

## Editorial

# What is it like to be a peahen?

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The 1970s and 1980s marked the apotheosis of Darwin's (1871) conjecture, dismissed in its day, that mate choice driven by individual aesthetic preferences – a “taste for the beautiful” – plays a central role in evolution. The major lines of mate-choice research were largely defined by 1990. Animal behaviorists and neuroethologists had shown that preferences were multidimensional (Burley, 1981) and contingent on a multiplicity of factors (Bateson, 1978). Evolutionary geneticists and behavioral ecologists argued that positive (Zahavi A, 1975), negative (Parker, 1979) or neutral (Lande, 1981) fitness effects could drive the evolution of mating preferences, or that preferences could emerge from functions unrelated to mating (Endler, 1992, Ryan, 1990). Under any of these scenarios, mate choice could play an integral role in the origin and maintenance of gene flow barriers among species and in the structure of natural populations (Lande, 1981, Searcy, 1982, West-Eberhard, 1983). Many of these ideas were crystallized in an eponymous volume edited by Bateson (1983); progress was summarized a decade later as part of Andersson's (1994) encyclopedic *Sexual Selection*.

Since then, the scholarly literature has ballooned to literally thousands of studies of mate choice, often employing technology undreamed of in the mid-to-late 20<sup>th</sup> century. Empirical studies have shown, for example, how single-nucleotide mutations can change sensitivity to stimuli and therefore mating preferences (Leary et al., 2012), how cognitive and perceptual biases influence mate choice (Akre et al., 2011), and how preferences are dependent on social experience (Bailey and Zuk, 2008).

Yet what we are left with is a vast set of case studies, some of them exquisite, adding complexity and detail to the outlines set up a generation ago. These studies have all but ignored a contemporary theoretical literature on mate choice heavily skewed towards a back-and-forth about mid-twentieth century ideas.

This stagnation remains because, like Darwin, we

continue to be more interested in the train of the peacock than the mind of the peahen. The study of mate choice is mostly concerned with collapsing preferences into selection gradients acting on sexual display traits. But in order to understand how mate choice works, how it evolves, and indeed how it acts as an agent of selection, we need to understand mate choice as a phenotype in its own right. In particular, we need to be able to make generalizations about how mate-choice mechanisms work, about how they vary among individuals and species, and about how they are shaped by selection both within and outside the context of mating decisions.

For obvious reasons of tractability, theoretical investigations of mate choice almost always focus on a narrow aspect of the mate-choice phenotype: searching for mates, choosing among conspecific courtiers, distinguishing conspecifics from heterospecifics. Each of these tasks, however, represents a special case of a general life-history problem that every individual faces: how to distribute resources among potential sexual partners over the course of one's lifetime.

As with other life-history problems, understanding mate choice revolves around the fitness costs and benefits of mate choice. Some straightforward rules emerge: sampling  $n+1$  mates often incurs more of a direct cost than sampling  $n$  mates; partnering with a devoted parent increases fitness relative to partnering with a poor one. In other cases, however, costs and benefits may not be intuitively obvious: for example, while sampling more *individuals* is often increasingly costly, it is not the case that sampling more *traits* on a potential partner carries increased processing costs - as theoretical models have assumed - since redundant cues can facilitate detection and discrimination (Guilford and Dawkins, 1991).

The most controversial questions involve the net *genetic* benefits surrounding mate-choice decisions. While it is almost universally true that mating with distantly related heterospecifics or full siblings is detrimental, the

spectrum of outcomes between these extremes is much more complicated: the last few decades have shown that interspecific hybridization, multiple mating, and mating with highly-ornamented courters can each have positive, neutral, or negative consequences. A further complication is that the mechanisms involved in mate choice must at once accomplish several tasks (Ryan and Rand, 1993): recognizing suitable conspecific mates, choosing among conspecifics, and avoiding close relatives, without compromising how they function in other contexts. Accordingly, mating preferences among conspecifics can arise as a result of selection pressures entirely unrelated to variation in conspecific phenotypes.

What can we glean from a theoretical and empirical corpus that tells us mate choice can yield virtually any possible fitness outcome? One approach is to do meta-analyses on large numbers of studies (Jennions et al., 2012). These studies can tell us, for example, that published studies on average report a weak positive effect of expressed mating preferences on chooser fitness. They do not, however, tell us why the offspring of a female house finch (Hill, 1991) who mates with colorful males are more likely to survive than those of a female guppy who does the same (Brooks, 2000). Understanding the ecological and evolutionary consequences of mate choice requires us to formulate general rules governing variation in mate choice; deriving these rules requires a detailed understanding of the proximate mechanisms underlying mating decisions, coupled with a more comprehensive, chooser-centered perspective on how mate choice operates. The same mechanisms that are used to discriminate potential mates are also used not only to discriminate relatives from nonrelatives and conspecifics from heterospecifics, but also can have general functions distinct from mating. Accordingly, it is important to resist the charms of blanket adaptationism: choosers often make decisions that are detrimental to their own fitness, and constraints on both display traits and preferences mean that mating decisions can fall far short of the ideal.

The six papers collected in this special column illustrate the challenges and rewards inherent in this more comprehensive approach to studying mate choice. Wiegmann and colleagues (this volume) synthesize optimality models of mate searching. These models ask the overarching question of how much time and energy individuals should allocate to sampling the distribution of potential mates; while we generally think of this problem in literal terms of individuals moving around and evaluating potential partners, the framework applies

equally to thinking about what share of one's sensory, perceptual, and cognitive resources should be given over to mate choice. Importantly, Wiegmann et al. relax the adaptationist assumption of previous mate-searching models that choosers can directly assay the fitness benefits of mating with particular individuals. Rather, choosers are sampling phenotypic distributions that may covary with fitness in multiple ways.

