Genotype-by-Environment Interactions and Sexual Selection in Guppies

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12.1 Introduction

12.1.1 Overview

No species is more prolific in the diversity of phenotypic and genetic responses to the environment than the guppy (Poecilia reticulata), a tropical freshwater fish that has long captivated biologists (Endler, 1995; Houde, 1997; Magurran, 2005). Studies of guppies are therefore expected to yield valuable empirical counterparts to the theoretical work on genotype-by-environment interactions (GEI; Chapter 2). In this chapter, I briefly introduce GEI and the models that predict how GEI influences variation in sexually selected traits. I then review the guppy system in light of the theoretical framework, by describing the traits important for sexual selection, the patterns of selection acting on those traits, and fluctuation in the environments to which the traits are subject. The theme that emerges is that there is evidence for all of the elements needed for GEI to influence variation in sexually selected traits in this system: guppies exhibit substantial genetic variation and plastic responses to the environment for a host of traits under strong selection, and individuals frequently encounter temporally and spatially varying environmental conditions. However, surprisingly few studies have uncovered GEI for sexually selected traits in this species, and there is a paucity of studies addressing whether GEI primarily acts to maintain or erode the strength of sexual selection. I suggest broad approaches that could be fruitful areas for future research on GEI and sexual selection in this charismatic species.
12.1.2 Phenotypic responses to environmental variation

Plasticity and GEI

Phenotypic plasticity, the production of multiple phenotypes by a given genotype in response to environmental variation, is ubiquitous across taxa and traits and is usually depicted as non-zero-sloped reaction norms (Dingemanse et al. 2009; Kelly et al. 2012; Figure 12.1; Scheiner, 1993; West-Eberhard, 1989). Adaptive phenotypic plasticity may allow individuals to broaden their ecological niches and facilitate evolutionary change by generating phenotypes that encompass those favored by selection (Ghalambor et al., 2007). Sexually selected traits are expected to be especially plastic because they are closely linked to condition (Price, 2006); however, adaptive plasticity can only evolve if its benefits sufficiently mitigate the costs (DeWitt et al., 1998; Ghalambor et al., 2007). Plasticity may be costly if information about the environment is unreliable or if phenotypic change is difficult (DeWitt et al., 1998; Hughes et al., 2002; also see Rodd &

Fig. 12.1 A generalized illustration of reaction norms for sexually selected traits. Each line represents a different genotype. The X-axis represents two environments, either in space or across time; the Y-axis represents the magnitude of a sexually selected trait (including the strength of preference for sexual displays). Panel (a) depicts a scenario in which there is no phenotypic plasticity but in which there is genetic variation in the mean phenotypic value. Panel (b) depicts a scenario with phenotypic plasticity, but without GEI (i.e., no variation among genotypes in the magnitude of the response). Panels (c) and (d) depict scenarios with GEI (with ecological crossover); Panel (c) depicts plasticity in the population mean value, and Panel (d) depicts no such plasticity. If the Y-axis depicts behavior, then Panels (a) and (b) illustrate behavioral syndromes.
Sokolowski, 1995), and may therefore be more common when it is particularly advantageous, such as in highly variable environments (Komers, 1997). Differences in the degree of plasticity among genotypes result in GEI (non-parallel reaction norms in Figure 12.1). GEI may reflect differences in quality among genotypes if higher quality genotypes are better able to exhibit adaptively flexible responses to a naturally occurring range of environments.

The pattern and magnitude of phenotypic plasticity are influenced by both the environment axis and the trait value axis of reaction norm plots. A more rigid set of conditions is required for plasticity to evolve in fixed traits such as structural ornaments, whose trajectory is established during development (Hughes et al., 2002; Scheiner, 1993) than in labile traits such as behavioral displays, which may be influenced by the environment throughout an individual’s lifetime (Ghalambor et al., 2010; West-Eberhard, 1989). I use “behavioral flexibility” to distinguish reversible behavioral traits from the fixed responses to the environment experienced during development (Dingemanse et al., 2009; Piersma & Drent, 2003).

In all cases, sufficient genetic variation for the trait must exist for plasticity to differ among genotypes such that GEI results (Ingleby et al., 2010). The range of environmental conditions also determines the phenotypic response pattern. If the y-axis in Figure 12.1 depicts a trait strongly related to fitness, then when the lines intersect within the range of environments examined (Figure 12.1c), the GEI involves ecological crossover, a situation which may be essential for GEI to maintain additive genetic variation as described below (Greenfield et al., 2012; Hughes et al., 2005; Kokko & Heubel, 2008; Rodriguez & Greenfield, 2003).

If the treatments in an experiment encompass the natural environmental range then GEI with crossover may represent a stronger response to the environment; otherwise, the distinction is less significant than whether the slopes differ at all (Boake, 1994; Ingleby et al., 2010).

**Demonstrating GEI**

The most effective method for establishing GEI within a population involves breeding experiments in which siblings from different families experience each environment, with a significant family-by-treatment interaction constituting evidence for GEI. This approach requires high statistical power to detect the interaction (e.g., Hughes et al., 2005; Ingleby et al., 2010; Miller & Brooks, 2005; Rodriguez & Greenfield, 2003). Assessing GEI for behavioral flexibility also requires a repeated measures or paired statistical design, and order effects may be substantial (Bell, 2013; Bretman et al., 2011; Dochtermann, 2010). However, studies of behavioral flexibility can be especially powerful if they simultaneously assess performance across developmental and adult environments. For example, by subjecting male guppies (*Poecilia reticulata*) to different light levels during development and testing courtship behavior under different light levels as adults, Chapman et al. (2009) were able to show that courtship is adjusted to testing but not rearing conditions.

A related approach for studying GEI involves comparing the degree of plasticity across isolated populations rather than across families (e.g., Bretman et al., 2011; Kolluru & Grether, 2005; Rodd & Sokolowski, 1995). In a depiction of
this population level GEI, each line in the reaction norm plot represents a pop-
ulation rather than an individual (also see Grether & Kolluru, 2011). Studies
of population-level GEI typically involve a common garden design in which the
population-by-treatment interaction constitutes evidence for GEI (Klefoth et al.,
2012; Kolluru & Grether, 2005; Rodd & Sokolowski, 1995). This approach
yields different information than the quantitative genetics design outlined pre-
viously, in that it indicates spatial variation in phenotypic plasticity, rather than
GEI within a population; information about the degree of movement of individ-
uals among populations is valuable for inferring whether population level GEI
influences sexual selection in the ways discussed below.

