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Decision-making in variable environments — a case of group selection and inter-generational conflict?

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Abstract

Suppose organisms need to engage in a particular action exactly once during some fixed period of time. Further suppose they can time this action to optimise their fitness based on the expected current payoff and the probability distribution of later payoffs. For an example we consider the timing of the annual nuptial flight in eusocial insects. Using two population genetics models, we ask whether stochasticity leads to evolutionary conflict between the queen and her offspring. We find that the winning phenotype is independent of who controls the timing. The best response to any non-equilibrium population strategy is the same in both control scenarios, a result that carries over to the diploid case. Although inter-generational conflict is therefore ruled out, the models support a previous observation that at equilibrium some of the offspring have a lower expected payoff than others. By measuring fitness in terms of *relative* reproductive success, we show that all individuals are in fact equally well off making group-selectionist arguments unnecessary. As such, the models should improve our understanding of the difficult conceptual problem of the unit of natural selection in stochastic environments.

Keywords: Environmental stochasticity; Bet-hedging; Evolutionary conflict; Fitness measures

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1. Introduction

Environmental stochasticity describes variation across time that affects all individuals alike. It is a well-established result from population genetics models (Dempster, 1955; Cohen, 1966; Lewontin and Cohen, 1969; Tuljapurkar, 1989) that the maximand of natural selection under such conditions is the geometric mean rate of growth,

$$\prod_{i=1}^{n} \gamma_i^{p_i}, \tag{1}$$

where γ_i is the rate of growth in terms of the absolute number of offspring in the ith state of nature (occurring with probability p_i). Since the absolute number of offspring is commonly seen as a reasonable measure of fitness, this product is often referred to as the geometric mean fitness. Because of its sensitivity to small values of γ, genotypes which do fairly well across all environmental states are expected to prosper relative to genotypes that excel in some environments but fail in others. This observation has given rise to the view that under environmental stochasticity a successful genotype should reduce variability in the number of offspring across environmental states, a strategy that has come to be known as bet-hedging (Seger and Brockmann, 1987).

Because individual fitness, when measured in terms of the absolute number of offspring of a bet-hedging genotype, may vary considerably between different phenotypes and thus between groups of individuals, the geometric mean result seems to imply that natural selection is not acting on individual fitness but on the fitness of the genotype (or the body of individuals sharing the same genotype). Fitness variability may then be seen as an expression of altruism on the part of the individual as has been suggested by Cooper and Kaplan (1982) when they state that bet-hedging constitutes "a sacrifice of immediate individual fitness for the sake of the long term advantage of the genotype" (Cooper and Kaplan, 1982, p. 145) and others have argued similarly (Ellner, 1986).

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It is only relatively recently with papers by McNamara (1995), Sasaki and Ellner (1995), Haccou and Iwasa (1995), and more explicitly by Grafen (1999), that "individual-as-maximising-agent" analogies for population genetics models with environmental stochasticity have been established. These allow us to view the individual as the focus of natural selection and suggest that all phenotypes of a bet-hedging genotype are in fact equally well off if only one employs the appropriate fitness measure.

The existence of such analogies does not preclude the possibility of a conflict between generations over the optimal phenotype distribution. Since the early work by Trivers (1974) the problem of evolutionary conflict has been dealt with extensively (Godfray, 1995). Yet, with the exception of Westoby (1981) and Ellner (1986), few papers have investigated its connection with stochastic environments. The existence of such conflict under stochasticity has first been suggested by Westoby (1981) in the context of seed dormancy. Phenotypic models predict that the most successful plants let a certain proportion of their seeds overwinter which clearly conflicts with the intuitive, individualistic view that "each and every seed ought to germinate at the single opportunity which gives the best chance of growing to maturity." (Westoby, 1981, p. 883).

The basic setting in which we investigate the problem of bet-hedging and evolutionary conflict is simple. We assume that individuals need to take some fitness-critical action exactly once during some period of time and that they can time this action to optimise their fitness based on the expected current payoff and the probability distribution of future payoffs. We set up two population genetics models in which we confer control over the timing to, respectively, the parent and the offspring. We then compare the evolutionary outcomes in terms of the distribution of the times chosen by individuals.

We have selected a particular problem for illustration: the timing of the nuptial flight in ants. The problem exhibits all the essential features we seek to model. The nuptial flight is a unique event in the life-cycle of the individual reproductive, and often of the colony as well. The flights are also periods of intense selection pressure often taking place only under a very narrow range of weather conditions (Boomsa and Leusink, 1981). If there is scope for evolutionary conflict, the colonial structure of ant societies provides the ideal setting for such conflict to manifest itself. Clearly, the models are a great abstraction not only because the life-cycle of ants is typically much more varied and complex, but also because most species are decidedly non-annual and have overlapping generations. The simplicity of the models comes with the prospect of illuminating some general principles that might be at work in more realistic settings where they tend to be occluded by the complexity of the problem.

