

Finding the one: optimal choosiness under sequential mate choice

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Abstract

When mates are encountered sequentially, each encounter involves a decision whether to reject the current suitor and risk not finding a better mate, or to accept them despite their flaws. I provide a flexible framework for modelling optimal choosiness when mate encounters occur unpredictably in time. The model allows for temporal variation in the fitness benefits of mating, including seasonal breeding conditions, accrual of mate search costs, survival of the choosing individual or senescence of gametes. The basic optimality framework can be applied iteratively to obtain mate choice equilibria in dynamically evolving populations. My model predicts that individuals should be choosier when the average rate of mate encounters is high, but that choosiness should decline over time as the likelihood of future mate encounters decreases. When mate encounters are uncertain, there is a trade-off between reproductive timing and mate choice (the ‘when’ and the ‘who’). Mate choice may be selected against when reproductive timing is highly important (e.g. when breeding conditions show a narrow peak in time). This can even lead to step-shaped mate choice functions, where individuals abruptly switch from rejecting to accepting all suitors as peak breeding conditions approach. The model contributes to our understanding of why individuals may not express mate preferences, even when there is substantial variation in mate quality.

For animals living in sparse populations, potential mates are most often encountered sequentially. Each such encounter comes with a dilemma: either accept the current suitor despite their imperfections, or reject them and risk not finding a better option, or indeed any option, before it's too late (Kokko & Mappes, 2005). This choice is particularly stark in species that mate only once, because a bad choice cannot be recovered from by ‘trading up’ later on (Jennions & Petrie, 2000; Bleu *et al.*, 2012).

Sequential mate choice is commonly characterized by two conditions. First, the timing of mate encounters is uncertain: after rejecting a potential mate, the chooser does not know when, or if, it will find another (de Jong & Sabelis, 1991; Kokko & Mappes, 2005). Second,

the fitness benefits of mating are time-dependent, due to the seasonality of reproductive conditions or mate availability, accrual of mate search costs, or senescence of the choosing individual or its gametes (Tinghitella *et al.*, 2013; Prasad *et al.*, 2015; Dechaume-Moncharmont *et al.*, 2016; Pérez *et al.*, 2016).

Previous mate choice theory generally neglects one or both of these conditions. Some models assume that the number of mate encounters is predictable or under the full control of the choosing individual. For instance, the chooser may encounter a fixed number of mates (Janetos, 1980; Janetos & Cole, 1981; Dombrovsky & Perrin, 1994; Mazalov *et al.*, 1996) or pay fixed costs to sample each additional mate (Parker, 1983; Real, 1990, 1991). Other models allow for uncertainty in mate encounters, but assume that so long as the chooser remains alive, the timing of reproduction does not affect fitness pay-offs (e.g. Kokko & Mappes, 2005, 2013; Courtiol *et al.*, 2016, who assume constant mortality over an infinite time horizon).

I provide a flexible framework for modelling sequential mate choice that allows for uncertainty in the

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number and timing of mate encounters, as well as temporal variation in the fitness benefits of mating. I present both a simple analytic model based on optimal control theory (Lenhart & Workman, 2007; Liberzon, 2012), and a more general approach based on dynamic programming (Houston *et al.*, 1988; Mangel & Clark, 1988; Kokko, 2007). The basic models derive the optimal behaviour of an individual assuming that the behaviour of all other individuals is fixed (i.e. they are optimality models). However, I show how equilibrium strategies in a dynamically evolving population can be estimated by iterative application of the optimality models (Johnstone, 1997). The most restrictive assumption of my models is that the choosing individual mates only once (see Discussion). I illustrate the dynamic programming framework with two simulated examples.

Analytic model

My models apply to mate choice by either sex, but for simplicity I present them from the perspective of a choosing female (for discussion of mate choice by both sexes, see Finding equilibria by iterating an optimality model). I assume the female must choose exactly one mate within a fixed window of time, or else go without mating. The time window might represent a breeding season, or the maximum period of viability of her eggs. Once she accepts a mate, she cannot change her choice, and rejected mates cannot be revisited later on. I assume that the female knows in advance the distribution of male quality that she is likely to encounter (cf. Mazalov *et al.*, 1996, where this assumption is relaxed).

Proportion of acceptable mates: a female's mate choice strategy

The female ranks potential mates based on the expected fitness gained by mating with them. She only accepts a male if his fitness value exceeds a certain threshold, where the threshold may vary with time. I express her mate choice strategy as a function $p(t)$, representing the proportion of acceptable mates at any time t . For example, if $p(t) = 0.25$, then a male encountered at time t would be accepted if his estimated fitness value is in the top quarter of all potentially encountered males at that time. Note that smaller values of $p(t)$ correspond to greater choosiness. For the analytic model, I assume (i) that males are encountered at a fixed rate λ , (ii) that the distribution of male quality is constant over time, and (iii) that the fitness benefits of mating do not depend on timing. I show how to relax these assumptions using a dynamic programming framework below.

Expected fitness gain from accepting a mate

Let $Q(r)$ be the mean fitness gained from mating with a male who is ranked on the r th quantile of all males.

Any imprecision in the assessment of mate quality (e.g. due to perceptual limitations, poor signal or background noise) will weaken the relationship between r and $Q(r)$ (Fisher *et al.*, 2006; Phelps *et al.*, 2006; Akre & Johnsen, 2016; Owen *et al.*, 2017). I assume, however, that higher ranked males always provide higher fitness gains on average (i.e. females do not make systematic errors in assessing mate quality). This means that $Q(r)$ is a nondecreasing function of the quality rank r . For mathematical tractability, I also assume that Q is continuously differentiable.

If a female accepts only the upper proportion $p(t)$ of males at time t , then the expected fitness value $v(p(t))$ of accepting a male at this time point is just the average of $Q(r)$ over the interval $[1 - p(t), 1]$:

$$v(p(t)) = \frac{1}{p(t)} \int_{1-p(t)}^1 Q(r) dr \quad (1)$$

Note that a higher proportion of acceptable mates $p(t)$ corresponds to a lower expected fitness gain $v(p(t))$ from mating. The expected fitness gain when mating at random is $\mu = v(1)$.

