Evolutionarily stable mating decisions for sequentially searching females and the stability of reproductive isolation by assortative mating

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Running title: Evolutionarily stable mating decisions

Keywords: optimal mate choice, sequential search, assortative mating, cost of choosiness, mistakes of assessment, reproductive isolation

Please cite as:
T. Priklopil, É. Kisdi & M. Gyllenberg (2015): Evolutionarily stable mating decisions for sequentially searching females and the stability of reproductive isolation by assortative mating. Evolution 69: 1015-1026.

Abstract

We consider mating strategies for females who search for males sequentially during a season of limited length. We show that the best strategy rejects a given male type if encountered before a time-threshold but accepts him after. For frequency-independent benefits, we obtain the optimal time-thresholds explicitly for both discrete and continuous distributions of males, and allow for mistakes being made in assessing the correct male type. When the benefits are indirect (genes for the offspring) and the population is under frequency-dependent ecological selection, the benefits depend on the mating strategy of other females as well. This case is particularly relevant to speciation models that seek to explore the stability of reproductive isolation by assortative mating under frequency-dependent ecological selection. We show that the indirect benefits are to be quantified by the reproductive values of couples, and describe how the evolutionarily stable time-thresholds can be found. We conclude with an example based on the Levene model, where we analyze the evolutionarily stable assortative mating strategies and the strength of reproductive isolation provided by them.

Mate choice is a decisive process that shapes the genotypic distribution of populations in the course of evolution. Females, who are often the active sex in mate choice, are faced with the task of selecting a male who gives the best chances for the production and survival of their progeny. In many species, the search for males is constrained to happen sequentially in time (Janetos 1980, Real 1990, Bakker and Milinski 1991, Backwell and Passmore 1996, Forsgren 1997, Houde 1997, Ivy and Sakaluk 2007, Lehmann 2007). In sequential search, the female faces a decision at each encounter with a male to be either satisfied with the male, in which case she accepts him for mating and terminates her search, or to decline him and continue searching for other males at the risk of running out of time. Ideally, the choice made at each encounter reflects the quality or quantity of benefits the encountered male is offering, where benefits could be either direct, e.g. a high-quality territory, nutrition, parental care or protection (Møller and Jennions 2001, Andersson and Simmons 2006) or indirect, i.e., genes for the offspring (Møller and Alatalo 1999, Andersson 2006, Andersson and Simmons 2006).

In the first part of this paper, we show that the best mating strategy, which maximizes the expected benefits for a sequentially searching female, is a particular time-threshold strategy. A female with a time-threshold strategy accepts a given male for mating if she encounters him after a time-threshold that depends on the type of the male. Some type(s) of males will have zero time-threshold, i.e., will be accepted from the beginning of the mating season, whereas others will be discriminated against by declining them until a time-threshold is passed. By the ”best” mating strategy, we mean a globally evolutionarily stable strategy or the globally optimal strategy (*sensu* Metz et al. 2008), depending on whether selection is frequency-dependent or not. We derive the best time-thresholds for arbitrary variation among males, i.e., genetic or environmental, discrete or continuous, for both optimization and frequency-dependent selection on the mating strategies. The best time-thresholds are expressed in terms of benefits various male types are offering. Females may however make mistakes in assessing a male. Such mistakes are incorporated in a natural way into our model, and we discuss the consequences of making mistakes via an example. Several theoretical papers have previously explored sequential mate search (e.g. Janetos 1980, Real 1990, 1991, Wiegmann et al. 1999, Fawcett and Johnstone 2003a, Fawcett and Johnstone 2003b, Wiegmann et al. 2007, Etienne et al. 2014); here we extend this work by generalizing female decisions to a time-threshold strategy.

In the second part of the paper, we focus on indirect benefits in populations where frequency-dependent ecological selection maintains the genetic polymorphism. We show how evolutionarily stable mating strategies can be found, and illustrate the method using a population genetic model where heterozygotes are selected against and conditions for ecological speciation are met. We investigate the stability of assortative mating that arises from homozygote females discriminating against the opposite homozygote or heterozygote males, investigate the conditions under which polymorphism is maintained (nonrandom mating implies sexual selection, which can interfere with ecological selection in maintaining the polymorphism), and explore when reproductive isolation between homozygotes is strong enough to maintain separate species.

The Model

Consider a large and well-mixed sexually reproducing population with k different types of males present. These types may represent any kind of variation, including genotypes or non-hereditary phenotypes. The type distribution may also be continuous; formulas for this case are given in Supporting Information S2. Females (the choosy sex) encounter males (who are always ready to mate) sequentially, such that at each encounter with a male, the female must either accept the male for mating and terminate her search or decline the male and continue searching. If a female of type f accepts a male of type g for mating, she will receive a positive benefit $\varepsilon_{f,g}$.

Encounters occur randomly at a rate λ during a mating season of length T. Importantly, the encounter rate depends on population density, because it is easier to find a male in a more dense population; we ease the notation by using λ for the encounter rate evaluated at the equilibrium density. Females who remain unmated till the end of the mating season cannot reproduce.

TIME-THRESHOLDS AS PREFERENCE TRAITS

Suppose that at time t in the mating season, a female f encounters a male of type g. In a sequential search, she has only two possible decisions: accept or reject. Thus the most general strategy the female may follow is to accept the male with probability $\Pi_{f,g}(t)$ and to reject with probability $1-\Pi_{f,g}(t)$. The benefit that this strategy yields on average is $B_{f,g}(t) = \Pi_{f,g}(t)\varepsilon_{f,g} + (1 - \Pi_{f,g}(t))E_f(t)$, where $E_f(t)$ denotes the benefit an unmated female of type f can expect to receive in the remainder of the mating season. $B_{f,g}(t)$ is a simple linear function of $\Pi_{f,g}(t)$, so that the best choice of $\Pi_{f,g}(t)$, which maximizes $B_{f,g}(t)$, is

$$\Pi_{f,g}(t) = \begin{cases} 1 & \text{if } \varepsilon_{f,g} > E_f(t) \\ 0 & \text{otherwise} \end{cases} \tag{1}$$

The female thus accepts the male if he provides a greater benefit than what the female can expect if she continues searching.

Let $\tilde{P}_m$ denote the frequency of male type g_m in the mating season (the symbol P_m is reserved for frequency at birth, see below). In Supporting Information S1, we show that the expected benefit of females who are still unmated at time t, $E_f(t)$, changes according to

$$\dot{E}_f(t) = \lambda \left[E_f(t) - \sum_{i=1}^{k} \tilde{P}_i \max\{E_f(t), \varepsilon_{f,g_i}\} \right] \tag{2}$$

with $E_f(T) = 0$ (at the end of the mating season, unmated females receive no benefit). Equation (2) is an extended version of the sequential search (or one-step decision) tactic introduced in Janetos (1980) and further developed in Real (1990), Wiegmann et al. (1999), Wiegmann and Angeloni (2007).

Because $E_f(t) \leq \sum_{i=1}^{k} \tilde{P}_i \max\{E_f(t), \varepsilon_{f,g_i}\}$ for all t, the expected benefit of unmated females, $E_f(t)$, decreases throughout the mating season towards $E_f(T) = 0$. If $E_f(0) > \varepsilon_{f,g_i}$ for a given male type such that, according to equation (1), the female should not accept males of this type at the beginning of the season, then there is a single time-threshold τ_{f,g_i} such that $\varepsilon_{f,g_i} > E_f(t)$ holds for all $t > \tau_{f,g_i}$ and the female should accept the male if she encounters him at any time after τ_{f,g_i} (see Figure 1). If $\varepsilon_{f,g_i} > E_f(0)$, then $\tau_{f,g_i} = 0$, as ε_{f,g_i} exceeds the expected benefit at all times and the male should be accepted right from the beginning of the mating season. For convenience, we index the male types in decreasing order of benefits, $\varepsilon_{f,g_1} \geq \varepsilon_{f,g_2} \geq ... \geq \varepsilon_{f,g_k}$ (note that this ordering may depend on the female), which implies $\tau_{f,g_1} \leq \tau_{f,g_2} \leq ... \leq \tau_{f,g_k}$, i.e., better males are accepted earlier in the season. Obviously, the best male type is accepted at any time such that $\tau_{f,g_1} = 0$. There might however be more than one male types that provide higher benefit than $E_f(0)$, in which case several of the thresholds are zero; we denote by n_f the number of male types that are accepted by a female f from the beginning of the season, so that we have $\tau_{f,g_1} = \cdots = \tau_{f,g_{n_f}} = 0$. Since unmated females receive no benefit, all male types have thresholds strictly less than T such that at the very end of the season, all males are accepted.

Equation (2) can be solved analytically and the best time-thresholds $\tau_{f,g_1}, \ldots, \tau_{f,g_k}$ of female f can be obtained (see Supporting Information S1) in the form

$$\tau_{f,g_{i+1}} - \tau_{f,g_i} = \frac{1}{\lambda \sum_{j=1}^{i} \tilde{P}_j} \ln \left[\frac{\bar{E}_f^i - E_f^{i+1}}{\bar{E}_f^i - E_f^i} \right] \qquad \text{for } n_f < i \leq k, \tag{3}$$

where $\tau_{f,g_{k+1}} = T$ by definition,

$$\bar{E}_f^i = \frac{\sum_{j=1}^{i} \tilde{P}_j \varepsilon_{f,g_j}}{\sum_{j=1}^{i} \tilde{P}_j} \tag{4}$$

is the average benefit provided by the male types $\{g_1, \ldots, g_i\}$ accepted in the time interval $[\tau_{f,g_i}, \tau_{f,g_{i+1}}]$, and where we use the shorthands $E_f^i = \varepsilon_{f,g_i}$ for $n_f < i \leq k$ for the benefits provided by males not yet accepted at the beginning of the season, $E_f^{k+1} = E_f(T) = 0$ for the expectation at the end of the season and $E_f^n = E_f(0)$ for the initial expectation given that $\tau_{f,g_1} = \cdots = \tau_{f,g_{n_f}} = 0$. If the benefits ε_{f,g_i} are known, then we can explicitly calculate all thresholds from equation (3) in the following way: First substitute $i = k$ to obtain τ_{f,g_k}. Then proceed backwards with $i = k-1$, $i = k-2$ etc. to obtain $\tau_{f,g_{k-1}}$, $\tau_{f,g_{k-2}}$ etc., until the time-thresholds are no longer positive; the remaining male types should be accepted any time. Hereafter we use the symbol $\tau_{f,g}$ to denote the best time-thresholds obtained from (3), and $t_{f,g}$ to denote any time-threshold strategy that does not necessarily give the maximum return of benefits.

