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Reconciling sexual selection to species recognition: A process-based model of mating decision

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Abstract

Mating signals often encode information important for both species recognition and mate quality assessment and endure selection pressures that combine both stabilizing and directional components. Here, we present a family of models of mate preference for multiple-message signals. Our models are process based rather than purely normative, they assume the existence of one (or more) ''utility function'' that order signals along a scale of perceived appropriateness, and interpret preferences either as the differential probability of signals recognition or as the combined effect of differential recognition and direct comparison between signal alternatives. These models show the critical role played by the proximate mechanisms of information processing in influencing the ultimate function of female mate choice. They show that if preferences are an emergent property of the way animals recognize signals then species recognition and mate quality assessment are expected to constrain each other severely and to limit the overall discrimination power of the system. In contrast, if preferences result from two computational processes, recognition and comparison, the constraining effects of species recognition and mate quality assessment are sensibly reduced. In these cases, females may improve discrimination in mate quality by adopting permissive recognition rules and limiting the risks of heterospecific mating.

Keywords: Sexual selection; Mate choice; Mate recognition; Preference function; Utility function

1. Introduction

Female choice is an important mechanism of both species recognition and sexual selection (Andersson, 1994; Cronin, 1992). In the past, species recognition and sexual selection have been often viewed as antithetical processes. Female choice in the mate recognition systems was thought to operate as a powerful stabilizing force that buffered rather than promoted signal evolution (Paterson, 1985; Templeton, 1979). In contrast, in sexual selection theory, female choice was considered as one of the most important mechanisms of signal evolution, that may eventually lead to behavioural isolation and speciation (Lande, 1981). In sexual selection theory, females are not thought to merely discriminate against potential mates of the inappropriate species, but to actively choose (to express a preference) among several appropriate mates of different appealingness. According to this point of view, species recognition forms a continuum with sexual selection because both result from the interaction between variation in signal and response to signal variation (Boake et al., 1997; Ryan and Rand, 1993).

The continuity of sexual selection and species recognition has been formalized in the mathematical concept of female preference function. In its most rigorous definition, the preference $\psi(z|y)$ of females with phenotype y for mating with males of phenotype z is assumed to be proportional to the probability that y-females will mate with z-males (Lande, 1981). A less rigorous definition does not consider variation in female preference and it defines the preference function $\psi(z)$ as the probability that males of phenotype z will be chosen as mate (Boake, 1989; Ritchie, 1996; Ryan and Rand, 1993). According to both definitions, females are thought to perceive variation in signals as variation in appealingness and to approach different

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signals with different probabilities. The preference-function hypothesis makes three (implicit) assumptions on the perceptual mechanisms that underlie mating decisions. The first is that females order prospective mates along a one-dimensional scale of values. The second is that recognition depends only on the probability that a male's perceived value be above the female's acceptance threshold (Reeve, 1989). The third assumption is that preferences arise from the differential probability of acceptance and, thus, that they are an emergent property of the way animals recognize signals.

Alternative models of mating decisions differ from the preference function model in one or more of these assumptions. In hierarchical models, females are thought to order signals along two or more scales of values and make their choice using the criterion, to which they assign the highest priority (Fawcett and Johnstone, 2003). In the best-of-n models, females are assumed to score prospective mates along a one-dimensional scale of values, to compare them, and to choose the one with the highest score (Real, 1990). Whether the preference function model views preferences as a stochastic process that may arise by an error-prone estimates of attractiveness (Reeve, 1989; Phelps et al., 2006), both the hierarchical and the best-of-n model do not assume assessment uncertainty and preferences are treated as deterministic rather than probabilistic phenomena.

Despite the acknowledged importance of mating decisions in influencing the evolution of reproductive isolation, there has been little empirical investigation addressing the underlying mechanisms of recognition and preferences. Bush et al. (2002) used no-choice phonotaxis experiments on female grey treefrogs, *Hyla versicolor*, to show that signal recognition is a graded (probabilistic) response rather than a Boolean categorization of 'recognized' versus 'not-recognized' stimuli. By comparing recognition functions obtained in no-choice tests with preference functions obtained in two-choice tests, Bush et al. (2002) found no cases in which the direction of a preference in a two-choice test was different from that predicted by the no-choice test. However, preferences were often stronger than those predicted by the recognition function (see also Doherty, 1985; Wagner et al., 1995 for similar results). Such qualitative similarities and quantitative differences between patterns of recognition and preference show that recognition strongly influences mating preferences, though it cannot fully explain them.

Recently, Phelps et al. (2006) have proposed a process-based model of mate choice that combines aspects of both preference-function and best-of-n models. As in the preference-function model, the authors assume that (i) females order prospective mates along a one-dimensional scale of values, (ii) females use error-prone estimates of mate attractiveness, and (iii) they recognize appropriate mates whenever perceived attractiveness exceeds some internal threshold. In this model, however, the preference between two alternatives not only depends on their differential probability of being recognized, but also on the probability that one alternative be perceived as better than the other. Phelps et al. (2006) found that, in *Physalaemus pustulosus*, the observed pattern of preferences is consistent with that predicted by the model, suggesting that a single perceptual process may explain both recognition and mating preference.

In this paper, as in Phelps et al. (2006), we adopt a process-based approach to investigate the roles of species recognition and sexual selection in mating decision. First, we present a general probabilistic model of mating preferences that enables us to express the relationship between recognition, preference, and the experimental protocols used to assess these processes. Second, by making different assumptions on the proximate mechanisms of information processing, we derive three specific models that share some similarities, respectively, with the preference-function, the hierarchical, and the best-of-n models. Third, we specify some ways in which the three models may be distinguished empirically. Finally, we use these circumstantial models to investigate how the way females perceive signals may pose different solutions to the conflicting demands of mate choice and species recognition.

2. Models of female preference

2.1. The model framework

We consider a signal $\mathbf{x} = (x_1, \ldots x_n)$ that can vary along n dimensions, where n represents the number of different biologically significant properties (e.g. call duration, fundamental frequency, and pulse rate for acoustic signals; patches extension, hue, and saturation for visual signals). For the sake of simplicity, we consider the case in which females compare and choose between two prospective mates, identified by their signals $\boldsymbol{x}$ and $\boldsymbol{y}$: we define the female preference function for signal $\boldsymbol{x}$ over the alternative $\boldsymbol{y}$, denoted by $P(\boldsymbol{x}, \boldsymbol{y})$, as the conditional probability of choosing $\boldsymbol{x}$ over $\boldsymbol{y}$, given that either $\boldsymbol{x}$ or $\boldsymbol{y}$ is chosen. This definition of preference function corresponds to the definition adopted in experimental studies of two-choice discrimination tests and, thus, allows a comparison between theory and empirical researches. Notice that by definition $P(\boldsymbol{x}, \boldsymbol{y}) = 1 - P(\boldsymbol{y}, \boldsymbol{x})$.

In order to make precise the relation between recognition and preference, we make the following assumptions:

(i) to each signal $\boldsymbol{x}$ is associated a recognition probability

$$r = r(\boldsymbol{x}), \quad 0 \leqslant r(\boldsymbol{x}) \leqslant 1, \tag{1}$$

which is the probability that the signal $\boldsymbol{x}$ be recognized and trigger the receiver behavioural response. We assume that $r(\boldsymbol{x})$ is statistically independent of $r(\boldsymbol{y})$ when $\boldsymbol{x} \neq \boldsymbol{y}$. This definition does not imply comparison and adheres to the definition of mate recognition proposed by Paterson (1985).