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## COMMENTARY

## Genotype–environment interaction and the reliability of mating signals

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*(Received 28 May 2003; initial acceptance 30 November 2003;  
final acceptance 22 January 2004; MS. number: AS-1285)*

It is a central tenet of animal communication theory that signals are reliable (Zahavi 1977). That is, the characteristics of a signal that are attended to by a receiver should be reasonably good predictors of the transmitter's current physical ability, internal state or motivation, social status, or acquired information. Signal characteristics should also predict the future consequences that a receiver, responding in a particular way, is likely to experience. Whereas the range of signals that animals transmit between one another may certainly include some messages that are not fully honest (Hasson 1994; e.g. Backwell et al. 2000), and partially withholding information or identity can sometimes be in a transmitter's best interest (Johnstone 1997), animal communications are generally expected to result in a net benefit to both signaller and receiver (see Hauser 1996; Bradbury & Vehrencamp 1998). This expectation rests on the reasoning that failure to meet the criterion of reliability, as when an 'inferior' individual broadcasts a 'strong' signal normally associated with superior physical prowess, should result in selection against receiver responses to the signal, which, in turn, would select against its continued transmission, without alteration, by the signaller. In terms of perfection, signal characteristics are expected to be reliable to the extent that an 'ideal receiver', one suffering no perceptual impairments, can respond in a manner that on average enhances its fitness (see Johnstone & Grafen 1993).

Within the realm of sexual selection, animal mating signals are expected to indicate the signaller's phenotype with some degree of reliability. Moreover, under the various coevolutionary mechanisms of sexual selection (wherein mate choice only yields indirect, genetic benefits), mating signals are also expected to indicate the

signaller's genotype and, more critically, the phenotype of offspring that the signaller would sire. This latter expectation is most apparent in those processes traditionally known as 'viability indicator' or 'good genes' mechanisms. Here, females (or males, in the case of sex-role reversal) choose males based on a signal or other advertisement feature that is a reliable indicator of a potential mate's (heritable) viability, the expected success in the natural selection arena (e.g. Moore 1994; Welch et al. 1998; Møller & Alatalo 1999; Doty & Welch 2001). Thus, a choosy female is ensured of producing offspring, daughters as well as sons, who are likely to enjoy superior survivorship and growth. The criterion of reliability is satisfied because males who do not show the viability trait are in poor condition and, on average, physically unable to generate an attractive signal, or the signal clearly reveals the male's poor condition (Maynard Smith 1991). In other words, a strong signal generally cannot be faked by a substandard individual; alternatively, it is a prerequisite for mating because a female cannot be certain that a male who lacks an attractive signal is a viable individual. It is assumed that both the signal and the preference for it are heritable traits, and the linkage disequilibrium established by mate choice maintains a genetic covariance between these two traits.

The reliability expectation is also inherent within those processes traditionally known as Fisherian, or arbitrary, mechanisms of sexual selection, although it may be less obvious here. But it is this common expectation, that mating signals reliably indicate the promise of fit offspring, that has led to a recent view that viability indicator and Fisherian mechanisms represent graded variations of a single process (Kokko et al. 2002).

In Fisherian selection, female preferences are based solely on heritable charm and appeal: females choose males who display attractive signals or other attributes, and they thereby produce sons who are likely to be attractive themselves and enjoy superior mating success (Fisher 1958; e.g. Jones et al. 1998). As above, preference and signal traits covary owing to linkage disequilibrium,

