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The Role of Ecology in Speciation by Sexual Selection: A Systematic Empirical Review

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Abstract

Theoretical and empirical research indicates that sexual selection interacts with the ecological context in which mate choice occurs, suggesting that sexual and natural selection act together during the evolution of premating reproductive isolation. However, the relative importance of natural and sexual selection to speciation remains poorly understood. Here, we applied a recent conceptual framework for examining interactions between mate choice divergence and ecological context to a review of the empirical literature on speciation by sexual selection. This framework defines two types of interactions between mate choice and ecology: internal interactions, wherein natural and sexual selection jointly influence divergence in sexual signal traits and preferences, and external interactions, wherein sexual selection alone acts on traits and preferences but ecological context shapes the transmission efficacy of sexual signals. The objectives of this synthesis were 3-fold: to summarize the traits, ecological factors, taxa, and geographic contexts involved in studies of mate choice divergence; to analyze patterns of association between these variables; and to identify the most common types of interactions between mate choice and ecological factors. Our analysis revealed that certain traits are consistently associated with certain ecological factors. Moreover, among studies that examined a divergent sexually selected trait and an ecological factor, internal interactions were more common than external interactions. Trait–preference associations may thus frequently be subject to both sexual and natural selection in cases of divergent mate choice. Our results highlight the importance of interactions between sexual selection and ecology in mate choice divergence and suggest areas for future research.

Subject areas: *Reproductive strategies and kinship analysis*

Key words: *ecology, natural selection, reproductive isolation, sexual selection, speciation, trait divergence*

Introduction

The role of sexual selection in population divergence and speciation remains an active area of research (e.g., Panhuis et al. 2001; Ritchie 2007; Kraaijeveld et al. 2011; Safran et al. 2012). One outstanding question is how sexual selection interacts with ecological context during population divergence, particularly in the evolution of divergent mate choice and consequent premating reproductive isolation (e.g., van Doorn et al. 2009; Maan and Seehausen 2011; Marie Curie SPECIATION Network et al. 2012; Langerhans and Reisch 2013; Safran et al. 2013). Ecological speciation, in which reproductive isolation arises as a by-product of adaptation to different ecological contexts, is comparatively well established (e.g., Schluter 2009; Nosil 2012). However, mate choice among divergent groups is frequently based on traits that have diverged as a result of sexual rather than natural selection (e.g., Safran et al. 2012; Seddon et al. 2013; Svensson and Waller 2013). For sexually reproducing organisms, mate choice is an important barrier to gene flow, and divergent mate preferences can result in premating reproductive barriers. This implicates critical roles for divergent sexual selection and for interactions between sexual selection and ecological context in cases of speciation by selection.

A recent conceptual framework for speciation by selection explicitly outlines criteria for testing the relative importance of sexual and natural selection in the evolution of behavioral premating isolation (Box 1 in Safran et al. 2013). Assessing the relative roles of natural and sexual selection in premating isolation requires identifying the traits that contribute to mate choice divergence between different populations or species and ultimately characterizing the sources of selection

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on those traits (Box 1 in Safran et al. 2013). This entails an examination of how mate choice behavior and ecological context separately and interactively influence sexual trait and preference variation both within and among closely related populations (Box 1 in Safran et al. 2013).

Safran et al. (2013, their Table 2) also describe four different pathways by which premating reproductive isolation can evolve between populations via selection. Premating isolation can evolve by divergent natural (ecological) selection alone, by divergent sexual selection alone, or by two types of interactions between sexual selection and ecological context; the latter three pathways involve divergence in traits used in mate choice and their corresponding preferences. In one type of interaction, natural and sexual selection act jointly on sexual traits and preferences, through either pleiotropy or linkage disequilibrium ("internal" interactions). In internal interactions, ecological context exerts natural (viability) selection on traits and preferences that are also used in mate choice (i.e., subject to sexual selection), leading to divergence among populations experiencing different environments. For example, traits that evolve for mimicry are often subject to both natural and sexual selection as shifts to different models results in selection on mimic traits and on preferences for individuals possessing those traits (e.g., Kronforst et al. 2007; Muñoz et al. 2010). In external interactions, ecological differences alter the dynamics of sexual selection when the environment acts as a filter, affecting the production, transmission, and/or perception of sexual signals (see Maan and Seehausen 2010 for a similar distinction), resulting in sexual selection but not natural selection on the signal or preference. For example, changes in light environment affect the perception of dewlap color in *Anolis* lizards, leading to trait divergence that maximizes contrast in different light environments (e.g., Leal and Fleischman 2004). There is thus divergent sexual selection on the signal due to biases of female perceptual space, but no viability selection. External cases also encompass context-dependent variation in mate choice, such as when females are more accepting of heterospecific mates in the presence of a predator despite preferring to mate with conspecifics (e.g., Bonachea et al. 2011). Distinguishing internal from external interactions is important in studies of speciation because variation in ecological context can exert different types of selection pressures on traits involved in mate choice divergence and ultimately premating isolation. Moreover, the type of interaction between sexual signals and the environment may affect the strength of isolation when divergent populations are brought into sympatry or a common garden. For example, external interactions, particularly between recently diverged populations, are predicted to yield weaker premating isolation than internal cases (Maan and Seehausen 2010; Safran et al. 2013) but may also serve as a crucial stage in early divergence.

Here, we conduct a systematic review of nearly 1500 published empirical studies related to sexual selection and speciation, leaving out the recently reviewed body of work on ecological speciation (Nosil 2012) and focusing on cases where the ecological context of mate choice divergence is analyzed. Because the traits and ecological factors affecting mating decisions are likely to vary across taxonomic groups and as a function of geographic context, we also collected data to evaluate whether patterns of mate choice divergence were associated with these factors. We addressed four main questions with these data (Table 1). First, we asked what types of sexual signal traits were involved in divergent mate choice and if these traits varied with taxa and geographic context. Second, we asked what types of ecological factors were involved in divergent mate choice and if these ecological factors varied with taxa and geographic context. Third, we tested for associations between sexual signal traits and the ecological context in which they are diverging to examine whether there are consistent associations between ecology and traits in divergent mate choice. Finally, we tested for associations between divergent traits/ecological factors and internal versus external interactions, asking whether one or the other type of interaction is more common and more frequently associated with particular traits or ecological contexts. Our goal in addressing these questions was to synthesize what is known about the role of ecology in mate choice divergence, assess the relative frequencies of internal versus external interactions in the empirical literature, and highlight areas to consider for future study.

Methods

Literature Search Terms

To identify studies related to the role of sexual selection in population divergence and speciation, we searched the Web of Science database using the search terms "sexual selection" AND "speciation" for publication dates between 1981 and September 2013. We chose 1981 as the start date for our search because it corresponds to the publication year of Lande's (1981) influential model for the evolution of reproductive isolation via divergence in male traits and correlated female preferences. Prior to publication of this model, very little work focused on the role of sexual selection in speciation; indeed, our search yielded only 30 articles published between 1990 and 1999, with increased interest in this topic occurring since 2000.

