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Phil. Trans. R. Soc. Lond. B 1998 **353**, 251-260
doi: 10.1098/rstb.1998.0207

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Sexual selection and natural selection in bird speciation

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The role of sexual selection in speciation is investigated, addressing two main issues. First, how do sexually selected traits become species recognition traits? Theory and empirical evidence suggest that female preferences often do not evolve as a correlated response to evolution of male traits. This implies that, contrary to runaway (Fisherian) models of sexual selection, premating isolation will not arise as an automatic side effect of divergence between populations in sexually selected traits. I evaluate premating isolating mechanisms in one group, the birds. In this group premating isolation is often a consequence of sexual imprinting, whereby young birds learn features of their parents and use these features in mate choice. Song, morphology and plumage are known recognition cues. I conclude that perhaps the main role for sexual selection in speciation is in generating differences between populations in traits. Sexual imprinting then leads to these traits being used as species recognition mechanisms. The second issue addressed in this paper is the role of sexual selection in adaptive radiation, again concentrating on birds. Ecological differences between species include large differences in size, which may in themselves be sufficient for species recognition, and differences in habitat, which seem to evolve frequently and at all stages of an adaptive radiation. Differences in habitat often cause song and plumage patterns to evolve as a result of sexual selection for efficient communication. Therefore sexual selection is likely to have an important role in generating premating isolating mechanisms throughout an adaptive radiation. It is also possible that sexual selection, by creating more allopatric species, creates more opportunity for ecological divergence to occur. The limited available evidence does not support this idea. A role for sexual selection in accelerating ecological diversification has yet to be demonstrated.

Keywords: sexual selection; natural selection; speciation; reproductive isolation; adaptive radiation; imprinting

1. INTRODUCTION

Natural selection, sexual selection and random drift have all been postulated to play roles in the origin of species. Natural selection has the strongest empirical support, because rapid speciation is best documented in adaptive radiations: the more or less simultaneous divergence of numerous lines from a common ancestor to exploit new adaptive zones (Simpson 1953, p. 223; Schluter 1998). Artificial selection experiments, mimicking natural selection, often produce reproductive isolation as a correlated response (Rice & Hostert 1993). Comparisons of sister clades with differing numbers of species have been used to identify traits that accelerate speciation rates. Heard & Hauser (1994) reviewed 47 proposed 'key innovations'. Thirty-five (74%) were traits enabling exploitation of new resources (such as phytophagous habit in insects; Mitter *et al.* 1988), ten (22%) affected dispersal, and just two (4%) were related to sexual selection.

Since Heard & Hauser's (1994) review more examples of traits accelerating speciation have been proposed, and some have implicated sexual selection. In birds, clades with relatively many species have been found to be associated with polygamous mating (Mittra *et al.* 1996; Møller & Cuervo 1998), with the frequency of sexually dichromatic species (Barraclough *et al.* 1995), and with the

presence of sexual dimorphism in feather ornamentation (Møller & Cuervo 1998). Polygamy and sexual dimorphism are both thought to be indicators of strong sexual selection, and sexual selection is thus invoked as an agent of speciation. Previously, many authors had suggested a role for sexual selection in speciation, based on comparative evidence demonstrating that closely related species often vary most strikingly in sexually selected traits (Sibley 1957; Kaneshiro 1980; West-Eberhard 1983; Dominey 1984; Ryan & Rand 1993*a*). One good example is that of the South American bellbirds (fig. 1, Snow 1976). The four species differ in facial ornamentation (figure 1). Snow (1976, p. 88) argued that 'some very powerful and arbitrary selective force is continually acting on the males'. West-Eberhard (1983) suggested that this force was sexual selection.

The attractiveness of sexual selection as an agent of speciation derives from three main observations. First, closely related species often differ in traits that appear to have evolved by sexual selection. Second, sexually selected traits can exhibit almost infinite variety, as is shown, for example, by the ornaments of the bellbirds (West-Eberhard 1983). Natural selection often produces convergences and parallelisms, and if traits subject to parallel evolution are used in species recognition, several derived populations may continue to recognize each

other, even as they do not recognize the ancestral type (Rice & Hostert 1993; Schluter & Nagel 1995). Third, because sexual selection requires communication between a signaller and a receiver, coevolution of the signalling trait and recognition system can result in members of some populations not being recognized by members of other populations (Kaneshiro 1980; Lande 1981). Premating reproductive isolation automatically develops in parallel with the evolution of the sexually selected traits. This is demonstrated most clearly in models of Fisherian sexual selection by female choice (Lande 1981; Iwasa & Pomiankowski 1995; Payne & Krakauer 1997). Given certain preference functions, females at different positions along lines of equilibria will most often mate with males from their own population, and ignore members of other populations (Lande 1981; Ryan & Rand 1993a; figure 2a).

Sexual selection offers an apparent mechanism for the generation of premating isolation, but none for the generation of ecological differences. Natural selection generates ecological differences, but the way in which species recognition develops is left to be explained. In this review I consider how the two processes, and random drift, might interact. I address two questions:

1. What is the role for sexual selection in the establishment of premating reproductive isolation among populations?
2. What is the role of sexual selection in adaptive radiations?

