

REVIEW

The role of genotype-by-environment interactions in sexual selection

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Abstract

Genotype-by-environment interactions (GxEs) in naturally selected traits have been extensively studied, but the impact of GxEs on sexual selection has only recently begun to receive attention. Here, we review recent models and consider how GxEs might affect the evolution of sexual traits through influencing sexual signal reliability and also how GxEs may influence variation in sexually selected traits and the process of reproductive isolation. We then assess the current empirical literature on GxEs in sexual selection and conclude by highlighting areas that need additional work. Research on GxEs and sexual selection is an important new area of study for the discipline, which has largely focused on relatively simple mate choice/competition scenarios to date. Investigators now need to apply this knowledge to more complex, but realistic, situations, to more fully explore the evolution of sexual traits, and in this review we suggest potentially useful directions for future research.

Introduction

Genotype-by-environment interactions (GxEs) occur whenever the relative performance of different genotypes is dependent on the biotic and/or abiotic environment in which they are expressed (Lynch & Walsh, 1998). GxEs have been extensively studied for over half a century in an agricultural context to improve crop yields and the efficacy of selective breeding programmes (see Falconer, 1952; Kang & Gauch, 1996). However, despite recent modelling attempts (e.g. Kokko & Heubel, 2008; Higginson & Reader, 2009) and increasing attention in empirical research over the last decade, relatively little is known about the role of GxEs in sexually selected traits and sexual trait coevolution (but see Greenfield & Rodriguez, 2004; Bussière *et al.*, 2008).

In this review, we summarize predictions from recent models which have investigated how GxEs might influence sexual selection and also consider current empirical research on GxEs in male sexual traits and female mating preferences. Our review highlights the paucity of empir-

ical studies of GxEs in sexual traits and how the theoretical work that has been carried out would benefit from further empirical testing. We therefore finish by outlining possible directions that future research may take to improve our understanding of the role that GxEs play in sexual selection.

GxEs and the expression of phenotypic traits

GxEs influence trait expression so that individuals with identical genotypes can have different phenotypes when exposed to different environments. This can be clearly illustrated as a reaction norm, where the phenotypic expression of a trait is plotted separately for each genotype in alternate environments (Fig. 1; Lynch & Walsh, 1998). In some recent theoretical papers, GxEs have been classified as either 'strong' interactions that cause ecological crossover between reaction norms (i.e. the ranked performance of genotypes changes between environment) or as 'weak' interactions that do not cause ecological crossover (see Fig. 1) (Kokko & Heubel, 2008; Higginson & Reader, 2009). These so-called weak GxEs change the scale of genetic variation across environments, but the rank order of genotypes remains the same in each environment, and only the relative strength of

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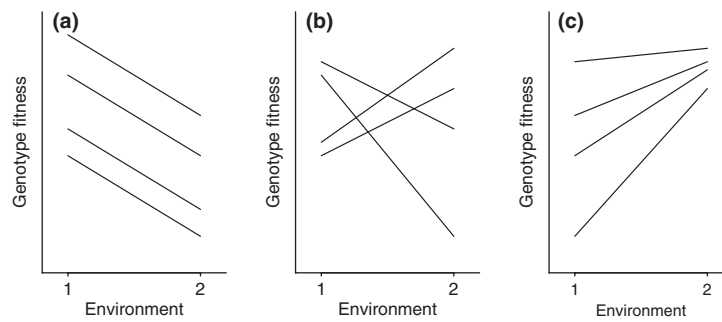


Fig. 1 Reaction norms for relative fitness of four genotypes each measured in two different environments. (a) No GxE. Genetic variation is indicated by the differences in trait expression within each environment, and the nonzero gradient between environments indicates an effect of environmental variation on trait expression, but there is no interaction between the two, and the effect is the same for all genotypes, as shown by the parallel gradients. (b) GxE with ecological crossover of reaction norms. The rank order of genotypes changes between environments, potentially affecting both the intensity and direction of selection, and the constancy of relative genotype fitness depends on the environmental constancy. The scale of variation is also likely to be affected under ecological crossover, as shown. (c) GxE where the scale of variation but not the rank order of genotypes differs between environments, which might affect the intensity of selection. A reaction norm for a GxE tested empirically may look like (b) or (c) depending on the range of environmental variation studied (see main text).

the selective advantage varies. That is, the variation in genotype performance is reduced in one environment relative to the other, under the assumption that selection on other traits remains constant between environments. However, this classification of GxEs as either ‘strong’ or ‘weak’ is somewhat idealized and depends strongly on the scale and extent of environmental variation which is considered. In other words, if GxEs are visualized graphically as nonparallel gradients of reaction norms for different genotypes (as in Fig. 1b, c), then every GxE will involve ecological crossover at some point along an infinite x -axis. Thus, whether a GxE is identified as ‘strong’ or ‘weak’ is merely a consequence of the scale and boundaries of the x -axis (i.e. the range of environmental variation which is studied). As such, these classifications may be useful theoretical concepts, but empirically they may be misleading. It might be more helpful empirically to compare the strength and influence of an interaction on trait expression by direct comparison of reaction norm gradients. It is also important to remember that the ‘strength’ of a GxE will be influenced by the genetic variation for the characters in question. For instance, a ‘strong’ GxE, with ecological crossover of reaction norms, may actually have less impact than a ‘weak’ GxE, with changes in the scale of variation, when additive genetic variation is lower in the former instance and larger in the second.

Modelling GxEs and their potential role in sexual selection

In the context of sexual selection, GxEs are likely to be very important. They could affect the expression of both male sexual traits and female mating preferences for them, which would ultimately influence how these traits co-evolve. Furthermore, GxEs might account for claims

that sexual selection generates limited evolution in some free-living populations (Grant & Grant, 2002). However, this is a relatively new field of research, and even theoretical studies are yet to consider many of the possible ways in which GxEs could potentially influence the evolution of male sexual traits. So far, models have explored how GxEs could disrupt the reliability of sexual signals (Higginson & Reader, 2009) and how they might facilitate the maintenance of variation in sexually selected traits (Kokko & Heubel, 2008).

The reliability of sexual traits as signals

Many models of sexual selection and the evolution of female mating preferences require that male sexual traits reliably signal some aspect of male quality that enables females to benefit from costly mate choice (Zahavi, 1975; Grafen, 1990; Johnstone, 1995). These benefits can be either direct to the female through materials and resources that might help her produce and raise offspring, or indirect through heritable genetic gains for offspring. If only high-quality males are capable of producing exaggerated sexual signals, then females can assess male quality via the sexual trait, secure fitness benefits, and female mate preferences will be advantageous (Grafen, 1990).

