

The Evolution of Intergenerational Discounting in Offspring Quality

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ABSTRACT: Intergenerational effects occur when an individual's actions affect not only its own survivorship and reproduction but also those of its offspring and possibly later descendants. In the presence of intergenerational effects, short-term and long-term measures of success (such as the expected numbers of surviving offspring and of farther descendants, respectively) may be in conflict. When such conflicts occur, life-history theory normally takes long-term measures to predict the outcome of selection. This ignores the fact that, because traits change in time—through mutation, sex, and recombination—long-term relations disintegrate. We study this issue with numerical simulations and analytical models combining intergenerational effects and evolutionary change. In the models, the parental investment per offspring, as well as the total reproductive effort, stand for investments in future generations. The models show that the rate of evolutionary change determines the level of those investments. Higher rates of mutation and of sexual as opposed to parthenogenetic reproduction favor lower parental investment per offspring and lower total reproductive effort. It follows that the level of investment of ancestors in descendants responds to the genetic relatedness between the generations of the lineage, in a manner unaccounted for by preexisting theory.

Keywords: offspring quality, parent-offspring conflict, inclusive fitness, maternal effects, intergenerational effects, mutation-selection balance.

The trade-off between offspring number and quality is an important aspect of an organism's reproductive strategy

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(Stearns 1992, pp. 158–159). Since the parental resource is limited, increasing offspring number reduces the parental investment per offspring, which reduces offspring quality and probability of survival (Lack 1947). Lack observed this trade-off in various bird species and hypothesized that natural selection optimized it—that is, that natural selection favored clutch sizes that maximized the expected number of surviving offspring (Lack 1947, 1954, 1966).

Smith and Fretwell (1974) isolated this trade-off from the one between investing in current versus future reproduction (residual reproductive value; Williams 1966; Charnov and Krebs 1974): assume that at any point in time, the organism's energy budget can be divided into two parts—one for current reproduction and one for survival and future reproduction—such that the two parts are in optimal balance. Using the current reproduction budget, how many offspring should the organism make? (Exclude cases where offspring from an early clutch help to provide for offspring from a late clutch and where offspring from subsequent clutches receive parental investment simultaneously [Smith and Fretwell 1974].)

Smith and Fretwell (1974) answered that natural selection maximized the product of offspring number and offspring "fitness." They also invented a graphical model that predicted the best clutch size for any given relationship between the two (an analytical model was provided by Lloyd [1987]). However, the fitness term must account for long-lasting consequences of the offspring's developmental conditions shaped by the parental reproductive strategy (maternal effects; Rossiter 1996; Mousseau and Fox 1998; Lindström 1999). In this connection, an important issue was ignored.

The parental reproductive strategy, through affecting offspring quality, affects not only offspring survival but also offspring reproductive success, which can affect the next generation of offspring in turn, and so on. In mice, Falconer (1965) observed that artificial selection for large litters made small litters more common in the next generation and inferred that large litters increased offspring competition for milk, reduced offspring size, and reduced

offspring litters. In the collared flycatcher, *Ficedula albicollis*, larger clutches produce smaller offspring that suffer higher mortality and make smaller first broods (Gustafsson and Sutherland 1988). Experimentally adding an egg to a mother's clutch reduced her daughter's clutch by 1/4 egg on average (Schluter and Gustafsson 1993). In the parasitoid wasps *Trichogramma*, smaller clutches produce larger offspring, among whom the female offspring have more eggs in the oviducts at emergence and a longer life span, which increases their lifetime fecundity (Waage and Ng 1984). The larger wasp offspring also move faster, show a lower frequency of brachyptery, and fly longer distances; this may improve their ability to choose hosts for their own clutches (Waage and Ng 1984). In the great tit, smaller clutches produce bigger offspring, and bigger offspring not only have higher survival rates but also are more dominant and acquire better territories (Verhulst et al. 1997). Among the great tit nestlings raised outside of Wytham Wood, a mature deciduous woodland near Oxford, United Kingdom, that provides a good diet and enhances reproductive success (Riddington and Gosler 1995), bigger offspring are more likely to disperse into Wytham (Verhulst et al. 1997) and, as a consequence, own a bigger resource with which to support their offspring.

The above are intergenerational effects (Andersson 1978). Relatively few studies have incorporated intergenerational effects into life-history theory (Stearns 1992; but see the illuminating contributions by Andersson [1978], Kirkpatrick and Lande [1989], and McNamara and Houston [1992, 1996]; sex allocation theory is also inherently intergenerational [Trivers and Willard 1973; Leimar 1996]). Intergenerational effects extend the trade-off between offspring number and quality: if offspring quality influences not only the probability of offspring survival throughout life but also offspring reproductive success, then it is more important relative to offspring number than it would have been otherwise.

Andersson (1978) formalized an instance of this idea by assuming that decreased clutch size hastened offspring maturity and increased the survival of offspring in adulthood from one breeding period to the next. He found that the clutch size that maximized long-term population growth rate in an annually breeding organism was substantially smaller than the Lack clutch size (as well as Charnov and Krebs's [1974] clutch size accounting for the residual reproductive value). McNamara and Houston (1992) further developed this idea with the powerful framework of state-dependent life-history theory. They assumed that an offspring's quality affected the number and quality of its own offspring through mechanisms involving body size, foraging ability, territory quality, and parasite load. They built a model that represented such mechanisms generally and showed that the optimal clutch size

depended on the number of generations considered (McNamara and Houston 1992; such timescale dependence is also in agreement with Lande and Kirkpatrick [1990]).

