

Opinion

Adaptive Plasticity as a Fitness Benefit of Mate Choice

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Phenotypic plasticity and sexual selection can each promote adaptation in variable environments, but their combined influence on adaptive evolution is not well understood. We propose that sexual selection can facilitate adaptation in variable environments when individuals prefer mates that produce adaptively plastic offspring. We develop this hypothesis and review existing studies showing that diverse groups display both sexual selection and plasticity in non-sexual traits. Thus, plasticity could be a widespread but unappreciated benefit of mate choice. We describe methods and opportunities to test this hypothesis and describe how sexual selection might foster the evolution of phenotypic plasticity. Understanding this interplay between sexual selection and phenotypic plasticity might help predict which species will adapt to a rapidly changing world.

Phenotypic Plasticity and Sexual Selection

Researchers have long recognized that sexual selection and **phenotypic plasticity** (see [Glossary](#)) can each play key roles in diverse ecological and evolutionary processes [1–4]. Less widely appreciated is that sexual selection and plasticity can interact in ways that influence how these processes unfold. One such process that this interaction can impact is adaptive evolution.

A way that sexual selection, acting alone, can promote adaptive evolution is when sexual traits (e.g., female **mate preferences** or male **sexual signals**) predict offspring fitness [5–8]. For example, males might produce condition-dependent sexual displays that predict the fitness of their offspring (e.g., because good-condition males transmit fewer deleterious and more beneficial alleles to their offspring relative to lower-condition males [5–10]). If females preferentially mate with males that express exaggerated forms of those condition-dependent displays, and produce fitter offspring as a result, sexual selection thereby fosters adaptation [7–10]. However, some have argued that maintaining this type of relationship between sexual traits and offspring fitness requires consistent selection [11–13]. This is problematic because most environments vary in space and time. Such variation can cause the selective environments that adults experience to differ from those that their offspring experience. In these situations, sexual traits would likely fail to predict offspring fitness, which would preclude sexual selection from promoting adaptation [3,13–16].

Sexual selection could promote adaptation in variable environments by favoring plasticity in mate preferences or sexual signals [3,6,12,16,17]. Under such circumstances, sexual traits that maximize offspring fitness in a particular environmental context would be expressed only in that context when parents assess the environment and respond by altering their sexual traits through plasticity. Yet, if parental and offspring environments are so different that parents cannot assess the conditions that their offspring will experience, then even plasticity in sexual traits would fail to promote adaptive evolution [11–16,18]. Moreover, offspring of a given pairing might experience selective pressures that differ not only from those experienced by the parents, but also from

Highlights

That offspring plasticity can serve as a fitness benefit of mate choice is relatively underexplored, but the ubiquity of both adaptive plasticity and mate choice suggests it may be common.

In contrast to some models of sexual selection, when offspring plasticity is a benefit of mate choice, environmental variation need not erode associations between sexual traits and offspring fitness. Thus, the hypothesis that offspring plasticity can serve as a fitness benefit of mate choice may help resolve longstanding questions regarding associations between sexual traits and offspring fitness.

That offspring plasticity can serve as a fitness benefit of mate choice has important implications for adaptive evolution in novel or variable environments and for the evolution of plasticity.

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those experienced by their siblings. Thus, plasticity in parents' sexual traits might be unable to optimize the fitness of all their offspring [3,13,19].

Yet, there is a way that sexual selection can promote adaptation, even in variable environments where parents cannot assess their offspring's environment(s) or in situations where parents cannot facultatively modify their sexual traits. Specifically, individuals could choose mates that produce adaptively plastic offspring. Essentially, individuals could select mates whose offspring adaptively assess and respond to their environment [18]; in other words, offspring plasticity could be a fitness benefit of mate choice. Such offspring plasticity would arise when individuals choose mates that either pass on genetic or nongenetic variation to offspring that enables offspring to respond facultatively to the environment, or provide resources to the choosy individual that enables the production of plastic offspring (e.g., nuptial gifts, *sensu* [20], that, when allocated to offspring, enable greater plasticity). Regardless of how the benefit of offspring plasticity is conferred, plasticity in offspring traits, as opposed to plasticity in adult sexual traits, should arise under conditions where parent and offspring environments differ and where parental plasticity is either not possible or disfavored (Table 1 and Box 1).

The hypothesis that offspring plasticity could function as a fitness benefit of mate choice rests on conventional predictions of mate choice theory (*sensu* [1]). Nevertheless, the potential for plasticity and sexual selection to interact in this way has important implications for both how adaptation can proceed in variable environments and the evolution of plasticity *per se*. Before discussing these evolutionary implications, we first develop the hypothesis in greater detail.

