IT'S ALL WHO YOU KNOW: THE EVOLUTION OF SOCIALLY CUED ANTICIPATORY PLASTICITY AS A MATING STRATEGY

Michael M. Kasumovic

Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales
Kensington, Sydney, New South Wales 2052 Australia

e-mail: m.kasumovic@unsw.edu.au

Robert C. Brooks

Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales
Kensington, Sydney, New South 2052 Australia

e-mail: rob.brooks@unsw.edu.au

abstract

Selection has led to the evolution of a variety of different mating strategies, each adapted to different competitive challenges. But what happens if the competitive challenges depend on the social environment? Here we discuss and review examples of socially cued anticipatory plasticity: irreversible developmental tactics in which resource allocation during the juvenile stage is altered to develop an appropriate phenotype for the competitive or mate choice environment that an individual encounters when mature. There are numerous theoretical and empirical examinations of the role of the social environment on the strength and direction of selection. However, only a handful of empirical studies examine how the social environment affects juvenile allocation and whether such tactics are adaptive. The goal of this review is to synthesize current knowledge about socially cued anticipatory plasticity, including the sensory modalities that individuals use to predict the adult competitive and mating environment. We then outline the various factors that are necessary for the evolution of socially cued anticipatory plasticity and discuss how this can affect phenotypic evolution. We conclude by suggesting some directions that future studies should take in order to understand how social variation can alter selection and the evolution of development.

INTRODUCTION

PHENOTYPIC PLASTICITY allows individuals to adaptively alter their phenotype in response to the environment in which they reside and can be behavioral, physiological, or developmental (Pigliucci 2001). Although reversible behavioral plasticity allows individuals to adjust their behavior in response to rapidly changing environments, the success of any individual can still be limited by the phenotype at maturity. On the other hand, developmental plasticity allows individuals to modify their developmental trajectories to match the competitive contexts that they are likely to encounter at maturity (West-Eberhard 2003). Such plasticity allows phenotype-context matching, but it requires available cues that reliably signal the future selective environment (Lively 1986). In the absence of such cues, individuals will develop an incorrectly matched phenotype, with fitness costs (Relyea 2002). Although both types of plasticity are of interest to evolutionary biologists, developmental plasticity that results in irreversible phenotypic changes is particularly intriguing as it has the potential to help explain the maintenance of variation.

Broadly, developmental plasticity is the ability of a genotype to produce different phenotypes in response to different environmental conditions and can be described by a reaction norm (Pigliucci 2001; West-Eberhard 2003). The majority of examples of developmental plasticity are in a response to large-scale environmental variation that is detectable during juvenile stages (e.g., temperature, photoperiod, and predator abundance) and there are numerous examples from a variety of taxa (Adler and Harvell 1990; Nylin and Gotthard 1998; Agrawal 2001; Pigliucci 2001; West-Eberhard 2003; Benard 2004). Some of the most familiar include induced defenses in response to the presence of predators (e.g., Green 1967), or seasonal variation in development in response to pond drying in frogs (e.g., Loman 1999; Laurila et al. 2002). In these examples, developing juveniles irreversibly alter their allocation of resources toward traits that will maximize fitness in their anticipated adult environment. As all of these heterospecific factors vary on large scales, and all individuals within a single population or even nearby populations experience the same suite of selective pressures.

Apart from variation in these abiotic and heterospecific factors (that normally vary on large temporal and spatial scales), populations can also deviate in conspecific cues that can vary in the temporal and spatial scales on which they occur. Even variation among siblings from the same litter can induce adaptive developmental plasticity. For example, late-hatched nestlings in many bird species follow a different developmental trajectory in order to compete with their larger, slightly older siblings. Late hatching spotless starling (*Sturnus unicolor*) chicks develop relatively larger gapes than their larger siblings in order to compete for provisioning from parents (Gil et al. 2008). Blue tit (*Cyanistes caeruleus*) hatchlings allocate more resources to leg growth, allowing them to reach higher while begging to outcompete larger, earlier hatched offspring (Mainwaring et al. 2010). Although juveniles alter allocation to different body parts in order to outcompete siblings, the cues that trigger these changes in allocation remain unresolved.

The density of conspecific rivals and available mates are strong determinants of the intensity and direction of sexual selection (Kokko and Monaghan 2001; Kokko and Rankin 2006) that vary on fine temporal and spatial scales (Kasumovic et al. 2008; Punzalan et al. 2010). Temporal shifts in the local abundance of mates and sexual competitors can be common in short-lived animals if the sexes have differences in maturation times or mortality rates. For example, in the soapberry bug (*Jadera haematoloma*), populations become more male-biased as the season progresses. As a result, there is stronger selection for larger males as they can more quickly locate and monopolize rare females (Carroll and Salamon 1995). Spatial variation in the social environment can also occur if there

is stratification as a result of the available habitat and low movement rates (Kasumovic et al. 2008; Punzalan et al. 2010) or if mating preferences and interaction rates between conspecifics vary as a function of age within a population (Dreiss et al. 2010).

Many demographic factors can affect the density of males, females, or both sexes. For example, the social environment can vary as a function of variation in sex differences in birth, death, and maturity rates (Foellmer and Fairbairn 2004; Kasumovic et al. 2007), immigration/emigration rates (Maxwell 1998; Matter and Roland 2002), time of arrival to breeding grounds (Grant et al. 1995; Wiklund and Fagerström 1977), predation rates (Gwynne and Bussière 2002; Su and Li 2006), and differences in mating optima between the sexes (Arnqvist and Rowe 2005; Parker 2006). Such changes in the social environment affect within-season variation in the intensity and direction of selection, making the fitness of any given phenotype context-dependent (Lailvaux and Kasumovic 2010; and e.g., Moya-Laraño et al. 2007; Kasumovic and Andrade 2009). As a result, there may be strong selection for adaptive developmental plasticity to match the competitive context each individual faces (Berrigan and Scheiner 2004; Garland Jr. and Kelly 2006).

The goal of this review is to outline a specific case of developmental plasticity where (a) individuals adaptively anticipate suitability for a life stage that is later than the one where the trait development occurs (i.e., prematuration life-history shifts) and (b) the cues used to determine these life-history shifts are the density of conspecific males and/or females (i.e., the social environment). We term this type of plasticity as "socially cued anticipatory plasticity" (SCAP). By definition, the prematuration resource allocation shifts of this type of plasticity result in irreversible postmaturation differences, but may not necessarily lead to irreversible postmaturation behavioral differences.

