

The causes and evolutionary consequences of variation in female mate choice in insects: the effects of individual state, genotypes and environments

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Sexual selection generally involves males evolving secondary sexual characters that satisfy the mating preferences of females. Behavioral ecologists have spent considerable research effort on identifying how variation in sexually-selected traits in insects is maintained among males at the expense of investigating the proximate and ultimate causes of variation in female mating preferences for those male traits. The past decade has witnessed improved effort in redressing this bias in insects with researchers identifying a host of factors intrinsic and extrinsic to the female as mediating flexibility in female mating behavior. Evidence is mounting that a female's social environment, whether experienced during development or as an adult, is key to shaping her mating preferences. Others have extended these observations to show that the genetic identity of the conspecific individuals comprising the social environment can have profound effects on female mating preferences via indirect genetic effects (IGEs), or through interspecific indirect genetic effects (IIGEs) if the genotype of heterospecifics influences plasticity in mating preferences. Considerably more work is needed to not only expand our list of mediating intrinsic and extrinsic factors but also to identify how their interaction influences individual variation in male and female mating preferences.

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The importance of phenotypic plasticity of mating preferences

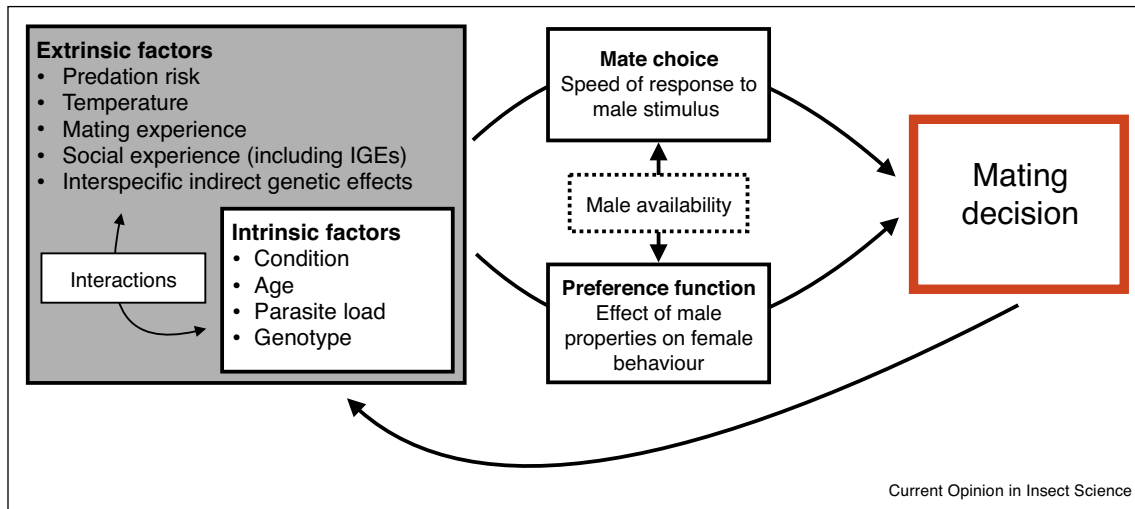
Females were long assumed to prefer mates with the most extreme expression of sexual traits because these males provided greater fitness benefits [1,2]. This notion has,

however, perplexed theoreticians because constant directional selection should exhaust genetic variation in male traits [3]. But this is clearly not the case, since males in nature express considerable heritable variation in their sexually-selected ornaments and displays (i.e. the lek paradox). Maintenance of this variation can be explained by heritable condition-dependent expression of male traits [4], parasite-mediated sexual selection [5], or by genotype × environment interactions [reviewed by 6]. This is only part of the story, however, since intrinsic and extrinsic factors can maintain genetic variation in female mating decisions. Variation in male traits and female mate preferences could lead to heterogeneity in sexual selection on male traits and thus, at least partially, resolve the lek paradox [7]. Across insects, females show phenotypic plasticity in their mate preference proximally either by adjusting their response speed (how quickly they respond to the appropriate stimulus) or the order in which they rank potential mates (i.e. preference function) [8]. Ultimately, there are two broad avenues by which variation in female mate preferences can be generated and maintained by selection. First, because exercising strong preferences can be costly to female fitness, adult females should adjust their mating preferences, as with other life-history traits, in order to maximize the reproductive benefits accrued within a given context or situation (e.g. females exhibit weaker preferences under predation risk) [2,9,10]. Second, females can develop mate preferences that depend upon the quality or composition of their developmental environment, or through the interaction between their genotype and the environment (e.g. if females reared in a high-density environment prefer larger males as adults) [11]. Both sources of variation undoubtedly maintain among population differences in male traits and female preferences and might help to explain how sexual selection can drive the evolution of new species [12**]. Despite Jennions and Petrie [8] noting more than twenty years ago that research needs to focus on the causes and evolutionary consequences of variation in mate choice, there remains a bias in insect research toward investigating the fitness benefits provided by males to females [1,6]. Over the past decade, however, investigators have taken great strides to redress this imbalance [13].

