

# Mate choice decisions by searchers

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**Abstract** For more than two decades rudimentary versions of the *fixed sample* and *sequential search* strategies have provided the primary theoretical foundation for the study of mate choice decisions by searchers. The theory that surrounds these models has expanded markedly over this time period. In this paper, we review and extend results derived from these models, with a focus on the empirical analysis of searcher behavior. The basic models are impractical for empirical purposes because they rely on the assumption that searchers—and, for applied purposes, researchers—assess prospective mates based on their *quality*, the fitness consequences of mate choice decisions. Here we expound versions of the models that are more empirically useful, reformulated to reflect decisions based on male phenotypic characters. For some organisms, it may be possible to use preference functions to derive predictions from the reformulated models and thereby avoid difficulties associated with the measurement of male quality *per se*. But predictions derived from the two models are difficult to differentiate empirically, regardless of how the models are formulated. Here we develop ideas that illustrate how this goal might be accomplished. In addition, we clarify how the *variability* of male quality should be evaluated and we extend what is known about how this variability influences searcher behavior under each model. More general difficulties associated with the empirical study of mate choice decisions by searchers are also discussed [*Current Zoology* 59 (2): 184–199, 2013].

**Keywords** Dispersive order, Fixed sample strategy, Mate choice, Preference functions, Sequential search, Stochastic dominance

*It seems to me—and my interest in such matters is admittedly casual—that the problem of determining characteristics of search rules empirically is a very difficult one.* Michael Rothschild

## 1 Introduction

Rothschild (1974) wrote this comment in a footnote to a rather dense theoretical paper on consumer search behavior, where he speculated on the imbalance between theoretical and empirical studies on rules followed by searchers. The behavior that leads searchers to a goal is indeed often complex and, as models of searcher behavior are modified to capture realism, so too is the associated theory. In this paper, we have several objectives. The first is to synthesize and extend results derived from two models that have been especially influential on the study of mate choice decisions by searchers. Here, we focus on versions of the models that capture sufficient realism to be applied. The second objective is to clarify how the variability of quality amongst prospective mates is specified under each model. Lastly, we show how the models might be

evaluated empirically and we offer a few suggestions that we believe may be usefully applied to the general study of mate choice decisions by searchers.

The study of search strategies has an extensive history in the field of economics (reviewed by McCall and McCall 2008). Two strategies, the *fixed sample* and *sequential search* strategies, appear prominently in this history (Stigler, 1961, 1962; McCall, 1965, 1970; Lippman and McCall 1976). Janetos (1980) proposed variants of these strategies—which he called, respectively, the *best-of-n-males* strategy and the *fixed threshold* strategy—as rules that females might employ to sample and choose amongst prospective mates. Real (1990) later used discoveries in economics to more fully characterize the models. These papers are now citation classics, which attests to the broad impact of these foundational models on studies of female mate choice decisions.

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Janetos (1980) supposed that decisions by females in search of a mate are tactical, shaped by selection to facilitate an encounter with a high quality individual (reviewed by Cronin 1991). The term *quality* evokes a variety of male attributes, such as physical condition, immune function or agility, but in this context *quality* refers to *the benefit that a mate conveys to a searcher*. The names he chose for the strategies reveal how this is presumed to be accomplished: a female who uses a best-of- $n$ -males strategy samples  $n$  males and mates with the highest quality male sampled, while a female who adopts a fixed threshold strategy terminates search when she encounters a male whose quality surpasses a predetermined, fixed threshold. The behavior of searchers is also apparent in names used in economics, and in this paper: a female who employs a fixed sample search strategy samples a fixed, predetermined number of prospective mates and a female who employs a sequential search strategy decides sequentially, after each encounter with a prospective mate, whether she should terminate search and mate with an encountered individual or continue the search process.

Because Janetos (1980) was concerned with the tactical nature of searcher behavior he focused on the performance of alternative search strategies, the fitness consequences of behavior. His analyses led him to conclude that the fixed sample search strategy is superior to the sequential search strategy. Real (1990) shared this interest and, indeed, one of his goals was to show that this conclusion is erroneous. But, more importantly, he animated his equations: he exposed search theory to empirical scrutiny. He predicted, for instance, how females who employ a sequential search strategy will respond if the mean or variability of quality amongst prospective mates is changed.

The papers by Janetos (1980) and Real (1990) also inspired a theoretical interest in search strategies and the development of alternative models, many of which capture more realism than the two foundational models (Wittenberger, 1983; Parker, 1983; Dombrovsky and Perrin, 1994; Getty, 1996; Luttbeg 1996; Johnstone, 1997; Fawcett and Johnstone, 2003; Colins et al., 2006; Fawcett and Bleay, 2009; Castellano and Cermelli, 2011; Castellano et al., 2012). The fixed sample and sequential search models have themselves been modified to add realism and, in particular, to confront problems related to the assessment of male quality (Wiegmann and Mukhopadhyay, 1998; Wiegmann et al., 1999; Wiegmann et al., 2010a, b; Seubert et al., 2011). These advances appear in technical papers and a primary objec-

tive here is to provide a general synopsis of these results and their implications for the empirical study of searcher behavior.

The models, as originally formulated, have limited applicability because searchers are presumed to evaluate prospective mates based on their quality, the fitness *consequences* of mate choice decisions. The versions of the models that we consider in this paper are more practical. In particular, they apply to situations in which mate choice decisions are founded on the expression of an *indicator character*, a phenotypic attribute like physical condition, that is somehow indicative of male quality (reviewed by Andersson, 1994; Byers et al., 2010). Indeed, the versions of the models featured in this paper can be applied, as we describe later, on male phenotypes without consideration of the fitness consequences of mate choice decisions. First we review the assumptions used to derive the original models and describe how the models were later modified to reflect decisions on indicator characters. The principal properties of the original models are then highlighted and their translation to decisions on indicator characters is discussed. This translation unveils a suite of problems that must be confronted when these models (and others) are empirically evaluated. Finally, we show how some of these problems may be circumvented and we offer a few suggestions that we believe can be usefully applied to the general study of search behavior and mate choice decisions.