12.1.3 GEI and sexual selection

Recent attention has focused on how GEI may strengthen or weaken sexual selec-
tion (Cornwallis & Uller, 2010; Greenfield et al., 2012; Chapter 2; Hunt et al.,
2004; Ingleby et al., 2010). GEI may maintain variation for a trait in the face of
directional sexual selection that ought to weaken it (Greenfield et al. 2012; Kirk-
patrick & Ryan, 1991). GEI provides a resolution to the lek paradox because
if no one genotype is the most successful across environments that vary either
temporally or spatially (with gene flow), then low quality males will always be
present, and costly female preference will continue to be favored (Bussiere et al.,
2008; Greenfield et al., 2012; Hunt et al., 2004; Ingleby et al., 2010; Kokko &
Heubel, 2008; Rodriguez & Greenfield, 2003). The detrimental effect of GEI is
that it can lead to a mismatch between genetic quality and phenotype, leading
to mate choice errors (Kokko & Heubel, 2008; Chapter 2). Models of sexual
selection stipulate that mating signals honestly indicate male quality (and hence
offspring quality; Zahavi, 1975) or attractiveness genes (Greenfield & Rodriguez,
2004). GEI may result in a weakening of signal honesty if the male moves to a
different environment between development of the signal and its use in a mating
display, or if the environment changes during this time (Ingleby et al., 2010).

The dual effect of GEI on sexual selection has been addressed in recent models
(Higginson & Reader, 2009; reviewed by Ingleby et al., 2010, Chapter 2;
model comparing GEI with crossover to the absence of GEI, varying parameters
including the timing and magnitude of dispersal, to predict the strength of
female choice. They demonstrated that GEI can maintain female preference by
generating variation among males, but that the timing and degree of mixing of
males among environments are key: GEI combined with low levels of mixing
promotes female choice by generating diversity among males, whereas if a
larger proportion of individuals moves among environments (or if environments
change) between when condition is determined and when mating occurs, then
GEI reduces signal honesty, and thereby erodes the net benefit of female choice
and contributes to its demise (Cornwallis & Uller, 2010; Ingleby et al. 2010).
Kokko and Heubel (2008) emphasize that the positive and negative effects of
GEI do not cancel each other out, but instead that the parameters determine
whether there is a net positive or negative effect. Higginson and Reader (2009)
use a model simulating weak GEI to demonstrate that GEI caused by heterogeneity in the levels of stress experienced during development can significantly disrupt the relationship between genotype and phenotype if genetic variation is relatively low and the environment plays a significant role in determining phenotype.

What emerges from this overview is that GEI may preserve genetic variation in male display traits, and consequently maintain costly female choice, but that GEI may also obscure the relationship between male genetic quality and phenotype, such that displays are inaccurate indicators of quality and offspring fitness. Which of these forces predominates depends on the extent of environmental influence on the traits in question, and the degree of mixing of males among environments (either temporally or via gene flow; for updated discussion of these models, see Chapter 2).

Guppies are particularly amenable to addressing the influence of GEI on sexual selection because they occur in habitats that vary along multiple environmental gradients, and because they exhibit strong sexual selection for a variety of traits. It is not my intention to exhaustively review the sexual selection or ecological genetics of this system, for which excellent reviews exist (e.g., Endler, 1995; Grether, 2010; Houde, 1997; Magurran, 2005). Rather, I highlight how guppy research has informed us about plasticity and GEI, and suggest areas for future consideration. I give an overview of the guppy mating system, traits that exhibit plasticity in response to environmental variation and the environmental axes responsible. I then discuss temporal and spatial heterogeneity of guppy habitats and address the mixing of individuals among spatially varying environments.

12.2 Plasticity, GEI, and the guppy system

12.2.1 The guppy mating system

Guppies have been intensively studied with respect to the responses to environment key for generating GEI. This live-bearing poeciliid fish native to Trinidad and adjacent parts of South America exhibits internal fertilization as part of a promiscuous mating system, with no defense of resources by males or parental care, and with strong pre- and post-copulatory sexual selection (Evans, 2010; Houde, 1997; Magurran, 2005). Early studies investigated opposing natural and sexual selection on male color patterns (Houde, 1997; Magurran, 2005). Since then, interest in this species has exploded (Endler, 1995; Grether, 2010; Houde, 1997; Magurran, 2005; Meffe & Snelson, 1989). Work on predation intensity gradients in the northern range of Trinidad has been so rewarding that other drivers of plasticity and GEI have received less attention until fairly recently. These include productivity gradients (Grether et al., 2001a; Grether, 2010; Reznick et al., 2001) and temporal variation in light environments (Archard et al., 2009; Chapman et al., 2009; Endler, 1987; Gamble et al., 2003). Likewise, exciting work on feral guppy populations such as those in Japan (Karino et al., 2005; Kudo & Karino, 2012a,b), South Africa (Brooks & Caithness, 1995) and Australia (Gamble et al., 2003; Head et al., 2008; Miller
Male guppies court females using a sigmoid courtship display, hovering before females in an S-shape while exhibiting their color patterns (Figure 12.2/Plate 9); males also sneak copulations by inserting the intromittent organ (gonopodium) into the female’s gonopore without displaying, and establish their dominance status via aggressive chases, bites and male-directed displays (Houde, 1997; Kodric-Brown, 1992; Kolluru & Grether, 2005). Although individuals switch between tactics, the degree to which a male sneaks versus displays is heritable, and males that sneak more have faster sperm but are less attractive to females (Evans, 2010). Harassment by males is costly for females and their offspring (Darden & Watts, 2012; Gasparini et al., 2012; Head & Brooks, 2006; Magurran & Seghers, 1994). Females respond positively to preferred males via a glide response, a behavior correlated with the likelihood of copulating (Houde, 1997). Males also exhibit choice, and tend to prefer larger, more fecund females (Benz & Leger, 1993; Herdman et al., 2004) and novel females (Kelley et al., 1999).

12.2.2 Sexually selected traits in guppies

The theory outlined in Section 12.1.3 assumes an interaction between genetic and environmental variation in determining phenotype, and guppies satisfy this assumption for a range of traits (Blows et al., 2003; Brooks, 2002; Brooks & Endler, 2001a; Brooks & Postma, 2011; Easty et al., 2011; Elgee et al., 2012; Endler, 1980; Endler & Houde, 1995; Houde, 1997; Hughes et al., 1999; 2005; Kudo & Karino, 2012a,b; Miller & Brooks, 2005; Ruell et al., 2013). Arguably the most important of these is coloration, a function of genotype and of the environment experienced both during development and throughout adulthood. Guppy color patterns include iridescent, structural violet-blue and green (Brooks, 2002; Grether et al., 2004a; Kemp et al., 2011), black (melanin), and yellow,
orange, and red spots resulting from the deposition of carotenoid (primarily tunaxanthin; Hudon et al., 2003) and pteridine pigments (drosopterin; Grether et al., 2001a). Because of the complexities of color signaling, such as amplification of orange spots by melanin borders, each color spot is a multicomponent trait within the larger multivariate display (Brooks & Caithness, 1996; Brooks, 2002; Grether et al., 2004a; Kemp et al., 2011).