The paper is structured as follows. We develop the two population genetics models in Section 2 and show that parents and offspring agree over the best response to any non-equilibrium population strategy. In Section 3, we use the models to demonstrate how the fitness variability across different phenotypes disappears upon measuring fitness not in terms of absolute reproductive success but in terms of the reproductive value as suggested by Grafen (1999). This result highlights the importance of employing appropriate fitness measures when analysing and interpreting the results of evolutionary models. It suggests that the notion of natural selection maximising individual fitness remains meaningful in stochastic models. We summarise and discuss the results in Section 4.

2. The models

The life-cycle of the modelled organism comprises the three following stages:

(1) male and female reproductives accumulate in colonies,
(2) the nuptial flight takes place during which prospective queens mate,
(3) queens found new colonies, males die.

The two models are very similar and only differ in whether it is the queen's or the offspring's genotype that determines the strategy adopted by the offspring. In both models we assume that there exist two points in time t_x and t_y at exactly one of which the nuptial flight needs to take place. We allow nature at t_y to be in one of only two states, which are independent of the state at t_x. We show in Appendix A that the results readily generalise to any distribution of states at t_y. The environmental state is the same for the entire population. The absolute reproductive success, which we will refer to as the payoff of an alate choosing t_x and t_y, is denoted by x and y, respectively, where y is a dichotomous random variable taking value y_1 with probability r and value y_2 with probability $1-r$. Without loss of generality we demand that $y_1 \leqslant y_2$, and we will occasionally refer to years with payoffs y_2 and y_1 informally as good and bad years, respectively. It is further assumed that the decision of whether or not to select t_x is informed by an accurate assessment of the environmental state at t_x. We consider a one-locus system where the trait under consideration is the probability s (henceforth referred to as the *split-ratio*) of an individual flying at t_x. To find the equilibrium split-ratio, we determine the spread conditions of a rare and dominant allele, A, with phenotypic effect s in a monomorphic population with phenotype $\tilde{s}$ associated with the focal locus. The evolutionarily stable strategy (ESS) is then found as the phenotype that resists invasion by any other deviant phenotypes when near fixation. For the second model it will be necessary to distinguish between the frequency of A in males, p^m, and in females, p^f, as these are generally different. We will also make this distinction in the first model but only to show that the two are, in fact, the same.

2.1. Model with offspring control

After assessing the conditions at t_x, each alate decides independently from all others whether or not to take action at t_x. Rejecting t_x implies acceptance of t_y. With p being small, we need to consider only three types of matings with relative frequencies $aa \times a$ (≈ 1), $Aa \times a$ ($\approx 2p^f$) and $aa \times A$ ($\approx p^m$). The mating combinatorics and descendant phenotypes are shown in Table 1. The split-ratios for the different genotypes are given in the bottom row (the split-ratios in the right column are those under parental control and will be of importance for the second model).

The expected payoffs for the 2 years are obtained as the average over the payoffs at t_x and t_y weighted by the probability of an alate choosing either time, i.e.

$$F(s) = \begin{cases} F_1(s) = sx + (1-s)y_1 & \text{with probability } r, \\ F_2(s) = sx + (1-s)y_2 & \text{with probability } 1-r. \end{cases}$$

Since y varies from generation to generation, so does F. The sequence of random variables form a discrete-time random process $\{F_n(s) : n = 0, 1, \ldots\}$ where n is the generation index. We shall often drop the variable s and write F for $F(s)$ and $\tilde{F}$ for $F(\tilde{s})$. Note that we use two types of subscripts in conjunction with F and $\tilde{F}$. One type specifies the different values taken by the random variable (F_1 and F_2), the other specifies the generation number: F_n denotes the random variable in generation n. The correct meaning will be evident from the context.