## 2 Basic Models

### 2.1 Assumptions

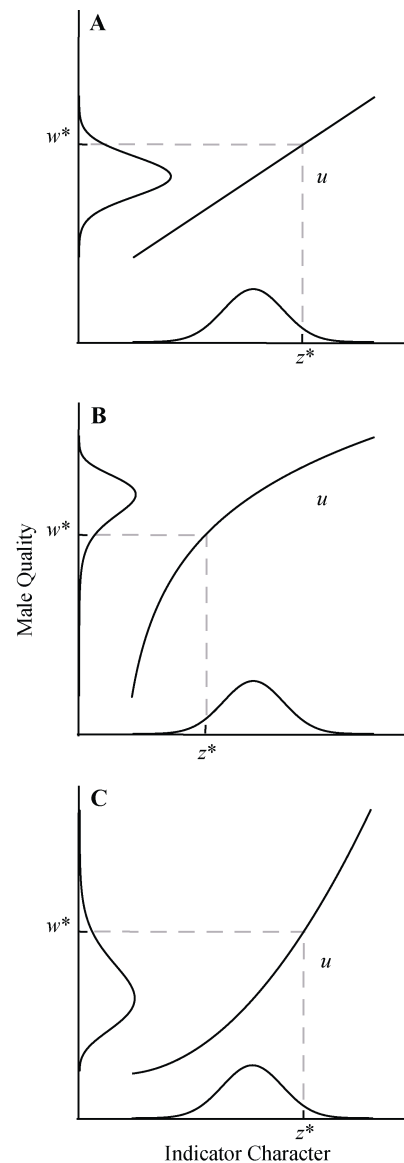
The assumptions used to derive the fixed sample and sequential search models are identical. Prospective mates are sampled for a cost from a static distribution that is known by searchers. The cost to sample a prospective mate is referred to as the *search cost* and when a male is sampled we say that he is *encountered*. The search cost is a random variable that is presumed to be independent of the quality of encountered individuals. The quality of encountered males is revealed to searchers without error. Importantly, the search cost and male quality *are measured in units of fitness to the searcher*. Females encounter prospective mates randomly and sequentially. Two additional assumptions maintain the constancy of the distribution from which prospective mates are sampled: males mate indiscriminately and the search process is not time limited. Females are presumed to behave within these constraints so as to maximize the expected net fitness return associated with

the search process. If a fixed sample strategy is employed, then the size of the sample of prospective mates to be inspected is optimized. When a sequential search strategy is used a threshold criterion, applied on male quality, is optimized. The optimal values of these decision variables are denoted herein by  $n^*$  and  $w^*$ , respectively.

Nearly all of the assumptions used to derive the original models have been modified to investigate their influences on searcher behavior (Wiegmann and Morris, 2005; McCall and McCall, 2008). The modification of particular interest to us, the modification that substantially improves the empirical usefulness of the models, relates to how prospective mates are evaluated. The quality of an encountered male is the fitness return that a female realizes *if* she elects to mate with him and terminate the search process. Thus, the quality of a prospective mate would appear to be unobservable *a priori*. Nonetheless, females are assumed to behave to the contrary, as if males announce their quality when they are encountered. The presence of model searchers arises because female sensory, perceptual and cognitive systems are presumed to have evolved to translate observations on male phenotypes into male quality. From the perspective of a researcher who studies the search process the decisions of searchers *appear* as decisions on observable male characters.

The models are more useful for empirical purposes if they are reformulated with this perspective in mind. Toward this end we imagine that male quality is revealed to females by inspection of an indicator character that has some functional relation to male quality and a distribution that is known by searchers. The behavior of females is then modeled as if they sample males from this phenotypic distribution and use the fitness function to formulate decisions on the indicator character. This simple alteration to the original models allows us to evaluate their predictions from mate choice decisions based on male characters that, unlike male quality, can be relatively easily quantified and manipulated. The original models, reformulated in this manner, are referred to here as the *modified* models.

Fig. 1 illustrates the conceptual relationship between the original and modified models. The fitness function  $u$  transforms values of an indicator character into an associated fitness return to searchers. For heuristic purposes it is useful to envision  $u$  as the lens of a searcher that has been designed by selection to seamlessly convert observations on indicator characters into observations on male quality. The distribution of the indicator



**Fig. 1 Relationship between the distribution of an indicator character and the distribution of male quality**

The distribution of male quality (shown on the y-axis) is the translation of the distribution of the indicator character (shown on the x-axis) through  $u$ . The translation of the indicator character through a **A** linear, **B** concave and **C** convex fitness function is depicted. The threshold male quality  $w^*$  under a sequential search strategy is observed as the phenotypic threshold  $z^*$ .

character, translated through  $u$ , prescribes the distribution of male quality, the distribution that dictates mate choice decisions by searchers.

The mate choices of searchers are observed as decisions on the indicator character. If a female chooses the highest quality male from a sample of prospective mates, then this is reflected in her choice of the male with the highest expression of the indicator character. (For simplicity, we assume that  $u$  increases with values of the male phenotypic character.) Likewise, a threshold criterion applied on male quality appears as a phenotypic

threshold. The phenotypic threshold tied to  $w^*$  is denoted  $z^*$ . Later, we discuss how observed decisions on indicator characters can be used to evaluate predictions derived from the original models. Fortunately, this is possible even when  $u$ —and, hence, the distribution of male quality—is not known in detail. To elucidate this assertion we first review several important properties of the original models.

**2.2 Model properties**

The predicted responses of searchers to changes of the search cost or to attributes of the distribution of male quality under conditions of the original models have been extensively studied. McCall and McCall (2008) summarize these results in technical detail. Here we highlight three principal predictions. The predictions are summarized in Table 1, where sources are also cited. Importantly, the results hold for *any* search cost and for *arbitrary* distributions of male quality.

*The cost to sample prospective mates.* The response of searchers to a change of the search cost is intuitive regardless of the search strategy that is employed. When a fixed sample search strategy is used the optimal sample size  $n^*$  decreases—strictly, does not increase—with an increase of the cost to sample prospective mates. When a sequential search strategy is used the optimal

acceptance threshold criterion applied on male quality  $w^*$  is likewise reduced. The proportion of males whose quality exceeds the adjusted, lowered threshold increases and females are expected to sample fewer males to find an acceptable individual.

*The mean quality of prospective mates.* The addition of a constant  $\delta$  to the quality of all males shifts their mean quality by  $\delta$ . The optimal sample size  $n^*$  is unaffected:  $n^*$  is independent of the mean quality of prospective mates. The optimal threshold criterion  $w^*$  is shifted by exactly  $\delta$  and, because the entire distribution of male quality is shifted, the proportion of males whose quality exceeds the adjusted threshold  $w^* + \delta$  is unchanged. The number of males that females are expected to sample to find an acceptable individual is consequently also unchanged.

*The variability of male quality.* The optimal sample size  $n^*$  increases—strictly, never decreases—with an increase of the variability of male quality. The optimal threshold criterion  $w^*$  likewise increases when the variability of male quality is increased. Whether the adjusted threshold causes females to sample more or fewer males in the search process depends critically on the cost to sample prospective mates.

