

Supporting Information for Mell, Baumard and André “Time is money. Waiting costs explain why selection favors steeper time discounting in deprived environments”

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November 28, 2019

1 Numerical derivation of the discount rate in the general case

In the main text, we defined the production function $p(w) = \kappa w^\alpha$ and mortality function $m(w) = \mu w^{-\beta}$, with $\alpha \in [0, 1]$ and $\beta > 0$, and the body weight at birth $w_0 \geq 1$. Here we also define the marginal functions

$$m_w(w) \equiv \frac{dm(w)}{dw} \tag{1}$$

$$p_w(w) \equiv \frac{dp(w)}{dw} \tag{2}$$

From these functions, the growth trajectory of an individual is derived:

$$w(t) = [(1 - \alpha)\kappa t + w_0^{1-\alpha}]^{\frac{1}{1-\alpha}} \tag{3}$$

Equation 7 of main text can be reformulated as

$$\frac{p_w(w_a)}{m(w_a)} - \frac{m_w(w_a)p(w_a)}{m(w_a)^2} = 1$$

and we can compute the evolutionarily stable (ES) adult body weight

$$w_a = \left(\frac{\kappa}{\mu} (\alpha + \beta) \right)^{\frac{1}{1-\alpha-\beta}} \tag{4}$$

From equations 3 and 4, we derive the ES age at maturity, t_a (not shown, see Mathematica notebook at https://github.com/hugomell/time_is_money).

Then, from equation 3 we can obtain the survival function during the growth phase $l(t) = e^{-\int_0^t m(w(s)) ds}$ (not shown; see Mathematica notebook). By definition of the switching age we know that the marginal value of body weight at the switching age must be equal to the survival function at the same age, which allows us to know that $\lambda_a \equiv \lambda(t_a) = l(t_a)$.

The lifetime reproductive success of individuals is given by $V_0 = l(t_a) \frac{p(w_a)}{m(w_a)}$, and the function $\lambda(\cdot)$ is found as the solution of the following system of differential equations

$$\dot{\lambda}(t) = V_0 m_w(w(t)) - \lambda(t) p_w(w(t)) \quad (5)$$

$$\lambda(t_a) = \lambda_a \quad (6)$$

These equations have no analytical solution hence we obtain a solution numerically (see Mathematica notebook). This allows us to obtain the discount rate during growth, given by

$$\delta(t) = p_w(w(t)) - V_0 \frac{m_w(w(t))}{\lambda(t)} \quad (7)$$

2 Numerical derivation of the degree of risk aversion in the general case

During the reproduction phase, individuals are risk-neutral (see main text). Hence we are only interested in the growth phase here. We imagine that we give a bonus resource ϵ to an individual at a certain age $t_b < t_a$. This bonus can actually be positive or negative, so it is better to see it as a “perturbation” in general. After this perturbation, the individual continues to invest in growth until she reaches her ES adult size, w_a , which is not modified by the perturbation and is therefore given by equation 4. The age at maturity is, however, affected by the perturbation. To calculate it, we derive the growth trajectory after the perturbation, given as a solution of the following system of differential equations

$$\dot{w}(t) = p(w(t)) \quad (8)$$

$$w(t_b) = \epsilon + [(1 - \alpha)\kappa t_b + w_0^{1-\alpha}]^{\frac{1}{1-\alpha}} \quad (9)$$

which allows us to obtain an expression for the growth trajectory $w(t)$ after the perturbation (not shown) and thus to calculate the age at maturity of the individual who experienced the perturbation, as the solution of $w(t) = w_a$ (not shown, see Mathematica notebook).

From these equations, we derive the survival function $l(t, t_b, \epsilon)$ of the individual during his growth. This allows us to calculate the probability $l(t_a, t_b, \epsilon)$ that the individual will actually reach adulthood when she has experienced a perturbation ϵ at age t_b . Thus, the lifetime reproductive success of the individual who experienced the perturbation is finally given by

$$V_0(t_b, \epsilon) = \frac{p(w_a)}{m(w_a)} l(t_a, t_b, \epsilon) \quad (10)$$

The degree of risk aversion at age t_b is finally given by (see main text):

$$\rho(t_b) = -\lim_{\epsilon \rightarrow 0} \frac{\partial^2 V_0(t_b, \epsilon)}{\partial \epsilon^2} \quad (11)$$

3 Measuring the effect of natural selection in a constant and in a variable environment

Here we consider a model of density-dependent regulation modified from Day and Gandon (2005) and André and Gandon (2006). We model demographic regulation and environment heterogeneity by considering a fixed set of sites that can each either be occupied by one individual or empty, that is available for colonization by the offspring of an established individual. Sites are of n different types ($n \geq 1$), varying with regard to some environmental properties (e.g. some are harsher than others).

