Sexual Selection and Speciation

Michael G. Ritchie

School of Biology, University of St. Andrews, Fife KY16 9TS, Scotland;
email: mgr@st-and.ac.uk

Key Words

Abstract

Sexual selection has a reputation as a major cause of speciation, one
of the most potent forces driving reproductive isolation. This rep-
utation arises from observations that species differ most in traits
involved with mating success and from successful models of sexual
selection–driven speciation. But how well proven is the case? Models
confirm that the process can occur, but is strongest in conjunction
with ecological or niche specialization. Some models also show that
strong sexual selection can act against speciation. Studies using the
comparative method are equivocal and often inconclusive, but some
phylogeographic studies are more convincing. Experimental evolu-
tion and genetic or genomic analyses are in their infancy, but look
particularly promising for resolving the importance of sexual selec-
tion. The case for sexual selection is not as strongly supported as,
for example, allopatric speciation. Sexual selection probably con-
tributes most effectively alongside ecological selection or selection
for species recognition than as a solitary process.

INTRODUCTION

The study of speciation has been dominated by debates about the geographic context in which speciation occurs, for example, Mayr's (1942) "Modes of Speciation," and by analyses of the genetics of reproductive isolation between species. The majority of the latter involves studies of hybrid sterility or inviability, inspired by Haldane's rule (1922). Since Dobzhansky (1937) categorized the causes of reproductive isolation, it has been acknowledged that the most common cause of reproductive isolation in sexual animals are obstacles to fertilization between species. Postinsemination but prezygotic effects on reproductive isolation are important, but it is likely that sexual isolation—premating isolation due to courtship traits and associated preferences—is the most common cause of reproductive isolation in animal species.

A probable resolution to the debate over modes of speciation is that allopatric speciation predominates. However, sympatric speciation is possible, although rare. If we were to ask what the most common processes generating reproductive isolation are—genetic drift, ecological adaptation inadvertently or pleiotropically causing isolation, direct selection for isolation, or sexual selection—there would probably be less consensus. Recently, sexual selection has attained widespread recognition as an engine of speciation, perhaps the most important of the forces that generates new species. But how does sexual selection influence reproductive isolation? By acting only directly on behavior, or also indirectly? Does it act in conjunction with ecological divergence? Can sexual selection inhibit speciation? What are the sources of evidence that implicate sexual selection, and are they unambiguous? Is the case as well proven as allopatric speciation?

HISTORY

Darwin's other great book, published 12 years after *The Origin of Species*, introduced the concept of sexual selection as a major source of selection on males and females (Darwin 1871). This had even less to say about the process of speciation than *The Origin of Species*, although the idea that this form of selection would influence speciation is clearly implicit (for example, Darwin regularly points out that sexually selected male traits are species or racially specific). Explicit discussion of the role of sexual selection in speciation is much more recent. During the modern synthesis, the processes of mate choice and species recognition were usually seen as fundamentally different, whereas most modern treatments (with important exceptions) recognize that these are part of a continuum: Females may discriminate against some males because they are of low quality or less stimulating, but when that process leads to discrimination between geographic races then it contributes to species recognition (Ryan & Rand 1993). Species recognition predominated in early discussions of sexual behaviors, with the concomitant assumption that change in species recognition systems arose owing to direct selection to avoid deleterious hybridization (reinforcement) or to avoid confusion with other species. This raised the problem of how speciation could be completed in allopatry, and some authors argued that the process was finalized only following hybridization or subsequent interspecific encounters (Dobzhansky 1940).

Others solved this by arguing that the fertilization system was finely tuned to environmental conditions and diverged in response to altered environments encountered in allopatry (Paterson 1985). Environmental adaptation of signals and preferences is a potent source of selection on sexual communication and can indirectly cause sexual isolation. Sexual selection will contribute to this process, but in a less direct manner than selection from intra- and intersexual selection.

As recently as the 1980s, researchers began to emphasize the continuity of mate choice within populations, between population divergence and speciation. This led to the natural conclusion that sexual selection within populations could lead indirectly to sexual isolation between populations, without requiring a link to the environment or other species. Fisher's (1930) verbal model of his runaway process of coevolutionary divergence between male traits and female preferences inspired several more formal models (Fisher's own account of the runaway process is explicitly framed as an intraspecific process, although calling hybridization "the grossest blunder in sexual preference" suggests a continuity of process). Initially, the most successful and influential models were those of Lande (1981, 1982), which showed that so long as there is genetic variation for a male trait and a female preference for that trait, assortative mating would generate a positive genetic covariance between the two. Usually the system remains at an equilibrium, where viability selection counters indeterminate changes in traits and preferences. However, if the disequilibrium is particularly strong, the system has the potential to become unstable and evolve away from the equilibrium. Clearly, if trait and preference distributions become nonoverlapping between populations, then sexual isolation is expected to follow. Lande's models were explicitly interpreted as models of speciation.

West-Eberhard (1983) also presented a highly influential review, which argued that social evolution, including both inter- and intrasexual selection, could cause speciation [Coyne & Orr (2004) credit this with being the first review "to emphasize what now seems an obvious link between sexual selection and speciation"]. While other authors, notably Paterson (1985), criticized the typological concepts of species recognition inherent in the new synthesis, West-Eberhard's (1983) paper contained the most cogent discussions of how social competition for mates could cause speciation in allopatry without any recourse to interspecific interactions. Analysis of the frequency of papers published on sexual selection and speciation shows a clear and significant upturn as recently as the 1990s, which probably reflects the natural lag time from the seminal West-Eberhard and Lande papers.