I draw on examples from birds, with some alternative taxa and speciation mechanisms considered in the discussion. I conclude, based on limited evidence, that sexual selection is important in producing a great diversity of traits that are used in species recognition, but may have little effect on rates of ecological diversification in adaptive radiations.

2. SEXUAL SELECTION AND SPECIATION

I equate speciation with the origin of reproductive isolation between diverging populations. Theories of sexual selection imply that correlated evolution of female preferences can automatically lead to reproductive isolation, as exemplified by the runaway (Fisherian) models. In this section I suggest two reasons why evolution of female preference as a consequence of a genetic correlation between male trait and preference is unlikely to play a major role in speciation. The reasons are first, most preferences are likely to be subject to some direct selection, and second, female preferences are often open-ended so that females from all populations prefer extreme males. Throughout the paper I concentrate on the evolution of female preferences for male sexually selected traits, but given these conclusions, speciation may result as easily if traits are evolving via competition between males or by competition for resources other than mates (West-Eberhard 1983).

In the runaway models of sexual selection, female preferences readily evolve and thereby amplify spatial patterns of variation in male traits (Lande 1982; Payne & Krakauer 1997). Divergence between populations in female preferences may be sufficient to cause speciation (Lande 1981; Iwasa & Pomiankowski 1995; Payne &

Krakauer 1997). The models rely on the female preference evolving as a correlated response to evolution of the male trait (Lande 1981), and depend critically on the female preference being subject to no, or at least very little, direct selection (Kirkpatrick 1996). Numerous studies have demonstrated that this is seldom likely to be the case. Indeed females usually seem to base their choice on traits that indicate male quality (e.g. Price *et al.* 1993). When there are benefits to choice, the mean female preferences deterministically evolve to a single point (Kirkpatrick 1985; Price *et al.* 1993). Opportunities for runaway sexual selection (Kirkpatrick 1985, 1996) and divergence via genetic drift (Kirkpatrick 1985; Price *et al.* 1993) become severely limited.

Although there are still some proponents of the importance of Fisherian mechanisms (Iwasa & Pomiankowski 1995; Payne & Krakauer 1997), direct selection on female preferences seems more likely to guide their evolution. Often females prefer extreme development of the male trait (Ryan & Keddy-Hector 1992), perhaps because the males with the most extreme development also provide most benefits. The potential for rapid diversification in the male trait as well as the female preference seems to be restricted, because we might expect one kind of male to provide maximum benefits. However, there are many situations where variation in the environment can cause geographical variation in expression of a male trait.

The mean expression of the male trait is attributable to a balance between benefits (mating success) and costs (Kirkpatrick 1985; Price *et al.* 1993). Therefore, geographical variation in sexually selected traits will arise if there is geographical variation in the intensity of sexual or natural selection. For example, the intensity of natural selection on male traits may vary in association with resource abundances (Hill 1994; Møller *et al.* 1995) or predators (Houde & Endler 1990; Endler & Houde 1995). The intensity of sexual selection can also vary if the male trait is more easily seen, or is a better indicator of male quality, in some environments (Schluter & Price 1993). Under all these mechanisms substantial geographical variation in the male trait may be accompanied by only modest variation in female preference (Schluter & Price 1993; see figure 2b). For example, in Hill's (1994) study of house finches, females from all populations showed strong preferences for bright males; variation in the male trait is attributed to the ease with which males can incorporate carotenoids into their diet.

If situations similar to the kind identified by Hill (1994) are common, geographical variation in male traits will not lead to speciation, because females from all populations still prefer one kind of trait. One way by which populations can diverge in the male trait, and also to some extent in female preferences for those traits, is by the spread and fixation of new male phenotypes in different populations. There are likely to be many female preferences latent in a population that are not expressed because the appropriate male phenotypes do not exist (Arak & Enquist 1993; Ryan & Rand 1993b). For example, Burley *et al.* (1982) working with zebra finches and Ryan & Rand (1993a,b) working with frogs, have shown how males can be made more attractive to females by enhancing aspects of their signals (in Burley's case by adding colour rings). Hidden preferences may arise as a

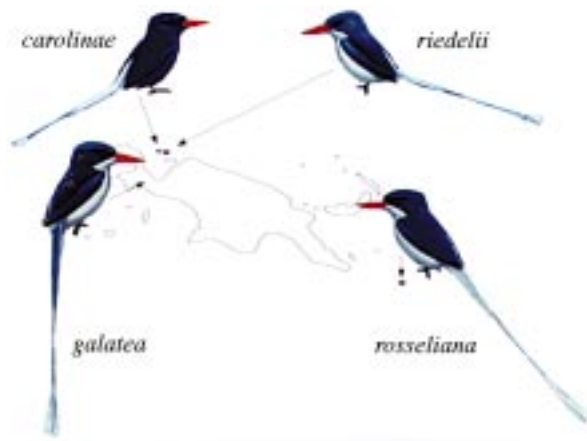


Figure 1. Four forms of the Paradise flycatcher. *galatea* and *rosseliana* are currently classified as subspecies of *Tanysepta galatea*. *T. caroliniae* is classified as a separate localized subspecies, and *T. riedelii* is sometimes considered to be a separate species and sometimes a subspecies of *T. galatea* (from Fry & Fry 1992).