With these conventions and from Table 1, the frequencies of A in males and females in generation $n+1$ are

$$p^f_{n+1} = \frac{1}{2}\left(p^m_n + p^f_n\right)\frac{F_n}{\tilde{F}_n},$$
$$p^m_{n+1} = p^f\frac{F_n}{\tilde{F}_n},$$

with $n \geqslant 0$ and $p^f_0 = p^m_0 = p_0$. It is easily seen that if $p^f_n = p^m_n$ the two will continue to be the same for all subsequent generations. But even if the two start off differently, they will quickly converge. We may therefore replace the second recurrence equation for males with the following

$$p_{n+1} = p_n\frac{F_n}{\tilde{F}_n}, \quad n \geqslant 0,$$

where $p_n = p^f_n = p^m_n$. The equation of motion for A then becomes

$$p_N = p_0 \times \prod_{n=0}^{N-1}\frac{F_n}{\tilde{F}_n},$$

with the average increase amounting to

$$w = \lim_{N\to\infty}\left(\frac{p_N}{p_0}\right)^{1/N} = \lim_{N\to\infty}\left(\prod_{n=0}^{N-1}\frac{F_n}{\tilde{F}_n}\right)^{1/N}.$$

Table 1
Mating combinatorics and offspring phenotypes

	aa	Aa	a	A	split-ratio (queen control)
$aa \times a$ (1)	1	0	1	0	$\tilde{s}$
$aa \times A$ (p^m)	0	1	1	0	$\tilde{s}$
$Aa \times a$ ($2p^f$)	1/2	1/2	1/2	1/2	s
split-ratio (alate control)	$\tilde{s}$	s	$\tilde{s}$	s	

It is useful now to take the logarithm on both sides. A split-ratio s that maximises w also maximises

$$W = \ln\, w = \lim_{N\to\infty}\frac{1}{N}\sum_{n=0}^{N-1}\ln\left(\frac{F_n}{\tilde{F}_n}\right).$$

Because $F_n/\tilde{F}_n$ are identically and independently distributed random variables (strictly speaking stochastic functions of the random variable y), for large N the average over generations can be replaced by the expectation with respect to the distribution of y,

$$W(s) = \mathbb{E}_y\left[\ln\left(\frac{F(s)}{\tilde{F}}\right)\right] = r\,\ln\left(\frac{F_1(s)}{\tilde{F}_1}\right) + (1-r)\ln\left(\frac{F_2(s)}{\tilde{F}_2}\right),$$

where $\tilde{F}$ only depends on the population strategy $\tilde{s}$. The standard condition for an ESS at s^* is that $W(s) \leqslant W(s^*)$ for all s (Maynard Smith and Price, 1973), that is s^* is the best response to itself when prevailing in the population. The best response is found by solving $\partial W/\partial s = 0$ which leads to the intermediate expression

$$rF_1'(s)F_2(s) = (r-1)F_2'(s)F_1(s). \tag{2}$$

Using the expressions of F_1 and F_2 from above, one finds the best response as

$$s^* = \frac{rxy_1 - rxy_2 - xy_1 + y_1y_2}{x^2 - xy_1 - xy_2 + y_1y_2}. \tag{3}$$

This gives the ESS if $x \in [y_1, y_2]$ (since $\partial^2 W/\partial s^2 < 0$), else Eq. (3) describes a minimum. In particular, if $x < y_1$, the value of s^* is larger than 1 and the optimal split-ratio is 0. If $x > y_2$, the value of s^* is smaller than 0 and the optimal split-ratio is 1. Both results are, in close accord with intuition.

It is worth noting that this is precisely the result obtained from a purely phenotypic model for a haploid asexual population with the fitness for an s-strategist given by $sx + (1-s)y_1$ in a bad year and $sx + (1-s)y_2$ in a good year with the optimal strategy maximising $W(s) = [sx + (1-s)y_1]^r \times [sx + (1-s)y_2]^{(1-r)}$.

It is instructive to consider the range of x values for which, given a particular distribution of y, the optimal split-ratio satisfies $0 < s^* < 1$, i.e. for which some alates fly at t_x and others at t_y. We can rearrange Eq. (3) thus

$$s^* = \frac{y_1y_2(1 - x/\mathbb{H})}{x(x - \mathbb{A}) + y_1y_2(1 - x/\mathbb{H})}, \tag{4}$$

where $\mathbb{A} = ry_1 + (1-r)y_2$ is the arithmetic mean and $\mathbb{H} = (r/y_1 + (1-r)/y_2)^{-1}$ is the harmonic mean of y_1 and y_2. From Eq. (4) we can derive a simple decision rule for alates at t_x: if $x \geqslant \mathbb{A}$ then $s^* = 1$, if $x \leqslant \mathbb{H}$ then $s^* = 0$. The first condition implies that alates should always choose the early point if the arithmetic average of the expected payoff at the later time is smaller than the current payoff, x. This part of the decision rule appears to be in accord with the idea of natural selection maximising individual fitness: if there is nothing to be gained on average from waiting, don't wait.