The first two results were derived from simple

**Table 1 Predicted adjustments to the optimal sample size  $n^*$  and the threshold applied on male quality  $w^*$  or an indicator character  $z^*$  in response to an increase of the cost to sample prospective mates and to an increase of the mean or variability of the distribution from which males are sampled**

Factor	Original Models			Modified Models		
	Fixed Sample	Sequential Search		Fixed Sample	Sequential Search	
	$n^*$	$w^*$	$E[n]$	$n^*$	$z^*$	$E[n]$
Search Cost	$n_2^* \leq n_1^*$ (1)	$w_2^* \leq w_1^*$ (1)	$E_2[n] \leq E_1[n]$ (1)	(a,b,c) $n_2^* \leq n_1^*$ (3)	$z_2^* \leq z_1^*$ (4)	$E_2[n] \leq E_1[n]$ (4)
Mean	$n_2^* = n_1^*$ (2)	$w_2^* = w_1^* + \delta$ (1)	$E_2[n] = E_1[n]$ (1)	(a) $n_2^* = n_1^*$ (3)	$z_2^* = z_1^* + \delta$ (4)	$E_2[n] = E_1[n]$ (7)
				(b) $n_2^* \leq n_1^*$ (3)	$z_1^* \leq z_2^* \leq z_1^* + \delta$ (4)	$E_2[n] \leq E_1[n]$ (7)
				(c) $n_2^* \geq n_1^*$ (3)	$z_2^* \geq z_1^* + \delta$ (4)	$E_2[n] \geq E_1[n]$ (7)
Variability	$n_2^* \geq n_1^*$ (2)	$w_1^* \geq w_2^*$ (1,6)	$dc$ (6)	(a) $n_2^* \geq n_1^*$ (8)	$z_2^* \geq z_1^*$ (5)	$dc$ (8)
				(b)?	$dc$ (5)	?
				(c)?	$z_2^* \geq z_1^*$ (5)	?

The sample sizes  $n_1^*$  and  $n_2^*$  are optimal before and after a term in the first column is increased. The adjustment of the optimal threshold  $w^*$  applied on male quality or the threshold  $z^*$  applied on an indicator character are likewise indicated. The number of males that a female who adopts a sequential search strategy expects to sample is  $E_1[n]$  and it is adjusted to  $E_2[n]$ . The mean is increased by the addition of a constant  $\delta$  to either the quality (original models) or phenotype (modified models) of all prospective mates. The variability of male quality or the indicator is assessed as illustrated in Figure 2. Rows under modified models apply when the fitness function  $u$  is (a) linear, (b) concave or (c) convex. Numbers in parentheses indicate where a result was derived (1: Real, 1990; 2: Wiegmann et al., 1996; 3: Wiegmann and Mukhopadhyay, 1998; 4: Wiegmann et al., 1999; 5: Wiegmann et al., 2010b; 6: Seubert et al., 2011; 7: Appendix A; 8: Appendix B). The symbols  $dc$  and  $?$  indicate that a result depends on the cost to sample prospective mates and that a particular result has not been published, respectively.

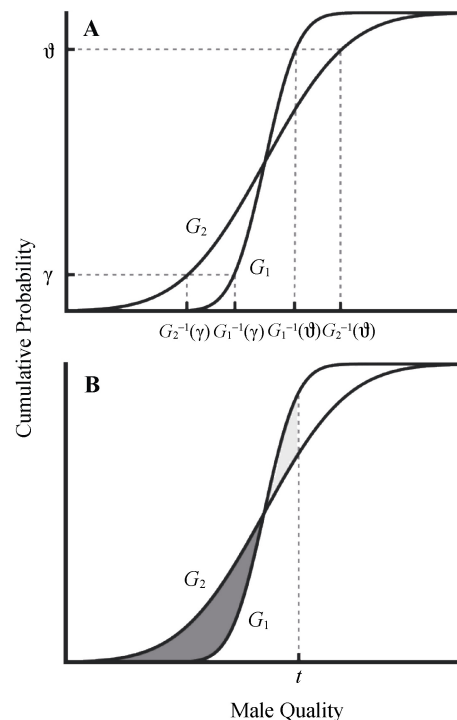
manipulations of model parameters. But predictions based on the variability of male quality are not so straightforward. In the next section of the paper, we consider how the variability of male quality influences the behavior of searchers in more detail.

### 2.3 Variability of male quality

Readers of early papers will find that the *variability* of male quality is imprecisely defined. For example, Real (1990) investigated how searchers respond to a change of the *spread* of the distribution of male quality. To understand his definition of spread requires a general familiarity with utility theory. Furthermore, the *variability* of male quality and the *variance* of male quality were loosely interchanged in his characterization of spread. (The lead author of this paper has regrettably also used these two words as synonyms.) But the term *variance* in this context is imposturous. Indeed, the variance of male quality reliably controls neither  $n^*$  nor  $w^*$ . Their control requires more stringent definitions of variability.

Fig. 2 illustrates how the variability of male quality is specified under each of the models. The *dispersive order* of male quality describes variability in the context of a fixed sample search strategy and in the context of a sequential search strategy variability is characterized by *stochastic dominance at the second order*. These conditions *define* the variability of male quality because they are the respective specifications of variability that control, all else equal, the optimal sample size  $n^*$  and the optimal threshold  $w^*$ . In particular,  $n^*$  is larger under one distribution of male quality, say  $G_2$ , than another, say  $G_1$ , whenever the dispersive order of male quality is higher under  $G_2$ . Likewise, the stochastic dominance of one of the distributions over the other at the second order ensures that for all search costs  $w^*$  will be higher under the distribution that is dominated.

These specifications of variability are hierarchically related to one another and to the variance of male quality *per se*. Dispersive order implies stochastic dominance at the second order, all else equal, but the latter condition does not strictly imply the former (Shaked and Shanthikumar, 1994). The variance of male quality also *necessarily* differs between two distributions of prospective mates if either of these conditions holds. But when two distributions have different variances neither dispersive order nor stochastic dominance at the second order is strictly implied. This is the reason that the variance of male quality fails to reliably control the behavior of searchers. Notice that the hierarchical relations imply that dispersive order controls  $w^*$  as well as  $n^*$ .



**Fig. 2 The variability of male quality**

The appropriate characterization of the variability of male quality specifies, all else equal, the relative magnitude of the decision variable associated with a particular search strategy. The mean quality of prospective mates is identical under the distributions  $G_1$  and  $G_2$  and the variability of male quality, appropriately characterized, is higher under  $G_2$ . **A.** The *dispersive order* of male quality determines the distribution under which the optimal sample size is larger when a fixed sample search strategy is employed (Wiegmann et al., 1996). The inverse of  $G$ , namely  $G^{-1}$ , is the value of male quality—the percentile—that equals or exceeds the qualities of some percentage of prospective mates. If the difference between all pairs of percentiles of male quality is larger under one distribution than another, then the dispersive order of male quality is higher under the former distribution than the latter. In this illustration,  $G_1^{-1}(\theta) - G_1^{-1}(\gamma) \leq G_2^{-1}(\theta) - G_2^{-1}(\gamma)$  for all  $0 < \gamma \leq \theta < 1$  and the dispersive order of male quality is higher under  $G_2$  (Shaked and Shanthikumar, 1994). The optimal sample size is larger—strictly, never smaller—for all search costs under  $G_2$ . **B.** The stochastic dominance of one distribution of male quality over another at the second order specifies, all else equal, the variability of male quality when females employ a sequential search strategy (Seubert et al., 2011). If the area under one distribution between the lowest value of male quality and any male quality  $t$  is never smaller than the area under another, then the former distribution is dominated by the latter (Harder and Russell, 1969). The dark-shaded and light-shaded regions show differences of areas under  $G_1$  and  $G_2$  where  $G_2 - G_1 > 0$  and  $G_2 - G_1 < 0$ , respectively. The dark-shaded region is never smaller for any male quality  $t$  and hence  $G_2$  is dominated by  $G_1$  stochastically at the second order. The optimal threshold criterion is higher for all search costs under  $G_2$ .