This is our point of origin. We begin by capturing it in an analytical model that is focused specifically on resources as carriers of the intergenerational effect in the clutch size trait. As in the case of the great tit, we assume that the clutch size affects both offspring survival and resources in adulthood. This will help to show how different clutch sizes maximize survival and reproduction over different numbers of generations. Our main point then follows. We incorporate the above into evolutionary models with mutation or Mendelian segregation and show that, in this context, a novel result emerges: the rates of mutation and sexual reproduction affect the distribution of clutch size strategies at equilibrium in a manner unaccounted for by preexisting theory. Specifically, mutation and sex favor larger clutches and smaller parental investment per offspring. Analogous complications are expected in other traits, as we will demonstrate with a model of reproductive effort.

We first present the mathematical models and then follow with an intuitive, verbal explanation of the analytical results ("Discussion"). Note that the models are "strategic," in the language of Holling (1968; see also May 1973); they are general and serve mainly as a proof of principle.

Intergenerational Effects in the Clutch Size Trait

We maintain the simplifying assumption of equal distribution to offspring made implicitly by Andersson (1978). Explicitly, if the parental resource, R_p , is distributed equally among n offspring, then the investment per offspring is R_p/n . Since offspring survival increases with parental investment per offspring, the probability of survival of any one offspring, S , is some nondecreasing function of R_p/n : $S(R_p/n)$. The expected number of surviving offspring is simply $nS(R_p/n)$.

We now define R_{t+1} as the resource that any one of the offspring grows to acquire in adulthood. As in the case of the great tit, offspring that receive more from their parents are more likely to become stronger adults and acquire better territories and therefore to be able to give more to their own offspring. Therefore, R_{t+1} is a nondecreasing function of R_t/n : $g(R_t/n)$. For any fixed, sufficiently small n , there is at least one stable (population-dynamic) equilibrium value of R .¹

Now, consider a lineage of a certain clutch size strategy,

¹ We assume that g is bounded above, nonnegative, and continuously differentiable. Furthermore, we restrict g such that there is a stable R for $n > 1$ to prevent the population from crashing. A sufficient (though not a necessary) condition for this is that the initial slope $g'(0) > 1$.

n_h , and a corresponding stable resource level, R_h . When a descendant to this lineage acquires a trait for laying a smaller clutch, of size $n_i < n_h$, each of its offspring receives $R_h/n_i > R_h/n_h$ and grows to acquire a resource $R_1 > R_h$. If these offspring maintain the new clutch size strategy (which is the case if the change is genetic and fully heritable), each of their offspring receives $R_1/n_i > R_h/n_h$ and grows to acquire a resource $R_2 > R_1$. In this manner, R will grow asymptotically toward a new, higher level, $R_i > R_h$.

Because of this resource accumulation, and because the resource affects offspring survivorship, it is possible that after a certain number of generations, n_i will surpass n_h in terms of the expected number of surviving offspring, even if it had been inferior in those terms originally. This is possible even in the case where n_h maximizes the expected number of surviving offspring under R_p , as demonstrated in figure 1. In the figure, while n_h strikes a better trade-off between offspring number and quality in the short term, it is n_i that is able to achieve and maintain the larger resource and better survivorship in the long term, through its investment in offspring quality. Thus, n_h is better in the short term and n_i is better in the long term.

Generally speaking, which clutch size is best depends on the timescale considered. This provides the basis for our main argument. We will show that the timescale dependence has an interesting consequence in an evolutionary context.

Mutation Favors Larger Clutches

To put the above in an evolutionary model, we make the smaller- and larger-clutch strategies, n_i and n_h , heritable and competing strategies with stable resources R_i and R_p , respectively ($n_i < n_h$, $R_i > R_h$). Let us call these two strategies “investor” and “spender,” respectively. The smaller clutch strategy, n_p , invests more per offspring and benefits future generations, while the larger clutch strategy, n_h , spends its resource on immediate offspring production.

Consider, for simplicity, an asexual organism with an entirely genetically determined clutch size trait, a single reproductive event, and nonoverlapping generations. Importantly, we need to represent evolutionary change in the model. While change can be generated biologically in a number of ways, we begin by adopting mutation as an agent of change, for a pedagogical purpose. The effect of mutation will not be strong, but it will be tractable. Later, we will examine the case of sexual reproduction.

To represent mutation, we assume that a spender gives birth to an investor with a small probability μ , and vice versa. Because of the intergenerational effect described, the resource of an investor lineage emanating from a mutated spender grows from R_h to R_p , and the resource of a spender lineage emanating from a mutated investor declines from