The total density of sites of type $i \in \llbracket 1, n \rrbracket$ is noted K_i . At time t , the density of empty sites of type i is noted $A_i(t)$, and the density of sites of type i occupied by an individual of age a is $N_i(a, t)$.

We assume that individuals colonize a new site at age $a = 0$ and only start growing once they have colonized a site. The fecundity of an individual of age a in a site of type i is denoted $b_i(a)$, its mortality rate is denoted $m_i(a)$, and the probability that it is still alive at age a is denoted $l_i(a) \equiv e^{-\int_0^a m_i(s) ds}$.

For simplicity, we assume that (i) only offspring disperse, leaving their parent's site to find an empty site for colonization, and that (ii) offspring colonize a random site among those that are available. Demographic competition is expressed through the fact that the probability for an offspring to effectively colonize a site is proportional to the density of available sites, that is when sites are highly occupied, the probability for an offspring to establish and be recruited as a reproducing individual becomes very low, which leads to a demographic equilibrium.

We first consider a given genotype, called the resident, established in this environment and we aim to characterize the demographic equilibrium of this genotype. The density of available sites of each type follows the following set of differential equations, expressing the fact that new available sites are produced at the death of individuals, and that available sites disappear when they are colonized by the offspring of living individuals:

$$\forall i \in \llbracket 1, n \rrbracket, \frac{dA_i(t)}{dt} = \int_0^{+\infty} N_i(a, t) m_i(a) da - A_i(t) \sum_{j=1}^n \int_0^{+\infty} N_j(a, t) b_j(a) da \quad (12)$$

The McKendrick – von Foerster equations expresses the fact that individuals either get older or die as time passes:

$$\forall i \in \llbracket 1, n \rrbracket, \quad \frac{\partial N_i(a, t)}{\partial a} + \frac{\partial N_i(a, t)}{\partial t} = -m_i(a) N_i(a, t) \quad (13)$$

With the boundary conditions expressing the fact that new sites are colonized by the offspring produced by individuals living on all sites

$$\forall i \in \llbracket 1, n \rrbracket, \quad N_i(0, t) = A_i(t) \sum_{j=1}^n \int_0^{+\infty} b_j(a) N_j(a, t) da \quad (14)$$

In demographic equilibrium (all changes with respect to time t are nil), the McKendrick – von Foerster equation tells us that $\frac{\partial N_i(a, t)}{\partial a} = -m_i(a) N_i(a, t)$. Hence, we have $N_i(a, t) =$

$N_i(0, t)l_i(a)$ at all time t and for all ages a . We then define $\hat{N}_i \equiv N_i(0, t)$, the equilibrium density of sites of type i colonized by an individual of age 0 and \hat{A}_i the equilibrium density of available sites of type i .

We now aim at characterizing \hat{A}_i , as controlled by the resident genotype in demographic equilibrium. To do so, we define $R_i \equiv \int_0^{+\infty} b_i(a)l_i(a)da$, which represents the total reproductive output of an individual living in a site of type i , per unit of empty sites available. Hence, from equation (12) above, the condition of demographic equilibrium becomes:

$$\forall i \in \llbracket 1, n \rrbracket, \quad \hat{A}_i \sum_{j=1}^n \hat{N}_j R_j = \hat{N}_i \quad (15)$$

We then define $R_0 \equiv \sum_{j=1}^n K_j R_j$, which represents the lifetime reproductive success (i.e. the fitness) of the resident genotype when introduced initially at very low density in the environment. Equations (15) then solves into:

$$\forall i \in \llbracket 1, n \rrbracket, \quad \hat{A}_i = \frac{K_i}{R_0} \quad (16)$$

Hence, we can characterize the demographic equilibrium as controlled by a resident genotype, in function of the total density of sites of each type (K_i) and in function of the fitness R_0 of this genotype.

