# Sequential search and the influence of male quality on female mating decisions

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**Abstract.** The patterns of phenotypic association between mated males and females depend on the decision rules that individuals employ during search for a mate. We generalize the sequential search rule and examine how the shape of the function that relates a male character to the benefit of a mating decision influences the threshold value of the male trait that induces females to terminate search. If the fitness function is linear the optimal threshold value of a male character increases with the slope of the function. The phenotypic threshold criterion declines, all else being equal, if the fitness function is made more concave (or less convex) by an increase of the risk of the function. The expression of the trait in females has no effect on the optimal threshold value of a male character if the fitness function is linear and phenotypic values combine additively to influence the benefit of a mating decision; the phenotypic threshold criterion is ubiquitous among females. A convex fitness function induces females with high trait values to adopt a relatively high phenotypic threshold criterion, whereas a concave fitness function induces such females to adopt a low threshold value for the male trait. Thus, linear, convex and concave fitness functions effect random, assortative and disassortative combinations of phenotypes among mated individuals, respectively. Changes of female search behavior induced by changes of the distribution of

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a male character similarly depend on the shape of the fitness function. A variance-preserving increase of male trait values produces a relatively small increase of the threshold criterion for the male character if the fitness function is concave, relative to conditions in which the fitness function is either linear or convex. Our results suggest that a sequential search rule can in principle induce the kinds of mating patterns observed in nature and that the phenotypic association between mated individuals is likely to depend on how a male character translates into fitness, the distribution of the trait among males and attributes of searching females.

**Key words:** Mate choice – Mate quality – Risk – Sequential search – Sexual selection

## 1. Introduction

Several studies of search behavior and mate choice suggest that females may often employ a sequential search rule, or some similar tactic that involves the use of a threshold acceptance criterion, during search for a mate (Moore and Moore 1988; Real 1990; Zuk et al. 1990; Bakker and Milinski 1991; Milinski and Bakker 1992). The type of search rule used by females is not likely to be universal, however, because the performance of a search tactic, as well as the behavior of a female using a particular rule, will generally depend on the conditions under which females search, constraints on information processing and memory (see Wittenberger 1983; Real 1990). Other rules may perform as well or better than a sequential search rule under some conditions and support for alternative forms of search behavior is evident from field studies of mate choice (Brown 1981; Bensch and Hasselquist 1992). The kind of search rule used by females may often be difficult to discern, however, because relatively detailed information about the distribution of males from which females choose and costs of search may be necessary to formulate rule-specific predictions of female behavior (Wiegmann et al. 1996). Furthermore, the behavior of females that adopt a particular search rule may depend on how the choice of a particular male translates into fitness, as well as the characteristics of the searcher.

The characteristics of searchers are known to influence mating decisions in many organisms, including fishes (Downhower and Brown 1980), frogs (Arak 1983; Robertson 1990), and pigeons (Trivers 1985), as well as humans (Berscheid and Walster 1974; Murstein 1977). Such

condition-dependent mate preferences induce a non-random combination of phenotypes between mated males and females, although other factors, like timing of reproduction, also likely influence observed mating patterns (see Andersson 1994). The phenotypes of mated individuals are often positively correlated (Boag and Grant 1978; Cooke and Davies 1983), particularly with regard to characteristics like body size (Trivers 1985; Alcock 1989), or, less frequently, negatively correlated (Murton et al. 1973; Bateson 1980; Partridge and Halliday 1984). Simple models of search behavior generally fail to reproduce such patterns (Janetos 1980; Real 1990), suggesting that some aspect of these search models is unrepresentative of either the conditions under which individuals search or the actual behavior of searchers (but see Real 1991).

Models of search behavior and mate choice are typically formulated on the assumption that females evaluate male quality directly and this assumption is one potential cause for the incongruency between predictions of search theory and the mating patterns observed under natural conditions (Wiegmann and Mukhopadhyay 1998; see McKenna 1975; Hall et al. 1979). Such a criterion for the evaluation of potential mates guarantees that the choice of the one male over another will yield the same fitness benefit to every female, regardless of the characteristics of a searcher, because male quality is measured in units of fitness. Searchers are, in actuality, likely to use a phenotypic indicator of quality to evaluate potential mates (Andersson 1994). The translation of fitness through a phenotypic character introduces the possible dependence of mating decisions on the phenotype of the searcher. An interdependency of male and female phenotypes on fitness may be particularly prominent in organisms with biparental care. A large female well suited to defend progeny may, for example, improve the survivorship of her offspring relatively little by pairing with a large male over a smaller individual, whereas a small female, less capable of defending progeny, could obtain a substantial benefit from such a mating decision.

The extent to which attributes of searchers influence mating decisions should depend on the functional relationship between fitness and the character used to evaluate potential mates. If a trait acts as a perfect substitute for the fitness benefit of a mating decision, then use of the character to select a mate is tantamount to a direct evaluation of mate quality and, as simple models of search behavior predict, the phenotypic characteristics of searchers may have no influence on search behavior (Janetos 1980; Real 1990). The phenotypic characteristics of potential mates are nevertheless unlikely to have such a perfect linear association with fitness. Embryo survivorship increases linearly

with male body size at a rate higher than unity in bullfrogs (Howard 1978; see also Woodward 1986), as does the growth rate of progeny in some cichlids (Perrone 1978). A character may even have a concave or convex relation to the benefit of a mating decision. In some fishes, the production of offspring increases with diminishing returns as male body size increases (Wiegmann et al. 1992; Wiegmann and Baylis 1995), while fecundity increases exponentially with female body size (Wootton 1990). The number of sperm transferred to female katydids, and other insects (Thornhill 1976), also increases with diminishing returns as male body size increases, as does the relationship between female fertility and sperm transfer (Gwynne 1984). Such fitness functions are likely to provide benefits that are dependent on attributes of searchers. Non-linear functional relationships between fitness and characteristics of potential mates may confer additional complications to the process of search, as the relative advantage of mating with one individual over another may depend on how the distribution of phenotypes is positioned with respect to the fitness function (see Real 1990; Wiegmann et al. 1996).

