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The evolution and evolutionary consequences of social plasticity in mate preferences

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In many animals, experience modifies behaviour in a variety of ways and contexts. Here we focus on experience of social environments and phenotypic plasticity in mate preferences. We first review adaptive hypotheses about the evolution of social plasticity in mate preferences, finding support for all of them across different species. We suggest that future work should assess which patterns of variation in social environments select for which forms of plasticity in mate preferences. We then highlight that social plasticity in mate preferences creates feedback loops between the role of social environments as causes of variation in phenotypes and the role of social environments as causes of selection on phenotypes. Fully understanding the consequences of these feedbacks will involve assessing both how selection shapes the plastic response to variation in social environments and how individuals in social environments are selected to influence the mate preferences of others. This task is just beginning, but we review evidence of genetic variation in both of these aspects of social plasticity in mate preferences.

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The experiences of animals often influence their behaviour in important ways (Danchin et al. 2004; Dingemanse & Wolf 2013; Dukas 2013). There is, for instance, increasing evidence that experience generates plasticity in mate preferences in a wide variety of animals (Hebets & Sullivan-Beckers 2010; Verzijden et al. 2012). The background for this research is a growing realization that mate choice unfolds in a dynamic milieu in which conspecifics, heterospecifics, natural enemies and the choosing individual's own characteristics all influence the context and outcomes of reproductive decisions (West-Eberhard 1983; Zuk & Kolluru 1998; Greenfield 2002; Costa 2006; Clutton-Brock 2007; Lyon & Montgomerie 2012). A consequence of this insight has been increased interest in the patterns of variation and plasticity in mate preferences because of their potential evolutionary consequences (Mayr & Dobzhansky 1945; Jennions & Petrie 1997; Cotton et al. 2006): mate preferences can strongly impact the fitness of the members of the choosing sex and their offspring (West-Eberhard 1983; Andersson 1994; Puurtinen et al. 2009; Prokop et al. 2012). Additionally, mate preferences are important causes of selection on sexual ornaments and displays (Darwin 1871; West-Eberhard 1983;

Andersson 1994). Thus, plasticity in mate preferences can have important consequences for sexual selection; it may, for example, influence the strength and form of sexual selection and determine whether divergence is promoted or opposed (Qvarnström 2001; Chaine & Lyon 2008; Hebets & Sullivan-Beckers 2010; Fowler-Finn & Rodríguez 2012a, b; Verzijden et al. 2012).

Here we review the patterns of plasticity in mate preferences that arise from experience of the social environment. We refer to this socially induced, experience-mediated plasticity as 'social plasticity in mate preferences'. Experience of the social environment should have particular influence on mate preferences because competitive and cooperative interactions with conspecifics are particularly strong sources of selection (Darwin 1871; West-Eberhard 1983; Andersson 1994; Hoekstra et al. 2001; Kingsolver et al. 2001). Furthermore, social plasticity in mate preferences can generate feedback loops between the social environment as a determinant of variation in mate preferences and the social environment as a product of selection arising from mate preferences (see below).

Understanding the causes and consequences of variation and plasticity in mate preferences will require refining and standardizing how behavioural ecologists describe such variation. We thus begin with a brief outline of the philosophy and methods behind quantitative descriptions of mate preferences and of how mate preferences relate to mate choice. We then address the following questions. (1) What sources of selection have favoured social

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plasticity in mate preferences? (2) How may social plasticity in mate preferences influence the process of sexual selection and its role in divergence and speciation?