This type of plasticity has received relatively less attention than the abiotic and predatory environment, possibly because social environments are considered to vary rapidly and unpredictably. Such a developmental tactic can, however, evolve in the same manner that sperm allocation strategies in relation to the risk of sperm competition in adults can (Drickamer 1977; Magellan and Magurran 2009), as studies demonstrate that the social environment can be predictable. But sexual competition should affect far more than sperm allocation; individuals could also benefit by altering the resources they allocate to growth, weight gain, fast development, or body condition. Care must be taken in examinations of SCAP to ensure that the social environment is the cue that individuals are using as although the social environment may be the factor shifting the selective environment, the cues that reliably predict shifts in the social environment may be distinct. For example, although the social environment determines the selective pressures in a butterfly (*Bicyclus anynana*), the seasonal environment is the cue that signals a developmental shift (Prudic et al. 2011). SCAP is also interesting to study as this type of plasticity may have fundamentally different evolutionary dynamics. For example, as individuals shift their development in response to the conspecific environment, indirect genetic effects play an important role in phenotypic expression that can result in interesting evolutionary feedbacks (Moore et al. 1997; Wolf et al. 1998).

Our review is thus organized along the lines of the three main requirements for developmental plasticity to evolve. First, there must be cues that reliably signal the competitive environment (i.e., the intensity and direction of selection, Lively 1986; Van Tienderen 1991; Getty 1996) since developmental shifts can be costly if they do not result in adult phenotypes that correctly match the environment (DeWitt et al. 1998; Relyea 2002). We first outline the various modalities that can be used by immature individuals to assess the adult social environment and discuss the type of information that can be gleaned from such cues. Second, the mean fitness of the plas-

tic phenotype must be greater than a non-plastic phenotype in the environments to which the animal is typically exposed (Via et al. 1995). Here we discuss how studies might test for the fitness benefits of SCAP and review the available evidence of fitness benefits. Third, the cue that signals the likely social environment must occur in a relevant time frame that will allow individuals to respond (Bradshaw 1965; Scheiner 1993). We then discuss the types of mating systems where such plasticity will likely be relevant, and the factors that are necessary for the evolution of such a developmental tactic. In the last section, we predict that SCAP will be widespread in animals, and discuss how researchers can test for SCAP in their study species as well as test for fitness benefits.

Socially Cued Anticipatory Plasticity

In general, when the fitness of a phenotype is context-dependent and the context an animal will find itself in is variable and predictable, then selection should favor the evolution of plastic allocation strategies. If the important determinant of the competitive context is the current developing cohort (i.e., a simultaneous univoltine emergence), then individuals should assess social factors associated with other developing juveniles. In contrast, if the competitive context is mainly determined by an earlier cohort (i.e., extended univoltine or multivoltine emergence), then developing juveniles would largely compete against adults already present in the population and should assess social factors associated with the adult population. Juveniles could detect the density of males or females from encounter rates or traces (e.g., feces) left by others, or by tuning into the presence, density, and quality of signals that adults use to attract mates and avoid/deter rivals.

Different signaling modalities will likely provide different types of information to eavesdropping individuals, varying from simple information on conspecific density to more complex information on the density of either sex or the sex ratio. Signals can also provide information on the qual-

ity of the signalers if such signals are reliably used for choice. Below we discuss the different signaling modalities and the information immature individuals might intercept through these modalities.

TACTILE CUES

Tactile cues require contact and only provide information regarding conspecifics in the immediate environment. Tactile cues will likely only be reliable in populations where individuals will be competing very locally, or where local cues represent population-wide phenomena. For example, a species of desert locust (*Schistocerca gregaria*) modifies its phenotype and social behavior in response to tactile stimulation signaling population density (Roessingh et al. 1998; Rogers et al. 2003). This developmental shift is thought to be a response to tactile cues of population size relative to food abundance (Simpson et al. 1999). As a result, the shift to a gregarious phase occurs in response to a signal of food availability (i.e., natural selection) rather than the intensity of competition for mates (i.e., sexual selection). Similar results can be seen in aggregating and nonaggregating species of cockroaches (Lihoreau and Rivault 2008).

Examples of allocation shifts in response to tactile cues of the intensity of competition occur in holometabolous invertebrates (Gage 1995; Stockley 1999) and leeches (Tan et al. 2004). In the moth *Plodia interpunctella*, females mate more frequently when population density is high, increasing the risk of sperm competition. Larval (juvenile) density is a reliable cue of adult density and is easily assessed by touch. When reared in high-population densities, males take longer to mature and develop larger testes for their body size, thus producing more sperm. If larvae are reared in low-density environments, males mature significantly more quickly and live longer, increasing their chances of successfully locating rare females (Gage 1995).

Similar results were found in yellow dung flies (*Scatophaga stercoraria*, Stockley and Seal 2001) and leeches (*Helobdella papillornata*, Tan et al. 2004). In all three cases,

species manipulated their testis size as a response to the intensity of sperm competition assessed from tactile cues. Although the tactile effects in these studies are difficult to separate from other potential cues that occur due to density (such as long-distance or contact pheromones or excreted wastes), these studies provide examples of the potential for touch to be assessed by juveniles as a cue of the social environment.

<div align="center">ACOUSTIC CUES</div>

Acoustic signals can propagate over long distances, allowing both communication and eavesdropping at a variety of spatial scales. Where acoustic signals are only produced by individuals of one sex to attract individuals of the opposite sex, juveniles can only use these signals to infer the density and quality of the displaying sex. As either sex can use these acoustic cues, the calling sex will have information on the intensity of competition they are likely to encounter, while the receiver will have information on the relative availability of mates of differing quality.

Acoustic communication in Orthoptera has been studied extensively, making them a particularly useful group to examine eavesdropping during immature stages. In a study on the Australian black field cricket (*Teleogryllus commodus*), males call to attract females and deter rivals. Although there is multivariate stabilizing selection on various calling traits (Brooks et al. 2005), there is directional selection on the male calling rate as females prefer males that call at a higher rate (Bentsen et al. 2006). As calling is energetically costly (Hoback and Wagner Jr. 1997) and determined by condition (Hunt et al. 2004), male calling rate may honestly indicate male quality. Thus, the calls that immature individuals hear can reliably signal the density and quality of nearby males.

By rearing individuals in six different social environments that varied in the density and quality of calling males, Kasumovic et al. (2011) demonstrated that both sexes altered their allocation strategies while immature as well as their reproductive strate-

gies as adults. Males matured more quickly, emerged smaller, and called more in environments signaling less competition with high-quality males. In contrast, males matured larger and heavier in environments that signaled a high density of high-quality males. Females had the opposite developmental strategy, allocating resources toward earlier maturity when reared in the presence of a high density of high-quality calls, as this would signal an environment with a greater number of high-quality mates. Females also allocated relatively more resources toward egg production in this environment to compensate for maturing smaller as a result of earlier maturation. These results demonstrate that different sexes respond differently to the same cues while immature, altering their developmental trajectories to make the most of the apparent conditions. Moreover, these results show that the ability of individuals to discriminate competitive environments is acute as individuals who can discriminate between environments with males of different quality and quantity, rather than simply the presence or absence of males.