Overall fitness

Let $[t_0, t_f]$ be the time window to choose a mate (hereafter the 'mating window') and let T be a random variable representing the time at which the female accepts a mate, if she ever does. Acceptable mates are encountered at an instantaneous rate of $\lambda p(t)$, which varies with time t . The total rate of such encounters over the interval $[t_0, t]$ is given by $\int_{t_0}^t \lambda p(\tau) d\tau$. The probability $\mathbb{P}(T > t)$ that no acceptable mate is encountered is this interval is then $\exp(-\int_{t_0}^t \lambda p(\tau) d\tau)$. Hence, the cumulative distribution function of T is:

$$F_T(t) = \mathbb{P}(T \leq t) = 1 - \exp\left(-\int_{t_0}^t \lambda p(\tau) d\tau\right) \quad (2)$$

The probability density function of T is then:

$$f_T(t) = \frac{d}{dt} F_T(t) = \lambda p(t) \exp\left(-\int_{t_0}^t \lambda p(\tau) d\tau\right) \quad (3)$$

The female's expected rate of fitness gain at time t is simply the probability density $f_T(t)$ of mating at that time multiplied by the expected fitness value $v(p(t))$ of such matings. Her total expected fitness over the interval $[t_0, t_f]$ is thus:

$$w = \int_{t_0}^{t_f} f_T(t) v(p(t)) dt \quad (4)$$

Optimal proportion of acceptable mates at any time

I now outline the derivation of the optimal choosiness function $p^*(t)$ (full details in Appendix). Suppose a female encounters a mate of quality r at time t' . She

should mate with him if the expected fitness gain $Q(r)$ exceeds her ‘remaining reproductive value’ for the current mating window (i.e. her expected fitness gain if she rejects him and then behaves optimally for the rest of the mating window). Her remaining reproductive value is given by (cf. eqn 4):

$$w_{T>t'}^* = \int_{t'}^{t_f} f_{T>t'}(t)v(p^*(t))dt \quad (5)$$

Here $f_{T>t'}(t)$ is the probability density function for the time she accepts a mate, given that she has not accepted one by time t' (cf. eqn 3):

$$f_{T>t'}(t) = \lambda p^*(t) \exp\left(-\int_{t'}^t \lambda p^*(\tau)d\tau\right) \quad (6)$$

No matter how male quality is distributed, the female’s remaining reproductive value $w_{T>t'}^*$ decreases steadily towards zero as she nears the end of the mating window (i.e. $w_{T>t'}^* \rightarrow 0$ as $t' \rightarrow t_f$). Suppose that all matings provide a positive expected fitness benefit, regardless of male quality (i.e. the minimum fitness benefit $Q(0) > 0$). Then there exists a minimum time point $t^* < t_f$ after which females should accept any encountered male (i.e. $p^*(t) = 1$ for all $t \geq t^*$). This time point is given explicitly by (proof in Appendix):

$$t^* = t_f - \frac{1}{\lambda} \log\left(\frac{\mu}{\mu - Q(0)}\right) \quad (7)$$

If there is little difference between the lowest-ranked and average males (i.e. $Q(0)$ is close to μ), then t^* is small, meaning that females should cease to be choosy long before the end of the mating window. In contrast, if average males are far superior to the lowest-ranked males (i.e. $\mu \gg Q(0)$), then females should remain picky until near the end of the mating window. Females should also remain choosy for longer when the rate of mate encounters λ is high (Fig. 1; see examples below).

For time points earlier than t^* , the optimal proportion of acceptable mates $p^*(t)$ is given by the solution to a second-order differential equation (proof in Appendix):

$$\lambda p^2 v'(p) - 2p'v'(p) - pp'v''(p) = 0 \quad (8)$$

with boundary condition $p(t^*) = 1$. This equation can be solved using numerical methods, although analytic solutions also exist for particular cases (see examples below).

On the other hand, suppose that some males are never worth mating with because they provide a negative expected fitness benefit (i.e. $Q(0) \leq 0$). This could occur e.g. if injuries or sexually transmitted infections acquired during mating greatly reduce future fitness. (Note that although I assume that the female only mates once in the current reproductive bout, she may still reproduce again in the future.) Females should