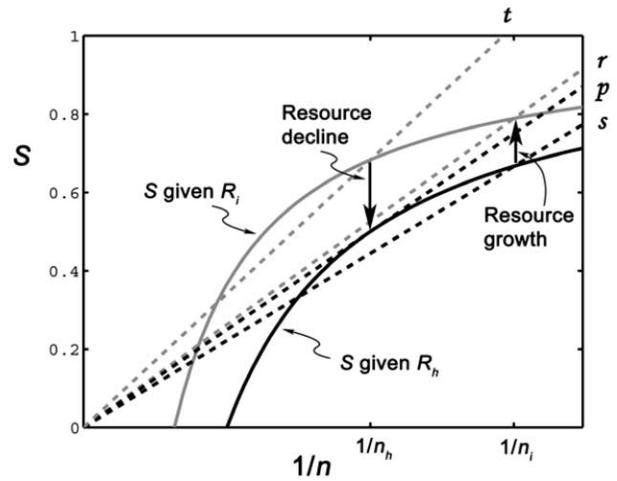


Figure 1: The probability of offspring survival, S , versus the reciprocal of offspring number, $1/n$, under each of two resources, R_h and R_i . Following the graphical method of Smith and Fretwell (1974), each straight line through the origin represents (S, n) pairs of equal expected number of surviving offspring; the steeper the line, the higher the expected number of surviving offspring. Accordingly, the tangent p crosses S at the best realizable (S, n) pair, given R_h . Because, in this example, it crosses S at $n = n_h$, n_h maximizes the expected number of surviving offspring under R_h . Specifically, since p is steeper than s ($p > s$), n_h is superior to n_i given R_h . However, unlike Smith and Fretwell (1974), the choice of n influences the very S curve. Because n_i leads to resource growth, it pushes the S curve upward and becomes superior to n_h in the long run ($r > p$). Given R_p , n_h is still superior to n_i in the short term ($t > r$), but it pushes S back down. This contradiction between short-term and long-term success occurs whenever the functional forms of g and S (the resource growth function and the survivorship function respectively) yield $t > r > p > s$.

R_i to R_h asymptotically. For simplicity, we assume that the resource changes from R_h to R_i or vice versa in just one generation. Figure 2 describes the model schematically.

To construct the analytical model, let $H_{h,t}$, $I_{i,t}$, $H_{i,t}$ and $I_{h,t}$ be the fractions of spenders with resource R_h , investors with resource R_p , spenders with resource R_i (mutated offspring of investors), and investors with resource R_h (mutated offspring of spenders) at generation t , respectively. Based on figure 2, the population dynamics are

$$H_{h,t+1} = \frac{H_{h,t}n_hS(R_h/n_h)(1-\mu) + H_{i,t}n_iS(R_i/n_i)(1-\mu)}{Q}, \quad (1a)$$

$$I_{i,t+1} = \frac{I_{i,t}n_iS(R_i/n_i)(1-\mu) + I_{h,t}n_hS(R_h/n_h)(1-\mu)}{Q}, \quad (1b)$$

$$H_{i,t+1} = \frac{I_{i,t}n_iS(R_i/n_i)\mu + I_{h,t}n_hS(R_h/n_h)\mu}{Q}, \quad (1c)$$

$$I_{h,t+1} = \frac{H_{h,t}n_hS(R_h/n_h)\mu + H_{i,t}n_iS(R_i/n_i)\mu}{Q}, \quad (1d)$$

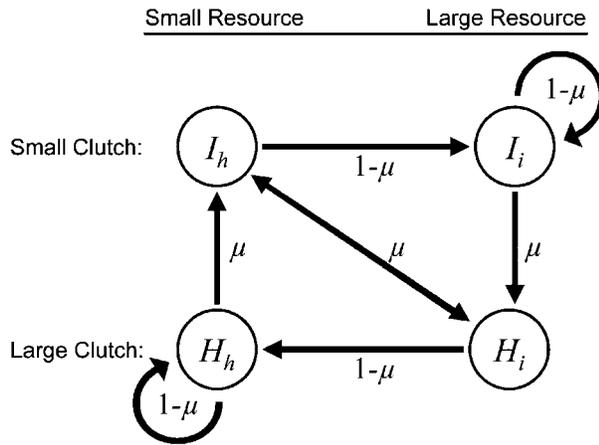


Figure 2: Because there are two strategies, spender and investor, and two resource sizes, R_h and R_p , we keep track of four categories: spenders with a small resource, spenders with a large resource, investors with a small resource, and investors with a large resource, with respective abundances H_h , H_p , I_h , and I_p . An individual of one category can give birth to an individual of another category if there is an arrow pointing from the one to the other, with probability μ or $(1-\mu)$ as shown. For example, an investor born to a spender is part of a large clutch and therefore grows to acquire the smaller resource, R_p ; it belongs to category I_h then. As another example, when this investor gives birth it has a small clutch. Each of its offspring then receives more parental investment than it received and grows to acquire the bigger resource, R_h . Those that do not mutate belong to category I_p , and those that do mutate belong to category H_p .

where Q , the normalization factor, is the sum of the numerators.

Numerical simulations of these equations under certain parameters show that, at low mutation rates, investors are more abundant, while at high mutation rates, spenders are more abundant (see app. E in the online edition of the *American Naturalist*, fig. E1). Given the details of the model, this reversal of abundance cannot be explained by the classical mutation-selection balance (Crow and Kimura 1970, pp. 258–287). The latter is acting here only to equalize the fractions of the two types. Yet another effect acts to tip the balance from one type to the other. The distinction between mutation-selection balance (as is currently known) and the new effect will be clarified in the next section. Interestingly, mutation here influences the direction of selection, and it does so in a manner that has not been addressed so far (e.g., in a manner different from McNamara et al. [2004]).