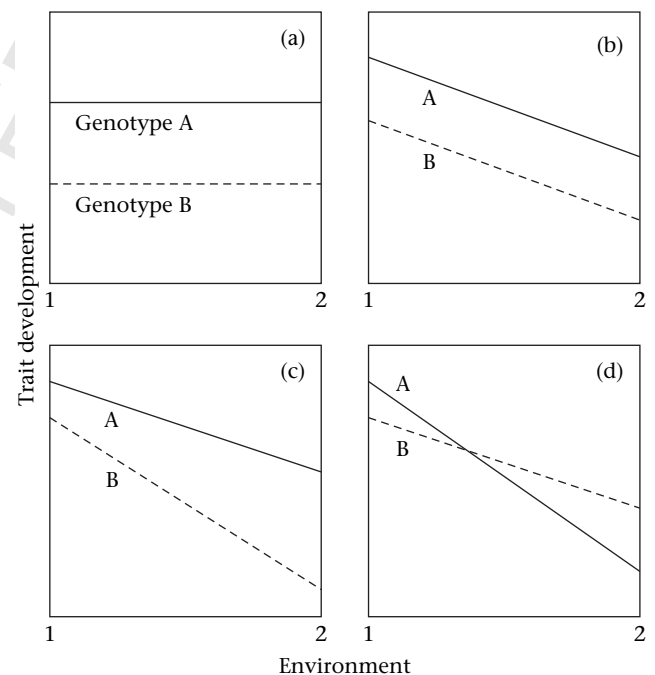
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and both traits may become exaggerated to an extent that is counterbalanced by natural selection. Unlike viability indicator selection, there exists no positive relationship between a male's attractiveness and viability, and a choosy female is not expected to produce offspring, sons or daughters, who show enhanced survivorship or growth. Reliability is central to the evolution of exaggerated sexual traits via Fisherian selection, because the attractive male that a female chooses to sire her offspring must carry the signalling gene(s) that covary, via linkage disequilibrium, in the population with her preference gene(s). This genetic covariance sets up a situation wherein a female's chosen mate will carry, but ordinarily not express, the same preference gene(s) that the focal female herself possesses. Consequently, each mate choice event strengthens ever so slightly the incidence of that preference trait within the population, which then strengthens the preferred signal. In addition to signal/preference genetic covariance, a female must also be ensured that the signalling gene(s) carried by her mate, and inherited and expressed by her sons, will confer attractiveness on these offspring when they mature in the next generation. Should a female be courted successfully and accept a male who lacks these genes, she will not necessarily produce sons with attractive features. Moreover, linkage disequilibrium would be disrupted, and, given a high incidence of such pairings, the process driving elaboration of the signal and preference traits within a population may eventually slow to a halt.

Formal analytical and simulation modelling (in which environmental constancy is generally implicit), complemented by empirical findings in various invertebrate and vertebrate species, lend support to the operation of both viability indicator (Pomiankowski 1988) and Fisherian mechanisms (Lande 1981; Kirkpatrick 1982) of sexual selection. These findings include observations of female choice in species where males do not provide direct benefits (Møller & Alatalo 1999), retention of additive genetic variance for male signal and female preference traits (Bakker & Pomiankowski 1995; Jang & Greenfield 2000; Greenfield 2002; Rodriguez & Greenfield 2003) in these species, and genetic correlation between the signal and preference traits (e.g. Bakker 1993; Gilburn et al. 1993; Hine et al. 2002). None the less, consideration of the environmental regimes that natural populations may experience, and the expected phenotypic responses to different regimes, presents a troubling dilemma: once certain assumptions of environmental and phenotypic constancy and lack of genotype–environment interaction are relaxed, signals may quickly become unreliable as either viability or Fisherian indicators. Because signal unreliability, whereby a female is led to choose a 'genetically inferior' male and produce offspring of below-average fitness, would seriously undermine either mechanism, the fundamental operation of these mechanisms should be reanalysed. In this paper we show explicitly how signal unreliability arises and explain why it would compromise operation of the coevolutionary mechanisms of sexual selection. We then consider the circumstances necessary for these mechanisms to work and the characteristics of signals whose reliability would be robust across a range of naturally occurring situations.

