
The evolution of mate choice and the potential for conflict between species and mate-quality recognition

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Understanding how individuals select mates becomes complex when high-quality conspecifics resemble heterospecifics. Individuals facing such a situation may be unable to effectively identify both conspecifics (species recognition) and high-quality mates that can confer fitness benefits to the choosy individual or its offspring (mate-quality recognition). Here I suggest when a conflict may occur between species and mate-quality recognition, discuss the evolutionary consequences stemming from this conflict, and present a model of mate-preference evolution in response to heterospecifics. Determining how species and mate-quality recognition interact to shape mate-choice decisions is important for understanding the diversification of sexually selected traits among closely related taxonomic groups, the use of complex sensory systems for detecting mates, and seemingly inappropriate mate-choice decisions.

Keywords: mate recognition; mate choice; species recognition

1. INTRODUCTION

Mate recognition—the process of identifying, assessing and deciding whether to accept or to reject a potential mate—serves at least two functions (Sherman *et al.* 1997): first, to identify a genetically compatible mate (i.e. a conspecific mate) (e.g. Loftus-Hills & Littlejohn 1971; Waage 1975; Kyriacou & Hall 1982; Ratcliffe & Grant 1983a; Claridge *et al.* 1984; Butlin *et al.* 1985; Verrell 1989; Gerhardt 1994; Noor 1995), and second, to identify a mate that can confer fitness benefits to the choosy individual or its offspring (i.e. a high-quality mate) (e.g. Nakatsuru & Kramer 1982; Møller 1990; Robertson 1990; Reynolds & Gross 1992; Petrie 1994). Mate recognition may therefore include, but is not limited to, the component processes of species recognition and mate-quality recognition (Rand *et al.* 1992; Sherman *et al.* 1997).

Individuals generally should engage in both species and mate-quality recognition because they can benefit by doing so. Heterospecific matings often result in no offspring or offspring with reduced fitness (e.g. Gerhardt 1982; Harrison & Hall 1993; Noor 1995; but see Arnold & Hodges (1995) and references therein). Thus, many organisms potentially engage in species recognition to avoid heterospecific matings (e.g. Loftus-Hills & Littlejohn 1971; Waage 1975; Kyriacou & Hall 1982; Claridge *et al.* 1984; Butlin *et al.* 1985; Verrell 1989; Gerhardt 1994; Noor 1995). Moreover, conspecifics often vary in their ability to provide fitness benefits to choosy individuals (reviewed in Andersson 1994). Thus, many organisms potentially engage in mate-quality recognition because of direct fitness benefits, which increase the reproductive output or survival of the choosy individual (e.g. Nisbet 1973; Thornhill 1976; Nakatsuru & Kramer

1982; Robertson 1990; Forsgren *et al.* 1996), or indirect fitness benefits, which increase the fecundity, attractiveness or survival of the choosy individual's offspring (e.g. Fisher 1958; Møller 1990; Reynolds & Gross 1992; Petrie 1994).

Species and mate-quality recognition are not independent of one another. Historically, attention has focused on how species and mate-quality recognition reinforce each other and how the two processes might jointly facilitate the speciation and diversification of sexually selected traits among closely related taxonomic groups (Fisher 1958; Lande 1981; West-Eberhard 1983; reviewed in Andersson 1994). Conversely, little attention has been paid to the possibility that species and mate-quality recognition can oppose one another (but see Gerhardt 1982; Rand *et al.* 1992; Ryan & Rand 1993). Yet, when high-quality conspecifics resemble heterospecifics, individuals may not be able to engage effectively in both species and mate-quality recognition. This potential for conflict between the two processes has important implications for the evolution of mate-choice behaviour and sexually selected traits. Here I examine this potential for conflict between species and mate-quality recognition, discuss the evolutionary consequences that follow from this conflict, and present a model of mate-preference evolution in response to heterospecifics.