To understand how this effect emerges, we simplify the model (app. A in the online edition, eqq. [A2]–[A4]). It turns out that

$$H_{h,t+1} = \frac{H_{h,t}\mathcal{P}(1-\mu) + I_{i,t}\mathcal{T}\mu}{Q'}, \quad (2a)$$

$$I_{i,t+1} = \frac{I_{i,t}\mathcal{R}(1-\mu) + H_{h,t}\mathcal{S}\mu}{Q'}, \quad (2b)$$

where $\mathcal{R} = n_i S(R_i/n_i)$, $\mathcal{P} = n_h S(R_h/n_h)$, $\mathcal{T} = n_h S(R_i/n_h)$, $\mathcal{S} = n_i S(R_h/n_i)$, and Q' is the sum of the numerators of equations (2a) and (2b), divided by $(1-\mu)$. Under the parameter range of interest, the ordering $\mathcal{T} > \mathcal{R} > \mathcal{P} > \mathcal{S}$ is satisfied. This ordering is not satisfied automatically; rather, it is satisfied when one type is better in the short term and the other is better in the long term, as explained in the previous section. Indeed, $\mathcal{T} > \mathcal{R} > \mathcal{P} > \mathcal{S}$ reflects the ordering of the slopes $t > r > p > s$ in figure 1.

We have now described the change of the two states H_h and I_i in terms of those two states alone. It is now possible to see why mutation actively favors spending: while spenders mutating into investors are weighted by \mathcal{S} , which is, under the parameters used (see figs. 1, E1), the smallest among the four terms \mathcal{T} , \mathcal{R} , \mathcal{P} , and \mathcal{S} , investors mutating into spenders are weighted by \mathcal{T} , the largest term. The larger μ is, the more this effect matters. This can be understood intuitively by looking at the chart (fig. 2). In the absence of mutation, the investors benefit from the bigger resource and the spenders suffer from the smaller resource. However, mutation carries the larger resource from investors to spenders and carries the smaller resource from spenders to investors. Hence mutation favors spending.

Here there is an analogy with the Prisoner's Dilemma (PD; Tucker 1950; M. Flood and M. Dresher, unpublished data, 1950; see also Axelrod 1984). In the PD, each of two players playing each other can choose either to cooperate or to be selfish (to “defect”). If both players cooperate, both get a reward, \mathcal{R} ; if both defect, both get a punishment, \mathcal{P} ; if one cooperates and the other defects, the cooperator gets a “sucker's payoff,” \mathcal{S} , and the defector gets a “temptation payoff,” \mathcal{T} , where $\mathcal{T} > \mathcal{R} > \mathcal{P} > \mathcal{S}$. The general case has been made that in an evolving population of individuals playing the PD repeatedly with their neighbors, less spatial mixing favors cooperation and more spatial mixing favors defection (Axelrod and Hamilton 1981; Axelrod 1984). In our model, investors “cooperate” with their future, spenders “defect” on their future, and mutation plays a role over time that is similar to the role of mixing over space. It therefore favors the “selfish” type—the spender (see more on that point in the “Discussion”).

It is now possible to solve the model analytically (eqq. [A5]–[A8] in the online edition). We find that the spenders are more abundant than investors at equilibrium if and only if

$$\mu > \frac{\mathcal{R} - \mathcal{P}}{\mathcal{T} - \mathcal{S} + \mathcal{R} - \mathcal{P}}. \quad (3)$$

This result can be interpreted as follows: $\mathcal{R} - \mathcal{P}$ is the advantage of investors and $\mathcal{T} - \mathcal{S}$ is the advantage given by mutation to spenders. The right side of equation (3) is therefore the proportional advantage of investors. If it is smaller than the mutation rate, μ , then spenders are more abundant than investors at equilibrium. The smaller $\mathcal{R} - \mathcal{P}$ and the larger $\mathcal{T} - \mathcal{S}$ are, the lower the mutation-rate threshold for spender majority.

In passing, note two points about the methodology. First, we assume that it takes only one generation for the resource to stabilize. The resulting simple model suffices for our purpose of demonstration. It would be worthwhile, however, to allow the resource to change more gradually and explore the effects of the rate at which it approaches stability. One might expect more gradual change to favor investors by reducing the flow between the different resource states. Second, the numerical results are intended mostly as illustrations of the analytical results and a proof of principle. Further work will be needed in order to explore the parameter ranges exhaustively.

Multiple Phenotypes Model

So far we have considered the two clutch size strategies, n_i and n_p , and their corresponding stable equilibria resources, R_i and R_p . We now consider a range of clutch size strategies, n_x , and their corresponding resources, R_x , $x = 1, \dots, m$, where $n_{x+1} < n_x$ and $R_{x+1} > R_x$ for all $x < m$. This will represent a range of phenotypes between spending and investing.

The purpose here is to clarify the novel aspect of the result. By considering a range of phenotypes, we can find the optimal phenotype. We can then see that the mutation rate determines that optimum by shifting it to the left or to the right. Thus, the mutation rate affects the direction of selection. It will also be easy to pinpoint how the model differs from the classical mutation-selection balance.

For this purpose we make a few assumptions. First, the expected number of surviving offspring (henceforth “fitness”) of an owner of a larger resource is bigger than that of an owner of a smaller resource: $n_{x+1}S(R_{x+1}/n_{x+1}) > n_xS(R_x/n_x)$, for all $x < m$. Second, offspring grow to acquire the same resource their parent had unless their parent mutated. If a mutant from a lineage of resource R_x lays a clutch of size n_{x+1} , smaller than the usual n_x , it invests more per offspring, $R_x/n_{x+1} > R_x/n_x$, and would upgrade the resource of its lineage from R_x to R_{x+1} in one generation. However, that mutant will pay a onetime cost in fitness because $n_{x+1}S(R_x/n_{x+1}) < n_xS(R_x/n_x)$. Conversely, if

a mutant of an R_x lineage makes more offspring, $n_{x-1} > n_x$, and invests less in each, $R_x/n_{x-1} < R_x/n_x$, it would be downgrading the resource of its lineage from R_x to R_{x-1} in one generation, while gaining a onetime benefit in fitness; that is, $n_{x-1}S(R_x/n_{x-1}) > n_xS(R_x/n_x)$. Third, let mutation change the clutch size strategy by exactly one step at a time, from n_x to either n_{x+1} or n_{x-1} with the same probability, $\mu/2$, and exclude mutating up from n_m or down from n_1 . These assumptions parallel those of the simplified version of the previous model (eqq. [A3a], [A3b] in the online edition). Any pair of equilibrium resources (R_x and R_{x+1}) is now analogous to the pair (R_i and R_j) previously discussed.