Offspring Plasticity as a Fitness Benefit of Mate Choice

When individuals prefer mates that produce plastic offspring, such offspring plasticity could constitute a fitness benefit of mate choice. Offspring plasticity could take many forms (Table 2), including: the expression of alternative morphologies in early development [18,21], greater behavioral flexibility in coping with their environment [22], or even the expression of adult traits [3,6,12,16,17]. However, our focus here is plasticity involving offspring (not parents) assessing and responding to their environment and that is expressed prior to sexual maturity (Table 1). Such plasticity is common in nature and frequently influences offspring survival (Table 2). Importantly, plasticity expressed prior to maturity is not only a potential fitness benefit of mate choice, but can also continue to be expressed and/or have important effects on phenotypes and fitness in sexually mature individuals (Table 2).

To illustrate how plasticity can serve as a fitness benefit of mate choice, consider Mexican spadefoot toads (*Spea multiplicata*; Figure 1). *Spea* tadpoles can develop as either an omnivore phenotype with generalized tadpole morphology and diet, or as a distinctive carnivore phenotype, which possesses features that allow it to specialize on large, mobile animal prey, such as anostracan fairy shrimp or other tadpoles [23]. This carnivore phenotype is induced when a young tadpole eats fairy shrimp or other tadpoles [24] (i.e., *Spea* tadpoles exhibit diet-induced phenotypic plasticity).

Neither alternative phenotype is intrinsically superior to the other. Rather, intraspecific resource competition gives rise to negative frequency-dependent disruptive selection, which maintains both phenotypes in the same pond [23]. Such selection generates equilibrium frequencies of the two phenotypes, which vary across ponds and years [23]. Consequently, the optimal developmental strategy for a tadpole is to possess plasticity to become either an omnivore or a carnivore [23,24]. Critically, this plasticity is greatest among *S. multiplicata* tadpoles sired by the relatively high-condition, fast-calling males with which females prefer to mate [18,25–27].

Glossary

Cryptic genetic variation: genetic variation that is not expressed phenotypically under normal conditions. Such variation can be revealed phenotypically when a population experiences a new environment (i.e., it can be revealed through plasticity).

Mate preference: any sensory, behavioral, or other trait of the choosing sex that shapes, in part, individuals' likelihoods of mating with members of the opposite sex that express certain phenotypes.

Nongenetic factors: any one of the various epigenetic factors (e.g., patterns of DNA methylation), behavioral factors (e.g., cultural transmission), or environmental factors (e.g., noncoding RNAs or microorganisms) that, independently of DNA sequence variation, can influence phenotype production, be transmitted across generations, and mediate evolutionary change.

Phenotypic plasticity: the capacity of an individual organism to alter its features in direct response to changes in environmental conditions; sometimes used synonymously with developmental plasticity. Although this capacity is often assumed to be adaptive (i.e., enhance the individual's fitness), it need not be.

Plasticity-led evolution: an evolutionary process that occurs when a change in the environment triggers a change in phenotype via phenotypic plasticity in an ancestral lineage and this pre-existing plasticity is subsequently refined by selection into an adaptive phenotype in a derived lineage; sometimes referred to as plasticity-first evolution.

Reaction norm: a graphical representation of the set of phenotypes that a single genotype produces in response to some specific environmental variable(s); individuals show plasticity if their reaction norm is nonhorizontal.

Sexual signals: behaviors, ornaments, or other traits that enhance mating success with the choosing sex in mating-related contexts.

Table 1. General Conditions Favoring the Evolution of Mate Preferences for Individuals That Produce Adaptively Plastic Offspring

Condition	Reason the condition matters	Situations in which condition might arise
Spatially or temporally variable environment that is predictable, owing to salient, reliable cues to impending or prevailing environmental conditions.	Favors the evolution of plasticity in general [37,38,79].	Any varying environment in which predictive cues occur.
Offspring fitness is frequency-dependent.	Parents cannot predict which offspring traits will be favored (because it will depend on what traits are assumed by others in the offspring's generation).	Competitive situations, which can generate negative frequency-dependent disruptive selection [80].
Reliable cues about the environment unavailable to parents or are more effectively assessed by offspring.	Parents cannot predict which offspring traits will be favored if cues are unavailable to them [16,18]. Plasticity in the offspring versus the parents is favored if offspring can better assess environmental cues (<i>sensu</i> [37,38,79]).	Any system where the parents' and offspring's environment are decoupled because adults mate in times or locations that differ from where offspring develop. This includes: (i) systems in which adults mate in a different season or location from when or where offspring develop (e.g., [38,74,75]); (ii) species with complex life histories in which adults and offspring inhabit disparate niches (e.g., aquatic and terrestrial) [73].
Parents' ability to express plasticity is too costly or limited relative to costs or limits of plasticity in offspring (<i>sensu</i> [81]).	Favors the evolution of plasticity in offspring as opposed to the parents.	Any system where plasticity is differentially favored or is differentially likely to evolve in parents versus offspring, including: (i) taxa with complex life histories in which plasticity is favored only in early life stages (e.g., [38,74,75]); (ii) taxa in which early (but not late) expression of plasticity is required for the development of optimal trait integration [46,76–78]; (iii) taxa in which adults have few, if any, opportunities for multiple matings (such systems would be less likely to evolve plasticity in sexual traits) [1,3]; (iv) systems in which sexual traits are under countervailing selective pressures that favor constitutive, as opposed to plastic, expression [1,3].