However, there are a number of circumstances in which GxEs in male sexual signals could disrupt signal reliability, causing females to effectively make the ‘wrong’ mating decision (Greenfield & Rodriguez, 2004). As an example, consider male bushcrickets that call to attract females using specialized structures on the wings that are fixed at eclosion to adulthood. During mate choice, females use calls to assess male quality, choosing to mate with high-quality males that are able to produce large, nutrient-rich spermatophores. However, if

the environment changes between when males develop their wings and when they become sexually mature and start calling, or similarly if migration occurs between these times, then wing morphology, and the resulting quality of song a male produces, represents his condition and quality in the initial environment which is no longer relevant. Consequently, females might choose a male based on an attractive call, but receive a poor quality spermatophore in return. In this way, GxEs in heterogeneous environments could cause the signal received by the female to be an unreliable indicator of the quality of the male and of the benefits he can provide (Higginson & Reader, 2009), and this will have implications in the evolution of mating preferences and could potentially eliminate any selective advantage to mate choice in the first place.

Equally, females can use male sexual signals to assess genetic quality. Indirect genetic benefits are generally mediated through genes that either confer sexual attractiveness or viability to offspring, and studies have found that attractive males do sire attractive sons, for example (e.g. crickets, Wedell & Tregenza, 1999; flies, Taylor *et al.*, 2007). However, the reliability of indicators of male attractiveness could be disrupted by GxEs and environmental fluctuations in the same manner as the direct benefits discussed earlier (Kokko & Heubel, 2008; Higginson & Reader, 2009), as could the reliability of viability indicators. For instance, male sticklebacks (*Gasterosteus aculeatus*) in good condition can produce brightly pigmented patterns that are attractive to females. In populations with parasites, condition is correlated with resistance to infection, and so females can use these sexual signals as indicators of viability genes which confer parasite resistance to her offspring (Barber *et al.*, 2001). However, parasite populations will vary both spatially and temporally, creating situations where a male might develop in the absence of parasites and then produce an attractive signal despite not being resistant to infection.

The issue of signal reliability is likely to be even more complex when females assess multiple sexual traits during mate choice, as appears common in many species (Candolin, 2003). For example, in the field cricket, *Gryllus campestris*, males produce an advertisement call to attract a mate, and females prefer males that produce calls with an increased chirp rate (Holzer *et al.*, 2003) and a lower carrier frequency (Simmons & Ritchie, 1996). Carrier frequency and chirp rate are uncorrelated components of the call (Holzer *et al.*, 2003; Scheuber *et al.*, 2003a), and carrier frequency, but not chirp rate, is negatively correlated with adult body size. Carrier frequency reliably signals juvenile, but not adult, condition with juveniles experiencing good nutrition during development growing larger and producing a call with a lower carrier frequency (Scheuber *et al.*, 2003b). Conversely, chirp rate is not influenced by juvenile condition but reliably signals adult condition, with adults fed a more nutritious diet calling at an increased chirp rate

(Scheuber *et al.*, 2003a). Consequently, if individuals occupy heterogeneous environments and there are GxEs for these traits, then the signal content of them can become uncoupled, making it difficult for a female to fulfil both preference criteria reliably. It is even possible that females will receive conflicting information from the traits they are assessing (i.e. a male producing a high carrier frequency but producing a high chirp rate).

The reliability of sexual signals is a key assumption in most models of sexual selection, because if not, selection for costly mate choice should be significantly weakened. Some models even predict that mate choice should not evolve in populations where this positive correlation does not exist (Kokko *et al.*, 2006). Two recent models that have considered how GxEs can influence signal reliability use different modelling approaches, but largely reach the same conclusion (see Box 1). That is, interactions modelled both with and without ecological cross-over can disrupt the reliability of sexual signals (Kokko & Heubel, 2008; Higginson & Reader, 2009) and, under certain conditions, can result in a negative correlation between female preference and male quality (Higginson & Reader, 2009). This situation is not predicted by classical models of sexual selection but clearly indicates how important GxEs could be in sexual selection.

Kokko & Heubel (2008) explored sexual signal reliability by modelling the costs of mating preferences tolerated by females, which is used as a proxy for the strength of female mating preferences (see Box 1). Where GxEs exist in sexual trait expression, a major cost could be the potentially low information content of male signals of quality, and the resulting increased chance that a female will make a mistake when expressing mate choice. The model looks at how gene flow between environments affects the costs of female mating preferences, and the results clearly indicate that selection for female mating preferences disappears under high levels of gene flow (with environmental structure) (see Box 1). This could be attributed to the high costs of female mate choice, which result from the low reliability of male sexual signals, which are in turn caused by GxEs and environmental variation (change).

Higginson & Reader (2009) test the potential effect of GxEs on sexual signal reliability by modelling the information content of sexual signals. Interestingly, the model highlights the importance of both genetic variation and environmental variation: signal reliability can potentially be compromised both by reduced genetic variation and by increased environmental variation (see Box 1). The model also emphasizes the influence of harsh, or stressful, environmental conditions that can severely reduce the information content of sexual signals.

The next obvious theoretical step would be to consider the consequences of unreliable sexual signals on the evolution of female mate preferences. It follows that selection for female choice will be weakened if

Box 1: Models of GxEs in sexual traits

Kokko & Heubel (2008) use a population genetics model to explore the effect of GxEs on the maintenance of female mating preferences, which are predicted to be selected for only when there is sufficient variation in sexual traits and when sexual signals reliably signal some kind of benefit for the female. Using the costs of mating preferences tolerated by females as a proxy for the strength of female mating preferences, Kokko & Heubel (2008) test how various scenarios with GxEs might affect the evolution of female mating preferences. The model compares the effect of no GxE against the effect of a GxE with ecological crossover.

The work highlights the importance of the timing of movement between environments (or, similarly, environmental change). Figure 2a describes the effect of migration, defined here as movement of males and females into a different environment immediately after birth, such that rearing conditions (the conditions in which viability selection takes place) are different from the conditions an individual is born in. Figure 2b shows the effect of male mixing, used in this model to quantify male-specific movement between environments which occurs after development (viability selection), but before mating (sexual selection). Male mixing therefore essentially describes the rate at which a given female encounters males from an alternative developmental environment than her own, as opposed to meeting males who developed in the same environment as herself. As levels of male mixing increase, the probability of a given female encountering a male from her own environment decreases. In both scenarios, the results suggest that generally selection for female mating preferences is low under high levels of gene flow (with environmental structure), although the exact effect of male mixing also depends also on the migration rate: low levels of

migration coupled with low levels of male mixing somewhat alleviates the costs of female preferences, although these costs increase as male mixing increases (Fig. 2b).

Higginson & Reader (2009) use stochastic simulations to explicitly test the effect of sexual trait GxEs without ecological crossover on sexual signal reliability. These simulations consider the information content of a male signal trait under GxEs, where each male is assumed to have a given value of genetic quality which indicates both his ability to survive environmental stress during development and his ability to produce an attractive sexual signal. First, signal reliability is considered under varying degrees of environmental heterogeneity (Fig. 3a), and then signal reliability is modelled in environmental conditions of varying 'harshness' (Fig. 3b). Harshness is used here to create a negative relationship between an environmental variable and a male's ability to both survive development and produce an attractive sexual signal, therefore simulating stressful or unfavourable conditions when environmental 'harshness' is high.