## Ecological Genetics of Sexually Selected Traits

Students of evolutionary biology recognize that, more often than not, traits are plastic (West-Eberhard 2003). As environmental conditions change, the morphological, developmental and behavioural features expressed by an organism or genotype are likely to vary, especially when these features are polygenic traits. This phenomenon is known as phenotypic plasticity (which can be adaptive per se; see Schlichting & Pigliucci 1998), and the function describing a genotype's level of expression of a particular trait under different environments is known as its norm of reaction (Fig. 1). Within a population, different genotypes may certainly show different levels of trait expression in a given environment (Fig. 1a, b), and they may also show different shifts in trait expression in response to an environmental change (Fig. 1c). That is, if the reaction norms of the various genotypes are not parallel, a genotype–environment interaction (GEI) is said to occur. Ecological crossover is a special case of GEI in which norms of reaction intersect (Fig. 1d). Thus, genotypes



**Figure 1.** Trait expression under different environmental conditions. (a) Genotypes A and B show different levels of trait development in both environments 1 and 2, but the levels expressed by both genotypes do not change across environments; that is, reaction norms (solid and dashed lines) are flat and phenotypic plasticity is not present. (b) Genotypes A and B show different levels of trait development, and both show comparable reductions in development in environment 2 (i.e. reaction norms are steep but parallel, and both genotypes show phenotypic plasticity). (c) Genotypes A and B show different reductions in development in environment 2 (i.e. reaction norms are not parallel, and a genotype–environment interaction is present). (d) Reaction norms of genotypes A and B intersect (i.e. ecological crossover is present, with genotype A and B, respectively, showing the greater trait development in environments 1 and 2).

A and B will respectively show the relatively higher level of trait expression in environments 1 and 2, a situation that can potentially maintain additive genetic variance within a population (Felsenstein 1976; Gillespie & Turelli 1989; Roff 1997).

While phenotypic plasticity, GEI, and ecological crossover are now core concepts in evolutionary and ecological genetics, remarkably little effort has been made to apply these concepts to sexually selected traits (e.g. Griffith et al. 1999; Jia et al. 2000; Proulx 2001; Rodriguez & Greenfield 2003; Welch 2003). Perhaps this oversight reflects a desire to retain an element of simplicity in models explaining the coevolutionary mechanisms; residue from the typological approach traditionally used to characterize a species' behaviour may represent an additional factor. But regardless of the source of neglect, any careful examination of sexual traits, including advertisement and courtship signals and the responses to them, shows that they are no more exempt from plasticity than other traits (e.g. see Maynard Smith 1991 on the conditional handicap model). For example, the acoustic characteristics of a male's sexual advertisement call may be closely associated with the male's body size (e.g. Brown et al. 1996), which might be strongly influenced by food, density, or temperature during development. If the growth, and hence advertisement calls, of several genotypes vary with density or temperature and norms of reaction also differ, the potential for ecological crossover in mating calls is clear: genotype A might produce a more attractive call (e.g. one with lower dominant frequencies or higher pulse rates) than genotype B under a particular environmental regime, but the sign of this phenotypic difference could be reversed as one or more environmental conditions change (Fig. 2; see Jia & Greenfield 1997; Jia et al. 2000; Welch 2003).

The potential for phenotypic plasticity and ecological crossover, in conjunction with dispersal or environmental change over time, is the major basis for the problem of signal unreliability in natural populations. While other sources, such as perceptual error and signalling noise (Bradbury & Vehrencamp 1998), may contribute to unreliability, ecological crossover is likely to be a more serious factor for several reasons. (1) Ecological crossover can generate unreliability immediately following dispersal or environmental change. (2) Animals may be unable to readily adapt (e.g. by sharpening perception via learned or evolved responses) to unreliability generated by ecological crossover. (3) A special conundrum arises because ecological crossover, while potentially maintaining additive genetic variance in a male trait and thereby sustaining female choice for that trait, may also counter the very operation of sexual selection by diminishing the indirect benefits accrued via mate choice.