The condition for which $s^* = 0$ is more interesting. For while alates are expected to choose t_x if the average payoff at t_y is lower, the reverse does not hold. If the offspring can expect a higher average payoff at t_y the model predicts a split-ratio below 1 but not necessarily 0, although the latter is seemingly the obvious choice from an individual alate's perspective. The second condition informs us that s^* takes the value 0 only when x is smaller than the harmonic mean of y_1 and y_2 (which is always smaller than or equal to the arithmetic mean). Let D be the difference between the arithmetic and the harmonic mean, i.e.

$$D = ry_1 + (1-r)y_2 - \frac{y_1 y_2}{(1-r)y_1 + ry_2} = \frac{(y_1 - y_2)^2 (r - r^2)}{r(y_2 - y_1) + y_1}.$$

Thus, if y has zero variance (i.e. $y_1 = y_2$) then $D = 0$ and the optimal strategy is pure. As the variance increases, so does D and the ESS becomes mixed with t_x being favoured under an increasingly wide range of x values. Fig. 1 shows the shape of the transition between $s = 0$ and 1 for different values of y_1 and y_2 when both are equally likely ($r = 0.5$). The mean is kept constant with the variance increasing from 0.0 ($y_1 = y_2 = 0.5$) to 0.2401 ($y_1 = 0.01, y_2 = 0.99$). Notice that, as the variance of y increases, the harmonic mean decreases and a growing number of alates begin to accept a lower payoff. We here seem to witness a trade-off between the mean and the variance in the absolute number of offspring, hence the notion of bet-hedging. As noted by Grafen (1999), this trade-off takes place, strictly speaking, only at the level of the genotype (or the body of individuals sharing the same genotype) not at the level of any particular individual, since situations can be conceived in which alleles specifying different degrees of variability in the number of offspring are selectively neutral at the level of the individual. Since "bet-hedging" is an intentional term, it may be misconstrued as a description of an optimisation principle applying to individuals, which is a role it cannot fulfil, and therefore may better be avoided.

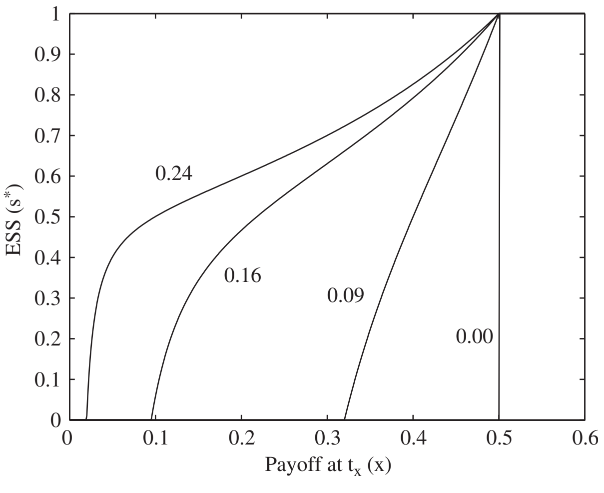

Fig. 1. Graph showing how the range of x values for which the optimal strategy is mixed ($0 < s^* < 1$) widens as the variance of y, the payoff at t_y, increases. For zero variance the optimal split ratio is either 0 or 1.

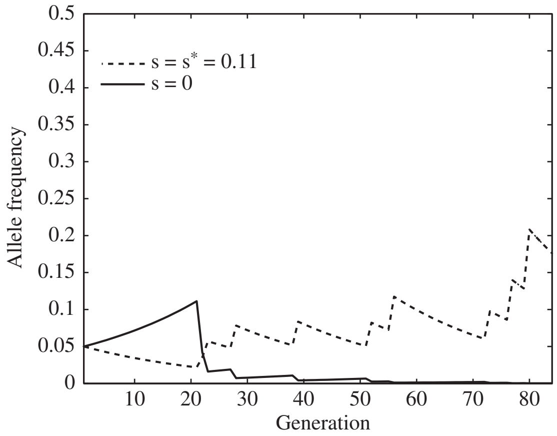

Fig. 2. Spread of two alleles in a population dominated by a non-equilibrium split-ratio. When the environment at t_y is highly variable ($y_1 = 0.1$, $y_2 = 0.9$), it pays to allocate a few offspring to t_x ($x = 0.3$) although it is on average worse. A strategy that favours the second time point (unbroken line) does better than the ESS (dotted line) in most years, but a few unfavourable years suffice for its frequency to vanish.

We show in Appendix A that this simple decision rule generalises to any distribution $p(y)$ of environmental states at t_y so that the optimal strategy is mixed whenever $x \in]x_{\min}, x_{\max}[$, where

$$x_{\min} = \left(\sum_{i=1}^{n} \frac{p(y_i)}{y_i} \right)^{-1} \quad \text{and} \quad x_{\max} = \sum_{i=1}^{n} p(y_i) y_i. \tag{5}$$

Fig. 2 shows a typical example of the spread of two initially rare alleles in a non-equilibrium population for the case of highly variable payoffs at t_y. The strategy that maximises average payoff across different years (by avoiding t_x altogether) spreads in good years but loses disproportionately in bad years leading to eventual extinction (see also caption).