Database Compilation

Search results (n = 1458) were downloaded and manually screened for relevance. Because we were interested in examining empirical patterns of association between divergence in sexual signal traits and ecological factors influencing mate choice, we focused on empirical studies and removed review articles, theoretical models, studies of plants, and other studies lacking empirical data. We also removed studies of mate choice within single populations that did not explicitly address divergence or speciation. To focus specifically on the interaction between sexually selected traits and ecological context in mate choice divergence, we further screened this database for studies that explicitly examined mating decisions, via preference trials, measurements of assortative mating, or isolation indices. We refer to these collectively as cases of "divergent mate choice." With these criteria, we identified 278 articles

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Table 1 Questions addressed and key results of this review

Question	Rationale	Comparison made	Sample size	Key result
What taxa are the focus of sexual selection and speciation studies?	The taxonomic groups studied may influence the types of traits and ecological factors involved in divergence.	Percentage of studies reviewed in each taxon category.	278	The majority of studies focus on insects (43%) and fish (31%).
What geographic contexts are studied, and are there associations between geography and taxa?	Geographic context and likelihood of gene flow influence the traits and ecological factors contributing to mate choice divergence.	Percentage of studies reviewed with different geographic contexts.	278	Even mix of sympatric and allopatric studies, and no association between taxon and geographic context.
Question 1a: Do patterns of trait and mate choice divergence differ across taxa?	Type of traits used in mate choice divergence may vary between taxa with different dominant sensory modalities.	Association between type of sexually selected trait and taxon (Figure 1).	188	Significant association between divergent traits and taxa mirrors dominant sensory modalities in those taxa (e.g. chemical signals in mammals, acoustic traits in birds).
Question 1b: Do patterns of trait divergence differ as a function of geographic context?	Different types of traits or sensory modalities may be used in reproductive isolation in allopatric vs. sympatric groups.	Association between type of sexually selected trait and geographic context of study.	188	No effect of geographic context on the type of divergent trait used in mate choice.
Question 2a: Do ecological factors involved in mate choice divergence differ across taxa?	The importance of different ecological factors to mate choice divergence should vary across taxa.	Association between divergent ecological factor and taxon (Figure 2).	138	Significant variation in ecological factors implicated in mate choice divergence across taxa linked primarily to light environment and habitat in fishes, host plant and heterospecifics in insects, and aposematism and heterospecifics in amphibians.
Question 2b: Do ecological factors involved in mate choice divergence differ across geographical contexts?	More divergent ecological factors are expected in allopatric comparisons than in sympatric comparisons.	Association between divergent ecological factor and geographic context of study.	138	No effect of geographic context on the ecological factor affecting mate choice. Surprising because sympatric groups should have the same ecology, but ecological factors are frequently cited as affecting mate choice divergence in sympatric comparisons.
Question 3: Are there associations between divergent traits and ecological factors in mate choice divergence?	Divergence in different types of traits should be affected by different ecological variables.	Association between divergent ecological factor and divergent trait (Figure 3).	116	Significant association between trait and ecological factor. Color and chemical signals interact with diverse ecological factors. Body size is linked primarily to habitat variation, acoustic signals to heterospecifics, and vibratory signals to host plant.
Question 4a: Are there associations between divergent traits and internal or external interactions?	Different types of traits may be more prone to internal vs. external interactions.	Association between divergent traits and type of interaction (Figure 4).	67	Significant association between trait and interaction type. Most cases are internal interactions involving color, followed by internal interactions with chemical cues, body size, and morphology.
Question 4b: Are there associations between divergent ecological factors and internal/external interactions?	Different ecological factors may be more or less likely to be involved in internal vs. external interactions.	Association between ecological factor and type of interaction (Figure 5).	67	Significant association between ecological factors and interaction type due to large number of internal interactions. Heterospecifics and mimicry exclusively internal. External interactions, and natural and sexual selection alone, are all rare.

Sample size is the number of articles reviewed that pertains to each question; some articles contained data on more than one trait or ecological factor.

from the original data set that included an analysis of mate choice (Supplementary Appendix).

We haphazardly assigned each of these 278 articles to one of the four authors of this article for review. To standardize data collection, all four reviewers initially reviewed the same studies until consistent data collection was achieved (approximately 10 articles were reviewed by all four reviewers at the start of this study). Throughout data collection, the reviewers periodically read the same articles to ensure consistency over time. For each article, we collected data related to study

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Table 2 Summary of information collected from each article in empirical literature review

Category	Definition	Options
Taxon	General taxonomic group.	Amphibian, arachnid, bird, fish, insect, mammal, mollusk, other invertebrate, reptile.
Focal species/study system	Scientific name of each species or subspecies used in the analysis.	N/A
Geographic context	Relative geographic distribution of the taxa studied. "No geographic element" includes within-population studies, phylogenetic comparative studies, and laboratory lines. "Not indicated" is used when geographic context was not mentioned.	Allopatric, sympatric, mix of allopatry and sympatry, no geographic element, not indicated.
Mate choice measured	Some component of mate choice or mating preference measured.	Yes/no
Divergent trait	Category of trait found to be involved in mate choice.	Acoustic, behavior, body size, chemical, color, color morph, electric or vibrational, morph, morphology.
Ecological context measured	Researchers consider ecological context of the focal taxa integral to the hypothesis or prediction being tested and/or the interpretation of the results.	Yes/no
Category of ecological divergence	Ecological variables that differ between focal taxa	Aposematism, conspecific density, elevation, habitat, heterospecifics, host plant, light environment, mimicry, predation, other.
Type of interaction between trait and ecological context	Type of interaction between sexual selection and ecological context.	Natural selection alone, sexual selection alone, internal interaction, external interaction, no reproductive isolation based on traits/ecology measured.

system, geographical context, mating traits, divergent ecological factors, and divergent mate choice (see Table 2 for summary of data collected). Of the 278 articles measuring mate choice, 138 also measured some aspect of ecology (Table 1). Of these 138 ecological studies, 116 also identified a divergent trait involved in mate choice divergence (Table 1). We were able to classify 67 of these studies into one of four categories: internal interactions between traits and ecology, external interactions between traits and ecology, sexual selection alone, or natural selection alone (cf., Safran et al. 2013).

Classifying internal versus external interactions required some inferences because most studies did not explicitly measure sexual and natural selection on traits and preferences. We classified studies as representing internal interactions if traits used in mate choice were also indicated as being related to ecological factors such as mimicry, predator avoidance, aposematic signaling, or reinforcement and character displacement. Studies that showed assortative mating by ecotype or morphotype also were classified as internal interactions. In all of these cases, natural and sexual selection on preferences for these traits would be expected but were rarely empirically tested.

We classified studies as representing external interactions if mate choice varied with context or ecological factor. The clearest cases were those in which divergent mate choice broke down in common gardens (e.g., at different light levels). Internal and external interactions need not be mutually exclusive as sexual signals can be shaped by multiple ecological factors, and organisms often have multiple signal traits. However, we did not find any studies that clearly examined effects of multiple ecological factors on different traits.

