Sexual Selection in Complex Environments

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Keywords

cryptic female choice, fluctuating selection, genotype-by-environment interactions, male-male competition, mate choice, phenotypic plasticity, sperm competition, selection analyses

Abstract

Sexual selection has resulted in some of the most captivating features of insects, including flashy colors, bizarre structures, and complex pheromones. These features evolve in dynamic environments, where conditions can change rapidly over space and time. However, only recently has ecological complexity been embraced by theory and practice in sexual selection. We review replicated selection studies as well as studies on variation in the agents of selection to delineate gaps in current knowledge and clarify exciting new directions for research. Existing work suggests that fluctuations in sexual selection may be extremely common, though work on the ecological factors influencing these fluctuations is scarce. We suggest that deeper ecological perspectives on sexual selection may alter some of the fundamental assumptions of sexual selection theory and rapidly lead to new discoveries.

INTRODUCTION

Sexual selection:
selection driven by
competition for
matings and
fertilizations

Mate choice:
differential mating by
females as a result of
mating preferences,
sampling strategies,
and environmental
conditions

**Male-male
competition:**
competition among
males for access to
potential mates

**Cryptic female
choice:**
a female-controlled
process or structure
that favors paternity by
some males over
others when multiple
matings have occurred

Sperm competition:
competition between
the sperm of two or
more males for
fertilization of an
egg(s)

The power of selection to produce magnificent adaptations of organisms to their environment
continues to captivate scientists and nonscientists alike. Selection has played a central role in
shaping much of the diversity seen in nature (131, 132, 143, 164). It has usually been divided
into natural and sexual selection, though precise categorization is still an area of lively and useful
discussion (e.g., 97). Darwin (32) was the first to argue that natural selection and sexual selection
were distinct, with sexual selection acting on the elaborate characteristics that increase mating
success, such as the peacock's tail and the horns of beetles. The evolution of such traits seemed at
odds with the theory of natural selection because of their presumed survival costs.

Natural selection varies over time and space in nature because environmental conditions (the
selective factors) themselves change over time and space (14, 145). Such fluctuations in natural
selection have long been appreciated (43, 53); however, only recently have researchers begun
to seriously examine fluctuations in sexual selection (27, 51, 146, 147). Two major agents of
sexual selection, female mate choice and male-male competition, have often been assumed to
exert strong, directional, and consistent selection pressures. However, these behavioral agents of
selection can vary in concordance with changes in the environment. Sexual selection may fluctuate
even more than natural selection because of the condition dependence and context dependence
of the many factors involved in sexual selection (9, 27, 29, 56, 85, 103, 125–127). For example,
the density of individuals (72, 124, 134), sex ratio (72, 124), level of female experience (76), and
presence of heterospecifics (141) can all change the strength, form, or direction of sexual selection.

More than three decades ago, Lande (90), Lande & Arnold (92), and Arnold & Wade (4) pro-
vided a robust theoretical framework for understanding selection and simple methods for quan-
tifying it. Selection analyses relate variation in some measure of fitness, e.g., survival, fecundity,
or mating success, with variation in the phenotypic trait(s) of interest. The slope of the regression
between the fitness measure and a focal trait (the covariance) provides a quantitative estimate of
the strength of selection (80). Selection analyses can document the strength of sexual selection
(e.g., stronger sexual selection at high density), the direction of sexual selection (e.g., larger males
might be favored at higher density and smaller males at lower density), and the form of sexual
selection (e.g., stabilizing sexual selection at moderate density and directional sexual selection at
high and low density). Information about these aspects is helpful for understanding the dynamics
and evolutionary consequences of selection.

Since the first influential papers in this area were published, hundreds of field and laboratory
studies have provided thousands of estimates of natural and sexual selection. Meta-analyses and
reviews of replicated selection studies have concluded that there is a clear signature of spatial
and temporal variation in selection in general (79, 145–147). Yet, replicated studies of sexual
selection are scarce (145–147). In this review, we discuss arthropod studies that have used selection
analyses to measure sexual selection repeatedly over space, time, or context. We highlight those
that have manipulated or attempted to identify the ecological factors responsible for differences
in selection (**Table 1**). While repeated studies of sexual selection are few in number, research
directly examining environmental influences on the agents of sexual selection—mate choice, male-
male competition, cryptic female choice, and sperm competition—is now becoming common
(27, 29, 73, 78). Many of these studies conclude that the agents of selection are highly sensitive
to ecological circumstances, leading to dynamics in the strength, direction, or form of sexual
selection. Thus, we augment what has been learned through selection studies *sensu stricto* by
reviewing evidence for plasticity in the agents of sexual selection. We note that the agents of
selection are themselves subject to selection, which may lead to complex evolutionary dynamics.
Finally, we discuss the role of ecological complexity in maintaining genetic variation. We focus