side effect of evolution of females under both natural and sexual selection (Ryan & Rand 1993*b*) or continually be gained and lost as a result of coevolutionary arms races between female and male (Arak & Enquist 1993; Krakauer & Johnstone 1995). One consequence of hidden preferences is that new male mutations may be favoured (i.e. attract females) even if the males that carry them are of low quality. In the only model of this process, females evolve resistance to such mutations as they appear (Krakauer & Johnstone 1995). However, if the new male traits are, or become, better indicators of quality than the old ones (e.g. because they are more easily perceived in the environment), then they can rapidly replace the old trait (Schluter & Price 1993). Population divergence will readily occur as different male mutations in the different populations become fixed (Muller 1942; Sibley 1957). The bellbird variation (figure 1) seems to be a good example of this sort of process.

If the male traits spread as a result of pre-existing biases in females and/or variation in the environment, sexually selected traits may relatively easily evolve, but female preferences show relatively little divergence between populations. Female preferences will evolve somewhat as the costs and benefits of searching for males in different environments varies (e.g. figure 2*b*), but the evolved differences are likely to be insufficient to generate reproductive isolation in themselves. This conclusion is apparently controverted by some artificial selection experiments (Wilkinson & Reillo 1994) and some studies of geographical variation (Houde & Endler 1990) which have demonstrated correlations between preference and trait. However, the selection experiments on stalk-eyed flies by Wilkinson & Reillo (1994) seem to include some direct selection on females, which is very difficult to eliminate in laboratory situations. In addition choice tests were apparently confounded by allowing females to choose between their own line versus stranger line males. In a re-evaluation and extension of their study on geographical variation in mate preferences of guppies, Endler & Houde (1995) found females preferred males with more

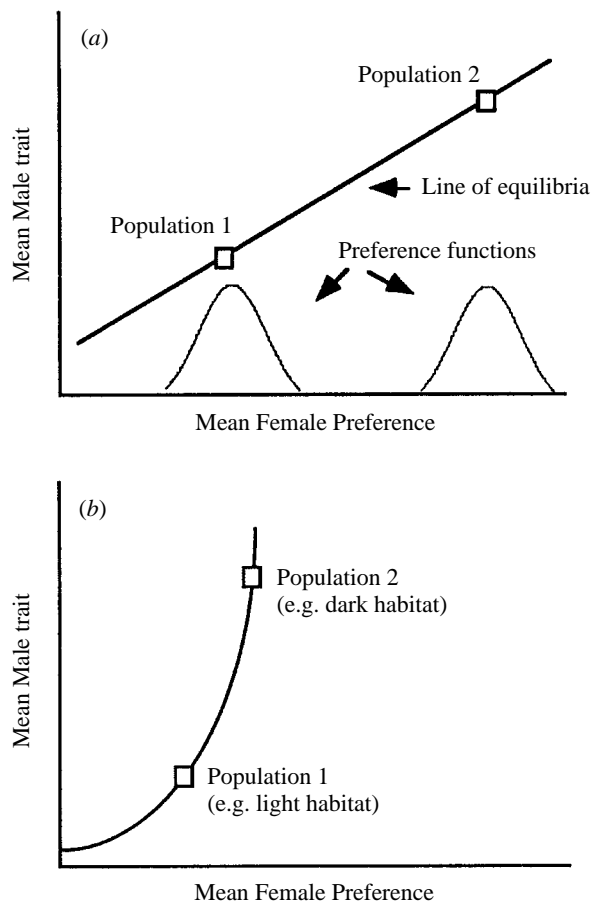


Figure 2 (*a*) Under a Fisherian model of sexual selection, two populations can easily diverge to different points along a line of equilibria (Lande 1981). The female preference functions coevolve with the male trait, and given the distribution of preferences illustrated, females would not recognize males of the other population as mates. Similar principles could apply when females have open-ended preferences for different traits (Lande 1981; Iwasa & Pomiankowski 1995). (*b*) One way by which sexually selected traits can evolve when they are indicators of male quality is if there is a cost to female search, and traits are more easily seen in some environments than others. The intensity of sexual selection on the male trait changes more rapidly than the female preference, which shows comparatively little evolution. In the example illustrated, the mean female preference and male trait lie along a curve in association with a habitat gradient (e.g. from lighter to darker; after Schluter & Price 1993).

orange coloration whatever their population of origin. The preference, although still directional, was less strong where the mean coloration was lowest, and this could reflect natural selection on females in predator-rich areas (Endler & Houde 1995).