2. THE POTENTIAL FOR CONFLICT BETWEEN SPECIES AND MATE-QUALITY RECOGNITION

The types of traits used for effective species recognition and mate-quality recognition can potentially differ (Rand *et al.* 1992; Ryan & Rand 1993). Consider, for example, that when engaging in species recognition,

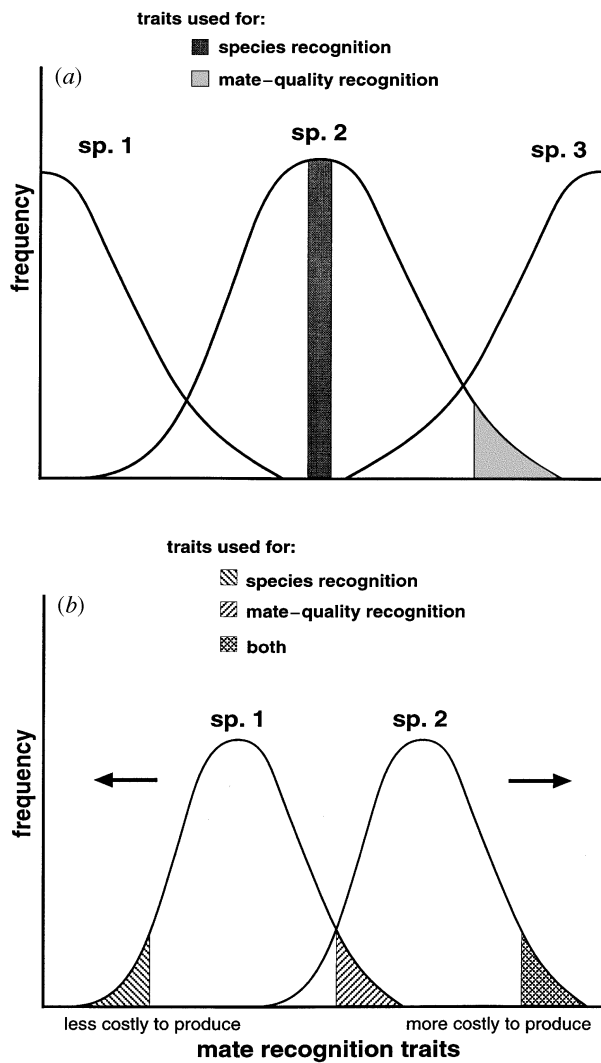


Figure 1. The potential for conflict between species and mate-quality recognition. Species and mate-quality recognition can impose conflicting demands, whether there is stabilizing selection (a) or directional selection (b) for species recognition traits. In both cases, species and mate-quality recognition potentially conflict because individuals engaging in species recognition risk mating with lower-quality mates, and individuals engaging in mate-quality recognition risk heterospecific matings. Although this figure assumes that costly, exaggerated traits reveal mate quality, conflict may occur whenever high-quality mates resemble heterospecifics.

individuals may prefer mates that possess traits closest to the mean or typical value for their population or species (Waage 1975; Kyriacou & Hall 1982; Claridge *et al.* 1984; Butlin *et al.* 1985; Gerhardt 1991; Barlow & Siri 1997), whereas for mate-quality recognition, individuals often use traits that are exaggerated and energetically costly to produce (e.g. Møller 1988; Andersson 1989; Zuk *et al.* 1990; Reynolds & Gross 1992; Thompson *et al.* 1997). In such a situation, individuals may not necessarily be able to engage in both species and mate-quality recognition simultaneously. Indeed, whenever the types of traits used in species recognition do not coincide with those used for mate-quality recognition, the potential for conflict between species and mate-quality recognition arises. If traits that indicate whether a potential mate is the appropriate species also indicate whether it is of high

quality, then species and mate-quality recognition coincide and reinforce one another. However, if high-quality conspecifics resemble heterospecifics, engaging in one form of recognition may detract from an individual's ability to engage in the other form (figure 1).

