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Mate choice and uncertainty in the decision process

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Abstract

The behavior of females in search of a mate determines the likelihood that a high quality male is encountered in the search process and alternative search strategies provide different fitness returns to searchers. Models of search behavior are typically formulated on an assumption that the quality of prospective mates is revealed to searchers without error, either directly or by inspection of a perfectly informative phenotypic character. But recent theoretical developments suggest that the relative performance of a search strategy may be sensitive to any uncertainty associated with the to-be-realized fitness benefit of mate choice decisions. Indeed, uncertainty in the decision process is inevitable whenever unobserved male attributes influence the fitness of searchers. In this paper, we derive solutions to the *sequential search strategy* and the *fixed sample search strategy* for the general situation in which observed and unobserved male attributes affect the fitness consequences of female mate choice decisions and we determine how the magnitude of various parameters that are influential in the standard models alter these more general solutions. The distribution of unobserved attributes amongst prospective mates determines the uncertainty of mate choice decisions—the reliability of an observed male character as a predictor of male quality—and the realized functional relationship between an observed male character and the fitness return to searchers. The uncertainty of mate choice decisions induced by unobserved male attributes has no influence on the generalized model solutions. Thus, the results of earlier studies of these search models that rely on the use of a perfectly informative male character apply even if an observed male trait does not reveal the quality of prospective mates with certainty. But the solutions are sensitive to any changes of the distribution of unobserved male attributes that alter the realized functional relationship between an observed character and the fitness return to searchers. For example, the standard sequential search model exhibits a reservation property—the acceptability of prospective mates is delimited by a *unique* threshold criterion—and the existence of this model property under generalized conditions depends critically on the association between the observed and unobserved male characters. In our formulations of the models we assumed that females use a single male character to evaluate the quality of prospective mates, but the model properties generalize to situations in which male quality is evaluated by a direct inspection of multiple male characters.

Keywords: Mate choice; Search strategies; Sequential search; Uncertainty

1. Introduction

The search behavior and mate choice decisions of females determine the force of sexual selection on male phenotypic characters. The behavior of females in search of a mate is also subject to selection, as alternative search strategies provide different fitness returns to searchers. In particular, the search strategy employed by a female determines the likelihood that a high quality male is encountered in the search process (Janetos, 1980; Real, 1990). The relative performance of alternative search strategies appears to be sensitive, however, to assessment errors and the magnitude of uncertainty associated with the to-be-realized fitness benefit of a mate choice decision (Luttbeg, 1996, 2002; see also Collins et al., 2006). Indeed, uncertainty in the decision process is an unavoidable consequence of imperfect sensory systems—which allow male signals to be erroneously identified—and it arises, perhaps more generally, whenever unobserved

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male attributes affect the fitness of searchers. In this paper, we derive solutions to the *sequential search strategy* and the *fixed sample search strategy*, two prominent models of search behavior, for the general situation in which observed and unobserved male attributes collectively determine the fitness consequences of mate choice decisions.

The sequential search strategy and the fixed sample search strategy are principal models of female search behavior partially because they provide females with a higher fitness return than a number of alternative search strategies (Janetos, 1980; Real, 1990). But, more importantly, these models capture many aspects of female search behavior (reviewed by Wiegmann et al., 1996; Jennions and Petrie, 1997). The fundamental characteristic of the sequential search strategy is its reservation property. A female who employs a sequential search strategy samples prospective mates until she encounters a male whose quality equals or exceeds a unique *reservation* or *threshold* male quality. The optimal reservation male quality and, hence, the choosiness of females depends on the variance of male quality and on the cost to search, both of which appear to influence female mate choice decisions (Milinski and Bakker, 1992; Gotthard et al., 1999; Wagner et al., 2001). The essential property of the fixed sample search strategy—also known as the best-of-*n* search strategy—is the establishment of an optimal number of males to sample in the search process. A female who adopts this search strategy samples *n* males and mates with the highest quality male in the sample of *n* individuals. The optimal *n* under a fixed sample search strategy likewise depends on the variance of male quality and on the cost to sample prospective mates.

These models were initially derived on an assumption that the quality of males encountered in the search process—the to-be-realized fitness benefit to a searcher—is revealed to females without error (Janetos, 1980; Real, 1990, 1991; Mazalov et al., 1996). The models were later modified to show how the inspection of a phenotypic *indicator character* with various functional relationships to fitness alters the optimal model solutions (Wiegmann and Mukhopadhyay, 1998; Wiegmann et al., 1999). These modified models provide an added level of realism to the search process, but they were similarly derived on an assumption that an indicator character reveals, with certainty, the quality of prospective mates. The standard models were adapted from economic theories on job search, where jobs are evaluated by wage offers, and it seems appropriate in this context to assume that a searcher may know the wage offer of a potential employer without error (reviewed by McKenna, 1985). However, the assumption that male quality is observed, like a wage offer, with certainty by a female in search of a mate is doubtful. The behavior of females of some bird species is indicative of uncertainty in the mate choice process (Bensch and Hasselquist, 1992; Dale et al., 1992; Hovi and Ratti, 1994; Getty, 1996). Indeed, it is unlikely that any method of evaluation reveals the quality of prospective mates to females with certainty, as unobserved male attributes must often contribute to the fitness of searchers.

In this paper, we derive solutions to the sequential search strategy and the fixed sample search strategy that allow for uncertainty in the mate choice process. In particular, we suppose that females evaluate prospective mates based on an indicator character that, due to unobserved male attributes, provides uncertain information on male quality. The distribution of unobserved male attributes associated with the observed indicator character determines the uncertainty of mate choice decisions and, in conjunction with the indicator character, determines the realized functional relationship between an observed male character and the fitness return to searchers. The model formulations allow us to determine how the optimal solutions to these models are modified by the magnitude of uncertainty in the decision process and, more generally, how unobserved male attributes influence female search behavior.

2. The models

The objective of a searcher is to maximize the net fitness benefit associated with the search process. In the standard formulations of the two search models females evaluate males based on a direct inspection of their quality and they pay a cost to sample prospective mates, where male quality and the cost to search are measured in fitness units to the searcher (Real, 1990, 1991). A female is assumed to encounter potential mates sequentially and randomly with respect to male quality. The distribution of potential mates from which females choose is also presumed to be immutable and known to searchers. The time horizon over which a female may search for a mate is assumed to be infinite and males are presumed to mate indiscriminately, two assumptions that effectively allow for a static distribution of the quality of potential mates.

The assumptions used to derive the standard models simplify the mathematics of the search problem and, in general, the essential properties of the models are qualitatively similar if more realistic assumptions—and more sophisticated mathematics—are used to derive the model solutions (McKenna, 1985). If search is assumed to occur over a finite time period, for instance, the sequential search strategy retains its principal characteristic, namely the adoption of a reservation male quality. In this situation the threshold criterion decreases, as anticipated, as unsuccessful search progresses (McKenna, 1985; Real, 1990). Likewise, the search strategy retains its reservation property if searchers estimate parameters of the distribution of male quality and modify mate choice decisions based on information acquired in the search process. The threshold criterion in this situation varies individually due to the probabilistic sequence of encounters experienced by searchers (Mazalov et al., 1996; see also Dombrovsky and Perrin, 1994). Furthermore, the behavioral responses of searchers to changes of the cost of search or parameters associated with the distribution of male quality in these more complicated models are qualitatively similar to the behavioral responses predicted by the standard models (McKenna, 1985; Mazalov et al., 1996; Wiegmann et al., 1996).