Intrinsic factors: female age, mating history and body condition

Although female mating preferences are undoubtedly influenced by male characteristics, factors intrinsic to

Figure 1



Schematic diagram showing that factors intrinsic and extrinsic to female insects (or males in the case of male mate choice scenarios) are sources of individual variation in the two properties of female mating preferences (mate choice and preference function) and, ultimately, female mating decisions. Intrinsic factors are specifically inset within extrinsic factors because females always mate within some ecological or environmental context that can also affect phenotypic variation in mating preferences. Different types of intrinsic and extrinsic factors will interact with each other (i.e. intrinsic \times intrinsic or extrinsic \times extrinsic) as well as between the two types of factors (i.e. extrinsic \times intrinsic interactions). Mating preferences in insects are influenced by the quality and quantity of available males in the environment at the time of mating. Female mating decisions could feedback to extrinsic and intrinsic factors if, for example, a female's choice of mate results in the transfer of parasites to her.

females, and unrelated to male phenotype, can also guide female mating decisions (Figure 1). For example, choosiness is expected to decline with age because older females have diminishing residual reproductive value and the time or energy costs associated with searching for preferred mates outweigh the relative benefits accrued by mating with them [14]. Several studies in insects support this prediction by showing that females become less selective of potential mates as they get older (Table 1). In one such study, Moore and Moore [15] found increased responsiveness to preferred males in older female cockroaches, *Nauphoeta cinera*. Older female cockroaches were also less fertile, which suggests that the decrease in choosiness might be a consequence of reduced reproductive potential. Atwell and Wagner [16] also showed that young female field crickets (*Gryllus lineaticeps*) were more choosy relative to older females but only under high male densities, presumably because of the greater variety of males from which to choose. On the contrary, Travers *et al.* [17^{*}] found that older female *Drosophila melanogaster* were choosier than younger females. They suggest that increased choosiness in older females is due to their having less to gain from additional matings because they have likely ensured fertilization of at least some of their eggs via previous matings. Because female age and mating history are positively correlated, female mating decisions might be driven by mating history rather than age [18]. Indeed, by experimentally disentangling these factors, Judge *et al.* [19] found that mating status had a significantly stronger effect on female

choosiness than age in *Gryllus pennsylvanicus* field crickets. These studies demonstrate that age-related changes in female choosiness are clearly driven by more than lowered reproductive potential or search costs; mating history certainly plays a role but, more specifically, the critical factor mediating mating decisions could be the quality or quantity of stored sperm that are available for future fertilizations [17^{*}]. Studies examining the effect of mating history on female choosiness need to account for patterns of sperm storage and usage by females.

Female mate choice decisions are likely to be condition-dependent and subject to trade-offs with other fitness-related traits [20]. By manipulating the acquisition of dietary protein throughout their lives (i.e. from hatching until death) of female black field crickets, *Teleogryllus commodus*, Hunt *et al.* [7] were able to show that high-condition females (i.e. reared on high-protein diet) more strongly preferred males having a high calling rate than did poor-condition females (i.e. reared on a low-protein diet). They argue that the observed decreases in responsiveness and preferences of poor-condition females are a product of choosiness being more costly for females with depleted energy stores. Support for this hypothesis evades us though as no study has yet quantified the energetic costs of sampling potential mates in an insect. Alternatively, experiencing a stressful environment during development might affect the development of sensory systems [21] resulting in some females lacking the ability to detect or differentiate sexual signals. Mate

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