

# Mate Recognition, Species Boundaries and the Fallacy of “Species Recognition”

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**Abstract:** If speciation is typically a process of allopatric divergence following vicariance or dispersal, then a priori, we might expect that individuals of separate lineages typically will retain the ability to “recognize mates” across species boundaries, especially if some components of mate recognition experience strong stabilizing selection. Confusion results from an over-reliance on the importance of reproductive compatibility, as emphasized by proponents of the Biological Species Concept, in contrast to other characters indicative of phylogenetic history. Lack of divergence in premating courtship implies nothing about the nature of species boundaries; rather, it is best viewed as the retention of a plesiomorphic genomic compatibility, not a violation of species boundaries. Until evolutionary biologists recognize that mate recognition systems need not diverge for the attainment of lineage status, misdirected debate will continue. Only by accepting the observation that heterospecifics need not differ in mate recognition systems will additional examples be documented.

**Keywords:** Mate recognition, species concept, species recognition, sexual selection.

## INTRODUCTION

Proponents of the Biological Species Concept (BSC) view divergence in mate recognition as integral to speciation [1]. For example, in their recent taxonomic investigations, both Padial *et al.* [2] and Friberg *et al.* [3] assume that divergence in mate recognition is required for attainment of species status in allopatric taxa. By contrast, those adhering to an Evolutionary Species Concept (ESC), and related views (e.g., Phylogenetic Species Concept, PSC), place less emphasis on the role of mating behavior in speciation [4, 5]; rather, they seek divergence providing evidence of the attainment of sufficient differences to indicate that lineages are distinct in time and space. de Queiroz [6] argued that most species concepts are united at their core by an assumption of an evolving metapopulation, and only differ significantly in their secondary diagnostic attributes (e.g., “intrinsic reproductive isolation” = BSC; “diagnosability” = PSC; etc.).

Like systematists, behaviorists also seek to explain divergence in mate recognition systems, but typically focus on the influence of intraspecific (social) interactions rather than interspecific interactions. Sexual selection was proposed by Darwin to account for traits inexplicable in light of natural selection alone, and it no doubt accounts for some or perhaps most evolutionary forces acting on mate recognition [7]. With renewed interest in sexual selection over the past 40 years, a number of workers championed it as the primary force accounting for divergence in mate recognition systems, especially since the role of interspecific interactions, such as reinforcement, were increasingly

questioned during this period [7-11]. The term “species recognition” is commonly used in these contexts to refer to situations in which individuals are expected to prefer conspecifics as mates (i.e., proponents of the BSC). Behaviorists often contrast these two perspectives on mate recognition divergence as alternatives: that is, sexual selection vs “species recognition” [e.g., 12-14]. Nonetheless, more recently, in reviewing the extensive literature on the relationship between sexual selection and speciation accumulated over the past three decades, Ritchie [15] formulated the over-riding question addressed by behaviorists in this context as: “*what does sexual selection have to do with reproductive isolation?*”

de Queiroz [6] argued convincingly that the “species problem” (i.e., debates over the numerous species concepts) derives in part from a misplaced focus on reproductive isolation, but nonetheless is more apparent than real. He suggested that: “*Alternative species concepts agree in treating existence as a separately evolving metapopulation lineage as the primary defining property of the species category*” (p. 879), and that differences arise because “*...they disagree in adopting different properties acquired by lineages during the course of divergence as secondary defining properties*” (p. 879). It is these differences in secondary defining properties (operational criteria) that lead to confusion with respect to mate recognition, species boundaries and “species recognition.” In practice, most species concepts assume a necessary relationship between speciation and divergence in mate recognition systems. The dominance of the BSC over the past fifty years has caused many to consider components of mate recognition systems as isolating mechanisms separating species in nature. Under the BSC, attainment of reproductive isolation is paramount to speciation [1, 15]. These views preclude one from considering that the evolution of mate recognition systems

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might occur independently of changes associated with cladogenesis.

Here I discuss the relationship between divergence in mate recognition and speciation, and the inappropriateness of assuming a necessary relationship between these phenomena. I suggest that adoption of the ESC from an operational perspective [6] frees one from the confusion arising from a priori expectations of a necessary relationship between divergence in mate recognition and speciation.