The model makes four explicit predictions about the conditions in which male sexual signals are likely to be unreliable indicators of male quality. These are as follows: (1) in highly heterogeneous environments (see Fig. 3a), (2) when variation in genetic quality is low (Fig. 3a), (3) in harsh environments where juvenile mortality is common (Fig. 3b) and (4) when environmental factors have a strong influence on sexual trait expression relative to the influence of genetic quality (Fig. 3b). This model is based on GxEs without ecological crossover, and yet it is clear that these so-called weak interactions can severely compromise the reliability of sexual signals, even causing a negative correlation between male attractiveness and genetic quality in particularly harsh environments (see Fig. 3b).

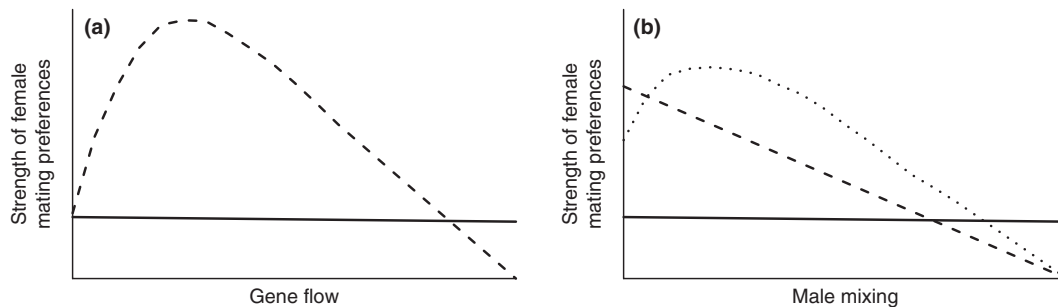


Fig. 2 The effect of gene flow between different environments on the strength of female preferences, measured as the costs tolerated by females before preference, is selected against and disappears from a population. (a) The effect of migration (or environmental change) immediately after birth (e.g. offspring dispersal). Migration is used here to describe an environmental change after birth such that offspring development and mating occur in a different environment from the one an individual is born in. In the absence of a GxE in sexual trait expression (solid line), the effect of migration is negligible. However, when there is a GxE with ecological crossover (dashed line) low levels of migration promote selection for female mating preferences, possibly through increased maintenance of variation in sexual traits. Selection on female mate choice decreases as migration increases, until at high levels of gene flow when individuals are equally mixed between environments, the advantages of female preferences disappear completely, likely to be an effect of unreliability of sexual signals. (b) The effect of male mixing, which describes male-specific movement between environments after trait development but before mating opportunities. As levels of male mixing increase, the probability of a given female encountering a male from her own environment decreases. With no GxE in sexual trait expression (solid line), the effect of male mixing is negligible. When there is a GxE with ecological crossover, the effect of male mixing depends on levels of migration (or environmental change). With high levels of migration (dashed line), the advantages of female mating preferences are high with no male mixing and then decrease steadily with increasing male mixing. With very low levels of migration (dotted line), the strength of female mating preferences is high with low male mixing and then decrease as male mixing increases further, and the reliability of sexual signals is increasingly disrupted. Figures adapted from Kokko & Heubel (2008).

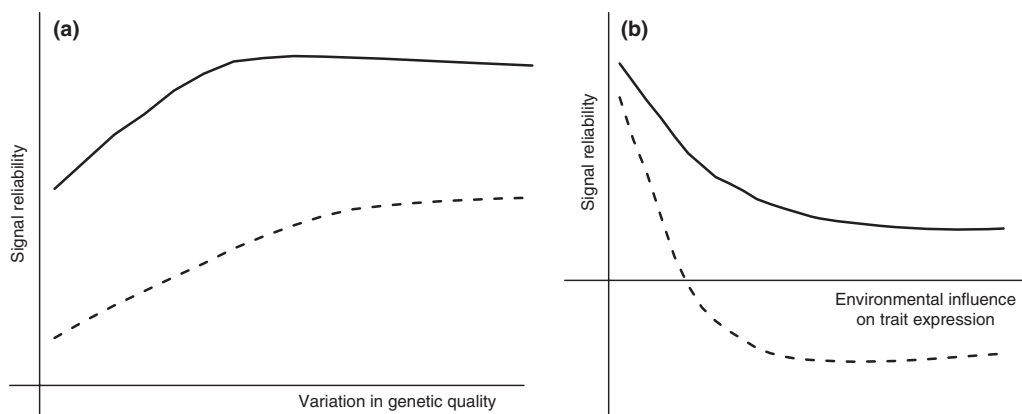
Box 1: (Continued)

Fig. 3 Reliability of sexual traits where GxEs affect the scale of variation between trait expressions in different environments but do not cause ecological crossover as modelled in different environmental conditions by Higginson & Reader (2009). (a) The effect of genetic variation in quality on the reliability of sexual signals, in environments with low heterogeneity (solid line) and in highly heterogeneous environments (dashed line). Signal reliability, measured here as the correlation between signal trait size and genetic quality, is lower in highly variable environments. However, in both types of environment, signal reliability increases with increasing variation in genetic quality, as the information content of the signal trait will be greater. (b) The effect on sexual signal reliability of the strength of environmental influence on trait expression in favourable environmental conditions (solid line) and harsh environmental conditions (dashed line). Signal reliability decreases with increasing strength of the environmental influence on trait expression. This effect could be magnified when environmental conditions are harsh (dashed line), even to the extent that the correlation between signal trait size and genetic quality becomes negative in some circumstances. Note that the line falls below zero, indicating this negative correlation. In these conditions, the most exaggerated sexual signals are produced by low-quality males, whereas high-quality males produce unattractive sexual signals, meaning that the reliability of sexual signals is so disrupted that the correlation between trait size and genetic quality is reversed. Figures adapted from Higginson & Reader (2009).

male sexual traits do not reliably signal some female benefit. This potentially has knock-on effects for trait and preference evolution. Indeed, Greenfield & Rodriguez (2004) suggested that signal reliability in traits affected by GxEs can only be fully maintained when the reaction norms for the size of the male trait and the corresponding female preference are parallel across environments.

Alternatively, it is possible that some information is better than none at all, meaning that even when GxEs exist for male sexual traits, females that utilize the little information in these signals have less variance in fitness than females not using 'unreliable' signals. Again, this needs explicit testing, by, for example, comparing female choice benefits in constant environments and fluctuating environments, with females not given a choice of mates. Either way, empirical research needs to look at both male trait expression and female mating preferences to account for the coevolution of sexual traits.