In our formulations of the two search models we suppose that females observe a male character that provides uncertain information about the to-be-realized fitness benefit associated with an encountered individual, where this uncertainty is derived from unobserved male attributes that contribute to the fitness return to searchers. Thus, there is uncertainty in the decision to mate with any particular male, even if females have perfect information on the distributions of observed and unobserved male characters. This uncertainty is sometimes referred to as *residual uncertainty* in problems related to search behavior (McKenna, 1985; Real, 1990). The complications associated with uncertainty in the search process may be particularly difficult to resolve if we attempt to determine how the variability of observed and unobserved male attributes independently influence the solutions to a search problem (Real, 1990). The development of generalized models of search behavior that include residual uncertainty is further complicated because the contributions of unobserved male attributes to the fitness of searchers may combine in an unknown manner—say, additively or multiplicatively—and they may have unknown interactions with an observed male character, which itself may have a complicated functional relationship to the fitness of a searcher.

The influence of residual uncertainty on mate choice decisions could be inferred from solutions to search models derived under a variety of plausible contributions of observed and unobserved male attributes to the fitness of searchers. For example, McKenna (1985) solved the sequential search problem for the situation in which job preferences are determined by the *sum* of a wage offer and the money equivalent of unobserved job characteristics. However, the aforementioned problems can be circumvented if we instead suppose that an observed male character and all unobserved male attributes that contribute to female fitness are jointly distributed, where combinations of the observed male character and unobserved male attributes determine—in an unspecified manner—the fitness return to a searcher. This approach allows us to effectively ignore the precise functional relations between male characters and female fitness and to derive solutions to the search models that can be used to determine more generally how the distribution of unobserved male attributes and residual uncertainty *per se* influence female mate choice decisions. The remainder of the search process in our formulations of the models follows the assumptions used to derive the standard models.

2.1. Sequential search strategy

The standard sequential search model establishes the existence of an optimal *reservation* or *threshold* male quality, the male quality that determines the acceptability of potential mates encountered in the search process. The sequential search strategy is consequently said to have a *reservation property*. In the standard model a female necessarily knows the to-be-realized fitness benefit of a mate choice decision with certainty at the time a male is encountered because the quality of males is evaluated directly. In this section of the paper we first derive a general solution to the sequential search strategy under conditions in which an observed male character provides uncertain information about the fitness return to searchers and we then establish the conditions under which the model retains a reservation property, the conditions under which females who employ this search strategy will impose a threshold criterion on the observed male character.

The search strategy involves an *a priori* selection of a set of male phenotypes that characterizes all of the individuals with whom a female would mate, if encountered, where this set maximizes the net fitness benefit associated with the search process. The optimal acceptance set of male phenotypes—the set that maximizes the net fitness return to searchers—is necessarily composed of observed male trait values, as the quality of a prospective mate is uncertain at the time he is encountered due to unobserved attributes that contribute to the fitness of searchers. In our development of the model we first determine the net fitness return to a female who employs an acceptance set that contains any *arbitrary* selection of values of the observed male character. The optimality conditions that maximize the net fitness return to searchers and the conditions under which females will impose a threshold criterion on the observed male character follow directly from the behavior of this searcher.

Let the random variable W be the total fitness return to searchers—the *realized* quality of prospective mates—derived from an observed male indicator character Z and from all unobserved male attributes that contribute to female fitness, where Z and W have a joint probability density h and probability densities f and g, respectively. The male character used by females to evaluate prospective mates is presumed to be an honest, but not necessarily precise, indicator of male quality, as selection should favor mate choice decisions based on male characters that provide accurate information on male quality (reviewed by Cronin, 1991; Andersson, 1994).

Now suppose that a female adopts an acceptance set A that is composed of any *arbitrary* selection of values of the observed male character. A female who employs this acceptance set terminates search and mates if she encounters a male with a phenotype $z \in A$ and she continues to search if she encounters any male of phenotype $z \notin A$ The fitness return to a female who adopts acceptance set

A is then

$$\begin{aligned} v(A) &= \int_A \int wh(w,z)\,\mathrm{d}w\,\mathrm{d}z + v(A) \\ &\quad \times \left(1 - \int_A \int h(w,z)\,\mathrm{d}w\,\mathrm{d}z\right) - c \\ &= \int_A \int w\,\mathrm{d}G(w|z)\,\mathrm{d}F(z) + v(A) \\ &\quad \times \left(1 - \int_A \int \mathrm{d}G(w|z)\mathrm{d}F(z)\right) - c, \end{aligned} \tag{1}$$

where c is the cost to sample prospective mates. The first term on the right-hand side of this equation is the expected fitness benefit associated with males who have a phenotype $z \in A$, multiplied by the probability that such a male is encountered. The second term is the expected fitness return to a female who encounters an unacceptable potential mate and continues to search, multiplied by the probability that a male with a phenotype $z \notin A$ is encountered. (Notice that the future fitness return, should search continue, is equal to the fitness return in the current search period because the distribution of potential mates from which females choose is identical in each search period). The third term, the cost to search, is expended by a female whether an encountered male is accepted or rejected. Rearrangement of this equation gives the expected net fitness return as

$$v(A) = \frac{\int_A \int w\,\mathrm{d}G(w|z)\,\mathrm{d}F(z)}{\int_A \int \mathrm{d}G(w|z)\,\mathrm{d}F(z)} - \frac{c}{\int_A \int \mathrm{d}G(w|z)\,\mathrm{d}F(z)}. \tag{2}$$

The first term on the right-hand side is the expected fitness benefit to a female who mates with a randomly encountered male in the acceptance set and the second term is the cost of search, multiplied by the number of potential mates a female expects to sample to find a male with a phenotype $z \in A$.

The objective of the searcher is to choose an acceptance set that maximizes $v(A)$. Let v^* equal the maximum of $v(A)$ and let A^* be the acceptance set for which the maximum is achieved. Then $v^* = v(A^*)$ and $v^* \geqslant v(A)$ for all A. It follows immediately from our last expression that

$$v^* = \frac{\int_{A^*} \int w\,\mathrm{d}G(w|z)\mathrm{d}F(z)}{\int_{A^*} \int \mathrm{d}G(w|z)\,\mathrm{d}F(z)} - \frac{c}{\int_{A^*} \int \mathrm{d}G(w|z)\,\mathrm{d}F(z)} \tag{3}$$

and, after rearrangement, we find that the optimized solution satisfies

$$c = \int_{A^*} \int (w - v^*)\,\mathrm{d}G(w|z)\,\mathrm{d}F(z). \tag{4}$$

A female who searches optimally effectively equates the marginal cost to sample potential mates, namely c, with the marginal fitness benefit associated with the search process (see also Real, 1990; Hey, 1979; McKenna, 1985).

But what values of the observed male character are actually contained in the optimal acceptance set? To answer this question consider the expected fitness return to a female who encounters a prospective mate with an observed phenotype z. Her anticipated fitness return by acceptance of this male as a mate is

$$r(z) = \int w\,\mathrm{d}G(w|z) = \hat{w}_z. \tag{5}$$

Now if $r(z) < v^*$ this female will prefer to continue to search over acceptance of the encountered individual as a mate because continued search offers a net fitness return of v^*. If $r(z) = v^*$ she will be indifferent between continued search and acceptance of the encountered male as a mate and she will clearly prefer to mate with the encountered male over continued search if $r(z) > v^*$. Because v^* is constant from one search period to the next the optimal strategy for a female is to continue to search until a prospective mate with an observed character value that satisfies $r(z) \geqslant v^*$ is encountered. The optimal acceptance set will, in general, contain all observed male character values that satisfy $r(z) > v^*$ and any subset of character values for which $r(z) = v^*$ (Fig. 1; see Hey, 1979; Wiegmann et al., 1999).