Similar results were seen in a congener, the oceanic field cricket (*T. oceanicus*). The population of males found on the Hawaiian island of Kauai have lost the ability to call, and this mutation is maintained in the population due to the high cost of parasitism from acoustically orienting flies that can only locate calling males (Zuk et al. 2006). Although silent males cannot call to attract females, they act as satellite males, mating with females that search for calling males. Bailey et al. (2010) have shown that males of both the silenced and normal wing morph shift their allocation toward body condition and reproductive tissue as well as their association behavior in response to acoustic cues of the competitive environment. Males reared in an environment that simulates an abundance of calling males invested more resources into body condition and reproductive tissue (Bailey et al. 2010). In contrast, males reared in silence matured in poorer body condition, invested less in reproductive tissue, and spent more time associated with

speakers playing looped male calls, suggesting they were more disposed to act as satellite males. These results demonstrate that the presence or absence of information on the social environment can affect juvenile allocation strategies.

Bailey et al. (2010) suggested that decreased allocation toward body condition and reproductive tissues is an alternative male reproductive tactic responding to the lower-density environment. Rather than an alternative reproductive strategy, however, males may have sacrificed body condition and reproductive tissue to develop more quickly in an environment signaling lower competition (the silence treatment) as in the other plasticity studies examined. As development time was not examined, it is impossible to assess whether this is the case.

It is interesting that such a developmental tactic is still present in this population given that calling is only a partial indicator of the competitive environment on Kauai where 90 percent of males have the silencing mutation (Zuk et al. 2006). Here, silence might indicate an absence of competition or merely an absence of calling males. The presence of the developmental shift in both *T. commodus* and *T. oceanicus* suggests that developing small and, possibly, being more inclined to act as satellites might be general responses to highly competitive circumstances. Whether the spread of the silencing mutation in *T. oceanicus* has altered the developmental plasticity of male development remains an important question for future study.

vibratory cues

Vibratory cues are widespread in arthropods (Cocroft and Rodríguez 2005) and can be found in some vertebrates (red-eyed treefrogs, Caldwell et al. 2010; club-winged manakin, Drickamer 1974). Although vibratory signals can be perceived acoustically by humans, many animals have separate receptors to identify vibrational signals (Hill 2008). Because vibrations propagate through the substrate and attenuate with distance, they are typically used for close-range communication between individuals (Hill 2009; e.g., intrasexual competitions, Elias et al. 2008; mating interactions, Elias et al. 2003) or by predators to locate and capture prey (e.g., Fertin and Casas 2007). Although this limits the utility of such cues to be used by conspecifics to eavesdrop, there are examples where immature individuals alter their development or behavior in response to vibrational cues of predation risk in both frogs (Warkentin 2005) and caterpillars (Castellanos and Barbosa 2006).

In both species, individuals altered their time to hatching in response to vibratory cues of the risk of predation. These results suggest that the vibrational signals used by adults could provide juveniles with cues of the social environment if population densities are high enough. Although studies that examine vibrational communication have increased with the advancement of technology to measure vibrations, studies that determine whether immature individuals use vibrational signals to estimate the selection pressures they will encounter as adults are still necessary.

chemical cues

Chemical cues can provide information on the sex, mating status, and quality of the signaler (Shorey 1976). Furthermore, as chemical plumes travel through the environment, and scent marks can persist for some time, individuals could also gain information on the density of nearby conspecifics (Murlis et al. 1992). As a result, receivers could infer the density, sex, and even the age structure of conspecifics, as well as the quality of rivals and mates in the near environment. This can potentially provide immature individuals with a very accurate description of the competitive environment. Chemical cues provide the best examples of SCAP and there are several cases from both vertebrates and invertebrates.

Excellent examples of SCAP have been documented in house mice (*Mus musculus*), two different species of fish, and a variety of arthropods. In mice, the effects of pheromones from mature males and females on the time it takes for juvenile fe-

males to mature (i.e., reach first estrus) are particularly interesting. Females reared in the presence of pheromones from mature males reached maturity earlier, while those housed with pheromones of females delayed maturation; although physical contact with females was required for the delayed effect to occur in females (Drickamer 1974, 1975). When examining both sexes and photoperiod simultaneously, photoperiod explained only 6% of variation in the onset of estrus and female presence explained 9%, while male presence explained 31% (Drickamer 1975). These results demonstrate a strong social component to the timing of first estrus. Surprisingly, this effect is only elicited when pheromones are present and experienced for at least seven days during the first week of weaning (Drickamer 1977), suggesting it is early development that is altered, rather than development immediately before maturity.

Examples in fish demonstrate a larger amount of variety in the circumstances and variance in the effects on the different sexes. This is, however, likely due to the increased number of studies that have examined the effect of the social environment on development in fish. In a study on the development of guppy males (*Poecilia reticulata*), immature males reared with other adult guppies developed gonopodia and secondary sexual characteristics later compared to males reared in isolation (Magellan and Magurran 2009). This is in contrast to a study examining the development of both males and females in the mosquitofish (*Gambusia affinis*) where males were not affected by chemical cues from either males, females, or a combination of the two, while females showed a reduction in growth rate and smaller ovary size when reared in the presence of pheromones from at least two other females (Lutnesky and Adkins 2003). Although the authors of both studies suggest the delayed development of these traits are a result of the inhibition of trait development by conspecifics, it is impossible to discern from developmental decisions in response to the presence of other rivals, as there was no comparison of the level of trait expression between individuals reared with rivals and in isolation. Regardless, it is interesting that the effects were sex specific for each species and were only triggered by the same sex.

Additional research on guppies was performed in the wild where the social environment was examined in conjunction with the presence of two different predators. In this study, Rodd et al. (1997) demonstrated that the developmental effect of the social environment was limited to males as above, but that the social environment had an effect on how females altered their reproductive strategies. Moreover, this effect was moderated by the predator community that they experienced as juveniles. Males matured later and larger when reared in increased densities, but this was limited to populations that originated with *Rivulus hartii* that feed on small guppies and absent from populations containing *Crenicichla alta* that feed on larger guppies. This suggests differential evolutionary shifts in response to both sexually and naturally selective environments. Female guppies did not show developmental shifts in response to the social environment, but instead demonstrated developmental and reproductive shifts in response to the predator community—a factor that is more likely to affect fitness in females.

In invertebrates, the currently available examples of SCAP in response to pheromones occur in spiders. Although jumping spiders and wolf spiders use visual cues to hunt, locate, and choose mates, the main form of communication in spiders is through pheromones (Foelix 1982; Gaskett 2007). As in most web-building spiders, male Australian redback spiders (*Latrodectus hasselti*) do not feed after maturity, and spend the remainder of their lives searching for females, competing with other males, and mating with a female (Foelix 1982). As a result, the pool of resources that adult males have available for all of these behaviors is limited to the resources they have when they first mature. In a study rearing penultimate-instar males in the presence or absence of female's

pheromones and in differing densities of immature males, the male redbacks modified their allocation toward development rate, body size, and body condition (Kasumovic and Andrade 2006). They matured significantly faster in the presence of females, but were smaller and in poorer body condition. Although smaller, this shift is adaptive as there is strong first male precedence and it allows males to reach and mate with nearby females quickly, denying competitors the chance to mate (Snow and Andrade 2004, 2005; Kasumovic and Andrade 2009). When females were absent and males were surrounded by an increasing number of rivals, males took longer to mature. They acquired more resources and eclosed larger and in better condition; traits that increase fitness in competition against rivals (Stoltz et al. 2009). This example demonstrates that males altered allocation toward various life-history traits that would allow them to maximize their fitness in different competitive environments.