To illustrate how species and mate-quality recognition can conflict, consider a situation where individuals use exaggerated signals or traits to assess mate quality. Such 'open-ended' preferences may mistakenly lead to heterospecific matings, if heterospecifics possess more extreme traits than conspecifics (Ryan & Rand 1993; see also Moodie 1982; Morris & Fullard 1983; Ryan & Wagner 1987; Basolo 1990; Grant & Grant 1997). For instance, when only given visual cues in laboratory choice tests, female swordtail fish, *Xiphophorus pygmaeus*, prefer allopatric *X. nigrensis* males over conspecifics (Ryan & Wagner 1987). *Xiphophorus nigrensis* males are larger than *X. pygmaeus* males and possess a more complex courtship repertoire (Ryan & Wagner 1987). Female *X. pygmaeus* preferences for exaggerated signals, possibly shaped by mate-quality recognition, may have led them to prefer heterospecifics in a novel situation. When females are given both visual and chemical cues from heterospecifics, females no longer prefer heterospecific males (Crapon de Caprona & Ryan 1990). Thus, engaging in mate-quality recognition can potentially confound an individual's ability to engage in species recognition, causing it to risk heterospecific matings (Ryan & Rand 1993).

Similarly, engaging in species recognition may confound an individual's ability to engage in mate-quality recognition (Gerhardt 1994; Barlow & Siri 1997). For instance, in several sympatric species of cichlid fish, males produce a swelling on their head during breeding (i.e. a nuchal hump). This hump is potentially condition dependent and may indicate male quality (Barlow & Siri 1997). Thus, females are predicted to prefer males with large nuchal humps, because the better a male's condition, the larger his hump. However, female Midas cichlids (*Cichlasoma citrinellum*) prefer males with medium-sized nuchal humps (Barlow & Siri 1997). These females may be selecting against conspecific males with large humps that resemble sympatric heterospecifics. Although there is no direct evidence that hump size indicates mate quality, this example illustrates that a conflict between species and mate-quality recognition may cause females to give up information on mate quality to ensure conspecific matings (Barlow & Siri 1997).

As suggested by the swordtail example, a conflict between species and mate-quality recognition is especially likely when the same trait or correlated traits are used for both species and mate-quality recognition. As will be discussed below, the use of multiple traits for both processes can mitigate the conflict between species and mate-quality recognition. If, however, individuals cannot assess multiple traits simultaneously, or if potential mates do not possess desired states of all traits, then individuals may still be unable to engage effectively in both species and mate-quality recognition.

When species and mate-quality recognition conflict, as in the examples described above, individuals may be seen to express seemingly inappropriate mate preferences (i.e. preferences for heterospecifics or lower-quality mates), because they engage in one form of recognition at the

expense of the other. This trade-off between the two processes may be a means by which individuals facing a conflict between species and mate-quality recognition, optimize the fitness benefits received through mate choice. Which form of recognition is emphasized in any particular situation depends on the likelihood of making a mistake in recognition and the fitness costs of doing so. Thus, I suggest that seemingly inappropriate mate preferences can perhaps be explained better as an adaptive response to a conflict between species and mate-quality recognition, rather than as an outcome of constraints on sensory systems (i.e. sensory bias mechanisms (e.g. Basolo 1990; Barlow & Siri 1997)).

Given that individuals may often face a conflict between species and mate-quality recognition, how do they minimize mistaken matings with heterospecifics or low-quality conspecifics? Below, I review the mechanisms by which these errors are minimized, and discuss the evolutionary consequences of these mechanisms.

3. CONSEQUENCES OF THE CONFLICT BETWEEN SPECIES AND MATE-QUALITY RECOGNITION

There are at least five means, which are not mutually exclusive, by which natural selection leads to a minimization of mistakes in species and mate-quality recognition. First, natural selection can favour individuals that identify high-quality conspecifics by relying on non-phenotypic cues instead of, or in addition to, phenotypic cues. Non-phenotypic cues indicate the time or place where desirable mates are found (Sherman *et al.* 1997). For example, to engage effectively in both species and mate-quality recognition, individuals may limit searching for high-quality mates to areas where, or during times when, heterospecifics are absent (e.g. specific host plants or times of day (Bush 1974)).