Orange spots are the main targets of sexual selection via female choice. Variation in orange spot brightness, chroma (color saturation), and hue (wavelength) mainly result from differences in the concentrations of carotenoid and drosopterin pigments (Grether, 2005; Grether et al., 2001a; 2005a; Hudon et al., 2003; Kemp et al., 2008; Pitcher et al., 2007). Whereas drosopterins can be synthesized from carbohydrates and amino acids (Grether et al., 2005a), carotenoids must be obtained from the diet (unicellular algae), and their availability can be limited (Grether et al., 1999; 2001b). Orange spot chroma, the most important aspect for female choice, thereby honestly indicates male quality by revealing heritable algal foraging ability (Endler, 1980; Karino et al., 2005). Supplementation with carotenoids enhances chroma (see Figure 12.3/Plate 10 and Grether, 2000; Kodric-Brown, 1989), and parasite infection reduces it (Houde & Torio, 1992), also supporting the value of chroma as an indicator trait. Furthermore, carotenoid intake is correlated with the strength of the immune response (carotenoids are immune system enhancers), such that chroma may also be an indicator of the quality of the immune system (Grether et al., 2004b). However, chroma is not the sole determinant of male attractiveness. Females prefer a specific hue of orange, which appears to be maintained across populations that vary in carotenoid availability via opposing, differential drosopterin allocation (Deere et al., 2011). In other words, environmentally induced interpopulation variation in carotenoid availability is hidden by opposing genetic variation in drosopterin production, such that the phenotype (hue) appears similar across environments (Grether et al., 2005b).

Orange spots also vary in area, and in contrast to the flexible characteristics discussed previously, spot area is highly heritable (Houde, 1997). Spot area is also sexually selected and positively correlated with male quality (Elgee et al., 2012; Houde, 1997; Locatello et al., 2006; Pitcher et al., 2007; but see Kemp et al., 2011), albeit in a complex fashion: there is geographic variation in female preference for spot area, (Elgee et al., 2012; Grether, 2000; Kemp et al., 2009; Kodric-Brown, 1993), and Blows et al. (2003) revealed a multivariate preference function favoring orange/black area, iridescent/fuzzy black area, and caudal fin area.

In addition to coloration, female guppies pay attention to a range of other plastic traits, including body size (Endler & Houde, 1995; Magellan et al., 2005; Reynolds, 1993; Reynolds & Gross, 1992; Reynolds et al., 1993), lateral projection area (MacLaren & Fontaine, 2012), relative gonopodium length (Elgee et al., 2012; Gasparini et al., 2012), sexual display rate (Kodric-Brown & Nicoletto, 2001a; Matthews et al., 1997) and duration (Nicoletto, 1996), boldness towards predators (Godin & Dugatkin, 1996) and learning ability (Shohet & Watt, 2009). Female preference exhibits flexibility with age (Kodric-Brown & Nicoletto, 2001b), parasite infection (Lopez, 1999), mate choice decisions by
Fig. 12.3  Plasticity in body size and coloration in adult male guppies from the Small Crayfish River in Trinidad, raised on either the low (a–c) or high (d–f) food level, and on either the trace (a, d), medium (b, e) or high (c, f) carotenoid level. For further details see Grether, G.F., Kolluru, G.R., Rodd, F.H., de la Cerda, J., and Shimazaki, K. (2005b) Carotenoid availability affects the development of a colour-based mate preference and the sensory bias to which it is genetically linked. *Proceedings of The Royal Society of London B* 272: 2181–2188. For color details, please see Plate 10.

other females (e.g., Godin *et al.* 2005), diet (Grether *et al.*, 2005b), and experience with male phenotypes (Breden *et al.*, 1995; Magurran, 2005; Rosenqvist & Houde, 1997). The latter includes the finding that females who see males with a range of orange spot areas during development subsequently exhibit stronger preference for high spot area than females that see males of uniform spot area (whether low or high; Rosenqvist & Houde, 1997).

12.2.3 Environmental influences on sexually selected guppy traits

As emphasized by the models discussed in Section 12.1.3, environmental heterogeneity is important for both the strengthening and weakening effects of GEI on sexual selection. The guppy system epitomizes the requirement of those models for environmental heterogeneity within and among populations. In this section, I describe the major axes of environmental variation experienced by guppies in Trinidad (Magurran, 2005): predation intensity, resource availability, light environment, social environment, and demography.
Predation intensity

Portions of Trinidadian guppy streams may be isolated from one another by waterfalls, which are barriers for the movement of predatory fish and which also restrict guppy movement upstream (Crispo et al., 2006). Downstream regions are therefore home to a variety of predators that are unable to cross the barrier waterfalls to colonize the upper reaches, leading to a repeated pattern of low predation intensity in the headwaters of streams and high predation intensity in the lower reaches (Endler, 1978; Magurran 2005; Reznick et al. 1996; Weese et al. 2011). In the low predation sites the primary predator is the gape-limited killifish Rivulus hartii, a relatively minor threat to guppies (Houde, 1997; Magurran, 2005; Reznick et al., 1996). In the high predation sites the pike cichlid Crenicichla alta and associated fish and crustaceans selectively prey on adults (reviewed in Endler, 1995; Magurran, 2005; Reznick et al., 1996). Although other predators such as the prawn, Macrobrachium crenulatum, have influenced guppy evolution (De Serrano et al., 2012; Kemp et al., 2008; Millar et al., 2006), fish have been the focus of most studies.

Predation intensity influences coloration, the most important target of sexual selection in guppies. Correlational studies suggest that males are more colorful in low predation sites (Endler, 1978; Millar et al., 2006), and a recent manipulation experiment showed that color elements are plasticly reduced in response to chemical predator cues experienced during development (Ruell et al., 2013), supporting the idea that coloration represents a balance between sexual selection favoring conspicuousness and natural selection acting against it (Endler, 1980). The correlational data have been corroborated using introduction experiments, in which guppies were moved from high predation to low predation sites, and the pattern and speed of evolution examined (Easty et al., 2011; Endler, 1980; Kemp et al., 2009). Some studies reveal remarkably rapid increases in conspicuousness via increases in the number and size of orange spots (Endler, 1980) and iridescence (Kemp et al. 2008; 2009) under predator release. However, the situation is more complex than a simple balance between sexual and natural selection (Easty et al., 2011). For example, Weese et al. (2010) found that although mortality rates were higher in high predation sites, selection against conspicuous coloration was sometimes stronger in low predation sites. They offered several explanations for this counterintuitive pattern, including decreased sexual selection in high predation sites, and natural selection against colorful males by parasites and the relatively minor guppy predators (Rivulus fish and Macrobrachium prawns) in low predation sites.