There are two additional examples of strong correlations between phenotypes and the social environment in field populations of two species of spiders; the golden orb-web spider (*Nephila plumipes*) and the St Andrew's cross spider (*Argiope keyserlingi*). In *N. plumipes*, females produce webs either singly or in aggregations of up to nine females (Herberstein and Elgar 1994; Kasumovic et al. 2007). Males mature either within or near these aggregations and then search for and preferentially settle on the webs of adult and then penultimate-instar females within these aggregations (Kasumovic et al. 2007, 2008). Most males only mate with a single female in their lifetime (Schneider and Elgar 2001), thus, a male's fitness is maximized by finding a virgin female and successfully mating with her. Kasumovic et al. (2009) found that a male's size and weight were positively correlated with the number of males and negatively correlated with the number of females within an aggregation—as predicted if males were matching the competitive context.

In contrast, male *A. keyserlingi* cannot distinguish between females of different age and mating status (Gaskett et al. 2004) and, as males attempt to mate with two separate females within their lifetime after guarding the first for a short period of time (Herberstein et al. 2005b), fitness is not limited to a single mating. In *A. keyserlingi*, males mature larger and heavier when the density of other males is high. These large males are better equipped to outcompete rivals (Herberstein et al. 2005a). Female density had no effect on male size or weight at eclosion because fitness is not as constrained by the availability of virgins as it is in *N. plumipes*. Although correlative, demography is a far stronger correlate of phenotype than any other measured environmental variable. Direct experimental tests are necessary to confirm if this is the case.

VISUAL CUES

The visual system allows assessment of conspecific density, quality, and sex ratio, and does not require individuals to actively produce signals as in the other modalities. However, one limitation is that individuals require line-of-sight access to other individuals. Thus, visual signals will likely play a strong role in species where individuals move within a population and can clearly see conspecifics.

Although visual cues may also have played a role in developmental tactics in some of the above fish examples, it is difficult to discern the relative role of visual and chemical cues as strict experimental guidelines that are required to tease apart the factors that affect development. The only example of SCAP in response to visual cues occurs in the green swordtail (*Xiphophorus helleri*). In this species, juvenile males and females were isolated from chemical and tactile cues and individuals altered their development time in response to the presence or absence of high-quality males in the adult population (Walling et al. 2007). Quality was determined by the size of the sword found on adult males. Females matured more quickly in the presence of high-quality males, sacrificing larger size and weight, while males

TABLE 1
The traits in the various examples that shift in response to social cues

Species	Traits	Sex	Reference
Plodia interpunctella	Head, thorax, abdomen size; testis size, lifespan, development rate	No distinction between sexes	Gage 1995
Scatophaga stercoraria	Testis size, mate searching behavior	Only males tested	Stockley and Seal 2001
Helobdella papillornata	Testis size	Male but no female plasticity	Tan et al. 2004
Latrodectus hasselti	Development rate, leg length, condition (regression of weight on leg length)	Only males tested	Kasumovic and Andrade 2006
Nephila plumipes and *Argiope keyserlingi*	Leg length, condition (regression of weight on leg length)	Only males tested	Kasumovic et al. 2009
Teleogryllus oceanicus	Male mating, tactics, testis and accessory glands and condition (regression of weight on leg length)	Only males tested	Bailey et al. 2010
Teleogryllus commodus	Development rate, pronotum width, weight, calling effort	Differential shifts by males and females	Kasumovic et al. 2011
Gambusia affinis	Growth rate, ovary size	Female but no male plasticity	Lutnesky and Adkins 2003
Poecilia reticulata	Sexual maturity	Only males tested	Magellan and Magurran 2009
Poecilia reticulata	Sexual maturity, size	Male but no female plasticity	Rodd et al. 1997
Xiphophorus hellerii	Development rate, weight, size	Differential shifts by males and females	Walling et al. 2007
Mus musculous	Sexual maturity	Only females tested	Drickamer 1974, 1975

took longer to mature in the presence of high-quality males. In this case, although individuals did not alter their development in response to the adult sex ratio, they did alter it in response to the quality of the potential mates or competitors, with females maturing fast to exploit the presence of high-quality mates, and males developing more slowly in order to mature at a more competitive size.

SUMMARY

Developmental plasticity clearly does occur in response to the variation in density of mates and rivals in many taxa (Table 1), and cues of the future competitive environment can be present in many forms (Table 2). In general, males increase their development rate to mature more quickly, therefore being smaller and lighter when competition is scarce, and will delay matu-rity in the presence of high-quality conspecifics to develop traits that increase fitness in a male-biased environment. In contrast, females mature more quickly when high-quality mates are likely to be available. The intensity and the effects on the different sexes can vary quite dramatically and are likely specific to the life history of the organism under study. Further studies are required to determine how taxonomically widespread these situations are, and to identify the diversity of cues and the interactions that are involved.

Is Socially Cued Anticipatory Plasticity Adaptive?

To determine whether any type of developmental plasticity is adaptive requires testing the different phenotypes across the various environments in which each phe-

TABLE 2

A summary of the modalities that immature individuals can use to assess the environment and the types of information that can be gleaned from each

Modality	Scale	Information	Examples
Tactile	Immediate neighbors	Information on density of conspecifics, but may not provide information on sex ratio	Gage 1995 Stockley and Seal 2001 Tan et al. 2004
Acoustic	Population	Limited to the information on the signaling sex Can provide information on quality and density of signalers	Bailey et al. 2010 Kasumovic et al. 2011
Vibratory	Immediate neighbors	Information on quality of signaler	None to date
Chemical	Population	Can provide information on the quality and density of both sexes and, potentially, the OSR Will be limited by wind movement through the environment	Drickamer 1974, 1975 Rodd et al. 1997 Lutnesky and Adkins 2003 Kasumovic and Andrade 2006 Kasumovic et al. 2009
Visual	Local	Can provide information on the density and sex ratio of both sexes and, potentially, the OSR Requires movement to assess population-wide density and sex ratio	Magellan and Magurran 2009 Walling et al. 2007

notype is purported to be adaptive (DeWitt et al. 1998). Each phenotype should be fitter than others within the environment in which it developed in order to be considered adaptive; moreover, a plastic strategy should have higher fitness than a nonplastic strategy across the relevant fluctuations in environmental conditions experienced in natural populations.

Testing for adaptive developmental plasticity of responses to abiotic factors such as temperature and photoperiod, as well as biotic variables such as predator presence is relatively simple as it involves simply rearing individuals in the different environments and then transplanting individuals in the opposite environments to compare their fitness. As the majority of examinations of environmental variables involve binary environments (e.g., predators present or absent) or ones that are simple to control (e.g., temperature, photoperiod), examinations and comparisons of fitness be-

tween environments is relatively simple. This is especially true because the scale of variation in abiotic and predatory factors in both pre- and postmaturation environments is well known in most species where plasticity is of interest.