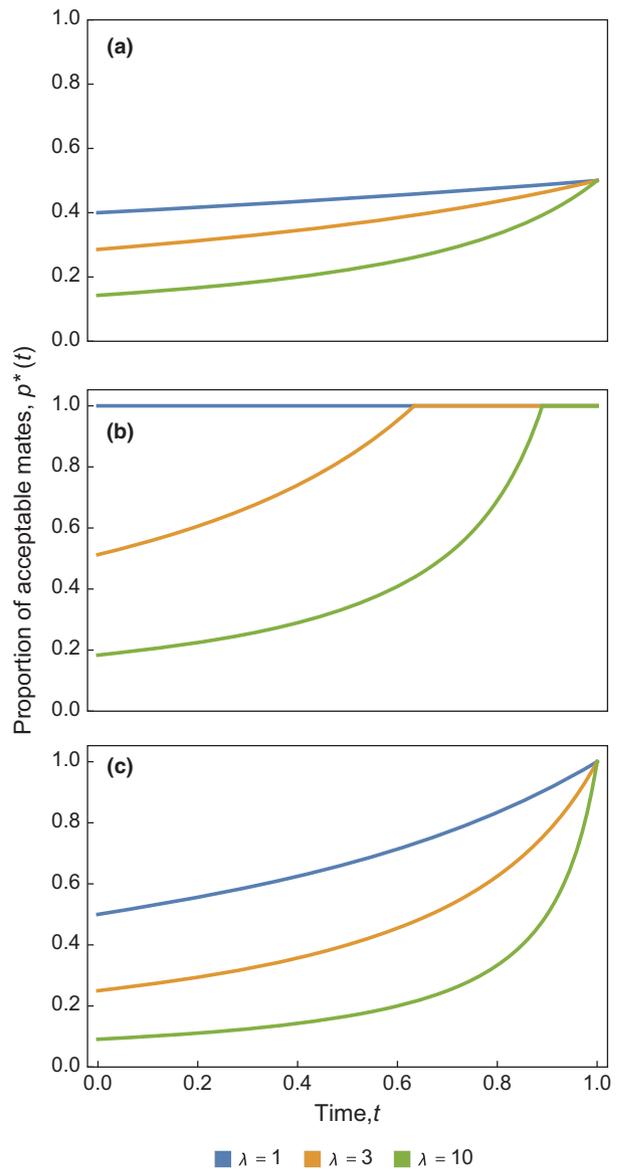


Fig. 1 Results for the analytic model, which assumes that the distribution of mate quality and the fitness benefits of mating are constant throughout the mating window. The optimal proportion of acceptable mates $p^*(t)$ increases over time t as the likelihood of future mate encounters declines. Higher average rates of mate encounters λ correspond to greater choosiness, as shown here with $\lambda = 1$ (blue); $\lambda = 2$ (orange); and $\lambda = 10$ (green). Mate quality is assumed to follow: (a) a uniform distribution on $[-1,1]$; (b) a uniform distribution on $[1,2]$; and (c) an exponential distribution.

always be somewhat choosy in this case. At the end of the mating window, an unmated female should accept any male whom she expects to provide a positive fitness benefit. The proportion p_{\max}^* of such males is given by the smallest p such that $Q(1-p) = 0$. The optimal proportion of acceptable mates is then given by the

solution to eqn 8 with the boundary condition $p(t_f) = p_{\max}^*$ (proof in Appendix).

Explicit solutions when mate quality follows a uniform or exponential distribution

In some cases, the optimal proportion of acceptable mates $p^*(t)$ can be solved for explicitly. Here are two examples:

Uniform distribution

First suppose that male quality $Q(r)$ (i.e. the expected fitness gain from mating with a male ranked on the r th quantile) is distributed uniformly on the interval $[a, b]$. The r th quantile of this distribution is $Q(r) = a(1-r) + br$. The expected fitness gain from mating with a male in the top p of the quality distribution is $v(p) = b - \frac{1}{2}(b-a)p$.

If $a \leq 0$ then there are some males a female should never mate with. The maximum value of p for an optimal strategy is then $p_{\max}^* = \frac{b}{b-a}$. This is simply the proportion of males that provide a positive expected fitness gain. Solving eqn 8 with the boundary condition $p(t_f) = p_{\max}^*$ then yields (Fig. 1a):

$$p^*(t) = \frac{2}{\lambda(t_f - t) + 2/p_{\max}^*} \tag{9}$$

On the other hand, if $a > 0$, then any mate is better than none, and so there exists a time point $t^* < t_f$ where females will begin to accept any mate. From eqn 7 this time point is given by:

$$t^* = t_f - \frac{1}{\lambda} \log\left(\frac{b+a}{b-a}\right) \tag{10}$$

Solving eqn 8 with the boundary condition $p(t^*) = 1$ then yields (Fig. 1b):

$$p^*(t) = \begin{cases} \frac{2}{\lambda(t^* - t) + 2}, & \text{for } t < t^* \\ 1, & \text{for } t \geq t^* \end{cases} \tag{11}$$

Exponential distribution

Now suppose that male quality follows an exponential distribution with parameter k . The r th quantile of this distribution is $Q(r) = -\frac{1}{k} \log(1-r)$. The expected fitness gain from mating with a male in the top p of the quality distribution is $v(p) = \frac{1}{k}(1 - \log p)$. Solving eqn 8 with the boundary condition $p(t_f) = 1$ then yields (Fig. 1c):

$$p^*(t) = \frac{1}{\lambda(t_f - t) + 1} \tag{12}$$

Note that this example is on the boundary of the two cases described above (i.e. all males provide a positive fitness benefit, but for the lowest quality males this benefit can be arbitrarily small).

Dynamic programming

A more flexible approach is to approximate the optimal mate choice function $p^*(t)$ using dynamic programming. Here, unlike in the previous section, I allow the fitness gained from mating $v(p(t), t)$ to depend explicitly on time, as well as the individual's mate choice function. The total rate of mate encounters $\lambda(t)$ may also vary over time. The model can then accommodate temporal variation of many kinds, including in (i) the availability and quality of mates; (ii) the fitness benefits of reproduction, for example under seasonal breeding conditions; (iii) the survival probability of the choosing individual or its gametes; and (iv) the costs of mate search.

Under these broader assumptions, the time T at which the female accepts a mate has probability density function (cf. eqn 3):

$$f_T(t) = \lambda(t)p(t) \exp\left(-\int_{t_0}^t \lambda(\tau)p(\tau)d\tau\right) \tag{13}$$

The expected fitness of an individual with mate choice function $p(t)$ is then (cf. eqn 4):

$$w = \int_{t_0}^{t_f} f_T(t)v(p(t), t)dt \tag{14}$$

Let us divide the mating window into n equal subintervals with endpoints given by $t_i = t_0 + \frac{i}{n}(t_f - t_0)$ for $i = 0, 1, \dots, n$. The length of these subintervals is $\ell = \frac{t_f - t_0}{n}$. I will approximate the optimal mate choice function by a constant over each subinterval (i.e. $p^*(t) = p_i$ for all $t \in [t_{i-1}, t_i]$).

Consider a female who is still unmated at time t_{i-1} . In the subinterval $[t_{i-1}, t_i]$, she will encounter $A_i = \int_{t_{i-1}}^{t_i} \lambda(t)dt$ potential mates on average, and she accepts each mate with probability p_i . If the subintervals are short enough relative to the rate of mate encounters, then the probability that she accepts a mate in this subinterval is approximately $p_i A_i$. Further, the time of mate acceptance is approximately uniformly distributed over the subinterval, so we can approximate the expected fitness benefit of mating by its local average:

$$v_i(p_i) = \frac{1}{\ell} \int_{t_{i-1}}^{t_i} v(p_i, t)dt, \text{ on } [t_{i-1}, t_i] \tag{15}$$

Alternatively, if the integrals for A_i and $v_i(p_i)$ are expensive to compute, they can be approximated by the value of the integrand at the midpoint of the subinterval (i.e. $A_i \approx \lambda(t_{i-1/2})$ and $v_i(p_i) \approx v(p(t_{i-1/2}), t_{i-1/2})$).