Because the issue of reliability is more straightforward in the viability indicator mechanism, we treat this category of coevolutionary sexual selection first. According to this mechanism, females choose a particular male because his signal is both heritable and reliably indicates heritable viability, the expected survivorship or development of sons and daughters. However, should phenotypic plasticity and GEI occur and generate ecological crossover for

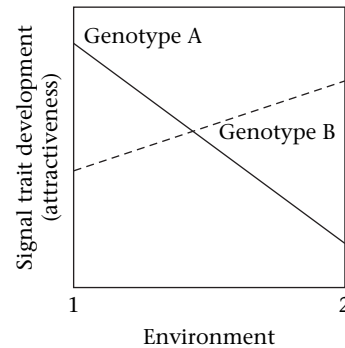


Figure 2. Potential signal unreliability under ecological crossover. Genotype A (solid reaction norm) males show the greater development of a signal trait and are the more attractive variant (to genotype A females) when maturation occurs under environment 1, whereas genotype B (dashed reaction norm) males are the more developed and attractive variant (to genotype B females) under environment 2. Thus, genotype A females in environment 1 may choose genotype B males who matured under environment 2 and then dispersed to environment 1, but offspring of these pairings who remain in environment 1 may be relatively unattractive, and possibly, nonviable as well. In addition, genotype A females in environment 1 who pair with genotype A males may produce offspring that will be relatively unattractive, and nonviable, should they disperse and mature under environment 2 or experience a comparable environmental change as they mature in situ (see Table 1). Whenever dispersal events or environmental changes lead to genotype A females in environment 1 pairing with genotype B males (or genotype B females in environment 2 pairing with genotype A males), the linkage disequilibrium between signal and preference traits is interrupted and genetic covariance is decreased incrementally. Lowered genetic covariance will ultimately hold the evolution of these traits in check (see Fig. 3).

signal expression, an environmental change over space or time may result in a female, which may be attracted to a male based on his signalling, choosing a genotype of uncertain, possibly inferior, viability (Fig. 2, Table 1). The severity of this problem may depend on the following factors: (1) the magnitude of ecological crossover, with greater crossover more likely to generate unreliable signals leading females to an unfortunate pairing; (2) the incidence of dispersal between environments or of environmental change over time, with high levels of dispersal or change more conducive to unreliability; (3) the mode of inheritance (autosomal or sex linked) and dominance of signalling and viability genes; (4) covariance between viability and signal development across environments; and (5) the nature of variability of the (female) preference trait (see below).

Similar problems beset the Fisherian mechanism of sexual selection. Fisherian females choose mates whose signals are aesthetically attractive, are likely to be attractive to most other females in the population, and, by virtue of the signal's heritability, will be displayed by their sons. However, when signal expression is plastic and subject to ecological crossover, Fisherian females may mate with a male bearing attractive features but whose sired offspring will fail to be attractive in a new environment (Fig. 2, Table 1). A female's chosen mate also may not carry the signalling gene(s) that covary with her

**Table 1.** Potential signal unreliabilities under dispersal or environmental change

Dispersal	Environmental change over time	Mating pair (female/male parental generation)	Male signal development level and attractiveness* (F <sub>1</sub> generation)	Viability (F <sub>1</sub> generation)	Linkage disequilibrium† (signal/preference* genes)
None	Environment shifts from 1 to 2 at site of population 1 before maturation of, and mating by, parental generation	Genotype A/genotype B	High; attractive to genotype A females	Viable in environment 2	Disrupted
		Genotype B/genotype B‡	High; attractive to genotype A females	Viable in environment 2	Not disrupted
None	Environment shifts from 1 to 2 at site of population 1 after maturation of, and mating by, parental generation	Genotype A/genotype A	Low; nonattractive to genotype A females	Nonviable in environment 2	Not disrupted
		Genotype B/genotype A‡	Low; nonattractive to genotype A females	Nonviable in environment 2	Disrupted
Female disperses from population 1 to 2 after maturation but before mating	None	Genotype A/genotype B in population 2 (environment 2)	High; attractive to genotype B females	Viable in environment 2	Disrupted
		Genotype B/genotype B in population 2 (environment 2)‡	High; attractive to genotype B females	Viable in environment 2	Not disrupted
Male disperses from population 2 to 1 after maturation but before mating	None	Genotype A/genotype B in population 1 (environment 1)	Low; nonattractive to genotype A females	Nonviable in environment 1	Disrupted
		Genotype B/genotype B in population 1 (environment 1)‡	Low; nonattractive to genotype A females	Nonviable in environment 1	Not disrupted

It is assumed that populations 1 and 2 experience environments 1 and 2, respectively, and that genotype A males show the more strongly developed signals when maturing under environment 1, whereas genotype B males show the more developed signals when maturing under environment 2 (cf. Fig. 2). Consequently, when signal development indicates viability, genotypes A and B are each the more viable variant when maturing under environments 1 and 2, respectively.