MATING PROBABILITIES AND THE EXPECTED BENEFITS

Here we derive the probability that a female f using the time-threshold strategy $t_{f,g_1}, \ldots, t_{f,g_k}$ mates with a male of type g_m and the expected benefit she eventually receives (this calculation applies to any time-threshold strategy, not only to the best time-thresholds $t_{f,g} = \tau_{f,g}$). To simplify the formulas below, we use the shorthand $t_{f,g_i} = t_i$ and set $t_{k+1} = T$. The probability for a focal female f and a male of type g_m to mate during a mating season of length T is obtained from the probability of mating within each time interval $[t_i, t_{i+1}]$ (where $i = 1, \ldots, k$), and then adding these up given that the female hasn't terminated her search. Because $1 - e^{-\lambda(t_{i+1}-t_i)\sum_{j=1}^{i}\tilde{P}_j}$ is the probability that acceptable males of types $\{g_1, \ldots, g_i\}$ are encountered between t_i and t_{i+1} and $\frac{\tilde{P}_m}{\sum_{j=1}^{i}\tilde{P}_j}$ is the probability that a particular type g_m is encountered out of the types $\{g_1, \ldots, g_i\}$, we have that a female f mates with a male of type g_m with probability

$$Q_{f,g_m}\tilde{P}_m = \sum_{i=m}^{k}\Bigg[\underbrace{\frac{\tilde{P}_m}{\sum_{j=1}^{i}\tilde{P}_j}}_{\substack{\text{choose } g_m \\ \text{out of } g_1,\ldots,g_i}} \times \underbrace{\left(1 - e^{-\lambda(t_{i+1}-t_i)\sum_{j=1}^{i}\tilde{P}_j}\right)}_{\substack{\text{encounter } g_1,\ldots,g_i \\ \text{between } t_i \text{ and } t_{i+1}}} \times \underbrace{\prod_{j=1}^{i-1} e^{-\lambda(t_{j+1}-t_j)\sum_{l=1}^{j}\tilde{P}_l}}_{\substack{\text{remain unmated} \\ \text{until time } t_i}}\Bigg]. \tag{5}$$

By similar arguments, we obtain the benefit a female f can expect to receive during the entire mating season, i.e., $E_f(t)$ evaluated at time $t = 0$, as

$$E_f(0) = \sum_{i=n}^{k}\left[\bar{E}_f^i \times \left(1 - e^{-\lambda(t_{i+1}-t_i)\sum_{j=1}^{i}\tilde{P}_j}\right) \times \prod_{j=n}^{i-1} e^{-\lambda(t_{j+1}-t_j)\sum_{l=1}^{j}\tilde{P}_l}\right]. \tag{6}$$

WHEN DOES NON-RANDOM MATING EVOLVE?

When all time-thresholds are zero, the female accepts the first male she encounters and therefore mates at random. According to equation (3), this is the best solution when the time-threshold of the worst male, τ_{f,g_k}, is not positive, i.e., when

$$\lambda T \leq \ln\left[\frac{\bar{E}_f^k}{\bar{E}_f^k - E_f^k}\right]. \tag{7}$$

λT is the expected number of males encountered during a mating season; if this is below a critical value, then the females run a high risk of remaining unmated and therefore the best strategy is to accept any male they encounter. Short mating seasons therefore select for random mating. The right hand side of condition (7) is large when there is only a small difference between $\bar{E}_f^k$, the average benefit from a random male, and $E_f^k = \varepsilon_{f,g_k}$, the benefit provided by the worst male type g_k. Therefore if there are only small differences between males, then mating at random is the best strategy unless the females are able to sample a great number of males. Equation (7) can be rewritten as $E_f^k > \bar{E}_f^k(1 - e^{-\lambda T})$, which says that random mating is the best strategy if even the worst male gives higher benefit than the average benefit times the probability of finding any male. If condition (7) holds for all females of the population, then random mating evolves; if it holds for some but not all females, then the population as a whole does not mate randomly, but some females do. Note that by equation (1), the best time-threshold strategy is better than any other conceivable mating strategy. Hence if condition (7) holds, no strategy is better than random mating; and the opposite of (7) is necessary for the evolution of any form of preferential mating.

MISTAKES IN EVALUATING MALES

Females may naturally make mistakes in estimating the correct type of the male. To incorporate such mistakes, we need to characterize the males not by their true type, but by their perceived type. For example, a male is of the type ”good-looking” either if the female assesses a good-quality male correctly or if a bad-quality male deceives the female so that she believes him to be good. Males of perceived type g vary in the real benefit they provide. We can however use the above results simply by substituting the mean of the real benefit from males of perceived type g for $\varepsilon_{f,g}$. With this, equation (3) yields the time-thresholds for females to accept males based on their perceived type, i.e., based on the information available to females. (Note however that with this, equation (5) gives the probabilities of mating with perceived types, not with true types. Supporting Information S1 explains how the probability of mating with a certain true type can be obtained.)

If mistakes are common, then the mean benefits from different perceived male types are similar to each other, because different perceived types are almost random samples from the entire male population. In this case, inequality (7) holds and random mating is the best mating strategy. In other words, females do not discriminate among the perceived male types when the available information is too unreliable.

Examples for optimal mating strategies

If the benefits $\varepsilon_{f,g}$ are constants, then the best time-thresholds of a given female are independent of what other females do. Finding the best mating strategy thus reduces to an evolutionary optimization problem *sensu* Metz et al. (2008). Here we give three simple examples for this case, assuming that all females are equal, whereas males and the benefits they give vary due to some environmental effects such as the quality of the microhabitat where the males grew up.

Example 1: Good vs bad males. Suppose that a fraction p_g of males are of good condition and able to provide ε_g

offspring, whereas the remaining $p_b = 1 - p_g$ fraction of males are of bad condition and can provide only $\varepsilon_b < \varepsilon_g$ offspring (since we assume all females to be equal, we suppress the female index f). Females can ascertain whether a male is good or bad without mistakes. The females should obviously accept a good male at any time, and therefore the only trait of interest is the time-threshold after which females accept also the bad males. Taking $i = k$ in equation (3) and substituting $\tau_{f,g_k} = \tau_b$, $\tilde{P}_1 = p_g$, $\tilde{P}_2 = p_b$, $\bar{E}_f^k = p_g\varepsilon_g + p_b\varepsilon_b$, and $E_f^k = \varepsilon_b$, we obtain the optimal threshold as

$$\tau_b = T - \frac{1}{\lambda}\ln\left[\frac{p_g\varepsilon_g + p_b\varepsilon_b}{p_g\varepsilon_g + p_b\varepsilon_b - \varepsilon_b}\right] = T - \frac{1}{\lambda}\ln\left[1 + \frac{\varepsilon_b}{p_g(\varepsilon_g - \varepsilon_b)}\right] \tag{8}$$

provided that this is positive; otherwise the females should accept also the bad males at any time. The threshold τ_b is high, i.e., discrimination against bad males is strong, when the difference between the benefits is large (relative to ε_b) and when encounters occur often and the good males are frequent such that females discriminating against the bad males do not run a high risk of remaining unmated.

Example 2: Mistakes in determining male type. Now we expand the above example allowing for mistakes that females might make in determining whether a male is good or bad. Suppose that with probability $q < \frac{1}{2}$, a good male the female perceives as bad, and with the same probability a bad male she perceives as good (in case $q > \frac{1}{2}$, the females should just make the opposite decisions). We assume the same probability for the two mistakes for simplicity, and hence consider situations where the mistake is due to extrinsic reasons such as visual constrains (e.g. turbid water, Seehausen et al. 1997), rather than due to male deception.

From the females' point of view, males are "good-looking" or "bad-looking", and these males occur with frequency $\pi_g = p_g(1-q) + p_b q$ and $\pi_b = p_b(1-q) + p_g q$, respectively. The benefit a good-looking male provides on average is $\eta_g = \frac{p_g(1-q)}{\pi_g}\varepsilon_g + \frac{p_b q}{\pi_g}\varepsilon_b$, whereas a bad-looking male provides $\eta_b = \frac{p_b(1-q)}{\pi_b}\varepsilon_b + \frac{p_g q}{\pi_b}\varepsilon_g$. It is easy to check that good-looking males give on average higher benefits ($\eta_g > \eta_b$), and therefore females should always accept good-looking males. The optimal time-threshold after which females should accept bad-looking males, τ_b, is calculated as in the previous example, but using $\tilde{P}_1 = \pi_g$, $\tilde{P}_2 = \pi_b$, and $E_f^k = \eta_b$; note that the average benefit $\bar{E}_f^k = \pi_g\eta_g + \pi_b\eta_b$ simplifies to $\bar{E}_f^k = p_g\varepsilon_g + p_b\varepsilon_b$ as above. This yields

$$\begin{aligned}\tau_b &= T - \frac{1}{\lambda}\ln\left[\frac{p_g\varepsilon_g + p_b\varepsilon_b}{p_g\varepsilon_g + p_b\varepsilon_b - \eta_b}\right] = \\ &= T - \frac{1}{\lambda}\ln\left[\frac{\varepsilon_b + p_g(\varepsilon_g - \varepsilon_b)}{p_g(1-p_g)(\varepsilon_g - \varepsilon_b)} \times \frac{1 - q - p_g(1-2q)}{1-2q}\right]\end{aligned} \tag{9}$$

As in the previous example, strong discrimination evolves when the difference $\varepsilon_g - \varepsilon_b$ is large (relative to ε_b) and when λ is high. τ_b decreases with increasing q, i.e., mistakes make the optimal discrimination less strong; this is because bad-looking males may well be good when mistakes are frequent. The effect of p_g is slightly more complicated (see Figure 2). At low values of p_g, τ_b increases with p_g and therefore discrimination against bad males becomes stronger; this is similar to the case without mistakes, but an additional factor is that at low p_g, most good-looking males are in fact of the common bad type, only mistaken for good, and therefore should not be preferred (thus random mating for very low p_g, Figure 2). At high values of p_g, however, τ_b decreases with the frequency of good males. This may seem counterintuitive because a higher frequency of good males should allow the females to be more discriminative against bad males without running the risk of remaining unmated. However, if bad males are rare, it is increasingly likely that a bad-looking male is in fact a good male, and therefore it doesn't pay off to discriminate against it.

Example 3: Continuous male type-distribution. If the distribution of male types is continuous, then the best time-thresholds of a female f are specified by a function $\tau_f(g)$ such that the female accepts a male of type g if she encounters him at a time $t > \tau_f(g)$ during the mating season. We derive the best time-threshold function for the general model in Supporting Information S2. Figure 3 shows two examples, one with uniform and one with log-normal distribution of male types, and with $\varepsilon_f(g) = g$ (note that this differs from the reverse ordering we used for the discrete case where low values of g provided the highest benefits). If the males are uniformly distributed over the interval $[0, 1]$, then we can obtain the optimal time-threshold function analytically (see Supporting Information S2),

$$\tau_f(g) = \max\left[T - \frac{2g}{\lambda(1-g)}, 0\right] \tag{10}$$

which is depicted in Figure 3a. Males with benefit higher than $g_0 = \frac{\lambda T}{2+\lambda T}$ have zero threshold, i.e., they are accepted from the beginning of the mating season. Notice that in this example, the females should never mate randomly; in particular, the worst male $g = 0$ is not accepted until time T. This is because at any time before T, the female has a chance to encounter a male with a positive benefit, and therefore she should not terminate her search with accepting a male with no benefit. Notice further that the time-threshold function $\tau_f(g)$ is concave down, which means that the discrimination between two similar male types is greater when both males are of better quality than when they are of the worse quality. In the beginning of the mating season, the females do not have a high risk of remaining unmated and therefore take a longer time during which they discriminate between males of similar qualities; but towards the end of the mating season, the females accept worse males sooner.