Box 1. A Context Where Offspring Plasticity Is Likely to Serve as a Fitness Benefit of Mate Choice

Many of the conditions that favor offspring plasticity as a benefit of mate choice are especially likely to arise among species with complex life histories, where juvenile and adult life stages are separated by a major developmental event: metamorphosis [73]. This developmental mode is predominant among animals [73], and animals with complex life histories (e.g., arthropods, fish, and amphibians) are frequently used to study mate choice and its fitness consequences [1,3]. A key feature of complex life histories is that parents and offspring express distinct phenotypes that are adapted to different ecological circumstances [73]. Moreover, in species with complex life histories, plasticity appears to be more commonly expressed in early, as opposed to later, life stages (e.g., [38,74,75]), possibly because adult environments are less variable than those of juveniles or because adults are more constrained in their ability to express plasticity than are juveniles [46,76–78]. Regardless of why plasticity is more likely in juveniles, species with complex life histories provide particularly good candidate systems for evaluating whether plasticity can serve as a fitness benefit of mate choice.

Table 2. Evidence of Genetic Variation in Plasticity as well as of Sexual Selection in Selected Animals^a

Taxon	Evidence of plasticity exhibiting G × E					Evidence of sexual selection		
	Trait(s)	Stimulus/source of environmental variation	Fitness enhancing?	Level of G × E	Refs	Mate choice	Sexual signals	Refs
Cladocera: water flea, <i>Daphnia pulex</i>	Size and age at maturity	Predator cue concentration	Possibly	Sibship, population	[82]	Cyclically parthenogenetic; whether and how mate choice occurs is uncertain; females flee from males that pursue them, possibly imposing selection on male pursuit ability	Unclear: males pursue females	[83]
Insect (Diptera): fruit fly, <i>Drosophila melanogaster</i>	Body size and wing length	Temperature	Possibly	Sibship, population	[84]	Mutual mate choice; males preferentially mate with larger females; females choose mates via a combination of male signals	Males express visual, auditory, and tactile signals in the course of 'courtship dances' and associated mating behaviors	[85]
Insect (Diptera): yellow dung fly, <i>Scathophaga stercoraria</i>	Rates of growth and development, body size	Resource availability, conspecific density	Yes	Sibship	[86]	Female choice is primarily cryptic and based on male genotypes at the phosphoglucosylase locus	Male phosphoglucosylase genotype may be signaled by hydrocarbons	[87]
Insect (Lepidoptera): squinting bush brown butterfly, <i>Bicyclus anynana</i>	Wing morphology and color	Developmental temperature	Yes	Sibship, sex, population	[88]	Females choose mates on the basis of a complex set of male mating traits	Males perform ritualized courtship behaviors, emit sex pheromones, and advertise wing pattern, coloration, and size to attract females	[89]
Insect (Blattodea): Chinese cockroach, <i>Eupolyphaga sinensis</i>	Rates of growth and development	Developmental temperature	Possibly	Sex, population	[90]	Unclear; exhibits sexual size dimorphism in which females are always larger	Like most cockroaches, females emit sex pheromones to attract males	[91,92]
Insect (Coleoptera): Asian lady beetle, <i>Harmonia axyridis</i>	Development time, adult size	Novel trophic resource	Possibly	Sibship	[93]	Females preferentially mate with males with bright elytra coloration	Elytra coloration	[94]
Insect (Coleoptera): leaf beetle, <i>Oreina</i> spp.	Development time, growth	Host-plant fungal infection	Yes	Population, species	[95]	Females choose mates on the basis of chemical-defense production and body size; males preferentially mate with large females	Male indicators of chemical-defense production unclear	[96]
Insect (Coleoptera): seed beetle, <i>Stator limbatus</i>	Survivorship, body size, female fecundity	Developmental temperature	Possibly	Population	[97]	Females prefer large males	Unclear whether females assess anything other than male body size	[98]
Insect (Hymenoptera): Ichneumon wasp, <i>Venturia canescens</i>	Body size, development rate, fecundity	Developmental temperature	Possibly	Population	[99]	Males preferentially mate with non-kin	Females emit sex pheromones that attract males	[100,101]
Echinodermata: pebble-collector urchin, <i>Pseudoboletia Indiana</i> , and crown of thorns	Embryonic and larval acidity and thermal tolerances	Ocean acidification and warming	Yes	Sibship	[102,103]	Gamete-mediated mate choice via bindin-protein recognition	No reported adult sexual signals	[104]

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Table 2. (continued)