3. SEXUAL SELECTION AND POPULATION DIVERGENCE IN BIRDS

The preceding review of the theory implies ample opportunity for sexually selected traits to diverge between populations, but less for female preferences to diverge in a way such that reproductive isolation can arise. In this section I concentrate on evidence that population divergence in male traits has indeed been driven by sexual

selection, without considering the evolution of female preferences and in the following section I consider ways by which variation among populations in sexually selected traits might lead to restricted patterns of female choice, and hence premating isolation. I concentrate on studies of birds. Many studies have demonstrated the operation of sexual selection within populations of birds (Andersson 1994). Sexually selected traits include song, plumage and courtship displays. Song and plumage patterns have been the main foci of studies, and some results are considered here.

(a) *Song*

Song variation has had a major role in bird speciation theory (Thielcke 1973; Baker 1996; Martens 1996), and the various competing hypotheses regarding song evolution are of interest for the differing weight they attribute to sexual selection. In many ways these hypotheses encapsulate debates about possible ways species recognition cues could diverge, incorporating arguments about small population size and founder effects, and natural and sexual selection. The debate does not centre on the evolution of female preferences. Rather it revolves around the mechanisms of song divergence. If song differences between populations are generated, recognition of those differences is automatically assumed to follow.

The mere fact that songs are largely sung during the breeding season indicates their importance in mating success, and suggests a role for sexual selection in their evolution. The most consistent finding with respect to sexual selection is that females exhibit preferences for complex songs (e.g. ones with more syllable types; Searcy 1992; Hasselquist *et al.* 1996). Such preferences are seen even in species that sing very simple songs (Searcy 1992), again illustrating the presence of hidden female preferences, and a failure of preference and trait to coevolve. Across species in the northern hemisphere, there is an association between song complexity and northerly breeding (Read & Weary 1992), suggesting that sexual selection is stronger, or opposing natural selection weaker, in more northern latitudes.

Sexual selection is an integral component to divergence in other aspects of song, in addition to complexity. In particular, some features of songs, such as frequency, are known to be adapted to physical characteristics of the environment, suggesting a role for habitat in driving song divergence (Morton 1975; Wiley 1991). Song divergence may also be affected by character displacement (or reinforcement) as a means of avoiding matings between closely related species, but there is very little evidence for this in birds (Thielcke 1969). Instead, song recognition rather than the song itself becomes refined in areas of sympatry (e.g. Gill & Murray 1972; Ratcliffe & Grant 1985; Lynch & Baker 1991); this may often be a result of learning.

Other hypotheses for song evolution are based on drift, and do not directly involve sexual selection. Songs have varying degrees of both learned and innate components depending on the species (Baptista 1996). The learning can be from fathers (Grant & Grant 1996), neighbours or other conspecifics (Payne & Payne 1993; Baptista 1996). Thielcke (1973) suggested that song evolution may result from a failure to learn components of songs in low-density founding populations and there are several apparent

examples (Thielcke 1973; Lynch & Baker 1991). It is not clear that the divergence in song is indeed driven by low population density of founders, however, and it is possible that the more rudimentary songs sung by outlying populations and species represent a response to relaxed sexual selection, assuming a cost to singing complex songs.

Most evidence for evolution by drift comes from changes in the form of the components of songs (i.e. syllables; Lynch 1996). For example, changes in syllable structure appear to play an important role in the evolution of songs in Darwin's finches, most likely as a consequence of drift (Grant & Grant 1996). Although syllable structure may be neutral, the evidence that syllable number is also determined by random drift (Baker 1996; Lynch 1996) is more questionable. For example, Baker (1996) showed that island populations of an Australian honeyeater have fewer syllable types (and that mainland and island populations did not recognize each other's songs). He suggested that syllables on the island had been lost through drift, but a relaxation of sexual selection pressures on the island remains a viable alternative hypothesis.

(b) *Plumage*

Most of the hypotheses discussed above for song have also been applied to the evolution of other putative sexually selected traits, such as courtship and plumage patterns. For example, geographical variation in patterns of sexual dichromatism have been explained on the basis of variation in sexual and natural selection pressures, species recognition, and drift (Peterson 1997). As in the case of song, some role for sexual selection has been established (Møller & Birkhead 1994), but a critical evaluation is still needed. Two studies have examined geographical variation in both the male trait and in female preferences from different geographical locations. Hill (1994) found that female house finches from all locations prefer red males, and Møller & de Lope (1994) found that female swallows from all locations prefer long-tailed males. The substantial geographical variation in the male trait was attributed in both cases to variation in the strength of natural selection opposing the sexual selection (Hill 1994; Møller *et al.* 1995). Both studies are thus in accord with the general idea that evolution of male traits need not be accompanied by evolution of female preference. As in song, there is a suggestion of increased sexual selection or reduced natural selection on plumage in more northerly latitudes, because dichromatism is more prevalent further north in Europe and in North America, both within species (Hill 1994; Møller & de Lope 1994), and between species (Curson *et al.* 1994, pp. 11–12; Fitzpatrick 1994).

In summary, there is clearly a role for sexual selection in divergence of both song and plumage. In the case of song, drift also seems to play a major part. The relative roles of drift and sexual selection largely remain to be evaluated, with perhaps a larger role for sexual selection than has been assigned.