We now aim to consider the rise of a rare variant genotype, when introduced in low frequency in the demographic equilibrium as controlled by the resident. To do so, we consider the first-order perturbation of the demographic equilibrium when the mutant is still very rare. To first order, we can consider that the density of available sites of each type is controlled only by the resident genotype and thus remains constant as the mutant rises (or falls) (see Day and Gandon, 2005). The density of sites occupied at time t by a mutant of age a is delineated as $N_i^*(a, t)$, which obeys the following differential equations :

$$\forall i \in \llbracket 1, n \rrbracket, \quad \frac{\partial N_i^*(a, t)}{\partial a} + \frac{\partial N_i^*(a, t)}{\partial t} = -m_i^*(a)N_i^*(a, t) \quad (17)$$

where $m_i^*(\cdot)$ is the mutant's mortality function in site i . With boundary condition:

$$\forall i \in \llbracket 1, n \rrbracket, \quad N_i^*(0, t) = \hat{A}_i \sum_{j=1}^n \int_0^{+\infty} b_j^*(a)N_j^*(a, t)da \quad (18)$$

where $b_i^*(\cdot)$ is the mutant's fertility function in site i .

Following Day and Gandon (2005) (and André and Gandon, 2006 for the case with multiple types of sites), the above equations solve into

$$\forall i \in \llbracket 1, n \rrbracket, \quad N_i^*(a, t) = C_i e^{r_i(t-a)} l_i^*(a) \quad (19)$$

where $l_i^*(\cdot)$ is the mutant's survival function in site i , for some constants C_i and r_i . The dynamics of the mutant genotype (its invasion or loss) depends on the values of these constants. In particular, the mutant rises in frequency iff $\max_i r_i > 0$, and the mutant disappears otherwise. Hence, we now aim at characterizing the values of C_i and r_i . To

do so, we introduce the above solution (19) into the boundary condition (18). Defining $h^*(t) \equiv \sum_{j=1}^n \int_0^{+\infty} b_j^*(a) N_j^*(a, t) da$, this gives us

$$\forall i \in \llbracket 1, n \rrbracket, \quad C_i e^{r_i t} = \hat{A}_i h^*(t) \quad (20)$$

Which must hold for all i and all time t . Hence, this implies that every r_i must be equal to the same value that we simply call r , and that every C_i must be proportional to its corresponding \hat{A}_i . Hence, mutant's dynamics follow $N_i^*(a, t) = k \hat{A}_i l_i^*(a) e^{r(t-a)}$, for some proportionality factor k . The set of equations (20) thus become a single equation

$$e^{rt} = \sum_{i=1}^n \hat{A}_i \int_0^{+\infty} b_i^*(a) l_i^*(a) e^{r(t-a)} da \quad (21)$$

Dividing both sides by e^{rt} gives us

$$1 = \sum_{i=1}^n \hat{A}_i \int_0^{+\infty} b_i^*(a) l_i^*(a) e^{-ra} da \quad (22)$$

With $R_i^* \equiv \int_0^{+\infty} b_i^*(a) l_i^*(a) da$, this equation entails that, if $\sum_{i=1}^n R_i^* \hat{A}_i > 1$, then we must have $r > 0$, and vice versa. Hence, the mutant will grow ($r > 0$) if and only if $\sum_{i=1}^n R_i^* \hat{A}_i > 1$. With $\hat{A}_i = K_i/R_0$ as controlled by the resident, and with mutant's fitness $R_0^* \equiv \sum_{i=1}^n K_i R_i^*$, this tells us that the necessary and sufficient condition for the mutant to rise in frequency is $R_0^* > R_0$. Hence, natural selection, i.e. the fixation of successive mutants, will maximize the lifetime reproductive success of individuals, i.e. their fitness, measured by summing the fertility of individuals across their life, and weighted by the density K_i of each type of environment:

$$R_0 \equiv \sum_{i=1}^n K_i \int_0^{+\infty} b_i(a) l_i(a) da \quad (23)$$

Under this model of density-dependence regulation, (i) in a constant environment ($n = 1$) natural selection maximises the lifetime reproductive success of individuals and (ii) when the environment is variable ($n > 1$) and in the absence of a cost of plasticity, natural selection favors the evolution of a reaction norm by which individuals maximize their life time reproductive success in each environment.

References

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