In this paper, we develop a general form of the sequential search rule which permits the relationship between a male character and fitness to take on any functional form. We examine how female search behavior is expected to depend on the functional relationship between a male trait and fitness and how attributes of females interact with a fitness function to alter search behavior. We also investigate how female search behavior is influenced by the interaction between the fitness function and changes of the distribution of a male trait.

## 2. A generalized sequential search model

### 2.1. Overview of the search problem

In the following section, we derive a general form of the (infinite time-horizon) sequential search rule and describe some characteristics of the rule with regard to mate choice. In our extension of the rule we presume that females evaluate male quality indirectly, by inspection of an indicator character, and our formulation of the search problem differs in this regard from earlier studies of sequential search and mate choice (Real 1990, 1991; Wiegmann et al. 1996). Our model is similar in other respects to earlier research on the problem.

In our model females are presumed to encounter males sequentially and evaluate male quality using an observable male phenotypic

character $Z$ with probability density function $f(z)$ and corresponding cumulative distribution $F(z)$. The choice of a mate with a trait value of $z$ is assumed to have an associated fitness benefit, determined by the function $W(z)$. The distribution of character $Z$ among males is presumed to be immutable and known to searchers (Real 1990; but see McKenna 1985; Dombrovsky and Perrin 1996). Females are presumed to encounter males randomly with regard to trait $Z$ and observe the trait values of encountered individuals perfectly. A cost $c$, measured in fitness units, is incurred to sample each potential mate and males are presumed to mate indiscriminately. The source of uncertainty for searching females is the realized sequence of encounters with potential mates.

### 2.2. The model

The optimal threshold acceptance criterion, the phenotypic value of male trait $Z$ that induces females to terminate search, is derived from the distribution of the indicator character among potential mates, the cost of search and the function that relates the indicator trait to fitness. Let $V(x)$ be the expected net benefit of search for a female that adopts $x$ as a critical threshold value for the male character. The value of $V(x)$ is given by the difference between the expected benefit of mating with a male of phenotype $Z > x$ and the expected cost of search to find such a male, or

$$V(x) = -c/(1 - F(x)) + \int_x W(z)f(z)\,dz/(1 - F(x)), \qquad (2.1)$$

where $F(x) = \int^x f(z)\,dz$ (see Lippman and McCall 1976). The expected number of males that a female will sample before encountering an individual of phenotype $Z > x$ equals $1/(1 - F(x))$, so the first term on the right-hand side of (2.1) equals the expected cost of search. The second term is simply the expected fitness benefit of mating with a male of phenotype $Z > x$, the mean quality of potential mates with character values higher than $x$.

The goal of a searching female is to maximize the net fitness gain of search. Setting the derivative of $V(x)$ with respect to $x$ equal to zero gives the first-order condition for maximization of $V(x)$ as

$$V'(x) = -cf(x) - W(x)f(x)(1 - F(x)) + f(x)\int_x W(z)f(z)\,dz = 0.$$

$$(2.2)$$

Thus, if $z^*$ is the value of trait $Z$ which satisfies (2.2), then

$$c = \int_{z^*} (W(z) - W(z^*)) f(z) \, dz. \tag{2.3}$$

This gives the generalized form of the sequential search rule (see also Hey 1979). The value of the phenotypic threshold $z^*$ is set to equate the cost of search with the expected gain of sampling an additional male and is the phenotypic value of male trait $Z$ for which females are indifferent between mating and continuing to search. We see immediately from (2.3) that as the cost of search increases the value of $z^*$ declines, just as under conditions in which females evaluate male quality directly. If $W(z)$ is linear with respect to $Z$ so that $W(z) = z$ and $W(z^*) = z^*$, then (2.3) reduces to the standard sequential search model (Real 1990).

   In this paper, we focus on how the shape of $W(z)$ influences the magnitude of $z^*$, given that $W(z)$ is a monotonic function of a male trait. If $W(z)$ is not monotonically related to the male character there may be no unique value of $z^*$. We briefly describe how the set of acceptable values of a male character relates to a more general form of $W(z)$ in Appendix A.

## 3. Influence of the fitness function on search behavior

### 3.1. Linear fitness functions

The decisions made by females depend on the exact form of the fitness function. The benefit of a mating decision may be linearly related to the value of a male character, or easily transformed to linearity, and we begin by evaluating how differences between simple linear fitness functions are expected to influence female decisions. Let the relationship between fitness and male character $Z$ be

$$W(z) = \alpha + \beta z, \tag{3.1}$$

where $\alpha$ corresponds to the intercept and $\beta$ equals the slope of the function. Values of $\alpha = 0$ and $\beta = 1$ correspond to the situation in which Real (1990) modeled the sequential search rule. Use of the optimality condition given by (2.3) allows us to examine properties of the search rule under more general conditions. Substituting (3.1) into (2.3) gives

$$c = \int_{z^*} ((\alpha + \beta z) - (\alpha + \beta z^*)) f(z) \, dz = \beta \int_{z^*} (z - z^*) f(z) \, dz. \tag{3.2}$$

From (3.2) we see that the cost of search is proportional to the slope of the association between male trait $Z$ and fitness. A fitness function with a low value of $\beta$ consequently induces a female to adopt a low optimal threshold value for male trait $Z$ and females sample few males before termination of search. The mean quality of males in a population, in contrast, has no influence on the magnitude of $z^*$ because the intercept parameter $\alpha$ is not retained in the solution. A uniform shift of the fitness function upward or downward, therefore, has no influence on the optimal threshold value of the male character.

## 3.2. Non-linear fitness functions

In this section, we evaluate how the curvature of a monotonically increasing fitness function influences female search behavior. The Arrow-Pratt coefficient of absolute risk aversion is frequently used in economics and behavioral ecology to characterize how the shape of a utility function influences choice behavior and we use this metric to characterize the local curvature of a fitness function. The coefficient $r(x|U)$ is defined as

$$r(x|U) = -U''(x)/U'(x), \qquad (3.3)$$

where $U'(x)$ and $U''(x)$ are the first and second derivatives of the utility function $U(x)$ with respect to the choice variable $X$ (Pratt 1964). If $r(x|U) > r(x|G)$ over all values of $X$, then $U(x)$ is, by definition, a more risk averse function than the alternative function $G(x)$. The sign of $r(x|U)$ describes the general shape of a monotonic, strictly increasing function. If $U(x)$ is concave, then $r(x|U) > 0$ at all values of $X$, whereas $r(x|U) < 0$ for a convex, accelerating function and $r(x|U) = 0$ at each value of $X$ for a linear function.