Cases that ruled out a role for ecology or sexual selection were classified as sexual or natural selection alone, respectively, and a small number of studies found no reproductive isolation based on the trait and ecological variable studied.

Statistical Analysis

To address questions related to the role of ecological context in mate choice divergence, we first summarized the prevalence of particular factors in our data set (i.e., number of studies focusing on different taxonomic groups, number of studies on allopatric vs. sympatric geographic contexts). We then statistically analyzed associations between different factors by applying generalized linear models with Poisson distributions to two-way tables of count data. We then compared saturated models (containing an interaction between the two explanatory variables) with models without the interaction term. A significant difference between the two models (based on a chi-square distribution with one degree of freedom) indicates that there is an interaction between the explanatory variables, whereas a nonsignificant difference between the saturated and simpler models indicates the two explanatory variables vary independently (Crawley 2012).

As with any literature review, our results are biased by multiple factors, including our search terms and the topics and taxa that researchers choose to study. Separating biological reality from researcher effort is a persistent challenge; therefore, we note whether resulting associations are likely to arise

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via differences in researcher effort and discuss apparent gaps in information that likely reflect true lack of biological associations. We also emphasize that prevalence of associations in our data set identifies current patterns that emerge from the empirical literature; in some cases, there are not enough data to summarize the prevalence of a particular association in nature.

Results and Discussion

Summary of Data Set by Taxonomic Group and Geographic Context

Taxonomic Representation in the Database

For each article, we classified study systems into broad taxonomic groups (Table 2). Taxa in the "other invertebrates" group were the subjects of three or fewer studies in the data set. Nearly half (43%) of the studies we reviewed investigated insects, and nearly a third used fish (31%), perhaps not surprising given the diversity of these groups and their tractability as research organisms. The remaining studies featured small proportions of birds (8%), amphibians (6%), and reptiles (4%); the rest were mammals, mollusks, arachnids, and other invertebrates. Among these broad classifications, we found 256 unique taxonomic groups (i.e., identified to species or subspecies level), 44% of which were insects and 31% of which were fish. Therefore, we did not find evidence for strong overrepresentation of particular species within broader taxonomic groups; that is, the taxon groups that comprised the greatest total number of studies (insects and fish) also included the greatest number of unique species (121 and 86, respectively). Although 121 species is a small subset of the total extant species of insects, it is a more diverse representation than the 16 amphibians, 23 birds, 7 mammals, 6 mollusks, and 10 reptiles in the data set. Any conclusions drawn about the traits and ecological factors involved in mate choice divergence are thus heavily influenced by information gleaned from studies of insects and fish, particularly *Drosophila* fruit flies (16% of total studies) and cichlid fishes (10% of total studies).

Geographic Context of Divergence

We classified the geographic context of each study as sympatric, allopatric, a mix of sympatry and allopatry (i.e., mate choice was tested within and between populations or species), or not relevant (e.g., in studies using laboratory lines, Table 2). Because they were relatively rare in our data set, studies of hybrid zones and parapatry ($n = 7$) were classified as sympatric. Of 278 cases, there was a roughly even split between the number comparing sympatric groups (32%) and allopatric groups (37%), with most of the remainder (24%) containing a mix of sympatric and allopatric comparisons. By definition, sympatric comparisons were among species, ecotypes, or subspecies, whereas allopatric comparisons also included comparisons among closely related populations.

Associations Between Geographic Context and Taxonomic Group

We found no significant associations between geographic context and taxonomic group ($P = 0.5$), indicating that certain taxa are not more likely to occur in studies of sympatry versus allopatry.

Traits and Ecological Factors Involved in Mate Choice Divergence

Traits used in mate choice can diverge for reasons other than sexual selection (e.g., genetic drift or natural selection), and divergence in these traits may not always result in premating isolation. Although sexual selection typically exerts directional selection on traits (Hoekstra et al. 2001; Siepielski et al. 2011), many traits that affect mate choice are currently subject to stabilizing sexual selection or may be fixed (e.g., Price 2008), leaving no signature of past directional selection that may have led to trait–preference divergence. Unfortunately, it was not possible to determine the nature of selection underlying trait and preference variation in our review (e.g., "good genes" or direct benefits models of sexual selection): most studies only examined variation in mate choice between populations, rather than describing selection on traits both within and between populations. This is likely a result of including "speciation" as a search term, which may have excluded studies that examine mate preferences within populations. Thus, in analyzing the types of traits used in mate choice divergence, we consider any trait that is a target of mate choice to be a putatively sexually selected trait, but recognize there are limitations to this assumption.

To understand the types of traits and ecological factors that influence mate choice divergence, we focused on studies that measured both divergence in sexual signal traits and mate choice in different species, subspecies, or populations, as well as ecological factors influencing traits and/or mate choice. The way in which "mate choice" was quantified varied widely across studies and included quantifying preference functions for specific traits within and among populations, measuring the amount of time a female spends in proximity to one or another male in experimental trials, calculating isolation indices based on matings observed in mixed cages of heterospecifics and conspecifics, and observing pairing patterns among ecotypes in nature. For the purposes of this review, we included all of these approaches under the heading "mate choice divergence."

Question 1: What Traits Are Involved in Mate Choice Divergence?

As variation in phenotype is the substrate of selection, understanding which aspects of phenotype constitute the basis of mate choice is the first step in identifying the processes driving speciation (Box 1 in Safran et al. 2013). For this analysis, we assigned traits to several categories based in large part on sensory modality (Table 2). Of the 278 studies that measured divergent mate choice, 188 indicated at least one trait on which mate choice was based. Of these, most were color (25%), acoustic (20%), and chemical (18%) traits. Approximately 6% of studies that tested preferences for a divergent trait found no reproductive isolation based on that trait; the remainder (94%) found some degree of isolation, assortative mating, or preference behavior. This may reflect a bias toward publishing "positive" results although records of traits that are not involved in reproductive isolation are equally as valuable for understanding the processes underlying divergence and their publication should be encouraged.

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Question 1a. Do Patterns of Trait and Mate Choice Divergence Differ across Taxa?

In the 188 studies that tested divergent mate choice for divergent traits, insects and fish were still the most prevalent study systems (35% and 32%, respectively). The decrease in the percent of insect studies relative to the full data set reflects the many insect studies that measure premating isolation but no specific aspects of phenotype.

There was significant variation among taxa in the types of traits found to be involved in mate choice divergence ($P < 0.001$, Figure 1), which is intuitive given the differences in dominant sensory modalities across taxa. For example, 55% of studies of birds and 30% of studies in insects focused on divergent acoustic signals, 41% of studies in fish focused on color signals, and 71% of studies in mammals and 54% in reptiles focused on chemical cues (Figure 1). It is notable that relatively few studies of fish (9%) examined divergent chemical cues, when these have frequently been found to be important in this group (e.g., Hankison and Morris 2003; Plenderleith et al. 2005). In addition, despite many studies reporting differences in behavioral variables like courtship intensity, very few (4%) quantify divergence in behavior (and corresponding preferences for behaviors) among groups. This is not surprising, as both chemical cues and behavior are difficult subjects for empirical data collection. Finally, of the studies focused on morphology and body size, half or more (58% and 50%, respectively) were in fishes, mostly in the form of assortative mating studies among different eco- and morphotypes. Studies of divergent mate choice for morphological traits and body size are largely absent in birds, amphibians, and mammals although studies of amphibians typically control for snout–vent length. This is perhaps an important omission given the prevalence of sexual dimorphism in all of these groups.