GxEs and the maintenance of genetic variation in sexual traits

The maintenance of genetic variation in sexual traits is important. If genetic variance is depleted, females may

not be able to reliably gain indirect benefits of mate choice. This is the essence of the 'lek paradox', which asks how genetic variation (on which mate choice depends when males provide only indirect benefits) can be maintained in the face of sustained directional sexual selection from female choice (Kirkpatrick & Ryan, 1991). Many studies have examined how environmental variation might maintain genetic variation, particularly with respect to the effects of stressful or unfavourable conditions, although the focus is typically not on sexually selected traits (reviewed by Hoffmann & Merilä, 1999). A recent meta-analysis of the effect of environmental stress on genetic variation in wild populations concluded that stressful conditions cause an overall reduction in genetic variation, although the effect was smaller in traits more closely correlated with fitness than in morphological traits (Charmantier & Garant, 2005).

Depletion of the genetic variation in male sexual traits in harsh environments could contribute to signal unreliability. Depending on the mechanism of female mate choice, a threshold for male attractiveness might not be met in harsh environments, or alternatively mating decisions based on relative male attractiveness might be difficult with decreased variation between males. Higginson & Reader's (2009) model of sexual signal

reliability with GxEs suggests as much, with the explicit prediction that signal reliability was greatly reduced in harsh environments and also that signal reliability was generally lowest with low genetic variation in male quality.

Genetic variation might not only be affected by stressful environmental conditions, but also simply by temporal and spatial environmental fluctuations which are a characteristic of most natural environments. It has long been recognized that environmental heterogeneity could potentially facilitate the maintenance of genetic variation in naturally selected traits (Hedrick *et al.*, 1976), and this idea was modelled explicitly for traits with GxEs by Via & Lande (1985). For a given trait expressed in different environments, evolution is not independent in each environment. With no GxE, there will be a positive correlation between trait expression in one environment and trait expression in another environment. However, where GxEs exist for trait expression, this across environment correlation can be weakened or become negative. Assuming there is some level of gene flow between environments (either spatially between populations or temporally through overlapping generations), genetic variation can then be maintained as a result of disruptive selection across environments. Gillespie & Turelli (1989) focussed on naturally selected traits with a model which demonstrated that significant trait variation could be maintained by the presence of GxEs in heterogeneous environments, and furthermore, that this effect could often be missed when only a narrow range of environmental variation is studied. A number of empirical studies support these predictions. For example, in laboratory populations of *Tribolium castaneum* kept on a variety of food substrates, body size evolution was not independent across environments (Via & Connor, 1995), and field-based experiments with *Drosophila melanogaster* have shown that genetic polymorphism in naturally selected traits can be maintained in heterogeneous environments (Mackay, 1980; Santos *et al.*, 1999).

More recently, there have been attempts to apply this general theory explicitly to GxEs in sexually selected traits (e.g. Kokko & Heubel, 2008; Box 1). The idea that GxEs might contribute to the maintenance of genetic variation in sexually selected traits is frequently proposed as a possible solution to the lek paradox, with genetic variance depleted through female mate choice but also maintained through the effect of GxEs. Kokko & Heubel (2008) modelled the potential of GxEs in sexually selected traits to maintain enough additive genetic variation to sustain indirect benefits of female mate choice when choice was costly and hence select for the evolution of female mate choice (Box 1). Their results demonstrate that GxEs can help to maintain enough genetic variation for the persistence of indirect benefits of female mating preferences but that this is heavily

dependent on the extent to which reproductive individuals from different environments mix (gene flow). With mixing of reproductive individuals from different developmental environments, there was increased genetic diversity within populations, maintaining the variation on which females could base mating decisions.

However, as described previously, migration or environmental change before mating can disrupt sexual signal reliability (see Box 1; Fig. 2a, b). As a result, low levels of gene flow between environments selected for female mate choice, but with high levels, costly mating preferences were selected against despite the genetic variation in male traits in the population. Kokko & Heubel's (2008) model highlighted the fact that it can be uninformative to consider how GxEs might maintain variation in sexually selected traits without also testing how they might disrupt sexual signal reliability. Indeed, the influence of genetic variation on the information content of sexual signals was also considered by Higginson & Reader (2009). Signal reliability increased with increasing variation in genetic quality, but this effect was weakened in heterogeneous environments where the correlation between male trait size and genetic quality was disrupted by GxEs (see Fig. 3a). In heterogeneous environments, GxEs can disrupt male sexual signal reliability and so weaken selection for female mating preferences, but conversely, environmental fluctuations can help maintain genetic variation and so maintain the advantages of mating preferences. A single model that includes both of these aspects would be enlightening.

Many aspects of sexual selection have been examined in quantitative genetics models, and many of these are built on Lande's (1981) original polygenic model. However, quantitative genetic modelling has yet to be applied directly to the role of GxEs in sexual selection. Arguably, the existing quantitative genetics models of sexual selection, combined with methods that have been developed for modelling GxEs (e.g. Nussey *et al.*, 2007), contain all the relevant details that need to be brought together to examine GxEs in sexual selection. Alternatively, new models that integrate tests of signal reliability and maintenance of genetic variation together would be useful, as would polygenic models which can account for male and female sexual trait coevolution in the context of GxEs. The nature of these traits means that quantitative genetics coupled with computer simulations could be another useful direction for theoretical research.

Currently however, existing theoretical models have explored the role of GxEs in sexual selection far more comprehensively than empirical research in this field. While the existing models provide us with a number of predictions on how GxEs might influence genetic variation in sexual traits and the reliability of sexual signalling, the field would benefit greatly from empirical tests of these predictions, as well as tests of the underlying assumptions of these models.

GxEs and population divergence

Given that speciation can be driven by local adaptation to different environmental conditions (Bush, 1975), it follows that GxEs in naturally selected traits could affect this process. If a population is subdivided and then subject to different environmental conditions, local selection will drive the evolution of genetic differences between populations, potentially leading to speciation (Wade, 2000). The potential role of GxEs in this process appears to depend strongly on whether there is gene flow between isolated populations. Where gene flow does occur, GxEs could act as a constraint on local adaptation (Via & Lande, 1985) and slow the rate of population divergence, particularly with disruptive selection acting between environments. This has been demonstrated empirically in experimental meta-populations of *T. castaneum* (Wade, 1990). However, the potential for GxEs to act as a constraint will be determined by the immigration of genes from other environments, as well as the relative strength of selection and the strength of the GxE. In the absence of gene flow between populations, this constraint is removed and genetic divergence should proceed (Wade, 2000).