Examining the adaptive nature of SCAP is relatively more difficult simply because of the more dynamic nature of social cues. First, less is known regarding the scale of variation in social factors as well as the scale that is relevant. As a result, it will be important to understand the life history of the species, or even the population under study. Second, pre- and postmaturation environments will vary for individuals that mature at different times of the season due to differences in the number of mature and mated individuals within the population. Designing relevant experiments depends on whether individuals are cueing into adults already present in the environment, the current cohort of juveniles (and,

therefore, future adults), or both. In fact, as the season progresses and the age structure of the population changes, the relative importance of the traits that are critical for fitness may also shift, resulting in a further feedback for individuals that develop in the future. This makes ascertaining the optimal phenotype difficult in such a dynamic environment, especially if the fitness benefit of plasticity is frequency dependent. Studies should start by examining how the social environment shifts throughout a breeding season and how mean phenotypes shift (Kasumovic et al. 2009). Although this would not answer whether the shifts are adaptive, it would highlight the scales at which social environment varies and the traits that are relevant.

Properly testing the adaptive nature of SCAP requires that the various environments that have triggered the developmental shift are easily reproducible for testing the fitness of multiple individuals. Each individual must also be tested in an independently replicated social environment in order to avoid pseudoreplication and because each experimental individual will itself change the social environment and, therefore, the competitive context. This can require a prohibitively large number of individuals for experiments of fitness. Further, it can be difficult to control the behaviors in the social environment that trigger the developmental shift as individuals can also alter behaviors in response to the social environment. Regardless, to truly understand SCAP and to determine its viability as a mating strategy, researchers must overcome the considerable hurdles if they are to formally test the fitness benefits of plasticity. In most species this goal remains a long way off.

As a result, most studies of SCAP have not yet progressed to formally test the adaptive nature of each phenotype across environments, relying instead on ad hoc arguments based on what is known about the life history and reproductive biology of the organism under study. For example, several studies have shown that rearing individuals at high density resulted in greater sperm numbers or larger testis than individuals reared at lower density (Gage 1995; Stockley 1999; Tan et al. 2004; Bailey et al. 2010). They have all argued that this response is adaptive because high densities are generally characterized by more intense sperm competition. Although this is certainly very likely to be the case as experimental evidence demonstrates that polygynous lines evolve larger testes compared to monogamous ones (e.g., Hosken et al. 2001), individuals were not tested in the various competitive environments to measure fertilization success and, thus, whether the documented plasticity is adaptive.

If adaptive, the magnitude of the fitness benefit remains to be formally established. For example, the adaptive nature of the allocation shifts in redback spiders was examined by utilizing known sperm use patterns associated with mating order that allowed fitness estimates (Kasumovic and Andrade 2009). In crickets, the adaptive nature of the allocation and behavioral shifts was tested by examining male satellite behavior in response to known calls played back to the test male (Bailey et al. 2010). Although fitness was not examined directly in the environment that the individuals were reared in, the experimental designs in both of the above examples allowed testing of behaviors and mating strategies associated with fitness in particular species-specific contexts. Through careful planning, an experimental setup that allows repeatable testing of the behavior (and potential fitness) of an individual's phenotype in different environments can be established.

Evolution of Socially Cued Anticipatory Plasticity

Although there are currently only a few examples of SCAP in animals, the taxonomic sweep of these examples suggests that SCAP is more common than initially thought. Here we outline various ecological, behavioral, and life-history factors that are likely necessary for the evolution of such a developmental tactic, as well as the factors that researchers must be aware of when designing experiments. Although examples of SCAP will not be limited to

species that demonstrate these particular traits, this will likely help in identifying species where such developmental tactics are likely present.

RELIABLE CUES OF FUTURE COMPETITIVE CHALLENGES

The predictability of the environment is an important determinant of the evolution of plasticity. Plasticity is more likely to evolve in accurately predictable environments (Scheiner 1993; Getty 1996). Although predicting variation such as demography initially seems more daunting then predicting large scale environmental variation, we outlined several different modalities that can reliably signal the competitive challenges in the near environment. In such instances, reliable cues that accurately predict future variation are necessary if SCAP is to be a viable strategy. These cues are likely to vary among taxa depending on the life history and ecology of the species under examination, and will further depend on whether generations are discreet or overlapping. Each modality would be ideal for specific environments and reproductive strategies, but a strong understanding of the reproductive biology of the system under study would provide insight into the cues that adults use, and the cues that would therefore be available to juveniles. Alternatively, species with a substantial wandering phase during the juvenile stage would allow individuals to estimate population demographics and may also be more likely to show plasticity in response.

PHYSICAL LIMITATIONS IN MATING OPPORTUNITIES

If mating opportunities are limited, individuals should develop the phenotype most appropriate to the particular challenges they face. Although this is most easily demonstrated in semelparous or monogynous species, limited mating opportunities for one sex can occur because of the high mortality risk during mate searching (Foellmer and Fairbairn 2005; Kasumovic et al. 2007) or mating (Barry and Kokko 2010). Further, the probability of locating the opposite sex may be low (e.g., mantids, Maxwell 1998) and males may not have a second opportunity. In addition, a short mating season or longer interaction time between mating pairs (e.g., mate guarding, biparental care) might also reduce mate searching opportunities (Carroll and Corneli 1995; Herberstein et al. 2005a).

MULTIPLE COMPETITIVE CONTEXTS AND STRONG PHENOTYPE-FITNESS CORRELATIONS

If the social environment fluctuates within a breeding season, the competition an individual experiences will depend on when they either mature or arrive in the population. In addition, if there are strong correlations between the fitness of a phenotype and the competitive context, different phenotypes will maximize fitness in each. This is especially important if opposing traits determine fitness at different times of the season, as can occur in species that have a reproductive life span that is shorter than the breeding season (e.g., most invertebrates). In contrast, a single optimum phenotype may be favored in species where populations have a single synchronous breeding attempt, or long-lived species in which individuals breed many times over successive breeding seasons (e.g., most birds and mammals). Here, individuals may experience multiple, different selective environments throughout their reproductive lifetime, and phenotypes that are able to flourish under a variety of conditions would probably enjoy relatively higher fitness (Van Tienderen 1991). Nonetheless, even in these systems there may be limited opportunities to mate and plastic rules that allow individuals to develop the phenotype with the greatest chance of success may be adaptive.

TEMPORAL VERSUS SPATIAL FLUCTUATIONS IN SELECTION

Theoretic models demonstrate that temporal variation is more likely to lead to the evolution of plasticity than spatial variation

(Levins 1963; Van Tienderen 1991; Moran 1992) simply because temporal variation is more predictable. Although the social environment within a population likely varies in a temporal fashion in the sense that a greater proportion of individuals are adults later versus earlier in the breeding season, if the social environment within a population was purely temporally structured, then plasticity could respond to temporal indicators such as temperature and photoperiod rather than cues of the social structure (e.g., Prudic et al. 2011). The density of males and females also strongly depends on habitat availability, resource abundance, and sex-specific use of the habitat such that the social environment can also be strongly spatially distributed (Kasumovic et al. 2008; Dreiss et al. 2010; Punzalan et al. 2010). The spatial structure within the environment may thus have a more important role in the evolution of SCAP relative to plasticity in response to other cues.