2.2. Model with parental control

We now turn to the situation where the split-ratio is determined by the parental genotype. We again consider the spread of A in a population of colonies with homozygous aa queens of phenotype $\tilde{s}$. The mating table and the genotype frequencies of the offspring are those of the first model but the phenotypes of the offspring are now given by the right column of Table 1. Again we assume A to be rare.

Recall that in the first model the mathematical treatment was greatly simplified by the fact that at any one time the frequencies of A are the same in both sexes and so we could restrict our attention to one sex. Under parental control, the rate of change in frequency of A is generally different in males and females. That this should be so can be seen intuitively by observing that some of the young Aa queens are reared in colonies with aa mothers, but all A males are reared in colonies with Aa mothers. As a consequence, A, if favoured over the wildtype, will spread faster in males than in females. From Table 1, we obtain the two following recurrence equations for the frequency of A in males (p^m) and females (p^f),

$$p^m_{n+1} = \frac{p^f_n F_n}{\tilde{F}_n} \quad \text{and} \quad p^f_{n+1} = \frac{p^m_n \tilde{F}_n + p^f_n F_n}{2\tilde{F}_n}. \tag{6}$$

We can separate the p^m and p^f by combining the two equations to form two stochastic second-order recurrence equations. Writing $\gamma_n = F_n/(2\tilde{F}_n)$ we obtain

$$p^m_{n+1} = \gamma_n(p^m_n + p^m_{n-1}) \quad \text{and} \quad p^f_{n+1} = \gamma_n p^f_n + \gamma_{n-1} p^f_{n-1}.$$

Each of these can be solved separately to find the strategy s that maximises the average rate of increase in each sex given some population strategy $\tilde{s}$. We do this for the first equation in Appendix B. We find that the optimal response s satisfies

$$rF'_1(s)\tilde{F}_2 = (1-r)F'_2(s)\tilde{F}_1.$$

This is just Eq. (2). We can now argue that this must also be the split-ratio that maximises the rate of increase in females by noting that the two recurrence equations, Eq. (6), imply that

$$p^f_{n+1} = \frac{1}{2}\left(p^m_{n+1} + p^m_n\right),$$

that is, the frequency in females in one generation lies halfway between the frequencies in that and the previous generation in males. A strategy that maximises the spread of A in males automatically maximises its spread in females. The optimal response to some population strategy $\tilde{s}$ is the same as under offspring control and so is the ESS, given by Eq. (3). We may conclude therefore that there is no inter-generational conflict over the timing of reproduction, neither at equilibrium nor away from it. That this is not merely a result of haplodiploidy but is of more general validity is demonstrated in Appendix C where we derive the same optimality condition for both control scenarios in the case of diploid inheritance.

3. Fitness variability at the ESS

In both models a mixed strategy is favoured over a pure strategy under a broad range of conditions. In particular, the optimal strategy is mixed whenever the payoff associated with the early time point, t_x, lies between the harmonic mean and the arithmetic mean of the payoffs associated with the later time point, t_y. The more variable the environment at t_y, the more likely are alates to choose t_x under "suboptimal" conditions even if the expected payoff at t_y may be substantially greater than that at t_x. Note from Fig. 1, for example, that for highly variable payoffs at t_y (variance of 0.24) some alates choose the early time even under conditions that confer less than a tenth of the payoff that could be expected at the later time.

This variability in the absolute number of offspring is well known from other models dealing with stochastic environments and seems to elude any interpretation in terms of a maximisation principle centred around the individual. In a recent series of papers (Grafen, 1999, 2000), attention has been drawn to the fact that such an "individual-as-maximising-agent" analogy can be found in the form of the expected reproductive value as introduced by Fisher (1930), or the arithmetic average of the relative reproductive success. The analogy is significant not only because it paves the way towards an elegant unification of the diverse strands of optimality theory in evolutionary biology (e.g Parker and Maynard Smith, 1990), but also because it re-emphasises the central role of the individual in evolutionary processes.