Taxon	Evidence of plasticity exhibiting G × E					Evidence of sexual selection		
	Trait(s)	Stimulus/source of environmental variation	Fitness enhancing?	Level of G × E	Refs	Mate choice	Sexual signals	Refs
starfish, <i>Acanthaster planci</i>								
Fish: three-spined stickleback, <i>Gasterosteus aculeatus</i>	Larval and juvenile growth rate, survival	Salinity of developmental environment	Yes	Sibship, population	[105]	Females choose mates on the basis of several male traits	Males advertise red coloration, courtship dances, and nest quality to attract females	[106,107]
Fish: pumpkinseed, <i>Lepomis gibbosus</i>	Body shape, trophic morphology	Interspecific competition, resource availability, microhabitat use	Yes	Sibship, population	[108]	Females are attracted to male nest sites; specific signals are unclear, but possibly a combination of male traits and nest characteristics	Specific signals are unclear, but males attract females to their nests, which are concentrated in shallow waters	[109,110]
Fish: mouthbrooder cichlid, <i>Pseudocrenilabrus multicolor victoriae</i>	Brain mass	Dissolved oxygen in developmental environment	Yes	Sibship, population	[111]	Females select mates on the basis of courtship displays and fin coloration	Males attract females via 'mating wiggle' displays and 'egg spots' on anal fins	[112]
Fish: Japanese rice fish, <i>Oryzias latipes</i>	Growth rate	Developmental temperature	Possibly	Sibship, population	[113]	Females choose mates on the basis of secondary sexual characters and courtship behaviors	Males advertise fin ornaments and perform courtship behaviors	[114,115]
Fish: crimson-spotted rainbowfish, <i>Melanotaenia duboulayi</i>	Gene expression at loci involved in responses to temperature	Developmental temperature	Possibly	Sibship	[116]	Females prefer males with high display rates and most commonly mate with dominant, large, bold males	Males compete for dominance and dominant males exhibit active, bold behavioral syndromes and high display rates	[117,118]
Amphibians (frogs): Cope's gray treefrog, <i>Hyla chrysoscelis</i> , and eastern gray treefrog, <i>Hyla versicolor</i>	Tadpole tail morphology, foraging behavior	Predation cues	Yes	Sibship, population	[119–121]	Females choose mates on the basis of call characteristics	Males form aggregations and call to attract females	[122,123]
Amphibian (frog): wood frog, <i>Lithobates sylvaticus</i> (<i>Rana sylvatica</i>)	Tadpole tail morphology, foraging behavior	Predation cues	Yes	Sibship, population	[124]	Sexual selection driven primarily by scramble competition among males, but males preferentially mate with relatively large females	Males form aggregations and call to attract females	[125]
Amphibian (frog): moor frog, <i>Rana arvalis</i>	Tadpole acidity tolerance	Pond acidification	Yes	Sibship, population	[126]	Sexual selection driven primarily by scramble competition among males, but females preferentially mate with males with high fertilization success	Males form aggregations and call to attract females; trait(s) associated with male fertilization success unknown	[127]
Amphibian (salamander): slender salamanders, <i>Batrachoseps</i> spp.	Number of trunk vertebrae	Developmental temperature	Possibly	Sibship, population, species	[128]	Unclear, but pheromones are implicated at least at the level of species recognition	Possibly pheromones	[129]

^aAll examples show plasticity prior to sexual maturity.