In Figure 3b, we assume the biologically more realistic log-normal distribution of male types,

$$p(g) = \frac{1}{\sqrt{2\pi}\sigma g} e^{-\frac{(\ln g - \mu)^2}{2\sigma^2}}. \tag{11}$$

In this case, the solution has to be evaluated numerically (Supporting Information S2), but its qualitative features are the same as with the uniform distribution.

Frequency-dependent indirect benefits

In the remainder of this paper, we assume that the male types correspond to genotypes and that the benefits the males provide are the genes inherited by the offspring. We also assume that the offspring undergo frequency-dependent viability (ecological) selection, which maintains the polymorphism. This raises two difficulties in quantifying the benefits and finding the best time-thresholds. Firstly, the offspring are of various genotypes, and therefore the number of offspring is not an appropriate measure of the benefit a female receives from a male; it is possible that the couple would have many offspring but these do not survive, or survive to reproduction but are then unable to find mates with whom they can reproduce successfully. In the first subsection below, we show that the benefit $\varepsilon_{f,g}$ is given by the reproductive value of the f, g couple. Secondly, the fitness of a given offspring genotype depends on the genotypic frequencies in the offspring population, and therefore the benefit from a given male to a given female depends on the mating preferences of other females. This means that the benefits $\varepsilon_{f,g}$ are not constants but depend on the mating strategy followed by the resident population. Our results enable us to determine whether certain time-thresholds are the best for an individual female assuming that all other females follow the same strategy. In the second subsection below, we discuss how this can be used to determine the evolutionarily stable mating strategy (ESS).

REPRODUCTIVE VALUES AS INDIRECT BENEFITS

Consider first a population with non-overlapping generations. If males contribute only their genes to the offspring, then the benefit a female f receives from a male g is the number of her offspring who survive and reproduce, weighted with the eventual success accrued from each reproducing offspring. The benefit is thus given by

$$\varepsilon_{f,g} = 2K \sum_r R_{f,g\to r} v_r \cdot \tfrac{1}{2}\Big(\sum_h Q_{r,h} \tilde{P}_h \frac{\varepsilon_{r,h}}{2} + \sum_h Q_{h,r} \tilde{P}_h \frac{\varepsilon_{h,r}}{2} \Big), \tag{12}$$

where $2K$ is the number of offspring (K daughters and K sons), $R_{f,g\to r}$ is the probability that parents with genotypes f and g produce an offspring with genotype r according to the Mendelian rules for autosomal loci, and v_r is the probability of survival of an offspring of genotype r. Importantly, v_r may be density- and frequency-dependent. $\frac{1}{2}Q_{r,h}\tilde{P}_h$ is the probability that the offspring is a female and that she gets mated with a male h, whereas $\frac{1}{2}Q_{h,r}\tilde{P}_h$ is the probability that the offspring is a male times the expected number of females of genotype h he is mated with. For time-threshold mating strategies, these quantities are given by equation (5). The weights attached to the offspring, $\frac{\varepsilon_{r,h}}{2}$ and $\frac{\varepsilon_{h,r}}{2}$, respectively, are halved because the offspring will pass the focal female's gene with probability $\frac{1}{2}$. Equation (12) is valid only at equilibrium, where the density- and frequency-dependent survival probabilities and the benefits are constants across generations. Because $R_{f,g\to r} = R_{g,f\to r}$, the benefits are symmetric such that $\varepsilon_{f,g} = \varepsilon_{g,f}$ (but $Q_{f,g}$ is generally different from $Q_{g,f}$). In Supporting Information S3, we show that the benefit given in (12) is the reproductive value of the couple f, g and generalize equation (12) to iteroparous populations. For a single locus under random mating, the benefits reduce to the expected viability fitness of the offspring of the couple (Supporting Information S3).

EVOLUTIONARILY STABLE MATING STRATEGIES

Since in any population the best mating strategy is a time-threshold strategy (cf. equation (1)), all evolutionarily stable strategies must be time-threshold strategies. To determine the evolutionarily stable time-thresholds, we assume non-overlapping generations (the extension to iteroparous organisms is tedious but straightforward). Let P_g denote the frequency of genotype g at birth, and let N be population size. To calculate the genotype frequencies after selection, we define $w_g = \frac{v_g}{\bar{v}}$, the relative viability of genotype g, where $\bar{v} = \sum_g P_g v_g$ is the average probability of survival; and since $\bar{w} = \sum_g P_g w_g = 1$, the frequency of genotype g after ecological selection and before mating is $\tilde{P}_g = P_g \frac{w_g}{\bar{w}} = P_g w_g$. v_g and therefore w_g depend on N and on $P_1, ..., P_k$.

Suppose that all females of the resident population mate using the (not necessarily best) time-thresholds $t_1, ..., t_k$. This resident population equilibrates at a population size and genotype frequencies that satisfy

$$\begin{aligned} P_r &= \frac{1}{\bar{Q}} \sum_{g,h} \tilde{P}_g \tilde{P}_h Q_{g,h} R_{g,h\to r} \\ &= \frac{1}{\bar{Q}} \sum_{g,h} P_g P_h w_g(N, P_1, ..., P_k) w_h(N, P_1, ..., P_k) Q_{g,h} R_{g,h\to r} \quad \text{for } r = 1, ..., k \end{aligned} \tag{13a}$$

$$N = K\bar{v}(N, P_1, ..., P_k)\bar{Q}(N, P_1, ..., P_k)N \tag{13b}$$

where $Q_{g,h}$ is given in (5) with λ evaluated at the equilibrium density N and $\bar{Q} = \sum_{g,h} \tilde{P}_g \tilde{P}_h Q_{g,h}$ is the fraction of females who mated by the end of the season.

Let us focus attention on an individual female in the equilibrium resident population. The benefits she obtains are determined by equation (12) evaluated at the resident equilibrium of $N, P_1, ..., P_k$. If the time-thresholds $t_1, ..., t_k$ are actually the best possible time-thresholds for an individual female who lives in this resident population, then they coincide with the time-thresholds obtained from equation (3). If it is so, then no other (mutant) mating strategy could invade this resident population, and therefore the resident time-thresholds correspond to an ESS. To determine the ESS time-thresholds, therefore, we need to solve equations (13) and (12) simultaneously for the unknowns $N, P_1, ..., P_k$ and $\varepsilon_{f,g}$ for $f, g = 1, ..., k$, substituting throughout the time-thresholds from equation (3) and $Q_{f,g}$ from (5) with λ evaluated at N. Once the solution of (12) is known, the ESS time-thresholds are obtained by substituting the benefits into (3). Since the equations are nonlinear, multiple solutions may exist, yielding multiple ESSs for the same model parameters. A further complication is that even though equation (3) gives the time-thresholds to be used in (5) explicitly, it supposes that we know, for each female genotype, the ranking of male genotypes (recall that male types must be indexed in decreasing order of benefits) and the number of male types n_f accepted by a female genotype f from the beginning of the mating season. Since with frequency-dependence this depends on the solution itself, one has to check each possible configuration of male rankings and n_f values separately, calculating the solution for a hypothetised configuration and checking whether the time-thresholds of the solution reproduce the configuration assumed. Every solution found gives a mating strategy $\tau_{f,g}$ for all f, g and the corresponding population equilibrium $N, P_1, ..., P_k$, where the evolutionary stability of $\tau_{f,g}$ is guaranteed by the fact that equation (3) yields the best time-thresholds, but the population dynamical stability of $N, P_1, ..., P_k$ (with the time-thresholds fixed) must be checked separately using the standard method of linear stability analysis.

Example: assortative mating in the Levene model

To demonstrate the method of finding the evolutionarily stable mating strategy under frequency-dependent selection, we consider a population that undergoes viability selection according to the multiple niche polymorphism model of Levene (1953). We assume that there are two habitats of equal size that support a population of fixed size (hence N

is constant). Two alleles, a and A, segregate in a single locus so that the possible genotypes are aa, aA and AA. The relative viabilities in the Levene model are given by

$$w_g = \frac{1}{2}\Big(\frac{u_g^{(1)}}{U_1} + \frac{u_g^{(2)}}{U_2}\Big), \tag{14}$$

where $u_g^{(i)}$ is the probability of survival for genotype g in habitat i, and $U_i = \sum_g P_g u_g^{(i)}$ is the average survival probability in habitat i. w_g is frequency-dependent because U_1 and U_2 depend on the genotype frequencies. For simplicity, we assume symmetric selection, i.e., $u_{aa}^{(1)} = 1$, $u_{aa}^{(2)} = 1 - s$ and $u_{AA}^{(1)} = 1 - s$, $u_{AA}^{(2)} = 1$ such that homozygotes aa (AA) are selected against in habitat 2 (in habitat 1) with the same selection coefficient s, and $u_{aA}^{(1)} = u_{aA}^{(2)} = 1 - hs$ (with $0 \leq h \leq 1$) such that heterozygotes are selected against equally in both habitats (Hoekstra et al. 1985). Figure 4 shows the selection regimes in this model under random mating.

We restrict our analysis to symmetric equilibria ($\hat{P}_{aa} = \hat{P}_{AA}$). Since half of the offspring of heterozygote females are heterozygote and the other half homozygote, and the two homozygote genotypes are under equal selection at the symmetric equilibrium, we have $\varepsilon_{aA,aa} = \varepsilon_{aA,aA} = \varepsilon_{aA,AA}$; this implies that heterozygote females do not benefit from any preference and thus their best strategy is random mating, $\tau_{aA,aa} = \tau_{aA,aA} = \tau_{aA,AA} = 0$. Moreover, at the symmetric equilibrium we have $\varepsilon_{aa,aa} = \varepsilon_{AA,AA}$, which means that we have just four unknowns in equations (12) and (13), $\varepsilon_{aa,aa}, \varepsilon_{aa,aA}, \varepsilon_{aa,AA}$ and $\hat{P}_{aa}$ (recall that $\varepsilon_{f,g} = \varepsilon_{g,f}$). Due to symmetry, the best time-thresholds are also symmetric, $\tau_1 = \tau_{aa,aa} = \tau_{AA,AA}$, $\tau_2 = \tau_{aa,aA} = \tau_{AA,aA}$ and $\tau_3 = \tau_{aa,AA} = \tau_{AA,aa}$, such that the two homozygote females discriminate equally against the opposite homozygote males and also equally against the heterozygote males.