Use of the Arrow-Pratt measure of risk aversion allows us to evaluate how changes of the curvature of a fitness function induce changes of the behavior of females in search of a mate. Suppose that a fitness function $W(z)$ is made more concave (less convex) by everywhere increasing the risk of the function and that $W(z)$ is altered in no other way; that is, presume $r(z|W) < r(z|\mathscr{W})$ for all values of male trait $Z$, where $\mathscr{W}(z)$ corresponds to the function after the change of risk (Fig. 1). The transformation of $W(z)$ implies that $W(\eta) = \mathscr{W}(\eta)$, $W'(\eta) = \mathscr{W}'(\eta)$ and $W''(\eta) > \mathscr{W}''(\eta)$, where $\eta$ is the lowest value of the male character, and the inequality of risk between $W(z)$ and $\mathscr{W}(z)$ insures that

$$\Delta W(z) = W(z) - W(\phi) > \Delta\mathscr{W}(z) = \mathscr{W}(z) - \mathscr{W}(\phi) \qquad (3.4)$$

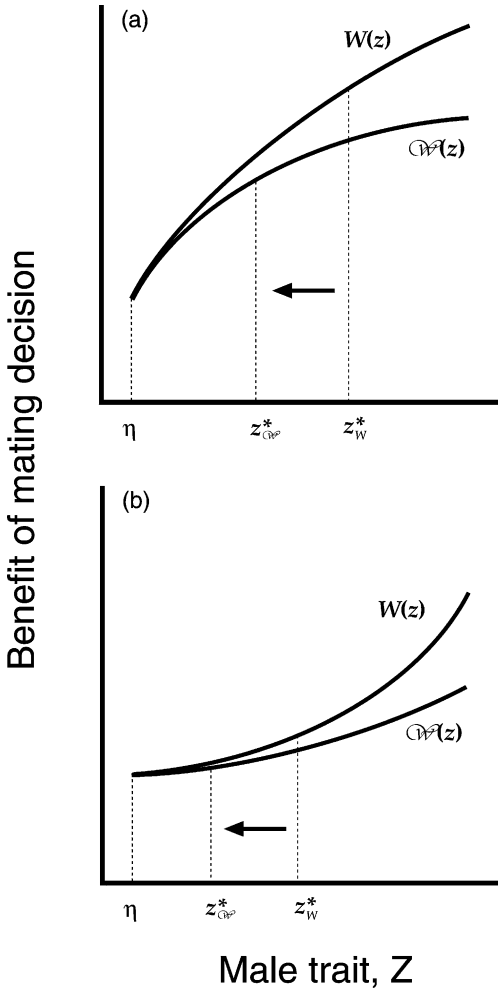for all $Z > \phi$ values of the male character.

**Fig. 1.** Change of the curvature of a fitness function by everywhere increasing the risk of the function. The increase of risk transforms the original (**a**) concave or (**b**) convex function $W(z)$ to $\mathscr{W}(z)$, such that $W(\eta) = \mathscr{W}(\eta)$, $W'(\eta) = \mathscr{W}'(\eta)$, and $W''(\eta) > \mathscr{W}''(\eta)$, where $\eta$ is the lowest value of the male character. The transformation results in a reduction of the optimal threshold value for the male character from $z_W^*$ to $z_{\mathscr{W}}^*$.

The optimality condition given by (2.3) for the fitness function $W(z)$ is just the integration of $\Delta W(z)$ over the distribution of male phenotypes, where $z^* = \phi$ is the optimal threshold value of the male trait. Thus, if $c$ is the cost of search, $z^* = \phi$ is optimal in the context of $W(z)$ and the distribution of the male character is given by $f(z)$, then

$$c = \int_{\phi} (W(z) - W(\phi))f(z)dz > \int_{\phi} (\mathscr{W}(z) - \mathscr{W}(\phi))f(z)\,dz. \quad (3.5)$$

The value of $z^* = \phi$ is, therefore, suboptimal in the context of the more risk averse fitness function, $\mathscr{W}(z)$. The inequality given by (3.5) indicates that the optimal phenotypic threshold value for a male character in the context of $\mathscr{W}(z)$ must be lower than $\phi$ for a given

cost of search and phenotypic distribution among males. Thus, an increase of the concavity (or decrease of convexity) of a fitness function due to an increase of risk, all else being equal, results in a reduction of the optimal threshold value for a male character. Females are consequently expected to sample relatively few males before mating if the function that relates a male character to the benefit of a mating decision is highly concave and risk averse (but see Appendix B).

## 4. Female contributions to fitness

### 4.1. *Additive contributions of male and female phenotypes to fitness*

The fitness benefit of a particular mating decision may often depend on the phenotypic attributes of a searching female. In the preceding development of the sequential search problem, we assumed that the fitness function was calculated with respect to the phenotypic contribution of females to fitness; that is, we presumed that trait $Z$ is either absent in females, that all females have the same phenotypic value for the character, or that differences of the trait among females have no influence on the benefit of a mating decision (see Real 1990, 1991). Under these conditions a sequential search rule induces an identical phenotypic threshold value for a male character among all females and, because males are presumed to be encountered randomly, the phenotypic values of mated males and females will be uncorrelated. The influence of female phenotypes on the fitness consequences of mating decisions can produce either assortative or disassortative mating, but the expected association between mated individuals depends on the shape of the fitness function.