1b. Do Patterns of Trait Divergence Differ as a Function of Geographic Context?

We found no significant association between the type of trait involved in divergent mate choice and geographic context ($P = 0.88$).

Question 2: Is Divergent Mate Choice Associated with Ecological Context?

To determine how ecological context is implicated in mate choice divergence, we identified 138 studies that indicated

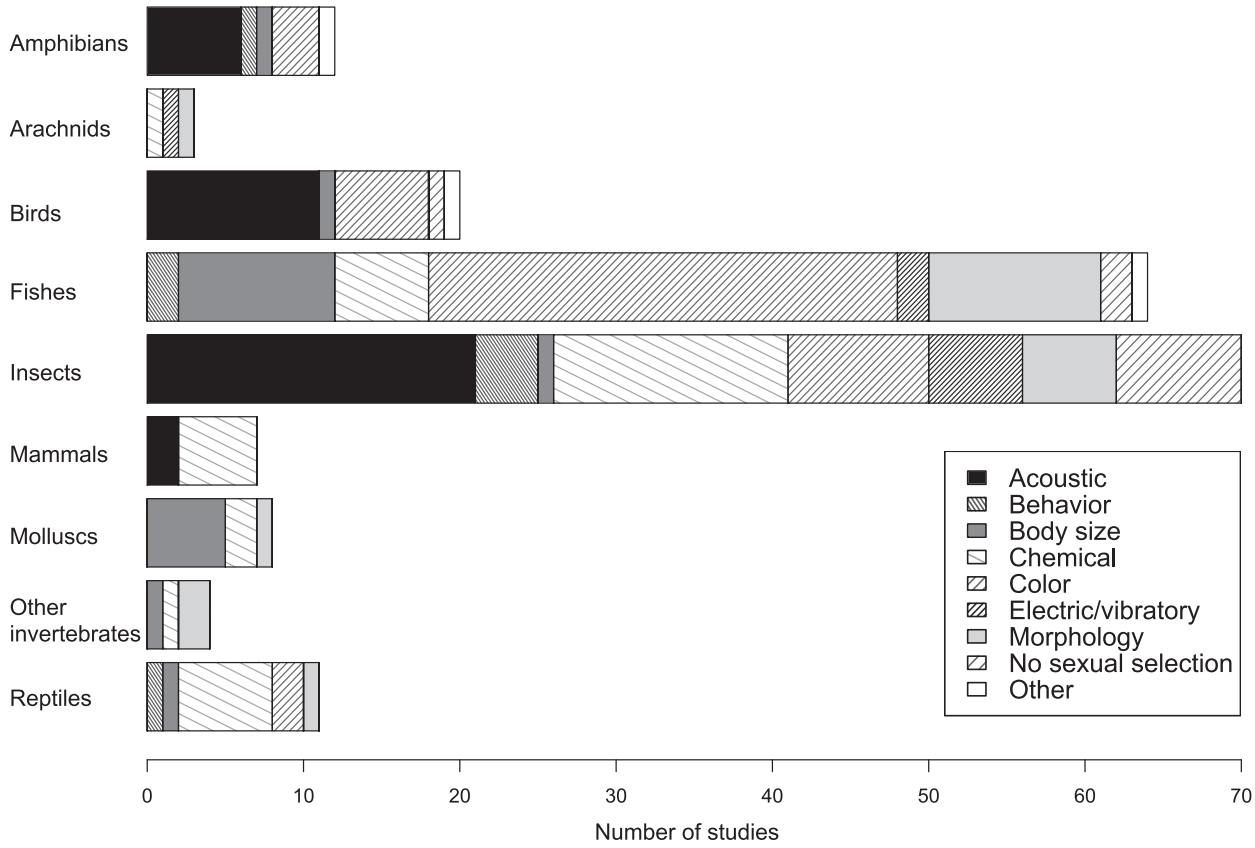

Figure 1. Association between type of sexually selected trait and taxon. The common categories of traits used in divergent mate choice mostly mirror the dominant sensory modality of that taxon.

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some role of ecology in preference divergence or assortative mating. As with the analysis of divergent traits, we classified divergent aspects of ecology into broad categories (Table 2) and then investigated how these ecological factors varied with taxon and geographic context.

The most common ecological factor considered in cases of mate choice divergence was habitat (33%). Although we classified some specific habitat characteristics separately due to their prevalence in the literature (i.e., light environment and elevation) habitat remained the broadest category, encompassing differences such as food, water depth, and climate. The next two most common ecological factors considered in studies of divergent mate choice were heterospecifics (15%, density and presence/absence of heterospecifics were lumped together) and host plants (12%). Studies focusing on heterospecifics reflect the large body of research on reinforcement and character displacement. The importance of reinforcement as a driver of diversification has been debated (Servedio and Noor 2003; Yukilevich and True 2006). Most studies that analyzed the effect of heterospecifics on mate choice divergence found an effect on patterns of assortative mating (e.g., females in sympatry with heterospecifics were choosier than those in allopatry), providing some empirical support for reinforcement (although this may be influenced by a publication bias toward studies with positive results). Cases of reproductive isolation concurrent with host plant switches are a central topic in discussions of ecological speciation (e.g., Drès and Mallet 2002; Nosil 2012). Their appearance in our sexual selection data set indicates that some of these studies concurrently examine divergent (putative) sexually selected traits and suggests that host plant fidelity may not be the only factor contributing to reproductive isolation in some of these groups (see Conclusions).

Q2a: Do Ecological Factors Involved in Mate Choice Divergence Differ across Taxa?