We aim this analysis at understanding the degree and stability of reproductive isolation by assortative mating. For this reason, we confine ourselves to ESSs where homozygote females benefit most from mating with identical homozygotes and least from the opposite homozygotes ($\varepsilon_{aa,aa} \geq \varepsilon_{aa,aA} \geq \varepsilon_{aa,AA}$), thereby disregarding situations where the production of heterozygotes is favoured and disassortative mating evolves. We therefore consider only three configurations of mating strategies for homozygote females ($f = aa$ or AA): *random mating* (RM) with $\tau_1 = \tau_2 = \tau_3 = 0$ (all males accepted equally; $n_f = 3$); *partial assortative mating* (PAM) with $\tau_1 = \tau_2 = 0$ and $\tau_3 > 0$ (opposite homozygotes discriminated; $n_f = 2$); and *assortative mating* (AM) with $\tau_1 = 0$ and $0 < \tau_2 \leq \tau_3$ (heterozygotes and opposite homozygotes discriminated; $n_f = 1$ and heterozygote males rank higher than opposite homozygotes). For these three configurations, we solved equations (12) and (13) (supplemented with (5) and (3)) numerically, using Maple 13.0, for various values of the three model parameters, the expected number of males encountered in the mating season λT, the strength of viability selection s, and heterozygote disadvantage h.

Figure 5 summarizes the results of this analysis, and Supporting Information S4 gives an extended discussion and derivations. We find ESSs with random mating (RM), with partial assortative mating (PAM), and with assortative mating (AM) in parameter regions that partially overlap, yielding multiple ESSs. Assortative mating is evolutionarily stable on the right of the thick line in Figure 5. For high s, we find two different ESSs of the AM configuration (the corresponding nonlinear equations have multiple solutions), which are denoted with superscripts $+$ and $-$ (for higher and lower homozygote frequency, respectively; see Figure 5b). At all ESSs shown, the solution is stable with respect to small perturbations of the genotype frequencies; the parameter regions where this is not the case are marked with NSS for no stable solutions. The subscripts PP and UP indicate whether the polymorphism is protected or unprotected. $NAMS$ marks regions which don't allow for assortative mating strategies, i.e., where no ESS exists with $\varepsilon_{aa,aa} \geq \varepsilon_{aa,aA} \geq \varepsilon_{aa,AA}$.

If heterozygotes are at an advantage during ecological selection ($h < 1/2$), then there is either AM or $NAMS$. The reason is that with RM or PAM, heterozygote males are not discriminated against by the females and hence suffer no disadvantage either in ecological selection or in sexual selection. With AM strategies, however, females do discriminate against heterozygote males, and when this sexual selection is sufficiently strong, it can override ecological selection and lead to an overall disadvantage of heterozygotes, thus making AM an evolutionarily stable mating strategy. This mechanism can stabilize reproductive isolation upon secondary contact even if the hybrids are at an ecological advantage.

The conditions under which random mating (RM) is evolutionarily stable can be obtained analytically (see Supporting Information S4). These conditions hold when λT is small, so that rejecting a male runs a high risk of remaining unmated; and also when h is close to $\frac{1}{2}$, so that all genotypes have similar viabilities (but at high λT, this region becomes too narrow to be seen in Figure 5). When h exceeds $h_{\text{int}} = (2-\sqrt{4-4s-s^2})/(2s)$, the RM equilibrium loses its population genetic stability, whereas above $h_0 = 1/(2-s)$, the RM and PAM polymorphisms are not protected.

Increasing λT increases the time-thresholds τ_2 and τ_3 of the AM/AM^+ strategy, so that homozygote females increasingly discriminate against other genotypes (but the same is not true for the AM^- strategy). As discrimination increases, the frequency of each homozygote approaches $1/2$ and the heterozygotes disappear. We measure the strength of reproductive isolation between the homozygotes by comparing the frequency of heterozygotes at birth to the frequency of heterozygotes under random mating, i.e., using the statistic $F = 1 - \frac{P_{aA}}{2P_aP_A} = 1 - 2P_{aA}$ (since

$P_a = P_A = \frac{1}{2}$ at the symmetric equilibrium). When the homozygote females adopt the AM/AM^+ strategy, F exceeds 0.99 in the shaded area in Figure 5. With strong heterozygote disadvantage during ecological selection (high s and high h), even a PAM strategy can sustain reproductive isolation ($F > 0.99$ for PAM in the darkly shaded area in Figure 5b), because heterozygotes are so rare during mating that discrimination against the opposite homozygotes alone suffices to maintain reproductive isolation. We thus conclude that with a sufficiently long mating season, reproductive isolation by assortative mating is evolutionarily stable.

Discussion

We have determined the best mating strategy for females who search for mates sequentially. We have shown that the best mating strategy is always a time-threshold strategy, such that a given female rejects a given type of male if she encounters him before a certain point in time during the mating season and accepts him after (this time-threshold may also be zero, meaning that the female accepts the male at any time). We have derived the best time-thresholds for both discrete and continuous male type distributions, calculated the probabilities that a given female will mate with a particular male type, and gave a condition under which non-random mating should evolve.

If the benefits are direct, as in our first set of examples, then the model reduces to an optimization model where time-thresholds always evolve to the values given by the best time-thresholds strategy. For the case of indirect benefits, i.e., when males contribute their genes to the success of the female's offspring, we have shown that the reproductive value of the couple is the appropriate measure of the benefit. We then embedded the sequential mate search model into a population genetic model of speciation, and established the conditions under which reproductive isolation by assortative mating is evolutionarily stable.

Females may make mistakes when assessing the type of the male. These mistakes are easily incorporated into our model by characterizing the males not by their true type but by their perceived type. We found that the distribution of true male types (p_g in Figure 2) influences whether females should discriminate among males in a somewhat surprising manner: When good males are common, it is not worth to discriminate against bad-looking males, even though finding a good male would not be difficult. This is because if bad males are rare, mistakes occur more often than encounters with bad males, i.e., it is quite likely that a bad-looking male is in fact a good male. On the other hand, if good males are rare, then the females should accept any mates or else they remain unmated. The females therefore should mate at random whenever they are prone to make mistakes and the frequencies of good and bad males are far from equal. In interspecific hybridization, conspecifics are usually ”good” and heterospecifics ”bad”. Our result is thus in agreement with the so-called Hubbs principle, which states that hybridization occurs more often when one of the species is rare (Hubbs 1955, Mayr 1963, Grant and Grant 1997, Randler 2002), and explains the puzzling fact that also females of the common species, who could easily find conspecific males, are often found in hybrid pairs (Randler 2002).

The best time-thresholds could be found by maximizing the expected benefit (given in equation (6)) with respect to $t_1, ..., t_k$ (for a continuous male type distribution, the same can be done using the calculus of variations, see e.g. Sagan 1992; Parvinen et al. 2006). We offer a more efficient way to find the best time-thresholds, which yields the explicit formula in equation (3). The globally optimal or (under frequency-dependent selection) globally evolutionarily stable mating strategies we have found are valid for any kind of variation, i.e., irrespectively whether the mating strategies are inherited or learned (Schimmel and Wasserman 1991, ten Cate et al. 1993, Kendrick at al. 1998, Irwin and Price 1999, Verzijden and ten Cate 2007, Dukas 2008, Kozak and Boughman 2009), whether they may take any form or are constrained to time-threshold strategies, whether they may change arbitrarily or only by small mutations, and what is the covariance structure of pleiotropic mutations affecting e.g. multiple time-thresholds (cf. Dieckmann and Law 1996; Durinx et al. 2008; Leimar 2009). In this article, we did not purse the dynamics of evolution leading to an evolutionarily stable mating strategy, which would be affected by all these details.

Our model addresses several issues that have received little attention in recent models of assortative mating and speciation. Firstly, it is often assumed that females have a fixed level of choosiness throughout the mating season. This is the case, for example, in the highly influential model of Gavrilets and Boake (1998), used e.g. by Kirkpatrick and Nuismer (2004), Schneider (2005), Schneider and Bürger (2006), Pennings et al. (2008), Ripa (2009), Peischl and Schneider (2010), and Kisdi and Priklopil (2011). In reality, however, females become gradually less choosy towards the end of the mating season, so as to avoid remaining unmated (Backwell and Passmore 1996, Thomas et al. 1998, Gray 1999, Kodric-Brown and Nicoletto 2001, Moore and Moore 2001; Tinghitella et al. 2013). Resorting to self-fertilization, despite the cost of inbreeding, at the end of the reproductive age also amounts to relaxing choosiness (Tsitrone et al. 2003). To account for this, Kopp and Hermisson (2008) assumed that at their very last encounter, females accept any male, but otherwise choosiness is constant. Our model quantitatively predicts how females should become less choosy as the mating season progresses. There is always a period at the end of the mating season when females should accept any male (unless some matings result in no offspring at all). If the mating season is short relative to the rate of encountering males, then random mating is the best strategy throughout the mating season (see inequality

(7)).

Secondly, many speciation models assume self-referent assortative mating, where females prefer males that are similar to themselves with respect to the ecological trait (Doebeli 1996, Matessi et al. 2001, Kirkpatrick and Nuismer 2004, Schneider 2005, Schneider and Bürger 2006, Pennings et al. 2008, Ripa 2009, Peischl and Schneider 2010, Kisdi and Priklopil 2011); but this means that maladapted females are constrained to prefer maladapted males. Our model imposes no constraint on which males a female may prefer. In particular, benefits from a given male may depend on the type of the female. This is often ignored in the so-called good genes models, where the effect of paternal genes are assumed to be independent of the recipient (Iwasa et al. 1991, Iwasa and Pomiankowski 1994, Proulx 2001, Lorch et al. 2003). Indiscriminate preference for fit males is problematic if females choose males from across an adaptive valley, which may result in producing unfit phenotypes and can cause chaotic dynamics of allele frequencies (van Doorn et al. 2009, Priklopil 2012).

Thirdly, most of the recent assortative mating models assume that each female can encounter a fixed number of males before the mating season runs out, or that there is no maximum number of encounters and all females are mated (see references above). In reality, the number of males a female encounters depends on population density and is affected by the stochasticity inherent in the search process. Our model incorporates both of these factors naturally by assuming that mate search is a Poisson process with a density-dependent encounter rate λ. It is also straightforward to extend the model such that λ depends on female type. For example, if mate sampling is costly due to time and energy expenditures (Thornhill 1984, Slagsvold et al. 1988, Alatalo et al. 1988, Milinski and Bakker 1992) or due to increased risk of predation (Sakaluk and Belwood 1984, Forsgren 1992), a female better adapted to the environment might bear the costs easier and sample more mates (Jennions and Petrie 1997, Cotton et al. 2006).

In the Levene model with disruptive ecological selection ($h > 1/2$), we found that an ESS with nearly perfect reproductive isolation exists if females encounter on average about 10 males during the mating season (Figure 5, shaded area), provided that the polymorphism is maintained. This number is roughly in agreement with the results of Kopp and Hermisson (2008), who assumed a fixed number of encounters and self-referent assortative mating in a different ecological model. There are, however, two facts that complicate matters. Firstly, genetic polymorphism may be lost due to the positively frequency-dependent sexual selection that is induced by assortative mating (see Matessi et al. 2001). If ecological selection is weak, then the polymorphism is stable only if a large number of males is encountered; for $s = 0.05$, this raises the necessary number of encounters to about 20. Secondly, the model can have alternative evolutionarily stable strategies without strong reproductive isolation at the same parameter values where an ESS with reproductive isolation exists. This happens when ecological selection is strong (Figure 5b) so that, surprisingly, weaker selection may sometimes be more conducive to reproductive isolation because then the alternative evolutionarily stable strategies are absent.