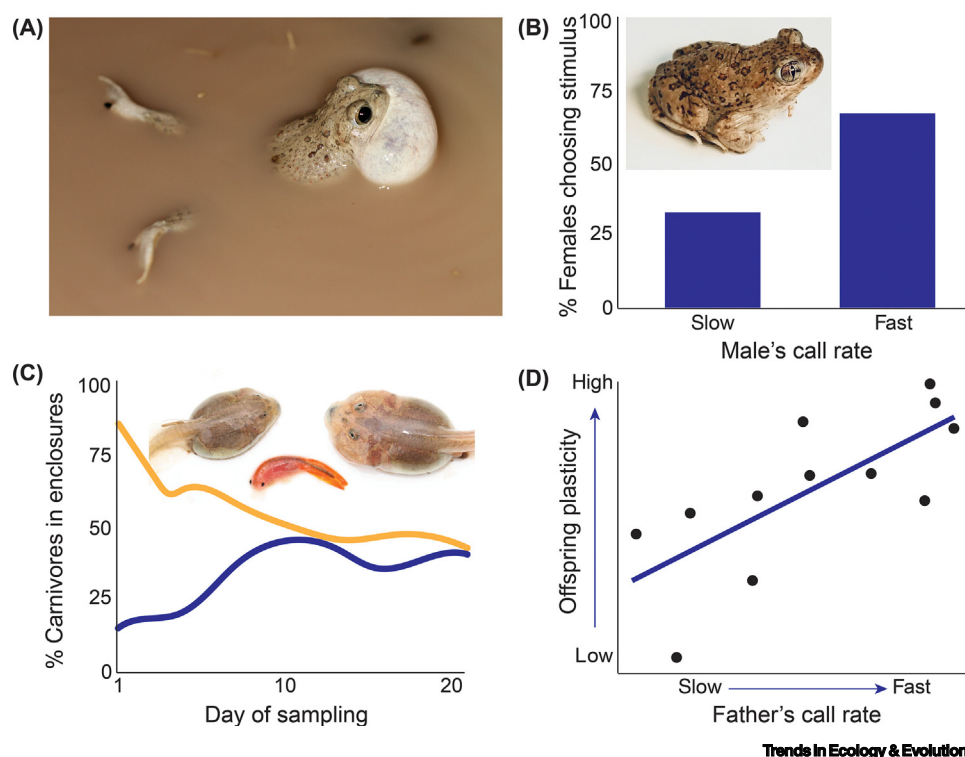


Figure 1. An Example in Which Offspring Plasticity Serves as Benefit of Mate Choice. (A) Male Mexican spadefoot toads, *Spea multiplicata*, call to attract females as mates, and (B) females prefer males that call faster [27]. (C) Their tadpoles have evolved pronounced diet-induced plasticity, developing into either an omnivore morph (left photo) or a carnivore morph (right photo), which is induced by, and specializes on, anostracan fairy shrimp (middle photo). This plasticity is favored by frequency-dependent natural selection, such that the optimal phenotype for an individual to produce depends, in part, on what others do. As evidence of such selection, when the frequency of carnivores in different experimentally enclosed areas of a natural pond is either increased (orange line in graph) or decreased (blue line), this frequency of carnivores later converges on a common, equilibrium frequency, which varies from pond to pond, depending on the relative abundance of shrimp [23]. (D) This also means that parents cannot predict the optimal tadpole phenotype; instead, selection favors adaptively plastic offspring because offspring are in a better position to evaluate their selective environment (i.e., the resource base and number of competitors). Consistent with this expectation, males that display the signal preferred by females (i.e., faster-calling males) sire offspring that are more likely to express carnivore-omnivore plasticity [18].

The *Spea* example underscores the key components of the hypothesis that offspring plasticity can serve as a fitness benefit of mate choice: sexual signals can predict the extent to which a prospective mate's offspring are plastic; individuals prefer mates who possess traits indicative of their ability to produce more plastic offspring; and, because tadpole fitness is frequency dependent, the offspring, not the parents, are best able to assess prevailing environmental conditions and express adaptive plastic responses to them (Figure 1 and Table 1).

Offspring plasticity might serve as a benefit of mate choice in many systems, given that both sexual selection and genetic variation in plasticity has been reported in numerous studies (Table 2). In particular, variation in the slopes, heights, and shapes of **reaction norms** among sibships (genotypes) suggests that heritable (e.g., genetic) variation among reaction norms could underlie a relationship between adult sexual traits and offspring plasticity. Importantly, in a number of the systems where sibship-level variation in reaction norms is observed, sexual selection has also been documented (Table 2). Although the details of male sexual signals and female mate choice are not always known, this broad distribution of both plasticity and sexual selection point to the general potential for plasticity to serve as a fitness benefit of mate choice.

Sexual Signals as Indicators of Offspring Plasticity

For offspring plasticity to serve as a fitness benefit of mate choice requires that individuals gauge a prospective mate's ability to produce plastic offspring. Direct assessment of a potential mate's ability to do so is unlikely [1,3], especially in contexts where offspring plasticity is most likely favored (Table 1 and Box 1). Instead, individuals should rely on sexual signals that predict a prospective mate's capacity to produce plastic offspring [1,3,28,29].

Generally, for sexual traits to predict offspring fitness, these traits must be condition-dependent or otherwise costly to produce [1,3,5,19,29,30] (i.e., they must be 'honest' signals) [29]. Thus, in the case of offspring plasticity, only those individuals capable of allocating resources to signaling can express preferred sexual signals and these signals would reliably predict an individual's ability to produce plastic offspring. Moreover, those individuals' offspring will inherit the capacity to produce the preferred sexual signals as a reflection of their fitness. If offspring plasticity is selectively favored in variable environments, then those offspring capable of facultatively expressing adaptive phenotypes in a given environment would attain the condition necessary to produce those signals as adults. Consequently, offspring plasticity might readily couple offspring fitness with the ability to express preferred signals (*sensu* [31–33]).

For sexual signals and offspring plasticity to become correlated does not require that mate preferences favor offspring plasticity *per se*, nor does it hinge on specific assumptions regarding the evolutionary origins of mate preferences. Indeed, if there is no variation in mate preferences (e.g., because the preference is fixed in the population or because individuals mate randomly with respect to sexual signals), then individuals that choose mates that produce more plastic offspring will benefit from those matings. Similarly, individuals might prefer mates that produce more energetic signals, either because such signals are more stimulatory to the nervous system or because they correspond to other fitness benefits (e.g., fertilization success, parental care, or nuptial gifts). However, if such mates also produce adaptively plastic offspring, then individuals will receive this benefit regardless of the origins of the preference.