For simplicity, we now consider only a specific case of the second assumption, namely, that in upgrading resources by one step in the spectrum, all mutants, irrespective of their strategy, merely experience the same onetime reduction factor, C , in fitness, and similarly, that in downgrading resources, all mutants experience the same onetime increase factor, B , in fitness. This restriction produces a simple model, given in appendix B in the online edition (eqq. [B1]–[B4]).

A numerical simulation of this model for various parameters shows that, for generation 1,000, which approximates the equilibrium distribution of strategies, higher mutation rates shift the distribution toward the larger-clutch strategies (online app. E, fig. E2). Because the larger-clutch strategies spend more on immediate offspring production and invest less in future generations through offspring quality, the results imply that larger μ favors more spending. Thus, the optimal level of spending depends on μ .

This result differs from the classical mutation-selection balance. In fact, the latter is a special case of the model, with $B = C = 1$. In that case, increased mutation would have flattened the distribution but would not have shifted its peak as in figure E2.

Note that Lloyd’s (1987) general formulation of the trade-off between quantity and quality does not take this effect into account. According to Lloyd, if quantity is a certain function, $f(x)$, of trait x , and quality is another function, $g(x)$, of that trait, then natural selection will favor the x that gives $[f'(x)]/f(x) = -[g'(x)]/g(x)$. However, the trade-off between quantity and quality also reflects short-term versus long-term success and will therefore be influenced by the mutation rate. In summary, the optimal balance between offspring number and quality depends on the mutation rate of the trait determining that balance.

Sexual Reproduction Favors Larger Clutches

Expression (3) shows that for the effect of interest to be visible, the mutation rate has to be high. Indeed, the ef-

fective mutation rate is high in some organisms. In plants, the meristem cells divide many times before they create the reproductive organs, and the cells accumulate mutations in the process (Buss 1987). In the RNA viruses, inaccurate replication mechanisms lead to high mutation rates (Alberts et al. 1994, p. 251). Apart from such cases, condition (3) is rather restrictive.

However, mutation is not the only mechanism that causes traits to change in time. Sex and recombination, for example, also cause change and can often make traits change substantially in just one generation. We therefore examine the clutch size trait in an evolutionary model with sexual reproduction instead of mutation as the agent of change. To do so, we make the following simplifying assumption. Although, in reality, traits are often shaped by the combined action of many genes and the environment, in order to construct a tractable theoretical model we examine a case where the trait is controlled by a single gene, in the hopes that the principle that arises from the model applies in more complicated situations, albeit with modifications.

Consider a population of random mating diploid individuals with a spender allele, H , and an investor allele, I . A spender homozygote (HH) gives birth to a large clutch, n_s , and an investor homozygote (II) gives birth to a small clutch, n_i . The heterozygote (IH) gives birth to a large clutch under spender dominance and to a small clutch under investor dominance. In any event, the maternal resource, whether R_s or R_i , is divided equally among the offspring (assume zero paternal investment for simplicity). As in the first model, both survival and resource growth are nondecreasing functions of the resulting investment per offspring. Offspring from small clutches grow to acquire the larger resource, R_s , and offspring from large clutches grow to acquire the smaller resource, R_i .

Our purpose is to examine how the sex rate affects the outcome of the evolution of the clutch size trait. Therefore, consider a theoretical model organism that is capable of both sexual and parthenogenetic reproduction, at rates X and $(1 - X)$, respectively. By varying the rate of sexual reproduction, X , we can observe its effect.

In a sense, figure 2 still represents the workings of the model, although because the transitions between types are now caused by sexual reproduction instead of mutation, their rates depend on the frequencies of the different types and are therefore themselves dynamic. The analytical model is now more complicated and is presented in appendix C in the online edition (eqq. [C1], [C2]).

Numerical simulations of this model show that sexual reproduction favors the spender allele, whereas parthenogenesis favors the investor allele. As an example, the results for spender dominance are given in figure E3 in the online edition. The figure shows that the investor

reaches fixation for low rates of sexual reproduction but that the pure investor equilibrium loses stability at a critical value of sexual reproduction (slightly above 0.2 in the simulation), above which all three genotypes persist.

This effect can be validated with the help of an invasion analysis (eqq. [C4]–[C10] in the online edition). It can be shown that the condition for the invasion of an investor population by a spender under spender dominance or codominance is

$$X > 2 \frac{\mathcal{R} - \mathcal{P}}{\mathcal{T} - \mathcal{P}}, \quad (4)$$

where \mathcal{R} , \mathcal{P} , and \mathcal{T} are defined as before. Indeed, it follows from inequality (4) that, under the parameters used in the simulation in figure E3, the threshold for invasion by spenders is $X > 2/9$, in agreement with the simulation results. More generally, inequality (4) shows that increasing X favors spender invasion. Conversely, as shown in appendix C online (eq. [C10]), in the case where a spender population is invaded by an investor under investor dominance or codominance, increasing X opposes investor invasion. In other words, a higher rate of sexual as opposed to parthenogenetic reproduction favors spending. Thus, the balance between offspring number and quality depends on the effective Mendelian segregation rate of the trait determining that balance. Since, in reality, X can be as low as 0 and as high as 1, the model's prediction is robust, albeit the one-locus assumption.