Acknowledgements

We thank two anonymous reviewers whose comments on an earlier manuscript greatly improved this paper. The research leading to these results received funding from the Academy of Finland and the People Programme (Marie Curie Actions) of the European Union's Seventh Framework Programme (FP7/2007-2013) under REA grant agreement n°[291734].

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Figure 1. Time-thresholds used by a female f during a mating season of length T. (a) A time-threshold strategy where males of types $g_1, \ldots, g_n$ are accepted right from the beginning of the season. Males of type g_i (with $i > n$) are accepted only after time t_{f,g_i}. For convenience, we set $t_{f,g_{k+1}}$ equal to the length of the mating season, T. (b) A particular solution to equation (2) which describes how the expected benefit $E_f(t)$ changes throughout the mating season. ε_i abbreviates ε_{f,g_i}, and similarly τ_i abbreviates τ_{f,g_i}. Males with types $g_1, \ldots, g_n$ offer higher benefits than the initial expectation $E_f(0)$, i.e. $\varepsilon_1 \geq \cdots \geq \varepsilon_n > E(0)$, and therefore they are accepted right from the beginning of the mating season. Males with type g_i offer higher benefits than the female is expected to receive in the future only after the time-threshold τ_i. To receive the maximum benefits, the female hence should reject male g_i before time τ_i and accept after τ_i. The expression for τ_i is given in equation (3).

Figure 2. Example 2: (a) A plot where the optimal time-thresholds lead to non-random and random mating. The parameter values are $\lambda T = 3, \varepsilon_g = 1$ and $\varepsilon_b = 0.75$. The dashed line indicates the cross section and the value of q used in plot (b). (b) The optimal time-threshold as a function of p_g, when $q = 0.2$. The other parameter values are as in (a).

Figure 3. The optimal time-threshold function $\tau_f(g)$ when male types are identified with the benefit they provide ($\varepsilon_f(g) = g$). (a) The benefits are uniformly distributed over the interval $[0, 1]$; (b) the benefits are lognormally distributed with $\mu = 1, \sigma = 1$. Parameters: $\lambda = 1$ and $T = 3$.

Figure 4. Ecological selection in the Levene model under random mating. Panels A-D show the relative viabilities w_{aa}, w_{aA}, w_{AA} as functions of the allele frequencies P_a and P_A at Hardy-Weinberg equilibrium. The middle panel shows for which parameter values s, h configurations A-D exist and whether the symmetric polymorphic equilibrium $(\hat{P}_{aa}, \hat{P}_{aA}, \hat{P}_{AA}) = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$ is stable. In panel A, near the fixation equilibria ($P_a = 0$ or $P_A = 0$) the heterozygotes have higher viability fitness than the common homozygotes so that the polymorphism is protected. Because the heterozygotes do better also at equal allele frequencies, selection is stabilizing at the symmetric equilibrium. In panel B, near the fixation equilibria selection is similar to panel A, but at equal allele frequencies the heterozygotes do worse than homozygotes, hence ecological selection is disruptive at the symmetric equilibrium. The symmetric equilibrium is globally stable in A and B. In C and D heterozygotes do worse than homozygotes at all allele frequencies and both fixation equilibria are stable. However, in C there exists a stable symmetric equilibrium (unprotected polymorphism) whereas in D the symmetric equilibrium is unstable and polymorphism is not maintained (not shown). In area C, the polymorphism is hence unprotected whereas in area D polymorphism is not maintained. In the middle panel, areas B

and C are separated by the line $h_0 = \frac{1}{2-s}$, whereas areas C and D are separated by the line $h_{\text{int}} = \frac{2-\sqrt{4-4s-s^2}}{2s}$ (see Supporting Information S4 for derivation). The dashed vertical lines mark the values of s used in Figure 5. Note that this figure would look different for non-random mating, because the genotype distribution is then different.

Figure 5. ESS mating strategies of the homozygote females for (a) $s = 0.3$ and (b) $s = 0.7$. See text for explanation. Note that in (a), $h_0 = 0.5882$ and $h_{\text{int}} = 0.5896$, so that the RM_{UP} region in-between is too narrow to be seen.

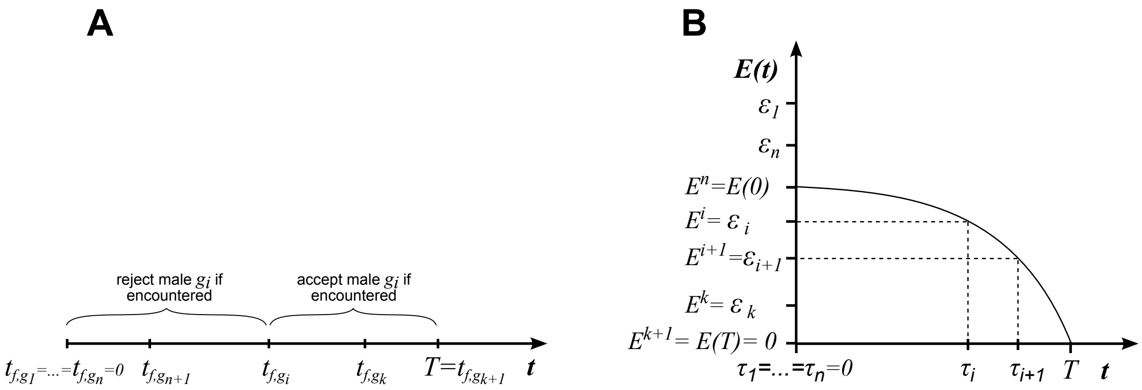
A
reject male g_i if encountered
accept male g_i if encountered
$t_{f,g_1}=\ldots=t_{f,g_n}=0$
$t_{f,g_{n+1}}$
t_{f,g_i}
t_{f,g_k}
$T=t_{f,g_{k+1}}$
t
B
$E(t)$
ε_1
ε_n
$E^n=E(0)$
$E^i=\varepsilon_i$
$E^{i+1}=\varepsilon_{i+1}$
$E^k=\varepsilon_k$
$E^{k+1}=E(T)=0$
$\tau_1=\ldots=\tau_n=0$
τ_i
τ_{i+1}
T
t

Figure 1:

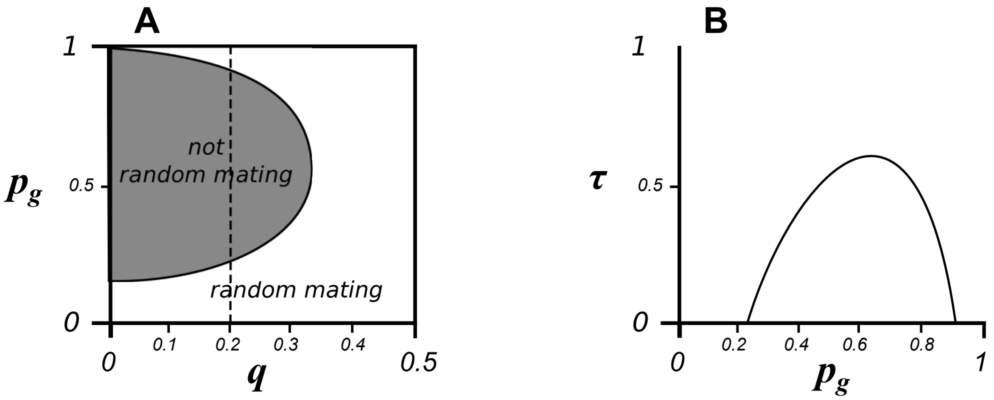
A
B
not random mating
random mating
1
0.5
0
0
0.1
0.2
0.3
0.4
0.5
p_g
q
τ
1
0.5
0
0
0.2
0.4
0.6
0.8
1
p_g

Figure 2:

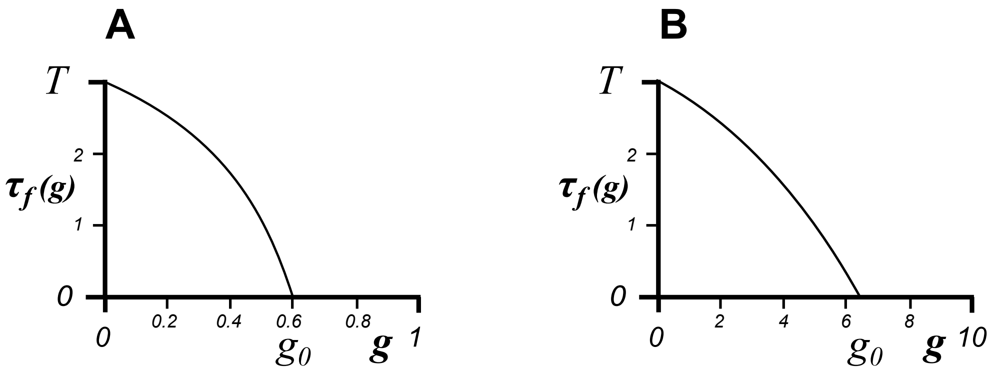

Figure 3:

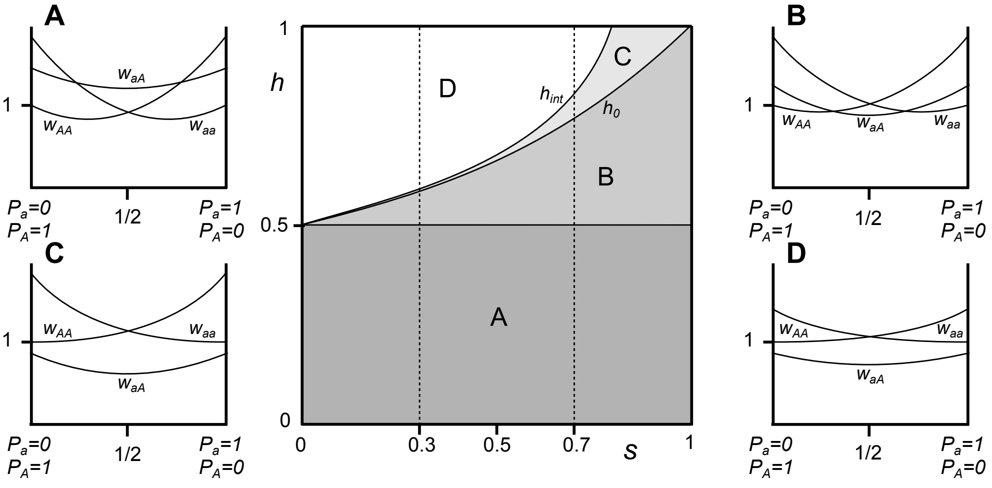
A
1
w_{aA}
w_{AA}
w_{aa}
P_a=0
P_A=1
1/2
P_a=1
P_A=0
C
1
w_{AA}
w_{aa}
w_{aA}
P_a=0
P_A=1
1/2
P_a=1
P_A=0
1
h
0.5
0
D
C
h_{int}
h_0
B
A
0
0.3
0.5
0.7
1
s
B
1
w_{AA}
w_{aA}
w_{aa}
P_a=0
P_A=1
1/2
P_a=1
P_A=0
D
1
w_{AA}
w_{aa}
w_{aA}
P_a=0
P_A=1
1/2
P_a=1
P_A=0