MATE PREFERENCE FUNCTIONS SUMMARIZE MATE CHOICE BEHAVIOUR

We begin with a distinction between mate choice and mate preferences. Mate choice occurs when the members of either sex discriminate among a set of potential reproductive partners rather than mating at random (Andersson 1994). Thus, mate choice is the outcome of interactions among individuals (Cotton et al. 2006). Mate preferences, by contrast, are the traits whose expression results in mate choice. Mate preferences are function-valued traits (Meyer & Kirkpatrick 2005; Stinchcombe et al. 2012); that is, they are expressed as a function of the sexual ornaments that are encountered by individuals choosing among potential mates. Describing a mate preference thus requires presenting individuals with a range of variation in ornaments and quantifying their responses across the tested range to generate 'mate preference functions' (Ritchie 1996). Figure 1 illustrates a preference function, obtained for a sample of females from one population of *Enchenopa* treehoppers (Hemiptera: Membracidae; Rodríguez et al. 2006). To describe preference functions we advocate nonparametric methods such as cubic spline regressions, which make no assumptions about the shape of the curves (Schluter 1988; Brodie et al. 1995; Ritchie 1996; Fowler-Finn & Rodríguez 2012a, b, 2013; Rodríguez et al. 2013).

Once preference functions have been generated, it is possible to describe variation in the shape of the curves with what we term 'preference function traits' (Bailey 2008; Fowler-Finn & Rodríguez 2012a; Rodríguez et al. 2013). Preference functions can be 'open' or 'closed' (Fig. 2). Open preferences favour extreme values in one direction; closed preferences favour intermediate trait values. Either type of preference can be further characterized in terms of peak preference and preference selectivity (Fig. 2). Preference functions that differ in peak preference exhibit different ornament trait values with highest attractiveness. Preference selectivity summarizes variation in aspects of preference shape other than peak preference, including for example how sharply the preference function declines as ornament trait values deviate from peak preference (Bailey 2008; Fowler-Finn & Rodríguez 2012a; Rodríguez et al. 2013). Preference selectivity predicts the strength of selection on sexual ornaments. We emphasize these two preference function traits because they can be used to describe patterns of variation in mate preferences useful in testing hypotheses about the evolution of social plasticity in mate preferences, as we detail below.

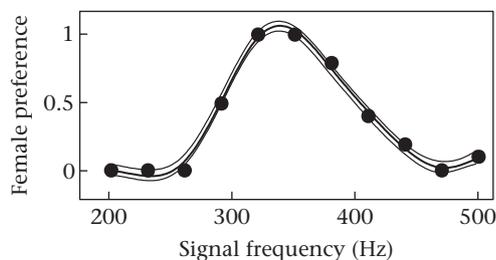


Figure 1. Example of a mate preference function. Depicted is the likelihood of female response to vibrational playback stimuli varying in dominant frequency in a member of the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). Symbols indicate the proportion of females responding to a playback stimulus. The curves show a cubic spline regression \pm SE curves based on the data points (see text). The curve peaks at a narrow range of stimulus frequencies and drops sharply as stimuli deviate from those frequencies. Note that in any one encounter between a male and a female, only a portion of the curve depicted would be expressed. Nevertheless, the entire curve is the trait of interest. Redrawn from Rodríguez et al. (2006).

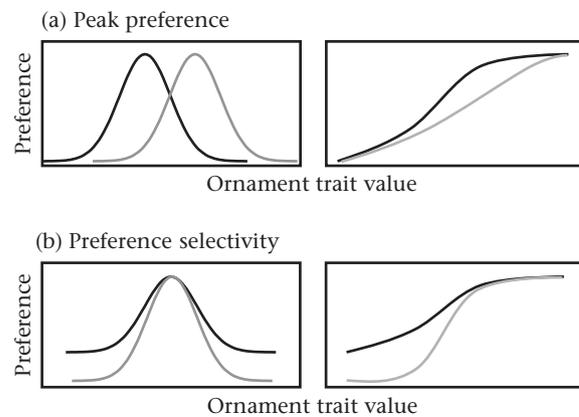


Figure 2. Describing variation in mate preference functions. Mate preferences may differ in shape. They may be 'closed' (unimodal), as shown in the left-hand panels in (a) and (b), or 'open-ended', as shown in the right-hand panels in (a) and (b). Mate preferences of either shape can be further characterized with two main traits: (a) 'peak preference' is the ornament trait value with highest attractiveness; each panel in the top row shows two mate preferences that differ in peak preference; (b) 'preference selectivity' summarizes variation in aspects of preference shape other than peak; each panel in the bottom row shows two mate preferences that differ in selectivity (see text).