Sexual selection has also been implicated in population divergence because of the strong potential for sexual selection on male sexual traits or female mating preferences to cause reproductive isolation (West-Eberhard, 1983). It is therefore likely that GxEs in sexual traits or mating preferences might also affect speciation but, in spite of this, this possibility has not been studied in any depth. Again, as the traits in question are polygenic, quantitative genetic models are ideally needed to account for the co-evolution of male and female sexual traits. Furthermore, like models of speciation with GxEs in naturally selected traits, gene flow between separated populations is likely to be important. For instance, GxEs in sexual traits combined with high levels of gene flow between populations will compromise the reliability of sexual signals, weakening selection for female mating preferences, as described previously. As a consequence, the presence of GxEs in sexual traits could act as a constraint on the evolution of reproductive isolation. Indeed, Etges *et al.* (2007) found that GxEs in the male courtship song of *Drosophila mojavensis* might slow population divergence because of the disruption of sexual signal reliability. However, without further attention, it is impossible to fully understand the complex ways that GxEs might affect reproductive isolation.

Empirical studies of GxEs in sexual selection

As a result of recent increased interest in the role of GxEs in sexually selected traits, there is a slowly growing body of empirical work examining the effect of genetic and environmental factors on sexual trait expression. We summarize some of these studies in Table 1. This is

unlikely to represent an exhaustive list of studies which have had the potential to test for GxEs in sexual traits, as negative results may not have been published. Most studies appear to have focussed on the identification of GxEs in the expression of male sexual traits (e.g. David *et al.*, 2000; Etges *et al.*, 2007; Engqvist, 2008; Morrow *et al.*, 2008). Table 1 illustrates that GxEs in male sexual traits are apparently common and found across a wide range of species, although notably not ubiquitous (see Miller & Brooks, 2005; Kemp & Rutowski, 2007). Furthermore, it is clear that GxEs frequently cause ecological crossover of reaction norms across environments, although as discussed previously, this does not necessarily indicate a strong influence of the GxE interaction on sexual trait evolution. The breadth of studies identifying GxEs in male sexual traits is in contrast to the mere two studies to date which have directly tested and found GxEs in female mate preference, both of which have involved laboratory model insect species: the lesser waxmoth, *Achroia grisella* (Rodriguez & Greenfield, 2003), and the fruit fly, *D. melanogaster* (C. Narraway *et al.*, unpubl. data). The latter study further demonstrated that the genetic variance underlying female preferences differed between environments.

It is also clear from Table 1 that research so far has primarily focussed on testing how trait expression is affected by abiotic environmental factors. For example, Olvido & Mousseau (1995) found significant GxEs for calling rate and call duration in male crickets (*Allonemobius fasciatus*) dependent on rearing temperature and photoperiod, and Jia *et al.* (2000) showed that the pulse rate of the acoustic signal in male *A. grisella* exhibited significant GxEs depending on both rearing temperature and food quality.

A few studies have, however, begun to consider the effect of biotic environmental factors (Table 1), which is reassuring because the biotic environment is probably subject to greater and more rapid change than the abiotic environment (Wolf *et al.*, 1999) and therefore likely to have a stronger influence on sexual selection. However, manipulation of the biotic environment has often involved altering density (e.g. Morrow *et al.*, 2008) or brood size (e.g. Mills *et al.*, 2007), and while these studies demonstrate GxEs in the male sexually selected traits examined, it is difficult to determine precisely what is causing the variation in the male trait: it could either be a direct consequence of social interactions or an indirect result of reduced food availability. This distinction between social environment and other environments is likely to be important, as different evolutionary dynamics might be caused by social environmental factors, which have a genotype and are subject to selection. However, a recent study by Kent *et al.* (2008) explicitly tested the effect of both abiotic and biotic environmental variations using *D. melanogaster* isofemale lines under different light cycles and different social environments. They found that

Table 1 Summary of some studies from the last 15 years which have tested genetic and environmental effects on sexual trait expression and/or the fitness consequences of potential GxEs in sexual traits.

Species	Environmental variable(s) manipulated	Breeding design	GxE in sexual trait	Ecological crossover	Fitness consequences	Reference
Bank vole (<i>Clethrionomys glareolus</i>)	Litter size	Full-sibling design	Yes- male testosterone levels (determine dominance)	No	Yes- indirect benefits to male offspring only in constant environments	Millis <i>et al.</i> (2007)
Coal tit (<i>Parus ater</i>)	Early/late in breeding season	Maternal half-sibling design	Not tested	-	Yes- indirect benefits to offspring only late in the season	Schmoll <i>et al.</i> (2005)
Collared flycatcher (<i>Ficedula albicollis</i>)	Year of study; brood size	Parent-offspring regression	Not tested	-	Yes- indirect benefits to sons (inheritance of attractive traits from father) only in favourable conditions	Qvarnström (1999)
Collared flycatcher (<i>Ficedula albicollis</i>)	Year of study	Parent-offspring regression	Not tested	-	Yes- indirect benefits of mating attractive	Hegyí <i>et al.</i> (2006)
Fruit fly (<i>Drosophila melanogaster</i>)	Host plant	Divergent populations	Yes- male courtship song traits	Yes	males varied between years	Etges <i>et al.</i> (2007)
Fruit fly (<i>Drosophila melanogaster</i>)	Photoperiod; social environment	Inbred lines	Yes- composition of cuticular hydrocarbons (male sexual signals)	Yes	Not tested	Kent <i>et al.</i> (2008)
Fruit fly (<i>D. melanogaster</i>)	Larval density	Inbred lines	Yes- sperm length	Yes	Not tested	Morrow <i>et al.</i> (2008)
Fruit fly (<i>D. melanogaster</i>)	Larval temperature (cold-shock)	Inbred lines	Yes- female mating preference intensity	Yes	Not tested	Narraway <i>et al.</i> (unpubl. data)
Gray tree frog (<i>Hyla versicolor</i>)	Tadpole density	Maternal half-sibling design	Not tested	-	Yes- female mate choice only conferred benefits in certain environmental conditions	Welch (2003)
Guppy (<i>Poecilia reticulata</i>)	Food quality	Full-sibling design	Yes- male carotenoid pigmentation	Yes	Not tested	Grether (2000)
Guppy (<i>Poecilia reticulata</i>)	Social environment	Full-sibling design	No- tested male pigmentation and display behaviour	No	Not tested	Miller & Brooks (2005)
Lesser waxmoth (<i>Achroia grisella</i>)	Larval density, food quality, temperature and photoperiod	Full-sibling design	Yes- pulse rate of male acoustic sexual signal	Yes	Not tested	Jia <i>et al.</i> (2000)
Lesser waxmoth (<i>A. grisella</i>)	Rearing temperature	Full-sibling design	Yes- female mating preferences	Yes	Yes- threshold for female mating preference differed between environments	Rodriguez & Greenfield (2003)
Lesser waxmoth (<i>A. grisella</i>)	Larval density	Inbred lines	Yes- male acoustic sexual signal	Yes	Not tested	Danielson-François <i>et al.</i> (2006)

Table 1 (Continued)