Under conditions in which the characteristics of females influence the fitness benefit of mating with a particular male we would ideally estimate the fitness function for each female, or each female phenotype, to determine the corresponding optimal threshold value for a male trait, an obligation that would generally be impractical, if not impossible. Alternatively, we can take the variability of female phenotypes into consideration in the sequential search model by making use of the simplifying assumption that the benefit of a mating decision depends on the combined value of male and female phenotypes. Let $W(z)$ be the function that relates male trait $Z$ to fitness for a female with a phenotypic value of trait $Z$ equal to $\gamma$. Suppose that the value of the female character is shifted by an amount $\Delta\gamma$ and that neither the female nor the conditions of search change in any other way. If

male and female phenotypic contributions to fitness act additively, then we can describe the revised function which relates trait $Z$ to fitness as $S(z, \Delta\gamma) = W(z + \Delta\gamma)$. The rationale underlying such a reformulation of the fitness function is simple. A female of phenotype $\psi = \gamma + \Delta\gamma$ is expected to use $S(z, \Delta\gamma)$ because mating with a male of trait value $z$ for such a female is equal to mating with a male of phenotype $z + \Delta\gamma$ for a female of phenotype $\gamma$. We presently explore how female contributions to fitness alter our previous findings under this condition.

## 4.2. Linear fitness functions

Suppose that the fitness function $W(z)$ is linear, as described by (3.1), for a female with a phenotypic value of trait $Z$ equal to $\gamma$. Let $z_\gamma^*$ equal the optimal threshold value of the male character for such a female and let $z_\psi^*$ be the corresponding value for a female with phenotype $\psi$ and fitness function $U(z, \Delta\gamma)$, where $\psi = \gamma + \Delta\gamma$. Finally, assume that fitness contributions attributable to character $Z$ combine additively for males and females.

Under these conditions, the fitness function for females of phenotype $\psi$ is given by

$$U(z, \Delta\gamma) = W(z + \Delta\gamma) = \alpha + \beta(z + \Delta\gamma). \qquad (4.1)$$

The difference of fitness for $\gamma$ and $\psi$ females that mate with a male of phenotype $\phi$ is

$$U(\phi, \Delta\gamma) - W(\phi) = W(\phi + \Delta\gamma) - W(\phi)$$
$$= \alpha + \beta(\phi + \Delta\gamma) - \alpha - \beta(\phi) = \beta\Delta\gamma \qquad (4.2)$$

and this relationship holds for all values of the male character (Fig. 2a). The only difference between the fitness functions $U(z, \Delta\gamma)$ and $W(z)$ is an intercept shift of $\beta\Delta\gamma$ which, as we found earlier, has no influence on the optimal threshold value of the male trait. As a consequence $z_\gamma^* = z_\psi^*$.

## 4.3. Nonlinear fitness functions

We found that the optimal threshold value for the male character does not depend on the value of the trait among females if the fitness function is linear; all females adopt the same threshold value for the male character. The reason for this result is that the curvature of
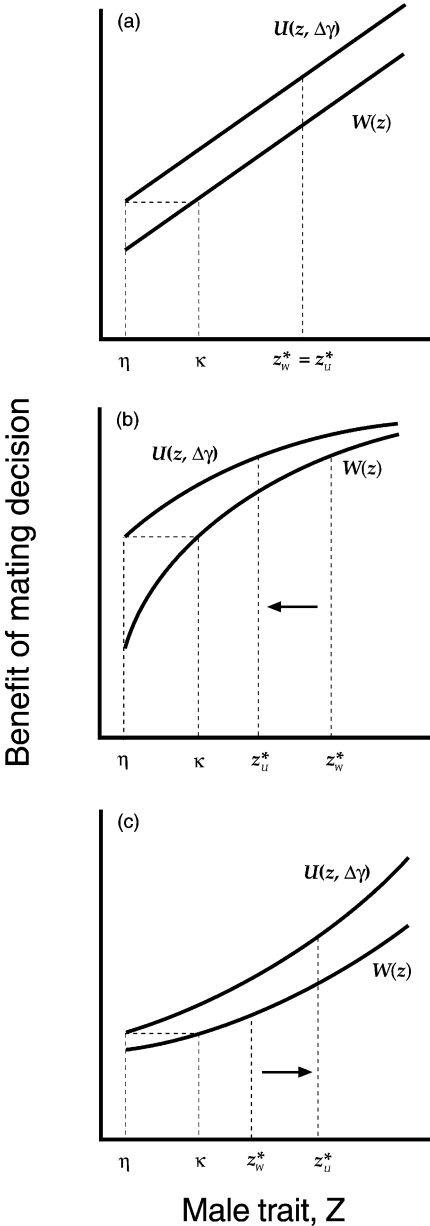
**Fig. 2.** Comparisons of the optimal threshold value for male trait $Z$ between two females that differ with regard to the same character under conditions in which the fitness benefit of a mating decision is (**a**) linear, (**b**) concave or (**c**) convex. The phenotypic contributions to fitness for males and females are assumed to be additive so that $U(z, \Delta\gamma) = W(z + \Delta\gamma)$, where $W(z)$ and $U(z, \Delta\gamma)$ are the fitness functions for females with phenotypes $\gamma$ and $\psi = \gamma + \Delta\gamma$, respectively. The fitness functions shown correspond to $\Delta\gamma = \kappa - \eta$. The curvature of the fitness function for each female determines the relationship between $U(z, \Delta\gamma) - U(\phi, \Delta\gamma)$ and $W(z) - W(\phi)$ for all $Z > \phi$ values of the male character and hence the value of the male phenotype that induces females to terminate search.

a linear fitness function is unaffected by the female phenotype. If the fitness function is non-linear, however, the curvature of the fitness function depends on the phenotype of a searching female and this property induces females with different phenotypes to adopt alternative threshold values of the male character.