\*The preference trait is not assumed to show phenotypic plasticity across environments, but see Fig. 3 for a more complete treatment of this issue.

†Linkage disequilibrium is expected to occur between signal and preference genes such that, under environment 1, genotype A males will tend to carry the preference genes that influence attraction (when expressed in females) specifically towards male signals that are produced by genotype A males that mature in that environment; conversely, genotype A females will tend to carry signal genes that influence production (when expressed in males) of signals that are attractive to genotype A females.

‡The pair is not expected to form: genotype B females are assumed to have preference genes, via linkage disequilibrium, that influence attraction specifically towards male signals that are produced by genotype B males that mature under environment 1.

preference gene(s), thereby interrupting the exaggeration process, especially when the various environments are similarly common. As with viability indicator selection described above, impediments to trait exaggeration via the Fisherian process should be greatest when plasticity and crossover are strong, environments change often, and dispersal between areas that are subject to different environmental regimes are regular events (cf. Proulx 2001). Under these circumstances, every time a dispersal event or an environmental change occurs, a female is liable to mate with a male who is attractive but who represents a genotype that had not been paired assortatively with her recent ancestors. Because each such pairing will sever linkage disequilibrium and incrementally reduce genetic covariance in the population between signal and preference traits, a pattern of regular dispersal or environmental change could keep covariance at levels low enough to prevent preference, and signal, traits from attaining extravagance.

The various scenarios above are presented to show that viability indicator and Fisherian mechanisms of sexual selection may operate only under a circumscribed set of conditions. In the following sections we re-examine these constraints and indicate in greater detail the circumstances necessary for operation. We do not question fundamental workings of the mechanisms themselves, but we do assume that environments change over space and time and that traits, including sexually selected ones, often respond in a plastic manner to such change. Our findings therefore call into question the overall prevalence, and strength, of coevolutionary sexual selection mechanisms. They also point towards the sorts of traits that would be most subject to evolution via these selection mechanisms.

### When Can Coevolutionary Mechanisms Operate?

One fundamental condition under which a mating signal will retain a critical element of reliability is when the signal/viability phenotypic correlation remains consistent across environments (see Fig. 2, assuming that viability parallels signal trait development in both environments; cf. Proulx 2001). For example, in a population wherein a low dominant frequency in an advertisement call indicates the caller's viability, the combination of low frequency and high viability would simply transfer from one genotype to another as environmental conditions change. Thus, although the males that females choose as mates following the change would represent different genotypes than the males they chose before the change, the males' call features and (heritable) viability would remain the same. This scenario of fortuitous shifts in mate choice might at first seem contrived, but consideration of the potential role that life history traits can play as intermediary factors in sexual selection (see Rowe & Houle 1996) reveals that concern may be unfounded. Acoustic signal characters such as dominant frequency often reflect, or hitchhike along with, body development, size, and other aspects of condition that represent viability

under the current environment. Consequently, under the various environmental regimes, females would simply be choosing those males who sustain superior condition. None the less, females would be choosing different genotypes under these various regimes, and such shifts would reduce genetic covariance between condition (which determines the degree of signal development) and preference traits (see Table 1). We return to this insidious problem in the following treatments of Fisherian selection and the potential plasticity of preference traits.