Table 1   Existing arthropod studies that examined sexual selection repeatedly across time, space, or laboratory contexts and the ecological factors that were shown or suggested to influence changes[a]

Order	Species	Putative agent of selection	Putative ecological factor(s)	Reference
Coleoptera	*Stator limbatus*	Male-male competition	Temperature	111
Diptera	*Scathophaga stercoraria*	Male-male competition	Density	72
Hemiptera	*Narnia femorata*	Male-male competition	Presence of female	121
Odonata	*Ischnura elegans*	Male-male competition	Density of female color morph, female body size	51
Diptera	*Sepsis cynipsea*	Mate choice	Density	15
Diptera	*Drosophila serrata*	Mate choice	Cuticular hydrocarbons	141
Hemiptera	*Gerris odontogaster*	Mate choice	Density	5
Orthoptera	*Gryllus pennsylvanicus*	Mate choice	Experience of females	76
Orthoptera	*Teleogryllus commodus*	Mate choice	Male harassment	60
Araneae	*Latrodectus hasselti*	Not differentiated	Competitive environment	77
Coleoptera	*Bolitotherus cornutus*	Not differentiated	Density	26
Coleoptera	*Bolitotherus cornutus*	Not differentiated	Social network position	46
Hemiptera	*Phymata americana*	Not differentiated	Sex ratio density	124
Hemiptera	*Neacoryphus bicrucis*	Not differentiated	Density	99

[a]All studies detected changes in selection.

primarily on insects and other arthropods for this review, because research on these organisms has provided and will continue to provide many of the leading insights for the field of sexual selection. Insects provide great power for investigating the ecological influences on sexual selection because they typically have short generation times, are relatively easy to study in the field and the laboratory, and offer the potential for large sample sizes. New technology is allowing in-depth field studies of insect behavior with the promise to yield outstanding insights (138, 139). Although the focus here is on insects, it is our hope that this review will spark research across taxa.

VARIABILITY IN THE AGENTS OF SEXUAL SELECTION

Darwin (32) defined sexual selection as the advantage some individuals have over others of the same species and sex in relation to reproduction. He identified two agents of sexual selection: male-male competition and female mate choice. Subsequent theorists were largely unable to envision the advantage of female mate choice (69, 170), and sexual selection research focused almost exclusively on male-male competition for many years. Since the 1980s, theory on the evolution of female mate choice has grown rapidly (52, 61, 81, 91, 114, 119, 176), and empirical studies documenting female mate choice and mate preference and discussing their potential role in evolution have become commonplace (2). With the exploding interest in female mate choice over

the past three decades, male-male competition has tended to be somewhat neglected. Another issue is that researchers usually study the agents of sexual selection (including postcopulatory agents of selection) in isolation, ignoring their potential combined role and possible synergistic effects. We discuss insights gained about the operation of the agents of sexual selection in complex environments and the resulting consequences for selection. We argue that more studies are needed to examine the agents of selection in concert.

Mate Choice and Fluctuating Selection on Ornaments

Female mate choice has resulted in the evolution of conspicuous male ornaments, such as bright colors, courtship pheromones, and display behaviors (2). Early population genetic models on female choice assumed that decisions are made in homogeneous environments, that females largely converge on their mate choices, and that constraints limiting mate choice are nonexistent. However, a wealth of recent studies have challenged these assumptions, revealing that individual mating decisions can change according to age, experience, condition, and context (29, 73). Recently, many studies have been conducted on factors influencing variation in female mate preferences, but relatively little is known about whether that variation translates into fluctuating selection pressures on male traits (**Table 1**).

What environmental factors influence individual mate choice? To adequately address this question, first the components of mate choice must be considered. A central element of mate choice is mate preference. Female mate preference is a complex trait that describes the propensity to select some males over others. Mate preferences do not always lead to matings with preferred males because of the effects of sampling strategies and environmental conditions. Female mate choice denotes the actual male(s) a female mates with, not necessarily the most preferred male(s) (169). Thus, even if certain male traits are preferred by females or provide an advantage in male-male competition, they may confer no selective advantage for males if they are not ultimately associated with increased fitness.