Consider a concave fitness function $W(z)$ that increases monotonically in value and decreases with respect to risk as male trait $Z$ increases; that is, presume $r(z|W) > 0$ and $r(\phi|W) > r(\theta|W)$ for all $\phi < \theta$ values of the male character. The fitness functions $W(z) = \alpha + \beta \ln(z)$ $(z \neq 0)$ and $W(z) = \alpha + \beta \sqrt{z}$ $(\sqrt{z} > 0)$ are two examples of such a function, where $\alpha$ and $\beta > 0$ are constants. Let $r(z|W)$ be the coefficient of local risk aversion for a female with a trait value of $Z$ equal to $\gamma$ and a fitness function $W(z)$ and let $r(z|U)$ equal the coefficient of risk for a $\psi = \gamma + \Delta\gamma$ female, where $U(z, \Delta\gamma) = W(z + \Delta\gamma)$ (Fig. 2b). Then $U'(z, \Delta\gamma) = W'(z + \Delta\gamma)$ and $r(z|U) = r(z + \Delta\gamma|W)$ which implies that $U'(z, \Delta\gamma) < W'(z)$ and $r(z|U) < r(z|W)$ if $\Delta\gamma > 0$, or $U'(z, \Delta\gamma) > W'(z)$ and $r(z|U) > r(z|W)$ if $\Delta\gamma < 0$, for all values of the male trait; that is, $U'(z, \Delta\gamma)$ and $r(z|U)$ are either uniformly higher or uniformly lower than $W'(z)$ and $r(z|W)$, respectively. Thus, $\Delta W(z) = W(z) - W(\phi) > \Delta U(z, \Delta\gamma) = U(z, \Delta\gamma) - U(\phi, \Delta\gamma)$ if $\Delta\gamma > 0$ and $\Delta W(z) < \Delta U(z, \Delta\gamma)$ if $\Delta\gamma < 0$ for all $Z > \phi$ values of trait $Z$ among males. A direct application of (3.5) to these inequalities gives $z_\gamma^* > z_\psi^*$ if $\gamma < \psi$. Thus, a concave fitness function results in disassortative mating under sequential search.

The concept of risk can be easily applied to examine the impact of the phenotype of a searching female on the optimal threshold value for a male character under conditions in which the fitness function is convex, rather than concave, and increasing with respect to local risk aversion; that is, situations in which $r(z|W) < 0$ and $r(\phi|W) < r(\theta|W)$ for all $\phi < \theta$ values of the male character. An example of such a fitness function is $W(z) = \alpha + \beta z^2$, where $\alpha$ and $\beta > 0$ are constants. The coefficients of risk for females of phenotypes $\gamma$ and $\psi = \gamma + \Delta\gamma$ with fitness functions $W(z)$ and $U(z, \Delta\gamma) = W(z + \Delta\gamma)$ are then related as $r(z|U) > r(z|W)$ if $\Delta\gamma > 0$ and $r(z|U) < r(z|W)$ if $\Delta\gamma < 0$ for all values of the male character. Furthermore, if $\Delta\gamma > 0$, then $U'(z, \Delta\gamma) > W'(z)$ over the domain of trait $Z$ among males, a condition which guarantees that $U(z, \Delta\gamma) - U(\phi, \Delta\gamma) > W(z) - W(\phi)$ for all $Z > \phi$ values of the male character. Thus, in contrast to the situation in which the fitness function is concave, use of (3.5) yields $z_\gamma^* < z_\psi^*$ if $\gamma < \psi$ (Fig. 2c). Sequential search leads to assortative mating if the function that relates male trait $Z$ to the benefit of a mating decision is convex.

The value of risk over the fitness function also explains the failure of a shift of the female phenotype to produce a change of the optimal threshold value for the male trait when the fitness function is linear. The phenotype of a searching female has no influence on local risk aversion if the male trait is linearly related to fitness and the fitness contributions of male and female phenotypes combine additively; that is, $U'(z, \Delta\gamma) = W'(z)$ and $U''(z, \Delta\gamma) = W''(z) = 0$ at all values of the

male character so that $r(z|U) = r(z|W) = 0$, regardless of whether $\Delta\gamma$ is positive or negative. Thus, $U(z, \Delta\gamma) - U(\phi, \Delta\gamma) = W(z) - W(\phi)$ for all $Z > \phi$ values of the male character and $z_\gamma^* = z_\psi^*$.

## 5. Changes of the distribution of the male character

### 5.1. Variance-preserving shift of the male trait

The optimal phenotypic threshold criterion depends on the distribution of trait $Z$ among males, as well as the shape of the fitness function and the cost of search. Real (1990) showed that a variance-preserving shift of male quality, a shift that alters the mean value of male quality while leaving the variance of male quality unchanged, results in a predictable change of female search behavior if females use a sequential search rule. The degree that $z^*$ is changed as a result of a variance-preserving shift of trait $Z$ depends, however, on the shape of the fitness function.

### 5.2. Linear fitness functions

Suppose that $W(z)$ is linear, as described by (3.1), and that all values of the male character are shifted by a constant amount $\Delta z$. Let $z' = z + \Delta z$ represent the value of the male phenotype after the shift and let $f(z')$ be the probability density function of the shifted trait. The shift alters the male phenotype such that $E(Z') = E(Z + \Delta z) = E(Z) + \Delta z$, $E[(Z' - \bar{Z}')^2] = E[(Z - \bar{Z})^2]$ and $f(z') = f(z)$. The fitness function pursuant to the shift of the male character is given by

$$W(z') = \alpha + \beta z' = W(z + \Delta z) = \alpha + \beta(z + \Delta z) \qquad (5.1)$$

and from (3.2) the optimality condition is

$$c = \beta \int_{z'^*} (z' - z'^*) f(z') \, dz' = \beta \int_{z'^*} (z + \Delta z - z'^*) f(z) \, dz \qquad (5.2)$$

where $z'^*$ is the optimal threshold value for the male trait in the context of the shifted distribution. If the cost of search is unaffected by the shift of the male character, then

$$c = \beta \int_{z^*} (z - z^*) f(z) \, dz = \beta \int_{z'^*} (z + \Delta z - z'^*) f(z) \, dz \qquad (5.3)$$

Thus, the value of the optimal threshold male phenotype in the context of the shifted distribution that satisfies (5.3) is $z'^* = z^* + \Delta z$ (Fig. 3a). Because the shift of $z^*$ does not depend on the magnitude of $\beta$, the result is identical to that predicted if $W(z) = z$ and females choose males by observing male quality directly (Real 1990).

## 5.3. Non-linear fitness functions

A variance-preserving shift of the male character, like a shift of the female phenotype, has no influence on the level of risk to a searching female if the fitness function is linear. If the function that relates the male trait to fitness is non-linear, however, the risk associated with the fitness function depends on the location of the male phenotypic distribution.