In our models the phenotype distribution that maximises the geometric mean of the absolute reproductive success does indeed maximise the arithmetic average of the relative reproductive success, as we shall now show. In the second model, the average reproductive value R of an s-queen in an $\tilde{s}$-dominated population with N queens is equal to

$$R(s) = r\frac{F_1(s)}{N\tilde{F}_1} + (1-r)\frac{F_2(s)}{N\tilde{F}_2}.$$

The derivative with respect to s is

$$\frac{\partial R}{\partial s} = \frac{1}{N}\left(r\frac{F'_1(s)}{\tilde{F}_1} + (1-r)\,\frac{F'_2(s)}{\tilde{F}_2}\right),$$

which has an internal optimum at s satisfying

$$rF'_1(s)\tilde{F}_2 = (r-1)F_2(s)'\tilde{F}_1. \tag{7}$$

The ESS is the best response to itself, so at equilibrium $s = \tilde{s}$ and Eq. (7) becomes

$$rF'_1(s)F_2(s) = (r-1)F'_2(s)F_1(s). \tag{8}$$

This is just Eq. (2) which describes the condition for the optimal split-ratio when alates control the timing. Thus, the ESS maximises R. It is but a small step from Eq. (8) to show that at equilibrium all alates have the same fitness when measured in terms of the expected relative number of offspring. If one replaces in Eq. (8) F'_i by $x - y_i$, we can rearrange it to give

$$\frac{rx}{F_1} + \frac{(1-r)x}{F_2} = \frac{ry_1}{F_1} + \frac{(1-r)y_2}{F_2}.$$

But the LHS and the RHS are now just the expected relative payoffs of an alate choosing t_x and t_y, respectively. Thus, the timing decision can be understood without taking recourse to group selectionist arguments and the notion of individual sacrifice. It can justly be viewed as an adaptation at the level of the individual. More informally, "an offspring produced for a rare and little-populated eventuality may regret that their day of glory is unlikely to arise, but this will be exactly compensated by the extent of their relative triumph should it do so." (Grafen, 1999, p. 802).

4. Discussion

We have presented two simple population genetics models to understand how uncertainty about future environmental conditions affects the timing of some fitness-critical action and to what extent the results depend on whether the timing decision is under parental or offspring control. The particular situation modelled is the nuptial flight in ants as there is some evidence that its success depends critically on the weather conditions at the time of flying, and because the colonial organisation provides an ideal setting for manipulation of the offspring.

Concerning the first question, we have shown that individuals should not all wait until the later time even if the expected payoff exceeds the present payoff (x). Rather, individuals should continue to choose the present time with a non-zero probability until the current payoff is smaller than the harmonic mean of future payoffs. We obtain a simple decision rule whereby the split-ratio is pure if x is smaller than the harmonic mean ($s = 0$) or larger than the arithmetic mean ($s = 1$) of the payoff at the second time point. We have further shown that the apparent fitness variability among the offspring at the ESS is compatible with the idea of individual fitness maximisation and that neither group selection nor altruism need to be invoked if fitness is measured in terms of the arithmetic average of relative reproductive success.

We explicitly model the problem of evolutionary conflict by giving control over the timing to either the parent or the offspring. We find that the best response of individuals to a non-equilibrium split-ratio is the same in both control scenarios and that, therefore, our models do not support the view frequently associated with bet-hedging that stochastic environments provide scope for inter-generational conflict.

Many complications of the basic model are conceivable: our decision problem is effectively one of binary choice. One could instead assume, more realistically, that nature varies according to a continuous-time random process where reproduction can take place anywhere along a continuum as has been assumed in Satake et al. (2001). Also, it seems reasonable to assume that the payoffs of the offspring are modulated through factors such as local mate competition (Hamilton, 1967) and local resource competition (Clark, 1978). These complications have proven useful in modelling offspring dispersion and sex-ratio (Frank, 1987; Wild and Taylor, 2004, and references therein). Finally, it can often be advantageous to synchronise timing decisions with that of others. In our particular case, a reproductive would gain little when flying under perfect weather conditions if no-one else joins. The selective advantage of synchronisation would lead towards greater temporal cohesion of the optimum phenotype distribution than predicted on the basis of Eq. (5). We venture to believe that in all these extensions our qualitative conclusions will retain their validity.

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Appendix A. Derivation of general decision rule, Eq. (5)

Let x be the payoff at t_x and $y_1, y_2, \ldots, y_n$ the n possible payoffs at t_y with probability distribution $p(y)$. The geometric mean fitness of a genotype with a split-ratio s, $G(s)$, is

$$G(s) = F_1^{p(y_1)} \times F_2^{p(y_2)} \times \cdots \times F_n^{p(y_n)},$$

where $F_i = sx + (1-s)y_i,\ i = 1, \ldots, n$. Let $H(s) = \ln G(s)$ then

$$H(s)' = \sum_{i=1}^{n} \left(p(y_i) \frac{F_i'}{F_i} \right).$$

Setting $H(s)'$ equal to zero and rearranging one obtains

$$\sum_{i=1}^{n} \left(p(y_i) F_i' \prod_{\substack{j=1 \\ j \neq i}}^{n} F_j \right) = 0. \tag{A.1}$$

For $s = 1$, F_j reduces to x and thus

$$x^n \sum_{i=1}^{n} p(y_i)(x - y_i) = 0.$$

With $\sum_{i=1}^{n} p(y_i) = 1$, this simplifies to

$$x = \sum_{i=1}^{n} p(y_i) y_i,$$

which is the arithmetic mean of the payoffs at t_y.