### PROXIMATE BASIS OF MATE RECOGNITION

A great deal of debate has surrounded the terms "mate recognition," "mate selection" and "species recognition" (e.g., [10, 16-18]). All of these terms have been applied to the act of (or some component of) pairing between males and females during reproduction. Many suggest or imply that there exist distinct proximate mechanisms of sensory system processing associated with different forms of mate recognition even though a distinction between mate recognition ("species recognition") and mate selection (sexual selection) is considered fallacious by some [10, 17, 18]. The mechanistic basis of mate pairing should be fundamentally similar with respect to sensory system detection and processing. Gerhardt *et al.* [17] noted that species and mate recognition inappropriately imply not only a separation between the proximate basis of neural processing for types of recognition (typically species versus mate), but also imply a proximate process of categorization (conspecific vs heterospecific) during mate pairing. Indeed, Ryan *et al.* [19] recently investigated mate recognition across closely related anuran amphibians and concluded "*females perceive variation in male signals (even heterospecifics) in a continuous manner with no evidence of perceptual category formation*" [see also 20]. Use of the term "species recognition" is problematic not only because it suggests unique proximate mechanisms but also because it inappropriately contrasts an outcome (the effect of "species recognition") with a causal process (typically sexual selection).

### ULTIMATE SIGNIFICANCE OF MATE RECOGNITION

Some workers have suggested that different mate recognition terms are appropriate depending on the ultimate consequences associated with mating behavior (cf. "species recognition" and mate selection). Many authors have suggested that mate recognition for species identity and mate recognition in the context of classical sexual selection are separable, and potentially useful as alternative hypotheses in explaining the diversity of courtship behavior [7-9, 18, 21-23], and may even act in opposition [12, 14, 24]. This suggests that "species recognition" applies to recognition among conspecifics in which all individuals are equivalent as mating partners, whereas a mate selection viewpoint is appropriate when directional selection (*i.e.*, classical sexual selection) operates within populations.

Under many circumstances females (and males) will experience ultimate consequences from mate recognition. It seems inappropriate to single out reduced fitness from mating with individuals of low genomic compatibility (heterospecifics), as unique. Females no doubt benefit by

avoiding matings with close relatives (inbreeding avoidance) or distantly related conspecifics (e.g., those adapted to a different microhabitat); both concern genomic compatibility. And even when individuals benefit by avoiding mating with certain genotypes, such as heterospecifics, sexual selection may be the critical process resulting in divergence of mate recognition systems during reinforcement [25-28]. Servedio [29] noted this similarity between mate selection from a sexual selection and "species recognition" perspective: "...hybrids have low fitness...similar in its effects...of mating with low condition males in good genes [scenarios]." In general, we expect variation in preferences and courtship traits; whenever social interactions lead to a covariance between these traits and fitness differences, sexual selection results. When females benefit by mating with males exhibiting an extreme development of a trait because it is most different from genomically incompatible heterospecifics, the fallacy of any distinction between selection for "species recognition" and sexual selection is obvious. But, sexual selection is also a process that can produce stabilizing selection [26, 30]; hence, even the most traditional notions of "species recognition" are compatible with the action of sexual selection. Only if all conspecifics are precisely equivalent (an unlikely event?) could one envision a scenario in which there is mate recognition without any sexual selection since the question for a female reduces to either mating with a heterospecific at a fitness cost, or mating with any conspecific at an equivalent fitness benefit.

Many recent investigations have examined mate recognition within a framework of conflicts between mate choice for quality (*i.e.*, sexual selection) and mate choice for species status (*i.e.*, "species recognition"; [see 12-14, 31]). A number of workers have suggested that mate selection can be thought of as a complex process in which some variables are under sexual selection and some under selection for "species recognition" with this being the solution to the problem of how selection can act in both contexts [13, 31]. For example, Pfennig [12] showed that female spadefoot toads living in sympatry with a close relative exhibit preferences that make it less likely they will mate with low quality heterospecifics even though it also means they are less likely to mate with high quality conspecifics. However, fundamentally, the processes are similar: in allopatry or in sympatry, females have apparently been selected to maximize fitness in the context of the genomic compatibility of their mate. It is certainly interesting to find that different solutions occur in the different environments, and the outstanding investigations of Pfennig and her colleagues are in no way diminished by adoption of the perspective outlined herein. I submit that it is simply inappropriate to suggest that fundamentally different evolutionary processes are at work in their amphibian system, either proximately or ultimately.

