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COMMENTARY

On the functional design of mate preferences and receiver biases

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Mate preferences may evolve under selection related to mate choice benefits (Andersson 1994; Møller & Alatalo 1999; Kokko et al. 2003). However, preferences may originate as, or be influenced by, 'receiver biases' that evolve under selection in nonsexual contexts or as consequences of signal recognition mechanisms (West-Eberhard 1984; Ryan 1990, 1995, 1998; Ryan & Rand 1990, 1993; Ryan & Keddy-Hector 1992; Arak & Enquist 1993, 1995; Shaw 1995; Endler & Basolo 1998). Some receiver bias models are not exclusive of mate choice benefits: selection favouring signal transmission efficiency does not preclude selection favouring the acquisition of resources or good genes from males, and a bias may facilitate mate searching, mate recognition, or the establishment of preferences for signals conveying mate quality (Dawkins & Guilford 1996; Endler & Basolo 1998; Payne & Pagel 2001; Kokko et al. 2003). Nevertheless, preferences influenced by receiver biases may not be adaptations for mate choice, in the sense of being the product of selection related to the performance of mate choice (Darwin 1859; Williams 1966; Sober 1984; Ryan & Keddy-Hector 1992; West-Eberhard 1992; Autumn et al. 2002). In some receiver bias models, signallers exploit the properties of receiver sensory systems or co-opt receiver responses shaped by selection in contexts such as foraging or predator evasion (Endler & Basolo 1998). Furthermore, preferences that arise as receiver biases before the preferred male traits, or that are constrained by selection in other contexts, may not coevolve with the male trait as entailed by models of indirect mate choice benefits (Fisher 1958; West-Eberhard 1983; Kirkpatrick & Ryan 1991; Andersson 1994).

Cases of receiver bias thus present a challenge for the study of adaptation, because they require fine discrimination of the functions that receiver responses perform. The diversity of cases where there is evidence that receiver bias is involved in mate preferences (Table 1; see also West-Eberhard 1984, 2003) suggests that it may be a widespread and important influence on the evolution of signalling systems. Although studies have dealt mainly with visual and acoustic systems, any trait involved in reproductive interactions (e.g. reproductive tract pH levels, Eberhard 1996; sperm manipulation triggered by egg-like objects in the female genital duct, von Helversen & von Helversen 1991) may show similar dynamics. The question of whether mate preferences are adaptations for mate choice is therefore general.

It is often expected that costly responses resulting from a bias will be modified such that costs are lowered or benefits are obtained (Reeve & Sherman 1993, 2001; Bradbury & Vehrencamp 1998, 2000). However, the response to novel selection may be constrained by selection in another context, or by the genetic architecture of the trait (Roff 1997; Bieri & Kawecki 2003; Sih et al. 2003), which can itself be influenced by the effects of selection in the functional context of the bias (e.g. Sih et al. 2003). Thus, when a receiver bias influences a mate preference, the question is whether the expected modification under selection in the mate choice context has occurred. Here we outline how empirically to ask this question.

Receiver Bias and the Functional Design of Mate Preferences

The relationship between a receiver bias and the preference it influences includes: (1) the selection that promoted the origin of the bias and its initial form; (2) the mechanism that results in the bias and influences the preference; and (3) the resulting selection on the receiver in the context of mate choice. If receiver responses have

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Table 1. Receiver bias studies of female mate preferences