PATTERNS OF SOCIAL PLASTICITY IN MATE PREFERENCES

A review of the literature reveals that social plasticity in mate preferences is widespread. Different species exhibit different patterns of plasticity (e.g. plasticity in peak preference versus preference selectivity). Species also vary in the degree of this plasticity.

The literature includes several cases of social plasticity using measures corresponding to peak preference (e.g. Miller & Fincke 1999; Hebets 2003; Walling et al. 2008), and this is without examples from studies of classical imprinting, wherein animals such as many birds learn their mate preferences during a critical window of time, typically at an early age (Irwin & Price 1999; Moore 2004; Servedio et al. 2009; Hebets & Sullivan-Beckers 2010). As an example, consider the study that is perhaps most responsible for sparking current interest in social plasticity in mate preferences (Hebets 2003). In this study, Hebets demonstrated that mating decisions of adult female *Schizocosa uetzi* wolf spiders (Araneae: Lycosidae) were influenced by experience with either brown-legged or black-legged males when the females were immature. Adult females preferred to mate with the type of male with which they were familiar, and they were also more likely to cannibalize males of the unfamiliar type. By contrast, females lacking experience with either type of male showed no preference between them.

There also exists evidence of numerous cases of social plasticity in measures that correspond to preference selectivity (De Winter & Rollenhagen 1993; Collins 1995; Wagner et al. 2001; Magurran & Ramnarine 2004; Hebets & Vink 2007; Bailey & Zuk 2008, 2009; Kozak & Boughman 2009; Fowler-Finn & Rodríguez 2012a, b). For example, in *Ribautodelphax imitans* planthoppers (Hemiptera: Delphacidae), De Winter & Rollenhagen (1993) showed that experimental manipulation of the type of female signal (conspecific versus heterospecific) experienced by males throughout their lives (egg to adult) influenced their adult mate preferences: all males preferred conspecific playbacks, but males that experienced conspecific signals were more likely to show this preference than were males that experienced heterospecific signals or males that had no experience with female signals.

FUNCTIONS OF SOCIAL PLASTICITY IN MATE PREFERENCES

When is social plasticity in mate preferences favoured by selection? And, how do different patterns of variation in social

environments favour different forms of plasticity in mate preferences? We address these questions with the general rationale for the evolution of adaptive plasticity. We envision a social environment that is sufficiently variable to disfavour any one fixed mate preference, but wherein variation occurs at such scales, and with such cues, as to allow the adaptive regulation of plasticity (cf. Via & Lande 1985; West-Eberhard 2003; Hollander 2008; Kasumovic 2013; Snell-Rood 2013). We then suggest that evaluation of the kinds of variation in the social environment that induce different forms of plasticity in mate preferences can be used to test hypotheses about the source of selection on this plasticity. The rationale for these evaluations is based on predictions for evolutionary change in mate preferences in response to long-term changes in the social environment (e.g. Irwin & Price 1999; McPeck & Gavrillets 2006), but applied to the evolution of plasticity in mate preferences in response to shorter-term changes in the social environment (Fowler-Finn & Rodríguez 2012a, b). The goal is to implement a functional design criterion, which seeks evidence that a trait has been selected to perform a particular function (cf. Williams 1966; West-Eberhard 1992; Autumn et al. 2002). Specifically, we seek evidence that plasticity in preference functions traits have been selected to perform particular functions related to variation in the social environment. For example, if there is seasonal variation in the extent to which mate choice confers benefits to females, and if females adjust their mate preferences accordingly, one might infer that plasticity has been favoured under selection to optimize the trade-off between the costs of performing mate choice and the benefits accrued from it (Qvarnström et al. 2000; Qvarnström 2001). A similar conclusion might be drawn from plasticity in preference selectivity related to variation in the risk of predation (Johnson & Basolo 2003).