Mate choice is subject to various environmental constraints, including the timing of reproduction and predation risks associated with searching (169). In addition, the distribution and availability of males can affect mate choice. For example, the most preferred males may themselves be choosy and be occupied with only a subset of females. Alternatively, preferred males may not be available for mating because they are less successful in male-male competition and thus have limited access to females (73). For example, in the cockroach *Nauphoeta cinerea* the male-produced pheromone blend most attractive to females and the blend most likely to confer high status to males in male-male competition are not the same. Thus, male-male competition may limit female access to preferred males (109).

Female condition and ecological context can affect countless elements of mate preference and choice, including female ability to detect differences among males, mate sampling rules, male availability, and interference from other females and other species (29, 101). Younger females or those in good condition may exert stronger preferences or invest more time and energy into sampling potential mates (63, 110). For example, female stalk-eyed flies of the species *Diasemopsis meigenii* and *Teleopsis dalmanni* in good condition appear to be more selective for males with long eyestalks (28, 67). Although context can constrain mate preferences, behavioral changes may at times not reflect constraints but instead be an adaptive response. For example, female collared flycatchers, *Ficedula albicollis*, breeding late in the season show heightened preference for mates with large forehead patches. Males with larger patches provide better parental care than males

Mate preference: an internal property of females that affects responses of females to males based on the expression of male traits; preference affects, but does not determine, female mate choice

with a smaller ornament, but only later in the season (126). Thus, female preferences appear to change according to the information conveyed by the male ornament (see also 25).

Another form of context-dependent mate preferences is mate-choice copying (35, 123). Mate-choice copying occurs when the probability that a female chooses a given male increases if other females have chosen that male. When mate-choice copying is present, females can converge more strongly on their mating decisions, increasing variance in male mating success and thus in the strength of sexual selection (168). Females across many taxa copy the mating decisions of others, but knowledge about mate-choice copying in insects is rather scarce. Recently Mery et al. (100) demonstrated that *Drosophila melanogaster* females show evidence of mate-choice copying and are able to generalize learned information. The researchers created two male color phenotypes that were unrelated to male quality, and then they staged matings. Females preferentially selected males of the color type they observed copulating. These results suggest that females copying other females can lead to selection of arbitrary trait values in males, and furthermore that the trait values preferred in one season or one location may easily differ from those preferred at another.

Individuals may receive indirect (genetic) benefits and direct (resource) benefits from being choosy. Direct benefits include nuptial gifts, access to superior territories for feeding and laying eggs, and protection from harassing males. Direct benefits, when present, are likely to be more influential than indirect benefits in mating decisions because of immediate and greater fitness returns (6, 82, 108, 142). Yet, the availability and quality of direct benefits may vary in a population depending upon resource availability and other environmental factors. When direct benefits are absent, females may switch to using cues indicating indirect benefits, leading to changes in selection (23, 73).

Intersexual selection is often used synonymously with female mate choice, although males in many species are also choosy (16, 39). The relative cost of breeding for each sex is a fundamental factor in determining which sex competes for matings and the intensity of sexual selection (162; but see 87). Often, females invest more in a single breeding event, and males compete for the gametes of these females. However, male sperm production and mating rate are not infinite, and many ecological circumstances can lead to males being choosy (16, 39). When male mate choice is present, some females may receive fewer sperm or have the opportunity to mate only with suboptimal males (165). Other females may be prevented from mating at all (58, 130).

Few studies have estimated selection gradients on females by males (173; but see 93, 136), and no published studies to our knowledge have investigated how these selection gradients change under different ecological circumstances. However, a few studies have investigated the role of social and other environmental factors on male mate choice. For example, males in the damselfly *Ischnura senegalensis* (158) and the field cricket *Gryllus bimaculatus* (12) initially do not exhibit mate preferences, but they become discriminating after gaining mating experience. Thus, the strength of sexual selection on females may fluctuate according to proportion of virgin versus experienced males in the population. In the annual orb-weaving spider *Zygiella x-notata* (Araneae: Araneidae), male mate choice varies according to the level of male-male competition. Interestingly, male spiders exhibit no detectable mate preferences when competition level is low, but at high competition levels, males increase their choosiness. When the level of competition is high, larger, more competitive males pair with larger, more fecund females, whereas smaller males choose smaller females as mates (13). In a species of Tettigoniidae (katydid), sex roles reverse depending on seasonal food availability. Male katydids produce a large, nutrient-rich spermatophore that is given to females during mating. This spermatophore is an important food source for females and increases their fecundity. When food is plentiful, and many males can produce spermatophores, females are choosy. However, when food is limited, fewer males are able to produce sufficient spermatophores.