Let $W(z)$ be the fitness benefit attributable to mating with a male of phenotype $z$, where $W(z)$ is concave and $r(z|W) > 0$ and $r(\phi|W) > r(\theta|W)$ for all $\phi < \theta$ values of the male trait. Let the male character undergo a variance-preserving shift of $\Delta z > 0$ and let $W(z') = W(z + \Delta z)$ be the fitness benefit attributable to mating with a male of phenotype $z' = z + \Delta z$ after the shift (Fig. 3b). Thus $W'(z) > W'(z') = W'(z + \Delta z)$ and $r(z|W) > r(z'|W)$ for all values of the male trait. If $z^*$ is the optimal threshold value for male trait $Z$ in the context of $f(z)$ and $z'^* = z^* + \Delta z$, the phenotypic value that would be optimal in the context of $f(z')$ if fitness were linearly related to the male character, then

$$c = \int_{z^*} (W(z) - W(z^*)) f(z)\,dz > \int_{z'^*} (W(z') - W(z'^*)) f(z')\,d(z'). \quad (5.4)$$

This inequality contradicts the optimality condition given by (2.3) and we can immediately conclude that $z'^* \neq z^* + \Delta z$. The inequality given by (5.4) indicates that, if the fitness function is concave and decreasing with respect to risk, a shift of the male phenotype values by $\Delta z > 0$ will result in an increase of the optimal threshold male trait value by less than $\Delta z$; that is, $z'^* < z^* + \Delta z$. If the fitness function is convex and increasing with respect to risk as male trait $Z$ increases, a straightforward comparison of $W(z) - W(z^*)$ and $W(z') - W(z'^*)$ over the original and shifted values of the male trait confirms that the opposite result will hold; that is, $z'^* > z^* + \Delta z$ after a positive shift of the male character if $r(z|W) < 0$ and $r(\phi|W) < r(\theta|W)$ for all $\phi < \theta$ values of the male trait (Fig. 3c).
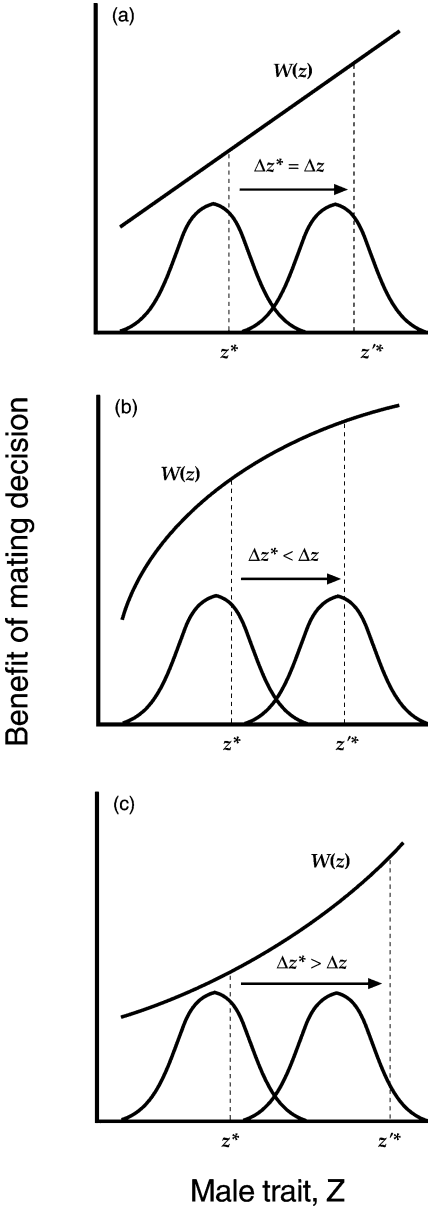
**Fig. 3.** The influence of a shift of a male character $Z$ by $\Delta z > 0$ on the optimal threshold value for the trait under conditions in which the fitness benefit of a mating decision is **(a)** linear, **(b)** concave or **(c)** convex. The phenotypic value of the trait after the shift is $z' = z + \Delta z$. The shift preserves the variance of the male character. The change of the curvature of $W(z)$ associated with the shift of the male trait determines the magnitude of the change of the optimal phenotypic threshold criterion $\Delta z^*$, where $\Delta z^* = z'^* - z^*$.

## 6. Discussion

### 6.1. Sequential search and the contour of fitness functions

In this paper, we derived a generalized model of sequential search and examined how the shape of the function that translates a male character

into fitness, the distribution of the male trait and differences of quality among females influence female search behavior. In the model of sequential search developed by Real (1990) searching females were assumed to evaluate male quality directly. In our development of the problem, in contrast, we assumed that females choose among potential mates using a phenotypic character with some unspecified relationship to fitness.

We focused our examination of the search model on monotonically increasing linear, concave and convex fitness functions, although our approach could be extended to a variety of other, more complex, fitness functions (Appendix A). Our results indicate that an increase of the slope of a linear function, all else being equal, increases the optimal threshold value of the male character. In order to describe the contour of non-linear fitness functions we made use of the economic concept of risk (Pratt 1964; Arrow 1965; see also Real 1981; Stephens and Krebs 1986; Harder and Real 1987; Cartar and Smallwood 1996). The optimal threshold value for a male character decreases if a fitness function is made more concave (or less convex) by increasing the risk of the function, all else being equal (Fig. 1). An analogous relationship exists in the economics of job search; a utility function with a high level of risk results in termination of search for a relatively low wage offer (Hall et al. 1979). The fitness difference that would result from mating with one male over another is, however, not entirely constrained by the coefficient of risk. The optimal threshold value for a male trait increases with the slope of a linear fitness function, but all linear functions encode the same level of risk. Thus, we can use the concept of risk to describe how a change of the curvature of a fitness function will alter female behavior during sequential search, but a simple comparison of the risk of two arbitrary fitness functions will not generally be sufficient to determine which function will induce a higher threshold value for a male character (Appendix B).

## 6.2. Female contributions to the net benefit of a mating decision

Female contributions to the fitness benefit of a mating decision can interact with the shape of the fitness function to alter the value of the male phenotype that induces termination of search. The fitness function used to predict female behavior during sequential search is calculated with respect to the qualities of a searching female and, in theory, we should determine the optimal threshold value for a male character from the fitness function that corresponds to each female, or female phenotype (Real 1990; see McKenna 1985). This unfortunate requirement could impede an experimental approach to the study of sequential search, but the

importance of the restriction depends on how the value of an indicator character translates into fitness and the way in which male and female phenotypes combine to influence the benefit of a mating decision.