	Male trait favoured	Functional context of bias	Nature of bias	Resulting selection on females in mate choice context	References
Australian grassfinches	Colour bands on legs and white crests on head	Identification of mate age?	Sensitivity to colour bands on legs and white crests on head	?	Burley et al. 1982; Burley 1986, 1988; Burley & Symanski 1998
Zebra finches	Song repertoires	?	Habituation	?	Collins 1999
Common grackles	Song repertoires	?	Habituation	?	Searcy 1992
Túngara frogs	Calls with whine and chuck components	Frequency resolution?	Frequency tuning of inner ear organs	? Possible fertilization benefits	Ryan 1985, 1990; Ryan & Rand 1990; Wilczynski et al. 1999
Fiddler crabs	Build and signal near mud pillars or hoods	Landmark orientation for predator evasion	Run to and hide behind objects	?	Christy 1995; Christy et al. 2002, 2003a, b
Oriental fruit moths	Sequester compound found in fermented fruit juices	Food location	Approach odour of fermented fruit	?	Christy 1995
Swordtail fish	Elongated caudal fin	?	?	?	Basolo 1990, 1995a, b, 1998, 2002; Rosenthal & Evans 1998; Basolo & Trainor 2002
Tiger moths	Incorporate plant compounds into sex pheromones, produce ultrasonic calls	Host plant and predator detection	Sensitivity to plant compounds and ultrasound	Fecundity, offspring viability	Conner 1999; Iyengar & Eisner 1999; Weller et al. 1999
Bush crickets	Genitalia that mimic the stimulus of oviposition	Egg fertilization	Release sperm when stimulated by egg-like object in genital chamber	?	von Helversen & von Helversen 1991
Damselflies	Genitalia that stimulate vaginal sensilla involved in sperm release	Egg fertilization and oviposition	Release sperm when stimulated by male genitalia	Offspring genetic diversity, sexual conflict?	Córdoba-Aguilar 2002
True crickets	Provide nuptial gift (spermatophylax)	Gustatory response to food items	Feeding on nuptial gift delays spermatophore removal	? (evidence against direct benefits)	Sakaluk 2000
Water mites	Tremble legs to mimic vibrations of copepod prey	Prey capture	Orient and clutch towards copepod-like vibrations	?	Proctor 1991, 1992
Pisaura mirabilis spiders	Wrap nuptial gifts in silk	Maternal care	Orient towards objects resembling egg sacs	?	Stålhandske 2002
Wolf spiders	Tufts on male forelegs	?	Preference for tufts on male forelegs	?	McClinctock & Uetz 1996

A question mark indicates that information is lacking or insufficient.

been modified by selection through point (3), there should be a fourth component: a mechanism that mediates the performance of the preference independently of the bias. Thus, responses may be modified such that they differ between behavioural contexts (e.g. between foraging and mate choice), or are influenced by different stimulus characteristics in the different contexts. The expectation of independent or context-modified responses suggests a test to consider their functional design. Its rationale is implicit in the suggestions that, if receiver biases explain female preferences, diversity in male traits and female preferences should be largely determined by ecological factors (Endler & Basolo 1998), and that experimental changes in the bias should result in equal changes in responses to males (Christy 1995).

The test requires knowledge about the functional context of the bias (point 1 above), a condition that can be met in several of the cases of proposed receiver biases (see Functional context of bias, Table 1). This condition will most easily be met when the adaptiveness of a mate preference is most questioned by the presence of a receiver bias. If the wrong context is used to test the functional design of the preference, the results will incorrectly show that the performance of the preference is independent of the performance of the bias. The test can be used when phylogenetic information is available (see below), but does not require it. It can also be framed in terms of a trait under selection in a context unrelated to mate choice that influences a mate preference. Thus, the test requires either knowledge that the bias originated before the preference or knowledge that selection in the alternative context is stronger than selection in the mate choice context, and that it is thus likely to overwhelm selection in the mate choice context and constrain the evolution of the preference.

To ask whether receiver responses have been modified under selection related to the performance of mate choice, one can measure the performance of the trait in its original or alternative context and its performance in the mate choice context, and then evaluate the correlation that exists between these measurements. As a hypothetical example, consider a case where it is simple to envision the original context of the bias: in *Neumania papillator* water mites, males mimic swimming copepods by trembling their legs, and an ancestral hunting behaviour is involved in the clutching responses of females that lead to pair formation and spermatophore uptake (Proctor 1991, 1992; Table 1). Female responses exert selection on the males but may not yield mate choice benefits.

The first step of the test is to take two types of measurement per female, to quantify the performance of responses in the different contexts. In the water mite example, the measurements might be a female's pursuit of copepods according to the frequency of the vibrations they generate in the water, and her approach to males according to the frequency of the trembling of their legs. Such measurements may be taken in many ways (e.g. response thresholds or preference functions: Ritchie 1996; Sinervo & Basolo 1996; Wagner 1998). The choice of method should reflect convenience and relevance according to the biology of the experimental animal, but it is important that the measurements be comparable across contexts. For example, use threshold measures in both contexts, and avoid mixing threshold measures with preference functions, or individual measures with population means. The second step is to evaluate the correlation between the two types of measurement. Do females discriminate similarly between potential prey and mates? Is there no correlation between how females respond to prey and to males? Are females that prey indiscriminately more reserved with males? Or do females discriminate differently between prey and males?