The optimal proportion of acceptable mates over the whole mating window can now be approximated by starting with the final subinterval and working backwards. In the final subinterval $[t_{n-1}, t_n]$, an unmated female accepts a mate with probability $p_n A_n$.

The expected fitness value of these matings $v_n(p_n)$. If she doesn't mate, which occurs with probability $1 - p_n A_n$, then her reproductive value at the end of the interval is $w_n^* = 0$. Consequently, her reproductive value at time t_{n-1} , assuming she behaves optimally thereafter, is approximately:

$$\begin{aligned} w_{n-1}^* &= \max_{p_n} \{p_n A_n v_n(p_n) + (1 - p_n A_n) w_n^*\} \\ &= \max_{p_n} \{p_n A_n v_n(p_n)\} \end{aligned} \quad (16)$$

The optimal acceptable proportion of mates p_n^* in the final subinterval is the argument that maximises this expression. Both w_{n-1}^* and p_n^* can be found numerically.

The same logic applies for all previous subintervals. I write w_i^* for the reproductive value of an unmated female at time t_i (i.e. her expected fitness gain over the remainder of the mating window $[t_i, t_f]$, assuming she behaves optimally). Her reproductive value at time t_{i-1} is approximately:

$$w_{i-1}^* = \max_{p_i} \{p_i A_i v_i(p_i) + (1 - p_i A_i) w_i^*\} \quad (17)$$

The optimal proportion of acceptable mates p_i^* on $[t_{i-1}, t_i]$ is the argument that maximizes this expression. Both p_i^* and w_{i-1}^* can be obtained numerically if the value of w_i^* is known. Starting with the final value $w_n^* = 0$, we can then work backwards, calculating the approximate reproductive value and optimal acceptance rate from the final subinterval to the first (Houston *et al.*, 1988; Mangel & Clark, 1988; Kokko, 2007).

Example: Temporal variation in offspring survival

In the analytic model, I assumed that matings achieved at any time in the mating window are equally valuable in fitness terms. However, the fitness benefits of mating are often sensitive to e.g. temporal variation in climate or resource availability (Pérez *et al.*, 2016), the accrual of mate search costs, or the senescence of the individual or its gametes (Prasad *et al.*, 2015). We can accommodate such factors by defining $v(p(t), t)$ to include a term $s(t)$ that depends explicitly on the time of mating (cf. eqn 1):

$$v(p(t), t) = \frac{s(t)}{p(t)} \int_{1-p(t)}^1 Q(r) dr \quad (18)$$

For particular choices of $s(t)$, the optimal mate choice function $p(t)$ can then be approximated using dynamic programming as above.

For instance, suppose that $s(t)$ represents the survival probability of offspring produced by a mating at time t . I assume that survival is highest in the middle of the breeding season, with both early and late breeders suffering low offspring survival (Fig. 2a). The rate of mate encounters $\lambda(t)$ is assumed constant, as in the analytic

model. At the beginning of the season, females should reject all suitors due to the poor breeding conditions and the likelihood of better conditions to come. As the season progresses, future conditions are increasingly unlikely to beat the current ones, and so females should accept a steadily wider range of mates (Fig. 2b–d).

When the offspring survival curve $s(t)$ has a broad peak, selection favours a gradual increase in the proportion of acceptable mates $p^*(t)$ over time (e.g. the green lines in Fig. 2). In contrast, for tightly peaked survival curves, $p^*(t)$ resembles a step function, with an abrupt shift from rejecting all mates (i.e. $p^*(t) = 0$) to accepting all profitable mates (i.e. $p^*(t) = p_{\max}^*$) just prior to peak offspring survival (e.g. the blue lines in Fig. 2). Temporal variation in reproductive conditions can thus select against mate choice, even when mates differ markedly in quality. For instance, if male quality is distributed according to a uniform distribution on $[1, 2]$, then the highest quality males provide twice the fitness benefit of the lowest quality males. Nonetheless, if offspring survival is tightly peaked, then females barely discriminate among individual males, rather rejecting all males early in the season and accepting all males later on (see blue line in Fig. 2c). The importance of mating at a favourable time overrides the benefits of mate choice.

Finding equilibria by iterating an optimality model

Both the analytic and the dynamic programming methods above are types of optimality model, where the mate choice strategy with the highest fitness payoff is calculated by treating the behaviour of all other individuals as fixed. In biological applications, the optimal mate choice strategy is often sensitive to the behaviour of potential mates or competitors, which may also be evolving. I mention two examples. First, when recently mated individuals are unreceptive to potential suitors (e.g. because they are engaged in parental care), mate availability depends on the choosiness of both same- and opposite-sex individuals (Johnstone, 1997; Courtiol *et al.*, 2016; Dechaume-Moncharmont *et al.*, 2016). Second, the expected fitness value of mating with a particular female may depend on how often she is chosen by other males, and hence on the level of sperm competition for her eggs (McDonald & Pizzari, 2018).

In such cases, evolutionarily stable strategies (ESS) can be found by iterated use of an optimality model (Johnstone, 1997). One first chooses arbitrary starting strategies for males and females in a population. Given this background mating behaviour, one can then calculate the optimal mate choice strategies for mutants of each sex (i.e. their 'best response' to the population strategies). These are then taken as the new population strategies. Repeating this procedure will approximate