Consistent use of the term mate recognition as shorthand for all aspects of courtship or premating isolating behavior that brings mates together during reproduction avoids this confusion. It may be that mate recognition leads to pairing with conspecifics, but it may not (see below). In general, during reproduction individuals are seeking to identify mates rather than recognize conspecifics per se; we, as taxonomists, are the only ones to engage in "species recognition." In this sense, mate recognition encompasses premating isolating mechanisms of the BSC, but does not

entail any implications regarding particular neural processing mechanisms or the ultimate significance of mate choice. Because sexual selection is a process (i.e., differential mating success as a result of social interactions) and "species recognition" an outcome, or pattern, it is inappropriate to erect them as competing alternative hypotheses.

### MATE RECOGNITION AND SPECIATION

Cracraft [4, 5] reviewed relationships among Australian birds and concluded that many valid species hybridize. He argued that a reliance on attainment of pre- or post-mating isolation as an indicator of speciation may distort our understanding of behavioral evolution among species, particularly of certain groups. *"The phylogenetic species concept does not deny the importance of reproductive cohesion or disjunction...it simply claims that incorporating reproductive criteria in a species concept not only obscures the analysis of historical pattern but also impedes our understanding of the reproductive relationships themselves* [4, 5].

Many would agree that entities recognized as species, both near and distant relatives, can interbreed and produce offspring under natural and especially artificial conditions. Hybridization is relatively common among birds, amphibians, insects, and flowering plants [32]. For example, McRobert and Tompkins [33] found that two drosophilids that differ in chromosome number retain the ability to interbreed, suggesting that genomic compatibility may be retained across speciation events, and in the face of dramatic divergence in other traits. Abundant examples of natural hybridization between demonstrably different species, which have retained sufficient genomic compatibility to allow interbreeding, suggest that ability to hybridize is not a phylogenetically informative trait since the potential to interbreed can be a shared-ancestral character state [34]. Because evolutionary species are recognized as historical units and not as reproductive communities, measurements of genomic compatibility are often inconsequential to the existence and determination of species [35]. Hybridization between relatively distantly related species, however, may provide unique opportunities for studying the evolution of mate recognition systems and other traits that may or may not have diverged following speciation.

Systematists largely agree that speciation is generally expected under conditions in which an ancestral population has been divided due to vicariance or dispersal [36-38]. Under such circumstances, it is not expected that divergence in mate recognition would be a necessary consequence of lineage divergence. In fact, a number of studies have documented the retention of mate recognition systems across speciation events; acoustically signaling organisms, such as crickets, mosquitoes, fruitflies, katydids and anurans have proved especially useful examples [39]. In North American field crickets, *Gryllus* [40], some distantly related forms, existing allopatrically, have retained "virtually identical" chirping songs. For wasps [41] and bark beetles [42], it appears that across a group of related species, courtship behavior is not necessarily associated with species boundaries. These investigations found an increase in homoplasy with addition of courtship behavior to phylogeny based on morphology. Of course, this may simply indicate

that to be phylogenetically informative courtship traits must be used at the appropriate phylogenetic level, but it reveals there may be little correspondence between divergence in mate recognition and speciation.

Coyne and Orr [43] found that premating isolation diverges more rapidly for taxa in sympatry than allopatry, but that premating and postmating isolation diverge at about the same rate for allopatric taxa. These observations are not inconsistent with the present view: a general relationship between time since separation (i.e., speciation) and divergence in genomic compatibility and mate recognition is expected. If mate recognition is under stabilizing selection, then in allopatry one might expect that postmating divergence would occur at some steady rate, whereas premating would remain unchanged in the absence of selective forces favoring divergence. However, this is not to imply that divergence in some components of mate recognition due to sexual selection would not occur (as suggested by Coyne and Orr for fruitflies). Additionally, under the present view, a more appropriate assessment of the relationships between divergence in premating and postmating traits awaits analysis of a greater variety of sympatric and allopatric taxa that were not initially recognized primarily on the basis of reproductive isolation. Interestingly, Ryan *et al.* [44] found that genetic divergence was unrelated to degree of divergence in mate recognition in Neotropical frogs.

Only under reinforcement, or sympatric speciation, should we expect a necessary relationship between divergence in mate recognition and speciation. During reinforcement, by definition taxa diverge in premating isolating mechanisms: these are properly termed "mechanisms" in this case because they serve the purpose of isolating taxa. However, in general, under the widely accepted view of allopatric speciation, there is no reason to expect a necessary relationship between speciation and divergence in mate recognition systems. Lofstedt [45] found that pheromones important to mate recognition in ermine moths of Europe exhibit within population consistency and between population divergence; additionally, it appears that heterospecific interactions may have shaped the divergence of mate recognition systems among related, sympatric taxa. Appropriately, in these instances these communication systems would represent "species recognition" assuming all conspecifics are equally attractive; the scarcity of such examples suggest that they are the exceptions that prove the rule.