What defines the variability of male quality is the weakest condition that reliably controls the decision variable under each model.

How is searcher behavior predicted to differ under two distributions of male quality when neither of these

conditions holds? In these situations, the actual values for  $n^*$  and  $w^*$  under each distribution need to be computed and compared. The distribution under which either decision variable is higher will depend critically on the cost to sample prospective mates. The predicted behavior of searchers is, unfortunately, even more complex if mate choice decisions involve indicator characters. Indeed, rigid experimental control may be necessary to evaluate model predictions related to the variability of male quality.

#### 2.4 Indicator characters

The modified models have been to some extent similarly analyzed. How search costs and distributional properties of indicator characters influence mate choice decisions under the modified models is complicated by the fact that there are countless possible expressions for the fitness function  $u$ . Nonetheless, many useful insights have been obtained by considerations of three general shapes for  $u$ , namely situations in which  $u$  is a linear, convex or concave function of an indicator character. Examples of these functions were illustrated in Fig. 1.

The predicted responses of searchers to changes of the search cost or distributional properties of an indicator character are listed in Table 1 for comparison with predictions derived from the original models. (New results, derived in the appendices of this paper, are included.) Two results are particularly noteworthy. From Table 1 we observe that adjustments to  $n^*$  under the original and modified formulations of the fixed sample search strategy parallel one another when  $u$  is linear. The same parallel adjustment of  $w^*$  and  $z^*$  is observed when a sequential search strategy is employed. These results reveal that male quality and the indicator character are effectively *synonymous* whenever  $u$  is linear.

The second noteworthy result is that *the variability of an indicator character has no universal control on the optimal phenotypic threshold*. If  $u$  is linear or convex and the mean associated with two distributions of an indicator character is equal, then the stochastic dominance of one of the distributions over the other at the second order ensures that for all search costs  $z^*$  will be higher under the distribution that is dominated. (The optimal sample size is likewise controlled by the dispersive order of the indicator character when  $u$  is linear.) However, when  $u$  is concave we know of no measure of the variability of a male trait that reliably controls the phenotypic threshold. It also seems likely that the variability of an indicator character fails to control  $n^*$  under a fixed sample search strategy when  $u$  is either concave or convex, but this is yet to be determined.

### 3 General Considerations

In this section of the paper, we consider aspects of the models that are likely to generalize to any strategic process related to the search for prospective mates. These considerations illuminate general difficulties associated with the empirical study of mate choice decisions by searchers. In particular, we discuss issues related to the evaluation of male quality and problems that can arise when experience influences searcher behavior. In addition, we illustrate how predictions derived from the two models might be empirically differentiated. Lastly, we recommend a specific direction for additional theory, which we believe would particularly benefit empirical inquiries into decision rules used by searchers.

#### 3.1 Fitness functions and male quality

When we observe female mate choice decisions on male indicator characters, rather than choices based on male quality *per se*, we apply the modified models. This means that we need an adequate characterization of  $u$ , which translates a male character into the currency of fitness to searchers. The behavioral responses of searchers to manipulations of the search cost or properties of the distribution of an indicator character can be predicted, as illustrated in Table 1, when we know the general curvature of  $u$ . But in many situations even the shape of a fitness function may be difficult to determine empirically. In these situations, a suitable alternative currency needs to be identified.

Fitness proxies are regularly substituted into predictive models of forager behavior (Stephens and Krebs, 1986). Indeed, this practice is arguably why optimality models have proven to be such a useful tool in this context (Hamilton, 2011). Forager responses to reward variability are reliably predicted, for instance, by optimality models formulated on the currency of *utility*, the *perceived value* of a reward (reviewed by Kacelnik and Bateson, 1996, 1997). This particular currency substitution could likewise prove to be highly profitable for studies of mate choice decisions by searchers.

The modified models are in fact ideally suited to a utility currency: a conceptual twist is all that is needed to accommodate a utility-based decision process. The function  $u$  is interpreted as a *utility* or *preference function* and the distribution derived from the translation of an indicator character through  $u$  is interpreted as the *subjective distribution of male quality* experienced by searchers. The predictions listed in Table 1 then apply directly to the curvature of the utility function and to the subjective distribution of male quality.

This conceptual shift expands the usefulness of the models because the currency of utility allows us to effectively bypass the fitness consequences of mate choice decisions and use rather simple techniques to characterize  $u$ . In particular, the utility function describes female preferences on a male character—the attractiveness of males with different trait expressions—and procedures adapted from economics can be used to elucidate its curvature (reviewed by Davis and Holt 1993). Excellent examples of these techniques are found in the seminal paper by Caraco et al. (1980) on risk-sensitivity in yellow-eyed juncos *Junco phaeonotus* and in a detailed study by Gerhardt et al. (2000) on mate choice decisions by female gray tree frogs *Hyla versicolor*. For many commonly studied organisms female preference functions are rather easily estimated (reviewed by Wagner, 1998; Widemo and Sæther, 1999). Perhaps most importantly, preference functions provide a representation of  $u$  that we expect to exert immediate control over mate choice decisions. Indeed, a utility substitution for fitness directs our attention toward proximate influences on the decisions of searchers.

### 3.2 Searcher attributes and experiences

The value of a decision variable can be fixed by selection or adjusted through individual experiences. The balance is shifted toward the latter solution when there is high spatial or temporal heterogeneity in the quality of prospective mates (Collins et al., 2006; see also Hutchinson and Halupka, 2004). Indeed, developmental processes and social experiences have substantive influences on mate choice decisions in many animals (reviewed by White, 2004; Dukas, 2006; Witte, 2006; Hebets and Sullivan-Beckers, 2010). The practical repercussion of these experiences is that the behavior of no two searchers will be identical. But how substantially do these experiences impede the investigation of search strategies?

Experiences can alter searcher *choosiness* or *partiality* for one male over another (*sensu* Jennions and Petrie, 1997). The choosiness of a searcher—the number of males that she is prepared to evaluate before a mate is selected—is influenced primarily by the time and energy costs demanded to sample prospective mates. The models adjust searcher choosiness via the decision variables  $n^*$  or  $w^*$ . The relation between  $n^*$  and choosiness is transparent:  $n^*$  specifies precisely how many males will be sampled. But  $w^*$  also specifies choosiness because, all else equal, a female expects to reject more encountered males as the threshold  $w^*$  is increased.