Other stimulants to this upturn of interest include many detailed comparisons of sister species that emphasize divergence in relevant behaviors such as male morphology, courtship song or genitalia, the rise of the comparative method in evolutionary studies, and recent experimental and genomic analyses. Studies of sexual selection within behavioral ecology have increased exponentially through this period, and there have been several very important changes in basic paradigms. The covariance between traits and preferences predicted in the Lande models has sometimes been found within populations. However, expectations for between-population covariances (more important for speciation) are more complex. Alternative sources of selection on traits or preferences can act against covariance among populations, and

Coevolutionary divergence: traits (or species) that mutually influence each other's evolution, e.g., male mating signals and female mating preferences

Assortative mating: nonrandom mating, usually due to similar individuals mating more often than expected, which can contribute to sexual selection

Comparative method: analyses of the evolution of traits upon an explicit phylogenetic hypothesis of species relationships, e.g., whether a trait influences speciation

noncoevolutionary models predict that traits and signals may be substantially out of step during evolutionary change. Male traits may evolve to exploit arbitrary or biased female preferences that have evolved in another context (Ryan 1990), for example, feeding behavior (Macías Garcia & Ramirez 2005). Sometimes this can lead to females preferring attributes of heterospecific males (Ryan & Wagner 1987). There has also been an upsurge in the importance of sexual conflict underlying the coevolution between traits and preferences, which originates with Parker (1979), with males evolving traits to overcome female reluctance to mate and female counteradaptations to these male exploitatory traits. Predictions of sexual conflict for coevolution between populations are not so clear. Although we may expect a broad correspondence between traits and preferences, it is possible for males and females to be out of step while one sex (probably temporarily) has the upper hand in the antagonistic coevolution (Arnqvist & Rowe 2002). This move away from an expectation of simple stepwise coevolution perhaps calls into question one of the underlying principles behind sexual selection as a generative force in speciation. Here I review the theoretical background and the main sources of empirical evidence presented to support the idea of speciation by sexual selection (this is a representative rather than comprehensive set of examples). Throughout, emphasis is placed on what constitutes decisive rather than supporting evidence, as much of the evidence in this area is rather indirect.

THEORETICAL STUDIES OF SEXUAL SELECTION AND SPECIATION

Coevolution

Lande's quantitative genetic models (1981, 1982) [and Kirkpatrick's (1982) similar few-loci models] were of what may be called pure sexual selection in that there was only viability selection on the male trait and coevolution on the mate recognition system. Major changes since have included the incorporation of other forms of selection, emphasis on the possibility of sexual selection facilitating sympatric speciation, and sexual conflict. Simulation studies confirmed that the Fisher-Lande process was possible (Wu 1985), at least in large populations (Nichols & Butlin 1989). Initial models of the effects of direct selection on preferences (direct or indirect costs of being choosy, for example) suggested that runaway coevolution was less likely (Bulmer 1989, Kirkpatrick & Ryan 1991). More recent studies have clarified the restrictive conditions under which runaway coevolution may occur (Hall et al. 2000). An intriguing additional component to coevolutionary models of trait-preference evolution is the incorporation of learning into the dynamics of population divergence. Noting that songbirds are a particularly speciose group, Lachlan & Servedio (2004) modeled coevolution in which males were predisposed to learn songs. Learning favors common traits, leading to faster divergence between populations via drift. Learning therefore leads to more rapid allopatric speciation, although if female preferences are costly (or trait and preference unlinked), the system behaves more like a conventional Fisher-Lande system, or worse. However, most empirical studies of song dialects in birds find weak or no relationships between song and genetic variation

Antagonistic coevolution: conflict influences the outcome of an interaction, e.g., predator and prey behaviors, or many sexual interactions

(e.g., Nicholls et al. 2006, MacDougall-Shackleton & MacDougall-Shackleton 2001, Wright & Wilkinson 2001). Condition dependence of male traits can lead to accelerated and extended evolution of male signals (Lorch et al. 2003). It seems likely that this would also accelerate allopatric speciation, but this has not been modeled explicitly.

Sexual Selection Against Hybrids: Parapatric and Sympatric Speciation

The issue of defining species recognition and sexual selection as different processes is critical when discussing speciation by reinforcement (selection against deleterious hybridization) or the evolution of behaviors to avoid signal confusion or mating competition from heterospecifics. In these cases, behavior is evolving to be species specific; therefore, species recognition is clearly a valid description of the function of the behavior. However, the underlying process is selection on variation in mating success or, in the case of reinforcement, a form of sexual selection of good genes or genetic complementarity. Reinforcement has been extensively reviewed elsewhere (e.g., Butlin 1989, Servedio 2004), so this section is restricted to situations where sexual selection is explicitly incorporated into interspecific interactions.

Speciation by reinforcement can occur when sexual selection is the main source of selection against hybrids. Hybrids often have aberrant behaviors, in addition to low viability or gametic sterility, and there are cases where postmating isolation is entirely due to behavioral abnormalities. Kawata & Yoshimura (2000) modeled hybridization in which the interacting populations differed in trait and preference distributions in the absence of postmating isolation. Selection against hybrids was frequency-dependent sexual selection on males. Nonoverlapping distributions evolved under a range of choice models. The probability of speciation was, not surprisingly, related to trait overlap between species, but even large overlap could result in speciation. In real populations, drift may counter the frequency-dependent selection favoring extinction of one form, or a hybrid swarm may form. Servedio (2004) attempted to examine the interaction between multiple sources of selection that contribute to reinforcement, including selection against hybrids, assortative mating, and local adaptation of mating signals. The importance of sexual selection is distinguishable from indirect viability selection in these models. Sexual selection alone can contribute to isolation, but is much more powerful when the traits involved are under environmental selection (or there are also incompatibilities). This makes the important point that sexual selection on locally adapted signals may be an important component of many systems usually interpreted as reinforcement or reproductive character displacement (see also Liou & Price 1994).