The reservation property of the sequential search strategy, which is a principle feature of the standard model, is a special case of this generalized model. The use of a threshold criterion on the observed male character occurs only if females unambiguously prefer encountered individuals with high values of the character. Thus, the generalized model exhibits a reservation property if and only if

$$\frac{\mathrm{d}}{\mathrm{d}z} r(z) = \int w\,\mathrm{d}\left[\frac{\partial}{\partial z} G(w|z)\right] = \frac{\mathrm{d}}{\mathrm{d}z} \hat{w}_z > 0. \tag{6}$$

This condition effectively demands that higher values of the observed male character are not associated with lower expected fitness returns to searchers as occurs, for example, if the contribution of the observed male character to female fitness increases monotonically with higher values of the observed male character and higher z-values induce distributions of unobserved male attributes that stochastically dominate the distributions of unobserved male attributes associated with lower values of the observed male character (McKenna, 1985). This condition ensures that there is exactly one observed male character value z^* that satisfies

$$r(z^*) = \int w\,\mathrm{d}G(w|z^*) = \hat{w}_{z^*} = v^* \tag{7}$$

whenever $v^* > 0$ and it is, hence, profitable for a female to engage in the search process (Fig. 1). In this situation, the optimal acceptance set is uniquely defined by

$$A^* \equiv \{z | z \geqslant z^*\} \tag{8}$$

and the optimal solution to the search problem becomes

$$c = \int_{z^*} \int (w - \hat{w}_{z^*})\,\mathrm{d}G(w|z)\,\mathrm{d}F(z). \tag{9}$$

The reservation value of the observed male character—the value of the male character that females use to demarcate the acceptability of prospective mates—is the value of the observed male character for which this equality is satisfied.

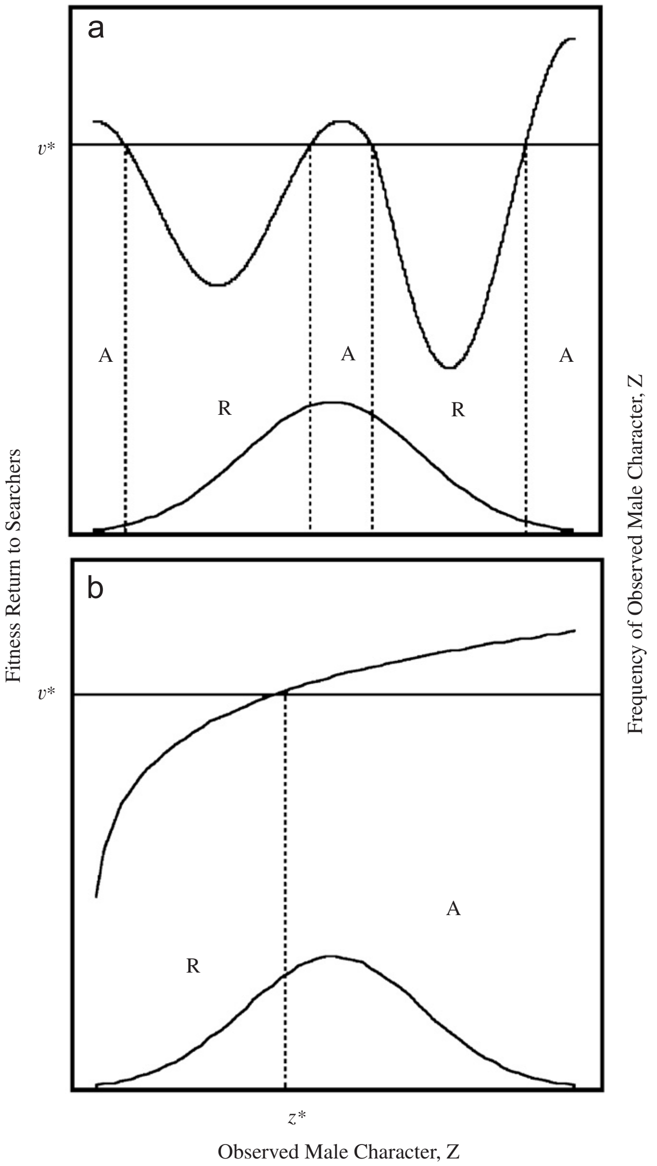

Fig. 1. The optimal acceptance set and the necessary condition for the sequential search strategy to exhibit a reservation property. The optimal acceptance set includes the observed character values of all potential mates who provide an expected fitness return higher than v^* and any subset of character values of potential mates who provide a fitness return equal to v^*. (a) The optimal acceptance set may include disjoint groups of male character values if a fitness function is complex and, in this situation, the sequential search model may not exhibit a reservation property. (b) If the net fitness return increases monotonically with values of the observed male character, then there is a unique reservation criterion, the observed character value associated with a fitness return v^*. In this situation, a female mates with any encountered male who has an observed character $z \geqslant z^*$. The observed male character values included in and excluded from the optimal acceptance set are indicated by the letters A (*acceptable* prospective mates) and R (*reject* male if encountered and continue to search) above the probability density of the observed male character.

Later in this paper we examine various properties of the sequential search model and we focus on the restricted formulation of the model that exhibits a reservation property. This approach simplifies our mathematics and, more importantly, it lends itself to direct comparisons with the standard model and to comparisons with earlier modifications of the model that incorporate the use of a perfectly informative indicator character (Real, 1990; Wiegmann et al., 1996, 1999). However, the conclusions to our analyses—unrelated to the adjustment of the threshold criterion *per se*—apply generally. The conditions that cause an increase or decrease of z^* result in a contraction or expansion of the optimal acceptance set in the unrestricted, generalized model, respectively.

2.2. Fixed sample search strategy

A female who uses a fixed sample search strategy samples n potential mates sequentially and she then returns to mate with the highest quality male in the sample of n individuals (Janetos, 1981; Real, 1990; see also McKenna, 1985). The decision variable is n and the objective of a searcher is to determine *a priori* the value of n that maximizes the net fitness benefit associated with the search process.

First consider the general structure of the search problem. The cost to sample n potential mates is cn and, hence, a female who samples n males has an expected net fitness return of

$$v(n) = E_n - cn, \tag{10}$$

where the first term on the right-hand side of this equation is the expected *maximum* male quality in a sample of n individuals. Likewise, a female who samples $n+1$ potential mates has a net fitness return of

$$v(n+1) = E_{n+1} - c(n+1). \tag{11}$$

In the standard model it is simple to establish that the expected maximum quality male in a sample increases with n and that the incremental benefit to an increase of n decreases with n (McKenna, 1985; Real, 1990). Thus, a female searcher who behaves optimally increases n provided

$$\Delta v(n) = v(n+1) - v(n) = E_{n+1} - E_n - c > 0 \tag{12}$$

and she chooses the largest n that satisfies

$$\Delta v(n) = E_n - E_{n-1} \geqslant c. \tag{13}$$

Now consider how a female evaluates males in a sample of potential mates when inspection of a phenotypic character provides uncertain information about male quality due to unobserved male attributes that affect the fitness of searchers. The quality of any particular male in a sample is unknown and the preferred male in a sample of potential mates is consequently the individual who provides the highest expected fitness return to a searcher. Thus, the males in a sample are ranked by

$$E[W|z] = \int w \, \mathrm{d}G(w|z) = \hat{w}_z. \tag{14}$$

This expression allows us to derive an explicit solution to the search problem. If F is the distribution of the observed male trait, where z-values are now *ordered* with respect to the expected fitness return to a searcher, then the probability that a female encounters a male with an expected quality no higher than some w is equal to the probability that she encounters a male with an observed phenotype no higher than the trait value that yields an expected fitness return of w. In a sample of n potential mates the probability that all individuals in the sample have an expected quality no higher than some w is consequently

$$X_n(w) = F(z)^n, \tag{15}$$

where z is the observed male trait value that yields an expected fitness return of w. This is also the probability that w is the maximum expected male quality in the sample of n potential mates. The derivative of this function with respect to the observed male character is