In this model, the effective segregation rate was determined by the rate of sexual versus asexual reproduction. However, a similar effect should emerge if it was determined by the rate of inbreeding or assortative mating. Alternatively, one may consider a two-locus model with recombination instead of segregation as the mechanism of evolutionary change and again expect similar results. When the trait under consideration is controlled by a number of genes, genetic linkage, as well as the number of genes involved, can affect the rate of change of the trait.

Sexual Reproduction Favors Smaller Reproductive Effort

The result that the optimum of a trait can depend on the evolutionary rate of change of the trait is not unique to the clutch size trait but follows from the fact that different clutch sizes dominate over different timescales. Thus, other traits whose variants dominate over different timescales should exhibit similar effects. So far we have considered the balance between offspring quantity and quality given a certain reproductive effort, that is, a certain fraction of energy spent on all offspring together. Let us now consider that reproductive effort. It has been discussed in the lit-

erature as a trade-off between investing in the current clutch versus investing in parental survival to improve the parent's chance of having future clutches (Williams 1966; Charnov and Krebs 1974). However, even without future reproduction, the parent's survival is important because during gestation, and in many species also after birth, the parent protects the young; if the parent dies, the young can also die. Therefore, investing in parental survival is investing indirectly in immediate offspring survival, while investing in offspring growth is investing in later offspring success. This is also an intergenerational effect—a trade-off between growth and survival of the lineage.

To put this effect in an evolutionary model, assume that an adult acquires one unit of energy, consumes a fraction of it, c , for survival up to birth giving, and saves the rest, $1 - c$, for its offspring in yolk quality (divided equally among offspring); furthermore, assume that the probability of parental survival to birth giving is proportional to the amount consumed, and the probability of offspring survival to adulthood is proportional to the amount saved. A farsighted investor strategy then spreads survival chances equally between parent and offspring ($c_i = 1/2$), whereas a shortsighted spender strategy spends more on parental survival ($c_h > 1/2$), gaining a very short lasting benefit. Consider a one-locus, two-allele model with a spender allele and an investor allele, where individuals reproduce either sexually or parthenogenetically. In sexual reproduction, let the two parents make together twice as many offspring as each would have made parthenogenetically, and let each parent divide its reproductive effort equally among the offspring. A numerical simulation of this model (given analytically in app. D in the online edition, eqq. [D1], [D2]) shows that sexual reproduction favors the spender allele whereas parthenogenesis favors the investor allele (fig. 3). Furthermore, an invasion analysis can now provide the evolutionarily stable strategy (ESS) in terms of X (eqq. [D3]–[D9]). It turns out that the ESS (Maynard Smith and Price 1973) is also convergence stable (CSS; Eshel and Motro 1981; Apaloo 1997; Levin and Muller-Landau 2000) and is of the form

$$C_{\hat{R}\hat{R}} = \frac{2}{4 - X}. \quad (5)$$

This expression shows that the convergence stable strategy rises from $C_{\hat{R}\hat{R}} = 1/2$ in the absence of sexual reproduction ($X = 0$) to $C_{\hat{R}\hat{R}} = 2/3$ when all reproduction is sexual ($X = 1$). In other words, the higher the sex rate, the more energy the CSS consumes and the less it saves for offspring. Thus, sexual reproduction promotes spending. The balance between investing in self and investing in offspring depends on the segregation rate of the trait determining that balance.

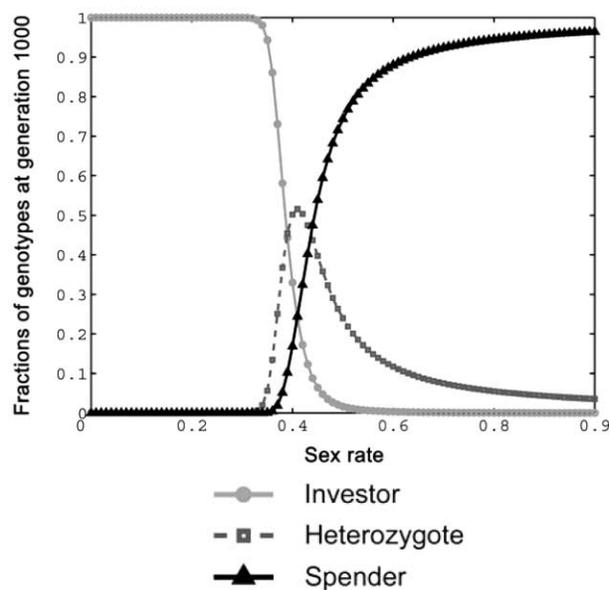


Figure 3: Results of a simulation based on equations (D1) and (D2), with parameters $c_i = 1/2$ and $c_h = 6/10$, under spender dominance. The simulation starts with a population of 99% homozygote investors and 1% heterozygotes at generation 1. The fractions of the three genotypes at generation 1,000 are then calculated. This is done under various sex rates. The figure shows that sex favors spending. A similar effect emerges for investor dominance and for other $c_h > 1/2$.

We have now examined four models toward a common purpose. The models employed population genetic analysis vis-à-vis phenotypic analysis, as suggested by Eshel et al. (1998), while addressing the question of intergenerational effects in life-history theory, promoted by Stearns (1989, 1992) and McNamara and Houston (1996). They call for further exploration of the effects that were found.