Under these conditions, female mate selectivity decreases and mating rate increases, likely to allow females to obtain adequate resources. Males that are able to replenish their spermatophore glands are choosy, preferentially mating with heavier, more fecund females. Females physically fight for access to males when food is scarce, but not when it is abundant (59). This example highlights that in some cases simple changes in resource availability can reveal male mate choice and completely alter patterns of sexual selection. Environmentally induced sex role reversal has also been demonstrated in butterflies, where it may lead to fluctuating selection for ornamentation in both sexes (122).

Male-Male Competition and Fluctuating Selection on Weapons

Male-male competition has resulted in a spectacular array of elaborate traits used to signal competitiveness and used in male-male combat (42). Many insect mating systems are characterized by intense male-male competition over females (11) or the resources that females need (160) and by male-female sexual conflict over mating rates (8). As a result, insect researchers interested in sexual selection are probably well aware that sexual selection is not solely a result of female preferences. As with selection on ornaments via female mate choice, selection on weapons and size via male-male competition is influenced by ecological factors (102, **Table 1**). The most commonly studied biotic factor relevant to male-male competition is population density. Many studies have been unable to differentiate the contributions of mate choice and male-male competition to selection (**Table 1**).

Depending on the species, its natural history, and the type of mating system, sexual selection can become stronger at either high density or low density (44, 88, 157) (**Table 1**). For example, populations of the soapberry bug, *Jadera haematoloma*, become more male-biased later in the season. As a consequence, selection for larger males appears to increase in intensity, because larger males can more quickly locate and mate with rare females (24). Positive relationships have been reported between population density and weapon size in pseudoscorpions (177) and the earwig *Forficula auricularia* (161). However, some species, including the mite *Sancassania berlesei* (128), the fly *Sepsis cynipsea* (15), the forked fungus beetle *Bolitotherus cornutus* (26), and various dung beetles (106, 118), appear to experience decreased selection for size at low densities. At low density, some mating systems may shift away from resource- and female-defense polygyny to scramble-competition polygyny, in which weapons and large size are not as useful (19, 115, 118). Thus, it is not possible to provide a simple answer to the question "Does high density lead to stronger sexual selection in favor of large males?" without a deep knowledge about the study species. This lack of universal pattern should caution against laboratory studies of sexual selection that do not take these considerations carefully into account (e.g., using artificially high or low densities).

Social factors other than density can also affect selection. Procter et al. (121) demonstrated that the presence or absence of a single female can change the strength and form of selection via male-male competition in the leaf-footed cactus bug, *Narnia femorata*. When females are not present, small males may reduce risk of injury and expenditure of energy by avoiding competition, but when females are present, the risk may be worth the investment. Insects rarely compete for matings under a highly standardized set of circumstances, and simple and localized changes in the presence or absence of other individuals or the sex ratio may introduce variation in selection.

Microhabitat structure likely influences selection on the size and shape of weapons and may be one reason for the great diversity of weapons seen in even closely related taxa (42). For example, the style of male-male competition can change depending on whether competitions occur on

the soil, on a complex host plant, on a dead tree, or in a tunnel. Changes in female oviposition behavior, resource availability, and male density, among other factors, could change the location where males compete, and thus the form, direction, or intensity of selection.

Sperm Competition and Cryptic Female Choice

For many years researchers argued that females required only one or a few mates to reach their maximal reproductive potential (11). However, recent research has demonstrated that females in many species mate more than predicted by theory (148). Polyandry can improve female fitness via resources provided by males, the production of genetically diverse offspring, insurance against male infertility, and the ability to further evaluate male quality (7, 148). A major consequence of polyandry is that sexual selection can continue well after mating (89). Both male-male competition and female mate choice have postcopulatory equivalents. The postcopulatory equivalent of male-male competition is called sperm competition (116), and the postcopulatory equivalent of female mate choice is called cryptic female choice (37, 38, 159). Thus, the common definition of sexual selection as selection via differential mating success is incomplete.