Ecological factors were not distributed equally across taxa, as revealed by a significant interaction between ecological factor and taxonomic group ($P < 0.001$, Figure 2). In fishes, 54% of cases of divergent mate choice were linked to divergence in habitat and 23% to differences in light environment (Figure 2), likely reflecting the relatively easily measurable habitat stratification that occurs in aquatic environments. In insects, 27% of cases where mate choice divergence was linked to ecological factors were a result of host plant divergence, 18% were due to heterospecifics, 16% to habitat, and 15% due to mimicry (Figure 2). Amphibians were the only other taxonomic group with more than five studies identifying an ecological variable related to mate choice, due mainly to studies of aposematic signaling in poison dart frogs (40%)

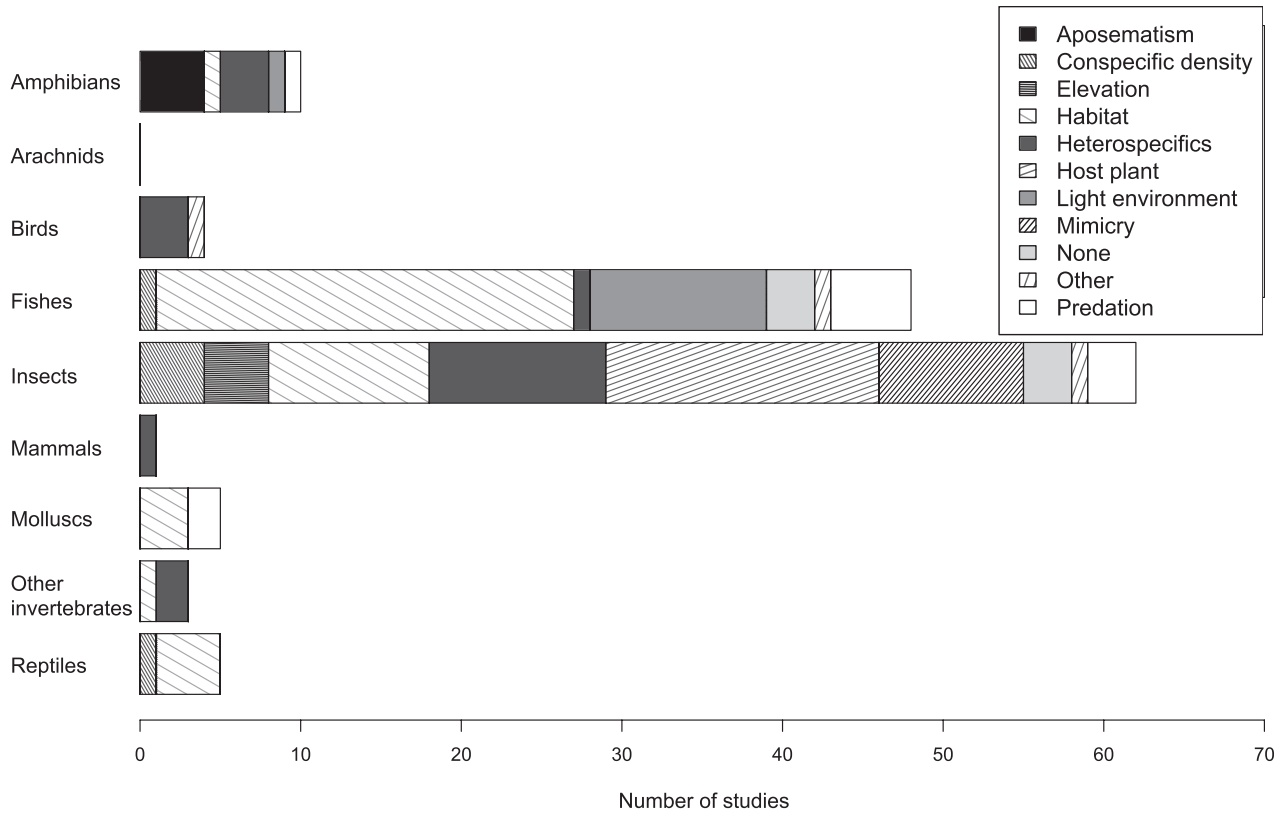

Figure 2. Association between divergent ecological factor and taxon. Most studies that examine associations between ecology and mate choice divergence are in fishes and insects. A diverse array of ecological factors influences mate choice divergence in these groups.

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and reproductive character displacement in choruses (30%, Figure 2). By comparison, therefore, birds, mammals, mollusks, arachnids, and reptiles are something of a black box when it comes to understanding the ecological factors that influence divergent mate choice.

Question 2b: Do Ecological Factors Involved in Mate Choice Divergence Differ across Geographical Contexts?

We found no significant associations between ecological factors and geographic context ($P = 0.08$). Habitat was the most common divergent ecological factor across all geographic contexts. No ecological factor was overwhelmingly associated with allopatry or sympatry, indicating that allopatric and sympatric populations are equally likely to experience different ecological contexts. This suggests that groups classified as "sympatric" in studies of speciation by sexual selection are rarely syntopic, and may instead inhabit different ecological niches despite physical proximity.

Question 3: Are There Associations between Divergent Traits and Ecological Factors in Mate Choice Divergence?

In the 116 studies that identified both a trait upon which divergent mate choice was based and an ecological factor affecting divergent mate choice, we examined associations between the types of traits and types of ecological variables involved. We found a significant interaction between trait category and divergent ecological factor ($P = 0.001$, Figure 3), indicating that different divergent traits are consistently associated with different aspects of ecology. Color divergence was both the most common type of trait–ecology association (32% of all trait–ecology interactions) and had the broadest range of ecological interactions, with 24% of cases of divergent color traits linked to different light environments, 22% to general habitat differences, 22% to mimicry, and 11% to predation (Figure 3). Chemical signals were the second most common type of trait associated with a divergent ecological factor (16% of total). Divergent preferences for chemical signals were associated mainly with habitat (42%), heterospecifics (26%), and host plant (16%, Figure 3). For acoustic signals, 46% of ecological interactions were due to heterospecifics (Figure 3), mainly reflecting studies of character displacement due to heterospecifics and otherwise noisy environments. In cases of divergent body size, 60% were associated with habitat differences (Figure 3), most from studies of different morpho- and ecotypes. Electric and vibratory signals were the most ecologically specific traits; 71% of cases of divergence in these signals were associated with differences in host plants (all of