Discussion

We have focused on the trade-off between offspring number and quality. There, we found that different clutch size strategies differed in their temporal orientation. We assumed that investing in offspring quality improved not only offspring survivorship but also offspring reproductive success. A higher-quality offspring was more likely to have higher-quality offspring of its own. By this assumption, the investment in offspring quality was carried down the generations. Therefore, a shift in the balance from quantity to quality represented a shift in the strategic orientation from short term to long term, and vice versa. It turned out that because of this element, increased evolutionary change through mutation or sexual reproduction favored the short-term strategy—that is, the larger-clutch variant.

We then found that the effect above applied not only to the clutch size trait but also to the total reproductive effort trait. There, the balance was between the chance of parental survival up to birth giving and the chance of offspring survival after birth. The short-term trait variant invested more in parental survival relative to the long-term variant. Again, it turned out that increased evolutionary change favored the short-term strategy.

We can now suggest an intuitive, verbal description of the workings of the mathematical models. The crucial element in the modeled traits is that they bear on a trade-off between short-term and long-term survival of the lineages carrying them. The so-called spender and investor trait variants are short-term and long-term strategies, respectively. Investors donate more to descendants at a higher short-term cost. Mutation and sexual reproduction are two mechanisms of evolutionary change. With slow evolutionary change, descendants inherit donations mostly from same-type ancestors. In this case, investors fare better in the long term as long as the benefits of the donations outweigh the costs. With fast change, however, the correlation in type between ancestors and descendants is reduced. Spenders inherit more similarly to investors but pass less to future generations and therefore fare better. Thus, intergenerational donations are more adaptive when donor and recipient are more alike.

This is a cost-benefit analysis of altruism in light of relatedness. In this sense, it is in accord with inclusive fitness (Hamilton 1964). However, inclusive fitness implies that parents may reduce the investment in an offspring under relatedness considerations only to the extent that they have a better way to invest in the next generation through other offspring or relatives. Accordingly, the parent-offspring conflict in its classical form (Trivers 1974; Feldman and Eshel 1982; Godfray 1995) is about how to allocate resources between born offspring, unborn offspring, and other relatives. Our results stand in contrast. In the reproductive effort model, even though the parent reproduces only once and is not given a choice to donate to relatives other than its offspring, it still saves less for all of its offspring together, the less related they are to it. In the clutch size models, relatedness alone suffices to put selection pressure on the clutch size trait, even while the expected relatedness between the parent and each of its offspring is identical. It appears from our models that individuals evolve to act as though they favor earlier generations more and later generations less, the faster relatedness drops in time. This can be called "intergenerational discounting" (to borrow a term from Schelling [1995]).

It is the combination of evolutionary change and intergenerational trade-offs that allows intergenerational discounting to evolve. Change, however, occurs by various means, namely, mutation, sex, recombination, and envi-

ronmental influence. In addition, intergenerational trade-offs exist in various traits.

We mentioned the clutch size trait in the great tit. A parent that makes a smaller clutch invests more per offspring. The offspring then grow bigger and stronger and become more dominant adults (Verhulst et al. 1997). This enables them to acquire and defend territories of higher quality in adulthood that ensure a better diet for their own offspring (Riddington and Gosler 1995; Verhulst et al. 1997). The ability of the high-quality offspring to own high-quality territories is the element through which the investment in offspring quality percolates down the generations.

In the parasitoid wasps *Trichogramma*, as mentioned, the resource available per offspring has multiple long-term consequences. Offspring from smaller clutches obtain a larger share of the host. They grow bigger and healthier, move faster and fly farther, and may be able to find better hosts for their own offspring (Waage and Ng 1984). The females among them also have more eggs in the oviducts and a longer life span, which further promote their lifetime reproductive success (Waage and Ng 1984).

The clutch size trait and the total reproductive effort trait modeled are only two examples of traits that carry intergenerational effects. In fact, there are many routes through which an individual's action can affect the fitness of future generations down the line. The transfer of social status to offspring is one case in point. In various group-living mammalian species where food is monopolizable, dominance relations emerge that give higher-ranking individuals and their kin better access to food and physical protection (Silk 1987; Pusey et al. 1997). In addition, the social rank is often transferred to offspring as a maternal effect (Hausfater et al. 1982; Holekamp and Smale 1991). Therefore, investing in rank acquisition and maintenance has a long-term benefit: not only does it improve the fitness of the focal individual, but through the transfer of rank to offspring, it improves the fitness of the offspring (McNamara and Houston 1996).

Pusey et al. (1997) relate the following three points about female chimpanzees. First, dominance improves fitness substantially: higher-ranking females experience far less infant mortality due to better protection and nutrition of the young, and, in addition, their daughters reach sexual maturity earlier. Second, dominance is partly transferred matrilineally, through the support that the mother and her kin give the daughter in acquiring social rank. Third, the social status can be improved independent of heritage through aggression. This last point allows for variance in the individuals' tendencies to invest or take risks in order to improve their social status (McNamara and Houston 1996). In combination, these points allow for the existence of short-term and long-term variants in traits for invest-

ment in status. They also seem generalizable to other apes and to the hyenas. In female baboons, social rank, sociality, and infant survival (which is a crucial fitness factor [Altmann and Alberts 2003]) are all correlated (Silk et al. 2003). In addition, social rank is transferred to offspring (Hausfater et al. 1982). In the spotted hyena, sons of high-ranking females obtain preferential access to food and are expected to benefit in maturity in terms of reproductive success (Frank 1986*b*). Again, the social status is transferred to offspring reliably (Frank 1986*a*).