Differences among traits in genetic canalization (see Kawecki 2000), or other bases for plasticity of expression, may offer another partial solution to the reliability problem. Are the traits that do serve as highly exaggerated sexual advertisement signals those whose canalization is high or whose expression is otherwise invariant across a range of commonly experienced environmental regimes or at least not subject to high amounts of ecological crossover? Environmental insensitivity (cf. Fig. 1a) or lack of genotype–environment interaction (GEI; cf. Fig. 1b) could ensure that the same genotypes are preferred under the various regimes encountered, reducing interruptions to linkage disequilibrium and declines in genetic covariance. On the other hand, traits whose expressions are altered significantly by environmental change and subject to significant GEI may never evolve to an exaggerated state. Thus, observers might fail to recognize them as sexual signals. More to the point, females cuing on these traits would often fail to produce viable offspring or attractive sons: males chosen as mates may not carry the genes that would confer viability or attractiveness in a new environment if conditions change before offspring mature in the subsequent season or offspring disperse (Fig. 2, Table 1). Under these circumstances, the continued evolution of the preference, and the corresponding signal, could be threatened.

### Phenotypic Plasticity and Ecological Crossover in Preference Traits

Thus far, our discussion of plasticity has focused largely on the signal trait, expressed in males, and treated the preference trait, expressed in females, as fixed and invariant. To a great extent, this emphasis is a bias that results from the relative difficulty of studying the genetic and environmental influences acting on preferences, which has led to a general lack of information on these behaviours as heritable, yet potentially variable, traits (see Jennions & Petrie 1997). None the less, there are no identifiable a priori reasons for us to expect preference traits to be less plastic than signals (e.g. Bakker et al. 1999; Lesna & Sabelis 1999; Qvarnström et al. 2000; Qvarnström 2001; Rodriguez & Greenfield 2003). Like signal traits, preference traits may reflect overall body condition and development, also hitchhiking along with these general features. Because development may influence an animal's locomotory ability and movement as well as its peripheral (e.g. Bailey 1998) and central neural processing, any plasticity in development may lead to plasticity in responses to signals and in preferences among them. That is,

life history traits can play the same mediating role in shaping preferences as they may do for signals.

When condition-dependent plasticity in female preference traits exists, signal reliability as a Fisherian indicator may be retained across a range of environments provided that both signal and preference traits have roughly parallel norms of reaction (see Fig. 3a, b). That is, (a prevalent) genotype P prefers the signals of genotype A under both environments 1 and 2, even though A's signals are modified strongly as the environmental regime changes from 1 to 2. But when signal and preference reaction norms are mismatched, an environmental change might result in preference shifting towards another genotype and a concomitant decrease in signal/preference genetic covariance (see Fig. 3c, d, noting the potential influence of the mode of female choice, i.e. open ended versus absolute). Can we then infer that signal traits that have evolved to exaggerated development via Fisherian selection are those whose reaction norms parallel the norms of associated preference traits?

When signals are viability indicators, though, parallel reaction norms in males and females may not necessarily retain signal reliability. Unless viability and signal development covary strongly, linkage disequilibrium between the signal and preference might be preserved but

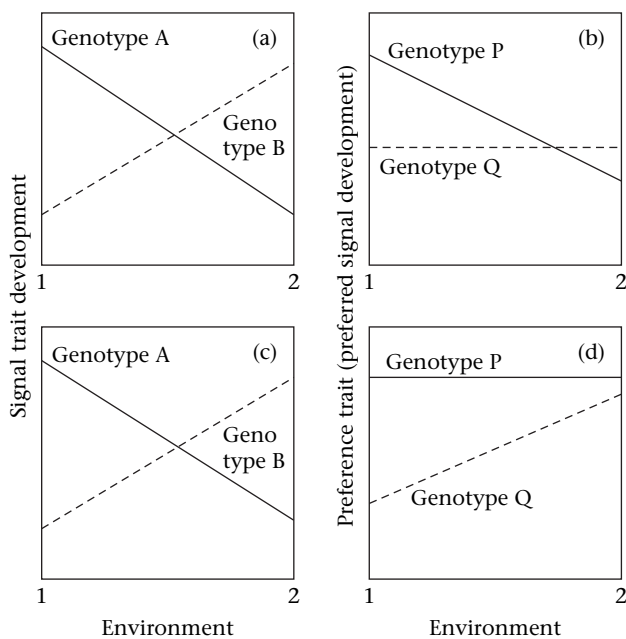
at the expense of choosing mates of inferior condition. Conceivably, however, offspring might disperse in a way that leads to settlement and maturation in the environments where they develop and perform best. Thus, assortative dispersal in the face of environmental variability is another factor that could preserve reliability and be prerequisite for signal evolution in some cases.