4. PREMATING REPRODUCTIVE ISOLATION IN BIRDS

The evidence that sexual selection is involved in the evolution of traits such as song and plumage is strong. In this section I ask how females might come to use male traits, which have diverged as a result of sexual selection,

as species recognition cues. Again, I restrict my evaluation to birds. In this group, sexual imprinting is often of central importance in the establishment and maintenance of premating isolation (Immelman 1975). Sexual imprinting has actually been defined as the process by which young birds learn species-specific cues that enable them to find a conspecific mate when adult (Clayton 1993). The learning is usually from the parents (Clayton 1993). The cues are largely auditory and visual, and both are typically employed (e.g. Baker & Baker 1990; Grant & Grant 1997*a,b*). The evidence for the importance of sexual imprinting in the field comes from heterospecific clutch swaps in gulls, sparrows, flycatchers and geese (Harris 1970; Fabricius 1991), which have always resulted in some adults entering into mixed species pairs. The mixed pairs are often due to just one misimprinted bird and one raised elsewhere in a normal brood, thus demonstrating the remarkable power of imprinting to determine mating preferences. In captivity similar results have been shown for many other taxa, including ducks, doves, quail and finches (Immelman 1975; ten Cate & Mug 1984; Clayton 1993). Imprinting itself may evolve to avoid mating with distantly related conspecifics (ten Cate & Bateson 1988) or to avoid mating with heterospecifics, if some post-mating isolation is present.

Sexual imprinting should stabilize mate choice towards the common type and makes it more difficult for traits to evolve under directional selection (Laland 1994). The apparent conflict between the stabilizing nature of any mechanism of mate choice involved in species recognition and the directional nature of sexual selection has long been used as an argument against the importance of sexual selection in the origin of mate recognition cues, as discussed by Ryan & Rand (1993*a*). Several resolutions to the conflict have been suggested, specifically with reference to imprinting. Female preferences can at times override the imprinting process, which may be stronger in males than females (Immelman 1975; ten Cate & Mug 1984). ten Cate & Bateson (1988) suggest that imprinting provides a crude internal representation, and sensitivity to contrasts or bright colours also contributes to preferences. ten Cate & Bateson (1988) and Weary *et al.* (1993) argue that the imprinting itself, by producing aversions to some types, incidentally produces preferences for deviant types in the opposite direction. Such arguments imply a creative role for imprinting, and indeed Immelman (1975) suggests that those groups that provide the most typical examples of imprinting (e.g. ducks, doves, estrildid finches) are also known for their extensive radiation, with several closely related species occurring in the same area. More work needs to be done to quantify Immelman's suggestion.

Sexual imprinting is clearly a powerful mechanism for maintaining premating isolation, and can work on traits produced by natural selection and drift, as well as sexual selection. In Darwin's ground finches (*Geospiza*) the main species recognition cues are morphological differences (Ratcliffe & Grant 1983) produced as a result of natural selection (Schluter & Grant 1984) and song differences, produced as a result of cultural drift (Grant & Grant 1996). The employment of these cues in species recognition is attributable to the early experience of the female (Grant & Grant 1997*a,b*). The most extreme example of a role for imprinting comes from the parasitic Viduine finches of

Africa. Males mimic the songs of their foster species, and these songs are used as mate recognition cues. A group of closely related species has been produced by the invasion of several Estrildid finch hosts. Payne (1973) labels these 'cultural species'. They are the best candidates for sympatric speciation in birds.

Obviously, not all species recognition arises through sexual imprinting. For example, adult parasitic cuckoos, *Cuculus*, are not likely to interact with their young at all, and up to five similar congeneric species co-occur in the Himalayas. The selection pressures that cause the evolution of innate recognition mechanisms are unclear and need further study, but presumably include the disadvantages of mating with the wrong species (Mayr 1942, 1992). Habitat selection (through an imprinting-like mechanism) also seems to be involved in species recognition. It has been noted that hybridization between some closely related species occurs mainly in human-altered habitats (Chapin 1948; Sibley 1954).

5. THE ROLE OF SEXUAL SELECTION IN ADAPTIVE RADIATION

Sexually selected traits may rapidly diverge between populations, and these traits are used in species recognition. Potentially, therefore, sexual selection could elevate the rate of speciation, and there is some evidence for this in birds; groups that are apparently subject to strong sexual selection are particularly speciose (Barraclough *et al.* 1995; Mitra *et al.* 1996; Møller & Cuervo 1998).

The influence of sexual selection on adaptive radiation is unexplored. One possibility is that sexual selection simply creates a large number of species that are ecological equivalents and allopatric replacements of one another (West-Eberhard 1983), with no influence on adaptive radiation. The production of reproductively isolated, ecologically equivalent species could create increased opportunities for the establishment of sympatry and lead to accelerated adaptive diversification driven by ecological character displacement. But this need not be the case. Ecological character displacement requires that at least some ecological differences are established in allopatry (reviewed by Taper & Case 1992). These ecological differences may be accompanied by sufficient divergence in traits that can be used in species recognition, even in taxa subject to only low levels of sexual selection. If this is so, then mildly and strongly sexually selected taxa will show no differences in rates of adaptive diversification.