A second means by which natural selection can minimize mistakes in species and mate-quality recognition is by favouring high-quality conspecifics that produce signals distinct from heterospecifics. The immense diversification of sexually selected traits among closely related taxonomic groups may be evidence of such an outcome (Littlejohn & Loftus-Hills 1968; Phelan & Baker 1987; Coyne & Orr 1989; Otte 1989; reviewed in Andersson 1994). This hypothesis is one answer to the open question of why sexually selected traits are so diverse among closely related taxonomic groups.

A third means by which natural selection can minimize mistakes in species and mate-quality recognition is by favouring individuals that detect differences between high-quality conspecifics and heterospecifics. For example, the túngara frog, *Physalaemus pustulosus*, responds preferentially to signals from high-quality conspecifics (Rand *et al.* 1992). The frog's amphibian papilla is tuned to frequencies associated with conspecific calls (Rand *et al.* 1992), and the tuning of the basilar papilla is biased toward low frequencies that are possibly indicative of high-quality mates (Ryan *et al.* 1990). Other species may have similar, finely tuned sensory systems for preferentially detecting high-quality conspecific mates (Ryan & Wilczynski 1988; Brenowitz 1991; Mello *et al.* 1992; Whaling *et al.* 1997). Such a possibility is intriguing because it is currently unclear as to what degree selec-

tion has shaped sensory systems for specific recognition tasks.

A fourth means by which natural selection can minimize mistakes in species and mate-quality recognition is by favouring decision rules that optimize fitness. To see how this might be accomplished, consider that organisms possibly possess an internal representation, or template, of the characteristics of desired mates (Reeve 1989; Sherman *et al.* 1997). Individuals often must compromise on their choice of mate, because it is unlikely that any given potential mate will conform exactly to this template. This willingness to accept a mate that does not exactly fit the template can be measured by a mate-acceptance threshold (i.e. a threshold value of the dissimilarity between the template and the perceived recognition cues (Reeve 1989)). Below this threshold, potential mates are accepted, whereas above this threshold, potential mates are rejected. The lower an individual's threshold, the less willing it is to compromise (Reeve 1989). Note that if undesirable mates (e.g. heterospecifics or low-quality conspecifics) resemble desirable mates (e.g. high-quality conspecifics), then individuals may mistakenly reject desirable mates (rejection errors) or accept undesirable mates (acceptance errors) (Reeve 1989). If an individual's threshold is too low, it may frequently reject desirable mates, but if its threshold is too high, it will frequently accept undesirable mates. Selection should favour settings of the mate-acceptance threshold that maximize fitness (Reeve 1989; Deutsch & Reynolds 1995; Sherman *et al.* 1997) by minimizing either error.

Modification of the mate-acceptance threshold can be achieved evolutionarily or facultatively. Facultative, or context-dependent mate choice, can result from experience, information from others (i.e. mate copying) or assessment of environmental factors (Warner *et al.* 1995; Dugatkin 1996; Godin & Briggs 1996; Gabor & Halliday 1997; Rosenqvist & Houde 1997). Thus, individuals may facultatively adjust their mate-acceptance thresholds depending on the costs of heterospecific matings, the frequency of interactions with heterospecifics and the benefits of conspecific matings (*sensu* Reeve 1989). Alternatively, individuals from different populations may have different 'fixed' mate-acceptance thresholds. Different preferences between populations that are allopatric and sympatric with heterospecifics (Waage 1975; Markow 1981; Ratcliffe & Grant 1983b; Gerhardt 1994; Noor 1995; Márquez & Bosch 1997) suggest that mate-acceptance thresholds may evolve in response to the likelihood or costs of heterospecific matings.