Sperm competition selects for larger testes and greater sperm production and, most likely, ejaculate composition, sperm form, and sperm function (149). As with other agents of sexual selection, sperm competition takes place in variable environments that may change the form, strength, and direction of selection. Variability in the intensity of sperm competition should result in selection for the ability to modify the amount of sperm ejaculated. Indeed, empirical studies in insects and other taxa have demonstrated that males ejaculate more sperm when mating with females in the presence of other males (33, 48, 49), suggesting an adaptive plastic response to variable selection pressures. The nutritional environment also may be quite important to postcopulatory mechanisms of sexual selection. Fricke et al. (47) found that female diet in *Drosophila melanogaster* altered the effects of a male ejaculate compound on female egg laying, receptivity, and life span. The authors concluded that the food environment may shape the strength and direction of selection on postcopulatory reproductive traits.

Selection via cryptic female choice is presumably responsible for the evolution of courtship behaviors that occur during mating [i.e., copulatory courtship (37, 38)], though it is also likely a selective agent for typical male ornaments such as color and pheromone composition. Some variables potentially influencing selection via cryptic female choice include prior mating experience (129), the timing of mating relative to reproductive cycles, factors influencing internal ions and pH (140, 174), and postcopulatory male behavior. Hall et al. (60) examined the opportunity, form, and intensity of sexual selection on components of the male courtship call and body size in the black field cricket, *Teleogryllus commodus*. After mating, females may attempt to remove the spermatophores deposited by males from their reproductive tracts. However, males often harass females after copulation, hampering the ability of females to remove spermatophores. The researchers found that when males harassed females, there was a reduced opportunity for selection, a change in the form of selection, and a reduced intensity of selection relative to when harassment was absent. These findings demonstrate that male behavior after mating can influence postcopulatory choice by female crickets and, furthermore, that factors limiting male harassment should alter selection. Thus, in complex microhabitats where females can escape from harassing males, selection via postcopulatory choice may have a more pronounced role in evolutionary change.

Most sexual selection analyses use mating success as a proxy for fitness, ignoring the potential selective processes occurring after mating (89). Postcopulatory selection can be included in selection analyses by measuring fitness as fertilization success instead of simply mating success (for

caveats, see 50). Furthermore, insights can be gained by combining a selection analysis approach with experimental manipulations of the agents of selection individually and in concert.

SELECTION ON THE AGENTS OF SEXUAL SELECTION THEMSELVES

The selective agents for ornaments and weapons, mate choice and male-male competition, are themselves targets of selection. Thus, variation in these agents can be a cause of fluctuating sexual selection but also an evolutionary consequence of fluctuating sexual selection. The potential for very complex evolutionary dynamics should be apparent. Although selection on these agents is often inferred, rarely has selection been quantified. As an exception, Robinson et al. (135) found that selection on mate choice in collared flycatchers (*Ficedula albicollis*) varies according to climatic conditions in a given year. Females who chose highly ornamented males had increased reproductive success during drier breeding seasons but decreased reproductive success during wetter years. Mate choice in this species has a heritable component, suggesting that selection can lead to an evolutionary response. Fluctuations in selection due to abiotic factors may lead to evolution and/or adaptive phenotypic plasticity in mate choice, which in turn may lead to fluctuating selection on ornaments. Similarly, in lark buntings (*Calamospiza melanocorys*) male traits associated with offspring success in one year are not associated with success at other times. Thus, selection on females to pursue males with certain trait values likely changes year to year (25). These studies demonstrate that selection on female mate choice can change rapidly over time.