This is demonstrated by a study on two spiders (*N. plumipes and A. keyserlingi*) where male size and body condition correlated strongly with the local social environment and not with the time of the breeding season (Kasumovic et al. 2009). The relevant spatial scale for each species, however, differed and depended on the life history of the species under study. These results demonstrate the necessity of understanding the life history and behavior of the organism in order to correctly identify the relevant scale that needs to be examined. Apart from an a priori understanding of the appropriate scale, studies of SCAP would benefit from the use of spatial analyses that would allow spatial hypothesis testing.

the importance of the adult versus juvenile cohort and population feedback

The rivals and mates that immature individuals will interact with depend on the life history of the species under study, including how synchronously individuals mature/ arrive to breeding grounds and whether there are overlapping generations. The time frame over which individuals mature will af-fect who newly maturing individuals will be competing against. For example, if individuals within a population mature more synchronously, then newly mature individuals will be competing against others of the same age, and individuals should be assessing the juvenile cohort. The more asynchronous the timing between the first and last emergence, the more likely individuals will be competing against adults that are already present in the population. As maturation (or arrival to breeding grounds) becomes less synchronous, there will likely be a point at which individuals will be competing equally with both individuals from the juvenile and adult cohort. Currently, studies of SCAP only focus on the effect of either the juvenile or adult cohort, but in other species, individuals may use cues of both.

Understanding the link between the juvenile social environment and the selective pressures is undoubtedly complex, as the phenotype-fitness association is partly a consequence of the biotic and abiotic environments in which an individual develops (i.e., ecogenetic feedback, Kokko and López-Sepulcre 2007). As a result, the degree of plasticity can change the intensity and direction of selection that individuals encounter as shifts in development change phenotypic distributions and the resulting interactions between individuals (Agrawal 2001; Fordyce 2006).

Conclusion

An individual's fitness depends on the match between its phenotype and the environment; with the number, quality, and strategies of rivals being an essential component of the environment. Just like other types of plasticity, a developmental response to a social environment can evolve if it allows individuals to enjoy higher fitness than fixed phenotypes in a variable, but predictable, environment. In recent years, several examples of socially cued plasticity have been published in a variety of taxa and in which juveniles use cues across each of the available modalities. We predict that SCAP is probably more widespread than appreciated.

It is the developmental system as much as the developed phenotype that deter-

mines individual fitness. To truly determine if this is the case requires further examinations of the fitness benefits and costs of SCAP across multiple environments. We urge researchers to use the knowledge regarding the life history and behavior of their study organisms to examine the role social environments play in introducing and maintaining variation within and between populations. Insights from the plant literature may be particularly useful in this case. For example, although plants do not respond to the "social" environment in the same way as animals do, plants alter their allocation of resources toward root (Casper and Jackson 1997) or leaf (Schmitt and Wulff 1993) structures in response to competition from both conspecifics and heterospecifics. How individuals interact through competition is well understood (Callaway et al. 2003; Novoplansky 2009), and how these interactions can limit plasticity and phenotypes are also relatively more explored in plants (Cipollini 2004; Valla-

dares et al. 2007). Further integration of quantitative genetic tools such as isolines, inbred families, and animal models with research on developmental shifts will provide a greater understanding of how and why population phenotypes shift within and between breeding seasons, thereby providing insight into the evolution of the traits themselves. This is an exciting new direction that researchers can take by integrating the ecology, behavior, and natural history of an organism with development and genomics to improve our understanding of the evolution of complex traits and behaviors.

REFERENCES

Adler F. R., Harvell C. D. 1990. Inducible defenses, phenotypic variability and biotic environments. *Trends in Ecology and Evolution* 5:407–410.

Agrawal A. A. 2001. Phenotypic plasticity in the interactions and evolution of species. *Science* 294:321–326.

Arnqvist G., Rowe L. 2005. *Sexual Conflict*. Princeton (NJ): Princeton University Press.

Bailey N. W., Gray B., Zuk M. 2010. Acoustic experience shapes alternative mating tactics and reproductive investment in male field crickets. *Current Biology* 20:845–849.

Barry K. L., Kokko H. 2010. Male mate choice: why sequential choice can make its evolution difficult. *Animal Behaviour* 80:163–169.

Benard M. F. 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. *Annual Review of Ecology, Evolution, and Systematics* 35:651–673.

Bentsen C. L., Hunt J., Jennions M. D., Brooks R. 2006. Complex multivariate sexual selection on male acoustic signaling in a wild population of *Teleogryllus commodus*. *American Naturalist* 167: E102–E116.

Berrigan D., Scheiner S. M. 2004. Modelling the evolution of phenotypic plasticity. Pages 82–97 in *Phenotypic Plasticity: Functional and Conceptual Approaches*, edited by T. J. DeWitt and S. M. Scheiner. Oxford (UK): Oxford University Press.

Bradshaw A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13:115–155.

Brooks R., Hunt J., Blows M. W., Smith M. J., Bussière L. F., Jennions M. D. 2005. Experimental evidence for multivariate stabilizing sexual selection. *Evolution* 59:871–880.

Caldwell M. S., Johnston G. R., McDaniel J. G., Warkentin K. M. 2010. Vibrational signaling in the agonistic interactions of red-eyed treefrogs. *Current Biology* 20:1012–1017.

Callaway R. M., Pennings S. C., Richards C. L. 2003. Phenotypic plasticity and interactions among plants. *Ecology* 84:1115–1128.

Carroll S. P., Corneli P. S. 1995. Divergence in male mating tactics between two populations of the soapberry bug. II. Genetic change and the evolution of a plastic reaction norm in a variable social environment. *Behavioral Ecology* 6:46–56.

Carroll S. P., Salamon M. H. 1995. Variation in sexual selection on male body size within and between populations of the soapberry bug. *Animal Behaviour* 50:1463–1474.

Casper B. B., Jackson R. B. 1997. Plant competition

underground. *Annual Review of Ecology and Systematics* 28:545–570.

Castellanos I., Barbosa P. 2006. Evaluation of predation risk by a caterpillar using substrate-borne vibrations. *Animal Behaviour* 72:461–469.

Cipollini D. 2004. Stretching the limits of plasticity: can a plant defend against both competitors and herbivores? *Ecology* 85:28–37.

Cocroft R. B., Rodríguez R. L. 2005. The behavioral ecology of insect vibrational communication. *BioScience* 55:323–334.

DeWitt T. J., Sih A., Wilson D. S. 1998. Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* 13:77–81.

Dreiss A. N., Cote J., Richard M., Federici P., Clobert J. 2010. Age- and sex-specific response to population density and sex ratio. *Behavioral Ecology* 21: 356–364.

Drickamer L. C. 1974. Sexual maturation of female house mice: social inhibition. *Developmental Psychobiology* 7:257–265.