Figure 4:

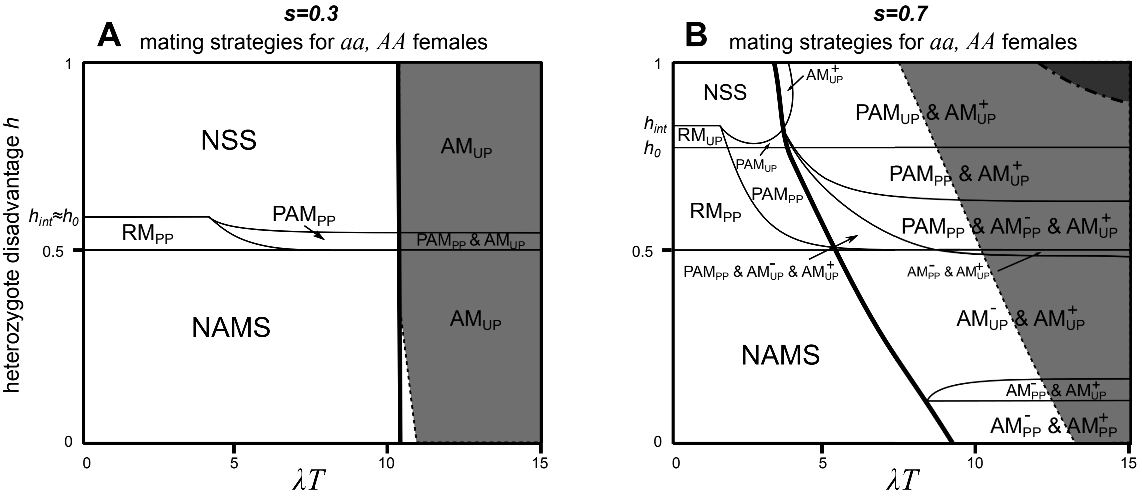
A
s=0.3
mating strategies for aa, AA females
heterozygote disadvantage h
1
$h_{int}≈h_0$
0.5
0
NSS
RM_{PP}
PAM_{PP}
PAM_{PP} & AM_{UP}
AM_{UP}
AM_{UP}
NAMS
0
5
10
15
λT
B
s=0.7
mating strategies for aa, AA females
1
h_{int}
h_0
0.5
0
NSS
AM^+_{UP}
RM_{UP}
PAM_{UP}
PAM_{PP}
RM_{PP}
PAM_{UP} & AM^+_{UP}
PAM_{PP} & AM^+_{UP}
PAM_{PP} & AM^-_{PP} & AM^+_{UP}
PAM_{PP} & AM^-_{UP} & AM^+_{UP}
AM^-_{PP} & AM^+_{UP}
AM^-_{UP} & AM^+_{UP}
NAMS
AM^-_{PP} & AM^+_{UP}
AM^-_{PP} & AM^+_{PP}
0
5
10
15
λT

Figure 5:

Supporting Information S1: Derivations for discrete male types

DERIVATION OF EQUATION (2)

We can write the expected benefit at time t in two parts, corresponding to the possibilities that in the next time interval dt the female will or will not encounter a male:

$$E_f(t) = (\lambda dt)\left[\sum_{\varepsilon_i < E_f(t+dt)} \tilde{P}_i E_f(t+dt) + \sum_{\varepsilon_i > E_f(t+dt)} \tilde{P}_i \varepsilon_{f,g_i}\right] + (1-(\lambda dt))\, E_f(t+dt) \tag{S1.1}$$

Here (λdt) is the probability that the female encounters a male in the time interval $[t, t+dt]$. In this case, the female either rejects the male, and then she has $E_f(t+dt)$, the expected benefit of unmated females dt time later (first summation within the brackets); or accepts the male, in which case her search is terminated and receives the benefit provided by the male (second summation within the brackets). The summations $\sum_{\varepsilon_i < E_f(t+dt)}$ and $\sum_{\varepsilon_i > E_f(t+dt)}$ mean that we sum over all $i = 1, \ldots, k$ for which ε_{f,g_i} is smaller or greater, respectively, than the expected benefit $E_f(t+dt)$. If the female does not encounter a male, which happens with probability $(1-(\lambda dt))$, then she has the expected benefit of unmated females dt later, $E_f(t+dt)$. Equation (S1.1) can be rearranged into

$$\frac{1}{dt}\left[E_f(t+dt) - E_f(t)\right] = \lambda\left[\sum_{\varepsilon_i > E_f(t+dt)} \tilde{P}_i E_f(t+dt) - \sum_{\varepsilon_i > E_f(t+dt)} \tilde{P}_i \varepsilon_{f,g_i}\right], \tag{S1.2}$$

and taking the limit $dt \to 0$, we get

$$\begin{aligned}\dot{E}_f(t) &= \lambda\left[\sum_{\varepsilon_i > E_f(t)} \tilde{P}_i E_f(t) - \sum_{\varepsilon_i > E_f(t)} \tilde{P}_i \varepsilon_{f,g_i}\right] = \lambda \sum_{\varepsilon_i > E_f(t)} \tilde{P}_i \left[E_f(t) - \varepsilon_{f,g_i}\right] = \\ &= \lambda\left[E_f(t) - \sum_{i=1}^{k} \tilde{P}_i \max\{E_f(t), \varepsilon_{f,g_i}\}\right].\end{aligned} \tag{S1.3}$$

SOLUTION OF EQUATION (2)

In the main text, we have proven that $E_f(t)$ is a decreasing function of time, and therefore there exist time-thresholds τ_{f,g_i} and $\tau_{f,g_{i+1}}$ such that the male types $g_1, ..., g_i$ are accepted at times $\tau_{f,g_i} < t < \tau_{f,g_{i+1}}$. In this time interval, equation (S1.3) simplifies to

$$\dot{E}_f(t) = \lambda\left(\sum_{j=1}^{i} \tilde{P}_j\right)\left[E_f(t) - \frac{\sum_{j=1}^{i} \tilde{P}_j \varepsilon_{f,g_j}}{\sum_{j=1}^{i} \tilde{P}_j}\right] = \lambda\left(\sum_{j=1}^{i} \tilde{P}_j\right)\left[E_f(t) - \bar{E}_f^i\right] \tag{S1.4}$$

This separable differential equation is readily integrated over $[\tau_{f,g_i}, \tau_{f,g_{i+1}}]$ to yield

$$\ln \frac{\bar{E}_f^i - E(\tau_{f,g_{i+1}})}{\bar{E}_f^i - E_f(\tau_{f,g_i})} = \lambda\left(\sum_{j=1}^{i} \tilde{P}_j\right)(\tau_{f,g_{i+1}} - \tau_{f,g_i}) \tag{S1.5}$$

and with $E_f(\tau_{f,g_i}) = \varepsilon_{f,g_i} \equiv E_f^i$, this is equivalent to equation (3).

MATING PROBABILITIES WHEN MISTAKES OCCUR IN EVALUATING MALES

Suppose that females can distinguish the perceived male types $g_1, ..., g_k$ in a population with true male types $h_1, ..., h_{k_T}$. The number of true male types, k_T, need not be the same as the number of perceived types, k; for example, there may be several true types with different benefits whom the females cannot distinguish from each other. To keep with the notation of the main text, we denote the frequencies of perceived types in the mating season with $\tilde{P}_1, ..., \tilde{P}_k$, whereas the frequencies of true types are $\tilde{P}_1^T, ..., \tilde{P}_{k_T}^T$. Let q_{ij} be the probability that a female evaluates a male of true type h_j as a male of perceived type g_i. The probability that a female f eventually mates with a male of true type h_i is given by

$$Q_{f,h_i}^T \tilde{P}_i^T = \sum_{j=1}^{k} r_{ij} Q_{f,g_j} \tilde{P}_j \tag{S1.6a}$$

where Q_{f,g_j} is from equation (5), r_{ij} is the probability that a male of perceived type g_j is of true type h_i, given by Bayes' theorem,

$$r_{ij} = \frac{q_{ji} \tilde{P}_i^T}{\sum_{l=1}^{k_T} q_{jl} \tilde{P}_l^T} \tag{S1.6b}$$

and from the identity $r_{ij} \tilde{P}_j = q_{ji} \tilde{P}_i^T$, the frequencies of perceived types are

$$\tilde{P}_j = \frac{q_{ji} \tilde{P}_i^T}{r_{ij}}. \tag{S1.6c}$$

Equations (S1.6) express the mating probabilities among true types in terms of the frequencies of true types (which derive from the ecological model that describes the origin of variation) and the probabilities of making mistakes, q_{ij}. Note that the probabilities q_{ij} (or even the number of perceived male types) may depend on the female's type f. In this case, r_{ij} and the frequencies of perceived types ($\tilde{P}_i$) are different for different female types, but the formulas above can be used for each female type separately.

Supporting Information 2: Continuous distribution of male types

Suppose that the male type g has a continuous distribution with a probability density function $p(g)$. In this case, the best mating strategy of female f is specified by a function $\tau_f(g)$, which gives the time-threshold after which the female should accept a male of type g. Let $\varepsilon_f(g)$ denote the benefit a female f receives if she mates with a male of type g; we assume that the benefit is a continuously differentiable function of male type.