In this section I consider the potential roles sexual selection may play in adaptive diversification. First, I ask if mildly and strongly sexually selected taxa differ in one measure of adaptive diversification (the number of species occurring in sympatry). Second, I investigate potential roles for sexual selection in promoting divergence in species recognition traits when an adaptive radiation is proceeding. I suggest that the presence of some sexual selection is necessary for adaptive diversification, but different levels of sexual selection in different groups may have little effect on rates of adaptive diversification.

(a) *Sexual selection and ecological diversity*

Sympatry is the ultimate test of good species, and it is usually thought that the establishment of sympatry

requires both ecological differences and reproductive isolation (e.g. Mayr 1951). As one way to assess a role for sexual selection in adaptive radiation, I investigated the extent to which sexual selection is associated with high sympatric species' diversity. To do this, I extended the analysis of Barraclough *et al.* (1995), based on the compilation of Sibley & Monroe (1990). Sexually dichromatic species seem to be subject to generally stronger sexual selection than monochromatic species, because there is a higher variance in mating success among males (Møller & Birkhead 1994). Barraclough *et al.* (1995) demonstrated an association between the fraction of species in a clade that are sexually dichromatic and the number of species diversity in that clade. The findings of Barraclough *et al.* (1995) suggest that an elevated intensity of sexual selection translates into an increased rate of speciation.

For their main analysis Barraclough *et al.* (1995) compared 20 pairs of sister tribes (the taxon just above the genus), and estimated frequency of dichromatic species in each tribe from a sample of all the species. Fifteen pairs had differences in the estimated fraction of species which are dichromatic greater than 0.2, and an analysis restricted to these pairs showed a strong association between species number and dichromatism (in 12 of the 15 comparisons tribes which were more dichromatic were also more speciose). I restricted my analysis to these 15 pairs, although similar results were obtained when all 20 pairs are used. I divided the world distribution into approximately 40 country-sized regions (e.g. Colombia, S. Africa), and tabulated distributions of all species in the tribes according to the compilation of Sibley & Monroe (1990). I recorded the number of species occurring in each region, and the number of regions spanned by a tribe. Dichromatic tribes have wider distributions (ten wider, three smaller, two equal, sign test $p < 0.05$), but not significantly more species in their most speciose region than monochromatic tribes (however, this is due to a single reversal, nine more, four less, two equal, sign test, $p > 0.1$). Because the regions I evaluated are larger than a generally accepted notion of sympatry, I also compared the residuals from a regression of number of species in the most speciose region on number of regions occupied by the tribe. Here there was no evidence of an increased number of species in a region than expected on the basis of distribution; the more dichromatic tribes had the higher residual eight times, and the more monomorphic tribes had the higher residual seven times.

This crude first test finds no evidence for an increase in the number of sympatric species—and by extension ecological diversity—due to sexual selection. Rather, the elevated number of species in sexually dichromatic clades may be due to allopatric replacements. The test clearly could be refined, for example, by studying correlates of morphological diversity and sexual dimorphism. It also needs to be extended to specific case studies. The most speciose 'sympatric' assemblage in the data set is that of the estrildine finches in central Africa (40 species). These are colourful and often sexually dichromatic birds. Although a role for sexual selection is plausible in generating the sympatric diversity in this case, correlates between ecology and sexual dichromatism have been identified in birds. Sexual dichromatism and/or plumage coloration is associated with nest height (Martin &

Badyaev 1996), foraging height (Garvin & Remsen 1997), geographical distribution (this study) and, specifically in finches, with habitat (Price 1996). Thus ecological differentiation could be occurring into those habitats which also favour sexual dichromatism.

Given the ease with which song, displays and plumage characteristics can evolve, premating isolation based on such traits may evolve relatively easily, even in groups that are only mildly sexually selected. Ecological differentiation of isolated populations, and not the generation of premating isolation, may be the more important rate-limiting step in adaptive radiation. The conclusion is in accord with the observation that rates of speciation slow down as an adaptive radiation proceeds (Nee *et al.* 1992; Zink & Slowinski 1995). The slowdown is best attributed to filling of ecological niche space (Nee *et al.* 1992)

(b) *Evolutionary sequences in adaptive radiations*

If sexual selection does not drive ecological differentiation, what part does it play in adaptive radiations? Traits subject to natural selection may also be used in species recognition, with a classic example being body size in Darwin's finches (Ratcliffe & Grant 1983). In this case sexual selection need play no role in speciation. Rice & Hostert (1993) suggested that speciation arising as a correlated response to natural selection is likely to be most important during the early stages of an adaptive radiation, presumably because relatively large morphological differences are needed if they are to be adequate species recognition traits, and such differences may be generated early in adaptive radiations. The implication is that other processes, such as sexual selection, may be more important later in an adaptive radiation, when the morphological differences generated between new species may be smaller. In particular, divergence into different habitats may often promote divergence in sexually selected traits (Endler 1992; Marchetti 1993; Schluter & Price 1993), but be accompanied by only subtle changes in shape (Lack 1947; Grant 1986; Richman & Price 1992). I evaluate a possible role for sexual selection in adaptive radiation, by asking when and where ecological differences arise, and especially how habitat shifts occur.