$$\frac{\mathrm{d}}{\mathrm{d}z} X_n(z) = nf(z)F(z)^{n-1}. \tag{16}$$

Because the maximum expected fitness return to a female who samples n potential mates may be associated with any particular value of the male trait the expected highest quality male in a sample of n potential mates is

$$E_n = n\int^{\zeta}\int wg(w|z)f(z)F(z)^{n-1}\,\mathrm{d}w\,\mathrm{d}z, \tag{17}$$

where ζ is the value of the observed male trait that yields the highest possible expected fitness return to a searcher. Integration by parts shows that

$$\begin{aligned} E_n &= \hat{w}_{\zeta}F(\xi)^n - \int^{\zeta}\int w\,\mathrm{d}\left[\frac{\partial}{\partial z}G(w|z)\right]F(z)^n\,\mathrm{d}z \\ &= \hat{w}_{\zeta} - \int^{\zeta}\int w\,\mathrm{d}\left[\frac{\partial}{\partial z}G(w|z)\right]F(z)^n\,\mathrm{d}z. \end{aligned} \tag{18}$$

Likewise, the fitness return to a female who samples $n+1$ males is

$$E_{n+1} = \hat{w}_{\zeta} - \int^{\zeta}\int w\,\mathrm{d}\left[\frac{\partial}{\partial z}G(w|z)\right]F(z)^{n+1}\,\mathrm{d}z. \tag{19}$$

The difference between the maximum male quality in a sample of $n+1$ potential mates and a sample of n males is

$$\begin{aligned} E_{n+1} - E_n &= \int^{\zeta}\left(F(z)^n - F(z)^{n+1}\right)\int w\,\mathrm{d}\left[\frac{\partial}{\partial z}G(w|z)\right]\mathrm{d}z \\ &= \int^{\zeta}\int (F(z)^n(1-F(z)))w\,\mathrm{d}\left[\frac{\partial}{\partial z}G(w|z)\right]\mathrm{d}z. \end{aligned} \tag{20}$$

This difference is greater than zero for all n because the distribution of the observed male trait is ordered on the expected quality of potential mates and

$$\frac{\mathrm{d}}{\mathrm{d}z}E[W|z] = \int w\,\mathrm{d}\left[\frac{\partial}{\partial z}G(w|z)\right] = \frac{\mathrm{d}}{\mathrm{d}z}\hat{w}_z > 0. \tag{21}$$

Thus, the expected fitness return to a female increases with n. (Notice that this derivative was used to establish a reservation property on the male character in the sequential search model and females who use a fixed sample search strategy will also prefer higher z-values if the observed male character is naturally ordered on the expected quality of potential mates.) However, the incremental fitness benefit decreases, as in the standard model, with successive increases in n, as

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}n}(E_{n+1} - E_n) = \int^{\zeta}\int \ln\,F(z)(F(z)^n(1-F(z))) \\ \times w\,\mathrm{d}\left[\frac{\partial}{\partial z}G(w|z)\right]\mathrm{d}z < 0. \end{aligned} \tag{22}$$

The optimal n is consequently the largest integer that satisfies

$$\begin{aligned} \Delta\upsilon(n) = E_n - E_{n-1} = \int^{\zeta}\int \left(F(z)^{n-1}(1-F(z))\right) \\ \times w\,\mathrm{d}\left[\frac{\partial}{\partial z}G(w|z)\right]\mathrm{d}z \geqslant c. \end{aligned} \tag{23}$$

The number of males in a sample is effectively increased until the marginal benefit from the addition of another male to the sample is less than the cost to include the additional male in the sample of potential mates.

3. Model properties

The optimal values of the decision variables in the standard formulations of the two search models are influenced by the variability of male quality and by the cost to search (Real, 1990; Wiegmann et al., 1996, 1999; Wiegmann and Mukhopadhyay, 1998). In this section of the paper, we specify how, in our formulations of the two models, the cost to sample potential mates influences female search behavior. In addition, we show how the distribution of unobserved male attributes amongst potential mates contributes to the overall variance of male quality and we determine how shifts of this distribution alter the optimal model solutions.

3.1. Search costs

3.1.1. Sequential search strategy

The influence of search costs on the optimal solution to our formulation of the sequential search model is intuitive, as in the standard model. If the cost to search increases, then the benefit of continued search declines and we find that the fitness return to search and the search cost are related by

$$\frac{\mathrm{d}}{\mathrm{d}c}\hat{w}_{z^*} = \frac{-1}{1-F(z^*)} < 0. \tag{24}$$

Furthermore, the reservation value of the observed male character increases or decreases concomitantly with $\hat{w}_{z^*}$ and

$$\frac{\mathrm{d}}{\mathrm{d}c}z^* = \frac{-1}{\int w\,\mathrm{d}\left[(\partial/\partial z^*)G(w|z^*)\right](1-F(z^*))} < 0 \tag{25}$$

(Appendix A). A female who behaves optimally can terminate search earlier, in the context of this search strategy, only through an expansion of her acceptance set and, hence, by a reduction of z^* (Fig. 2). Indeed, the proportion of acceptable males is $1-F(z^*)$ and the number of males a female expects to sample to encounter a male with an observed character in the optimal acceptance set is consequently

$$E[n] = \frac{1}{1-F(z^*)}, \tag{26}$$

which clearly decreases as z^* decreases. Thus, an increase of the search cost causes females to become less choosy and, as a result, lowers the probable duration of the search process.