Below we summarize hypotheses concerning (1) aspects of the social environment that vary in such a way as to favour plasticity in mate preferences, (2) aspects of preference functions selected to be plastic and (3) the functions performed by this plasticity (Table 1, Fig. 2). The hypotheses are not mutually exclusive, because different patterns of variation in social environments may select for different forms of plasticity in mate preferences, and multiple patterns of variation in the social environment can occur simultaneously. However, each hypothesis makes distinctive predictions about the presence and pattern of plasticity that should be expressed according to different aspects of the experience of the social environment (Table 1).

Common Mate Types Hypothesis

This hypothesis posits that (1) there is variation in which of several equally acceptable (or equally beneficial) mate types is present or common in the social environment, (2) this variation selects for plasticity in mate preferences that allows recognition of these common mate types and (3) the function of this plasticity is to ensure that mating takes place and to reduce mate-searching costs. In prior work we have also referred to this hypothesis as the 'learned preference' hypothesis (Fowler-Finn & Rodríguez 2012b).

This hypothesis predicts shifts in peak preference according to experience of cues of the mate types present in the environment (Table 1). Note that this prediction is not confounded by the rare male effect, whereby unique, novel or uncommon ornaments may be preferred (Knoppien 1985; Zajitschek & Brooks 2008; Mariette et al. 2010; Rutledge et al. 2010), because the prediction of a shift in peak preference towards experienced common types is the opposite of the expectation under the rare male effect (shift towards uncommon types).

Evidence in support of this hypothesis includes studies of classical imprinting (Irwin & Price 1999; Moore 2004; Servedio et al. 2009; Hebets & Sullivan-Beckers 2010). Additionally, recent work shows that shifts in peak preference occur in a variety of animals, including species where the learning mechanisms of imprinting might not have been expected. There are, for example, documented cases of shifts in peak preference to the mate types experienced in damselflies (Miller & Fincke 1999; Fincke et al. 2007), swordtail fish (Walling et al. 2008) and wolf spiders (Hebets 2003). Such shifts in peak preference suggest that certain mate types may be preferred over others, not only or mainly because of benefits obtained from mating with them, but as a means of expediting processes such as pair formation. It is early to ask how commonly this may occur in nature, but it seems clear that it is widespread. There is, however, a variant of this hypothesis, which posits selection on plasticity in peak preference in relation to variation in which mate type is most advantageous. There are examples of such variation, and of the predicted shifts in peak preference, in soil mites (Lesna & Sabelis 1999), spadefoot toads (Pfennig 2007) and lark buntings (Chaine & Lyon 2008). However, in these cases the regulating cue is environmental rather than social. We are unaware of examples where the regulating cue is purely social.

Mismating Avoidance Hypothesis

This hypothesis posits that (1) there is variation in whether preferred versus nonpreferred types (e.g. conspecifics versus heterospecifics) are present or common in the social environment, (2) this variation selects for plasticity in mate preferences that facilitates recognizing and avoiding the nonpreferred mate types and (3) the function of this plasticity is to help prevent mismating when the risk of mismating is high and to reduce the cost of mate discrimination when the risk of mismating is low (Fowler-Finn & Rodríguez 2012a, b).

This hypothesis predicts either shifts in peak preference away from experienced nonpreferred types; and/or higher selectivity with experience of nonpreferred types (Table 1). Cases supporting this hypothesis include work on damselflies (Svensson et al. 2010), guppies (Magurran & Ramnarine 2004) and planthoppers (De Winter & Rollenhagen 1993). Interestingly, there are also cases in which selectivity decreases with experience of nonpreferred types (Fowler-Finn & Rodríguez 2012a, b; see below), suggesting that the prevention of mismating may not be the primary function of plasticity in mate preferences. This may indicate that features other than plastic adjustment of mate preferences have been selected to

Table 1
Hypotheses seeking to explain the evolution of social plasticity in mate preferences (summarized from Fowler-Finn & Rodríguez 2012a, b)

