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Introduction to the Symposium: Mechanisms of Mate Choice[1]

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The processes and consequences of choosing a mate have provided a constant impetus for empirical and theoretical research. For example, the problem of speciation was a cornerstone of the New Synthesis that revolutionized evolutionary thought in the middle of this century (Mayr, 1982), and an attempt to answer the hows and whys of species recognition resulted in a synergism of population genetics, animal behavior, and neurobiology.

The problem of mate choice is still central to many evolutionary debates, but the emphasis has shifted to the intraspecific level. Because mate choice among conspecifics generates sexual selection, it can be responsible for the evolution of elaborate and bizarre animal morphologies and behaviors; for example, the peacock's tail has become a common exemplar of the outcome of sexual selection by female mate choice.

Despite some obvious parallels between mate choice among and within species, the latter has not generated the multidisciplinary approaches that have been applied to the "species problem." Instead, much of the current research has been dominated by two fields. Behavioral ecologists have concentrated on how mate choice can generate differential mating success in nature, how this mating success can be correlated to variance in male phenotypes, and what might be the immediate advantage, if any, to females exercising choice. Theoretical population geneticists have evaluated various proposals as to why females evolve such preferences. For example, two popular hypotheses suggest that by choosing males with traits indicating viability, females promote the genetic quality of their offspring (good genes hypothesis), or that female mate preferences evolve because they are genetically linked to the male traits that they promote (Fisher's runaway sexual selection; Kirkpatrick and Ryan, 1991). But what has often been ignored is how intraspecific mate choice actually takes place.

Without denying the importance of the behavioral ecology and population genetic research paradigms, we convened this symposium to address the mechanisms that actually generate intraspecific mate choice. We believe knowledge of these mechanisms is important for several reasons: sexual selection can be generated by mate choice, so understanding mechanisms of mate choice is necessary for understanding the dynamics that generate selection; female preferences are expressions of underlying genetic and sensory mechanisms, thus these are the loci for evolution of mate preferences; and finally, preferences may result from selection in contexts other than mate choice, and this potential pleiotropic effect can not be deduced unless one realizes the mechanisms involved. Toward this end, we have invited researchers studying mechanisms of mate choice in three areas: genetics, sensory biology, and learning.

It is important to understand the genetic mechanisms that generate variation in female preferences, but there are few studies bearing directly on this issue. Studies of the period locus in *Drosophila* might offer the greatest promise. Previous research has shown that variation in both circadian rhythm and male song frequency have the same genetic control, thus it is possible that this male courtship trait could evolve as a pleitropic effect of selection outside of the

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context of courtship; that is, selection on circadian rhythm rather than song itself. Now Kyriacou and his colleagues have extended their studies to examine how the female response is mediated by this gene, and these studies are beginning to yield a more complete understanding of the degree of interaction between trait and preference at the molecular-genetic level.

There is a general consensus that an important consequence of species recognition is in effecting matings between genetically compatible individuals. The same suggestion has been made for intraspecific mate choice. Lennington and her colleagues have been investigating mate choice based on the t-complex genotype in rodents, and here they review data showing how this genotype is discriminated using chemical cues in mate choice. They consider the contribution of this discrimination to patterns of assortative mating in nature. Kinship concerns are not restricted to the "higher" vertebrates. Waldman previously had shown that toad tadpoles differentially associate with siblings, and he now shows that kinship also influences mating decisions. By comparing mitochondrial haplotypes he concludes that there is evidence for incest avoidance. It is not known how kinship is evaluated by the toads, but DNA fingerprints show that individuals that are genetically more similar also produce more similar advertisement calls, suggesting the intriguing and testable hypothesis that females might attend to call differences to avoid incestuous mating. Good genes hypotheses often have been invoked to explain the evolution of female preferences. But these hypotheses are based on absolute genetic quality of the male. The studies by Lennington *et al.* and Waldman suggest that relative genetic quality might be an important consideration.

How the female perceives the male courtship signals is crucially important to understanding why she might discriminate among conspecific mates. In the túngara frog one call component is necessary and sufficient for species recognition while the other component further enhances the attractiveness of the call to females. Rand and his colleagues have shown that the receiver is fairly strict regarding acceptable variation in the call component used for species recognition, while the component that enhances call attractiveness can be varied considerably, and even replaced by novel stimuli, and be equally effective in making the call more attractive. This receiver permissiveness suggests that female preferences based on some parts of the call can be exploited by newly evolved male traits. Searcy also addresses female mate choice based on acoustic cues in his studies of bird song repertoires. Females of the common grackle prefer songs containing different song types (*i.e.*, repertoires) to songs that repeat the same call type, and his data suggest the enhanced attractiveness of repertoires is due to release from habituation. This is especially interesting considering that male grackles do not have repertoires. As with the study of the túngara frog, this appears to be another example of males evolving traits that exploit preexisting female preferences, and offers a different view of how trait and preference evolve than suggested by hypotheses of good genes and runaway sexual selection (Ryan, 1990).

Most studies of female choice have addressed single male traits and have not considered the role of learning or experience in shaping the preferences. As Keddy-Hector shows with primates, however, female preferences can be based on suites of characters that are socially rather than morphologically based, such as familiarity, social status, and parenting abilities. Barlow, reviewing his studies of the gold and wild-type color morphs in cichlid fish, emphasizes the interaction of visual and chemical cues in mate choice, as well as the color of one's siblings and parents, and the amount of aggression between males and females of each color morph. And finally, Domjan has shown that in quails cues used for mate discrimination can be learned, and the receiver can be quite malleable. The cues that are learned might depend on the earlier sexual experience of the animal as well as the environmental context in which they are presented. This suggests that factors external to the trait-preference dyad could influence the diversity of sexual signals in the absence of genetic evolution.

Our hope is that these studies give a flavor of the diversity of issues implicated in mechanisms of mate choice, and especially that they will convince evolutionary biologists interested in sexual selection that it is crucial to understand these mechanisms. We also hope that these studies highlight the advantages to a multidisciplinary approach and encourage others to exploit the rich biological diversity of this phenomenon.

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