Species	Environmental variable(s) manipulated	Breeding design	GxE in sexual trait	Ecological crossover	Fitness consequences	Reference
Lesser waxmoth (<i>A. grisella</i>)	Larval competitive environment	Inbred lines	Not tested	–	Yes- indirect benefits of attractive males were dependent on environment	Danielson-François <i>et al.</i> (2009)
Orange sulphur butterfly (<i>Colias eurytheme</i>)	Larval food quality; temperature	Full-sibling design	No- tested male wing pigmentation	No	Not tested	Kemp & Rutowski (2007)
Scorpionfly (<i>Panorpa cognata</i>)	Larval food availability	Full-sibling design	Yes- male sperm transfer rate	Yes	Not tested	Engqvist (2008)
Stalk-eyed fly (<i>Cyrtodopsis dalmanni</i>)	Larval food quality	Full-sibling design	Yes- male eye span	No	Not tested	David <i>et al.</i> (2000)
Sticklebacks (<i>Gasterosteus aculeatus</i>)	Light environment	Paternal half-sibling design	Yes- male pigmentation	Yes	Not tested	Lewandowski & Boughman (2008)
Striped ground crickets (<i>Allonemobius fasciatus</i>)	Rearing temperature; photoperiod	Full-sibling design	Yes- male calling rate and duration	Yes	Not tested	Olvido & Mousseau (1995)

GxE, genotype-by-environment interaction.

the composition of cuticular hydrocarbons (CHCs), which act as male sexual signals in this species, exhibits significant GxEs with both the abiotic (i.e. light : dark cycle) and social (i.e. social competitors) environmental factors examined.

Another interesting pattern that emerges from the empirical studies on GxEs presented in Table 1 is the diversity of breeding designs used to account for the genetic component of sexual trait expression. Although a single given breeding design is not always amenable to all study species, it is important to recognize that these designs differ markedly in the quality of information they provide on GxEs. For example, some studies have quantified GxEs by regressing the sexual trait of the father against that of the son when expressed in alternate environments (i.e. parent–offspring regression) (e.g. Qvarnström, 1999). Other studies have measured genetic divergence between isolated populations under different environmental conditions to test for GxEs (e.g. Olvido & Mousseau, 1995) or have used either a full-sibling breeding design (e.g. Etges *et al.*, 2007) or isofemale (inbred) lines (e.g. Danielson-François *et al.*, 2006) (Table 1). The limitation of these approaches is that while they show that genes differ in their expression across environments, they are unable to differentiate between genes with an additive effect from those that have a nonadditive effect (i.e. dominance and/or epistasis) (Lynch & Walsh, 1998). Most quantitative genetic models that examine the evolutionary implications of GxEs are based on additive genetic variance (e.g. Via & Lande, 1985), and as such, if empirical results are to be directly linked to existing theory, they should make this distinction also. Of the variety of breeding designs shown in Table 1, only the paternal half-sibling design is able to partition the effects of additive and nonadditive genetic variance on the expression of sexual traits in alternate environments (Lynch & Walsh, 1998).

As well as the breeding design, another consideration when designing experiments should be the substantial statistical power which will be needed to detect a GxE interaction. In Table 2, we have extracted standardized effect sizes, where possible, from the studies cited in Table 1 which identify GxE interactions. GxE effect sizes are clearly very small. In fact, the effect sizes we found are generally slightly lower than those found for ‘good genes’ effect sizes by Møller & Alatalo (1999), who used similar methods to calculate the effect sizes from sexual selection studies. As testing for GxEs generally involves measurement of how much phenotypic variation is attributed to the interaction between environmental and genetic factors, they will be subject to a lot of noise, and so to detect a significant GxE of such a small effect size will require large studies with high statistical power.

Table 1 also highlights the extensive empirical research conducted on GxEs in the waxmoth, *A. grisella*. Not only have GxEs been identified in male sexual traits (e.g. male acoustic sexual signals; Danielson-François *et al.*, 2006),

Table 2 Effect sizes of GxE interactions identified in some of the studies shown in Table 1.

Species	Sexual trait	<i>P</i> value	Effect size*	References
Bank vole (<i>Clethrionomys glareolus</i>)	Male dominance	0.006	0.017	Mills <i>et al.</i> (2007)
Fruit fly (<i>Drosophila mojavensis</i>)	Male acoustic signal	0.006†	0.009	Etges <i>et al.</i> (2007)
Fruit fly (<i>Drosophila melanogaster</i>)	Male cuticular hydrocarbons	0.2138†	0.046	Kent <i>et al.</i> (2008)
Fruit fly (<i>D. melanogaster</i>)	Female mate choice	0.0001	0.006	Narraway <i>et al.</i> (unpubl. data)
Guppy (<i>Poecilia reticulata</i>)	Male pigmentation	0.077†	0.015	Grether (2000)
Lesser waxmoth (<i>Achroia grisella</i>)	Female mate choice	0.013	0.008	Rodriguez & Greenfield (2003)
Lesser waxmoth (<i>A. grisella</i>)	Male acoustic signal	0.035	0.003	Danielson-François <i>et al.</i> (2006)
Scorpionfly (<i>Panorpa cognata</i>)	Male sperm transfer rate	0.016	0.013	Engqvist (2008)
Stalk-eyed fly (<i>Cyrtodiopsis dalmanni</i>)	Male eye span	0.0001	0.013	David <i>et al.</i> (2000)
Sticklebacks (<i>Gasterosteus aculeatus</i>)	Male pigmentation	0.059†	0.007	Lewandowski & Boughman (2008)

GxE, genotype-by-environment interaction.

*Effect size, *r*, calculated from standardized *z* values [see method described in Rosenthal (1991)].

†Average *P* value of multiple sexual traits measured in the study.

but the first positive identification of a GxE in female mate choice was demonstrated in this system (Rodriguez & Greenfield, 2003) and remains to date one of only two studies demonstrating that GxEs in female mating preferences exist (see also C. Narraway *et al.*, unpubl. data). Furthermore, although a few studies have considered the fitness consequences of potential GxEs, this is the only system in which GxEs in sexual traits have been studied in any depth. Having identified GxEs in both male sexual traits and female mating preferences (Rodriguez & Greenfield, 2003; Danielson-François *et al.*, 2006), research then began to consider the role of GxEs in sexual selection. The potential of GxEs to facilitate the maintenance of variation in male sexually selected traits has been demonstrated (Jia *et al.*, 2000), and it has also been shown that GxEs can alter the fitness consequences of mate choice (Jia & Greenfield, 1997; Danielson-François *et al.*, 2009). This is an important finding and highlights that whilst demonstrating that GxEs exist for sexual traits is an essential starting point for determining the role of GxEs in sexual selection, the next step is to test whether these GxEs alter the fitness consequences of female mate choice. Few of the studies in Table 1 have considered the effects GxEs in male sexual traits have on female mate choice and the possible benefits gained by the female. Furthermore, those which have assessed the fitness consequences have only focussed on indirect benefits (e.g. Qvarnström, 1999; Welch, 2003), and as discussed previously, it is possible that GxEs could also affect the relationship between a male sexual signal and the direct benefits he can offer a female.