Mate preferences can be learned in a number of different animal taxa, including several insect and arthropod species (36, 62, 166). Such learning may be a special form of phenotypic plasticity in response to a temporally and spatially variable mating environment. For example, females of the banded demoiselle damselfly (*Calopteryx splendens*) exhibit plastic mate preferences for a male secondary sexual trait, the size of melanized wing patches, depending on the presence (sympatry) or absence (allopatry) of a congeneric species (*C. virgo*) (151). Males of these two species differ in the amount of wing melanization; *C. splendens* males have a wing patch that covers 50% of the wing, whereas *C. virgo* males have almost entirely melanized wings (152). Although interspecific matings occur, hybrids are few and probably have very low fitness (153, 163). Thus, although some studies have indicated female preference for large melanin wing patches in males and hence directional selection for this trait (150), when *C. splendens* is sympatric with *C. virgo*, such a *C. splendens* female preference for large male melanin wing patches might be selected against because of direct costs of heterospecific matings, indirect costs of hybridization, or both (163). In southern Sweden, sympatric and allopatric populations of *C. splendens* and *C. virgo* occur in mosaic, with "microallopatric" *C. splendens* populations embedded within a larger matrix of sympatry at the regional level and with a low level of genetic differentiation between the two types of populations (151, 154). This is exactly the ecological setting where one would expect learning and adaptive plasticity in female mate preferences to play an important role, as gene flow between populations would tend to erode genetic population divergence in mate preferences between sympatric and allopatric populations. Interestingly, female *C. splendens* do show radically different mate preferences toward male wing melanization at this small spatial scale of weakly genetically differentiated populations, and experiments in outdoor cages suggest that these population differences in female mate preferences result from learning, rather than genetic differences. Physical exposure of sexually naive (virgin) females to either con- or heterospecific males for only a few hours in outdoor cages is sufficient to induce different mate responses (151).

To examine selection on mate choice and male-male competition, trait differences and seasonal or (ideally) lifetime reproductive success should be quantified. This problem would be best studied where all offspring can be followed through development and where maternity, paternity, or both

can be assigned accurately. For example, Robinson et al. (135) were able to capitalize on 25 years of data on pairing patterns, reproductive success, survival, and phenotypic measurements for a wild collared flycatcher population. They calculated annual female reproductive success for 4,522 females and compared that to the patch size of a female's social partner for each breeding season. Such studies should typically be relatively easy to perform in insects and other invertebrates, where larger samples can often be obtained and there are ample opportunities for spatial and/or temporal replication. When field studies are not possible, large numbers of insects can often be reared and followed in seminatural conditions.

THE MAINTENANCE OF GENETIC VARIATION

Sexually selected ornaments and weapons were long assumed to undergo consistent and directional selection for increased expression (2). Such directional selection should eventually erode genetic variation in these traits, yet genetic variation in sexually selected traits is common (120). With regard to female mate choice, if benefits to mate choice were meager, choice behaviors should diminish. However, females in many species continue to exhibit mate preferences, even when they appear to receive only sperm from mating. This perplexing situation is termed the lek paradox, and it has received considerable attention (e.g., 18, 83, 104). Study of the lek paradox has focused on mate choice, but directional selection for male weapons through male-male competition should also result in the erosion of genetic variation.

The lek paradox rests on the premise that selection is directional and generally consistent (83). As mentioned above, there is now much cause to question this assumption. The expression of sexually selected traits can be strongly influenced by developmental conditions (17, 56, 103, 107), small males or males with smaller weapons can in some circumstances achieve access to females (57, 76, 78), and females sometimes choose less elaborated males (73). These changes can result in fluctuations in selection and the evolutionary response to selection (e.g., 78, 121). One result is that the erosion of genetic variation can be slowed (14, 41). In addition, it is now recognized that genotype-by-environment interactions (G × E) may be common for sexually selected traits, and they may play an important role in delaying the loss of genetic variation (55, 71).

G × E occur whenever the relative performance of genotypes is different across environments (96). For example, a genotype may have the highest performance in one context, but a different genotype may succeed in another. If gene flow does not occur across the contexts, then fixation of the different high-performing alleles should occur in each situation. However, gene flow across spatial or temporal contexts will mix genotypes and maintain variation. Thus, G × E can provide one solution to the lek paradox. G × E have been extensively investigated with regard to many phenotypic traits (1, 45); however, they have only recently attracted attention in the field of sexual selection.

For an example of how G × E can operate, consider the situation in which insects develop on a host plant that produces flowers early in the year and fruits later in the year. If nutritional differences are associated with the phenological changes in the host plant, then some genotypes may be relatively more successful developing on flowers, whereas other genotypes may perform better when they develop on fruits. In this case, G × E would be present. Because generations overlap, potential mates would include those reared on flowers and those reared on fruits. Expression of a sexually selected ornament, such as a pheromonal blend, coloration, or a display behavior, may be an honest indicator of genetic potential, but only if the developmental context can be discerned. If a male phenotype cannot be associated with a particular developmental context, females could easily make "mistakes" (66), selecting fathers for their offspring that developed successfully on flowers, even though offspring would be developing on fruits.