It is possible that following speciation, taxa could be favored to retain the ability to recognize what are now heterospecifics. For example, in birds and lizards, interspecific territoriality may favor such ability. Korner *et al.* [46] found that male cordylids exhibit interspecific territoriality even though the taxa they studied are allopatric; they attributed this result to "poor species recognition," but their investigation assumes that individuals normally categorize conspecifics relative to all other life forms. By contrast, there is some evidence that mate recognition may diverge among populations that are still part of a single lineage. Plant hoppers show divergence in mate recognition systems without speciation [47]. Similarly, fruitflies have been described as "incipient species" [48]. The critical issue

is the connection of divergent populations by gene flow. Even if there is little within population variation in mate recognition systems, divergence may occur between populations [45]. In these instances we find divergence in mate recognition in the absence of speciation.

## SUMMARY

“Species Recognition” is a widely used term predicated on a misconception of proximate causes and ultimate significance of mate recognition, and an underlying assumption of reproductive isolation as a necessary requirement of cladogenesis. Proximate processes of mate recognition are not fundamentally distinct whether the ultimate significance has to do with a high quality conspecific choice that provides sexual selection benefits in the classical sense (*e.g.*, good genes) or heterospecific avoidance (in the same sense, good genes). Further, the fallacy of “species recognition” is more and more apparent from recent studies showing mate recognition may include acceptance of heterospecifics as appropriate mates. Although biologists “recognize species,” the term is best avoided when discussing proximate or ultimate aspects of reproductive behavior, even when “species recognition” is an effect of mate recognition. A reduction in reliance on the operational criteria (*sensu* [6]) associated with the BSC (*i.e.*, reproductive isolating mechanisms) avoids the pitfall of expecting a necessary relationship between speciation and attainment of reproductive isolation.

If it is accepted that speciation in general is a process of allopatric divergence following vicariance or dispersal, then *a priori*, we might expect that individuals of separate lineages typically will retain the ability to recognize mates across species boundaries simply because some components of mate recognition experience strong stabilizing selection [11, 17, 35, 49]. This does not preclude divergence due to sexual selection on any number of other components of the mate recognition system; in anurans, it is now well documented that sexual selection on traits associated with male vigor (call effort) can occur in spite of strong stabilizing selection on traits critical to mate recognition (*e.g.*, amplitude modulation of calls). However, it suggests that formulation of Ritchie’s question (“*what does sexual selection have to do with reproductive isolation?*”) is problematic: speciation need not have anything to do with reproductive isolation. Mate recognition in many circumstances may often encompass more than current, local conspecifics and thus not necessarily represent “species recognition.”

A realization that mate recognition systems need not diverge for the attainment of lineage status avoids misdirected debate. For example, Sinsch and Schneider [50] used the lack of variation in advertisement calls of *Rana lessonae* in south central Europe to argue that a newly described species, based on fixed allozymic differences, should not be recognized given a lack of divergence in advertisement calls relative to sister taxa. Only by accepting the observation that heterospecifics need not differ in mate recognition systems will such examples be documented. Gleason *et al.* [51] noted that a phylogenetic analysis of the *Drosophila willistoni* group was incompatible with the existing taxonomy based on reproductive compatibility (*i.e.*,

ability to hybridize). They suggested that the problematic nature of the group is due in part to a conflict between the BSC and ESC. This conflict results from an over-reliance (*i.e.*, character-weighting) on the importance of reproductive compatibility in the face of other characters indicative of phylogenetic history.

The present perspective suggests that the attention focused on “speciation genes” [52-54] is misdirected. Divergence in courtship, if sufficient to prevent mating among populations, is certainly sufficient evidence for speciation. But lack of divergence in premating courtship does not necessarily contribute to our understanding of the nature of species boundaries in particular instances. Species even may retain genomic compatibility such that postmating isolation is not attained. A lack of pre- or postmating isolation, as often observed among amphibians [46] and birds [4, 5], is best viewed as the retention of a plesiomorphic genomic compatibility, rather than a violation of species boundaries.

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## ABBREVIATIONS

BSC = Biological species concept

ESC = Evolutionary species concept

PSC = Phylogenetic species concept

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