These studies show that GxEs can often cause the indirect benefits of mate choice to be dependent on environmental variation, and as a result, GxEs are likely to be highly influential in the evolution of female mating preferences. With knowledge of the frequency of GxEs in male sexual traits and how they might influence fitness, more complex evolutionary questions can then be addressed, concerning the identification of GxEs for

female mating preferences, and the effect of GxEs on the co-evolutionary dynamics between female preference and male sexual traits.

Future directions

Further research on GxEs in sexual selection needs to begin by focussing on female mating preferences, as these have largely been neglected in studies so far. The lack of research on this subject could be in part attributed to the poor understanding of the evolution and genetics of female mate choice in general (Bakker, 1999; Mead & Arnold, 2004). Empirical data on GxEs in female mating preferences will first allow us to determine whether GxEs are as strong and as widespread as the interactions already documented for many male sexually selected traits. There are only two studies that have identified GxEs in female mating preferences, one in the lesser waxmoth (Rodriguez & Greenfield, 2003) and one in *D. melanogaster* (C. Narraway *et al.*, unpubl. data). The potential for GxEs in female mate choice has largely been ignored to date and could represent another way (in addition to unreliable male sexual signals) in which females could make the 'wrong' mating decision and fail to gain benefits from mate choice. The fitness consequences of a mating decision should drive the evolution of mate choice, and as such, it is likely that GxEs in sexual traits could have a strong impact on the evolution of mate preferences. It is also possible that female preferences demonstrate adaptive plasticity (Shuster & Wade, 2003) and vary between environments such that preferences track variation in male signals across environments. This possibility requires additional research as so far the influence of GxEs on the adaptive plasticity of mating preferences has only been assessed in female waxmoths (Rodriguez & Greenfield, 2003).

Once the occurrence and strength of GxEs has been identified in both male sexual traits and female mating preferences, research should focus on testing the

potential roles of GxEs in sexual selection and in the evolution of sexual traits and mating preferences. With this aim in mind, we have outlined the following possible avenues for future research. We discuss: (1) why it is important that research integrates male and female sexual traits in GxE studies to consider sexual trait coevolution, (2) gaps in our understanding of how abiotic environmental variation might affect sexual trait expression, (3) the influence of biotic environmental factors and social environment on sexual trait expression, (4) the relevance of the 'strength' of GxE interactions and (5) the potential for future research into the genetic mechanisms which underlie GxEs. We hope to emphasize how these research directions could support the existing theory and further develop our understanding of the role of GxEs in sexual selection.

Integration of male and female traits

Mating involves an interaction between a male and female through sexual signalling and a mate-choice response, and because these male and female traits are expected to co-evolve, incorporating both into one study is essential to understand evolutionary dynamics. So far, neither modelling nor empirical studies of GxEs have fully attempted this. From a modelling perspective, the existing single-locus models of GxEs in sexual selection represent a good start, but these models remain inadequate because the traits in question are likely to be polygenic. The utility of quantitative genetic models in the study of sexual selection is illustrated by a direct comparison between the one or two loci models of O'Donald (1980), which demonstrated linkage building up between male sexual signal and female preference traits, with Lande's (1981) polygenic model, which not only showed this but additionally was able to fully demonstrate Fisher's runaway process. Quantitative genetics are necessary to incorporate patterns of both inheritance and selection on continuously varying traits into models, which is vital when modelling the coevolution of sexual signal and preference traits (Mead & Arnold, 2004). More realistic multilocus models should also be used to examine how GxEs affect the expression of both male and female sexual traits and how this, in turn, affects the interaction between the individuals during mate choice. If GxEs exist in the expression of either the male sexual trait or the female mating preference, then the co-evolution of the two traits could be strongly disrupted by environmental heterogeneity, particularly in the light of the results of the recent models which have demonstrated how GxEs can affect sexual signal reliability and levels of genetic variation in sexual traits.

Empirical studies that integrate GxEs in male sexual traits and female mating preferences could specifically test how GxEs influence the coevolution of male and female sexual traits by assessing genetic associations

between the two. Empiricists should also evaluate the extent to which sexual signal reliability is disrupted or otherwise altered by GxEs, and the role this might have in the evolution of female mating preferences and on the fitness consequences of mate choice.

Abiotic environmental variation

Our review of the empirical literature clearly illustrates that most studies of GxEs in sexual selection have looked for interactions between abiotic environmental factors and the expression of male sexual traits, and there is compelling evidence from a number of species that such GxEs exist. However, these studies should now be developed to directly address the assumptions and predictions of theory. For example, Gillespie & Turelli (1989) pointed out that to thoroughly test for maintenance of genetic variation in traits with GxEs, a broad range of environmental variables should be investigated, as there is a risk of failing to detect an effect when studying limited environmental heterogeneity. Identifying GxEs based on multivariate environments might be useful for a number of other reasons, including making studies more realistic and enhancing our ability to identify interactions between environmental variables that affect trait expression.

Additionally, an explicit prediction made by Higginson & Reader (2009) is that sexual signals should become less reliable with increasingly harsh developmental environments. Indeed, Charmantier & Garant's (2005) meta-analysis suggested that genetic variation is depleted in wild populations under harsh environmental conditions, which could contribute to unreliable sexual signals. However, it is also thought that in particularly harsh environments, only high-quality males are able to afford the costs of exaggerated sexual signals, illustrating Zahavi's handicap principle and how the honesty of sexual signals can be enforced (Hoffmann & Merilä, 1999). It is clear that whilst GxEs have been identified, we are still unsure of how trait expression is affected by relative degrees of environmental heterogeneity along one axis of environmental variation, and what the consequences of this are for signal reliability. By widening the range of environments employed in an empirical study, it should be possible to quantify the effects and strengths of GxEs and relate these results to existing models.

Biotic environmental variation and social environments

Previous research has also largely been limited to identifying GxEs in sexual traits that result from variation in abiotic environmental factors. These abiotic factors are probably the simplest to manipulate experimentally, but the paucity of studies examining biotic environmental factors, and especially social environmental factors, is

surprising as sexual selection typically involves male–male competition, female choice of mates and/or sexual conflict, all of which involve social interactions. It therefore follows that the outcome of sexual selection will be influenced by the surrounding biotic and social context and that this effect could be strong given the potential for these biotic environmental factors to vary widely over relatively short timescales (Wolf *et al.*, 1999).