The above problems suppressing evolution of exaggerated features disappear, of course, if the genetic covariance between signal and preference traits results from pleiotropy or very close physical linkage between genes (e.g. location on the same arm of a chromosome). Sexual selection operating under such circumstances is by the above definition noncoevolutionary, and we have too little information on the genetic architecture of sexually selected traits to assess the likelihood of its occurrence. Moreover, findings in some insect species do show that signal and receptor (preference) traits are not controlled by the same or closely linked genes (e.g. Löfstedt et al. 1989; also see Butlin & Ritchie 1989), and in the case of viability indicator selection, physical linkage would be demanded of the viability trait as well.

### Phenotypic Plasticity, Ecological Crossover and Population Divergence

When environmental conditions vary and signal and/or preference traits show differential phenotypic plasticity and ecological crossover, there exist two possible consequences for sexual selection. Declining genetic covariance, which holds signal evolution in check as outlined above, can be expected when environmental change or dispersal and interbreeding occur frequently among populations experiencing the different conditions. Here, females are selected to lose the preference in proportion to the cost of exercising it, which is the degree of signal unreliability; none the less, this loss may be countered by higher genetic variance for the signal trait arising under elevated gene flow, which would increase the benefits females accrue by being choosy. However, a second, very different consequence may arise if such environmental change or dispersal occurs but rarely. In the latter case, we may expect a build up of differences in signals, and preferences, between populations that experience dissimilar environments (e.g. Sattman & Cocroft 2003). Using Fig. 2 (or Fig. 3) as an example, populations that are subject to environments 1 and 2 may become quite differentiated in signal and preference traits, and in underlying gene frequencies. To the extent that preference differences between these populations are strong enough to preclude interbreeding should dispersal occur at a later date, divergence (and speciation) could be the end result (cf. Kawecki 1996, 1997).

The predictions we have presented here are all qualitative assessments based on generalized responses of traits to environmental change. Obviously, our assessments will need more rigorous confirmation via formal population and quantitative genetic modelling, which specify numbers of loci and alleles, degree of dominance, mode of inheritance, and potentially additional variables.



**Figure 3.** Reaction norms of male signal and female preference traits. (a, b) Reaction norms of genotype A males and genotype P females are roughly parallel, a situation that may sustain signal/preference genetic covariance, leading to signal evolution via Fisherian selection. (c, d) Reaction norms of genotype A males and genotype P females are not coincident, a situation that may erode signal/preference genetic covariance, holding signal evolution via Fisherian selection in check. In either situation, the outcome may depend on the incidence of other preference genotypes (Q) in the population and whether preferences are open ended (accept any level of signal development equal to or greater than a specific value) or target a specific level of signal trait development.

Empirical studies of the extent to which GEIs affect sexually selected traits and the degree to which signal and preference reaction norms match will also be needed. None the less, the predictions put forth make it clear that coevolutionary sexual selection mechanisms will seldom, if ever, operate in straightforward textbook fashion and that a reaction norm approach can offer much insight. Expressed in terminology relevant to fundamental criteria of these mechanisms, phenotypic plasticity and GEI may lead to marked decreases in signal heritability and genetic covariance between signal and preference traits. Reflecting the general outlook for behavioural genetics put forth by Boake et al. (2002), future investigations of the coevolutionary mechanisms cannot afford to ignore the effect of plasticity and its several consequences on the overall strength of selection or on population divergence.

We thank Rex Cocroft, Anne Danielson-François, Carl Gerhardt, Michael Jennions, John Kelly and an anonymous referee for critical reading of this manuscript. Many of the ideas presented were stimulated by research conducted under U.S. National Science Foundation grants IBN-9807915 and DEB-0131708.

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