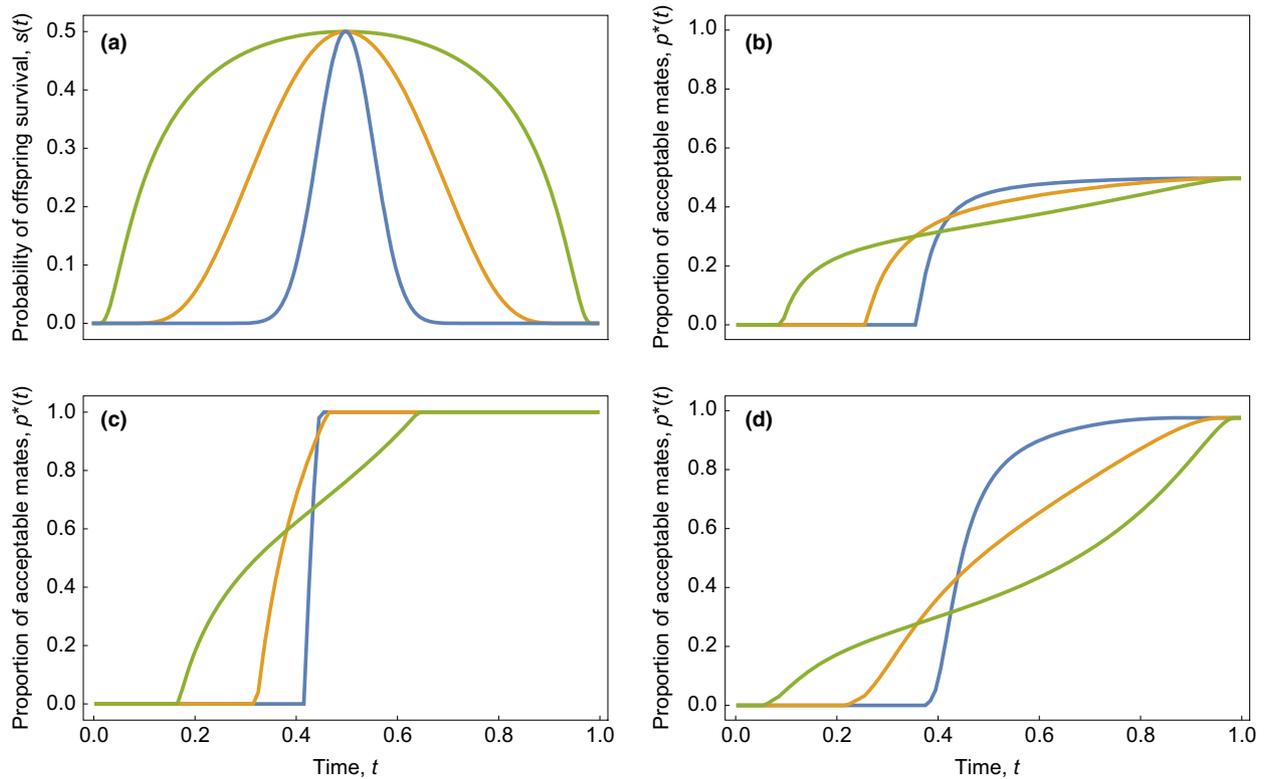


Fig. 2 Results for the example ‘Temporal variation in offspring survival’, where offspring survival is assumed highest for matings near the middle of the mating window. (a) The assumed probability of offspring survival $s(t)$ after mating at time t . (b–d) The optimal proportion of acceptable mates $p^*(t)$ over time t when mate quality is assumed to follow: (b) a uniform distribution on $[-1, 1]$; (c) a uniform distribution on $[1, 2]$; and (d) an exponential distribution. All panels are shown with survival curves $s(t) = \frac{1}{2} \exp\left[\frac{(1-2t)^2}{at(t-1)}\right]$, where $a = 0.1$ (blue); $a = 1$ (orange); and $a = 10$ (green). Mates are encountered at an average rate of $\lambda = 5$ per unit time. The functions $p^*(t)$ were approximated by piecewise constant functions over $n = 100$ equal subintervals using dynamic programming. For ease of viewing, the piecewise constant functions were then transformed into continuous functions by linear interpolation of their values at the midpoints of each subinterval.

evolutionarily stable strategies in well-behaved cases (Hofbauer, 2000).

Example: Sexually cannibalistic spiders

I illustrate the ‘best response’ approach to calculating ESS mate choice strategies with an example of male mate choice, inspired by sexually cannibalistic spiders (Schwartz *et al.*, 2013). I assume here that female behaviour is fixed, although the best response approach can also be used when behaviour varies in both sexes. When a male approaches a potential mate, she either mates with him and then eats him (if she is receptive) or just eats him without mating (if she is not receptive). Successful males damage the female’s reproductive organs during mating, so that females can mate only once during the mating window (Uhl *et al.*, 2010; Mouginot *et al.*, 2015; Nakata, 2016). The number of available individuals of both sexes consequently declines as the mating window progresses. Males can distinguish mated from unmated females, and only approach

the latter. However, males cannot tell whether an unmated female is receptive without approaching her.

I assume that the probability of female receptivity follows a curve $a(t)$ over the mating window and is independent of both male and female quality. I write β for the ratio of males to females at the beginning of the mating window. The sex ratio becomes progressively more female-biased over time due to nonreceptive females eating their male suitors. Males encounter potential mates at a rate of $\lambda(t) = \lambda_0 \pi_f(t)$, where $\pi_f(t)$ is the proportion of females remaining unmated at time t , and λ_0 is the rate of mate encounters at the beginning of the mating window.

Rather than consider the *proportion* of acceptable females $p(t)$ at each time point, it is mathematically more convenient to consider the *threshold* female quality $b(t)$ that is acceptable to a male. I define $b(t)$ relative to the distribution of female quality at the beginning of the mating window: a female encountered at time t is accepted if her quality exceeds the quantile $1 - b(t)$ of the initial quality distribution.

For any population strategy $b(t)$, a mutant's best response $\text{br}(b(t))$ can be approximated analogously to the previous section (details in Appendix). One can then choose a strategy intermediate between $b(t)$ and $\text{br}(b(t))$ by taking a constant $\delta \in (0, 1)$ and setting:

$$b'(t) = (1 - \delta)b(t) + \delta\text{br}(b(t)) \quad (19)$$

The strategy $b'(t)$ is then taken as the new population strategy. An ESS $b^*(t)$ can be approximated by repeating this procedure until $b(t)$ and $\text{br}(b(t))$ are sufficiently close (Johnstone, 1997). For Fig. 3, I used $\delta = \frac{1}{2}$ and iterated eqn 19 until $b(t)$ and $\text{br}(b(t))$ differed by no more than 10^{-4} for any t .