In fact, there are many empirical studies which demonstrate that variation in social environment can indeed affect female mating preferences, which illustrates adaptive plasticity of preference, although not explicitly testing for GxEs. These studies generally focus on the effect of a female's previous social experiences; for example, copying the mating preferences of other females (e.g. White & Galef, 2000), or expressing preference for males with 'familiar' phenotypes to those which they have experienced or interacted with previously (e.g. Hebets, 2003; Dukas, 2008). These studies represent a diverse range of species and suggest that an effect of social environment on mating preferences could be common. Furthermore, work on the field cricket *Teleogryllus oceanicus* has not only demonstrated that previous social environment can affect mating preferences but has also showed how this affects the outcome of sexual selection through changing the female's preference function and mate choice strategy (Bailey & Zuk, 2008, 2009). These studies clearly demonstrate that female mating preferences can be strengthened or weakened dependent on the social environment experienced by the focal individual.

The importance of social environment is further highlighted by recent work on indirect genetic effects (IGEs), where the phenotypic expression of a focal individual is affected by interactions with conspecifics, be these parents, siblings or unrelated conspecifics (Wolf *et al.*, 1998). There is a considerable body of evidence showing that IGEs are important in sexual selection and the evolution of mating preferences (reviewed by Miller & Moore, 2007). Furthermore, modelling has shown that evolutionary dynamics can be dramatically altered when IGEs are taken into consideration (e.g. Wolf *et al.*, 2008) and that this seems to be attributed to two effects that arise when environmental variation is heritable. First, the environment itself will be subject to selection as well as causing selection on the focal individual, and secondly, IGEs can alter the covariance between genotype and phenotype. This covariance is important as it defines how phenotypic selection is translated into changes in gene frequency and thus evolution (Wolf *et al.*, 1998).

The distinction between GxEs for social environment and IGEs will depend partly on the question being studied (see Wolf *et al.*, 2004 and Wolf & Moore, 2010 for more in-depth discussion). Arguably, the theory developed for IGEs could generally be applied to genotype-by-social environment interactions for sexual traits.

However, GxEs describe particular cases where trait expression in the focal individual is not only dependent on the genotypes of surrounding conspecifics (i.e. the social environment) but also on the genotype of the focal individual itself, because a GxE for social environment describes variation between focal genotypes in their response to variation in the social environment. This added layer of complexity may mean that predictions about the effects of genotype-by-social environment interactions on sexual traits are slightly different than those concerning the effect of IGEs.

GxEs for biotic environmental variation are also somewhat more general than the GxEs for social environment and IGEs. An important point is that whereas social environment covers the influence of interacting individuals of the same species as the focal individual, GxEs can involve interactions with other species in the environment. Interactions with other species could affect the phenotypic expression of a sexual trait, as illustrated in the earlier example of male stickleback pigmentation as a signal of male resistance to parasites, which females use during mate choice. There are no studies of GxEs in sexual traits which have directly addressed the effect of biotic interactions with other species, such as parasite prevalence or nonconspecific competitors for resources. However, a few studies have recognized the importance of biotic environment and have attempted to test for GxEs in male sexual traits through manipulation of biotic environmental variables. For example, Welch (2003) manipulated population density, which might alter the intensity of competition or levels of mate availability. However, there is the potential to confound biotic factors, such as competition, with abiotic factors, such as food availability, and this may mean that more direct tests of the effect of social interactions through manipulation of the social environment (*sensu* Kent *et al.*, 2008) may be more revealing. As the outcome of a female's mating decision is based mainly on behavioural responses and the signalling interaction between the male and female, more studies are required if we are to understand how social environments might affect the evolution of sexual traits where GxEs exist.

The 'strength' of a GxE interaction

As discussed previously, sexual selection models of GxEs have made a distinction between 'strong' GxEs which have ecological crossover of reaction norms, and 'weak' GxEs which do not (Kokko & Heubel, 2008; Higginson & Reader, 2009). This has enabled theoretical predictions to be based on an assumption of the strength of the influence a GxE has on trait expression; however, the distinction between these 'types' of GxE does not translate easily into an empirical programme. A 'strong' GxE under this definition might have very little effect on sexual selection if there is low genetic variation for the traits in question, whereas a 'weak' GxE could be

hugely important where there is a lot of genetic variation.

Empirically, it might be more useful to estimate the 'strength' of a GxE interaction as some measure of the genetic effect size of the interaction, or as some measure of the genetic variation between environments. To more easily apply some measure of interaction 'strength' to empirical studies, we could consider trait heritability between environments, the relative gradients of reactions norms, or even the genetic effect size of the interaction directly. Alternatively, quantification of the strength of an interaction might involve measuring genetic correlation of sexual traits between environments, or measuring the covariance between male and female sexual traits, but this again is something that requires further assessment. The 'strength' of a GxE should be measured in terms which are comparable and can easily relate empiricism to theory. In doing so, there is the potential to test whether the 'strength' of the GxE interaction is important in the outcome of sexual selection.

The mechanistic basis of GxEs

The research directions suggested earlier largely aim to improve understanding of the evolutionary consequences of GxEs in sexual traits. However, to fully explore the role of GxEs in sexual selection, insight into the genetic mechanisms which underlie GxEs will also be necessary. To this end, research into GxEs in sexual selection can begin to make use of what is already known about the genetics of sexual traits, although research in this field has so far largely focussed only on male sexual traits (reviewed by Emmons & Lipton, 2003). This information could be used in studies which look at the genetic control of differential gene expression between environments, which is indeed beginning to be investigated in naturally selected traits in yeast, *Saccharomyces cerevisiae* (Landry *et al.*, 2006), and the nematode worm, *Caenorhabditis elegans* (Shook & Johnson, 1999; Li *et al.*, 2006). DNA microarrays have been used to identify quantitative trait loci for plasticity of expression in traits which are known to have GxEs. These genomic techniques could similarly be applied to test for pleiotropy and epistatic gene interactions in the expression of sexual traits with GxEs, both of which have the potential to control the genetic mechanism behind GxEs in phenotypic trait expression.

Conclusions

In conclusion, research into the effect of GxEs on sexual selection has to date primarily concentrated on identifying GxEs in male sexual traits and making predictions based on models of the effects these GxEs might have on sexual selection. Research now needs to test more thoroughly for GxEs in female mating preferences and

then move on to evaluating the theoretical implications of GxEs, such as how GxEs affect sexual signalling and genetic variance, and ultimately the influence they might have on the co-evolution of male and female sexual traits. We have suggested that advances in this field of research will involve theoretical progress, through quantitative genetics models, and empirical progress, through dedicated research programmes similar to that applied to the lesser waxmoth, where GxEs in both male and female traits are identified, and the specific effects of these GxEs on sexual trait co-evolution can be quantified. With this aim in mind, we have detailed five potential research directions which we feel are important to increase understanding of the role of GxEs in sexual selection. The last 30 years of sexual selection research has largely been about documenting sexual selection and its mechanisms. It is now time to move beyond this and to consider more complex scenarios and how they influence sexual selection and sexual trait evolution.

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