Experiences that affect searcher choosiness are often incident to the search process. Female sticklebacks *Gasterosteus aculeatus* forced to swim against a current to sample prospective mates, for instance, are relatively more receptive to otherwise less attractive males (Milinski and Bakker, 1992; Luttbeg et al., 2001). Female field crickets *Gryllus integer* exposed to the threat of a predator in the vicinity of a highly attractive male call are relatively more likely to approach an alternative, less attractive call (Hedrick and Dill, 1993). The choosiness of female túngara frogs *Physalaemus pustulosus* is also adjusted in response to predation risks (Baugh and Ryan, 2010; Bonachea and Ryan, 2011). Higher encounter rates with individuals of the opposite sex also generally enhance choosiness (Berglund, 1994, 1995; deRivera et al., 2003; Bateman et al., 2004; Willis et al., 2011; Bleu et al., 2012; Heuschele et al., 2012). These selected examples illustrate that the immediate circumstances in which prospective mates are sampled can induce search costs that have a direct impact on choosiness. But costs can also be propagated through experiences that affect the physical condition of a searcher, which later exerts an influence on her choosiness (Rintamäki et al., 1995; Byers et al., 2006; Hebets et al., 2008; Moskalik and Uetz, 2010).

Experiences that influence choosiness are not overly troublesome for the empirical study of search strategies because it is choosiness that is directly or indirectly optimized in models of searcher behavior: experiences that alter choosiness induce responses by searchers that can, generally, be predicted. Experiences that alter searcher preferences, on the other hand, introduce potentially serious complications, particularly for studies conducted in the field. In some situations, the experiences that influence the preferences of a searcher are conveniently recorded in her phenotype (deRivera, 2005; Hebets et al., 2008; Moskalik and Uetz, 2010). In other situations, however, experiences leave little trace other than their profound impact on mate preferences. Indeed, the experiences of a searcher may even modulate the importance of the sensory cues that are used to evaluate prospective mates. When female swordtails *Xiphophorus birchmanni* are food deprived, for instance, the strength of preferences on male olfactory cues is enhanced (Fisher and Rosenthal, 2006a, b). Preferences may also be sexually imprinted (Immelmann, 1972; Bateson, 1978; Slagsvold et al., 2002; ten Cate et al., 2006; Verzijden et al., 2008; Kozak and Boughman, 2009; Kozak et al., 2011).

These kinds of experiences are potentially problema-

tic because they tend to jumble the phenotypic standard by which males appear to be judged. In these situations, detailed information on ontogeny or strict control over experiences may be required to decipher the strategy used by searchers. Indeed, these are the experiences that make the empirical study of search strategies so complicated. In the next section of the paper we consider potential empirical approaches with these complications in mind.

### 3.3 Identification of decision variables

Here we illustrate how model predictions could be used to identify the decision variable—a sample size or threshold—used by searchers. The first approach that we describe is experimental and the second is observational.

**3.3.1 Manipulation of searcher experiences** The experiment described here uses males that differ in their expression of an indicator character to manipulate female experiences. In the design of the experiment attention is, however, rightfully focused on  $u$  because it is the quality or attractiveness of prospective mates that controls the decisions of searchers. The experiment consequently requires that  $u$  can be adequately characterized. The experimental design is based on ideas proposed in several earlier papers (Wiegmann et al., 1996, 1999; Wiegmann and Morris, 2005; Wiegmann and Angeloni, 2007).

Isolation of the decision variable used by searchers requires that we identify a set of conditions that induces strategy-specific patterns of behavior. To accomplish this the experiment is divided into two distinct phases. The initial phase controls the information that females obtain and it establishes a known distribution of male quality. (The decision variable used by searchers is presumed to be malleable and adjusted to their experiences.) The second phase of the experiment controls the set from which a prospective mate can be sampled. Two-tiered experimental designs of this kind are commonly employed to study mate choice decisions. For example, Beckers and Wagner (2011) and Izzo and Gray (2011) used a similar two-staged design to investigate the mate choice decisions of female field crickets.

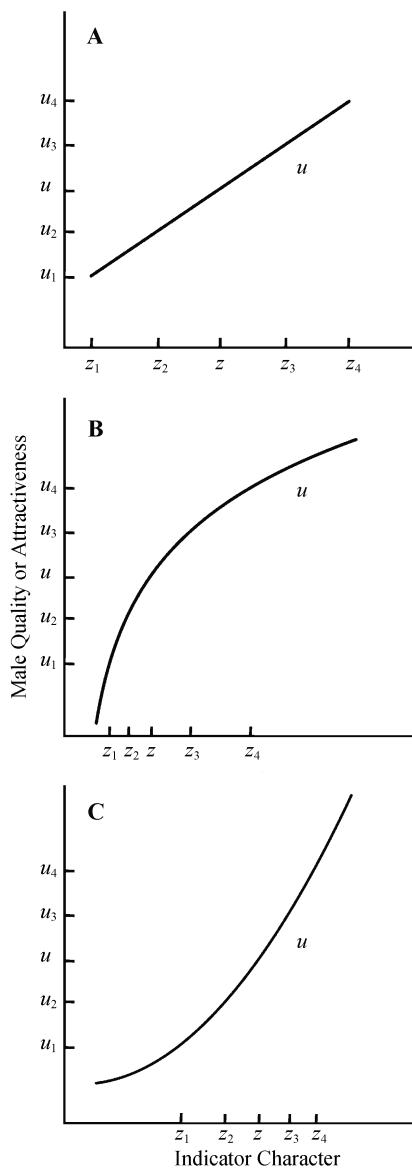
First consider a hypothetical situation in which male quality can be manipulated, where the quality of any male can be augmented by a positive constant  $\delta$ . In the initial phase of the experiment naïve females are allowed to preview males in one of two groups. For simplicity, suppose that each group contains two males. The males in one group are of quality  $w_1$  and  $w_2 = w_1 + \delta$  and the males in the other group have qualities  $w_3 = w_1$

+  $3\delta$  and  $w_4 = w_2 + 3\delta$ . Notice that each male in the second group is equivalent in quality to a male in the first group plus  $3\delta$ . Thus, the mean quality of males in the second group is higher by  $3\delta$ . Importantly, the dispersive order of male quality between the two groups of males, which does not depend on the mean quality of prospective mates, is identical.

In the second phase of the experiment every female is allowed to sample a test male of quality  $w_1 + 2\delta$ . (This male quality is chosen because it holds the dispersive order of male quality experienced by every female constant even if females update their appraisal of the distribution of male quality when the test male is sampled.) Their responses to this male can, as we explain presently, reveal which decision variable—a sample size or threshold—is more likely employed.

Table 1 reveals how  $n^*$  and  $w^*$  depend on the qualities of males initially previewed. The second row of Table 1 shows that  $n^*$  is unaffected, all else equal, by the mean quality of prospective mates. The optimal sample size for a fixed search cost depends only on the dispersive order of male quality, which is preserved by the hypothetical manipulations. Thus, the responses of females to the test male should not depend on which group of males is previewed and any observed difference of responsiveness implies that a sample size is *not* the decision variable used by searchers. From the second row of Table 1 we also observe that  $w^*$  increases when the mean quality of prospective mates is positively shifted by the addition of a constant to the quality of each individual. Hence, females who preview the second group of males should exhibit a lower average level of responsiveness to the test male if a threshold is used.