The predation intensity axis also influences behavioral flexibility. Visually conspicuous displays are reduced in favor of sneak copulations under high-risk conditions (Archard et al., 2009; Endler, 1987; Godin, 1995; Houde, 1997; Magurran & Nowak, 1991; Magurran & Seghers, 1990; Reynolds, 1993; Reynolds et al. 1993), and males from high predation sites are more responsive to predation risk (Godin & Briggs, 1996; Magurran & Seghers, 1990; but see Archard et al., 2009). However, even in sites classified as low predation based on fish predators, there may be mortality from other visually orienting predators such as birds (reviewed in Magurran, 2005), some of which forage most actively
when light levels are high (Endler, 1987). Templeton and Shriner (2004) showed that guppies respond defensively to simulated avian attacks, and that there are differences in the response between low and high (fish) predation populations. Less attention has been paid to other aspects of male guppy mating behavior, but there is evidence for reduced aggression under high predation risk (Kelly & Godin, 2001).

Sexual selection itself may also fluctuate with predation intensity. Female guppies reduce or even reverse their preference for colorful males when predation risk is high, because of increased risk to themselves (Godin & Briggs, 1996; Gong, 1997; Gong & Gibson, 1996; Pocklington & Dill, 1995). Dill et al. (1999) demonstrated that when females alone could see a predatory cichlid, males reduced the frequency of courtship displays in a manner similar to when they themselves could see the predator, presumably in response to reduced female receptivity, suggesting that plasticity in the behavior of both sexes is important (Dill et al., 1999). Long-term sperm storage by female poeciliids may be an evolutionary response to predation risk, in that females can mate with conspicuous males when risk is low and use stored sperm for fertilizations when risk is high (Johnson & Basolo, 2003). There is evidence for population level GEI for flexibility in female preferences. Females from some low predation sites do not reduce their preference for colorful males as readily as high-predation females after seeing a predator (Godin & Briggs, 1996), whereas females from other low predation sites do (Archard et al., 2009).

**Resource availability**

Resource availability is usually an important driver of variation in sexually selected traits because of its direct effects on body size and energetically expensive behaviors. However, for guppies, the primary food source is also the primary source of carotenoid pigments, such that variation in resource availability also affects coloration. Grether and his colleagues describe a productivity gradient independent of, but concomitant with, variation in predation intensity: lower reaches of Trinidadian streams have more open canopies than their headwater counterparts, resulting in differences in primary productivity (Grether, 2000; Grether et al. 1999; 2001b; also see Reznick et al., 2001). To formally describe the productivity gradient, Grether et al. (2001b) compared phylogenetically paired low predation sites, to exclude variation due to predation regime differences (e.g., low predation guppies eat more algae; Palkovacs et al., 2009). They demonstrated that more open-canopied streams receive greater levels of photosynthetically active radiation than closed-canopy streams within the same drainage system (Grether et al., 2001b). This difference translates into greater algae availability per fish, such that guppies grow faster and males reach larger asymptotic sizes in the more open-canopied sites. Because algae are a primary food source for guppies, both food and carotenoid availability are greater in high-resource streams (Grether, 2010; Grether et al. 2001b). Varying food availability and varying carotenoid availability have both yielded complex patterns of GEI in guppies, and I address each separately in the following.
Food availability

Kolluru and Grether (2005) employed a common garden design to examine behavioral flexibility and population-level GEI as a function of food availability. They raised males from low- and high-food-availability sites on either low or high food levels and predicted a population level GEI with less flexibility among males from high resource sites, because food availability is less variable there than in low resource sites (Komers, 1997). Males from low resource sites and males raised on low food foraged more than their high food counterparts, and males from all sites were less aggressive when raised on low food. These results suggest a flexible adjustment of current reproductive effort (male–male aggression) and investment into future reproduction (foraging) with food intake. There was also GEI for courtship displays as predicted: males performed more displays when raised on high food, but only if they were from low resource availability sites. However, males from high resource availability sites were more flexible in their aggressive behavior. Kolluru et al. (2007) followed with a field survey demonstrating that males in high resource availability sites are more aggressive. These studies reveal a complex pattern of flexibility in response to food intake, and GEI at the population level, for intermale aggression. However, covarying factors such as body size and light levels may be at least partially responsible for the pattern, illustrating the need for studies varying multiple factors simultaneously (Grether & Kolluru, 2011).

Hughes et al. (2005) directly addressed whether GEI maintains variation in guppy populations, focusing on the effect of food availability on body size and coloration. They found evidence for GEI for body size across populations (Figure 12.4), such that variation could be maintained with sufficient gene flow. However, as in Miller and Brooks (2005), there was no evidence for GEI for coloration. Lack of GEI for coloration may be characteristic of guppy populations, although the environmental factors studied limit the generality of that conclusion (Hughes et al. 2005; Miller & Brooks, 2005).

Several studies have addressed flexibility in female guppy mate preferences as a function of food level. Archard et al. (2006) found no effect of short-term (5-day) food restriction on female preference for male coloration, and in general found that female preference was not repeatable in any treatment group over that time. Although females who were food limited for a longer period (4 weeks) also showed no difference in preference functions (females in food restricted and control groups both preferred the same males), they did show reduced responsiveness to male displays (Syriatowicz & Brooks, 2004). Grether et al. (2005b) raised females from birth to maturity in crossed carotenoid level and food level treatments, and found that food limited females exhibited stronger plasticity in mate preferences with carotenoid intake. The relationship between carotenoid intake and mate preference was not present in females raised on high food amounts, presumably because the costs of choosing were not as high for that group (Grether et al., 2005b). Condition-dependent variation among females in responsiveness may relax the strength of sexual selection (Syriatowicz & Brooks, 2004).
Fig. 12.4  GEI for standard length (a and c) and body mass (b and d) for adult male guppies from two Trinidadian populations, raised on two food levels. Bars show least-squares means ± SE. (Hughes et al. 2005. Reproduced with permission of John Wiley & Sons.)

**Carotenoid availability**

The gradient in carotenoid (algae) availability results in corresponding differences in carotenoid content of male guppy orange spots; males in high-resource streams have higher orange spot chroma (reviewed in Grether, 2010; Grether & Kolluru, 2011). Orange spot chroma is an honest indicator of immune system strength (Grether et al., 2004b) and heritable ability to forage on algae (Kudo & Karino, 2012a,b), and is a target of sexual selection by female choice.