In some situations the net benefit of mating with one male over another may depend only on the phenotypic differences between potential mates. Such a situation might occur if males alone provide for progeny, as is relatively common in freshwater fishes (Baylis 1981; Gross and Shine 1981), or if males and females perform separate roles with regard to defense of offspring (Saito 1986; Yamamura 1987). A male characteristic, like body size, or some extension of the male phenotype, like attributes of a nest site, might be used under such conditions to evaluate the paternal qualities potential mates (Orians 1969; Downhower and Brown 1980; Wiegmann and Baylis 1995). In other situations the net benefit of a mating decision may depend on female attributes, as well as the characteristics of males. The same phenotypic character, like body size, may influence the ability of males and females to defend progeny against predators under conditions in which both parents provide for offspring. The advantage of mating with a male of a particular body size may then depend on the body size of a searching female.

In this study we evaluated how the phenotypes of females influence search behavior under conditions in which male and female phenotypes contribute additively to the benefit of a mating decision. If the fitness function is linear, then risk is constant over the domain of the male trait and the optimal value of the phenotypic threshold for the male character is unaffected by the phenotype of a searching female; all females adopt the same phenotypic criterion for termination of search and no phenotypic correlation between mated individuals is expected (Fig. 2a). If the fitness function is linear, or can be transformed to a linear function, the results of empirical studies of search behavior may consequently be unaffected by the phenotypes of females. If the fitness function is concave and decreases in risk as the male trait increases, in contrast, then females with a high value of the phenotypic character adopt a relatively low threshold value for the male character and mating will be disassortative (Fig. 2b). A convex fitness function that increases in risk as the male trait increases effects assortative mating because females with a high value of the phenotypic character adopt a relatively high threshold criterion for the male trait (Fig. 2c).

## 6.3. Changes of the distribution of a male character

An experimental manipulation of male quality can provide decisive information about the search rule that females actually employ

(Wiegmann et al. 1996). Real (1990) showed that a variance-preserving shift of the mean quality of potential mates produces an identical shift of the optimal acceptance criterion for male quality. The prediction follows whether the shift is a result of direct experimental manipulation or a consequence of the process of search, provided that searchers evaluate the distribution of mate quality accurately. An analogous result follows from a shift of a male phenotypic character if the fitness function is linear; that is, a shift of the mean value of an indicator character which preserves the variance of the trait produces an equivalent shift of the optimal threshold value for the male character (Fig. 3a). The number of males that females are expected to sample before mating is unaffected by a variance-preserving shift of the male trait because the proportion of males with phenotypic values higher and lower than the threshold criterion is unchanged by such a shift. Thus, if we wish to evaluate whether females use a sequential search tactic or some alternative search rule, like a best-of-$n$ rule (Janetos 1980), an experimental manipulation of a male trait that has a linear relationship to fitness is just as powerful as a direct manipulation of male quality *per se* (see Wiegmann et al. 1996; Wiegmann and Mukhopadhyay 1998).

The predicted behavioral response of females that use a sequential search rule to a shift of the male phenotype is more complicated if the fitness function is non-linear. If the fitness function is concave, and decreases in risk as the male trait increases, a positive (negative) shift of the mean value of the male trait produces a less extreme increase (decrease) of the optimal phenotypic threshold value (Fig. 3b). If the function that relates the benefit of a mating decision to a male character is convex and increases in risk as the value of the male trait increases, in contrast, a variance-preserving positive (negative) shift of the average value of the male character produces a more extreme positive (negative) shift of the optimal threshold value for the male phenotype (Fig. 3c). A precise prediction of changes of search behavior under conditions in which the fitness function is non-linear consequently requires specifying the exact form of the function. Non-linear fitness functions are further complicated by the fact that the optimal threshold criterion for a male trait may depend on the phenotype of a searcher if the character is also expressed among females.

All of our results indicate that only the shape of the function that relates a male trait to the fitness benefit of a mating decision influences the threshold value of the male phenotype; the mean benefit of a mating decision has no influence on female search behavior, whether the fitness function is linear, concave or convex (Fig. 2; Appendix B). Thus, any phenotypic differences among females which result only in

differences of mean fitness should have no influence on search behav-
ior. This result also implies that a high net benefit of search to females
need not result from a high threshold value for a male character and
vice versa, whether we compare the fitnesses of females with different
phenotypic values in a single population or the fitnesses of females with
similar phenotypes in different populations.

In this paper, we generalized the sequential search rule to examine
how the shape of the function that relates a male character to the
benefit of a mating decision, the distribution of a male trait and
differences of phenotypic values among females interact to influence
the behavior of females in search of a mate. A sequential search rule
fails to induce assortative or disassortative mating under conditions in
which females evaluate male quality directly (Real 1990), but an in-
corporation of these complexities into the model yields the general
patterns of phenotypic associations observed between mated indi-
viduals (see also Real 1991).

## Appendix A

In this appendix we examine properties of the sequential search model
under conditions in which the relationship between a male character
$Z$ and the benefit of a mating decision takes on any arbitrary funct-
ion, $W(z)$. The optimal threshold value for the male phenotype
which induces females to terminate search may not be unique if $W(z)$
is not monotonically increasing (or decreasing) with respect to the
male trait; that is, there may be no unique lower (upper) value of
character $Z$ for which females are indifferent to mating or continuing
search. Our proof of this property of the sequential search rule follows
Hey (1979).