Sympatric speciation has been extensively modeled because of its controversial nature. Early models implied that gene flow and recombination restricted the buildup of assortative mating between sympatric morphs (e.g., Felsenstein 1981). More recent models can be divided into those that incorporate sexual selection into disruptive selection by ecological niche divergence or those that examine if sexual selection alone can cause sympatric speciation. The former are much more convincing, although there is debate about whether speciation due to enhanced assortative mating

constitutes speciation by sexual selection. For example, Kondrashov & Kondrashov (1999) showed that disruptive selection on traits involved in ecological adaptation can drive bimodality within a population. If a behavioral trait became involved, then it was effectively recruited to facilitate assortative mating between the morphs. Even if female preference for the trait was influenced by an independent set of loci, assortative mating deterministically built up isolation between the morphs under a broad range of conditions. Dieckmann & Doebeli (1999) reached similar conclusions with an adaptive dynamics model of resource competition driving sympatric divergence. Even if an indicator mating character was independent of the resource specialization, sympatric morphs could appear with alternative characters in disequilibrium with the specialization (see also Drossel & McKane 2000). However, Kondrashov & Kondrashov (1999) were insistent that such models, with sexual traits facilitating assortative mating, are not examples of speciation by sexual selection but of natural selection driving adaptation (perhaps this is another case in which behavior can be thought of as a species-recognition trait rather than one evolving primarily under sexual selection). This is potentially a critically important point in assessing the importance of sexual selection in speciation. If a trait that contributes to assortative mating is intimately associated with niche specialization (beak size in finches, body size in sticklebacks), then the trait may have facilitated speciation by ecological selection rather than sexual selection. However, distinguishing assortative-mating-facilitating adaptation from, say, sexual selection for good genes may seem a rather subtle and empirically fraught proposition (Schwartz & Hendry 2006), and other authors (e.g., Kirkpatrick & Ravigne 2002) do not make this distinction (it seems inevitable that frequency-dependent selection against individuals struggling to mate assortatively will generate sexual selection).

Models of sympatric speciation by assortative mating independent of ecology have been proposed, but are less convincing. Turner & Burrows (1995) modeled a situation where extremes of a unidimensional male trait were opposed by viability selection (visually driven predation, for example). A mutation in female preference that altered the direction of preference could spread until the alternative forms became fixed. This was inspired by the species flocks of African cichlid fishes, where closely related species differ by color and sometimes ecology. Incorporation of the peculiarities of cichlid sex determination into such models also facilitates sympatric speciation by assortative mating (Lande et al. 2001). These studies show that given the (exacting) conditions of the models, sympatric speciation can occur by sexual selection. However, Kondrashov & Kondrashov (1999) believe that their ecological-selection model with the secondary recruitment of behavior is "more economical and explains all the evidence" (see also Arnegard & Kondrashov 2004).

Higashi et al. (1999) produced a model of sympatric divergence in traits and preferences. In a large population starting with continuous normal distributions of male traits and preferences, assortative mating generates three possible outcomes: The population remains stable, the trait shifts, or trait and preference diverge to produce two species. They describe the latter as like two bouts of Fisher's runaway process for higher and lower values of the trait. However, most models have implied that pure sexual selection is unlikely to promote sympatric speciation. Sexual selection

against rare forms will oppose sympatric speciation (Kirkpatrick & Nuismer 2004), and the circumstances favoring it are rare (see also Kondrashov & Shpak 1998). Numerous factors act against sympatric speciation by sexual selection alone, including polygenic determination of the traits involved and frequency-dependent selection that eliminates the rarer forms (requiring symmetrical distributions, disruptive selection, or some strong counteradvantage to favor the process) (Arnegard & Kondrashov 2004, Gourbiere 2004, van Doorn et al. 2004).

Sexual Conflict and Speciation

Sexual conflict arises when the sexes differ in the optimal outcome of an interaction and underlies most processes in sexual selection, from copulation to polyspermy and female postmating fecundity (Parker 1979). The first model to explicitly address the influence of sexual conflict on speciation concerned conflict over mating at a parapatric secondary contact (Parker & Partridge 1998, 1999). This proposed that the effect of conflict on speciation depended on which sex gained the upper hand in determining the outcome: If female preference predominated a mating system, speciation was more likely, but if male competition overcame female preference, then speciation would be less likely. This is one of a few models (see also Kirkpatrick & Nuismer 2004, Gavrilets & Waxman 2002) to argue that strong sexual selection can sometimes inhibit speciation, a logical conclusion that is underappreciated (some comparative studies employ one-tailed tests).

More recently, Gavrilets and colleagues (Gavrilets et al. 2001) modeled the influence of sexual conflict on speciation. Preference functions evolve to resist male traits and potentially give rise to isolation, although other possibilities include asymmetrical isolation or extinction. Another model illustrated the potential for allopatric speciation (Gavrilets 2000). The preference function determined the number of compatible males available to females, and conflict led to perpetual changes in traits and preferences, in a manner reminiscent of Fisher's runaway process, but with females perpetually evolving to decrease the mating rate while males evolved to increase it. Holland & Rice (1998) term such antagonistic sexual coevolution a chase-away process. This process was intimately related to population size, with larger populations facilitating conflict and consequently divergence rate. The dynamics of conflict coevolution in sympatry are particularly interesting (Gavrilets & Waxman 2002). If females evolve two differing resistance strategies, males can chase them and can themselves separate into two distinct assortative mating types. Alternatively, males can become immobilized in a trough of low mating success between them, like Buridan's ass (trapped by being equidistant between two equally attractive sites, like a Scotsman between a chip shop and a pub). The message of these models is that if female preference evolves as resistance against males, a strong evolutionary dynamic can be set up that can facilitate sexual isolation between populations, although one would imagine that conflict would lead to unpredictable or asymmetric isolation more readily than Fisher-Lande coevolution.