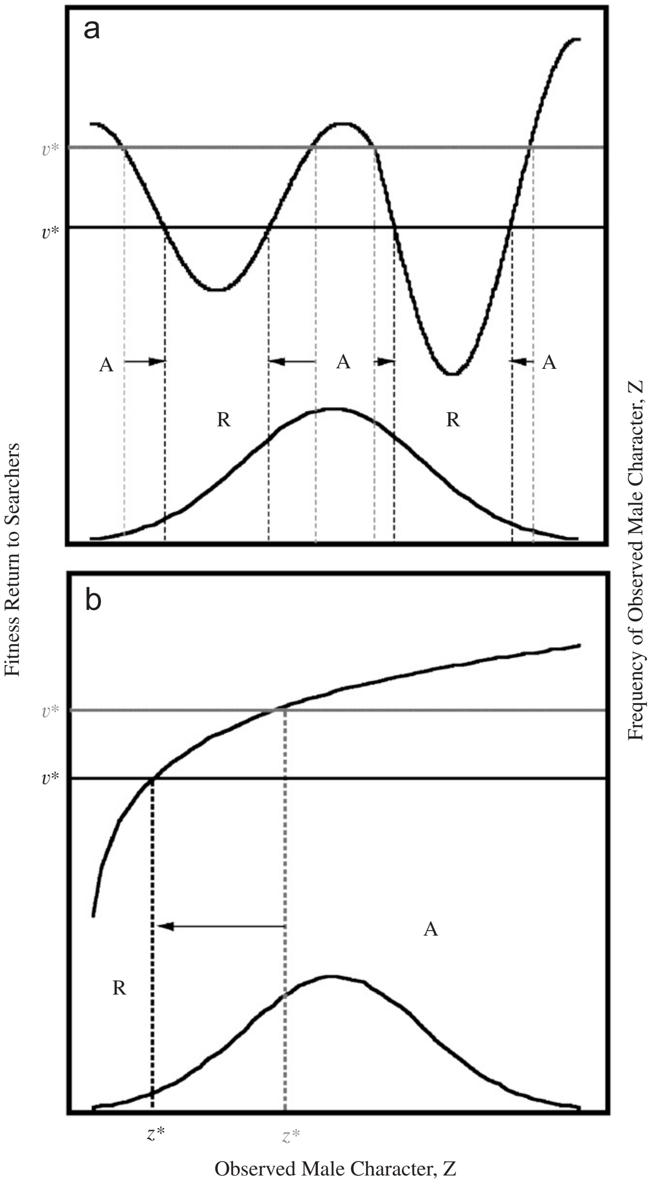

Fig. 2. The relationship between the cost of search, the fitness return to searchers and the contents of the optimal acceptance set under a sequential search strategy. The net fitness return v^* declines as the cost to search c increases. (a) In general, the reduction of v^* induced by an increase of c causes an expansion of the optimal acceptance set and lowers the expected duration of the search process. (b) If the model exhibits a reservation property the expansion of the optimal acceptance set is accomplished by a reduction of z^*. The observed male character values contained in and excluded from the optimal acceptance set are indicated by the letters A and R, respectively, above the probability density of the observed male character. Light-colored vertical lines set the boundaries on character values included in the optimal acceptance set under a lower search cost and dark vertical after an increase of c and the concomitant reduction of v^*. Arrows indicate the magnitude of expansion of the optimal acceptance set caused by the increase of the cost to sample potential mates.

3.1.2. Fixed sample search strategy

The anticipated fitness return to a female who adopts a fixed sample search strategy also declines as the cost to search increases and, as we show presently, the optimal n decreases as the cost to search increases. The incremental fitness increase that results with each increase of n declines with n and the optimal n is the highest integer for which the fitness increase between a sample of $n-1$ and n potential mates is at least c and an increase of the sample from n to $n+1$ yields a fitness increase less than c. Thus, if n_1^* and n_2^* are the optimal n for search costs c_1 and c_2, then n_1^* and n_2^* satisfy

$$E_{n_1^*} - E_{n_1^*-1} \geqslant c_1 > E_{n_1^*+1} - E_{n_1^*} \tag{27}$$

and

$$E_{n_2^*} - E_{n_2^*-1} \geqslant c_2 > E_{n_2^*+1} - E_{n_2^*}. \tag{28}$$

Furthermore, if c_2 is higher than c_1, then

$$c_2 > E_{n_1^*+1} - E_{n_1^*}. \tag{29}$$

This result establishes that the optimal n for higher search costs can never be higher than the optimal n under lower search costs. Indeed, there is a c_2 larger than c_1 that satisfies

$$c_2 > E_{n_1^*} - E_{n_1^*-1} \geqslant c_1 > E_{n_1^*+1} - E_{n_1^*} \tag{30}$$

for all non-zero n^* (Fig. 3). Thus, the optimal n decreases—strictly, does not increase—as the cost of search increases.

3.2. Variance of male quality

The total variance of male quality in our formulations of the two models depends on how unobserved male attributes are distributed amongst potential mates. In the next two sections of the paper we show how the magnitude of the variance of male quality modifies female search behavior, but it is useful to first describe how this variance is structured by unobserved male characters. The total variance of male quality can be partitioned into components attributable to the differences of mean quality *amongst* males with different values of the observed character and to differences of quality *within* males that have the same expression of the observed character, or

$$\sigma^2 = \iint (w-\hat{w})^2 \, \mathrm{d}G(w|z) \, \mathrm{d}F(z) = \int (\hat{w}_z - \hat{w})^2 \, \mathrm{d}F(z) + \iint (w-\hat{w}_z)^2 \, \mathrm{d}G(w|z) \, \mathrm{d}F(z), \tag{31}$$

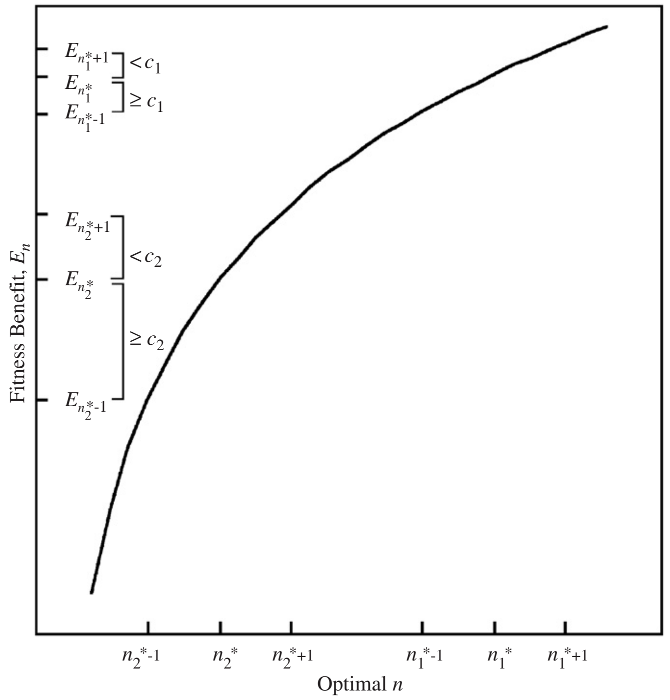

Fig. 3. The relationship between the cost to search and the optimal n under a fixed sample search strategy. The sample of potential mates is increased until the fitness benefit from the addition of another male to the sample is less than the cost c to add a male to the sample of potential mates. Because the incremental fitness benefit to the addition of a male to the sample decreases with n for any distribution of male quality the optimal n is higher for lower search costs.

where $\hat{w}$ is the overall expected male quality. The first term on the right-hand side of this equation is the variance of expected quality amongst males with different expressions of the indicator character, the variance of conditional expected male quality. The magnitude of this term depends on the direct fitness impact of the observed male character and on the association between this character and all unobserved male attributes that influence the fitness of searchers. This term essentially describes the variance of male quality that is attributable to the realized functional relationship between the observed male character and the fitness return to searchers, where this function might be fitted, say, by a simple linear regression of fitness on the observed male character.

The second term is the expected variance of male quality at each value of the observed male character. The inside integral of this term describes the magnitude of uncertainty associated with a particular mate choice decision, the variance of potential fitness returns to a searcher who mates with a male of phenotype z due to unobserved male attributes that contribute to female fitness. The second term is the expected *residual variance* of fitness, the variance of fitness returns not accounted for by the realized functional relationship between fitness and the observed male character.

3.2.1. Sequential search strategy

The distribution of unobserved male attributes may in principle alter female search behavior through either of the two components of the total variance of male quality. First consider how the solution is altered by the variance of conditional expectations of fitness. The solution to the model can be rewritten and expressed in units of fitness expectations as

$$c = \int_{z^*} \int (w - \hat{w}_{z^*})\, \mathrm{d}G(w|z)\, \mathrm{d}F(z) = \int_{z^*} (\hat{w}_z - \hat{w}_{z^*})\, \mathrm{d}F(z) \tag{32}$$

from which we observe that the right-hand side of the solution, the marginal fitness return to searchers, *decreases* with an increase of the reservation value of the observed male character.

Now suppose S and T are two distributions of conditional fitness expectations, X and Y, with inverses S^{-1} and T^{-1}. The dispersion of fitness expectations increases if the distance between all percentiles of the distribution increases and, hence, the variability of X is less than Y if

$$T^{-1}(\gamma) - T^{-1}(\varphi) \geqslant S^{-1}(\gamma) - S^{-1}(\varphi) \tag{33}$$

for all $0 < \varphi \leqslant \gamma < 1$. In this situation X is said to be smaller than Y in *dispersive order* (Shaked and Shanthikumar, 1994). The dispersion of $X + \varepsilon$ is identical to the dispersion of X and, likewise, the dispersion of $Y + \varepsilon$ equals the dispersion of Y, where ε is any real number. Furthermore, the inverse of $X + \varepsilon$ is $S^{-1}(\cdot) + \varepsilon$ and

$$\begin{aligned} T^{-1}(\gamma) - T^{-1}(\varphi) &\geqslant S^{-1}(\gamma) + \varepsilon - (S^{-1}(\varphi) + \varepsilon) \\ &= S^{-1}(\gamma) - S^{-1}(\varphi). \end{aligned} \tag{34}$$

Thus, the dispersive order of X and Y are independent of their overall expectations; that is, either X or Y may be shifted by a constant with no impact on their dispersive order.