Because the relationship between carotenoid availability and carotenoid content of orange spots is a diminishing returns function, carotenoid availability is far more limiting in low-resource sites than in high-resource sites (reviewed in Grether & Kolluru, 2011).

The indicator value of orange spots should be greater in more carotenoid-limited sites, generating a correspondingly stronger preference for orange spot chroma in those sites (reviewed in Grether, 2010; Grether & Kolluru, 2011). Grether (2000) and Grether et al. (2005b) tested this prediction by rearing full sib males on one of three dietary carotenoid levels and determining the preference strength of females from sites differing in carotenoid availability, paired within five drainages. These experiments revealed substantial population-level GEI for
chroma and brightness (Figs. 12.3/Plate 10 and 12.5); however, although there was female preference for higher chroma across all sites, and geographic variation in preference strength, preference strength did not vary predictably with the carotenoid availability of the site of origin of the females (Figure 12.5). These results appeared to contradict the indicator value prediction of stronger preferences in more carotenoid-poor environments. However, Grether et al. (2005b) demonstrated that there is instead a reaction norm for female preference such that the strength of preference is reduced by increased carotenoid intake by females. Female carotenoid intake is expected to be lower in low resource sites, where carotenoid spots are expected to be a better indicator of male quality. Therefore, these results support the indicator hypothesis via flexibility in female preference, and females are expected to preferentially use other traits to evaluate males in carotenoid-rich areas (Grether et al., 2005b).
Rodd et al. (2002) support the intriguing idea that orange spots originated via sensory bias, as mimics of carotenoid-rich orange fruit that periodically fall into streams. These authors and Grether et al. (2005b) demonstrated a strong preference by both sexes for orange disks over disks of other colors, supporting the hypothesis of a pre-existing bias for orange foods. Grether et al. (2005b) found that the carotenoid-dependent reaction norm for orange preference extended to preference for orange disks (a foraging context) as well as for orange males. However, the flexibility for orange disk preference was present only in females, suggesting that whereas the bias favoring orange foods is a foraging adaptation, flexibility in the bias in response to carotenoid intake is a mating adaptation.

**Light environment**

Light conditions are especially important for visually displaying species such as guppies. Light conditions in guppy streams vary with canopy cover, water depth, stream structure, turbidity, and time of day (Archer et al., 2009; Chapman et al., 2009; Endler, 1987; Gamble et al., 2003; Grether et al., 2001a; Kolluru et al., 2007; Luyten & Liley, 1991; Magurran & Phillip, 2001; Reznick et al., 2001). Temporal fluctuations in selection imposed by changing light conditions should be especially important in the context of GEI and sexual selection, because GEI can maintain costly female preferences if males differ in their abilities to track the fluctuations (see Chapters 2 and 3).

The intensity of photosynthetically active radiation is the most well studied aspect of light conditions in guppy streams. The light is less intense, and males are consequently less visible to predators and conspecifics, early and late in the day compared to midday, generating predictably fluctuating levels of risk (Brooks, 2002; Endler, 1991, 1993; Gamble et al. 2003). Although the ability of females to discriminate male quality is greatest at high light intensities, males generally display less and sneak more in high intensity light (Archer et al. 2009; Endler, 1987; Godin, 1995; Kolluru et al. 2007; Long & Rosenqvist, 1998; Magurran & Seghers, 1990; Magurran & Nowak, 1991; Reynolds et al., 1993a, b). Chapman et al. (2009) described decreased courtship at even lower “twilight” intensities, suggesting that courtship levels change throughout the day, maximized when visibility is high and predation risk is low. Perhaps to compensate for lower visibility, males court females at closer distances under low light (Long & Rosenqvist, 1998).

The color and quality of light (spectral composition) may also influence male traits and selection on them (Archer et al., 2009; Brooks & Caithness, 1995b; Long & Houde, 1989). Archer et al. (2009) found differences in factors such as the proportion of UV light in the spectrum between two Trinidadian rivers (Quaré and Aripo), suggesting that different streams represent different light environments even at the same time of day. These authors also manipulated the light spectrum using filters and showed that males increased courtship displays under light conditions simulating early/late in the day (i.e., lower total irradiance), suggesting that observational patterns seen in other studies are caused directly by light levels, rather than by time of day.
**Social environment**

Social groups constitute an important aspect of the biotic environment, and indirect genetic effects may result in variation in behavior contingent upon the genotypes of other group members (e.g., Bleakley & Brodie, 2009; Chapter 5). Studies involving guppies have addressed the influence of conspecifics on sexually selected traits, although to our knowledge this work has not yet extended to the influence of indirect genetic effects on mating behavior. Although not yet studied from the perspective of GEI, there is evidence that the environment experienced during development influences the adult phenotype. Field and Waite (2004) found that males exhibit “homosexual” behavior more frequently when deprived of females during rearing. Although these behaviors may constitute intermale aggression rather than sexual behavior (for example, male-directed displays are common even when males have access to females; Kolluru & Grether, 2005), the results suggest developmental flexibility in behavior in the form of learning (Kelly et al. 2012). Guevara-Fiore (2012) similarly demonstrated that males deprived of visual contact with other males but allowed to see females during development performed more sneak attempts, whereas males raised in visual contact only with other males performed longer courtship displays.

Studies varying the social environment guppies experience as adults have revealed that males exhibit reduced preference for large females in the presence of other males, an audience effect that may persist even after the other male is removed (Makowicz et al., 2010). These results may be attributed to avoidance of intermale aggression over the preferred female, or to sperm competition. Males are known to avoid females they have seen recently mating, supporting the latter idea (reviewed in Makowicz et al., 2010). Male-male aggression also varies plastically with the presence of other males. Price and Rodd (2006) demonstrated that males raised together are less aggressive than strangers, presumably because the latter have not yet established dominance hierarchies. Although this study could not exclude effects of relatedness (brothers were raised together), familiarity alone likely reduces aggression.

Demography varies in concert with predation risk in Trinidad, such that high predation sites have lower densities and more even sex ratios than the female-biased low predation sites (Rodd & Sokolowski, 1995). In a factorial experiment designed to test for differences between sites in the form of genetic divergence, plasticity, and/or population-level GEI, Rodd and Sokolowski (1995) raised males from low and high predation populations under conditions representing the demography of each type of site, and found a stronger response to demography in males from low predation sites. The authors suggest that plasticity is more limited in high predation sites because the costs of a delayed or incorrect response to the environment are greater due to higher mortality in high predation sites, whereas the benefits are lower because the demographic environment is less variable, food availability is higher and sexual selection is less intense (Rodd & Sokolowski, 1995).