Equation (2) directly generalizes to the continuous case in the form

$$\dot{E}_f(t) = \lambda \left[E_f(t) - \int\limits_{-\infty}^{\infty} p(g) \max\{E_f(t), \varepsilon_f(g)\} dg \right] \tag{S2.1}$$

As in the discrete case, a female should start accepting a male of type g when the benefit from this male equals the benefit she can expect if she keeps searching, i.e., we have

$$E_f(\tau_f(g)) = \varepsilon_f(g) \tag{S2.2}$$

Differentiating both sides of this equation yields $\dot{E}_f(\tau_f(g))\tau_f'(g) = \varepsilon_f'(g)$ (where prime denotes differentiation with respect to g). Substituting $\dot{E}_f$ from (S2.1) and using (S2.2) again yields

$$\tau_f'(g) = \frac{\varepsilon_f'(g)}{\lambda \left[\varepsilon_f(g) - \int_{-\infty}^{\infty} p(\tilde{g}) \max\{\varepsilon_f(g), \varepsilon_f(\tilde{g})\} d\tilde{g} \right]} \tag{S2.3}$$

The right hand side of this differential equation contains only known functions and therefore can readily be integrated to obtain $\tau_f(g)$ up to a constant. To find the integration constant, one possibility is to (numerically) integrate equation (S2.1) with $E_f(T) = 0$, and find a male type g_0 such that $\varepsilon_f(g_0) = E_f(0)$; then we have $\tau_f(g_0) = 0$, and we can use this as the initial value to go with the differential equation in (S2.3). There is a simpler way (not involving an integral with the $\max$ function in (S2.1)) to find the integration constant if the benefit has a global minimum at some male type g^* (i.e., if $\varepsilon_f(g^*) \leq \varepsilon_f(g)$ for all g in the support of the male type distribution). If $\varepsilon_f(g^*) > 0$ such that even the worst male type gives a positive benefit, then there is a time interval $[\tau_f(g^*), T]$ of positive length at the end of the mating season when $\max\{E_f(t), \varepsilon_f(g)\} = \varepsilon_f(g)$ for all g and the female should accept all males. Integrating equation (S2.1) over this interval of time yields

$$\tau_f(g^*) = T - \frac{t}{\lambda} \ln \left[\frac{\bar{E}_f}{\bar{E}_f - \varepsilon_f(g^*)} \right], \tag{S2.4}$$

where $\bar{E}_f = \int_{-\infty}^{\infty} p(g)\varepsilon_f(g) dg$ is the expected benefit from a random male (this result is analogous to equation (3) of the case of discrete male types, with $\bar{E}_f = \bar{E}_f^k$ and $i = k$). If $\varepsilon_f(g^*) = 0$, then $\tau_f(g^*) = T$.

The solution of equation (S2.3) can be negative for those male types g who should be accepted from the beginning of the mating season. As in the discrete case, these negative values must be truncated to zero. Since the right hand side of equation (S2.3) does not depend on τ_f, the truncation has no effect on the non-negative part of the solution.

Suppose now that $\varepsilon_f(g) = g$ and g assumes only non-negative values. In this case, equation (S2.3) simplifies to

$$\tau_f'(g) = \frac{1}{\lambda \left[g - \int_0^{\infty} p(\tilde{g}) \max\{g, \tilde{g}\} d\tilde{g} \right]} = \frac{-1}{\lambda \left[\int_g^{\infty} p(\tilde{g})(\tilde{g} - g) d\tilde{g} \right]} \tag{S2.5}$$

with the initial value $\tau_f(0) = T$, so we have the solution explicitly as

$$\tau_f(g) = T - \frac{1}{\lambda} \int\limits_0^g \frac{1}{\int_{\hat{g}}^{\infty} p(\tilde{g})(\tilde{g} - \hat{g}) d\tilde{g}} d\hat{g} \tag{S2.6}$$

If the benefits are uniformly distributed over the interval $[0, 1]$, then

$$p(g) = \begin{cases} 1 & \text{if } 0 \leq g \leq 1 \\ 0 & \text{otherwise} \end{cases} \tag{S2.7}$$

and the solution simplifies to

$$\tau_f(g) = T - \frac{1}{\lambda} \int\limits_0^g \frac{1}{\int_{\hat{g}}^1 (\tilde{g} - \hat{g}) d\tilde{g}} d\hat{g} = T - \frac{2g}{\lambda(1-g)} \tag{S2.8}$$

The optimal time-threshold is given by this formula when its value is positive, and zero otherwise (cf. equation (10) in the main text; Figure 3a). If the benefits follow the lognormal distribution (equation (11) in the main text), then the integrals in formula (S2.6) must be evaluated numerically to obtain $\tau_f(g)$ as shown in Figure 3b.

Supporting Information 3: Reproductive values as indirect benefits

REPRODUCTIVE VALUES

Let $N_{fg}(t)$ denote the number of couples where the female and the male have genotypes f and g, respectively and let $\mathbf{N} = [N_{11}, N_{12}, \ldots, N_{1k}, N_{21}, \ldots]^T$. Recall that a male can mate several times and can thus be part of several couples. The population dynamics are given by the matrix model $\mathbf{N}(t+1) = \mathbf{A}(t)\mathbf{N}(t)$, where $\mathbf{A}(t)$ is a $k \times k$ block matrix of $k \times k$ blocks with elements

$$A_{rh,fg} = \tfrac{1}{2}\left[KR_{f,g\to r}v_r Q_{r,h}\tilde{P}_h + KR_{f,g\to h}v_h Q_{r,h}\tilde{P}_r\right]. \tag{S3.1}$$

The two terms of this expression correspond to the daughters and the sons of the couple (f,g), respectively, who become half of a couple (r,h) a generation later. At equilibrium, the elements of $\mathbf{A}$ are constants and the dominant eigenvalue of $\mathbf{A}$ is 1. The (fg)'th element of the dominant left eigenvector of $\mathbf{A}$,

$$\begin{aligned}\varepsilon_{fg} &= \sum_r\sum_h \varepsilon_{rh}A_{rh,fg} = \\ &= \frac{K}{2}\left[\sum_r\sum_h R_{f,g\to r}v_r Q_{r,h}\tilde{P}_h\varepsilon_{rh} + \sum_r\sum_h R_{f,g\to h}v_h Q_{r,h}\tilde{P}_r\varepsilon_{rh}\right] = \\ &= \frac{K}{2}\sum_r\sum_h R_{f,g\to r}v_r\tilde{P}_h\left(Q_{r,h}\varepsilon_{rh} + Q_{h,r}\varepsilon_{hr}\right)\end{aligned} \tag{S3.2}$$

is the benefit that a female f receives from being part of a couple (f,g), as given by equation (12) in the main text. Equation (12) determines the benefits only up to a constant, but this is irrelevant to finding the best time-thresholds as they depend only on the ratios of benefits. The elements of the left eigenvector are the reproductive values of the corresponding couples (Caswell 2006). The best time-thresholds of a female maximize her reproductive value by choosing to be part of a couple with the highest reproductive value (cf. McNamara 1991).

INDIRECT BENEFITS FOR A SINGLE LOCUS UNDER RANDOM MATING

For a single locus under random mating, the reproductive value of a couple simplifies to the expected viability fitness of their offspring. To see this, recall that under random mating, the probability that a female f is mated to a male g is the probability that she is mated at all times the frequency of genotype g, i.e., using the notation introduced at equation (13) in the main text, $Q_{f,g}\tilde{P}_g = \bar{Q}\tilde{P}_g$, from which we obtain that $Q_{f,g} = \bar{Q}$ is the same for all f, g. Equation (12) therefore simplifies to

$$\varepsilon_{f,g} = K\sum_r R_{f,g\to r}v_r\bar{Q}\Big(\sum_h \tilde{P}_h\varepsilon_{r,h}\Big) \tag{S3.3}$$

Since at equilibrium $K\bar{v}\bar{Q} = 1$ (cf. equation (13)), $Kv_r\bar{Q}$ equals the relative viability fitness $w_r = \frac{v_r}{\bar{v}}$ and we have

$$\varepsilon_{f,g} = \sum_r R_{f,g\to r}w_r z_r \tag{S3.4}$$

with $z_r = \sum_h \tilde{P}_h\varepsilon_{r,h}$. Now we prove that for a single locus and under random mating, $z_r = z$ is the same for all genotypes r. Multiplying both sides of equation (S3.4) with $\tilde{P}_g$ and summing over all g yields

$$z_f = \sum_g \tilde{P}_g\sum_r R_{f,g\to r}w_r z_r \quad \text{for } f = 1, ..., k, \tag{S3.5}$$

which is a linear system of equations for $z_1, ..., z_k$. This linear system is satisfied by $z_r = z$ for all r if

$$\sum_g \tilde{P}_g\sum_r R_{f,g\to r}w_r = 1 \tag{S3.6}$$

holds for all f. This is indeed the case for a single locus under random mating, where $R_{ij,mn\to im} = \frac{1}{4}$ and $\tilde{P}_{ij} = p_i p_j w_{ij}$ (where p_i is the frequency of allele A_i and we used that $\bar{w} = 1$). Substituting these into the left hand side of equation (S3.6) and using repeatedly that in equilibrium, all allelic (marginal) fitnesses are equal and thus $\sum_j p_j w_{ij} = 1$ for all i, we obtain for the female genotype $f = A_m A_n$

$$\begin{aligned}\sum_g \tilde{P}_g \sum_r R_{f,g\to r} w_r &= \frac{1}{4}\sum_i \sum_j p_i p_j w_{ij}(w_{im} + w_{in} + w_{jm} + w_{jn}) \\ &= \frac{1}{4}\sum_i p_i(w_{im} + w_{in}) + \frac{1}{4}\sum_j p_j(w_{jm} + w_{jn}) \\ &= \frac{1}{4}(1+1) + \frac{1}{4}(1+1) = 1\end{aligned}$$

This proves that $z_r = z$ is the same for all genotypes r, and therefore equation (S3.4) reduces to $\varepsilon_{f,g} = z\sum_r R_{f,g\to r} w_r$ where z is an arbitrary constant (recall that the reproductive values are determined only up to a constant, and the constant z cancels in equation (3)).

EXTENSION TO ITEROPAROUS POPULATIONS

Equation (12) can straightforwardly be extended to iteroparous organisms. Let $l_r(a)$ denote the probability that a newborn of genotype r is alive at age a (with non-overlapping generations, $l_r(1) = v_r$ and $l_r(a) = 0$ for $a \geq 2$), and let $2K_r(a)$ be the number of offspring born to a female of of genotype r and age a. In general $l_r(a)$ and $K_r(a)$ are density- and frequency-dependent, but we consider their equilibrium values only. The reproductive value accrued by a female of age a and genotype f in one season from mating with a male of genotype g is then

$$\varepsilon_{f,g}(a) = 2K_f(a)\sum_r R_{f,g\to r}\cdot\frac{1}{2}\sum_{a'=1}^{\infty} l_r(a')\Big(\sum_h Q_{r,h}\tilde{P}_h\frac{\varepsilon_{r,h}(a')}{2} + \sum_h Q_{h,r}\tilde{P}_h\sum_{a''=1}^{\infty}\frac{l_h(a'')}{L_h}\frac{\varepsilon_{h,r}(a'')}{2}\Big), \quad \text{(S3.7)}$$

where $\tilde{P}_h$ is the frequency of genotype h in the entire population, $L_h = \sum_{a=1}^{\infty} l_h(a)$ is the expected life span of an individual with genotype h, and $\frac{l_h(a)}{L_h}$ is the probability that a female of genotype h is of age a at equilibrium. Note that when femle fecundity depends on her age and genotype, the benefits are no longer symmetric, i.e., $\varepsilon_{f,g}(a)$ is not the same as $\varepsilon_{g,f}(a)$.

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Supporting Information 4: Detailed discussion and derivations for the Levene model

MAINTENANCE OF ASSORTATIVE MATING

In the Levene model, two mechanisms maintain assortative mating by stabilizing the AM strategy: ecological selection against heterozygotes (for $h > \frac{1}{2}$ only) and sexual selection against heterozygotes (by the AM strategy itself; see main text). When the strength of ecological selection is moderate, then it is mainly sexual selection that disfavours heterozygote males and therefore h has little effect on whether an AM strategy is evolutionarily stable; in Figure 5a, the thick line, which separates the region where the AM strategy is stable, is almost vertical. When ecological selection is strong, then a disadvantage of heterozygotes ($h > \frac{1}{2}$) facilitates AM, whereas an advantage of heterozygotes ($h < \frac{1}{2}$) hinders it (Figure 5b).

