertility to cycles with high mortality and high fertility, although the full picture of life-cycle variation is more complicated (Promislow and Harvey 1990; Blackburn 1991; Ricklefs and Wikelski 2002; Oli and Dobson 2003; Gaillard et al. 2005; Bielby et al. 2007; Owen et al. 2008; Salguero-Gómez et al. 2016). A trade-off between survival and fertility is generally invoked to explain the existence of this continuum (Stearns 1992; Dobson 2007). In a vast number of species, the quantity that best captures where a life cycle is found in the continuum is the generation time (Gaillard et al. 2005). But there is more than one measure of generation time (Cochran and Ellner 1992; Caswell 2001; Steiner et al. 2014; Bienvenu and Legendre 2015). Different measures have been used to characterize the slow-fast continuum, for example, the time it takes for a population to grow by a factor equal to the net reproduction rate or the average age at parenthood in a demographically stable population (Gaillard et al. 2005). Ellner (2018) recently showed that under assumptions that

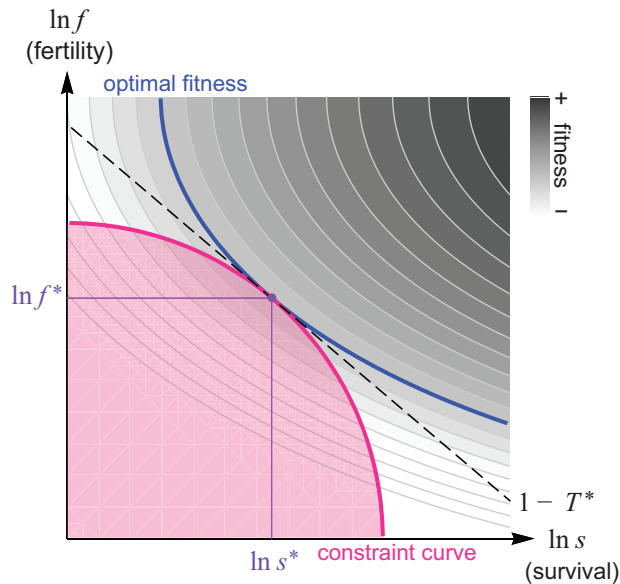


Figure 1: Trade-off between survival s and fertility f at evolutionary equilibrium in a life cycle. The two traits s and f are under selection with a negative trade-off between them. In this log-log plot, each point $(\ln s, \ln f)$ is a life cycle with an associated fitness value. Level curves of fitness are plotted. Darker shades of gray correspond to greater fitness. Feasible life cycles are within or on the constraint curve. The optimal life cycle subject to the constraint is $(\ln s^*, \ln f^*)$. At this point, both the constraint curve and the level curve of optimal fitness have slope $1 - T^*$, where T^* is the generation time of the optimal life cycle.

natural populations often fulfill, such as a roughly stationary demographic regime (demographic stability and unit geometric growth), distinct measures of generation time are essentially equivalent to T as defined in Bienvenu and Legendre (2015), which gives the average age at parenthood in stage-structured models (Cochran and Ellner 1992). Therefore, in many cases different measurements of the generation time may be inconsequential for studies of the slow-fast continuum. However, Gaillard et al. (2005) argued for the superiority of T because it integrates all vital rate elasticities of population growth. But it is left unclear exactly why elasticities would matter in this respect. Despite the limitations inherent to the linear time-homogeneous demographic model from which it was derived, our result gives a more solid theoretical foundation to this argument. Accordingly, T should be the most appropriate measure in studies of the slow-fast continuum because this measure is intimately related to the survival-fertility trade-off that is postulated to be at the very basis of this continuum.

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APPENDIX

Stages as Age Classes

Survival-fertility trade-offs may exist between portions of the life span, for example, trading late-life survival in favor of early-life fertility (Kirkwood and Rose 1991). Our approach cannot account for these, as it presupposes a contrast between survival and fertility over all stages. Moreover, a stage can comprise individuals of different ages, while individuals of the same age may be in different stages. There are methods to extract age-specific quantities from stage-structured models (Cochran and Ellner 1992; Caswell 2001). But such methods are numerical in essence, and there is little hope of parametrizing matrix models with generalized demography to target specific segments of the life span. We can, however, tailor our method to the case of age-classified populations. The matrix population model is then the $k \times k$ Leslie matrix:

$$\mathbf{L} = \begin{bmatrix} F_1 & F_2 & \dots & F_{k-1} & F_k \\ U_1 & 0 & \dots & 0 & 0 \\ 0 & U_2 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & U_{k-1} & 0 \end{bmatrix}, \quad (\text{A1})$$

where U_i is the probability of surviving from age class i to $i + 1$, F_i the fertility in age class i , and k the maximum attainable age. The characteristic equation of \mathbf{L} is the Euler-Lotka equation:

$$\sum_{j=1}^k \left(\prod_{i=1}^{j-1} U_i \right) F_j e^{-rj} = 1, \quad (\text{A2})$$

where $r = \ln \lambda$, as in the main text. Implicitly differentiating this equation leads to

$$\begin{aligned} U_m \frac{\partial r}{\partial U_m} &= T^{-1} \sum_{j=m+1}^k \left(\prod_{i=1}^{j-1} U_i \right) F_j e^{-rj}, \\ &\quad m = 1, 2, \dots, k-1, \\ F_m \frac{\partial r}{\partial F_m} &= T^{-1} \left(\prod_{i=1}^{m-1} U_i \right) F_m e^{-rm}, \\ &\quad m = 1, 2, \dots, k, \end{aligned} \quad (\text{A3})$$

(Hamilton 1966; Baudisch 2005), where the first and the second expressions account for multiplicative changes in survival and fertility, respectively, at age m . In both expressions, T is the generation time as defined in Bienvenu and Legendre (2015). We then introduce the set $G \subseteq \{1, 2, \dots, k-1\}$ con-

taining the ages at which survival is involved in the trade-off and the corresponding set $K \subseteq \{1, 2, \dots, k\}$ for fertilities. The scalar traits s_G and f_K govern survival and fertility at the relevant ages in the following way: $U_j = s_G p_j$ with p_j a constant such that $0 < s_G p_j \leq 1$ whenever $j \in G$ and $F_j = f_K b_j$ with $b_j > 0$ a constant whenever $j \in K$. Assume that a constrained local maximum of r subject to $h(s_G, f_K) = c$ is at $\mathbf{x}^* = (s_G^*, f_K^*)$ with $s_G^* p_j < 1$ for $j \in G$. Note that

$$\begin{aligned} s_G \frac{\partial r}{\partial s_G} &= s_G \sum_{j \in G} \frac{\partial U_j}{\partial s_G} \frac{\partial r}{\partial U_j} \\ &= s_G \sum_{j \in G} p_j \frac{\partial r}{\partial U_j} \\ &= \sum_{j \in G} U_j \frac{\partial r}{\partial U_j} \end{aligned} \tag{A4}$$

and, similarly,

$$f_K \frac{\partial r}{\partial f_K} = \sum_{j \in K} F_j \frac{\partial r}{\partial F_j}. \tag{A5}$$

Using the same approach as in the main text, we get

$$\left. \frac{d \ln f_K}{d \ln s_G} \right|_{\ln s_G = \ln s_G^*} = - \left(\sum_{j \in G} U_j \frac{\partial r}{\partial U_j} \right) \Big|_{x=x^*} \Big/ \left(\sum_{j \in K} F_j \frac{\partial r}{\partial F_j} \right) \Big|_{x=x^*}, \tag{A6}$$

which is a local measure of the strength of the trade-off between survival and fertility, both considered at the specified ages only, around the given optimum.

It is hard to gain some general analytic insight from the combination of equations (A3) and (A6) for arbitrary ages in G and K . However, in at least one case, equation (A6) simplifies considerably. Suppose there is a trade-off between present survival and future reproduction. In the water flea, for example, young individuals may form an armor that is protective against juvenile-specific predation, but if they do so, less resources are left for egg production in adulthood (Bateson 2015). We then let $G = \{j\}$ and $K = \{j + 1, j + 2, \dots, k\}$ so that survival at any age $1 \leq j < k$ constrains fertility at all subsequent ages. Substituting from equation (A3) into equation (A6) leads to

$$\left. \frac{d \ln f_K}{d \ln s_G} \right|_{\ln s_G = \ln s_G^*} = -1, \tag{A7}$$

with $G = \{j\}$ and $K = \{j + 1, j + 2, \dots, k\}$.

Hence, at a constrained optimum, a given percent change in survival at one age is worth exactly as much as the same percent change in fertility at all later ages. The result is independent of properties of the optimal life cycle, and therefore it

should be considered as an invariant in the sense of Charnov (1997). As noted by a reviewer, the result is not tied to a small neighborhood of the optimum. Let

$$\phi_i = \left(\prod_{j=1}^{i-1} U_j \right) F_i \tag{A8}$$

be the age-specific net fertilities so that Euler-Lotka's equation is reexpressed as $\sum_{j=1}^k \phi_j e^{-rj} = 1$. Multiplying a particular U_j by $c > 0$ and dividing all fertilities F_j , $j = j^* + 1, \dots, k$, by c leave the net fertilities ϕ_i ($i = 1, \dots, k$) and, therefore, r unchanged without the requirement $c \rightarrow 1$.

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A rose chafer (*Cetonia aurata*) after the rain in Bad Malente, Germany. This beetle, like most organisms, is likely to face a trade-off between survival and reproduction. Photo credit: Stefano Giaimo.