The relationship between the observed male character and X and Y is revealed if we apply this result to the restricted sequential search model, where $r(z)$ increases with z. The conditional expected fitness returns to searchers are related to the observed male character by $y = T^{-1}(F(z))$ and $x = S^{-1}(F(z))$ and by the dispersive order of X and Y,

$$T^{-1}(F(z_j)) - T^{-1}(F(z_i)) = \Delta y \geqslant S^{-1}(F(z_j)) - S^{-1}(F(z_i)) = \Delta x \tag{35}$$

for all $z_i \leqslant z_j$. Division of both sides of this inequality by $\Delta z = z_j - z_i$ reveals that $\Delta y/\Delta z \geqslant \Delta x/\Delta z$ over all values of the observed male character (Fig. 4). Thus, the dispersion of X and Y effectively defines the slope of the functional relationship between the expected fitness return to a searcher and the observed character under S and T, respectively.

Now suppose $T^{-1}(F(z^*))$ is the expected fitness return to a female who mates with a male with an observed character z^*, where z^* is the optimal reservation value of the male

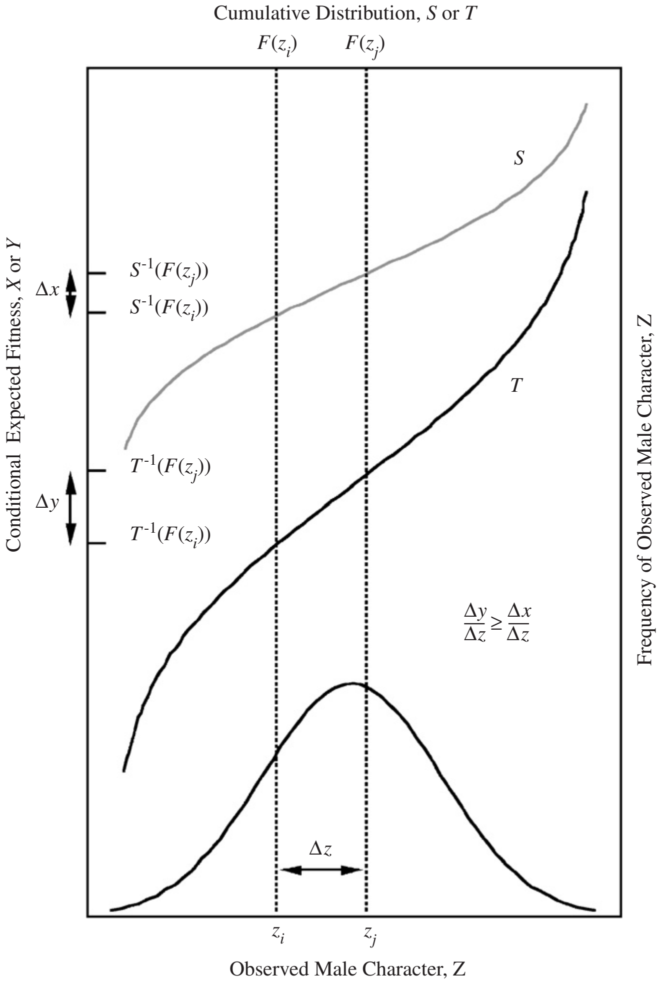

Fig. 4. The relationship between the dispersion of conditional fitness expectations and the optimal solutions to the search models. The conditional fitness expectations X and Y have distributions S and T with inverses S^{-1} and T^{-1}, where X is smaller than Y in dispersive order. The dispersion of conditional fitness expectations effectively defines the curvature of the realized functional relationship between the expected fitness return to searchers and the observed male character and the curvature of the fitness function determines the optimal solutions to the models. In general, an increase of the dispersion of conditional fitness expectations causes a *contraction* of the optimal acceptance set under the sequential search model and an *increase* of the optimal n under a fixed sample search strategy.

character under the more disperse distribution T. It then follows from the dispersive order of X and Y that

$$T^{-1}(F(z)) - T^{-1}(F(z^*)) \geqslant S^{-1}(F(z)) - S^{-1}(F(z^*)) \tag{36}$$

for all $z \geqslant z^*$. Integration of both sides of this inequality from z^* to infinity gives

$$\begin{aligned} c &= \int_{z^*} (T^{-1}(F(z)) - T^{-1}(F(z^*)))\, \mathrm{d}F(z) \\ &\geqslant \int_{z^*} (S^{-1}(F(z)) - S^{-1}(F(z^*)))\, \mathrm{d}F(z). \end{aligned} \tag{37}$$

This result and our earlier observation that the marginal fitness return to a searcher decreases with an increase of z^* establish that the optimal reservation value of the observed male character under T is higher than under S and that females become choosier—the optimal acceptance set contracts—as the variance of conditional fitness expectations increases. Thus, any shift of the distribution of unobserved male attributes that alters the dispersion of conditional expectations of fitness to searchers modifies female choosiness.

Next consider how the magnitude of uncertainty associated with mate choice decisions influences the optimal solution to the model. The uncertainty of a mate choice decision increases with the variance of the potential fitness returns to a female who chooses a male with any particular value of the observed character. Let an increase of a parameter α increase the variance of male quality at each observed male phenotypic value, where this parameter has no effect on the conditional expected male quality. The optimal solution to the sequential search strategy for a particular α can then be written as

$$c = \int_{z^*} \int (w - \hat{w}_{z^*})\, \mathrm{d}G(w|z,\alpha)\, \mathrm{d}F(z). \tag{38}$$

The fact that the model solution can be written in terms of conditional fitness expectations implies that α has no influence on female search behavior and in Appendix B we provide a formal proof that the model solution is indeed unaffected by the magnitude of uncertainty associated with mate choice decisions.

3.2.2. Fixed sample search strategy

First consider how the variance of conditional expectations of fitness influences the optimal solution to the fixed sample search model and suppose again that S and T are two distributions of conditional fitness expectations, X and Y, where X and Y are ordered on the observed male character and X is smaller than Y in dispersive order. The incremental fitness benefit that results from increase of the sample of potential mates from $n-1$ to n can be rewritten as

$$E_n - E_{n-1} = \int^{\zeta} (F(z)^{n-1} - F(z)^n) \left[\frac{\mathrm{d}}{\mathrm{d}z}\hat{w}_z\right] \mathrm{d}z, \tag{39}$$

which clearly reveals that the model solution depends on the slope of the functional relationship between the observed male character and fitness expectations to searchers. And if X is smaller than Y in dispersive order the derivative in this expression is, as we determined earlier, higher under T than under S at all values of the observed male character. Thus, the optimal n under a fixed sample search strategy increases as the dispersion of conditional fitness expectations increases and any shift of the distribution of unobserved male attributes that alters the dispersion of these expectations also alters the optimal number of prospective mates females sample in the search process.

Next consider how the magnitude of uncertainty associated with mate choice decision influences the model solution and suppose again that an increase of the parameter α increases this uncertainty. In this situation, it is straightforward to show that the magnitude of α has no impact on the optimal solution to the model (Appendix C). The behavior of females who adopt a fixed sample search strategy is, like the behavior of females who employ a sequential search strategy, unaffected by the magnitude of uncertainty associated with mate choice decisions.