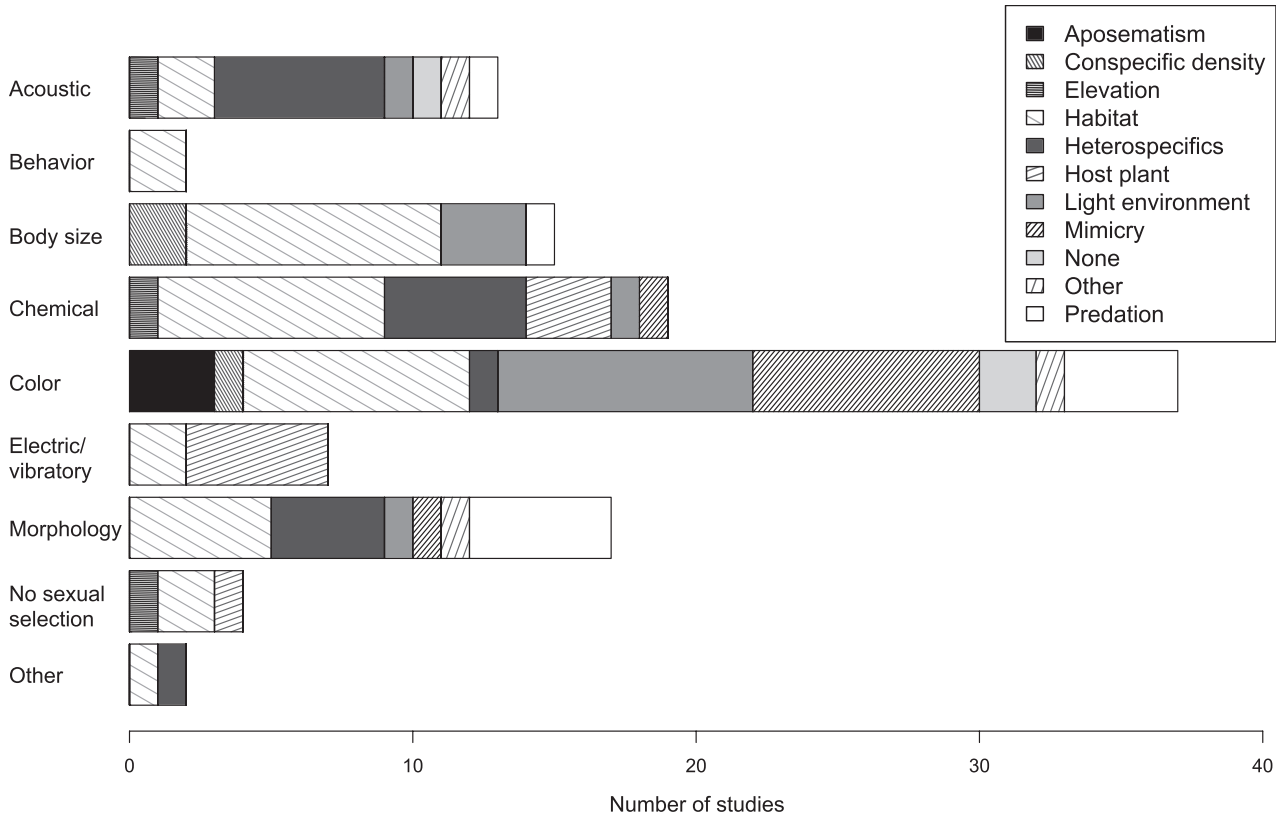

Figure 3. Associations between divergent traits and ecological factors. Divergence in different traits is associated with variation in different ecological factors. Color is both the trait most frequently associated with ecological divergence and is associated with the widest array of ecological factors.

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which were vibratory rather than electric signals, Figure 3), likely because vibratory signals transmit differently on different substrates. Notably, the only divergent traits associated with host plant shifts were chemical and vibratory cues. Given the importance of host shifts to speciation in a wide range of insects (e.g., Drès and Mallet 2002; Nosil 2012), it is interesting that other traits contributing to reproductive isolation have not been identified.

Question 4: Are There Associations Between Specific Traits or Ecological Factors and Internal/External Interactions?

To assess the relative frequencies of the four pathways by which premating isolation can evolve, we classified studies that included both a divergent trait and a divergent aspect of ecology as having internal interactions (natural and sexual selection on trait or preference) or external interactions (sexual selection on trait or preference due to variation in signal transmission environment) with their ecological context. We were able to classify 67 studies according to this framework and determine if the different types of interactions were associated with specific traits and ecological factors. Note that because we did not specifically search the ecological selection literature, the studies classified as "natural selection alone" are those that examined both ecological factors and some aspect of sexual selection and found no evidence for divergent sexual selection. Because these studies explicitly examined both forms of selection, they are most likely to represent "real" cases of divergence by natural selection alone. Nonetheless, this limited data set does not allow us to generalize about the relative prevalence of natural selection alone versus sexual selection alone in the speciation process.

We found that internal interactions were overwhelmingly more common than external interactions: 70% of the classified cases were internal, 14% found no reproductive isolation associated with the divergent traits and ecological variables measured, and only 7% were clear examples of external interactions. Although it is very difficult to rule out a role for ecology or sexual selection in divergence (Safran et al. 2013), 7% of cases of reproductive isolation were plausibly driven by sexual selection alone and 3% by ecological selection alone.

Question 4a: Are There Associations Between Divergent Traits and Different Types of Interactions?

We found a significant association between the types of traits used in mate choice and the type of interaction (internal vs. external plus sexual and ecological selection alone; $P = 0.04$, Figure 4). Internal interactions involving color divergence were again the most common (30% of all interactions, Figure 4). All interactions involving chemical cues (12%) and body size (14%) were also classified as internal (Figure 4). Surprisingly, very few acoustic studies could be confidently

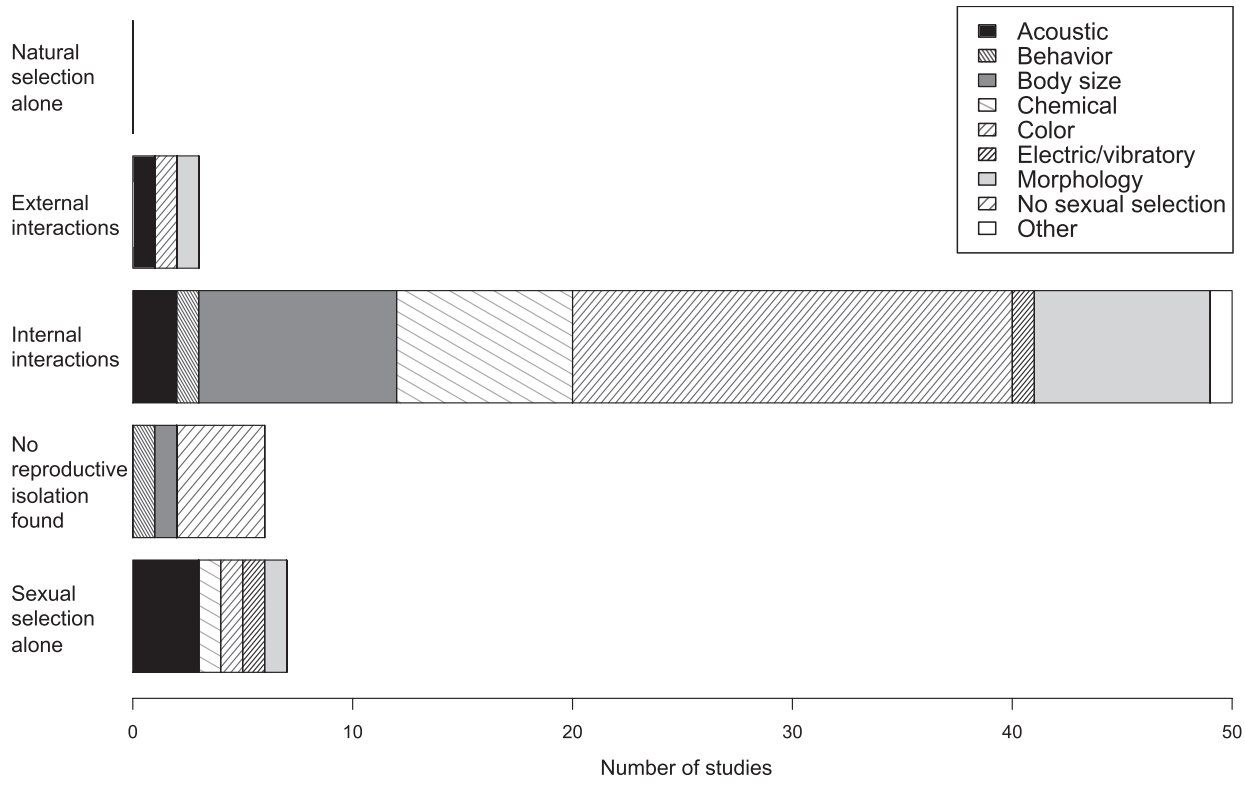

Figure 4. Associations between divergent traits and internal/external interactions: internal interactions with color are the most common type of associations between divergent traits and ecological context. Note that studies that found "natural selection alone" are those that ruled out a role for sexual selection.