For any ESS threshold strategy $b^*(t)$, the ESS proportion of acceptable mates is given simply by:

$$p^*(t) = \frac{\int_{1-b^*(t)}^1 \pi_f^*(r, t) dr}{\pi_f^*(t)} \quad (20)$$

Here $\pi_f^*(r, t)$ is the proportion of females of quality rank r that remain unmated at time t and $\pi_f^*(t)$ is the overall proportion of unmated females remaining at time t , assuming that all males play the ESS strategy $b^*(t)$.

Like in the previous examples, both the mate acceptance threshold $b^*(t)$ and the proportion of acceptable mates $p^*(t)$ are predicted to increase steadily over time (Fig. 3a,b). When the initial sex ratio is male-biased, the number of unmated females diminishes rapidly as the mating window progresses (Fig. 3c). This reduces the reproductive value of unmated males, and consequently males accept a higher proportion of females when the sex ratio is male-biased (Fig. 3a,b). The average fitness payoff $v(b^*(t))$ when a male approaches a female is mainly determined by the probability of female receptivity, which is assumed to peak at the midpoint of the mating window (Fig. 3f). However, fitness payoffs peak earlier than female receptivity, both because males are choosier early in the mating window and because high-quality females mate and leave the mating pool faster than low-quality females.

The rate at which males approach females is determined by the product of female availability and male choosiness, which leads to interesting dynamics. For all sex ratios, males are initially very choosy, due to low female receptivity and the likelihood of better opportunities to come (Fig. 3d). Approach rates are consequently low at the beginning of the breeding season. If the sex ratio is even or male-biased, approach rates then increase to a peak, after which a shortage of unmated females forces approach rates down again (Fig. 3d, green and orange lines). If the sex ratio is female-biased at the beginning of the mating window, the shortage of females never occurs, and so approach rates continue to increase right up until the end of the mating window (Fig. 3d, blue line).

Discussion

I have provided a flexible framework for modelling the evolution of sequential mate choice. The most restrictive assumption of my models is that the choosing individual mates only once. The models are consequently applicable to those rare species that are genetically monogamous (Griffith *et al.*, 2002; Coleman & Jones, 2011; Schaedelin *et al.*, 2015), as well as to the choice of social partner under social monogamy (Reichard, 2003; Lukas & Clutton-Brock, 2013). It can also be applied to strict polyandry or polygyny viewed from the perspective of the singly mating sex. For instance, males of many barnacles (Chan & Høeg, 2015; Lin *et al.*, 2015) and anglerfish (Pietsch, 2009) attach themselves permanently to their mates, and obligate sexual cannibalism occurs in some spiders (Schwartz *et al.*, 2013). Males of these species consequently have only one shot to get it right. Similarly, females of many eusocial hymenopterans mate monandrously (Strassmann, 2001; Shilpa *et al.*, 2012), and some female springtails take up a single deposited spermatophore to fertilize their eggs (Zizzari *et al.*, 2009).

Even when there is multiple mating, the choice of the first mate can be of decisive importance, and here the model is also informative. One example is first-male sperm precedence, in which the first-mated male is disproportionately likely to fertilise a female's eggs (Simmons, 2014). This can result from the mechanism of female sperm usage (Jones *et al.*, 2002) or from male adaptations like mating plugs or damage to female reproductive anatomy (Uhl *et al.*, 2010; Mouginit *et al.*, 2015; Dougherty *et al.*, 2016; Nakata, 2016). Sufficiently strong first-male sperm precedence can even lead to genetic monandry (Pardo *et al.*, 2016).

Previous theory has predicted that in an idealised world with high mate availability, females should be highly selective about whom they mate with, but that they should settle for less if there is a risk of remaining mateless (the 'wallflower effect': de Jong & Sabelis, 1991; Kokko & Mappes, 2005; Dechaume-Moncharmont *et al.*, 2016). My model confirms this effect in two ways. First, females are predicted to be less choosy when the average rate of mate encounters is low (e.g. due to low population density or mobility). Second, choosiness is predicted to decline over the breeding season as the likelihood of future mate encounters declines (Figs 1 and 2). Consistent with these predictions, Breedveld & Fitze (2015) found that female common lizards (*Zootoca vivipara*) were less choosy after being artificially separated from males for a long period, which they perhaps interpret as a cue of mate scarcity. Passos *et al.* (2014) found that female killifish (*Austrolebias reicherti*) preferred larger males early in the reproductive season, but became unselective towards the end of the season.