For $s = 0$, F_i reduces to y_i and thus Eq. (A.1) becomes

$$\sum_{i=1}^{n} \left(p(y_i)(x - y_i) \prod_{\substack{j=1 \\ j \neq i}}^{n} y_j \right) = 0.$$

Dividing both sides by $\prod_{j=1}^{n} y_j$ yields

$$\sum_{i=1}^{n} \left(\frac{p(y_i)(x - y_i)}{y_i} \right) = 0$$

and after some rearrangement

$$x \sum_{i=1}^{n} \frac{p(y_i)}{y_i} = \sum_{i=1}^{n} p(y_i).$$

With $\sum p(y_i) = 1$, this becomes

$$x = \left(\sum_{i=1}^{n} \frac{p(y_i)}{y_i} \right)^{-1},$$

which is the harmonic mean of the payoffs at t_y.

Appendix B. Optimal response under parental control

The frequency of allele A in males and females under queen control in generation n is given by the following recurrence equation:

$$p_{n+1} = \gamma_n (p_n + p_{n-1}), \quad n \geqslant 1$$

with initial conditions $p_0 = p$ and $p_1 = 2\gamma_0 p_0$, and γ_n being identically and independently distributed random variables with distribution

$$\gamma = \begin{cases} \frac{F_1}{2\tilde{F}_1} = \frac{sx+(1-s)y_1}{2(\tilde{s}x+(1-\tilde{s})y_1)} & \text{with probability } r, \\ \frac{F_2}{2\tilde{F}_2} = \frac{sx+(1-s)y_2}{2(\tilde{s}x+(1-\tilde{s})y_2)} & \text{with probability } 1-r. \end{cases}$$

Let $\langle p_n \rangle$ be the expectation of p_n over the distribution of γ. For example, $\langle p_0 \rangle = p_0$ because it is fixed, $\langle p_1 \rangle$ can take two values depending on the value of γ_0. We now define the generating function

$$P(x) = \sum_{n=0}^{\infty} \langle p_n \rangle x^n.$$

Multiplying each side of the recurrence equation by x^n and summing over all $n \geqslant 1$ gives

$$\sum_{n \geqslant 1} p_{n+1} x^n = \sum_{n \geqslant 1} \gamma_n p_n x^n + \sum_{n \geqslant 1} \gamma_n p_{n-1} x^n,$$

which can be rewritten as

$$\begin{aligned} \frac{1}{x} \left[\sum_{n \geqslant 0} p_n x^n - p_1 x - p_0 \right] = & \sum_{n \geqslant 0} \gamma_n p_n x^n - \gamma_0 p_0 \\ & + x \sum_{n \geqslant 0} \gamma_{n+1} p_n x^n. \end{aligned}$$

Now taking expectation on each side leads to

$$\begin{aligned} \frac{1}{x} \sum_{n \geqslant 0} \langle p_n \rangle x^n - \langle p_1 \rangle - \frac{p_0}{x} = & \sum_{n \geqslant 0} \langle \gamma \rangle \langle p_n \rangle x^n - \langle \gamma \rangle p_0 \\ & + x \sum_{n \geqslant 0} \langle \gamma \rangle \langle p_n \rangle x^n. \end{aligned}$$

This can be rewritten in terms of our generating function $P(x)$ as

$$\frac{1}{x} P(x) - \langle p_1 \rangle - \frac{\langle p_0 \rangle}{x} = \langle \gamma \rangle P(x) - \langle \gamma \rangle p_0 + x \langle \gamma \rangle P(x).$$

With $\langle p_1 \rangle = 2\langle \gamma \rangle p_0$ and after rearrangement we get

$$P(x) = \frac{p_0 \langle \gamma \rangle x + p_0}{1 - x^2 \langle \gamma \rangle - x \langle \gamma \rangle} = \frac{p_0}{\langle \gamma \rangle} \left(\frac{\langle \gamma \rangle x + 1}{\frac{1}{\langle \gamma \rangle} - x^2 - x} \right).$$