Looking across these models, the most obvious way in which sexual selection could accelerate speciation (independent of direct selection for speciation by reinforcement)

is via increased coevolution of male traits and female preferences in allopatric populations or if traits involved in mate recognition were under direct environmental selection. Behavioral traits that facilitate assortative mating can act alongside ecological selection in parapatry or sympatry (although in this case there is debate about whether sexual selection is really the driving force or simply facilitates ecological divergence). Sympatric speciation by sexual selection alone is not impossible, but remains controversial (whether sexual selection between sperm- and egg-recognition proteins is a special case is an intriguing possibility; van Doorn et al. 2001). Sexual conflict can drive speciation in a manner similar to Fisher's runaway process, but can also lead to asymmetrical preferences. Models of sympatric speciation by sexual conflict seem more convincing than those relying on assortative mating or coevolution alone.

EMPIRICAL WORK

Comparative Studies

The most consistently quoted source of evidence that sexual selection causes speciation has been the observation of closely related species that differ primarily or solely in traits involved in sexual communication or sexual selection. However, many of these examples are largely anecdotal. Proving that sexual selection has caused speciation in such cases requires demonstrating that the traits have evolved by sexual selection and that they were the first traits to diverge and cause reproductive isolation (Panhuis et al. 2001). Detailed comparisons to assess the rate of evolution of sexual behaviors versus other traits, such as ecological specialization or incompatibilities, are usually lacking. In an influential study, Coyne & Orr (1989; see also Coyne & Orr 1997) surveyed the rate of evolution of pre- and postmating isolation in species pairs of *Drosophila* using genetic distance as a measure of divergence time. They found that these evolve at similar rates unless species are sympatric or parapatric, when sexual isolation accelerates over postmating isolation (the inferred average time to speciation is 2.7 My for allopatric species versus 0.2 My for sympatric, a remarkable difference). This pattern is liable to multiple interpretations. It suggests that interspecific encounters promote sexual isolation, which is compatible with reinforcing selection or reproductive character displacement. Coyne & Orr (1989) also speculated that sexual selection alone may lead to increased divergence in sympatry, but it would have to be accentuated by the presence of another species, as there is no reason to suppose that sexual selection should be less important in allopatry. Resource competition may be greater where closely related species meet, and ecological selection could favor behavioral separation by a Kondrashov-like (Kondrashov & Kondrashov 1999) process. Funk et al. (2006), in a similar but more taxonomically widespread study, found that ecological differentiation was related to sexual but not postmating isolation. Sperm proteins of marine invertebrates evolve more quickly in sympatry (van Doorn et al. 2001). Mendelson (2003) examined divergence rates of assortative mating and egg inviability in some species of darters (fish) and found that behavioral divergence occurred more quickly. Dealing with traits potentially under sexual selection, Gleason

& Ritchie (1998) found that courtship song diverged particularly quickly in the *willis-toni* group of *Drosophila*, sometimes before any postmating isolation was detectable. More studies like these are sorely needed. However, even accurately quantifying that sexual isolation evolved most quickly in a group would not necessarily prove that sexual selection caused this, especially if we consider species recognition a distinct process.

Another way of asking if sexual selection influences speciation is to perform comparisons using the comparative method, which assesses if number of species or rates of speciation are greater in species that show signals of sexual selection while controlling for phylogenetic relatedness. The first study addressing this was done by Barraclough et al. (1995), who examined species richness in passerine birds and found that clades with more sexually dichromatic species contained more species. They discussed potential confounding factors such as species recognition and issues of species definition. Price (1998) reanalyzed these data and found that the pattern was mainly due to allopatric comparisons and argued that ecological equivalents were of uncertain importance. Owens et al. (1999) confirmed an effect of dichromatism in birds, although they found no effect of polyandry or sexual size dimorphism on species richness. Similar studies in birds include those by Møller & Cuervo (1998) and Mitra et al. (1996), both of which found marginal effects of feather ornamentation or mating system on species richness when making sister group comparisons in birds.

Arnqvist et al. (2000) compared species richness in insect clades differing in levels of polyandry; 25 phylogenetic contrasts were possible, and inferred speciation rates were approximately four times greater in the polyandrous clades (an even stronger pattern was seen when restricted to more closely related groups). This is an impressive and seemingly robust study. The mechanism is unknown, but candidates include sperm competition, cryptic female choice, or antagonistic coevolution, emphasizing the need for speciation biologists to study postinsemination effects (Howard 1999). Fast evolution of male genitalia is a well-characterized phenomenon (Eberhard 2004), and accelerated genital evolution is also seen in comparative studies of mono- and polyandrous insect clades (Arnqvist 1998). Although rapid genital evolution was originally interpreted in terms of species recognition, recent studies have suggested that male coercion is more important (more "male lock" than "lock and key") (e.g., Jagadeeshan & Singh 2006).