Genotype-by-environment interactions (G × E): G × E occur whenever the relative performance of different genotypes is dependent on the environment in which they are expressed

Thus, G × E for male ornaments may result in unreliable signaling (55). In such situations, females may pay a cost for their mate choice but gain few or no benefits (144). Even when signals are "honest on average" (84), mate choice should be stable only as long as the benefits of choice outweigh the costs. Thus, as the information content of the trait declines, so should females' use of that trait as an indicator of the genetic quality of males. Thus, almost paradoxically, G × E can both maintain and weaken female choice for genetic benefits. Maintenance of choice depends upon such factors as the degree of generational overlap or gene flow and the timing of dispersal (86).

Many, but not all, studies of male sexually selected traits have found evidence of G × E. Bussière et al. (21) and Ingleby et al. (71) provide important summaries of work on G × E and sexual selection. Studies since this time have generally confirmed the presence of G × E for sexually selected traits. G × E have been found for morphological traits in oceanic field crickets, *Teleogryllus oceanicus* (113); chemical signals in decorated crickets, *Gryllodes sigillatus* (171), and *Drosophila simulans* (70); viability and body size in the seaweed fly, *Coelopa frigida* (40); and a suite of traits including sperm defense ability in *Tribolium castaneum* (94). Studies in the lesser wax moth have shown that G × E may help maintain genetic variation in a male signaling trait (75) and alter the fitness consequences of mate choice (31, 74).

Studies of G × E and sexual selection have almost exclusively focused on male traits; however, G × E may also exist for behaviors associated with mate choice and male-male competition. Rodriguez & Greenfield (137) found phenotypic plasticity in traits associated with female preferences, body and ear size, and development time in the lesser wax moth. They also found plasticity and possible G × E in the threshold by which females respond to male calls. In contrast, Delcourt et al. (34) found no evidence for G × E in female preference for male contact pheromones in a laboratory population of *Drosophila serrata*. In an unusual twist to existing G × E methodology, Brommer et al. (20) investigated G × E on *D. melanogaster* when the environments tested involved sexual conflict instead of variation in resources or temperature. They used artificial selection to create high-conflict versus low-conflict strains by altering the amount of exposure females had to males. They found a female genotype by sexual conflict interaction on female fitness metrics potentially capable of slowing the erosion of genetic variation.

That G × E exist for mate choice as well as ornaments and weapons complicates the simple picture of sexual selection portrayed by early population genetics models (71). Genetic covariance between male ornaments and female preferences is often widely assumed (65), but G × E could easily alter this correlation. For example, Narraway et al. (112) found G × E and a change in the genetic variance of female preferences with variation in temperature exposure of *Drosophila melanogaster* during development. Their results demonstrate that any genetic correlation between female preference and male attractiveness should vary in strength across environments (10). The strength of the association between female preference and male attractiveness is central in determining certain evolutionary trajectories (3, 91). Thus, the implications of G × E for sexual selection go beyond the maintenance of genetic variation, potentially challenging other fundamental assumptions of sexual selection theory.

Most of the existing work on G × E in insects has been conducted using artificial stressors instead of a realistic set of environmental conditions. For instance, many lab strains are fed artificial diets instead of natural foods. These studies are very important for showing patterns of variation that can appear when novel environments occur, but they are not as informative about actual G × E in existing natural populations. Realistic environments will yield insight into not only whether G × E are possible but also whether they do occur in the wild. If field studies are not possible for a particular species, studies using seminatural enclosures or natural resource variation in the laboratory will be informative.