At $h = \frac{1}{2}$, all genotypes have equal viabilities at the symmetric equilibrium so that whether or not the AM solution exists is independent of the strength of selection. However, the stability of this solution with respect to perturbing the genotype frequencies still depends on s (see below) such that with weaker selection, stable solutions exist only at higher λT (compare Figure 5a and b).

At $h = \frac{1}{2}$, also reproductive isolation reaches the level $F = 0.99$ at the same value of λT irrespectively of s, provided that the polymorphism is stable in the population genetic sense. When heterozygotes are at a disadvantage during ecological selection ($h > \frac{1}{2}$), stronger selection facilitates reproductive isolation because heterozygote disadvantage selects for stronger discrimination. For $h < \frac{1}{2}$, this effect is the reverse, yet sexual selection from assortative mating alone can lead to strong reproductive isolation if λT is sufficiently high.

PROTECTED VERSUS UNPROTECTED POLYMORPHISMS

A polymorphism is protected if the fixation equilibria are unstable. In this section, we investigate the stability of the fixation equilibrium $(\hat{P}_{aa}, \hat{P}_{aA}, \hat{P}_{AA}) = (1, 0, 0)$ with respect to perturbations of the genotype frequencies for RM, PAM and AM mating strategies with fixed time-thresholds (by symmetry, the stability conditions of the opposite fixation equilibrium $(\hat{P}_{aa}, \hat{P}_{aA}, \hat{P}_{AA}) = (0, 0, 1)$ are the same).

The fixation equilibrium $(\hat{P}_{aa}, \hat{P}_{aA}, \hat{P}_{AA}) = (1, 0, 0)$ is unstable when the marginal fitness of allele A in a population monomorphic for allele a exceeds 1, i.e., when

$$W_a(A) = \frac{1}{2}\left(\frac{Q_{aa,aA} + Q_{aA,aa}}{Q_{aa,aa}}\right) w_{aA} > 1, \tag{S4.1}$$

(Kisdi and Priklopil 2011). In this condition, w_{aA} is to be evaluated at the fixation equilibrium, which in the Levene model yields

$$w_{aA} = \frac{1}{2}\left(\frac{1-hs}{1} + \frac{1-hs}{1-s}\right) \tag{S4.2}$$

$Q_{aa,aA}$, $Q_{aA,a}$ and $Q_{aa,aa}$, defined in equation (5), are evaluated at the fixation equilibrium using the time-thresholds of the RM, PAM and AM mating strategies as follows:

RM: Under random mating, $Q_{aa,aA} = Q_{aA,aa} = Q_{aa,aa} = 1 - e^{-\lambda T}$, and condition (S4.1) is reduced to $W_a(A) = w_{aA} > 1$. Using (S4.2), this can be written as

$$h < h_0 = \frac{1}{2-s}. \tag{S4.3}$$

PAM: Under partial assortative mating with time-thresholds $t_1 = t_2 = 0$ and $t_3 > 0$, equation (5) yields

$$Q_{aA,aa} = 1 - e^{-\lambda T} \tag{S4.4}$$

$$Q_{aa,aA} = \frac{1}{\tilde{P}_{aa} + \tilde{P}_{aA}}(1 - e^{-\lambda(\tilde{P}_{aa}+\tilde{P}_{aA})t_3}) + (1 - e^{-\lambda(T-t_3)})e^{-\lambda(\tilde{P}_{aa}+\tilde{P}_{aA})t_3} \tag{S4.5}$$

$$Q_{aa,aa} = Q_{aa,aA}, \tag{S4.6}$$

which reduces to $Q_{aa,aA} = Q_{aA,aa} = Q_{aa,aa} = 1 - e^{-\lambda T}$ when evaluated at $(\hat{P}_{aa}, \hat{P}_{aA}, \hat{P}_{AA}) = (1, 0, 0)$. The condition for stability is thus the same as in the RM case, see (S4.3). This result is intuitive, since under both RM and PAM, the homozygote females do not discriminate against the heterozygote males and therefore mating does not influence the marginal fitness of the rare allele.

AM: Under assortative mating with time-thresholds $t_1 = 0$ and $t_2, t_3 > 0$, equation (5) at the fixation equilibrium $(\hat{P}_{aa}, \hat{P}_{aA}, \hat{P}_{AA}) = (1, 0, 0)$ reduces to

$$Q_{aA,aa} = 1 - e^{-\lambda T} \tag{S4.7}$$

$$Q_{aa,aA} = e^{-\lambda t_2} - e^{-\lambda T} \tag{S4.8}$$

$$Q_{aa,aa} = 1 - e^{-\lambda T}, \tag{S4.9}$$

which leads to the condition

$$W_a(A) = \left[1 - \frac{1}{2} \cdot \frac{1 - e^{-\lambda t_2}}{1 - e^{-\lambda T}}\right] w_{aA} > 1. \tag{S4.10}$$

for the instability of the fixation equilibrium with w_{aA} given in (S4.2). For $t_2 > 0$ we have $w_{aA} > W_a(A)$, so that the fixation equilibrium is easier unstable (i.e., the polymorphism is easier protected) for RM and PAM strategies than for AM strategies. This is because under an AM strategy, the resident homozygote females discriminate against the heterozygote males carrying the rare allele. AM strategies therefore imply sexual selection against heterozygote males, whereby they stabilize the fixation equilibria and hinder protected polymorphisms.

To determine whether the polymorphism is protected under an ESS strategy of the AM configuration, the ESS time-threshold τ_2 must be substituted for t_2 in (S4.10). For ESSs of the RM and PAM configurations, the condition of protected polymorphism in (S4.3) does not depend on the ESS time-thresholds.

EXISTENCE AND STABILITY OF THE RANDOM MATING SOLUTION

We can obtain the conditions under which random mating is an evolutionarily stable mating strategy analytically using inequality (7) and checking the population genetic stability of the symmetric equilibrium $(\hat{P}_{aa}, \hat{P}_{aA}, \hat{P}_{AA}) = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$ of the Levene model. We assume $h > \frac{1}{2}$ such that heterozygotes are at a disadvantage during ecological selection. (Note however that the RM solution exists also for $h < \frac{1}{2}$, in the region marked $NAMS$ in Figure 5, but since here heterozygotes are at an advantage so that the condition $\varepsilon_{aa,aa} \geq \varepsilon_{aa,aA} \geq \varepsilon_{aa,AA}$ is violated, we do not pursue the analysis of this part.)

Heterozygotes always mate at random (see the main text), and therefore it suffices to evaluate inequality (7) for the homozygote females $f = aa$ (by symmetry, the same condition applies also to AA). For a single locus under random mating, the benefits are given by the expected viability fitness of the offspring (see Supporting Information S3); and with heterozygote disadvantage during viability selection, AA males give the least benefit to aa females so that we have

$$E^k_{aa} = \varepsilon_{aa,AA} = w_{aA} = \frac{1 - hs}{1 - \frac{1}{2}s(h + \frac{1}{2})}.$$

The expected benefit $\bar{E}^k_{aa}$ is given by

$$\begin{aligned}\bar{E}^k_{aa} &= \frac{1}{4}\varepsilon_{aa,aa} + \frac{1}{2}\varepsilon_{aa,aA} + \frac{1}{4}\varepsilon_{aa,AA} \\ &= \frac{1}{4}w_{aa} + \frac{1}{2}\left(\frac{1}{2}w_{aa} + \frac{1}{2}w_{aA}\right) + \frac{1}{4}w_{aA} \\ &= \frac{1}{2}w_{aa} + \frac{1}{2}w_{aA} = 1\end{aligned}$$

where the last step can be confirmed by direct substitution of the viability fitnesses, but also follows from the fact that $w_{aa} = w_{AA}$ by symmetry and $\bar{w} = 1$. Substituting E^k_{aa} above and $\bar{E}^k_{aa} = 1$ into inequality (7) yields

$$\lambda T \leq \ln \frac{1}{1 - E^k_{aa}} = \ln \frac{4 - s(2h+1)}{s(2h-1)} \quad \text{for } h > \frac{1}{2}.$$

This condition is satisfied to the left of the curve that delimits the RM area in Figure 5.

To establish the population genetic stability of the symmetric equilibrium under random mating, we need to evaluate the Jacobian of the population genetic recursion

$$P'_r = \sum_{g,h} P_g P_h w_g w_h R_{g,h\to r}$$

where prime denotes the next generation (cf. equation (13); recall that under random mating, $Q_{g,h} = \bar{Q}$). With the three genotypes aa, aA, AA, this reads

$$\begin{aligned}P'_{aa} &= P^2_{aa}w^2_{aa} + P_{aa}P_{aA}w_{aa}w_{aA} + \tfrac{1}{4}P^2_{aA}w^2_{aA} \\ P'_{aA} &= P_{aa}P_{aA}w_{aa}w_{aA} + 2P_{aa}P_{AA}w_{aa}w_{AA} + \tfrac{1}{2}P^2_{aA}w^2_{aA} + P_{AA}P_{aA}w_{AA}w_{aA} \\ P'_{AA} &= P^2_{AA}w^2_{AA} + P_{AA}P_{aA}w_{AA}w_{aA} + \tfrac{1}{4}P^2_{aA}w^2_{aA}\end{aligned}$$

with the relative viability fitnesses from the Levene model from equation (14),

$$\begin{aligned}w_{aa} &= \frac{1}{2}\left(\frac{1}{P_{aa} + P_{aA}(1-hs) + P_{AA}(1-s)} + \frac{1-s}{P_{aa}(1-s) + P_{aA}(1-hs) + P_{AA}}\right) \\ w_{aA} &= \frac{1}{2}\left(\frac{1-hs}{P_{aa} + P_{aA}(1-hs) + P_{AA}(1-s)} + \frac{1-hs}{P_{aa}(1-s) + P_{aA}(1-hs) + P_{AA}}\right) \\ w_{AA} &= \frac{1}{2}\left(\frac{1-s}{P_{aa} + P_{aA}(1-hs) + P_{AA}(1-s)} + \frac{1}{P_{aa}(1-s) + P_{aA}(1-hs) + P_{AA}}\right)\end{aligned}$$

After some algebra, we get that the dominant eigenvalue of the Jacobian evaluated at the symmetric equilibrium $(\hat{P}_{aa}, \hat{P}_{aA}, \hat{P}_{AA}) = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$ is greater than 1, i.e., the symmetric equilibrium is unstable, if

$$h > h_{\text{int}} = \frac{2 - \sqrt{4 - 4s - s^2}}{2s}. \tag{S4.11}$$

h_{int} gives the upper border line of the RM area in Figure 5.

References

[1] Kisdi, E., and T. Priklopil. 2011. Evolutionary branching of a magic trait. J. Math. Biol. 63: 361–397.