4. Discussion

The behavior of females in search of a mate is subject to selection because the strategy employed by a searcher determines the probability that a high quality mate is encountered in the search process. The sequential search strategy and the fixed sample search strategy were first derived—like most other models of female search behavior—on an assumption that the quality of males encountered in the search process is revealed without error to searchers (Janetos, 1980; Real, 1990; see Sullivan, 1990, 1994; Gibbson and Högland, 1992; Luttbeg, 1996, 2002). However, the decision to mate with a particular male is inherently uncertain whenever unobserved male attributes contribute to the fitness of searchers. In this paper, we derived solutions to these two models of search behavior under the general condition in which both observed and unobserved male attributes determine the fitness return to searchers and we evaluated how search costs and the variance of male quality influence female search behavior and mate choice decisions.

The fundamental feature of the standard sequential search model is its reservation property (McKenna, 1985; Real, 1990). In the standard model females use a threshold male quality w^* to differentiate between acceptable and unacceptable prospective mates. The generalized sequential search model derived in this paper also exhibits a reservation property, but only if the anticipated fitness return to searchers increases monotonically with the value of the observed male character. This association is implicit in earlier modifications of the model that incorporate the use of a perfectly informative indicator character (Wiegmann et al., 1999). In this situation females impose a threshold criterion z^* on the observed male character. The reservation property of the standard model arises *de jure* because the to-be-realized fitness return w is revealed to females with certainty at the time a male is encountered and the expected fitness return to acceptance of any encountered male as a mate *necessarily* increases with w.

The optimal reservation value of the male character z^* under the generalized sequential search model behaves qualitatively like w^* under the standard model. The threshold value of the male character in our restricted formulation of the model and w^* both decrease, for example, as the marginal cost to sample prospective mates c increases. In general, the net fitness return associated with the search process declines as c increases and this effectively causes an expansion of the optimal acceptance set in all formulations of the model. In the standard model and in the generalized model that exhibits a reservation property this occurs through a reduction of w^* and z^*, respectively. The optimal n under the standard and generalized fixed sample search rule also decreases as the cost to search increases. These parameter changes in response to increased search costs ultimately reduce the expected duration of the search process.

The optimal solutions to the two search models in their standard formulations also depend on the variance of male quality. In particular, the optimal threshold criterion w^* and the optimal n both increase as the variance of male quality increases (Real, 1990; Wiegmann et al., 1996). In our formulations of the models we assumed that an observed male character and unobserved male attributes contribute to the total variance of male quality. The observed male character and unobserved male attributes determine the realized functional relationship between an observed male character and the fitness return to searchers—the dispersion of conditional fitness expectations—and the distribution of unobserved male attributes associated with each value of the observed male character determines the magnitude of uncertainty associated with mate choice decisions. These two sources of fitness variation together comprise the total variance of male quality experienced by searchers and a primary goal of our study was to evaluate how the magnitude of these sources of fitness variation impact female search behavior.

The optimal solutions to the models are sensitive to the dispersion of conditional fitness expectations. Indeed, the generalized sequential search model is guaranteed to exhibit a reservation property if and only if the expected fitness return to searchers that results from the combined contributions of the observed male character and unobserved male attributes increase monotonically with the observed character. The dispersion of conditional fitness expectations effectively describes the curvature of the realized functional relationship between the fitness return to searchers and the observed male character. The results of this study reveal that highly inclined fitness functions induce a higher optimal z^* under a sequential search strategy and a higher optimal n under a fixed sample search strategy, irrespective of the specific form of the functional relationship between an observed male character and fitness or the mean quality of prospective mates. The variance of conditional fitness expectations in our development of the models is equivalent of the fitness variance induced by the translation of a perfectly informative indicator character into the fitness benefit to searchers (see Wiegmann and Mukhopadhyay, 1998; Wiegmann et al., 1999). The expected fitness return to searchers increases as the dispersion of conditional fitness expectations increases; that is, an increase of the dispersion of conditional fitness expectations implies a shift of the realized functional relationship between the fitness return to females and the observed male character that, in general, causes a contraction of the optimal acceptance set under the sequential search model and an increase of the optimal n under a fixed sample search strategy.

The uncertainty of mate choice decisions induced by unobserved male attributes, in contrast, has no influence on the optimal solution to either search model. This property of the models has important implications for studies of mate choice and search behavior. The sequential search model and the fixed sample search model have motivated numerous empirical studies of female search behavior and there is some controversy over evidence used to determine the search strategy that females actually employ (reviewed by Gibbson and Langen, 1996; Valone et al., 1996; Jennions and Petrie, 1997; Luttbeg, 2002). The controversy developed in part because the search behavior of females who adopt alternative search strategies may often appear superficially similar (Wiegmann et al., 1996). For example, the number of males a female is expected to sample under a fixed sample search strategy decreases as the cost to search increases, but, as we showed, the number of males a female expects to sample under a sequential search strategy also decreases with the cost to sample prospective mates. The results of this study imply that experiments proposed in earlier theoretical studies to resolve this issue—experiments that rely on the manipulation of a perfectly informative indicator character—apply even if an observed male character does not reveal the quality of prospective mates with certainty (Wiegmann et al., 1996; reviewed by Wiegmann and Morris, 2005).

Unfortunately, this property of the models will likely be difficult to verify empirically because, while it is simple to manipulate the distribution of an indicator character, it is not obvious how to manipulate the variance of the fitness benefit associated with a particular value of a male trait *and* reveal the magnitude of this variance to searchers. However, this property might be falsified by comparisons of the behavior of females from, say, two populations for which there is a similar functional relationship between an observed male character and female fitness and dissimilarity in the uncertainty of mate choice decisions. In this situation, the behavioral responses of females to experimental manipulations of an observed character should follow predictions of the aforementioned theoretical studies on the use of indicator characters in the search process, regardless of the magnitude of uncertainty associated with mate choice decisions. The comparative approach we propose is not as implausible as it might perhaps first appear because, as we showed, the optimal solutions to the models depend only on the curvature of the fitness function and not on the overall expected fitness return to searchers. In addition, the indicator trait used by females in the different populations need not in principle be the same male character. This comparative approach requires only that the fitness functions within each population have—or can be transformed to have—the same curvature and that these functions have different variances of residual fitness.

In our formulations of the search models we assumed that females use a single male character to evaluate prospective mates. The mate choice decisions of females may, however, often involve an assessment of multiple male characters (Backwell and Passmore, 1996; Dale and Slagsvold, 1996; Jang and Greenfield, 2000; Møller and Petrie, 2002; Olvido and Wagner, 2004). This situation can be accommodated within our formulations of the models if the distribution of *combinations* of observed male characters is substituted for F, the distribution of the observed male character, in the initial equations of the generalized models. The model solutions are then derived exactly as we solved the problems. The number of male characters evaluated in the decision process is likely to influence the uncertainty of mate choice decisions and the quantitative solutions to the models will depend on how the acquisition of this additional information alters the search cost and on how this information alters the curvature of the function that describes the fitness return to searchers. In this situation, the optimal acceptance set under a sequential search strategy is the set composed of the combinations of observed male characters that equates the marginal cost to search and the marginal fitness benefit to searchers and the existence of a reservation criterion on any particular male character will depend on its correlation with any observed or unobserved male traits that have a particularly strong influence on female fitness. In general, the model will exhibit a reservation property if the net fitness return to searchers increases monotonically with the value of any of the observed male characters. The optimal n under a fixed sample search strategy is likewise determined from the distribution of combinations of observed male attributes ordered on the expected fitness return to searchers. Thus, the results of our analyses apply qualitatively to situations in which females use any number of male characters to evaluate the quality of prospective mates.