Experience with females also influences mating traits. Miller and Brooks (2005) addressed whether mating traits exhibit GEI across levels of reproductive effort by assigning full sib males to different social environments: reared alone,
with visual contact only with a female, or with free contact with a female. Although they found genetic variation and flexibility for courtship behaviors and coloration, they found no GEI, suggesting that the same genotypes are the most successful across social environments. Jordan and Brooks (2012) investigated how the abundance and size range of females experienced in the recent past contributed to male mating behavior. Males invested more effort into courtship displays when they encountered females sequentially rather than simultaneously, suggesting that they are able to use mate encounters to predict mating opportunities. Males also favored large females only if they had encountered a range of sizes, possibly because experience was required to assess relative size. Because guppies in the wild are subject to continually changing social conditions, assessment of the general social environment in the recent past may enable males to behave appropriately without having to constantly assess environmental fluctuations (Jordan & Brooks, 2012).

Because the types of behavioral changes in response to social environment outlined in this section are so labile, it would seem that the strengthening effects of GEI (maintenance of variation among males in the ability to track social environmental cues) would be more likely than the weakening effects (mismatch between male phenotype and quality). However, these ideas remain to be tested explicitly.

**Sex ratio and density**

Greater densities and more male-biased operational sex ratio (OSR) are expected to intensify sexual selection (Emlen & Oring, 1977; Head et al., 2008). However, males sneak more and court less under such conditions (Jirotkul, 1999a,b; Kolluru et al., 2007; Magellan & Magurran, 2007; Price & Rodd, 2006; Rodd & Sokolowski, 1995), and the increased harassment of females may actually reduce the opportunity for sexual selection (Head et al., 2008). Using more natural densities than previous studies, Head et al. (2008) found no influence of density on behavior or on the direction of sexual selection. Similarly, although males followed females and competed more under more male-biased OSR, there was no change in selection for male traits, as determined by genetic paternity tests. Furthermore, the increased harassment of females did not alter the opportunity for or the strength of sexual selection, prompting the authors to suggest that being choosy may not be costly enough to outweigh the benefits (Head et al., 2008).

12.2.4 Environmental heterogeneity in guppy populations

Having reviewed the evidence for genetic variation in guppy traits important for mating success and the multitude of environmental influences on those traits in the previous sections, I now turn my attention to temporal and spatial fluctuations in environmental conditions. Such changes may allow the opportunity for GEI to maintain variation because different genotypes have different abilities to track the changes. Alternatively, fluctuating environments may lead to a mismatch between the developmental environment and the environment in which
displays occur, such that GEI leads to a mismatch between a male’s signal and his quality, causing incorrect mate choice decisions (Chapter 2). The net effect of GEI on sexual selection depends on the degree of temporal and spatial heterogeneity among environments, and the extent of mixing of males among those environments (Higginson & Reader, 2009; Hunt et al., 2004; Ingleby et al., 2010; Kokko & Heubel, 2008).

**Temporal environmental fluctuation**

Guppy environments fluctuate on a variety of time scales, due to changing light conditions and variation in predation, parasitism and resource availability. Regular temporal changes in Trinidadian streams result from the sometimes dramatic seasonal flooding. Grether et al. (2001a) addressed whether changes in algae availability occur as a consequence of flooding. As outlined earlier, the carotenoid pigments in algae are key for the production of sexually selected guppy coloration; seasonal changes in algae availability due to flooding may therefore result in fluctuating selection pressures by altering the availability of carotenoids specifically, and of resources in general. However, Grether et al. (2001a) found no net effect of flooding on algae availability, because the biomass of both guppies and algae decreased after the floods. This result suggests that algae availability may not fluctuate due to flooding sufficiently to generate the temporal variation in selection pressures required for GEI to maintain variation. In contrast, in feral guppy populations in Japan, temporally fluctuating sexual and natural selection pressures have been invoked to explain within- and among-year changes in orange and black spot areas, orange spot chroma, body and fin sizes, and female preference (Kudo & Karino, 2012a,b).

Diurnal fluctuations in light levels are a potentially important source of environmental heterogeneity, given the significance of the light environment for visibility of displaying males to females and to predators. Male guppies are selected to alter courtship display rates to meet changing light levels across the day; however, conspicuousness may nonetheless fluctuate diurnally such that “a winner at dawn may become a loser at noon” (Reynolds, 1993; also see Archard et al., 2009; Brooks, 2002; Gamble et al., 2003; Reynolds et al., 1993).

There is evidence for GEI in how males respond to changing light environments: Reynolds (1993) and Reynolds et al. (1993) demonstrated that larger, more attractive males (Reynolds & Gross, 1992) display less often than small males under high light intensity (presumably because the cost-benefit ratio differs with body size), but that this difference is reversed under low light intensity, such that larger males display more and achieve higher reproductive success under low light levels. Interestingly, Gamble et al. (2003) demonstrated increased preference for larger males under the low light intensities. Reduced courtship by large males under high light intensity may therefore in part be driven by reduced female responsiveness (Reynolds, 1993).

Gamble et al. (2003) addressed the lek paradox using guppies, by altering the ambient light spectrum using filters to simulate different times of day, and examined behavior, coloration and attractiveness of males. They found that sneak copulations were more infrequent, and female responsiveness to courtship more
intensified, under “midday woodland shade” conditions than under “early morning/late afternoon” or “midday forest shade.” Because the success of sneaks versus courtship varied with light levels, males who differentially employ each tactic (see Evans, 2010) may be favored at different times. Female preference for body size varied across treatments, suggesting that fluctuating selection may maintain variation in this trait; however, preference for orange spot area, a fixed trait, was consistent across treatments, suggesting that GEI would not be able to prevent erosion of variation for this trait (Gamble et al., 2003). Gamble et al.’s (2003) results suggest the potential for temporal environmental heterogeneity to maintain variation in at least some sexually selected guppy traits. In addition to different males being favored at different times, it is also possible that different males are able to achieve a high fitness phenotype in different ways, such that there is not just one fitness-enhancing alternative (also see Blows et al., 2003).