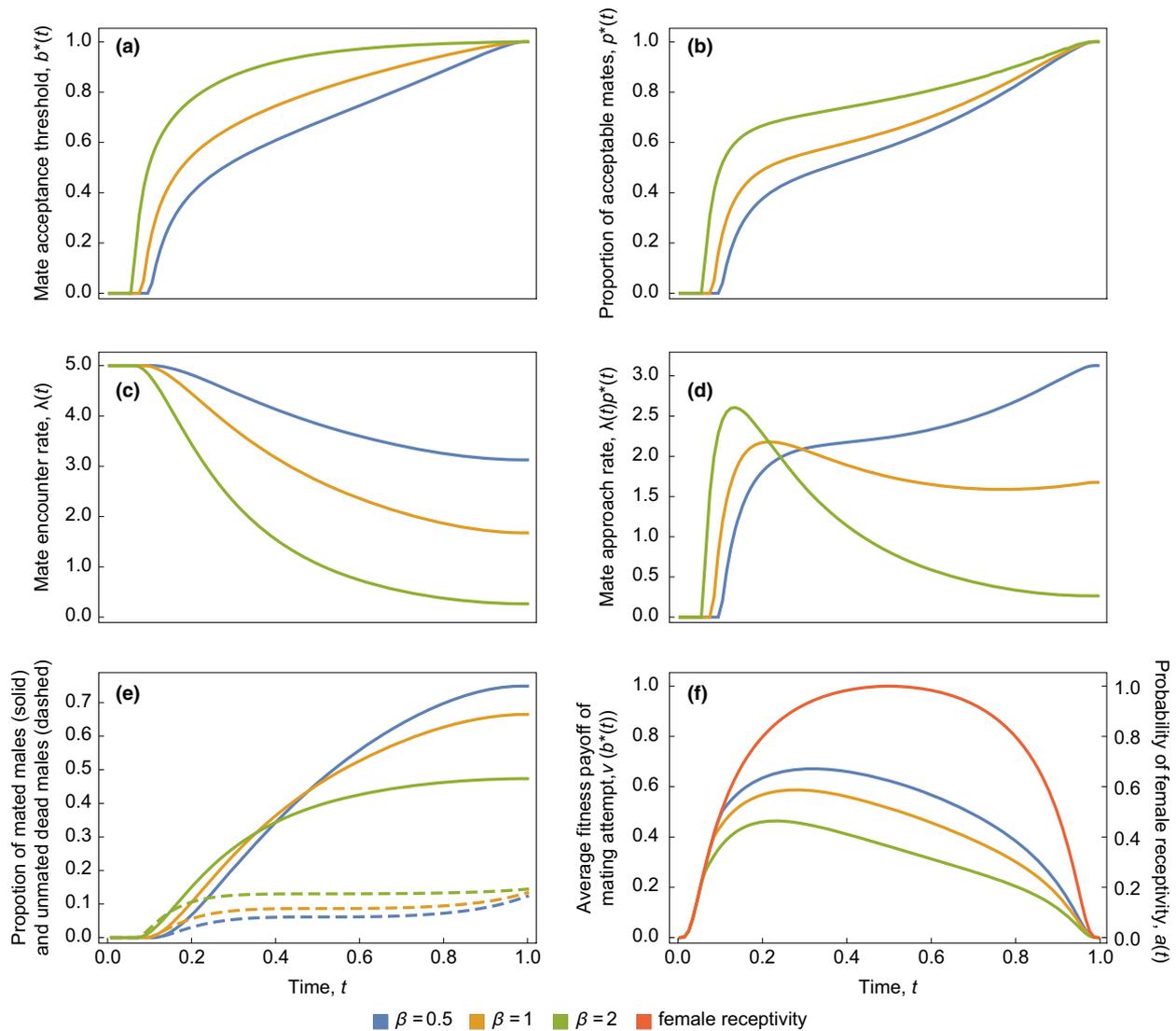


Fig. 3 ESS strategies and population states for the example ‘Sexually cannibalistic spiders’ as functions of time t : (a) Threshold of female quality above which males will approach her, $b^*(t)$; (b) Proportion of unmated females that are acceptable to males (i.e. that exceed the quality threshold), $p^*(t)$; (c) Instantaneous rate at which a male encounters unmated females, $\lambda(t)$; (d) Instantaneous rate at which a male approaches females, $\lambda(t)p^*(t)$; (e) Cumulative proportion of males that have mated successfully (solid lines) or that unwittingly approached an unreceptive female and were consumed (dashed lines); (f) Average fitness payoff of approaching a female, $v(b^*(t))$ (shown in blue, orange, green: see below) and the probability of female receptivity, $a(t) = \exp\left(\frac{(1-2t)^2}{10t(1-t)}\right)$ (red). All panels are shown with initial ratio of males to females $\beta = 0.5$ (blue); $\beta = 1$ (orange); $\beta = 2$ (green). At the beginning of the mating window, female quality is assumed to follow a uniform distribution on $[0,1]$ and mates are encountered at an initial rate of $\lambda_0 = 5$ per unit time. All functions were approximated by piecewise constant functions over $n = 100$ equal subintervals using dynamic programming. For ease of viewing, the piecewise constant functions were then transformed into continuous functions by linear interpolation of their values at the midpoints of each subinterval.

A second ecological effect on mate choice has received less attention: the importance of reproductive timing. Many species face seasonal change in climate, food or the availability of nesting or oviposition sites (Williams *et al.*, 2014; Visser *et al.*, 2015; Pérez *et al.*, 2016). At an individual level, the developmental schedule of eggs may also shape the optimal timing of mating (Henshaw *et al.*, 2014; Prasad *et al.*, 2015). In

some taxa, mate choice and reproduction can be partially decoupled in time, for instance by storing sperm until it is needed or by prolonging association with a chosen mate prior to reproduction (Birkhead, 1993; Pfeiffer & Mayer, 2013). Many species lack such mechanisms, however, and must consequently align their mating and reproductive schedules (Breedveld & Fitz, 2015).

When mate encounters are uncertain, there is a trade-off between reproductive timing and mate choice (the ‘when’ and the ‘who’). Narrow temporal peaks in the fitness benefits of mating may consequently select against mate choice, even when mates differ markedly in quality. This can even lead to step-shaped mate choice functions, where individuals switch abruptly from rejecting to accepting all comers in a short space of time (Fig. 2). This phenomenon may be self-limiting if species with narrow breeding windows evolve to breed with higher synchronicity or in tighter aggregations, leading to higher rates of mate encounter and hence greater choosiness. All else being equal, however, my model predicts that the duration of good breeding conditions should correlate positively with the strength of mate choice. This could be tested by comparing choosiness among lines that evolved under mating windows of varying, experimentally imposed lengths.

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Appendix

Analytic model: derivation of the optimal proportion of acceptable mates

Here I derive the optimal proportion of acceptable mates $p^*(t)$ for the analytic model (eqns 7 and 8 in the main text and associated boundary conditions). It is convenient to first consider the case where some males are never worth mating with (i.e. $Q(0) \leq 0$). I then consider what happens when any mating is better than none at all (i.e. $Q(0) > 0$).