There have been only a few attempts to address the sequence whereby niche differences are built up during adaptive radiations (Diamond 1986; Richman & Price 1992; Schluter *et al.* 1997; for a similar analysis in lizards see Losos (1992)). Diagrammatic representations of some major ecological splits for Darwin's finches (Schluter *et al.* 1997) and Old World warblers (Richman & Price 1992) are shown in figure 4. In both Darwin's finches and the warblers, a major early split appeared to be between ground and tree habit (Lack 1947). Within these major modes there are splits based on body size. Then, within the body-size clades (of the leaf warblers) there are splits based on altitudinal (habitat) partitioning. Such partitioning has hardly evolved in the ground finches (Schluter & Grant 1982). The patterns appear to be consistent across these two quite different groups, with the adaptive radiation of the Darwin's finches having progressed no further than an earlier stage seen in the warblers. These conclusions are tentative and there are many statistical difficulties (Schluter *et al.* 1997). For example, an alternative interpretation of the observation



Figure 3. The four species of bellbirds (genus *Procnias*). Females of all species are greenish and similar; two are illustrated. Males of all four species are illustrated. *P. averanno* apparently has a disjunct range. Ranges and illustrations are from Snow (1982).

that closely related sympatric species are separated by altitude is that such segregation represents the first step in ecological differentiation whenever new species are formed, even during the early stages of the radiation. This was the interpretation given by Diamond (1986) and Richman & Price (1992) in their analyses of evolutionary sequences. It differs radically from the interpretation here, but both scenarios agree in that changes in habitat (tree/ground and/or altitude) occur both early and late in the adaptive radiations. Firm conclusions await more studies.

Taking the analysis as it stands, there is only modest support for the contention that reproductive isolation, arising solely as a side effect of natural selection, predominates early in adaptive radiations (cf. Rice & Hostert 1993). Major morphological differences in size which are known to be involved in species recognition, appear after a tree/ground split. Both the tree/ground split and altitudinal partitioning seem to be accompanied by subtle shape changes (Lack 1947; Grant 1986; Richman & Price 1992), which may be less useful as species-recognition cues than large shifts in body size. However, both tree/ground and altitude involve large changes in habitat. Habitat differences can affect the evolution of both song (Morton 1975) and colour patterns (Endler 1992; Marchetti 1993). Specifically, in both the finches and the warblers variation in song and plumage patterns is correlated with habitat (Bowman 1979; Grant 1986; Marchetti 1993; Badyaev &

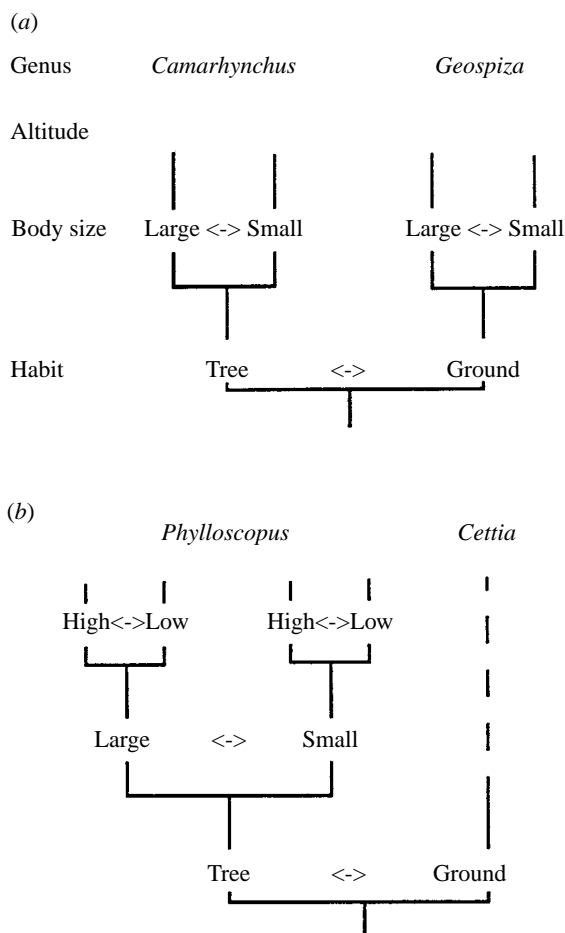


Figure 4. Diagrammatic representation of the build-up of ecological differences in body size, altitude and arboreal habit, based on parsimonious reconstructions. (a) Darwin's finches; (b) Old World warblers. For details of phylogeny and ecology see Grant (1986), Richman & Price (1992), Stern & Grant (1996) and Schluter *et al.* (1997). Each terminal branch represents a cluster of several species. There is little altitudinal segregation in Darwin's finches (Schluter & Grant 1982).

Leaf 1997). Thus ecological change associated with exploitation of new habitat will often be accompanied by change in mate recognition traits; traits which may be used in species recognition. Divergence in sexually selected traits, through the changing selection pressures in association with habitat may play an important role in speciation both early and late in adaptive radiations.