Although largely unexplored, temporal fluctuations in carotenoid availability should be especially important for guppies. Tree fall gaps (Schwartz & Hendry, 2010) or increases in carotenoid rich fruits dropping into streams (Rodd et al., 2002) may create localized increases in carotenoid availability in otherwise low-resource (low carotenoid availability) sites. As described earlier, female preference for orange spot chroma is intensified under carotenoid-poor conditions (reviewed in Grether, 2010). The local surfeit of carotenoids resulting from tree fall gaps or fruit may allow a poor quality male (e.g., one that is genetically poor at foraging on algae; Karino et al., 2005) to deceptively signal high quality to a highly choosy female in a different part of the stream that did not experience the increased carotenoid availability. If tree fall gaps via deforestation cause rapid localized changes in carotenoid availability, then such a blurring of the honesty of the male signal could constitute an “evolutionary trap” (Ghalambor et al., 2010; Sih et al., 2011). Although Schwartz and Hendry (2010) found no effect of short-term decreases in canopy cover on guppy coloration, they did not measure orange spot saturation (chroma), a key characteristic expected to change in response to carotenoid availability. It also remains to be addressed whether other aspects of the guppy mating system, such as female preference for high carotenoid males (Grether, 2000), are influenced by rapid changes in carotenoid availability.

Spatial environmental fluctuation and gene flow

Guppy habitats are highly subject to spatial variation, most notably in predation risk and resource availability. The visual environment is also likely to differ spatially, even in different parts of the same stream, due to localized variation in background and stream structure (Brooks, 2002; Endler, 1980; Millar et al., 2006). Because movement generates the mixing among individuals that is key to the influence of GEI on sexual selection (Kokko & Heubel, 2008), it is important to know the likelihood and nature of movement of males among locations that differ environmentally.

Guppies appear to move infrequently within a stream in the short term, as revealed by mark-recapture studies (Reznick et al., 1996; Grether et al., 2001a), and Crispo et al. (2006) determined that geographic barriers such as waterfalls
are more important than selection against migrants in limiting gene flow (also see Schwartz et al., 2010; Weese et al., 2011). In the longer term, however, there is ample evidence that gene flow occurs and includes movement among predation and parasitism risk environments (Brooks, 2002; Hughes et al., 2005; Magurran & Phillip, 2001; Labonne & Hendry, 2010; Schwartz et al., 2010; Suk & Neff, 2009; van Oosterhout et al., 2007). Movement caused by flooding is likely to carry males from low to high predation sites within a stream, and selection may act against migrants, both because they are colorful and because high predation females may discriminate against them, such that reinforcement acts to prevent maladaptive hybridization with the migrants (Schwartz et al., 2010). However, movement may also be more active (Schwartz & Hendry, 2010). Croft et al. (2003) found that males moved more frequently than females (presumably to find mates), and that movement increased with body size in both sexes. These studies suggest that mixing of individuals among Trinidadian microhabitats is likely sufficient to allow for GEI to both generate variation in local adaptation among males, and also to lead to a mismatch between male mating signals and genetic quality.

12.3 Summary and future directions

12.3.1 Guppies and the positive and negative effects of GEI on sexually selected traits

This review has identified strong, naturally occurring environmental influences on a range of sexually selected traits in guppies, combined with substantial temporal variation in and gene flow among environments. Therefore, the conditions are met for GEI to both maintain variation in the face of directional sexual selection, by altering the relative fitness of males in different environments, and to disrupt the honesty of mating displays (Ingleby et al. 2010; Chapter 11).

The potential for GEI to maintain diversity in mating traits in guppies has received considerable attention (Brooks, 2002; Brooks & Postma, 2011; Gamble et al., 2003; Weese et al., 2010), as have other mechanisms (Bro-Jorgensen, 2009; Brooks, 2000; Brooks & Endler, 2001b; Cornwallis & Uller, 2010; Grether et al., 2004a; Hampton et al., 2009; Hughes et al., 1999; Johnson et al., 2010; Kemp et al., 2011; Kudo & Karino, 2012a,b; Mariette et al., 2010; Olendorf et al., 2006; Zajitschek & Brooks, 2008). In general, it appears that the rank order of attractiveness does not change markedly across the environments that have been examined to date. Guppies did not exhibit GEI in coloration across social, food availability or light spectrum conditions, or in mating behavior across social environments (Brooks & Postma, 2011; Gamble et al., 2003; Hughes et al., 2005; Miller & Brooks, 2005). However, the responsiveness of females, their preference for large males, and male mating tactics all vary with the light environment (Gamble et al., 2003). Therefore, GEI may maintain variation among males in the ability to track changes in at least some traits, and should be examined further (Blows et al., 2003; Brooks, 2002; Gamble et al., 2003; Weese et al., 2010).
The influence of GEI is also dependent on the degree of movement of males among environments. Studies of guppy movement patterns have focused on colorful migrants moving downstream, who are disfavored under natural selection by predators in downstream regions, but favored under sexual selection (Labonne & Hendry, 2010). However, GEI can generate migrants that are disfavored by sexual selection itself. Deere et al. (2011) demonstrated that female preference for orange spot hue results in “genetic compensation” (Grether, 2010), genetic variation in drosopterin allocation to orange spots across environments differing in carotenoid availability, such that males across environments achieve the preferred hue (pigment ratio). However, if a male moves to a location differing in carotenoid availability from his population of origin, his genetically based drosopterin levels may yield a suboptimal hue, compromising the honesty of the mating signal. All of the movement patterns discussed here may result in males developing in an environment that is different from that in which selection takes place, such that there is a mismatch between a male’s color phenotype and his genetic quality as a consequence of GEI. In contrast, sexual selection for behavioral traits may be enhanced by GEI. For example, female response to courtship display changes with predation risk, such that females may prefer males that are locally adapted to a given predation risk environment; GEI may act to reveal maladapted males and favor the preservation of mate choice, even if it is costly (Chapter 2).

Understanding the influence of GEI on sexual selection requires consideration of multiple traits simultaneously (Brooks & Endler, 2001b; Ingleby et al., 2010). Guppies epitomize multivariate displays, including complex color elements, behaviors, and morphology interacting to produce the preferred phenotypes. Males are evaluated by females whose preferences may themselves be subject to GEI, adding to the complexity. Some male traits may emerge as more important than others to choosy females. For example, in populations where sneak is more common than displays due to increased predation risk, relative gonopodium length (a predictor of sneak copulation success) may be a better predictor of siring success than ornaments (Becher & Magurran, 2004; Elgee et al., 2012). Alternatively, several traits may be evaluated together by females, either because they modify each other or because they indicate different aspects of quality (e.g., Grether et al., 2004a), and studies addressing whether traits are independently subject to GEI or linked together in their response to the environment would be useful.