However, other apparently equally detailed comparative studies fail to support a role of sexual selection or sexual conflict in speciation. Gage et al. (2002) carried out a large independent-contrasts study of mammals, butterflies, and spiders. They found that species richness was unrelated to sexual size dimorphism (across more than 700 genera) or measures of polyandry (120 genera). They discuss a number of factors that might act against finding a result, but the contrast with Arnqvist et al. (2000) is difficult to understand, as the methods are similar. Gage et al.'s (2002) paper is more extensive taxonomically, although it has been suggested that it does not control for phylogeny so well (the butterflies are a geographic, not a phylogenetic, assemblage, although comparative approaches were used within that constraint). Morrow et al. (2003) carried out probably the most comprehensive study of the influence of sexual size dimorphism, sexual dichromatism, and testes mass on species richness in birds.

They identified 130–180 independent contrasts with which to test the hypothesis. None of the predictors were significant; in fact two had a negative effect on species richness (see also Morrow et al. 2003).

Some studies are difficult to interpret. Katzourakis et al. (2001) analyzed predictors of species richness including male testes size and female spermathecal width—indicators of sperm competition—in an extensive phylogeny of hoverflies. The results were equivocal, with contrasts in testes size significantly different from zero ($p = 0.014$) but no significant regression of these contrasts on species richness. Stuart-Fox & Owens (2003) analyzed a fairly complete lizard phylogeny with sexual size dimorphism, sexual dichromatism, and the possession of sexual ornaments as predictors of species richness. Ornaments did not predict species richness—dichromatism was marginal ($p = 0.056$)—but sexual size dimorphism did, but in the opposite direction to that predicted, with more species in groups with less sexual dimorphism. Stuart-Fox & Owens (2003) conclude the latter may reflect a process other than sexual selection, for example, resource partitioning. They also suggest that dichromatism may represent male competition or species recognition, considerable caveats to the previous studies supporting an association in birds.

Ritchie et al. (2005) examined inferred rates of speciation in a monophyletic group of Mexican fish in which body shape dimorphism was thought to reflect sexual conflict. In 10 out of 16 phylogenetically independent contrasts, speciation occurred more quickly in dimorphic lineages, but this was not statistically significant. However, Mank (2007) recently completed a sister group comparison across all fish and found consistent evidence of more species in groups containing a greater proportion of species with apparent sexually selected traits.

The comparative method has been proposed as a particularly appropriate way to assess the influence of traits on speciation, but is fraught with difficulties. Looking across the studies currently available, supporting evidence for a role of sexual selection is not overwhelming (although some authors find it to be "particularly convincing" regarding measures of sexual dichromatism in birds). Of 11 studies considered here, two were convincing in support of the hypotheses, two apparently equally convincing against the hypothesis, and the remainder either gave inconsistent results with different traits thought to correlate with the intensity of sexual selection or were of marginal statistical significance (at most, five or six provide positive evidence). Tests are often understandably statistically weak owing to a low number of independent contrasts, but we should expect a strong effect to be more consistently detectable. Furthermore, species richness depends on the net diversification rate; clades vary in richness owing to extinction as well as speciation. If both processes are potentially influenced by the traits of interest, it may not be possible to resolve their relative importance simply by analyses of the number of extant species. It does seem likely that extreme sexual selection may be associated with an increased risk of extinction (Gavrilets et al. 2001), and there is empirical evidence that, for example, dichromatic bird species have elevated extinction rates (Doherty et al. 2003). Morrow et al. (2003) actually concluded that the role of sexual selection in promoting speciation was so well established that increased extinction in sexually selected species must explain their inability to find such a relationship in their analysis. A rather more subtle

potential bias of the comparative approach concerns deciding what to include. A species complex where different pheromone blends distinguish reproductively isolated insect species may have the number of described species underrepresented. It is perhaps not too surprising that more species of birds have been described in clades with elaborate sexual dichromatism.

There are other problems with cause and effect in correlations between species richness and apparently sexually selected traits: What if adaptive radiation favors polyandry (Gage et al. 2002), or what if ecological diversification increases the need for species recognition? Price (1998) has argued that sexually selected traits may be particularly prone to diverge during adaptive radiation (different traits may propagate better in different environments) but that coevolution of preferences may be unlikely. For example, in bird species, females may all prefer males with larger tails, but male tail length reflects varying costs in different environments. Price (1988) argued that imprinting in birds (and possibly cichlid fish) may mean that some striking morphologies evolve as recognition traits not under sexual selection (see also Lachlan & Servedio 2004). In many of the species groups where male traits are species specific (e.g., cichlids, *Anolis*, lacewings, Hawaiian *Drosophila*, or crickets), female preferences have been studied in detail in only one or two species, so covarying female preferences are usually an assumption. Price (1998) argues that this is unjustified, as preferences may be asymmetrical, costly, or have evolved under sensory exploitation. More empirical studies examining Fisher-Lande coevolution between preference and trait variation within and between populations are required. Although comparative approaches are likely to continue to be used extensively in this area in the future, the caveats associated with this approach perhaps mean that more decisive results are to be obtained from other types of study.