Now consider a more realistic situation in which male phenotypes are manipulated. To apply this experimental design females are first allowed to preview two males in one of two groups, where males in one group have expressions of an indicator character of  $z_1$  and  $z_2$  and males in the second group have phenotypes  $z_3$  and  $z_4$ . The phenotypes for the males in the two groups are chosen so that their respective qualities or attractiveness  $u_1, u_2, u_3,$  and  $u_4$  follow  $(u_2 - u_1) = (u_3 - u_2)/2 = (u_4 - u_3)$ . (From the second row of Table 1 we see that if  $u$  is linear we can shift the phenotypes  $z_1$  and  $z_2$  by a constant  $\delta$  in exactly the same manner that male quality was shifted to obtain the phenotypes  $z_3$  and  $z_4$ .) In the second phase of the experiment females are allowed to sample a test male whose quality or attractiveness is  $(u_2 + u_3)/2$  (Fig. 3). These phenotype choices



**Fig. 3** Experiment designed to evaluate whether the decision variable used by searchers is a sample size or threshold

Naïve females are exposed to two males with phenotypes  $z_1$  and  $z_2$ , with qualities or measures of attractiveness  $u_1$  and  $u_2$ , or to two males with shifted phenotypes  $z_3$  and  $z_4$ , with qualities or attractiveness  $u_3$  and  $u_4$ . Their responsiveness to a male of phenotype  $z$  is then tested. Phenotypes for males in the two groups are chosen so that  $(u_2 - u_1) = (u_3 - u_2)/2 = (u_4 - u_3)$  and the phenotype for the test male is chosen so that his quality or attractiveness is  $u = (u_2 + u_3)/2$ . These phenotype choices ensure that the optimal sample size does not differ for females exposed to either set of two males when a fixed sample search strategy is used. Phenotypes that satisfy these conditions when the fitness or preference function  $u$  is **A** linear, **B** concave and **C** convex are depicted.

hold constant the dispersive order of  $u$  experienced by all females so that the optimal sample size should again not depend on which set of males is previewed. If a threshold is used, however, it should be higher for females that preview males with phenotypes  $z_3$  and  $z_4$ .

Hence, the predicted responses of females to the test male are the same as those described when male quality itself was manipulated.

**3.3.2 Encounter sequences** The position of accepted males in sequences of encounters have been used to infer the strategy employed by searchers. These positions are indeed informative when the assumptions used to derive the original or modified models hold. When a fixed sample search strategy is employed, and  $n^*$  males are sampled, the highest quality or most attractive male encountered by a searcher is equally likely to occupy any one of the  $n^*$  positions in the sequence of encounters. Thus, the position of accepted males in sequences of a particular length should be uniformly distributed. When a sequential search strategy is used the threshold criterion is, like  $n^*$ , fixed. Hence, the accepted male should always be the last prospective mate encountered.

The latter prediction follows from the assumption that search is not time-limited. When search occurs within a finite time period the model predictions are blurred. The threshold criterion adopted by a female who employs a sequential search strategy may not be surpassed before the search time elapses and, in this situation, the optimal solution for a searcher is to mate with the highest quality male sampled (Lippman and McCall, 1976). This male is equally likely to occupy any position in the encounter sequence and, hence, the behavior of females who are forced by time limitations to mate with a previously encountered male will be indistinguishable from the behavior of females who employ a fixed sample search strategy. Furthermore, prospective mates are likely to be resampled if the pool of candidates is limited when either strategy is employed (Appendix A). These considerations reveal why observations on the position of mated males within encounter sequences have generally failed to provide indisputable evidence of the strategy that underlies the mate choice decisions of searchers (reviewed by Wiegmann et al., 1996; Gibson and Langen, 1996; Jennions and Petrie, 1997; Luttbeg, 1996, 2002).

How a female responds to the first male that she encounters is, however, a decisive indicator of the likely use of a sample-based decision process. The probability that a female rejects the first male that she encounters should be independent of his quality if a sample size is used. (When a threshold is used, on the other hand, initial encounters with high quality males should generate larger probabilities that search is terminated.) This prediction is robust to time constraints as well as individual experiences that induce variability of the sample size

adopted by searchers. Moreover, this prediction can be evaluated without detailed information on fitness or preference functions, provided that the quality or attractiveness of prospective mates is not too disordered amongst searchers.

The search process for many animals cannot be easily observed, but natural patterns of searcher behavior provide invaluable insights into the decision process (Uy et al., 2001; Byers et al., 2005, 2006). Luttbeg and Langen (2004) used a novel statistical approach to study how western scrub-jays *Aphelocoma californica* sample and evaluate nuts (they naturally store large quantities of acorns) and, with sufficiently detailed information on encounter sequences, similar techniques could be applied to uncover the strategies used by females as they sample prospective mates. Procedures used to study job search strategies in economics might also be employed (Keane et al., 2011).

### 3.4 Theoretical considerations

The fitness returns to individuals that employ alternative strategies are regularly compared to determine the theoretically best solution to various problems. Real (1990) showed, for instance, that the expected fitness return to searchers is higher—strictly, never lower—under a sequential search strategy than a fixed sample strategy when the distribution of male quality is truncated normal. Indeed, this result holds for *any* distribution of male quality or cost to sample prospective mates under conditions of the original or modified models (Wiegmann et al., 2010b). The rationale for such comparisons is that selection is expected to favor the use of strategies that perform well.

The conclusion that *there is no distribution of male quality or search cost that favors a fixed sample strategy over a sequential search strategy* is a powerful statement with some theoretical appeal. But what is its importance to the empirical study of searcher behavior? Its main contribution is conceptual rather than practical. In particular, the result is a decisive contradiction to the misconception that low search costs favor the use of a fixed sample search strategy and, more generally, it casts doubt on the notion that variability of search costs diversifies the number of strategies used by searchers (reviewed by Jennions and Petrie, 1997).

The empirical relevance of this result depends, nonetheless, on the extent to which the model assumptions hold. In some situations, the performance of the two strategies is known to be reversed. Luttbeg (2002) explored how imperfect information alters the performance of search rules and he showed, for instance, that

when searcher estimates of the mean quality of prospective mates are biased a fixed sample search strategy can be favored over a sequential search strategy. His approach was numerical and he supposed that male quality is normally distributed, but the generality of his result is evident in Table 1. There we find that for *any* distribution of male quality  $n^*$  is, unlike  $w^*$ , insensitive to a shift of the mean quality of prospective mates. Thus, if searchers formulate an inaccurate estimate of the mean quality of prospective mates the sample size  $n^*$  will still be optimal, all else equal, whereas the threshold criterion applied on male quality will be inappropriately shifted and suboptimal. Additional theoretical attention to potential causes of *reversals* of strategy performance is needed to illuminate other potentially important cognitive and ecological influences on the strategic behavior of searchers.

## 4 Discussion

The quote by Rothschild (1974) with which we opened this paper speaks to the general complexity of search processes. The apathy he expressed toward endeavors to uncover the strategies that are actually used by searchers perhaps also speaks to the very phenomenon he noticed: an imbalance between the number of theoretical and empirical studies of rules used by searchers. In this paper, we reviewed and extended predictions of two prominent search models, the fixed sample strategy and the sequential search strategy, with an eye toward their application to empirical studies of mate choice decisions by searchers. The versions of the models we focused on accommodate how we as researchers typically assess male quality, via the expression of an indicator character (reviewed by Byers et al., 2010).