Moreover, the possibility that offspring plasticity serves as a fitness benefit of mate choice addresses one of the general arguments that environmental variation disrupts predictive relationships between sexual traits and offspring fitness. In particular, some have argued that environmental variation, and even the expression of phenotypic plasticity in response to that variation, should weaken correlations between genotypes and phenotypes, thereby diminishing the likelihood that sexual signals predict offspring fitness [3,11,13–15]. Yet, such arguments likely only apply when the environment varies unpredictably (see, e.g., [13]). By contrast, adaptive plasticity is not expected to evolve in unpredictable environments [34–38]. Instead, adaptive plasticity is expected to evolve in variable environments where salient cues reliably predict prevailing or impending environmental conditions [37,39]. For example, as highlighted above, reaction norms evolve in response to selection favoring individuals that express the appropriate phenotype in a given environment [2,40–42]. Thus, selection can refine both the extent to which offspring are plastic and the phenotypes that are expressed in different environments, given those environments are of the sort that are expected to favor plasticity in general [2,37,43,44]. In these situations, plasticity does not preclude a predictive relationship between sexual traits and offspring fitness, but could instead reinforce such a relationship.

Establishing that plasticity serves as a fitness benefit of mate choice requires evaluating whether preferred sexual traits predict offspring plasticity and fitness (Figure 2; e.g., [18]). In performing such tests, it is critical to measure offspring fitness across different environments (Figure 2). Indeed, in any given environment, offspring with fixed phenotypes that are optimal for that environment might achieve

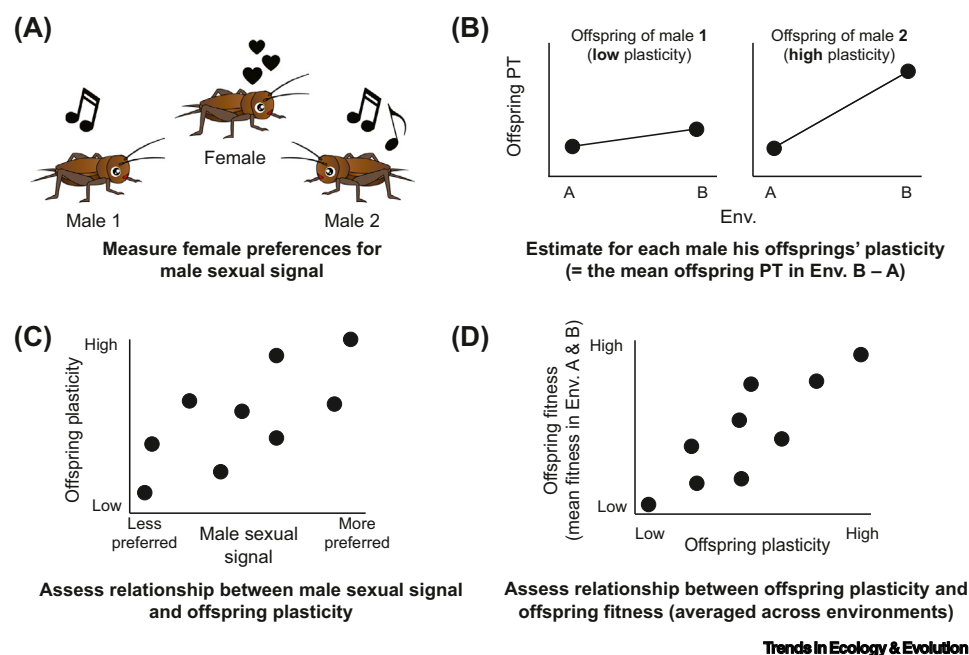


Figure 2. A Method for Evaluating if Offspring Plasticity Is a Fitness Benefit of Mate Choice. (A) First, determine if certain male signals are preferred by females. (B) Second, use a common-garden approach to determine if offspring of different males vary in degree of ecologically relevant plasticity (note that in doing so one should incorporate methods that account for possible parental effects, such as differential maternal resource allocation, impacting offspring plasticity [19]). From this, ask whether the slopes of the reaction norms are steeper for preferred than for nonpreferred males or, alternatively, (C) examine the relationship between the male signal and offspring plasticity, where the latter can be estimated by taking the family mean difference in phenotype when offspring are exposed to two (or more) environments (e.g., obtained from a reaction norm experiment as shown in panel B). (D) Finally, determine if the plasticity is adaptive by measuring the fitness of the offspring from different males when they are reared in the different environments that they would normally encounter in nature; more plastic offspring should have higher fitness than less plastic offspring across these different environments. Note that more plastic offspring might not have the highest fitness in a given environment (see main text), but they should have higher average fitness across environments.

higher fitness than offspring with facultatively expressed phenotypes (*sensu* [45,46]). Yet, those same offspring with that fixed phenotype would do poorly in an alternative environment compared with offspring that can facultatively express traits that are better suited to the alternative environment. Thus, offspring that express different phenotypes in response to the environment should have higher fitness overall when averaged across multiple environments [4].

In this regard, offspring plasticity differs from other fitness benefits ascribed to mate choice. If plastic individuals are unable to express the optimum phenotype in a given environment, then the offspring of preferred mates or those with exaggerated sexual signals might not be those with the highest fitness in that environment. The possibility that offspring plasticity could serve as a benefit in this way could explain why preferred males with exaggerated sexual signals do not always sire the fittest offspring in any particular environment [3]. Thus, identifying whether offspring plasticity constitutes a fitness benefit of mate choice could reconcile, at least in part, longstanding issues about the nature and prevalence of indirect, ‘good genes’ benefits of mate choice [3,19].