Hypothesis	Function of plasticity	Predictions
Common mate types	Ensure mating; reduce mate-searching costs	Shift in peak preference to type experienced to be common
Mismating avoidance	Prevent mismating; reduce mate choice costs	Shift in peak preference away from nonpreferred type experienced
Mismating avoidance	Prevent mismating; reduce mate choice costs	Preference selectivity increases with experience of nonpreferred types
Mating assurance	Ensure choice of preferred type; ensure mating	Preference selectivity decreases with experience of nonpreferred types
Mate variability assessment	Ensure choice of preferred type; reduce mate choice costs	Preference selectivity increases with experience of heterogeneity in mate types present, if preferred mate types are included

reduce mismating. Alternatively, mismating may often not be the main cost related to mate choice. For example, the risk of forgoing reproduction may be important, and it may sometimes pay to relax mate preference criteria.

Mating Assurance Hypothesis

This hypothesis posits that (1) there is variation in whether preferred types are present or common in the social environment, (2) this variation may select for plasticity in mate preferences that promotes discrimination only when the preferred types are present or common and (3) the function of this plasticity is to help secure mating with preferred types when those are available and to ensure that mating occurs when the preferred types are rare or absent (Fowler-Finn & Rodríguez 2012a, b).

This hypothesis predicts lower selectivity with experience of nonpreferred types relative to experience of preferred types (Table 1). There is widespread support for this hypothesis, including studies in crickets (Bateman et al. 2001; Wagner et al. 2001; Bailey & Zuk 2008, 2009; Rebar et al. 2011), fruit flies (O’Hara et al. 1976; Dukas 2006), sticklebacks (Kozak & Boughman 2009), treehoppers (Fowler-Finn & Rodríguez 2012a, b) and wolf spiders (Hebets & Vink 2007).

Mate Variability Assessment Hypothesis

This hypothesis posits that (1) there is variation in the level of heterogeneity or variability in the composition of the social environment, (2) this variation may select for plasticity in mate preferences that promotes mate choice when there is variability in the composition of mate types in the social environment (i.e. when there is a choice to be made) but promotes reduced discrimination when there is little variability in the composition of the social environment and (3) the function of this plastic adjustment in preference selectivity is to secure the benefits of mate choice when there is a range of mate types to choose from and to reduce the costs of mate choice when there are few or no options from which to choose (Real 1990; Getty 1995; Jennions & Petrie 1997; Fowler-Finn & Rodríguez 2012b). That is, plasticity is favoured because

the payoff of mate choice changes with the level of variability in the composition of the social environment.

This hypothesis predicts higher selectivity with experience of greater variability in mate types, provided that the preferred mate types also are present (Table 1). Few studies have assessed how social plasticity in mate preferences is influenced by the effect of experience of variability per se. There is, however, support for this hypothesis in guppies (Jordan & Brooks 2012) and treehoppers (Fowler-Finn & Rodríguez 2012b).

CONSEQUENCES OF SOCIAL PLASTICITY IN MATE PREFERENCES

Social plasticity in mate preferences can generate feedback loops between the social environment as a determinant of variation in mate preferences and as a product of selection arising from mate preferences. These feedback dynamics may arise when (1) variation in the social environment induces plasticity in mate preferences and (2) mate preferences influence the strength and form of social and sexual selection, thereby (3) altering the patterns of variation in the social environment.

Feedback between the causes of variation in fitness and the causes of variation in phenotypes can take various forms (Fowler-Finn & Rodríguez 2012a, b). For example, if preference selectivity increases with variability in the social environment, the strength of sexual selection may increase and in turn reduce variability in subsequent generations. By contrast, if preference selectivity decreases with reduced variability in the social environment, the strength of sexual selection may decrease and allow a subsequent increase in variability. These dynamics can potentially establish a negative feedback loop that may contribute to the maintenance of variation (Fig. 3a).