We begin by substituting $V(S)$ for $V(x)$ in (2.1), where $S$ is any
arbitrary set of values of male trait $Z$ that causes a female to terminate
search. We can then rewrite (2.1) as

$$V(S) = -c/\int_S f(z)\,dz + \int_S W(z)f(z)\,dz/\int_S f(z)\,dz. \qquad (A.1)$$

Females choose a set of values of character $Z$ that maximizes the net
fitness benefit of search, $V(S)$, and we denoted that set by $S^*$. Thus,
$V(S^*) > V(S)$ for all $S$. The optimality condition analogous to (2.3) is

then given by

$$c = \int_{S^*} (W(z) - V(S^*)) f(z) \, dz. \tag{A.2}$$

Our goal is to determine what values of the male trait may be included in $S^*$ when $W(z)$ is an arbitrary function of the male phenotype. Let $J$, $K$, and $L$ be sets of values of trait $Z$ for which $W(z) > V(S^*)$, $W(z) = V(S^*)$ and $W(z) < V(S^*)$, respectively, so that all values of the male character are contained within the three sets. Suppose that $S^*$ contains some trait values of set $L$; that is, presume $S^* \equiv S \cup l$, where $S \cap L = \varnothing$, $l \subseteq L$, $l \neq \varnothing$ and $S \neq \varnothing$. Then, from (A.1) we observe that

$$V(S) = \left( -c + \int_S W(z) f(z) \, dz \right) \bigg/ \int_S f(z) \, dz \tag{A.3}$$

and

$$V(S^*) = \left( -c + \int_S W(z) f(z) \, dz + \int_l W(z) f(z) \, dz \right) \bigg/$$

$$\left( \int_S f(z) \, dz + \int_l f(z) \, dz \right). \tag{A.4}$$

With use of (A.2) we subtract $V(S^*)$ from $V(S)$ to obtain

$$V(S) - V(S^*) = \int_l (V(S^*) - W(z)) f(z) \, dz \bigg/ \int_S f(z) \, dz, \tag{A.5}$$

which contradicts the optimality condition that $V(S^*) > V(S)$ for all $S$ because $W(z) < V(S^*)$ throughout all of $L$. Thus, $S^*$ can contain no values of male trait $Z$ for which $W(z) < V(S^*)$; that is, $S^* \cap L = \varnothing$.

We can similarly show that $S^*$ must contain all of the value of character $Z$ that are contained in $J$. Suppose that some values of trait $Z$ contained in $J$ are not also contained in $S^*$; that is, suppose $S \equiv S^* \cup s$, where $s \cap J \neq \varnothing$, $S^* \cap s = \varnothing$ and $s \cap L = \varnothing$. From (A.1) and (A.2) we find that subtraction of $V(S^*)$ from $V(S)$ then gives

$$V(S) - V(S^*) = \int_s (W(z) - V(S^*)) f(z) \, dz \bigg/ \int_S f(z) \, dz, \tag{A.6}$$

which is also positive and contradicts the optimality condition because $W(z) > V(S^*)$ throughout all or part of $s$. Thus, $S^*$ must contain all of the phenotypic values of the male trait that are contained in $J$.

The reason that the set of acceptable male phenotypic values is not unique results from the arbitrary inclusion of trait values in $K$. Let $S^* \equiv J$ and $S \equiv J \cup k$, where $k$ is any subset of $K$. Use of (A.1) and (A.2) gives

$$V(S) - V(S^*) = \int_k (W(z) - V(S^*)) f(z) \, dz \Big/ \int_S f(z) \, dz = 0 \quad \text{(A.7)}$$

because $W(z) = V(S^*)$ throughout all of $k$. Thus, $V(S) = V(S^*)$ and $S^*$ may contain any subset of male phenotypic values contained in $K$.

The non-uniqueness of $S^*$ implies that the male phenotypic values contained in $S^*$ can be discontinuous with respect to the domain of trait $Z$; that is, the values of the male character that induce females to terminate search may be located in disconnected groups across the domain of the trait. The sequential search rule and other search rules may consequently be difficult to study if the benefit of a mating decision is a highly unusual function of the male phenotype.

## Appendix B

A comparison of the coefficients of risk of two arbitrary fitness functions is not generally sufficient to establish which function will induce females to adopt a higher threshold value for a male trait. In this appendix, we determine the conditions that are necessary to insure that such a comparison will unambiguously reveal the rank order of optimal threshold values for a male character.

Let $r(z|W)$ and $r(z|U)$ be the risk coefficients of strictly increasing, concave fitness functions $W(z)$ and $U(z)$, respectively, and let $r(z|U) > r(z|W)$ over all values of male character $Z$. We transform function $W(z)$ so that the transformed function $\mathscr{W}(z)$ and $U(z)$ have the same slope at an arbitrary value $\tau$ of the male phenotype. We define $\mathscr{W}(z)$ as a positive affine transformation of $W(z)$, or

$$\mathscr{W}(z) = \alpha W(z) + \beta, \quad \text{(B.1)}$$

where $\alpha > 0$ and $\beta$ are constants. Differentiation of (B.1) yields $\mathscr{W}'(z) = \alpha W'(z)$ and $\mathscr{W}''(z) = \alpha W''(z)$ so that

$$r(z|\mathscr{W}) = -\mathscr{W}''(z)/\mathscr{W}'(z)$$
$$= -\alpha W''(z)/\alpha W'(z) = -W''(z)/W'(z) = r(z|W). \quad \text{(B.2)}$$

The transformation thus preserves the risk associated with the original function (French 1986). Any value can be assigned to the constant $\beta$ without changing this result; the risk associated with a function does

not depend on the mean value of the function. We complete the transformation by assigning a value to $\alpha$ so that $\mathscr{W}'(\tau) = U'(\tau)$, a requirement satisfied by $\alpha = U'(\tau)/W'(\tau)$.

The transformation of the fitness guarantees that $U''(\tau) < \mathscr{W}''(\tau)$ because $r(\tau|\mathscr{W}) < r(\tau|U)$ and $\mathscr{W}'(\tau) = U'(\tau)$. The function $U(z)$ consequently decelerates from $\tau$ at a more rapid rate than $\mathscr{W}(z)$. Furthermore, the inequality of risk insures that $\mathscr{W}(z) - \mathscr{W}(\tau) > U(z) - U(\tau)$ for all $Z > \tau$ values of the male character. A direct application of (3.5) indicates that if $z_{\mathscr{W}}^* = \tau$, then $z_{\mathscr{W}}^* > z_U^*$. This result establishes the conditions under which we can use the coefficient of risk to unambiguously determine which of two monotonically increasing fitness functions will induce females to adopt a higher threshold value for a male trait. If $r(z|W) < r(z|U)$ over all values of the male character and $z_W^* \geq \tau$, where $\tau$ is the value of the male phenotype at which $W'(z) = U'(z)$, then $z_W^* > z_U^*$.

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