Inheritance of Plasticity: Genetic and Nongenetic Mechanisms

A predictive association between sexual signals and offspring plasticity does not require a genetic basis to plasticity in offspring (or to sexual traits) but such a genetic basis may exist. Indeed, as

highlighted in Table 2, numerous studies have documented variation among sibships and populations in whether and how they respond to any particular change in their environment. Moreover, plastic traits commonly exhibit additive genetic variance in the heights and slopes of reaction norms [40,42,47,48]. Both observations suggest the presence of underlying heritable variation in plasticity.

Attempts to identify specific genes that regulate plasticity, and that could serve as the targets of sexual selection for offspring plasticity, are still in their infancy [49], but such attempts have produced some intriguing possibilities. For instance, researchers have identified several developmental switch genes that influence plasticity (e.g., [50–52]). In situations where, as a result of mate choice, offspring inherit alleles at specific genes that render them more plastic, plasticity could constitute an indirect, ‘good genes’ benefit of mate choice.

However, the hypothesis that offspring plasticity can serve as a fitness benefit of mate choice does not necessitate that offspring actually inherit alleles for plasticity. Rather, offspring may inherit **nongenetic factors** (*sensu* [53]). Indeed, increasing evidence suggests that nongenetic factors such as epigenetic modifications of DNA play a key role in mediating plasticity [53,54]. For instance, some of the aforementioned developmental switch genes that regulate plasticity are themselves influenced by epigenetic factors [51,52]. This suggests that mechanisms of nongenetic inheritance and the genetic architecture of plasticity can both be targets of selection and together shape the evolutionary trajectories of plastic traits in offspring.

In short, the mechanisms mediating the inheritance and expression of plasticity, and that could therefore serve as targets of selection for offspring plasticity, are varied and complex [4,49]. Indeed, both genetic and nongenetic mechanisms might play important roles in the expression of offspring plasticity and these mechanisms will differentially impact whether and how sexual selection is exerted on the genome and the subsequent evolutionary response. Thus, a key challenge is to uncover the factor(s) actually transmitted across generations that influences offspring plasticity (see Outstanding Questions). Regardless of whether sexual signals become correlated with genetic or inherited nongenetic (e.g., epigenetic) variation underlying plasticity [5,7], offspring plasticity would still constitute a fitness benefit of mate choice.

An important consideration regarding offspring plasticity as a benefit of mate choice is the subsequent impact of directional selection exerted by mate choice on the underlying genetic or nongenetic variation. If mate choice exerts strong selection on sexual signals that are indicative of adaptive, facultatively expressed traits, then any underlying heritable variation for those signals or the facultatively expressed traits could be lost over time [1]. Historically, variable selection (and, therefore, shifting optima) was one explanation for how variation could be maintained in the face of strong selection [1,11,14]. Yet, under the scenario we outline here, the same genetic variants would be favored regardless of environment (because the plastic variants exhibit higher fitness when averaged across all environments). Thus, genetic variation could decline as populations approached optima for sexual signals and offspring plasticity.

However, the genetic (and/or nongenetic) architecture of plasticity likely consists of a sufficiently large mutational target to maintain heritable variation in the face of persistent selection by mate preferences (analogous to ‘genic capture’; *sensu* [5,30]). Indeed, the genetic architecture of adaptive plasticity, and of the resulting facultatively induced phenotypes, likely consists of numerous loci with diverse functions, ranging from elements of the sensory system involved in detection of environmental cues to the threshold amount of hormone needed to trigger a specific plastic response [4,49]. Such diversity would provide ample potential sources of heritable variation across the genome that is unlikely to

be exhausted by sexual selection, especially if multiple routes exist by which facultative expression of adaptive phenotypes exist [55].

Generally, the complexity of mechanisms underlying adaptive plasticity is thought to explain the maintenance of genetic variation in plasticity in natural populations [48,56] and it suggests that the potential for a single, optimally plastic genotype to approach fixation is low. Whether this is the case remains to be tested, but we suspect that the variation underlying offspring plasticity and sexual traits might be especially resistant to depletion. Moreover, if condition-dependent direct benefits, such as the provisioning of nuptial gifts and subsequent maternal resource allocation to offspring, also contribute to mate choice favoring offspring plasticity, then heritable variation should readily be maintained [3,20]. As greater attention is given to offspring plasticity as a benefit of mate choice, theoretical and empirical work should evaluate how variation in phenotypic plasticity (whether caused by genetic or nongenetic mechanisms) is impacted by mate choice and the subsequent effect of this variation on sexual selection.