Case Studies

African cichlids and other fish. The cichlids from the crater lakes of central Africa (particularly Victoria and Malawi) represent a remarkable recent radiation. Inferred speciation rates rival or exceed any other, with speciation intervals of as little as a few thousand years for Lake Victoria (Turner 1999) and the fastest rates of all in Lake Nabugabo (Coyne & Orr 2004). Several authors have argued that sexual selection is an important driving force behind this, as many of the most closely related species are distinguished by body color, a target of female mate choice (Seehausen et al. 1999). These have become a flagship example of sexual selection and sympatric speciation and have inspired several models of this process (including those of Turner & Burrows 1995, van Doorn et al. 1998, and Lande et al. 2001). However, many species also differ in ecological niche and there is debate over the relative importance of ecologically driven selection or if the divergence of color between species is driving speciation or is recruited into ecological adaptation to facilitate assortative mating (Kondrashov & Shpak 1998, Arnegard & Kondrashov 2004). Unfortunately, the rapidity of the radiation means that attempts to obtain a molecular phylogeny within Lakes Victoria and Malawi have been of limited success, precluding careful comparisons of the divergence rates in ecology and behavior. Seehausen et al. (1999) examined the evolution

of cichlid color patterns against a phylogeny of a wider assemblage of cichlids. Interestingly, they were able to detect the influence of ecology on the characteristic dark banding patterns of cichlids, but in contrast, nuptial hue coloration varied with mating system rather than ecology. Speciation in promiscuous species was associated with changes in hue, but it was not clear that their speciation rate was accelerated over other groups. Seehausen et al. (1999) compared the distribution of species within Lake Victoria and found that color heteromorphic pairs were more likely to be found in sympatry; if these pairs have large niche overlap (see also Haesler & Seehausen 2005), this would imply that behavior diverges more quickly. Color (and vision) also diverges under direct natural environmental selection for efficient propagation and detection as light quality changes in different regions within lakes (Terai et al. 2006).

Quantitative trait loci have been identified for morphologies involved in niche adaptation in cichlids, and their genetic architecture implies a role of directional selection in divergence between species (Albertson et al. 2003). Decisive genetic evidence for strong sexual selection on nuptial color could be found if similar quantitative trait loci analyses of color differences between sibling species occupying similar ecological niches found evidence for strong selection. Quantitative genetic studies suggest that relatively few genes may be involved (Haesler & Seehausen 2005, Barson et al. 2007). Most of the behavior genetic studies have concentrated on finding a match between the predictions of models of speciation derived for cichlids, but these architectures will probably be compatible with other interpretations (predictions of the number of loci and the likelihood of sympatric speciation vary between different models). Adaptive radiation, direct ecological selection involving behavior, and sexual selection have undoubtedly all contributed to the extremely rapid divergence of these cichlids, but the relative importance of these is uncertain and difficult to ascertain.

Wilson et al. (2000) attempted to distinguish the roles of assortative mating and ecological adaptation to genetic differentiation among morphs of a Midas cichlid from Nicaragua. Phylogeography was used to examine whether genetic variation was structured by trophic morph or nuptial color. Both mtDNA and microsatellites were partitioned more by color than jaw morph in at least one lake. Similar studies in the African cichlids would be most interesting. Studies of genetic differentiation between populations of four species of Mexican Goodeid fish found greater differentiation between populations within two dimorphic than two monomorphic species, and evidence for greater sex-biased gene flow in the dimorphic species (Ritchie et al. 2007).

Assortative mating by size contributes to some of the recent radiations of sticklebacks into different ecological niches in Canada and elsewhere (Nagel & Schluter 1998). Hybrids have low mating success, which would contribute to their isolation, but in this case ecological selection seems to be the main source of selection (Schluter 2000). Morphological traits such as body size (or divergence in nest structure in an Icelandic radiation; Ólafsdóttir et al. 2006) probably provide examples of traits intimately associated with the ecological selection facilitating speciation, as in some of the models of sympatric ecological speciation (e.g., Dieckmann & Doebeli 1999).

The guppy provides an intriguing potential counterexample of the role of sexual selection in fish speciation (Magurran 1999). Guppies show rapid evolution, and

Quantitative trait loci: genes influencing a trait whose approximate genomic location, magnitude, and directionality have been inferred statistically

Phylogeography: analyses of patterns of geographic variation in traits or genetic markers among related populations or closely related species

transplantation experiments have shown adaptation to local conditions within a few generations. Why, then, have divergent populations of the guppy from Trinidad not completed speciation? Female guppies are subject to numerous encounters with amorous males who can "sneak mate," bypassing female mating preferences. Magurran (1999) has argued that the guppy may provide an example of nonspeciation due to male-biased sexual conflict (Parker & Partridge 1998).

Hawaiian *Drosophila* and crickets. The iconic example of sexual selection and island speciation is the Hawaiian *Drosophila* (Templeton 1978, Boake 2005). Their radiation is similar to that of cichlids, with rapid evolution on these oceanic islands (around 25% of the world's species of *Drosophila* are endemic to Hawaii). There is also a great ecological radiation, with the flies occupying a much broader range of niches than are usually occupied by fruit flies and elaborate and unusual secondary sexual traits, including painted wings, unusual morphologies, and elaborate courtship songs (Hoikkala et al. 1989). Carson, Kaneshiro and colleagues (e.g., Kaneshiro & Boake 1987) have argued that sexual selection has been particularly important for this radiation. Genetic revolutions during founder-flush cycles are thought to have facilitated switches between different coadapted gene complexes and the evolution of unusual courtship behaviors (Carson & Templeton 1984). Sexual selection is an important component of the elaborate models of speciation inspired by these flies, including asymmetric isolation due to relaxation of preferences and simplification of courtship repertoires (Kaneshiro 1989). Barton & Charlesworth (1984) produced cogent criticism of these models of speciation, arguing that details of the genetic transilience model of speciation are unnecessary and direct ecological selection may suffice. The Kaneshiro hypothesis of asymmetrical sexual selection and speciation (Kaneshiro 1989) has also had a rough reception and lacks widespread acceptance. The Hawaiian *Drosophila* are difficult to breed, and detailed studies of their postmating isolation are lacking. Sexual isolation is clearly important to their speciation, but its relative role, and even the contribution of the elaborate traits to isolation, is unclear (Boake 2005). The Hawaiian *Drosophila* have probably been the single most important radiation giving credence to the role of sexual selection in driving speciation, but the evidence is almost wholly indirect. Rather depressingly, the possible loss in the wild of iconic species such as *D. heteroneura* means we may never be in a position to resolve these issues.