To my knowledge, few studies employing guppies have addressed GEI from the perspective of signal honesty. A fruitful area for research in this regard would be to examine host-parasite interactions involving guppies. Common guppy parasites include monogenean trematodes in the genus Gyrodactylus (Cable, 2011; Scott & Anderson, 1984). Gyrodactylus loads (numbers of parasites per fish) vary geographically in at least one Trinidadian stream, with higher parasite loads upstream than downstream on the Aripo River (reviewed in McMullan & van Oosterhout, 2011). Parasite loads also fluctuate temporally, decreasing after seasonal flooding (van Oosterhout et al., 2007). Females are expected to enhance their fitness by mating with males signaling resistance to Gyrodactylus, which may be conveyed via orange spot chroma and rates of intermale aggression and
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courtship displays (Houde & Torio, 1992; Kolluru et al., 2009; Lopez, 1998). However, GEI may disrupt signal honesty if, for example, a male develops his orange spots in a low parasite prevalence environment but moves to an area with abundant parasites, or if parasite loads change over time, such that his coloration inaccurately indicates his actual likelihood of being resistant and of sexually transmitting an active infection (Ingleby et al., 2010). Alternatively, it is possible that the main role of GEI in the context of Gyrodactylus/guppy interactions is positive, generating variation among males in the ability to resist infection across changing parasite load environments.

12.3.2 Behavioral syndromes as an emerging focus

Recent attention has been drawn to the importance of behavioral syndromes, which occur in the absence of GEI (Dochtermann & Dingemanse, 2013; Sih et al., 2004a,b; 2012). A syndrome describes consistency across environments in the rank order of the behavioral types exhibited by individuals (Schuett et al., 2010). A behavioral syndrome results from intra-individual consistency in behavioral type across environments, including situations (e.g., low and high light intensity), and contexts (e.g., foraging and mating); this leads to maintenance of the rank order among individuals across environments, yielding parallel reaction norms, either with (Figure 12.1a) or without (Figure 12.1b) flexibility for the group as a whole (also see Schuett et al., 2010). By emphasizing genetic correlation in behavior across environments, the behavioral syndromes approach allows researchers to explain suboptimal behavior and constraints on evolutionary change (Dochtermann & Dingemanse, 2013; Sih et al., 2004a,b). For example, some males may be adaptively aggressive during male-male competition, and this behavioral type may carry over such that the same males are maladaptively aggressive towards potential mates (Bell, 2007). In other cases, consistency in behavior may be adaptive (Sih et al., 2004a,b). For example, female choice may preserve a behavioral syndrome for display rate if females specifically prefer males able to consistently display frequently across environmental conditions (Schuett et al. 2010). Because behavioral syndromes result in parallel reaction norms, the existence of a syndrome for any given sexually selected trait should both reduce the ability of GEI to maintain variation in sexually selected traits and reduce the likelihood that GEI erodes signal honesty.

As outlined earlier, plasticity and behavioral flexibility at the group level occur across a variety of sexually selected traits in guppies; however, there is a paucity of studies of individual patterns of response to the environment for these traits. Studies such as Reynolds (1993), which demonstrated that display rate under different light intensities is dependent on body size, and Gamble et al. (2003), which emphasizes the importance of the adjustment of heritable (Evans, 2010) mating tactics to changing light levels, hint at GEI rather than behavioral syndromes, because not all males appear to adjust their behavior in the same manner. In contrast, Magellan and Magurran (2007) demonstrated individual level consistency in guppy display rates with varying sex ratios, such that rank order of males was preserved. A focus on individual profiles of behavioral flexibility
across environments is likely to yield important results with respect to the extent to which GEI shapes behavioral variation in guppy populations.

### 12.3.3 The challenge of human-induced environmental changes

Environmental changes to natural ecosystems are occurring at an unprecedented rate (Sih et al., 2011). Because these alterations may be too rapid to generate adaptive evolutionary responses, plasticity may be key to survival for wild populations. GEI in response to human-induced rapid environmental changes may therefore influence the evolutionary trajectory of natural populations, for example, by favoring those genotypes best able to plastically alter traits to meet environmental demands (Ghalambor et al., 2007; Sih et al., 2012). Tropical rainforest areas in the northern range of Trinidad are subject to deforestation, resulting in more open canopies and increased resource availability (Grether et al., 2001a; Schwartz & Hendry, 2010). Although increased resources may enhance traits such as body size, increased carotenoids may cause a maladaptive alteration of the optimal hue of orange spots by disrupting the ratio of carotenoid and drosophetin pigments preferred by females (Deere et al., 2011; Grether, 2010). Because drosophetin production does not respond plastically to changes in diet, rapid evolutionary increases in drosophetin production to maintain the preferred hue would be the only way for male guppies to adaptively respond to such perturbations.

Other environmental changes may pose an even more difficult challenge. Pollution of freshwater ecosystems by endocrine disrupting compounds (EDCs), exogenous substances which alter normal hormonal functions, can have profound effects on reproductive biology, including generating maladaptive plastic responses (reviewed in Martin et al., 2011; Shenoy & Crowley, 2011). EDCs may reduce the discriminability of a mating signal (ability of the receiver to distinguish a given signal from that produced by other signalers in the population; Shenoy & Crowley, 2011), such that, although signal strength may still reliably indicate quality, females would be less able to distinguish the higher quality males from others. EDCs may also decrease the assessability of traits, the ability of receivers to make an accurate connection between trait and quality of the signaler (Shenoy & Crowley, 2011).

Not surprisingly, guppies are emerging as valuable for studies of the effects of EDCs on sexually selected traits (Baatrup, 2009; Bayley et al. 2003). The contamination of Trinidadian streams with EDCs has been documented (Magurran, 2005). Baatrup (2009) demonstrated that several EDCs reduce sigmoid courtship display rates. Shenoy (2012) exposed male guppies from three populations to atrazine and replicated Baatrup’s (2009) results, also showing reduced orange spot area and male-male aggression in treated males. Shenoy (2012) found no difference among populations in the degree to which atrazine reduced sexually selected traits, suggesting no population-level GEI. It is possible that the time of exposure to the chemicals was insufficient to reveal a complex population difference in response. Regardless, this scenario should generate within-population GEI favoring those genotypes exhibiting the least
reduction in display rate, orange spot area, and aggression in response to EDCs. Females prefer high courtship display rates, which signal high food intake (Kolluru & Grether, 2005) and freedom from Gyrodactylus parasites (Kolluru et al., 2009; Lopez, 1998), and high orange spot area, which signals a variety of aspects of male quality (Houde, 1997). Male-male aggression may also enhance fitness both by allowing males to monopolize access to females and via female preference (Kodric-Brown, 1992; 1993). The reduction in these traits and in discriminability and assessability in response to EDCs may reduce the benefits of mate choice. Reduced signal reliability can threaten population viability and have cascading ecological and evolutionary effects, especially for taxa such as guppies that exhibit strong sexual selection (reviewed in Shenoy & Crowley, 2011).

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References


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