The primary advantage to the reformulated models is the ease with which indicator characters can be measured, relative to male quality *per se*. But we are not liberated from concerns about male quality even when the models are reframed to reflect decisions on indicator characters. This is because the behavior of searchers is still presumably tactical. Ideally, we want to know how fitness returns to searchers and the indicator character are related, the curvature of the fitness function  $u$ , because when  $u$  is specified the distribution of male quality can be readily determined from the distribution of the indicator character. However,  $u$  need not be known precisely to make use of either model. Table 1 lists model predictions that were derived from limited information on the curvature of  $u$ . For some organisms it

may even be possible to bypass fitness functions altogether and instead use controlled observations to characterize  $u$  as a utility or preference function (reviewed by Wagner, 1998; Widemo and Sæther, 1999). Indeed, the value of a decision to a searcher, the curvature of  $u$ , is of concern for all studies of mate choice decisions.

The predictions listed in Table 1 also reveal why the two models are so difficult to differentiate empirically. The first row of Table 1 indicates that an increase of the cost to sample prospective mates causes the optimal sample size  $n^*$  to be lowered. Likewise, the number of males that a female expects to sample is reduced if she adopts a sequential search strategy. Further inspection of Table 1 reveals a general pattern:  $n^*$  and the number of males that we expect a female to sample when she employs the threshold strategy increase or decrease in parallel. Thus, the two strategies are not easily differentiated based on adjustments to the number of males that females sample in the search process. Isolation of the decision variable used by searchers requires that we identify conditions that lead to strategy-specific patterns of behavior. These conditions are often not easily recognized. Here we developed two ideas to accomplish this goal, one experimental and one observational.

Table 1 further reveals that comparatively little is known about how the variability of an indicator character influences searcher behavior. This particular issue is rather complicated. In Appendix B we show that the dispersive order of an indicator character controls  $n^*$  and that stochastic dominance at the second order controls  $z^*$  when  $u$  is linear. These are the very same conditions on variability that control searcher decisions under the original models: when  $u$  is linear, indicator characters and male quality are effectively synonymous. But a specification of variability that reliably controls  $n^*$  when  $u$  is concave or convex is yet to be discovered. The same statement applies to  $w^*$  for concave  $u$ . The responses of searchers to the *variance* of an indicator character have been explored (Itzkowitz et al., 2001; Draud et al., 2008). The variance of an indicator character cannot generally be used, however, to predict the behavior of searchers who adopt either of the search strategies we considered. Seubert et al. (2011) discuss issues related to search behavior and the characterization of variability in more detail.

Janetos (1980) and Real (1990) inspired the empirical and theoretical exploration of searcher behavior. The details of optimality models, like those they developed, are often less important than the ideas the models generate about how a particular problem *might* be solved, by

the identification of decision variables that *could* be optimized. In other instances, the goal is to capture realism in model details (Fawcett and Belay, 2009; Castellano and Cermelli, 2011; Castellano et al., 2012). Here we used the theoretical foundations established by Janetos (1980) and Real (1990) to illustrate how the decision variable used by searchers might be empirically isolated. A major challenge for theoretical and empirical biologists alike is to determine how more realistic and complex models can be differentiated to advance the empirical study of rules that dictate mate choice decisions by searchers.

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## Appendix A

In this appendix, we show how the number  $n$  of males sampled by a female who adopts a sequential search strategy is altered in response to a shift of the mean of an indicator character  $Z$ . In particular, we want to determine how the expectation of  $n$ , namely  $E[n]$ , is altered when  $Z$  is shifted by a constant  $\delta \geq 0$  and  $u$  is a linear ( $u'(z) = du(z)/dz \geq 0$ ,  $u''(z) = d^2u(z)/dz^2 = 0$ ), concave ( $u'(z) \geq 0$ ,  $u''(z) \leq 0$ ) or convex ( $u'(z) \geq 0$ ,  $u''(z) \geq 0$ ) function of the indicator character.

Let  $Z_2 = Z_1 + \delta$  and let  $F_1$  and  $F_2$  be the distributions of  $Z_1$  and  $Z_2$ , respectively. The addition of  $\delta$  to each  $Z_1$  shifts its mean by  $\delta$  and leaves the variability of the trait preserved. In particular,  $F_2(z_2) = F_1(z_2 - \delta) = F_1(z_1)$ . When  $u$  is linear, concave or convex the optimal phenotypic threshold criteria  $z_1^*$  (under  $F_1$ ) and  $z_2^*$  (under  $F_2$ ) are respectively ordered  $z_2^* = z_1^* + \delta$ ,  $z_1^* \leq z_2^* \leq z_1^* + \delta$  and  $z_2^* \geq z_1^* + \delta$  (Wiegmann et al., 1999). Notice that these orders are equivalent to  $z_2^* - \delta = z_1^*$ ,  $z_1^* - \delta \leq z_2^* - \delta \leq z_1^*$  and  $z_2^* - \delta \geq z_1^*$ .

The number of males that females expect to sample under  $F_1$  is  $E_1[n] = 1/(1 - F_1(z_1^*))$  (Real, 1990). Under  $F_2$  this expectation is likewise  $E_2[n] = 1/(1 - F_2(z_2^*)) = 1/(1 - F_1(z_2^* - \delta))$ . If  $u$  is linear  $z_2^* - \delta = z_1^*$  and  $F_1(z_2^* - \delta) = F_1(z_1^*)$ . Hence  $E_2[n] = E_1[n]$ . If  $u$  is concave  $z_2^* - \delta \leq z_1^*$  and  $F_1(z_2^* - \delta) \leq F_1(z_1^*)$  so  $E_2[n] \leq E_1[n]$ . And when  $u$  is convex  $z_2^* - \delta \geq z_1^*$  and  $F_1(z_2^* - \delta) \geq F_1(z_1^*)$  so  $E_2[n] \geq E_1[n]$ . Thus, the number of males that females are expected to sample when the mean of an indicator character is positively shifted remains unchanged whenever  $u$  is linear. When  $u$  is concave or convex the phenotypic shift causes an increase and decrease of  $E[n]$ , respectively.

A brief comment on the interpretation of  $n$  is useful. The expectation  $E[n]$  is strictly the expected size of the sample drawn from  $F$ . If  $F$  is not continuous  $E[n]$  does not necessarily equal the number of *distinct* individuals that a female expects to sample in the search process. In particular, a male could be resampled (by chance) because searchers are assumed to sample prospective mates randomly. The same interpretation of  $n$  applies under the fixed sample search model, where  $n^*$  is strictly the optimal size of the sample drawn from the distribution of prospective mates. In many natural situations it is consequently reasonable to expect that some males will be resampled when either rule is employed.