A key question for understanding how female mating decisions translate into fitness outcomes is how the phenotypic landscape of courters maps on to the preference landscape of choosers. Indeed, most studies of mate choice focus on preferences, or internal predispositions to mate with some phenotypes more than others. As Stafstrom et al. show in this volume, preferences are highly multivariate and interdependent. Their study shows that the elaborate tufts on males' legs, perhaps the most salient morphological feature of these spiders, influence female choice only when presented in the context of a multimodal (visual and vibrational) courtship display. Sexual selection via mate choice therefore acts only secondarily on brushes.

A major difficulty of conceptualizing multivariate preference space is that signalers (courtiers) and receivers (choosers) can vary along very different axes. For example, three very different traits – a color patch produced by deposition of a single carotenoid pigment; a color patch produced via structural properties of tissue; and a color patch produced by a mixture of pigments – can elicit an identical response from chooser sensory systems, while a single trait on a courter can address multiple sensory and cognitive registers within choosers. For example, the inflation of the vocal sac in frogs and toads produces both visual and acoustic cues. Accordingly, the space of display traits and the space of chooser preferences have very different shapes. This means that the most attractive stimulus combinations are, like the women represented by Barbie dolls, unlikely to exist in the physical world.

As the remaining papers in this column show, the complexities of mating preferences have important evolutionary consequences. Gabirot and colleagues show that preferences for a chemosignal varying within, but not between lizard populations overrode any preferences for pheromone components that diverged between populations. Preference for a shared trait therefore precludes assortative mating and the accumulation of genetic differences among species.

The relationships among multivariate traits and multivariate preferences are very much dependent on the

genetic architecture underlying both. Van der Sluijs and colleagues (this volume) estimate the genetic covariance among mating preferences, display traits, and intrasexual aggression. Genetic correlations between any of these traits can facilitate assortative mating and therefore speciation. Intriguingly, aggression and display traits were correlated with one another but preference was not, consistent with a misaligned preference space and with Gabirot et al.'s findings.

The fascinating thing about mate choice for evolutionary biologists is that mate choice is a complex trait that both shapes evolutionary processes like speciation and hybridization, and is in turn shaped by them. Oh et al. revisit a classic scenario posited by Kaneshiro (1980), whereby divergence of courter traits and chooser preferences among species arise from genetic bottlenecks in founder populations, which can lead to the loss of signal elements and to an initial weakening of chooser preferences. Finding behavioral evidence in support of Kaneshiro's hypothesis in a species pair of Hawaiian crickets, they posit that cuticular hydrocarbons (CHCs) and the corresponding pheromone receptors were lost in founder events.

Cuticular hydrocarbons varying in structure produce highly multivariate chemical cocktails that are ubiquitously used by insects in mate choice. Individuals attend to both absolute concentrations and ratios of specific combinations of compounds. Weddle et al. conclude this volume by reviewing how choosers attend to CHCs, focusing on their use in self-referential phenotype matching, which allows them to avoid inbreeding and remating. Weddle et al.'s work completes the circle from an expanded view of the fitness consequences of mate choice, through the need to understand genetic and functional mechanisms like the ones surrounding sensation and evaluation of pheromone blends.

As Weddle and colleagues show, a common mechanism for self-referential phenotype matching is simply for females to attend to their own pheromone cues that have remained on previously mated males. This mechanism hints at another major source of complexity for mate choice: the social, biological, and physical environment surrounding choosers. Most components of mate choice, from the overall effort invested in mate choice, to the molecular structure of sensory receptors, to the subjective value assigned to different males, are strongly influenced by variation in the physical, ecological, and social environment (Jennions and Petrie, 1997). There has been relatively little effort to incorporate such plasticity into theories of preference evolution

(but see e.g. Verzijden et al., 2012). A promising way forward lies in both life-history theory, which explicitly incorporates environmental parameters into allocation decisions (Alonzo, 2010) and in quantitative-genetic models incorporating indirect genetic effects (IGEs) which can explicitly incorporate learned mating preferences (Bailey and Moore, 2012).

We have known for over thirty years that mate choice is highly multivariate, highly constrained, and highly labile. Yet we have focused, rather myopically, on how mate choice imposes selection gradients on male traits. Our thinking on preference evolution has revolved around the extent to which preferences coevolve with traits, and we have devoted far, far too much effort to understanding mate choice through the lens of its minuscule, and ambiguous, genetic contribution to offspring viability (1.5%, Møller and Alatalo, 1999). Mate choice generates sexual selection on male traits, but sexual selection's feedback on mate choice itself may be of only minor importance.

Our mistake in this area over the past three decades has been sweeping the messy, multivariate, nonlinear nature of mate choice under the rug. Fortunately, there are signs of an emerging new framework for understanding mate choice. Exciting recent work has bridged the theoretical-empirical divide (Jennions et al., 2009, Phelps et al., 2006), and a burgeoning literature is shifting the center of attention away from display traits and towards mating preferences in their own right (e.g. Rubenstein, 2012 and accompanying special issue). Technology now allows us to collect large behavioral, neurophysiological, and genetic datasets more efficiently, and to sample multivariate preference space more thoroughly. What we need now is a synthetic framework that embraces the biological complexity of mate choice through the conceptual integration of evolutionary history, neural and genetic mechanisms, and multiple selective forces. Within this framework, we need much better communication between theoreticians and empiricists, grounded in a common vocabulary of quantitative parameters that we can measure in the real world. Specific, testable predictions within an integrative perspective should generate important insights into the fundamental role that mate choice plays in evolution, and into the intricate processes underlying this most important of individual decisions.

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