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classified as internal or external. This suggests that although variation in ecological factors is frequently invoked in studies of divergent acoustic signals (see Figure 3), few of these studies determine the explicit link between ecology and trait divergence (i.e., whether natural and sexual selection jointly drive the evolution of acoustic signals [internal interactions] or whether the transmission environment simply alters the dynamics of mate choice [external interactions]). Determining this link is particularly difficult in the case of acoustic signals, which are complex, labile, and, in the case of many birds, culturally transmitted.

Of the three studies containing clear examples of external interactions, one involved acoustic signals (*Physalaemus pustulosus*, Bonachea et al. 2011), one involved color (*Pundamilia nyererei*, Seehausen and Van Alphen 1998) and one involved morphology (*Corynopoma riisei*, Kolm et al. 2012, Figure 4). These were cases where ecological factors prevented females from expressing preferences for specific traits or temporarily shifted preferences for a particular trait due to the context of mate choice. Six studies provide potential examples of divergence due to sexual selection alone; three of these involved acoustic traits (pulse rate in *Laupala cerasina*, Oh et al. 2012 and Grace et al. 2012; courtship song in *Gryllus texensis* and *Gryllus rubens*, Gray and Cade 2000), one chemical signal (*Chorthippus parallelus*, Tregenza 2002), one color trait (*Etheostoma zonale* and *Etheostoma barrenense*, Williams and Mendelson 2013), and one vibratory signal (*Chrysoperla plorabunda* and *Chrysoperla downesi*, Henry and Wells 2004). Each of these studies examined at least one divergent ecological variable, but some simply stated that there were no obvious habitat differences among populations, whereas others ruled out specific ecological differences as not affecting trait variation. These systems are prime examples for future work on ecological factors that may (or may not) influence trait and mate choice divergence.

Question 4b: Are There Associations Between Divergent Ecological Factors and Different Types of Interactions?

We found a significant association between ecological factor and interaction type ($P = 0.05$, Figure 5). Internal interactions between habitat (18%) and heterospecifics (13%) accounted for the highest percentages of the total, followed by internal interactions with mimicry (10%) and light environment (10%, Figure 5). Internal interactions due to heterospecifics are likely a result of preference divergence due to reproductive character displacement and reinforcement; we considered these to be internal interactions because shifts in preferences and/or increased choosiness in sympatric populations are the result of selection against maladapted hybrids (i.e., viability selection) and are typically maintained in laboratory common garden experiments. Internal interactions due to mimicry likely arise via correlated trait–preference shifts concomitant with switches to new mimic models.

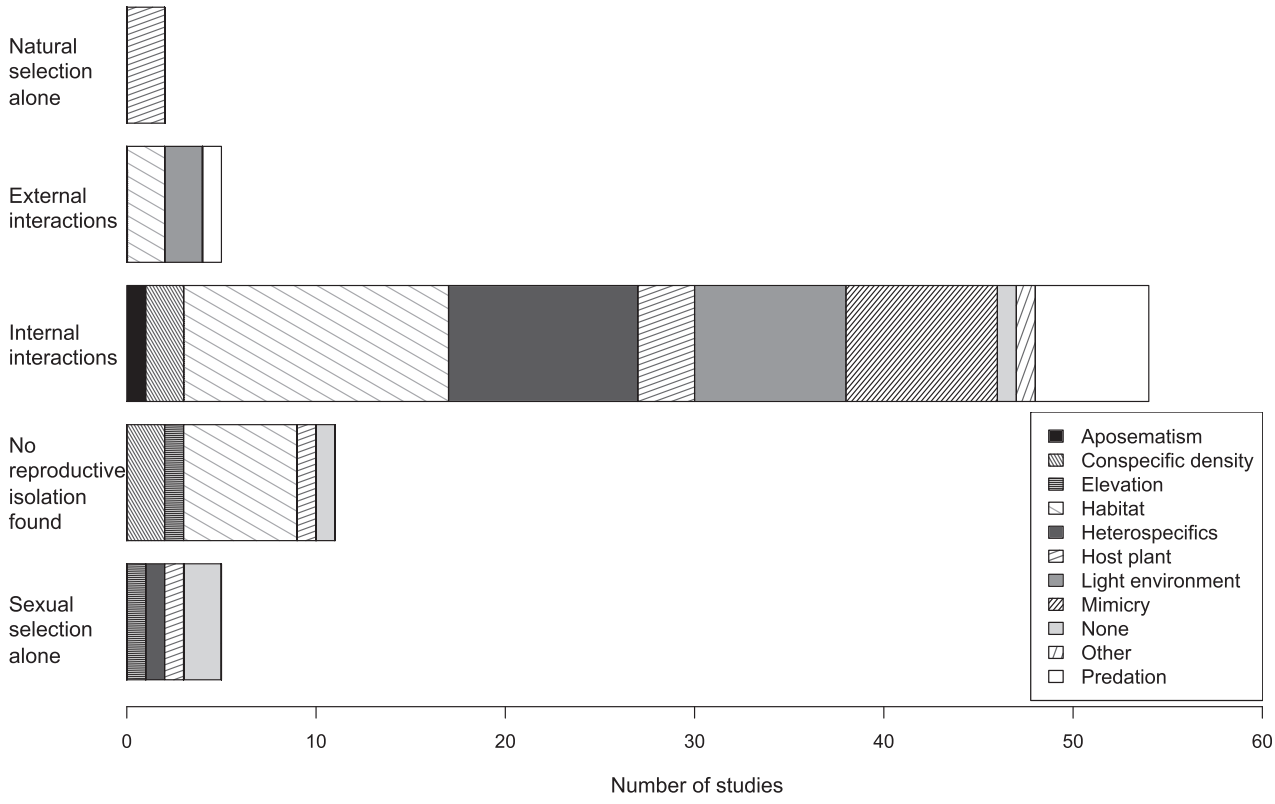

Figure 5. Associations between divergent ecological factors and internal/external interactions: internal interactions are the most common, particularly those involving habitat, heterospecifics, and mimicry. External interactions are comparatively rare.