Drickamer L. C. 1975. Female mouse maturation: relative importance of social factors and daylength. *Journal of Reproduction and Fertility* 44:147–150.

Drickamer L. C. 1977. Delay of sexual maturation in female house mice by exposure to grouped females or urine from grouped females. *Journal of Reproduction and Fertility* 51:77–81.

Elias D. O., Mason A. C., Maddison W. P., Hoy R. R. 2003. Seismic signals in a courting male jumping spider (Araneae: Salticidae). *Journal of Experimental Biology* 206:4029–4039.

Elias D. O., Kasumovic M. M., Punzalan D., Andrade M. C. B., Mason A. C. 2008. Assessment during aggressive contests between male jumping spiders. *Animal Behaviour* 76:901–910.

Fertin A., Casas J. 2007. Orientation towards prey in antlions: efficient use of wave propogation in sand. *Journal of Experimental Biology* 210:3337–3343.

Foelix R. F. 1982. *Biology of Spiders*. Cambridge (MA): Harvard University Press.

Foellmer M. W., Fairbairn D. J. 2004. Males under attack: sexual cannibalism and its consequences for male morphology and behavior in an orb-weaving spider. *Evolutionary Ecology Research* 6:163–181.

Foellmer M. W., Fairbairn D. J. 2005. Selection on male size, leg length and condition during mate search in a sexually highly dimorphic orb-weaving spider. *Oecologia* 142:653–662.

Fordyce J. A. 2006. The evolutionary consequences of ecological interactions mediated through phenotypic plasticity. *Journal of Experimental Biology* 209: 2377–2383.

Gage M. J. G. 1995. Continuous variation in reproductive strategy as an adaptive response to population density in the moth *Plodia interpunctella*. *Proceedings of the Royal Society, Series B: Biological Sciences* 261:25–30.

Garland Jr. T., Kelly S. A. 2006. Phenotypic plasticity and experimental evolution. *Journal of Experimental Biology* 209:2344–2361.

Gaskett A. C. 2007. Spider sex pheromones: emission, reception, structures, and functions. *Biological Reviews* 82:27–48.

Gaskett A. C., Herberstein M. E., Downes B. J., Elgar M. A. 2004. Changes in male mate choice in a sexually cannibalistic orb-web spider (Araneae: Araneidae). *Behaviour* 141:1197–1210.

Getty T. 1996. The maintenance of phenotypic plasticity as a signal detection problem. *American Naturalist* 148:378–385.

Gil D., Bulmer E., Celis P., López-Rull I. 2008. Adaptive developmental plasticity in growing nestlings: sibling competition induces differential gape growth. *Proceedings of the Royal Society, Series B: Biological Sciences* 275:549–554.

Grant J. W. A., Bryant M. J., Soos C. E. 1995. Operational sex ratio, mediated by synchrony of female arrival, alters the variance of male mating success in Japanese medaka. *Animal Behaviour* 49:367–375.

Green J. 1967. The distribution and variation of *Daphnia lumholtzi* (Crustacea: Cladocera) in relation to fish predation in Lake Albert, East Africa. *Journal of Zoology* 151:181–197.

Gwynne D. T., Bussière L. F. 2002. Female mating swarms increase predation risk in a "role-reversed" dance fly (Diptera: Empididae: *Rhamphomyia longicauda* Loew). *Behaviour* 139:1425–1430.

Herberstein M. E., Elgar M. A. 1994. Foraging strategies of *Eriophora transmarine* and *Nephila plumipes* (Aranea: Araneoida): nocturnal and diurnal orb-weaving spiders. *Australian Journal of Ecology* 19: 451–457.

Herberstein M. E., Barry K. L., Turoczy M. A., Wills E., Youssef C., Elgar M. A. 2005a. Post-copulation mate guarding in the sexually cannibalistic St Andrew's Cross spider (Araneae Araneidae). *Ethology Ecology & Evolution* 17:17–26.

Herberstein M. E., Gaskett A. C., Schneider J. M., Vella N. G. F., Elgar M. A. 2005b. Limits to male copulation frequency: sexual cannibalism and sterility in St Andrew's Cross spiders (Aranea, Araneidae). *Ethology* 111:1050–1061.

Hill P. S. M. 2008. *Vibrational Communication in Animals*. Cambridge (MA): Harvard University Press.

Hill P. S. M. 2009. How do animals use substrate-borne vibrations as an information source? *Naturwissenschaften* 96:1355–1371.

Hoback W. W., Wagner Jr. W. E. 1997. The energetic cost of calling in the variable field cricket, *Gryllus lineaticeps*. *Physiological Entomology* 22:286–290.

Hosken D. J., Garner T. W. J., Ward P. I. 2001. Sexual

conflict selects for male and female reproductive characters. *Current Biology* 11:489–493.

Hunt J., Brooks R., Jennions M. D., Smith M. J., Bentsen C. L., Bussière L. F. 2004. High-quality male field crickets invest heavily in sexual display but die young. *Nature* 432:1024–1027.

Kasumovic M. M., Andrade M. C. B. 2006. Male development tracks rapidly shifting sexual versus natural selection pressures. *Current Biology* 16: R242–R243.

Kasumovic M. M., Andrade M. C. B. 2009. A change in competitive context reverses sexual selection on male size. *Journal of Evolutionary Biology* 22:324–333.

Kasumovic M. M., Bruce M. J., Herberstein M. E., Andrade M. C. B. 2007. Risky mate search and mate preference in the golden orb-web spider (*Nephila plumipes*). *Behavioral Ecology* 18:189–195.

Kasumovic M. M., Bruce M. J., Andrade M. C. B., Herberstein M. E. 2008. Spatial and temporal demographic variation drives within-season fluctuations in sexual selection. *Evolution* 62:2316–2325.

Kasumovic M. M., Bruce M. J., Herberstein M. E., Andrade M. C. B. 2009. Evidence for developmental plasticity in response to demographic variation in nature. *Ecology* 90:2287–2296.

Kasumovic M. M., Hall M. D., Try H., Brooks R. 2011. The importance of listening: juvenile allocation shifts in response to acoustic cues of the social environment. *Journal of Evolutionary Biology* 24: 1325–1334.

Kokko H., López-Sepulcre A. 2007. The ecogenetic link between demography and evolution: can we bridge the gap between theory and data? *Ecology Letters* 10:773–782.

Kokko H., Monaghan P. 2001. Predicting the direction of sexual selection. *Ecology Letters* 4:159–165.

Kokko H., Rankin D. J. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society, Series B: Biological Sciences* 361:319–334.

Lailvaux S. P., Kasumovic M. M. 2010. Defining individual quality over lifetimes and selective contexts. *Proceedings of the Royal Society, Series B: Biological Sciences* 278:321–328.

Laurila A., Karttunen S., Merilä J. 2002. Adaptive phenotypic plasticity and genetics of larval life histories in two *Rana temporaria* populations. *Evolution* 56:617–627.

Levins R. 1963. Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. *American Naturalist* 97:75–90.

Lihoreau M., Rivault C. 2008. Tactile stimuli trigger group effects in cockroach aggregations. *Animal Behaviour* 75:1965–1972.