Finally, natural selection can minimize mistakes in species and mate-quality recognition by modifying templates of high-quality conspecific mates (Ratcliffe & Grant 1983b; Grant & Grant 1997). Specifically, increasing the number of attributes used for identifying high-quality conspecifics can refine templates. Thus, selection to minimize recognition mistakes may explain the use of multiple traits in mate assessment (e.g. Crapon de Caprona & Ryan 1990; Barlow 1992; Rand *et al.* 1992; Gerhardt 1994; McLennan & Ryan 1997; but also see Møller & Pomiankowski 1993). If, however, individuals cannot use multiple traits effectively for both species and mate-quality recognition, then individuals may

emphasize one form of recognition over the other. For instance, individuals sympatric with heterospecifics may weigh traits indicating species identity over those indicating mate quality, and individuals in allopatry may weigh traits indicating mate quality over those indicating species identity (Gerhardt 1994).

An alternative to incorporating more attributes into the template is to alter what attributes of an acceptable mate are considered desirable. For example, if high-quality conspecifics possessing exaggerated traits resemble heterospecifics, then, to avoid heterospecific matings, individuals may adopt a template that specifies that desirable mates possess less exaggerated values of the trait. Such a shift in template can have the counter-intuitive outcome that individuals will actually prefer low-quality conspecifics, even when high-quality conspecifics are available. To see how this shift in template can occur, a model of mate-preference evolution in response to heterospecifics is presented below.

4. A MODEL OF MATE-PREFERENCE EVOLUTION IN RESPONSE TO HETEROSPECIFICS

In this model, we seek to examine how fitness is optimized when species and mate-quality recognition conflict. A template may shift in response to the risk of heterospecific matings as follows. Imagine a template, t , corresponding to a preferred trait or suite of traits. Let $W(t)$ be the average fitness of individuals with a template, t . Let $h(t, I)$ and $(1-h(t, I))$ be the probability of mating with a heterospecific and a conspecific, respectively, where the probability of mating with a heterospecific is a function of the acceptable mate template, t , and the proportion of heterospecifics, I , in the population. Let $(1-c)$ be relative fitness due to mating with a heterospecific (I assume that mating with a heterospecific is never beneficial, so c ranges from 0 to 1, the maximum cost possibly accrued by mating with a heterospecific). Let $(1+q(t))$ be the mean quality of a conspecific mate, given that a conspecific mate is chosen. Here, 1 is the mean value of conspecific mates in the population and $q(t)$ is a continuous measure of the extra quality of a chosen mate. The value of $q(t)$ ranges from 0 to the maximum extra benefit that can be accrued from a high-quality conspecific mate. I assume that mates possessing exaggerated traits will provide greater benefits to the individual so that higher values of t result in greater benefits accrued through mate-quality recognition ($dq(t)/dt > 0$). Finally, let $S(t)$ be the cost of searching for a mate, given the template for a desired mate, t ; for simplicity, this cost is assumed to combine additively with the fitness resulting from mating. Thus, the total fitness is equal to

$$W(t) = h(t, I)(1 - c) + (1 - h(t, I))(1 + q(t)) - S(t). \quad (1)$$

Natural selection should favour templates that maximize $W(t)$. When $W(t)$ is maximized, $\partial W(t)/\partial t = 0$, and the optimal template, t^* , will lie under that fitness maximum. To determine how this optimal template (t^*) will change as any parameter, x , in the fitness function, $W(t)$, changes, we first must note that t^* is a function of x . Thus, when fitness is at a maximum, $t^*(x)$ is implicitly defined by $\partial W(x, t^*(x))/\partial t = 0$ (Reeve 1989). Using this

definition of t^* and the implicit function theorem, we can then find dt^*/dx , the change in an individual's optimal template, as any given parameter, x , is varied (Reeve 1989):

$$dt^*/dx = (-\partial^2 W(t)/\partial x \partial t)/(\partial^2 W(t)/\partial t^2), \text{ at } t = t^*. \quad (2)$$

For example, using equation (2) to examine how an individual's optimal template, t^* , changes as the cost of heterospecific matings, c , changes, we find

$$dt^*/dc = h^{(1,0)}(t^*, I)/(\partial^2 W(t)/\partial t^2), \text{ at } t = t^*, \quad (3)$$

where $h^{(1,0)}(t^*, I) = \partial h(t, I)/\partial t$. The denominator of equation (3) is always negative, because an individual's fitness is at a maximum at t^* ($\partial^2 W(t)/\partial t^2 < 0$), so attention can be focused on the numerator's sign.