Even dispersal may bear on the intergenerational trade-off, although it is a complicated case. Consider dispersal in annual plants (Levin et al. 1984). In various species, dispersing far necessitates morphological changes in the seed that entail a cost (Motro 1982*a*; Levin and Muller-Landau 2000). Far-dispersing seeds experience mortality en route and in establishment (Rousset and Gandon 2002). The fact that the parent plant is established suggests that local conditions are favorable and that far-dispersing seeds take an unfavorable risk (Hastings 1983; Olivieri et al. 1995). On the other hand, near dispersal leads to the proliferation of the species within the local patch, intensifies kin competition down the generations, and becomes a source of inefficiency in the long term (Hamilton and May 1977; Comins et al. 1980). Other factors complicate the problem, such as various sources of environmental stochasticity (Roff 1975; Levin et al. 1984), inbreeding depression (see, e.g., Bengtsson 1978), and genetic adaptation to the local environment (see, e.g., Balkau and Feldman 1973).

Concentrating on kin competition, Comins et al. (1980, p. 213) found that the dispersal strategy that maximized the chance of establishment differed from the strategy that maximized success farther into the future. Thus, there is room for variability in the temporal orientation of dispersal traits. In this light, it is interesting that sexual selection as opposed to parthenogenesis was found to reduce the tendency to disperse to some extent (Hamilton and May 1977; Comins et al. 1980; Motro 1982*c*). Although Hamilton and May (1977) attributed this result to the parent-offspring conflict in its classical form (Trivers 1974), which depends on the offspring being in control of the dispersal trait (Hamilton and May 1977; Motro 1982*b*), it may be possible that, under some conditions (such as multiple adults per site; Comins et al. 1980; Levin et al. 1984), sexual reproduction would reduce dispersal also due to intergenerational discounting, which is independent of whether the parent or the offspring is in control. While some preliminary results (A. Livnat and S. Levin, unpublished data, 2004) suggest that this is the case, we have yet to explore this issue more thoroughly.

There are other traits that share elements with the traits above but have additional elements as well that make them

more complicated. One such example is sexual reproduction. There, the cost of the search for mates applies immediately, while the benefits of combining good mutations seem to accumulate in the long run (Maynard Smith 1978; Barton and Charlesworth 1998). As evidence of the long-term consequences, selfers are more liable to extinction than sexually reproducing species (Barrett et al. 1996). However, unlike the cases discussed above, sexual reproduction plays a double role, in both being the focal trait and affecting its own rate of evolution. This makes it an intricate case.

The investment in biomass, through yolk or parental care, the investment in social status as in apes and hyenas, dispersal in plants, and even sexual reproduction are all traits that reflect intergenerational trade-offs, where trait variants can differ in their temporal orientation. These variants make different investments that mature at different schedules and pay different “interest rates” on the intergenerational timescale. It appears that life-history strategies provide plenty of opportunity for organisms to adjust their contributions to grandchildren and further descendants indirectly (contrary to Hamilton’s claim [1964, p. 33]). This becomes crucial in combination with evolutionary change due to mutation or sexual reproduction. With the help of analytical models and computer simulations, we found that faster evolutionary change favors short-term over long-term strategies. In other words, the tendency to invest in future generations decreases as the relatedness to those future generations decreases. We called this effect “intergenerational discounting.” Incidentally, the original framework of inclusive fitness was developed to deal with interactions between relatives of the same generation. Hamilton saw it as a first step toward a general theory that would account for all kinds of relatives (Hamilton 1964). In a sense, intergenerational discounting extends the approach of inclusive fitness over the time dimension.

As a matter of speculation, intergenerational discounting may have an interesting consequence as follows. Because of evolutionary constraints, different traits within the same organism evolve at different rates. It follows that they evolve different discounting rates and, much as they can mismatch in the degree of relatedness to a contemporary relative and the value of donating to it, they can conflict over the value of a donation to the future.

Consider the following thought experiment. The outcrossing rate in plants is shaped by a number of traits: stigma-to-anther distance, flower size, and the timing of sexual functions (Barrett and Eckert 1990). If outcrossing reflected an intertemporal trade-off as mentioned, and if the different outcrossing traits evolved at different rates, then some could have evolved to push for more outcrossing and some could have evolved to push for less. This

would have been an example of a biological conflict within the organism over the future. It could also connect to the question of why there are mixed mating systems (see, e.g., Lande and Schemske 1985; Yahara 1992).

As another thought experiment, consider a hypothetical immune system whose different cell lines fighting different pathogens compete for the body's resources. There, the long-lasting cell lines would be those that did not drain their target pathogens but rather maintained them at some optimal level. However, the evolution of those cell lines would make them defect on their own future and thereby cooperate with the future of their host. The spatial analog is that in a mixed population of bacteria with a number of species present, cheaters that do not produce colicins (antibacterials) but retain the ability to resist them break down the intraspecific cooperation in poisoning other species and thereby reduce conflict on the interspecies level (Durrett and Levin 1997; Riley and Gordon 1999; Kerr et al. 2002). The analogy suggests that the breakdown of cooperation over one timescale may promote cooperation over another timescale. Thus, considerations of cooperation and conflict over time may lead to a very complex view of sex and recombination. Further theoretical work and empirical testing would be needed to explore these interesting possibilities.

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