An alternative feedback dynamic may arise if preference selectivity increases with experience of preferred mate types, in which case the strength of sexual selection may increase and promote fixation of preferred mate types; but if preference selectivity decreases due to experience of lack of preferred mate types, the strength of sexual selection may decrease and promote the acceptance of nonpreferred types (Fig. 3b; also see Bailey & Moore 2012). In this case, the loops are self-reinforcing and external events are required to switch from the positive loop to the negative

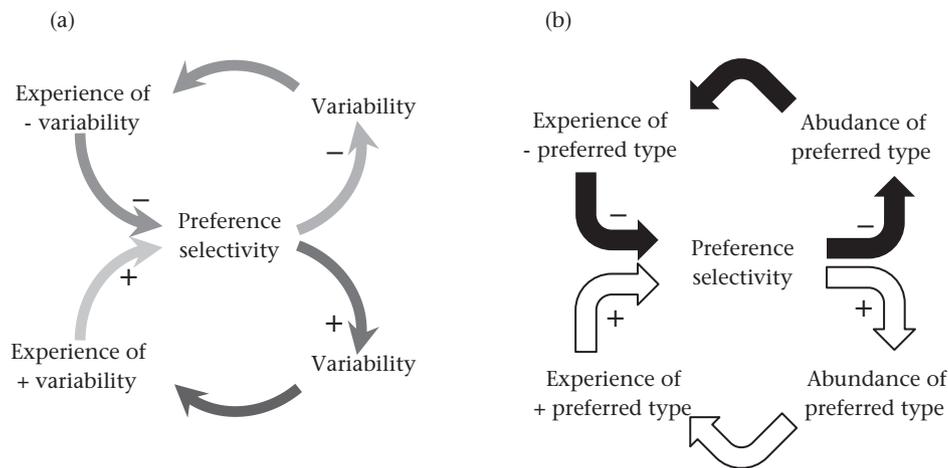


Figure 3. Potential feedback loops that may arise from the interplay between mate preferences as causes of selection and social environments as causes of variation in mate preferences. (a) Negative feedback loop between preference selectivity and variability in mate types in the social environment. The flow of ‘events’ follows arrow shading: experience of high variability increases preference selectivity, thus subsequently diminishing variability; experience of low variability decreases preference selectivity, permitting subsequent increases in variability. (b) Positive feedback loop between preference selectivity and abundance of preferred mate types. Here there are two possible, self-reinforcing loops (denoted by arrow shading): experience of high abundance of preferred mate types increases preference selectivity, and thus subsequently increases the abundance of preferred types even more (open arrows). Alternatively, experience of low abundance of preferred types decreases preference selectivity, thus permitting even greater abundance of nonpreferred types (black arrows).

loop. For example, a population in the positive loop in Fig. 3b (open arrows) could be shifted to the negative loop by an event that made preferred types rare, such as a bottleneck or a founder effect during colonization of a novel environment. In the case of such events, the feedback loops depicted in Fig. 3b could help the population survive and adapt by allowing reproduction in conditions in which preferred mate types are lacking.

GENETIC VARIATION IN SOCIAL PLASTICITY IN MATE PREFERENCES

Genetic Variation in the Plastic Response of Mate Preferences to the Social Environment

Understanding the adaptive nature of social plasticity in mate preferences requires addressing whether and how it responds to selection. There is evidence that social plasticity in mate preferences can evolve: studies in guppies and crickets have detected geographical variation in socially induced plasticity in mate preferences (Magurran & Ramnarine 2005; Bailey & Zuk 2012). An additional step in answering this question involves assessing the presence of genetic variation in the expression of social plasticity in mate preferences. This amounts to asking whether there is a genotype \times environment interaction in mate preferences, with the twist that 'environment' in this question refers to the social environment. We tested for evidence suggestive of genetic variation in social plasticity (i.e. genotype \times environment interaction, or $G \times E$) in mate preferences of *Enchenopa* treehoppers using a full-sib split-family design, with families split across developmental environments that showed variation both in the rearing plant environment and in the social groupings on the rearing plants (Rodríguez et al. 2013). We detected significant heritability in peak preference and preference selectivity (mostly medium to large effect sizes), and we found evidence suggestive of $G \times E$ in these preference function traits (Rodríguez et al. 2013).