GUIDE FOR FUTURE RESEARCH IN THIS AREA

Studies measuring selection gradients over time, space, and with changes in putative environmental influences are rare and much needed (**Table 1**; 146, 147). Temperature should be of particular interest in terms of how it affects sexual selection, given ongoing anthropogenic climate change. However, with a few exceptions (**Table 1**), existing quantitative data on how selection regimes and selection gradients change in relation to temperature are scant. This is surprising; such data should not be too difficult to obtain, at least not in laboratory settings. Temperature can potentially affect mate choice and male-male competition via changes in activity levels and the demographic environment (e.g., increased densities, longer seasons, changed operational sex ratios), changes in the expression of secondary sexual traits (54, 64, 95, 133), and direct influences on female mate preferences and male-male competition. Changes in sexual selection over latitudinal gradients are also largely unexplored. Large-scale comparative studies on birds suggest that both speciation and extinction rates might be elevated at higher latitudes (172), although the generality of this pattern has been questioned (105). Speciation and extinction rates may be influenced by sexual selection, but, to our knowledge, there are no direct comparisons of the strength of natural or sexual selection at high versus low latitudes. However, a recent comparative study on calopterygid damselflies and their allies suggested that northern species in colder climates were significantly more likely to have pigmented wings, a signaling trait involved in both sexual selection and premating reproductive isolation (156).

Estimating sexual and natural selection gradients from fitness data, mating data, and/or survival, which has a strong tradition in evolutionary ecology (80, 92), does not in itself tell us about the underlying ecological influences on selection or the agents of selection (167). Thus, major challenges in future empirical research on sexual selection are to develop quantitative and experimental assays to partition variation in sexual selection arising from male-male competition, female choice, and their (possible) interaction (68) and to also discern ecological factors affecting these mechanisms. The contributions of sperm competition and cryptic female choice also need to be considered (89, 117).

We suggest that a good way forward is to combine selection estimates from natural populations with short-term manipulative experiments conducted in the field or laboratory or under seminatural conditions. By comparing selection gradients from controlled environments with those from unmanipulated "noisy" field situations, inferences can be made about the relative importance of, for instance, female choice versus male-male competition in sexual selection under different circumstances (68). A first, critical step in identifying ecological influences on sexual selection would be to experimentally manipulate ecological variables, either in the laboratory or in the field, and quantify the resulting changes in sexual selection. Much can be adapted from similar experimental studies of natural selection (22, 167). For instance, Svensson & Sinervo (155) experimentally demonstrated that hatchling density influenced natural selection on egg size in juvenile side-blotched lizards (i.e., density-dependent natural selection). Calsbeek & Cox (22) examined the relative contributions of predation and competition to natural selection through whole-island manipulations of *Anolis* lizards. There is a growing interest in experimental manipulations and identification of ecological agents in natural selection studies (98), and sexual selection researchers should follow this path as well.

After identifying influential ecological factors, studies should manipulate these factors and examine the implications for behavior and selection. For example, an experimental decrease in food availability for a focal species may lead to an elevated intensity of male-male competition, which would subsequently limit female choice and increase the selection gradient. Such manipulative studies can also be informative in parsing the contributions of both natural selection and sexual

selection to fitness. When designing these studies, it will be important to recognize that the agents of selection may interact in ways that cannot be predicted by studying each mechanism in isolation. For example, females may incite male-male competition before mating (30), and the results of male-male competition may alter female mate preferences or mate choice (175). Importantly, laboratory contexts may fundamentally change the nature of sexual selection if not designed appropriately. Thus, in-depth knowledge of competitive and mating behaviors as they occur in nature is essential to determine suitable contexts for measurements of selection.

CONCLUSIONS

Sexual selection, like natural selection, takes place in ecologically complex environments. One of the most exciting and understudied questions in sexual selection research today is how such ecological complexity shapes the processes and outcomes of sexual selection. The agents of sexual selection, including male-male competition and female mate choice, are causes and consequences of fluctuating selection pressures. Thus, cascading evolutionary dynamics may result from even simple within-population differences in environmental variables. The central conclusion from this review is that it is time for a reappraisal of some of the fundamental assumptions about sexual selection, which should lead to new approaches in both empirical and theoretical research. Indeed, the field of sexual selection is currently primed for rapid growth and great discovery.

SUMMARY POINTS

1. Sexual selection, like natural selection, takes place in heterogeneous environments. Studies measuring sexual selection over time, space, or context are relatively rare. However, existing studies of mate choice and male-male competition suggest that fluctuations in sexual selection may be extremely common.

2. Much research on sexual selection has been focused on simply demonstrating the presence of mate choice, male-male competition, or postcopulatory agents of selection. Furthermore, these factors are usually examined in isolation. It is time to examine sexual selection as a whole, integrating these agents.

3. Ecological complexity may maintain genetic variation in sexually selected traits through the effects of both fluctuating selection and genotype-by-environment interactions.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

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