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Appendix A

In this appendix we show that the total expected fitness return to search and the reservation male character decrease as the cost to search increases. The solution to the sequential search problem is

$$c = \int_{z^*} \int (w - \hat{w}_{z^*})\,\mathrm{d}G(w|z)\,\mathrm{d}F(z) = w^* \int_{\infty}^{z^*} \mathrm{d}F(z) - \int_{\infty}^{z^*} \int w\,\mathrm{d}G(w|z)\,\mathrm{d}F(z). \tag{A.1}$$

Total differentiation of this equation with respect to z^* gives

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}z^*}c &= \frac{\mathrm{d}}{\mathrm{d}z^*}\hat{w}_{z^*}\int_{\infty}^{z^*}\mathrm{d}F(z) + f(z^*)\left(\hat{w}_{z^*} - \int w\,\mathrm{d}G(w|z^*)\right)\\ &= \frac{\mathrm{d}}{\mathrm{d}z^*}\hat{w}_{z^*}\int_{\infty}^{z^*}\mathrm{d}F(z),\end{aligned} \tag{A.2}$$

which after rearrangement shows

$$\frac{\mathrm{d}}{\mathrm{d}c}\hat{w}_{z^*} = \frac{1}{\int_{\infty}^{z^*}\mathrm{d}F(z)} = \frac{-1}{\int_{z^*}\mathrm{d}F(z)} = \frac{-1}{1-F(z^*)} < 0. \tag{A.3}$$

The fitness return to a searcher consequently decreases with c. Furthermore, the expected fitness return to a female who encounters a male with phenotype z^* is

$$\hat{w}_{z^*} = \int w\,\mathrm{d}G(w|z^*) \tag{A.4}$$

and differentiation of this expression with respect to z^* gives

$$\frac{\mathrm{d}}{\mathrm{d}z^*}\hat{w}_{z^*} = \int w\,\mathrm{d}\left[\frac{\partial}{\partial z^*}G(w|z^*)\right] > 0. \tag{A.5}$$

This derivative is positive because it is precisely the condition necessary for a reservation z^*. Thus, the expected fitness return to search and the value of the reservation male character increase (or decrease) concomitantly. Substitution of this expression into the total derivative gives

$$\frac{\mathrm{d}}{\mathrm{d}z^*}c = \left(\int w\,\mathrm{d}\left[\frac{\partial}{\partial z^*}G(w|z^*)\right]\right)\int_{\infty}^{z^*}\mathrm{d}F(z) \tag{A.6}$$

and, after rearrangement, we find that

$$\frac{\mathrm{d}}{\mathrm{d}c}z^* = \frac{-1}{\int w\,\mathrm{d}[(\partial/\partial z^*)G(w|z^*)](1-F(z^*))} < 0. \tag{A.7}$$

Thus, an increase of the search cost reduces the fitness return to a searcher and lowers the reservation observed male phenotype z^*. Notice that a reduction of z^* effectively expands the optimal acceptance set because the proportion of acceptable males is $1-F(z^*)$ and this proportion clearly increases as z^* decreases.

Appendix B

In this appendix we show that an increase of the variance of male quality about each value of the observed male character that preserves the conditional expected male quality has no influence on the optimal solution to the sequential search model. Let an increase of α increase the variance of male quality at each observed male character value, where this parameter has no effect on the conditional expected male quality. The optimal solution to the sequential search strategy for a particular α is

$$\begin{aligned}c = {}& \int_{z^*}\int w\,\mathrm{d}G(w|z,\alpha)\,\mathrm{d}F(z)\\ &- \hat{w}_{z^*}\int_{z^*}\mathrm{d}F(z) \equiv K(\hat{w}_{z^*}, z^*, \alpha).\end{aligned} \tag{B.1}$$

The total derivative of this expression with respect to α is

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}\alpha}c = {}& \frac{\partial}{\partial\hat{w}_{z^*}}K(\hat{w}_{z^*}, z^*, \alpha)\frac{\mathrm{d}}{\mathrm{d}\alpha}\hat{w}_{z^*}\\ &+ \frac{\partial}{\partial z^*}K(\hat{w}_{z^*}, z^*, \alpha)\frac{\mathrm{d}}{\mathrm{d}\alpha}z^*\\ &+ \frac{\partial}{\partial\alpha}K(\hat{w}_{z^*}, z^*, \alpha)\frac{\mathrm{d}}{\mathrm{d}\alpha}\alpha.\end{aligned} \tag{B.2}$$

The derivative of c with respect to α is zero and the first derivative on the right-hand side of this expression is

$$\frac{\partial}{\partial\hat{w}_{z^*}}K(\hat{w}_{z^*}, z^*, \alpha)\frac{\mathrm{d}}{\mathrm{d}\alpha}\hat{w}_{z^*} = -(1-F(z^*))\frac{\mathrm{d}}{\mathrm{d}\alpha}\hat{w}_{z^*} = 0. \tag{B.3}$$

The second derivative on the right-hand side is

$$\begin{aligned}\frac{\partial}{\partial z^*}K(\hat{w}_{z^*}, z^*, \alpha)\frac{\mathrm{d}}{\mathrm{d}\alpha}z^* &= f(z^*)\\ &\times\left(\int w\,\mathrm{d}G(w|z^*,\alpha) - \hat{w}_{z^*}\right)\frac{\mathrm{d}}{\mathrm{d}\alpha}z^* = 0\end{aligned} \tag{B.4}$$

and the third derivative is

$$\frac{\partial}{\partial\alpha}K(\hat{w}_{z^*}, z^*, \alpha)\frac{\mathrm{d}}{\mathrm{d}\alpha}\alpha = \int_{z^*}\int w\,\mathrm{d}\left[\frac{\partial}{\partial\alpha}G(w|z,\alpha)\right]\mathrm{d}F(z) = 0. \tag{B.5}$$

The first and third derivatives are zero because, by definition, an increase of α preserves the conditional mean quality of prospective mates and the second derivative is zero because $\hat{w}_{z^*}$ equals the expected fitness return to a female who encounters a male with observed character z^*. The total derivative is consequently zero. Thus, the magnitude of α does not affect the optimal solution to the search problem.

Appendix C

In this appendix we show that an increase of α has no influence on the optimal solution to the fixed sample search model. The probability that a male with any particular character z is included in a sample of potential mates is not affected by α because α shifts the distribution of unobserved male attributes and does not affect the marginal distribution of the observed male character. Thus, we need only consider how a shift of α influences which male in a sample of potential mates provides the highest fitness return to a searcher. If an increase of α preserves the conditional expected male quality, then

$$\frac{\mathrm{d}}{\mathrm{d}\alpha}E[W|z] = \int w\mathrm{d}\left[\frac{\partial}{\partial\alpha}G(w|z,\alpha)\right] = 0 \tag{C.1}$$

for all values of the observed male character. Now consider two random samples of $n-1$ and n potential mates, where males have expected quality $w_{1,n-1} \leqslant w_{2,n-1} \leqslant \cdots \leqslant w_{n-1,n-1}$ and $w_{1,n} \leqslant w_{2,n} \leqslant \ldots \leqslant w_{n,n}$, respectively. If an increase of the dispersion of residual male quality preserves the conditional expected quality, then the transformation of male quality also preserves the expected quality of all males in a sample of potential mates. The incremental fitness benefit $w_{n,n} - w_{n-1,n-1}$ is consequently independent of α. Furthermore, this result applies to *any* two random samples of $n-1$ and n potential mates. Thus, the derivative

$$\frac{\mathrm{d}}{\mathrm{d}\alpha}\Delta v(n) = 0 \tag{C.2}$$

for all n. The magnitude of the dispersion of male quality about each observed male phenotypic value, the degree of uncertainty associated with mate choice decisions, has no impact on the optimal n under a fixed sample search strategy.

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