Consider a situation where species and mate-quality recognition conflict. Increasing the template increases the probability of heterospecific matings if high-quality conspecifics resemble heterospecifics. Here, equation (3) is negative (because $h^{(1,0)}(t^*, I)$ is positive), and t^* decreases as the costs of heterospecific matings increase; i.e. individuals prefer less exaggerated traits when the costs of heterospecific matings increase. Similarly, the optimal template decreases when the interactions with heterospecifics, I , increase in frequency. Thus, the optimal template will result in preferences for relatively lower-quality mates.

This last result reflects a key assumption of this model: that the costs of species recognition errors are always greater than the costs of mate-quality recognition errors ($(1-c)$ is always less than $(1+q(t))$ except when c and $q(t) = 0$). However, mate-quality recognition errors may occasionally be more costly than species recognition errors; e.g. if matings with low-quality conspecifics lead to death from a sexually transmitted disease so that future reproduction is lost. Nevertheless, it seems likely that the costs of committing species recognition errors will normally outweigh those associated with mate-quality recognition errors.

To summarize, individuals might optimize the fitness benefits of mate choice by actually avoiding high-quality conspecific mates in order to ensure conspecific matings. Two examples potentially illustrate such preference evolution. First, recall that female Midas cichlids prefer males with average traits even though such males may be of relatively low quality (Barlow & Siri 1997). Presumably, females may select against conspecific males possessing traits that resemble heterospecifics (Barlow & Siri 1997). Similarly, female spadefoot toads (*Spea multiplicata*) prefer males with average call rates to males with fast call rates (K. Pfennig, unpublished data). Preferences for faster call rates can lead to costly mis-matings with a sympatric congener (*S. bombifrons*). Thus, spadefoot females apparently select against conspecific males resembling heterospecifics even though such males may be of relatively high quality.

5. CONCLUSION

Most species will, at some point in their evolutionary history, face a conflict between species and mate-quality recognition. In particular, individuals may be unable to

engage in both species and mate-quality recognition whenever high-quality conspecifics resemble heterospecifics. Such a conflict will most likely occur after recent speciation events or when closely related sympatric groups rely on similar secondary sexual signals. In a situation where individuals face a conflict between species and mate-quality recognition, they may engage in the form of recognition that minimizes the overall costs and likelihood of recognition errors.

Given the above prediction, (i) how do individuals mitigate this conflict and optimize the fitness benefits of mate choice, and (ii) what are the evolutionary consequences of minimizing the costs and risks of recognition mistakes? Regarding these questions, fruitful areas of future research will include examining how individuals engage in these recognition processes, and whether they preferentially engage in one form of recognition over the other. For example, comparing mate preferences between sympatric and allopatric populations will suggest whether individuals engage in the recognition process that minimizes the costs and likelihood of recognition mistakes (e.g. Waage 1975; Markow 1981; Ratcliffe & Grant 1983b; Gerhardt 1994; Noor 1995; Márquez & Bosch 1997). If individuals successfully mitigate the conflict so that they accrue fitness benefits through both species and mate-quality recognition, it is also important to understand how they do so. There are a variety of ways by which individuals may minimize recognition mistakes, and this may provide an evolutionary explanation for the diversity of sexually selected traits among closely related taxonomic groups, the use of complex sensory systems and non-phenotypic recognition for detecting mates, and seemingly inappropriate mate-choice decisions.

We are beginning to discover how species and mate-quality recognition interact to shape mate-choice decisions in important and non-intuitive ways (Morris & Fullard 1983; Ryan & Wagner 1987; Rand *et al.* 1992; Ryan & Rand 1993; Gerhardt 1994; Barlow & Siri 1997). Whether by reinforcing or by conflicting with one another, species and mate-quality recognition cannot be considered independently. Understanding how the two processes interact will provide further insight into the evolution of mate-choice behaviour and, perhaps, the speciation process as well.

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