If $Q(0) \leq 0$, then females should always be somewhat choosy, but should never reject all possible mates. The optimal acceptance rate consequently obeys $0 < p^*(t) < 1$ for all times $t < t_f$. Writing $P(t) = \int_{t_0}^t p(\tau) d\tau$, the integrand in eqn 4 of the main text can be written as a Lagrangian:

$$L[t, P', P] = \lambda P' \exp(-\lambda P) v(P') \quad (S1)$$

Finding the optimal choosiness function is equivalent to finding a function P that maximizes $w = \int_{t_0}^{t_f} L dt$. In this case, the solution stays in the interior of the interval $[0, 1]$, so the Euler-Lagrange equation gives us a necessary condition for the optimality of P (Lenhart & Workman, 2007; Liberzon, 2012):

$$\frac{\partial L}{\partial P} - \frac{d}{dt} \frac{\partial L}{\partial P'} = 0 \quad (S2)$$

Substituting in the Lagrangian from eqn S1 gives us:

$$\lambda(P')^2 v'(P') - 2P'' v'(P') - P' P'' v''(P') = 0 \quad (S3)$$

Since $P' = p$, this can be rewritten as:

$$\lambda p^2 v'(p) - 2p' v'(p) - p p' v''(p) = 0 \quad (S4)$$

This is eqn 8 in the main text. To solve the equation, a boundary condition is required. At the end of the mating window, an unmated female should accept any male who she expects to provide a positive fitness benefit. Consequently, we can take $p(t_f) = p_{\max}^*$ as a

boundary condition, where p_{\max}^* is the smallest value of p such that $Q(1-p) = 0$.

If $Q(0) > 1$, then there exists a minimum time point t^* such that $p^*(t) = 1$ for all $t \geq t^*$. I now calculate t^* explicitly. The instantaneous rate of mate acceptance at time t^* is $\lambda p(t^*)$, and such matings have an average fitness value of $v(p(t^*))$. On the other hand, accepting a mate at time t^* removes any possibility of accepting one later. If the female behaves optimally from time t^* onwards, then the likelihood that she accepts a mate after this time, given that none was accepted earlier, is $1 - e^{-\lambda(t_f - t^*)}$ (remembering that $p^*(t) = 1$ for all $t \geq t^*$). The mean fitness benefit from such a mating is $\mu = v(1)$. Putting these opposing factors together, the instantaneous rate of fitness gain from playing $p(t^*)$ at time t^* is

$$G = \lambda p(t^*) \left[v(p(t^*)) - (1 - e^{-\lambda(t_f - t^*)}) \mu \right] \quad (S5)$$

Since t^* is the earliest time point where $p^*(t^*) = 1$, we must have $\frac{\partial G}{\partial p(t^*)} \Big|_{p(t^*)=1} = 0$. Solving this equation yields:

$$t^* = t_f - \frac{1}{\lambda} \log \left(-\frac{\mu}{v'(1)} \right) \quad (S6)$$

From eqn 1 in the main text, we have $v'(1) = Q(0) - \int_0^1 Q(r) dr$. Using the identity $\mu = \int_0^1 Q(r) dr$ (see e.g. Kämpke & Rademacher, 2015) then yields eqn 7 in the main text. For time points earlier than t^* , we can then apply eqn S4 with boundary condition $p(t^*) = 1$, by similar logic to the previous section.

Sexually cannibalistic spiders: derivation of a mutant's best response strategy

Here I show how to approximate a mutant male's best response strategy for the sexually cannibalistic spider example in the main text. I divide the mating window into n equal subintervals of length ℓ . I assume that all males in the population play the same mate choice strategy, approximated as a piecewise constant function b_i on each subinterval $[t_{i-1}, t_i)$. I write $\pi_{m,i}$ for the proportion of males remaining unmated and alive at time t_{i-1} . Similarly, $\pi_{f,i}(r)$ represents the proportion of females of quality rank r remaining at time t_{i-1} .

The probability that a male approaches a female in the subinterval $[t_{i-1}, t_i)$ is approximately $\ell \lambda_0 \int_{1-b_i}^1 \pi_{f,i}(r) dr$. Hence, the proportion of males remaining at time t_i is approximately:

$$\pi_{m,i+1} = \left(1 - \ell \lambda_0 \int_{1-b_i}^1 \pi_{f,i}(r) dr \right) \pi_{m,i} \quad (S7)$$

Similarly, the probability that a female of quality $r \geq 1 - b_i$ is approached by a male in the subinterval $[t_{i-1}, t_i)$ is approximately $\ell \beta \lambda_0 \pi_{m,i}$, and she accepts him with probability $a_i = \frac{1}{\ell} \int_{t_{i-1}}^{t_i} a(t) dt$. Hence, the proportion of females of quality rank r that are still unmated at time t_i is approximately:

$$\pi_{f,i+1}(r) = \begin{cases} \pi_{f,i}(r) & r < 1 - b_i \\ (1 - \ell \beta \lambda_0 a_i \pi_{m,i}) \pi_{f,i}(r) & r \geq 1 - b_i \end{cases} \quad (S8)$$

We can iterate the recursive eqns S7 and S8 forward in time to approximate the proportions of males and females remaining alive and unmated in each subinterval, starting with the initial conditions $\pi_{m,1} = 1$ and $\pi_{f,1}(r) = 1$ for all r .

I now consider a single mutant male playing the strategy $\hat{\mathbf{b}} = \{\hat{b}_1, \hat{b}_2, \dots, \hat{b}_n\}$ in a population where all other males play $\mathbf{b} = \{b_1, b_2, \dots, b_n\}$. In the subinterval $[t_{i-1}, t_i)$, the mutant encounters acceptable mate at a rate of $\lambda_0 \pi_i(\hat{b}_i)$, where:

$$\pi_i(\hat{b}_i) = \int_{1-\hat{b}_i}^1 \pi_{f,i}(r) dr \quad (S9)$$

The mutant male's expected fitness gain from such matings is approximately:

$$v_i(\hat{b}_i) = \frac{a_i}{\pi_i(\hat{b}_i)} \int_{1-\hat{b}_i}^1 \pi_{f,i}(r) Q(r) dr \quad (S10)$$

The mutant's reproductive value at time t_{i-1} is then approximately (see main text):

$$w_{i-1}^* = \max_{\hat{b}_i} \{ \lambda \pi_i(\hat{b}_i) v_i(\hat{b}_i) + (1 - \lambda \pi_i(\hat{b}_i)) w_i^* \} \quad (S11)$$

The mutant's best response $br(\mathbf{b})$ against a population playing \mathbf{b} can be calculated by backwards iteration of this equation, starting with the final reproductive value of $w_n^* = 0$ (see main text).