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Divergent mate choice due to changes in light environment is a classic example of sensory drive, wherein traits evolve to be more conspicuous in a particular light environment. In many of these studies, female preferences collapse when a change in light environment inhibits detection of phenotypic variation (e.g., nuptial color in sticklebacks, Boughman 2001, and African cichlids, Seehausen et al. 1997), suggesting there are external interactions between sexual selection and the environment. One of the external cases in our data set is indeed an example of assortative mating collapse in turbid water (Seehausen and Van Alphen 1998). However, we found that all other studies reporting divergent mate choice as a result of different light environments or water color also found some degree of assortative mating maintained in a common garden (e.g., Haesler 2005; van der Sluijs et al. 2008; Maan and Seehausen 2010) or found additional assortative mating based on traits such as body size (Boughman 2005), which are unlikely to be affected by light environment. We therefore suggest that purely external interactions are relatively rare and/or fleeting in nature, a point we consider further below.

The two studies clearly showing ecological selection alone in our data set involved host plant shifts in insects; in these studies, insects that breed on different hosts are reared in a common environment and show no evidence of assortative mating or hybrid fitness effects. A breakdown in assortative mating in a common garden indicates that sexual traits and/or preferences have not diverged and implicates habitat preferences and/or other ecological adaptation in reproductive isolation. In the studies we reviewed (*Henosepilachna diekei*, Matsubayashi et al. 2011; *Callosobruchus maculates*, Rova and Björklund 2011), premating isolation based on traits other than host plant was also tested but ruled out. Two additional studies, also on host plant shifts (*Timema cristinae*, Nosil et al. 2002; *Rhagoletis* complex, Rull et al. 2012), found no reproductive isolation in a common garden but did not measure mate choice based on putative sexually selected traits; nonetheless, the breakdown of assortative mating in a common garden makes these good additional candidates for ecological speciation alone.

Conclusions

In this article, we reviewed the empirical literature on speciation and sexual selection in the context of a recent framework for understanding interactions between sexual selection and ecological context (Safran et al. 2013). We conclude by considering some of the larger patterns our review has illuminated.

Taxa, Traits, and Ecological Factors Studied

The literature on sexual selection and speciation is biased toward fish and insects, and there is a general bias toward more easily quantifiable traits (e.g., color, acoustic signals) and ecological factors (light environment, host plant), with the result that our understanding of interactions between sexual selection and ecology is largely informed by a few specific cases. In particular, we have a rather good understanding of how sexual selection and ecology interact in cases of light environment and color in fishes and host plant switches in insects. Broadening analyses to include additional taxa, types of traits, and ecological factors will better illuminate how trait–preference associations interact with ecology during mate choice divergence.

Our review also highlights some areas within the well-represented taxa that may be fruitful directions for future research. Chemical cues and courtship behaviors are understudied in fishes, and visual and acoustic cues are understudied in insect host plant races. In addition, many insect studies measure components of reproductive isolation very carefully but do not identify the traits used in mate choice. Considering that mate choice is typically based on multiple signals (i.e., Candolin 2003; Bro-Jørgensen 2010), identifying additional traits involved in mate choice and premating reproductive isolation in these groups could be both tractable and informative.

Geographic Context, Ecology, and Traits

We found no significant association between divergent ecological factors or divergent traits and geographic context, and sympatric groups in our analysis were just as likely to experience divergent ecology as allopatric groups. Speciation is thought to occur most commonly in allopatry (Coyne and Orr 2004; Price 2008), yet many studies of apparently sympatric taxa describe effects of divergent ecological factors on mate choice, indicating that groups in geographical proximity, nonetheless, differ in aspects of ecology that could affect mate choice divergence. This result is consistent with the hypothesis that sympatric speciation requires disruptive ecological selection (e.g., Bolnick and Fitzpatrick 2007); however, the difficulty of confirming true allopatry and sympatry in these studies may confound any real relationship between geography and ecological factors. A more rigorous analysis of gene flow in these cases might reveal a different pattern. Future work in recently diverged systems that still exchange genes may be the best way to identify the mechanisms at work in the early in stages of speciation.

Associations between Divergent Traits and Ecological Factors

We found a significant association between type of divergent trait and type of divergent ecological factor in studies of mate choice divergence, indicating that certain ecological factors interact with certain types of traits in consistent ways. Many of these associations are biologically intuitive, for example, the association between light environment and color. However, we found that "habitat" was the most prevalent form of trait–ecology interaction in our data set, but also the most difficult to interpret. In part, this is because we lumped many different ecological factors into this category (e.g., diet, temperature, season), but the difficulty of interpretation is also due to the lack of quantitative measurements of ecological variation in many studies; it was rarely clear how specific ecological factors affected phenotype. Studies that test specific hypotheses for how sexual signal traits vary with particular ecological factors

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are critical for understanding interactions between natural and sexual selection, particularly because different mechanisms of sexual selection (e.g., good genes, direct benefits) are predicted to have different interactions with ecology (Safran et al. 2013). Ideally, researchers should use similar methodology and measure similar traits and ecological factors within existing systems so that results of different studies are broadly comparable (Box 1 in Safran et al. 2013).

Roles of Internal and External Interactions in Divergence

Internal interactions, where we inferred the joint action of natural and sexual selection, were more common than external interactions, providing empirical support for the suggestion that "speciation by sexual selection" is most frequently a result of both natural and sexual selection. The relative rarity of external interactions, and the nature of those we found, suggests that such interactions may be more prevalent in the early stages of divergence and/or relatively fleeting. For example, shifts in color may initially be driven by changes in light environment that affect signal perceptibility. Over time, however, natural selection on sensory systems in divergent light environments may also cause divergence in preferences, changing this to an internal ecological interaction.

External interactions are not necessarily negligible or unimportant to speciation, as ecological and social context are critical to mate choice (Qvarnström 2001; Bro-Jørgensen 2010; Bailey and Moore 2012). Indeed, external interactions can both promote and inhibit divergence in sexual signals, promoting divergence when signals adapt to distinct transmission environments and inhibiting divergence when a change in the environment breaks down context-specific preferences. We reviewed multiple studies that showed females are more likely to mate with heterospecifics when a predator blocked access to a conspecific (e.g., Bonachea et al. 2011; Velema et al. 2012) or when the density of heterospecifics was higher than that of conspecifics (Saetre et al. 1999; Peterson et al. 2005). Even low levels of gene flow can break down local adaptation (Hey 2006; Smadja and Butlin 2011), and these kinds of context-specific interactions are likely to be very common in nature. Future work that explicitly links laboratory choice experiments to observational and experimental field studies of mate choice and gene flow will go a long way toward addressing how important ephemeral external interactions are in speciation by sexual selection.

We suggest the best way to move forward in understanding the mechanisms underlying trait–preference associations, mate choice divergence, and speciation is to 1) quantify natural and sexual selection on traits used in mate choice and corresponding preferences both within and between populations; 2) test hypotheses about the role of specific ecological factors in shaping divergence in trait–preference associations; and 3) broaden the scope of speciation studies to include a more diverse array of taxa, traits, and ecological factors. The advent of genomic techniques that allow measurement of current and historic gene flow, combined with studies that explicitly address how ecology and sexual selection interact in mate choice, are a powerful way to understand the generality of different mechanisms of divergence in natural systems.

Supplementary Material

Supplementary material can be found at http://www.jhered.oxfordjournals.org/.

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