More recently, explosive speciation of crickets of the genus *Laupala* on Hawaii has also been described (Otte 1989). Mendelson & Shaw (2005) generated a phylogeny of this genus and examined the timescales involved. The inferred rate of speciation on the Big Island exceeds that of *Drosophila* and is second only to the African cichlids. Each species of *Laupala* is characterized by a unique calling song, and studies of two species have indicated that female preferences are tuned to male song and that the species are reproductively isolated (Shaw & Parsons 2002). Mendelson & Shaw (2005) argue that ecological selection or reinforcing selection can be reasonably ruled out as an alternative to sexual selection as causes of speciation in this group. *Laupala* illustrates the difficulty of a conclusive broad comparison of a species group because it is difficult to know if sexual selection, drift, or other factors associated with speciation

on islands is consistently most important across the group. However, the crickets are more ecological generalists than Hawaiian *Drosophila*.

Other examples. As we have seen, broad comparisons among species groups can be indecisive. With fewer species, it may be possible to examine gene flow directly and correlate this with variation in traits known to be evolving under sexual selection. An example of assortative mating driving divergence in a natural context is a recent study of the Amazonian frog *Physalaemus petersi* (Boul et al. 2007). Different populations within this species have independently evolved two call types important to mate choice. Phonotaxis experiments between distinct but geographically close populations demonstrated assortative female call preferences, and genetic differentiation follows divergence in calls. Furthermore, mtDNA divergence implies that directional selection has fixed call types between populations. Boul et al. (2007) argue that the appearance of complex calls in some populations has altered female preferences for normal calls, driving assortative mating and reducing gene flow between diverging populations. The association between call, female preference, and gene flow is clear, but why sexual selection has favored males with complex calls is not [although sensory biases for such songs have been seen in related species (Ryan et al. 1990)]. A similar study compared populations of a jumping spider from Arizona (Masta & Maddison 2002). Phylogeographic analyses implied a role of positive selection in the fixation of sexually dimorphic male color and morphological ornaments, presumed to be sexual selection. Females showed a reluctance to mate with males of other morphs in some crosses between allopatric types (there was also some postmating isolation), but there was no direct comparison of genetic differentiation and behavior. These and the previously described fish studies (Wilson et al. 2000; Ritchie et al. 2007) perhaps suggest that phylogeographic studies are a more appropriate scale than broad comparative studies at which to detect an influence of sexual selection on evolutionary differentiation.

Most other studies only address components of the story. Gray & Cade (2000) examined variation in song and female preferences in the cricket *Gryllus texensis*. Females prefer songs of their own species over the geographically overlapping *G. rubens*, yet there is a lack of character displacement and no apparent postmating isolation or ecological divergence. This, and numerous other examples of primary divergence in mating signals and preferences, is compatible with speciation by coevolution of trait and preference (although song and preference were not positively correlated among populations of *G. texensis*) but does not satisfy all the criteria necessary to unambiguously demonstrate speciation by sexual selection (Panhuis et al. 2001).

Experimental Evolution

Ultimately the most decisive way of testing models of speciation is to examine their effectiveness during experimental evolution. There have been many studies of factors promoting reproductive isolation or assortative mating in the laboratory, and the most successful experiments have involved selection from a multiplicity of sources

(Rice & Hostert 1993). However, there have been few direct tests of the importance of sexual selection. Rice (1998) pioneered groundbreaking studies of responses to elevated sexual conflict and has argued that this could drive both pre- and post-mating reproductive isolation. Martin & Hosken (2003) performed one important experiment addressing this issue. They reared dung flies under three regimes: enforced monogamy and free mating, under high or low population density [following Gavrilets' model (2000) showing that sexual conflict would be especially important at high density because selection is more effective with more genetic variation and less drift]. After 35 generations, tests for assortative mating between replicates found increased positive assortative mating between lines within the free-mating regimes. Furthermore, this was greatest at high density and was driven by increased female reluctance to mate. This is consistent with sexual conflict driving allopatric divergence in assortative mating.

Wigby & Chapman (2006) have produced the only attempt to replicate such an experiment so far. They reared *D. melanogaster* for a similar period on male-biased, female-biased, or equal-sex ratios, again manipulating sexual conflict. However, they did not find any consistent pattern of increased reluctance to mate under higher sexual conflict or between lines or regimes. Sexual conflict is strong in *D. melanogaster* so the contrast is hard to explain, although perhaps postinsemination responses to the toxicity or manipulative effects of semen components rather than reluctance to copulate are more important in this species. Female postcopulatory resistance can evolve in the laboratory (Lew et al. 2006) and is a component of natural between-species variation (Sakaluk et al. 2006). It is critically important to see further replication of such laboratory evolution experiments, as these are much more decisive tests of theory (Rice & Hostert 1993). Traits with the potential to influence sexual isolation such as male courtship song have shown rapid laboratory evolution under increased sexual selection in *D. pseudoobscura* (Snook et al. 2005), although differences in mating rate within lines seem slight (Crudgington et al. 2005).

Genetic Studies

There has been a long history of attempting to identify genes that cause reproductive isolation (Coyne & Orr 2004). Probably the ultimate way of demonstrating the cause of speciation in nature would be to identify the sources of selection responsible for the substitution of genes causing reproductive isolation between species. There are too few examples of potential so-called speciation genes that have been characterized to enable general conclusions to be drawn, but some are contributing to the evidence that sexual reproduction (and by implication sexual selection) is a pervasive source of selection driving gene substitution.