Genetic Variation in Social Influence on Mate Preferences

In addition to genetic variation in the plastic response of mate preferences to the social environment, the way in which social environments influence this plastic response may also have an underlying component of genetic variation (i.e. social environments are composed of individuals whose phenotypes and interactions are partly influenced by their genotypes). That is, the feedback dynamics arising from social plasticity in mate preferences may involve 'indirect genetic effects' (IGEs), whereby genes expressed by one individual have phenotypic effects on another individual (Moore et al. 1997; Wolf et al. 1999; Miller & Moore 2007). Furthermore, genetic variation in these components would suggest that each component can evolve in response to selection exerted by the other component. With regard to IGEs, empirical work has lagged behind theory, because the required measurements are extremely challenging. Nevertheless, although there have been relatively few studies of IGEs (on any trait), it seems clear that they are likely to be widespread (Agrawal et al. 2001; Kent et al. 2008; Bleahey & Brodie 2009; Danielson-François et al. 2009; Biscarini et al. 2010).

We recently demonstrated IGEs on mate preferences; that is, we demonstrated the presence of genetic variation in the influence of the social environment on mate preferences (D. Rebar & R. L. Rodríguez, unpublished data). We used a simple quantitative genetics breeding design (full-sib split-family) to estimate genetic variation, with a twist: the phenotypes we described (i.e. the mate preferences) were not those of the individuals belonging to the full-sib families, but instead were those of randomly collected unrelated

individuals that we reared with the full-sib families. These indirect genetic effects influenced the overall shape of the mate preference functions and also had a detectable influence on both peak preference and preference selectivity.

CONCLUSION AND FUTURE DIRECTIONS

We provide an overview of plasticity in mate preferences arising from experience of the social environment. We advocate a function-valued approach for describing variation in mate preferences and a functional design approach to study its evolution. There are various hypotheses that seek to explain why social plasticity in mate preferences evolves. Each hypothesis is supported by some studies, suggesting that, in different species or populations, social environments vary in ways that select for different patterns of social plasticity in mate preferences. Progress will come from seeking a broad understanding of which patterns of variation in the social environment select for which forms of plasticity in mate preferences. The hypotheses may be tested by observing the patterns of plasticity that occur in the field (e.g. Qvarnström et al. 2000; Chaîne & Lyon 2008). However, variation in mate preferences in the field may not represent plasticity, but rather among-individual variation. It may also be difficult to pinpoint the environmental cue involved in the regulation of plasticity. Finally, mate preferences may be difficult to describe in the field (as opposed to describing realized mate choice decisions arising from interactions between males and females). We therefore advocate experimental manipulation of specific components of the social environment.

Perhaps the most powerful test of the above hypotheses would be a comparative study of multiple populations or closely related species varying in social context. This would allow testing for particular predicted patterns of plasticity according to the pattern of variation in social context experienced by each population or species. For example, shifts in peak preference towards familiar mate types would be predicted in species having multiple acceptable types that vary in abundance. By contrast, plasticity in preference selectivity would be predicted in species varying in the abundance of preferred and nonpreferred types (Table 1). Another way to implement this test would be with the ancestral-derived framework proposed by Foster (2013), if it were possible to reconstruct ancestral states for forms of plasticity and of variation in the social context.

Social plasticity in mate preferences brings evolutionary consequences that arise from the dual role of social environments as causes of variation in phenotypes and causes of selection on phenotypes. These roles interact to create feedback loops that may variously promote the maintenance of variation, strengthen sexual selection or facilitate mate recognition under conditions of sparse mate availability.

In the final analysis, understanding the evolution and evolutionary consequences of social plasticity in mate preferences will involve study not only of how selection shapes the plastic response to variation in social environments, but also of how individuals as components of those social environments are selected to influence the mate preferences of other individuals. With evidence of genetic variation in both of these aspects of social plasticity in mate preferences, we anticipate exciting and continuing discoveries about how social dynamics shape evolutionary processes.

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