Lively C. M. 1986. Canalization versus developmental

conversion in a spatially variable environment. *American Naturalist* 128:561–572.

Loman J. 1999. Early metamorphosis in common frog *Rana temporaria* tadpoles at risk of drying: an experimental demonstration. *Amphibia-Reptilia* 20: 421–430.

Lutnesky M. M. F., Adkins J. W. 2003. Putative chemical inhibition of development by conspecifics in mosquitofish, *Gambusia affinis*. *Environmental Biology of Fishes* 66:181–186.

Magellan K., Magurran A. E. 2009. The effect of social environment during ontogeny on life history expression in the guppy *Poecilia reticulata*. *Journal of Fish Biology* 74:2329–2337.

Mainwaring M. C., Dickens M., Hartley I. R. 2010. Environmental and not maternal effects determine variation in offspring phenotypes in a passerine bird. *Journal of Evolutionary Biology* 23:1302–1311.

Matter S. F., Roland J. 2002. An experimental examination of the effects of habitat quality on the dispersal and local abundance of the butterfly *Parnassius smintheus*. *Ecological Entomology* 27:308–316.

Maxwell M. R. 1998. Seasonal adult sex ratio shift in the praying mantid *Iris oratoria* (Mantodea: Mantidae). *Environmental Entomology* 27:318–323.

Moore A. J., Brodie III E. D., Wolf J. B. 1997. Interacting phenotypes and the evolutionary process. I. Direct and indirect genetic effects of social interactions. *Evolution* 51:1352–1362.

Moran N. A. 1992. The evolutionary maintenance of alternative phenotypes. *American Naturalist* 139: 971–989.

Moya-Laraño J., El-Sayyid M. E. T., Fox C. W. 2007. Smaller beetles are better scramble competitors at cooler temperatures. *Biology Letters* 3:475–478.

Murlis J., Elkinton J. S., Cardé R. T. 1992. Odor plumes and how insects use them. *Annual Review of Entomology* 37:505–532.

Novoplansky A. 2009. Picking battles wisely: plant behaviour under competition. *Plant, Cell and Environment* 32:726–741.

Nylin S., Gotthard K. 1998. Plasticity in life-history traits. *Annual Review of Entomology* 43:63–83.

Parker G. A. 2006. Sexual conflict over mating and fertilization: an overview. *Philosophical Transactions of the Royal Society, Series B: Biological Sciences* 361: 235–259.

Pigliucci M. 2001. *Phenotypic Plasticity: Beyond Nature and Nurture*. Baltimore (MD): John Hopkins University Press.

Prudic K. L., Jeon C., Cao H., Monteiro A. 2011. Developmental plasticity in sexual roles of butterfly species drives mutual sexual ornamentation. *Science* 331:73–75.

Punzalan D., Rodd F. H., Rowe L. 2010. Temporally variable multivariate sexual selection on sexually

dimorphic traits in a wild insect population. *American Naturalist* 175:401–414.

Relyea R. 2002. Costs of phenotypic plasticity. *American Naturalist* 159:272–282.

Rodd F. H., Reznick D. N., Sokolowski M. B. 1997. Phenotypic plasticity in the life history traits of guppies: responses to social environment. *Ecology* 78:419–433.

Roessingh P., Bouaïchi A., Simpson S. J. 1998. Effects of sensory stimuli on the behavioural phase state of the desert locust, *Schistocerca gregaria. Journal of Insect Physiology* 44:883–893.

Rogers S. M., Matheson T., Despland E., Dodgson T., Burrows M., Simpson S. J. 2003. Mechanosensory-induced behavioural gregarization in the desert locust *Schistocerca gregaria. Journal of Experimental Biology* 206:3991–4002.

Scheiner S. M. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* 24:35–68.

Schmitt J., Wulff R. D. 1993. Light spectral quality, phytochrome and plant competition. *Trends in Ecology and Evolution* 8:47–51.

Schneider J. M., Elgar M. A. 2001. Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea): female and male perspectives. *Behavioral Ecology* 12:547–552.

Shorey H. H. 1976. *Animal Communication by Pheromones.* New York: Academic Press.

Simpson S. J., McCaffery A. R., Hägele B. F. 1999. A behavioural analysis of phase change in the desert locust. *Biological Reviews of the Cambridge Philosophical Society* 74:461–480.

Snow L. S. E., Andrade M. C. B. 2004. Pattern of sperm transfer in redback spiders: implications for sperm competition and male sacrifice. *Behavioral Ecology* 15:785–792.

Snow L. S. E., Andrade M. C. B. 2005. Multiple sperm storage organs facilitate female control of paternity. *Proceedings of the Royal Society, Series B: Biological Sciences* 272:1139–1144.

Stockley P. 1999. Sperm selection and genetic incompatibility: does relatedness of mates affect male success in sperm competition? *Proceedings of the Royal Society, Series B: Biological Sciences* 266:1663–1669.

Stockley P., Seal N. J. 2001. Plasticity in reproductive effort of male dung flies (*Scatophaga stercoraria*) as a response to larval density. *Functional Ecology* 15:96–102.

Stoltz J. A., Elias D. O., Andrade M. C. B. 2009. Male courtship effort determines female response to competing rivals in redback spiders. *Animal Behaviour* 77:79–85.

Su K. F. Y., Li D. 2006. Female-biased predation risk and its differential effect on the male and female courtship behavior of jumping spiders. *Animal Behaviour* 71:531–537.

Tan G. N., Govedich F. R., Burd M. 2004. Social group size, potential sperm competition and reproductive investment in a hermaphroditic leech, *Helobdella papillornata* (Euhirudinea: Glossiphoniidae). *Journal of Evolutionary Biology* 17:574–580.

Valladares F., Gianoli E., Gómez J. M. 2007. Ecological limits to plant phenotypic plasticity. *New Phytologist* 176:749–763.

Van Tienderen P. H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution* 45:1317–1331.

Via S., Gomulkiewicz R., De Jong G., Scheiner S. M., Schlichting C. D., Van Tienderen P. H. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology and Evolution* 10:212–217.

Walling C. A., Royle N. J., Metcalfe N. B., Linström J. 2007. Green swordtails alter their age at maturation in response to the population level of male ornamentation. *Biology Letters* 3:144–146.

Warkentin K. M. 2005. How do embryos assess risk? Vibrational cues in predator-induced hatching of red-eyed treefrogs. *Animal Behaviour* 70:59–71.

West-Eberhard M. J. 2003. *Developmental Plasticity and Evolution.* Oxford (UK): Oxford University Press.

Wiklund C., Fagerström T. 1977. Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. *Oecologia* 31:153–158.

Wolf J. B., Brodie III E. D., Cheverund J. M., Moore A. J., Wade M. J. 1998. Evolutionary consequences of indirect genetic effects. *Trends in Ecology and Evolution* 13:64–69.

Zuk M., Rotenberry J. T., Tinghitella R. M. 2006. Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biology Letters* 2:521–524.

Handling Editor: Maria R. Servedio