Most early studies of speciation genes attempted to identify genes causing hybrid male sterility or inviability. One gene found in the *simulans* clade of *melanogaster* is *Odysseus*; when crossed into the wrong genetic background, it is responsible for approximately 40% of the sterility typically seen between species (Perez & Wu 1995). It shows classic signs of strong directional selection—rapid sequence divergence and a greatly elevated rate of synonymous over nonsynonymous substitutions within the

**Synonoymous/
nonsynonymous
mutations:** synonymous mutations do not change a protein (owing to code redundancy); diversifying selection will increase nonsynonymous but not synonymous replacements

clade (Ting et al. 1998). But what caused this selection? The normal function of *Odysseus* is not clear, but it does influence sperm production and potentially sperm competition in *D. simulans* (Sun et al. 2004), so postcopulatory sexual selection may have driven its divergence and indirectly contributed to hybrid sterility. Genes that show male-biased expression show greater signatures of selection across species of *Drosophila* (the ratio of nonsynonymous to synonymous mutations is approximately double in male-biased genes; Zhang et al. 2004). The excess of nonsynonymous substitutions is positively related to the recombination rate in male-biased genes but not those in females-biased or unbiased genes, an important observation as it supports the interpretation that strong directional selection (rather than relaxed constraints) underlies this rapid evolution (Zhang & Parsch 2005). Male-biased genes are also more likely to be misexpressed in sterile hybrid males (Michalak & Noor 2003). Why are male-biased genes evolving quickly? The fast-male evolution explanations of Haldane's rule (which argued that males are under stronger selection) were thought not to be of great general importance because hybrid female sterility is seen in butterflies and birds with opposite chromosomal systems of sex determination, but fast-male evolution does occur in species with conventional sex determination (Wu et al. 1996, Presgraves & Orr 1998).

Genes involved in sexual or gametic recognition (for example, mating-type loci in *Chlamydomonas*, sperm-egg recognition genes) also show strong signals of rapid directional selection compared to other loci (e.g., Metz & Palumbi 1996, Ferris et al. 1997; reviewed in Swanson & Vacquier 2002). Genes classified as involved in sexual reproduction (that is, known to influence mating behavior, fertilization, spermatogenesis, or sex determination) also show faster evolution and an excess of nonsynonymous substitutions in a range of organisms (e.g., Civetta & Singh 1998; reviewed in Singh & Kulathinal 2000). Many authors think that sexual selection, particularly antagonistic selection, is likely to drive elevated evolutionary rates in sex-biased or sex-related genes. Zhang et al. (2004) make the important point that male-male competition may be a more likely explanation than intersexual antagonism for fast-male evolution. Antagonistic coevolution alone cannot explain fast-male evolution, unless the interacting female loci are systematically underrepresented [faster evolution of sperm than egg proteins is seen in marine invertebrates, a system where the female counterparts are well known; van Doorn et al. (2001) suggest that intrasexual competition for fertilization drives this]. If fast-male evolution is driven by spermatogenesis rather than sperm competition or other intrasexual selection, this intriguing and strong correlation between sex and fast evolution of genes may have a relatively simple explanation (at least 12% of the genes in *D. melanogaster* are expressed only in testes; Boutanaev et al. 2002). The bias in sexual-function-related genes (rather than sex-biased ones) is also seen in genes expressed in female reproductive tracts (Singh & Kulathinal 2000) and must indicate a stronger selection, perhaps reflecting antagonistic coevolution. However, the nature of selection on female-biased genes may differ from that on male-biased ones, with directional selection on male-biased genes and purifying or balancing selection being more likely to be seen on female-biased genes (Proschel et al. 2006). It remains to be seen if such fast-evolving genes are more likely to be identified as speciation genes, which seems likely.

Clearly, genomic studies provide a great opportunity to identify which genes evolve most rapidly between species. Identifying the sources of selection acting on these gene replacements will require correlational or manipulative studies of individual loci. Recent studies of selection on loci thought to influence behavioral reproductive isolation, such as opsin genes in cichlids (Terai et al. 2006) and genes involved in pheromone production in moths (Groot et al. 2006) and *Drosophila* (Greenberg et al. 2003; but see Coyne & Elwyn 2006), have implicated ecological selection through environmental adaptation, efficient signal detection, or directional selection from interspecific interactions in their divergence. None of these studies provides examples of loci under primarily sexual rather than ecological selection.

CONCLUSIONS

The evidence that sexual selection is an important cause of speciation comes from numerous sources. Of necessity, much of this is theoretical, correlational, or indirect. Decisive studies are surprisingly thin on the ground, but some can be found. The concept of speciation by sexual selection is currently undergoing a surge in popularity, and perhaps as a consequence supporting evidence tends to be accepted rather uncritically and competing or alternative explanations not so thoroughly considered (as seen with other hypotheses; Simmons et al. 1999). Currently, the case for speciation occurring primarily by sexual selection is certainly not as well made as, say, the case for the preponderance of allopatric speciation. It seems highly likely that sexual selection (or sexual conflict) contributes to divergence in traits that influence sexual isolation in allopatry. The role of sexual selection in sympatric speciation is much more contentious, with theoretical support but no wholly convincing empirical example. So far, much of the evidence has come from comparative studies, but smaller-scale phylogeographic studies, genetic and genomic studies, and experimental evolution are perhaps more likely to provide conclusive evidence in the future. The major challenge for empirical studies is distinguishing between cases where sexual selection has directly driven reproductive isolation rather than acted as a secondary force alongside ecological selection, or where selection was for species recognition. It seems unlikely that sexual selection often acts alone.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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Errata

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