The values $\langle p_n \rangle$ are the coefficients of the power series expansion of $P(x)$, by the definition. The power series expansion is found by first writing $P(x)$ in terms of partial fractions

$$P(x) = \frac{p_0}{\langle \gamma \rangle} \left(\frac{H_2}{x - b_2} - \frac{H_1}{x - b_1} \right),$$

where

$$H_1 = \frac{1 + \langle \gamma \rangle b_1}{b_1 - b_2}, \quad H_2 = \frac{1 + \langle \gamma \rangle b_2}{b_1 - b_2},$$

$$b_1 = -\frac{1}{2} + \frac{1}{2} \sqrt{1 + \frac{4}{\langle \gamma \rangle}}, \quad b_2 = -\frac{1}{2} - \frac{1}{2} \sqrt{1 + \frac{4}{\langle \gamma \rangle}}.$$

The power series expansion of each partial fraction is a geometric series. In particular, we have

$$\frac{H_1}{x - b_1} = -\left(\sum_{n=0}^{\infty} \frac{H_1}{b_1^{n+1}} x^n \right)$$

and

$$\frac{H_2}{x - b_2} = -\left(\sum_{n=0}^{\infty} \frac{H_2}{b_2^{n+1}} x^n \right).$$

Putting everything together, we find the coefficients of the power series $P(x) = \sum_{n=0}^{\infty} \langle p_n \rangle x^n$ as

$$\langle p_n \rangle = \frac{p_0}{\langle \gamma \rangle} \left(\frac{H_1}{b_1^{n+1}} - \frac{H_2}{b_2^{n+1}} \right).$$

We are interested in the expected rate of increase per generation. This can be found as

$$R = \lim_{n \to \infty} \frac{\langle p_{n+1} \rangle}{\langle p_n \rangle}.$$

Substituting our expressions for H_1 and H_2, we find

$$\begin{aligned} R &= \lim_{n \to \infty} \frac{\langle p_{n+1} \rangle}{\langle p_n \rangle} \\ &= \lim_{n \to \infty} \frac{(1 + \langle \gamma \rangle b_1) b_2^{n+2} - (1 + \langle \gamma \rangle b_2) b_1^{n+2}}{(1 + \langle \gamma \rangle b_1) b_2^{n+2} b_1 - (1 + \langle \gamma \rangle b_2) b_1^{n+2} b_2} \\ &= \frac{1}{b_1} = \frac{2}{\sqrt{1 + \frac{4}{\langle \gamma \rangle}} - 1}. \end{aligned}$$

Finally, we need to find the strategy s that maximises R given some population strategy $\tilde{s}$. Since $\langle \gamma \rangle$ is a function of s, then by the chain rule,

$$\frac{\partial R}{\partial s} = \frac{\partial R}{\partial \langle \gamma \rangle} \frac{d \langle \gamma \rangle}{ds} = 0$$

and therefore we require

$$\frac{d \langle \gamma \rangle}{ds} = 0.$$

Recall that $\langle \gamma \rangle = r F_1 / \tilde{F}_1 + (1 - r) F_2 / \tilde{F}_2$ and that only F_1 and F_2 depend on s. Writing F_1' and F_2' for the derivatives with respect to s this is

$$\frac{\partial \langle \gamma \rangle}{\partial s} = r \frac{F_1'}{\tilde{F}_1} + (1 - r) \frac{F_2'}{\tilde{F}_2} = 0,$$

Table 2
Mating combinatorics under diploidy

	aa	Aa	split-ratio (parental control)
$aa \times aa$ (1)	1	0	$\tilde{s}$
$Aa \times aa$ ($4p$)	1/2	1/2	s
split-ratio (offspring control)	$\tilde{s}$	s	

whence we derive the same condition as for the case of offspring control

$$rF_1'\tilde{F}_2 = (1-r)F_2'\tilde{F}_1.$$

and the maximum rate of spread is found either at $s = 0$ or 1 with the ESS, s^*, given by solving the last equation for $\tilde{s}(= s^*)$

$$s^* = \frac{rxy_1 - rxy_2 - xy_1 + y_1y_2}{x^2 - xy_1 - xy_2 + y_1y_2}.$$

Appendix C. The case of diploid inheritance

For parental control we assume that the offspring exhibit the dominant phenotype if at least one of the parents carries the deviant allele A. Unlike in the genetically asymmetric case of haplodiploidy, we do not need to distinguish between the frequencies of A in males and females. The mating combinatorics for the diploid case are those in Table 2.

From the table we see that the control scenarios are indistinguishable. In both cases a heterozygous offspring will adopt a split-ratio of s because one of its parents will have to carry the A allele. The frequency of p in generation $(n+1)$ is just

$$p_{n+1} = \frac{1}{2} \times 4p \times \frac{1}{2} \times \frac{F_n}{\tilde{F}_n} = p_n \frac{F_n}{\tilde{F}_n},$$

which is the same as in the haplodiploid case.

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