Evolutionary Implications of Offspring Plasticity as a Fitness Benefit of Mate Choice

That offspring plasticity can function as a benefit of mate choice has at least two key evolutionary implications. First, it can help explain how sexual selection promotes adaptation in novel or variable environments. As noted earlier, a criticism of the notion that sexual selection promotes adaptation is that environmental variation will break down any correlations between adult sexual traits and offspring fitness. However, if sexual traits indicate the capacity for offspring to produce different traits in response to prevailing or impending environmental conditions, then adult sexual traits will predict offspring fitness even in variable environments [18] (Figure 2; see also Figure 1 and Table 1).

Moreover, exposure to novel environments can induce the expression of plasticity, which is then subject to novel selective pressures [57,58]. This plasticity can be adaptive in the sense that it allows rapid (within-generation) responses to selection and subsequent short-term population persistence, but whether it allows long-term persistence depends on the existence of underlying heritable variation in plasticity and, thus, the capacity for evolutionary responses to selection [48,56,58]. If inducing cues in a novel environment reliably predict environmental conditions (*sensu* [59]), then the potential for a long-term adaptive response may be increased by associations between sexual traits and offspring plasticity owing to the combined effects of direct ecological selection and indirect sexual selection. Indeed, because selection on sexual traits can be stronger than selection on viability and fecundity traits in natural populations [60,61], offspring plasticity as a benefit of mate choice might facilitate relatively rapid adaptive evolution and long-term persistence in novel environments. Testing this possibility is especially important in a time of global change.

A second implication of offspring plasticity as a benefit of mate choice is that it could impact the evolution of phenotypic plasticity itself [18]. Plasticity is increasingly thought to play diverse roles in ecology and evolution, including enabling populations to persist in novel or changing environments and facilitating speciation [2,57,58,62–64]. Plasticity can assume such diverse roles because plasticity can itself evolve [65] and its evolution can, in turn, have important downstream consequences [43,66]. For example, because environmental change is typically harmful to an organism (it reduces the match between its phenotype and environment), phenotypic plasticity has evolved in essentially all taxa [67], where it allows individuals to produce phenotypes that are better suited for any new conditions that they might encounter [2,4]. However, because different genotypes typically vary in whether and how they respond to any given environmental change (Table 2), selection can act on this formerly **cryptic genetic variation** for plasticity [68] and favor those genotypes that produce well-adapted phenotypes for the current environment.

Through this process of adaptive refinement (known as ‘genetic accommodation’ [2]), selection can cause a change in both the regulation of plasticity and form of the facultatively expressed phenotypes, leading to a better match between phenotype and environment [2,57,63,64].

Sexual selection might play a crucial role in this process of **plasticity-led evolution**. If mate choice enhances the reproductive success of individuals that produce plastic offspring, then mate choice would thereby increase the production of offspring capable of responding to cues that reliably indicate prevailing or impending environmental conditions. As more plastic offspring are produced and exposed to selection, the opportunity for selection to refine that plasticity is increased [2,18,43]. Thus, when adult sexual traits become associated with adaptive offspring plasticity, they may readily enable plasticity-led evolution to facilitate adaptation [2,18,43,64,66].

Concluding Remarks

The potential for offspring plasticity to constitute a fitness benefit of mate choice could arise whenever the environment is spatially or temporally variable and offspring are better able than their parents to accurately assess their environment or express plasticity (Table 1). Evaluating whether plasticity can serve as a fitness benefit of mate choice could explain patterns of sexual selection in diverse taxa and help resolve whether and how sexual selection contributes to adaptation, which is an enduring issue in evolution [1,10,12,69–72]. Moreover, because mate choice for plastic offspring could facilitate the evolution of plasticity, sexual selection could amplify plasticity-led evolution and its downstream consequences. Given that many species are experiencing rapid environmental change, and that plasticity might help populations ‘buy time’ until more permanent adaptive solutions can evolve [58], evaluating whether plasticity can serve as a benefit of mate choice is especially timely now (see Outstanding Questions).

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Declaration of Interests

No interests are declared.

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Outstanding Questions

What are the genetic, developmental, and evolutionary mechanisms by which offspring plasticity becomes associated with adult sexual traits? Addressing this question is fundamental to our understanding of whether and how plasticity serves as a fitness benefit of mate choice.

Are there particular traits, taxa, or conditions in which sexual traits are more likely to predict offspring plasticity? Evaluating these factors would provide insights into the processes by which plasticity serves as a fitness benefit of mate choice.

Can mate choice for offspring plasticity explain some of the conflicting evidence for indirect benefits of mate choice? If offspring plasticity commonly mediates connections between sexual traits and offspring fitness, then past tests of indirect benefits might have failed to capture important dimensions of how these models apply to natural populations (e.g., by rearing offspring in only one environment).

Can sexual selection, paradoxically, lead to the loss of plasticity? If offspring plasticity is associated with adult sexual traits, then any changes to those traits could result in the production of less-plastic offspring and indirectly facilitate the loss of plasticity, a process known as genetic assimilation. Such changes to mating traits might not arise because offspring plasticity is selectively disfavored *per se*. Instead, selection might favor mating traits that maximize other components of fitness that are under stronger selection

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