Interpretation of the Correlations

A lack of correlation between the measurements would indicate that performance in one context is independent of performance in the other context. In spite of evidence that the preference originated as, or is influenced by, a bias, it could be inferred that the preference has been influenced by selection other than that in the context of the bias. It would then be appropriate to invoke evidence of mate choice benefits. A negative correlation would indicate independent performance, and a trade-off between performances in the two contexts. For example, choosy female water mites might miss some feeding opportunities. A trade-off would mean that selection on the performance of the preference can counterbalance the cost in terms of the context unrelated to mate choice.

A positive correlation would be harder to interpret. On the one hand, $r \approx 1$ might indicate that receiver responses are intertwined among contexts. Given evidence about the prior origin of the bias, or about the greater strength of selection in the context unrelated to mate choice, such a positive correlation might indicate that the female preference is a by-product of selection in the context of the bias; female responses would exert selection on the males but not have been modified under selection related to the performance of mate choice. On the other hand, a weak positive correlation (e.g. $r < 1$ but significant) may indicate that selection in the mate choice context has modified receiver responses by weakening the relationship with performance in the nonsexual context. Such a correlation would not necessarily indicate that the preference is a by-product of the bias, and instead might reflect selection on the performance of mate choice. Thus, useful predictions about positive correlations may not be possible, unless knowledge on the original value of the correlation were available. Another problem would arise if selection in the two contexts converges on the same responses (Ryan 1985; Dawkins & Guilford 1996). For example, selection on foraging behaviour and mate choice might both result in water mite females that approach the same frequency of vibrations if optimal foraging based on prey size and selection on mate choice or mate recognition converge. Because of these concerns, the strength of the test lies in cases where negative or no correlations are detected. Consequently, statistical power will be an important consideration.

Comparative Tests

As well as with measurements of between-individual variation, the test can also be performed with measurements of between-population variation. In the water mite example, receiver performance in foraging and pair formation could be compared between populations hunting different prey with different vibration frequencies. Here, we comment on two studies that have used correlational tests to consider receiver bias and mate preferences. Rodd et al. (2002) evaluated the between-population correlation between responsiveness to orange discs (a measure that described performance in foraging for orange-coloured fruit, an important and rare food) and the female preference for orange males in guppies. A positive correlation between these measurements led to the conclusion that the female preference for orange males originated as a receiver bias and not under selection related to mate choice benefits. Similarly, Madden & Tanner (2003) presented experimentally coloured grapes to male and female bowerbirds of several species. An indication of a positive correlation in preferences for fruit colour between foraging females and bower-decorating males led to the conclusion that female preferences for bower decoration colours originated as a receiver bias.

These studies approach the aim of contrasting receiver performance in different behavioural functional contexts, but there is a major problem with their conclusions. The correlational procedure used can address the functional design of a preference given prior documentation of a receiver bias. It cannot be used to provide evidence of a receiver bias. For the latter purpose, one requires evidence of the prior origin of the bias (see Endler & Basolo 1998), or evidence that selection in the nonsexual context is stronger and therefore likely to constrain responses in the mate choice context. Making the assumption that the latter is likely to be the case may confound interpretation of the results. For example, Rodd et al. (2002) point to foraging for seasonally abundant fruit rich in protein, sugar and carotenoids as the context in which responses to orange objects are likely to experience the stronger selection, but previous studies also identify algae as important sources of nutrients and carotenoids (Grether 2000; Grether et al. 2001). It is thus necessary to have previous evidence of the presence of a receiver bias before the test is used to consider the functional design of mate preferences influenced by the receiver bias. Another consideration in evaluating these studies is the compatibility of the measures of performance across contexts (e.g. responses to orange discs versus live males in the guppie study, and female foraging responses versus male decorating preferences in the bowerbird study).

The test can also be performed at broader comparative scales. When phylogenies are available, the test can be applied by the use of comparative methods (Harvey & Pagel 1991). For example, one would evaluate the correlation between changes in performance in the original or alternative context and in mate choice. In the water mite example, different species might hunt prey of different sizes that produce different frequencies as they swim, and the correlation between changes in the frequencies that females approach for prey capture and changes in the preferred male signal frequencies could be measured. This application of the test will depend on how well it is possible to reconstruct ancestral character states and estimate phylogenetic correlations. Recent work has shown these to be challenging but fruitful endeavours (Schultz et al. 1996; Cunningham et al. 1998; Schultz & Churchill 1999; Martins 2000; Martins et al. 2002).

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