6. DISCUSSION

Mayr's (e.g. 1942, 1951, 1958, 1963) influential views on speciation were derived mainly from studies on birds. He studied geographical variation in particular and identified many patterns of the sort illustrated in figures 1 and 3. Mayr's 1958 paper starts with an account of the paradise kingfishers. There are three very similar subspecies on New Guinea, but four of the six taxa on offshore islands were classified as different species, and some still are (figure 3). Mayr discounted selection alone as the cause of the differentiation between mainland and island, because the substantially varying conditions across mainland New Guinea were not associated with much geographical

variation in plumage and morphology. This led him to emphasize the importance of gene flow in promoting homogeneity, and the necessity of its absence for differentiation. Mayr (1992) noted that one of the most surprising aspects of the evolutionary synthesis was the almost total neglect of sexual selection. In this discussion, I consider Mayr's views on speciation, in the light of sexual selection.

Mayr (e.g. 1963, p. 604) noted that behavioural changes in habitat and food selection play a major role in the shift into new adaptive zones, with structural changes in morphology acquired secondarily. He also emphasized that an incipient species 'can complete the process of speciation only if it can find a previously unoccupied niche' (Mayr 1963, p. 574). The limited evidence to date suggests that although sexual selection can speed up speciation rates, it has little effect on rates of adaptive diversification. However, habitat creates a link between adaptation and speciation via sexual selection: movement into new habitats is often associated with ecological diversification, and this will usually result in the evolution of communication signals used in mate identification.

Variation in habitat almost inevitably leads to variation in sexual selection pressures, by affecting the ease with which different traits are perceived (e.g. sound in a dense forest, colour in the open; Endler 1992), and also which traits are the best indicators of male quality (for example, a particular kind of parasite may occur in one habitat only). Variation in predators, parasites or resources affects natural selection pressures on sexually selected traits. The net result is that environmental variation may often lead to substantial variation in male traits. In addition to environmentally driven variation, a potentially important mechanism of sexually selected population divergence is the spread and fixation of new male traits as a consequence of pre-existing female preferences for many kinds of novelty (Arak & Enquist 1993; Ryan & Rand 1993*b*). If populations are isolated from one another, fixed mutations will often differ among populations (Muller 1942; Sibley 1957).

Roles of small population size and genetic drift have been emphasized in many works on speciation, including Mayr's (1958) founder effect theory. However, the two mechanisms of population divergence discussed here are likely to be accelerated by large population size. The rate of divergence due to fixation of new mutations by genetic drift is independent of population size, and the rate of divergence due to fixation of favourable new mutations under selection is actually higher in large populations (Crow & Kimura 1970, pp. 418–430). The kind of mass-selected change induced by a changing environment is also likely to be more efficient in large than small populations (see Weber (1996) for a recent discussion).

I have argued that female preferences may rarely evolve as a genetically correlated response to sexual selection on males in a manner which generates premating isolation between populations. If this is the case, the most critical need is an evaluation of the mechanisms by which sexually selected traits become involved in species recognition. Mayr (1992) stated that 'owing to change of function, sexual preference features become species recognition marks when two incipient species first come in contact with each other'. Such a change of function mechanism is implicated by the widespread occurrence of sexual

imprinting, whose connection with sexual selection remains unclear. Although it is apparent that the selection pressures which cause the evolution of species recognition sometimes result from contact between incipient species, as suggested by Mayr (and seen in the many cases of refined song recognition in areas of sympatry), it is not clear that this need generally be the case. Indeed, there are many allopatric replacements that are classified as good species. There are many selection pressures in the environment, such as the presence of other more distantly related species or individuals from differently adapted populations, which may directly favour the evolution of mechanisms used in species recognition, whether the recognition is by sexual imprinting or innate.

In this review I have concentrated on the evolution of premating isolation via sexual selection in birds, and it is worth asking how generally applicable the conclusions are. Sexual imprinting, a major mechanism of premating isolation in birds, seems to be restricted to a few groups. In other groups, the selection pressures which generate innate mechanisms of premating isolation remain largely an open question. Avoidance of mating with (not necessarily closely related) heterospecifics possibly plays a major role. One of the most spectacular adaptive radiations is that of the cichlid fish in East African lakes. The species are colourful, and both sexual selection and sexual imprinting are thought to be rampant. Dominey (1984) argued an important role for sexual selection, and Immelman (1975) for sexual imprinting. As in birds, most of the evidence for speciation by sexual selection comes from studies of allopatric replacements of ecological equivalents. Key innovations affecting ecological abilities have also been suggested as the cause of the rapid diversification in the cichlids, and Meyer (1993) concludes his review on the cichlid radiation with no conclusion: 'the jury is still out on a role for sexual selection'.

In conclusion, sexual selection is strongly implicated in the production of cues which are used in species recognition. The overall importance of sexual selection in leading to reproductively isolated sympatric species remains to be determined. It will require a better understanding of the way by which sexually selected traits become species recognition cues, and on the environmental pressures generating population divergence in sexually selected traits.

I thank M. Benowitz-Fredericks, P. Grant, D. Irwin, K. Marchetti, D. Schluter and A. Uy for advice.

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