## Appendix B

In this appendix, we show that in the context of the two search models the variability of a male indicator character  $Z$  is synonymous with the variability of male quality when male quality is a linear function of  $Z$ . Let the quality of prospective mates be  $W$ . The quality of an encountered male is then  $w = u(z) = \alpha + \beta z$ , where  $\alpha$  and  $\beta > 0$  are the intercept and slope of the fitness function  $u$ , respectively. Notice that  $z$  can also be expressed as a function of  $w$ , namely  $z = (w - \alpha)/\beta$ , and when male quality has lower and upper bounds  $A$  and  $\Omega$  that  $Z$  is bounded on the interval  $[(A - \alpha)/\beta, (\Omega - \alpha)/\beta]$ .

First consider the dispersive order of an indicator character and the optimal sample size  $n^*$  under two cumulative distributions  $F_1$  and  $F_2$ . The associated distributions of male quality, say  $G_1$  and  $G_2$ , are obtained by the translation of  $F_1$  and  $F_2$  through  $u$ . If the dispersive order of the indicator character is smaller under  $F_1$  than  $F_2$ , then the relationship between their inverses  $F_1^{-1}$  and  $F_2^{-1}$  is by definition

$$F_1^{-1}(\vartheta) - F_1^{-1}(\gamma) \leq F_2^{-1}(\vartheta) - F_2^{-1}(\gamma)$$

for all percentages  $0 < \gamma \leq \vartheta < 1$  of the indicator character (Shaked and Shanthikumar, 1994). The male quality that corresponds to  $F_1^{-1}(\vartheta)$  is  $G_1^{-1}(\vartheta) = \alpha + \beta F_1^{-1}(\vartheta)$ . Hence,  $F_1^{-1}(\vartheta) = (G_1^{-1}(\vartheta) - \alpha)/\beta$ . Likewise,  $F_1^{-1}(\gamma) = (G_1^{-1}(\gamma) - \alpha)/\beta$ . Expressions for the relationship between  $F_2^{-1}$  and  $G_2^{-1}$  are identical:  $F_2^{-1}(\vartheta) = (G_2^{-1}(\vartheta) - \alpha)/\beta$  and  $F_2^{-1}(\gamma) = (G_2^{-1}(\gamma) - \alpha)/\beta$ . Substitution of the right-hand sides of these equalities for  $F_1^{-1}$  and simplification gives

$$G_1^{-1}(\vartheta) - G_1^{-1}(\gamma) \leq G_2^{-1}(\vartheta) - G_2^{-1}(\gamma),$$

which defines the dispersive order of male quality under  $G_1$  and  $G_2$ . If male quality is a linear function of  $Z$  and the dispersive order of the indicator character is smaller under  $F_1$  than  $F_2$ , then the dispersive order of male quality is smaller under  $G_1$  than  $G_2$  and *vice versa* and the optimal sample size  $n^*$  will be higher for all search costs under  $F_2$ .

Next consider  $w^*$  and the second-order stochastic dominance relationship between  $F_1$  and  $F_2$ . If  $F_1$  dominates  $F_2$  stochastically at the second order, then by definition

$$D_F\left(\frac{w - \alpha}{\beta}\right) = \int_{\frac{A - \alpha}{\beta}}^{\frac{w - \alpha}{\beta}} (F_2(z) - F_1(z)) dz \geq 0$$

for all  $z = (w - \alpha)/\beta$ , where strict inequality holds for at least one  $z$  between  $(A - \alpha)/\beta$  and  $(\Omega - \alpha)/\beta$  (Harder and Russell 1969). Likewise, the distribution  $G_1$  dominates  $G_2$  stochastically at the second order when

$$D_G(t) = \int_A^t (G_2(w) - G_1(w)) dw \geq 0$$

for all  $w = t$  between  $A$  and  $\Omega$ . If the mean of the indicator character  $E[z]$  is identical under  $F_1$  and  $F_2$ , then the mean male quality  $E[u(z)] = E[\alpha + \beta z] = \alpha + \beta E[z]$  is identical under  $G_1$  and  $G_2$  and for any  $w = t$  we find that

$$\begin{aligned}
D_F\left(\frac{t-\alpha}{\beta}\right) &= \int_{\frac{A-\alpha}{\beta}}^{\frac{t-\alpha}{\beta}} (F_2(z) - F_1(z)) dz = \int_{\frac{A-\alpha}{\beta}}^{\frac{t-\alpha}{\beta}} (1 - F_1(z)) dz - \int_{\frac{A-\alpha}{\beta}}^{\frac{t-\alpha}{\beta}} (1 - F_2(z)) dz \\
&= \left[ \int_{\frac{A-\alpha}{\beta}}^{\frac{t-\alpha}{\beta}} (1 - F_1(z)) dz + \int_{\frac{t-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_1(z)) dz - \int_{\frac{t-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_1(z)) dz \right] - \left[ \int_{\frac{A-\alpha}{\beta}}^{\frac{t-\alpha}{\beta}} (1 - F_2(z)) dz + \int_{\frac{t-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_2(z)) dz - \int_{\frac{t-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_2(z)) dz \right] \\
&= \left[ \int_{\frac{A-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_1(z)) dz - \int_{\frac{t-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_1(z)) dz \right] - \left[ \int_{\frac{A-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_2(z)) dz - \int_{\frac{t-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_2(z)) dz \right] \\
&= \left[ E[Z] - \int_{\frac{t-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_1(z)) dz \right] - \left[ E[Z] - \int_{\frac{t-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_2(z)) dz \right] \\
&= \left[ - \int_{\frac{t-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_1(z)) dz \right] - \left[ - \int_{\frac{t-\alpha}{\beta}}^{\frac{\Omega-\alpha}{\beta}} (1 - F_2(z)) dz \right] \\
&= \left[ - \int_t^{\Omega} (1 - G_1(w)) dw \right] - \left[ - \int_t^{\Omega} (1 - G_2(w)) dw \right] \\
&= \left[ E[u(z)] - \int_t^{\Omega} (1 - G_1(w)) dw \right] - \left[ E[u(z)] - \int_t^{\Omega} (1 - G_2(w)) dw \right] \\
&= \left[ \int_A^{\Omega} (1 - G_1(w)) dw - \int_t^{\Omega} (1 - G_1(w)) dw \right] - \left[ \int_A^{\Omega} (1 - G_2(w)) dw - \int_t^{\Omega} (1 - G_2(w)) dw \right] \\
&= \left[ \int_A^t (1 - G_1(w)) dw + \int_t^{\Omega} (1 - G_1(w)) dw - \int_t^{\Omega} (1 - G_1(w)) dw \right] - \left[ \int_A^t (1 - G_2(w)) dw + \int_t^{\Omega} (1 - G_2(w)) dw - \int_t^{\Omega} (1 - G_2(w)) dw \right] \\
&= \int_A^t (1 - G_1(w)) dw - \int_A^t (1 - G_2(w)) dw = \int_A^t (G_2(w) - G_1(w)) dw \\
&= D_G(t) \geq 0.
\end{aligned}$$

If male quality is a linear function of the indicator character and  $F_1$  dominates  $F_2$  stochastically at the second order, then  $G_1$  dominates  $G_2$  stochastically at the second order and *vice versa* and the optimal phenotypic threshold  $z^*$  will be higher for all search costs under  $F_2$ .