REPEATED EVOLUTION OF SEXUAL COLOR DIMORPHISM IN PASSERINE BIRDS

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ABSTRACT.—We present a survey of passerine birds designed to investigate the frequency with which sexual dimorphism in coloration or color pattern has evolved from monomorphism (or the converse). Based on the number of genera that have both a monomorphic and a dimorphic species, and the minimum number of changes inferred to have occurred between genera, the transition between dimorphism and monomorphism has occurred at least 150 times. Using the Sibley/Ahlquist phylogeny, we obtain maximum likelihood estimates of the probability that one state will be in the other after one million years of 0.01 to 0.02 (monomorphism to dimorphism) and 0.03 to 0.04 (dimorphism to monomorphism). The rate of transition from dimorphism to monomorphism appears to be higher than the converse, and there are more monomorphic than dimorphic species. We conclude that the transition between alternative states is not difficult, and that the evolution of sexual dimorphism, given appropriate selection pressures, is unlikely to be constrained. *Received 15 August 1995, accepted 1 April 1996.*

MANY SPECIES OF BIRDS are sexually dimorphic in color or color pattern. This often is thought to be a consequence of sexual selection, and sexual dimorphism in color has been used as an index of the intensity of sexual selection in comparative studies (Hamilton and Zuk 1982, Read and Harvey 1989, Fitzpatrick 1994, Møller and Birkhead 1994, Barraclough et al. 1995). Population studies have confirmed that male plumage patterns in sexually dimorphic species are subject to sexual selection (Price 1984, Møller 1989, Hill 1990, Petrie and Halliday 1994), and Møller and Birkhead (1994) show that dimorphism is correlated with the frequency of extrapair copulations across species.

The evolution of sexual dimorphism requires not only appropriate selection pressures but also sufficient genetic variation. Lande (1980) suggested that the evolution of sexual dimorphism might be constrained, because many of the genes affecting variation in males similarly affect variation in females. Selection on males therefore results in a high correlated response in females, and sex-limitation may require many generations of selection to separate the expression of those few genes that affect the male and female differently. The presence of rudimentary male traits in females, such as reduced epaulets in female Red-winged Blackbirds (*Agelaius phoen-*

iceus), suggests that correlated responses do occur (Muma and Weatherhead 1989). However, rudimentary female traits, at least in some species, may be maintained at their observed level of expression by selection. Several analyses have implicated selection on female plumages as a main cause of the presence or absence of dimorphism (Björklund 1991, Irwin 1994).

Therefore, the degree to which the evolution of dimorphism is limited or prevented by a high genetic correlation between the sexes remains unclear. In this paper we estimate the minimum number of times dimorphism has evolved in the Passeriformes. We find it has evolved at least 150 times. We suggest that this is a high number, and that the evolution of dimorphism from monomorphism (or its converse, monomorphism from dimorphism) is not constrained greatly by an absence of genetic variation for dimorphism.

METHODS

Throughout this paper, monomorphism and dimorphism are used as shorthand for sexual monochromatism and sexual dichromatism. The trait "sexual dimorphism" is particularly suitable for study because of the many species whose phenotypic state is known. Therefore, even low frequencies of transition between states should be detectable. We do not consider sexual dimorphism in size, or in ornaments such as wattles, plumes, and elongate tails. We studied the 5,398 passerine bird species in the

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1,125 genera listed in Clements' (1981) check-list of birds of the world. A more recent list by Sibley and Monroe (1990) is similar to Clements in the classification of species to genera (but with 5,705 species in 1,164 genera), and the results are identical regardless of which compilation is used. Using field guides, we were able to determine the presence or absence of sexual dimorphism in color or color pattern for species in all but 54 of the genera (66 species). We classified a species as sexually dimorphic if the sexes were described separately in species' descriptions, or if the sexes appeared different in illustrations. Therefore, minor differences, such as more spots on a larger bird, would not be counted. Nevertheless, the degree of dimorphism varies from strong to mild. Examples of species with weak sexual dimorphism are the Tropical Parula (*Parula pitayumi*), in which the female lacks the male's orange breast band, and the White-browed Tit-Warbler (*Leptopoecile sophiae*), in which the female is paler and without much of the male's blue wash.

Species that are seasonally dimorphic (e.g. Scarlet Tanager [*Piranga olivacea*]) were classified as dimorphic, whereas those with polymorphisms that are not sex limited (e.g. Scaly-breasted Wren-Babbler [*Pneopyga albiventer*], Ali and Ripley [1983]; and several Wheatear species [*Oenanthe*], Mayr and Stresemann [1949]) were classified as monomorphic. We did not record the plumage state of every species, but rather whether a genus consisted entirely of monomorphic species, entirely of dimorphic species, or a mixture. Therefore, we are unable to place an exact figure on the proportion of all species that are monomorphic. We estimate that at least 60% of all species are monomorphic (Fig. 1). Barraclough et al. (1995), in a smaller sample of passerines, found that 69% were monomorphic. Some species may be cryptically dimorphic in ultraviolet light, in which case the number of dimorphic species would be underestimated. However, no species has been discovered to be sexually dimorphic in ultraviolet light but monomorphic to humans, despite an extensive search (Staffan Andersson pers. comm.).

The main goal of the study was to estimate the frequency of transitions between monomorphism and dimorphism. To do this we used two approaches, i.e. within genera and among genera.

Within genera.—We tallied the number of genera containing both a monomorphic and a dimorphic species, excluding from consideration species that are both monomorphic and dimorphic in different parts of their range. If genera are assumed to be monophyletic, then each genus containing both a monomorphic and a dimorphic species represents an independent evolutionary transition between the two states.

Among genera.—We located 399 of the genera on Sibley and Ahlquist's (1990) phylogenetic tree based on DNA–DNA hybridization data. The tree clearly will have inaccuracies, but it provides the best esti-
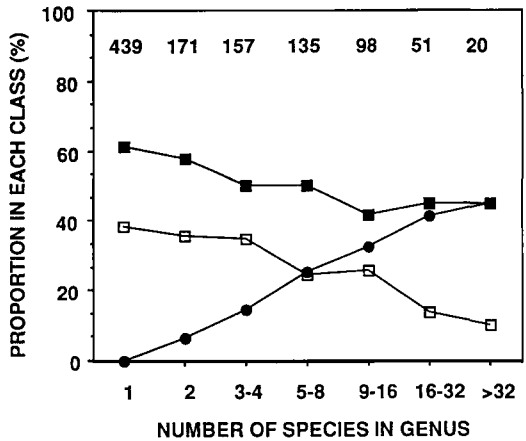

FIG. 1. The proportion of passerine bird genera containing all monomorphic (filled squares), all dimorphic (open squares), or mixed monomorphic and dimorphic species (filled circles) for genera with different numbers of species. Numbers of genera in each class are listed at the top of the figure.

mate of relationships among genera currently available. Using parsimony we then reconstructed ancestral states on the tree using the ACCTRAN method (Maddison 1989). This gives a single parsimonious estimate, and there may be other equally parsimonious trees (Maddison 1989). We did not search for these because we were interested mainly in estimating minimum frequency of change. The method assigns each node below the tips of the tree as monomorphic (M), dimorphic (D), or monomorphic or dimorphic (M/D) depending on the state of the genera above the node. One then works down the tree scoring each node according to the states of the two nodes above (e.g. if the two nodes above were M/D and D, the node below is D). Finally, when all nodes had been assigned we worked back up the tree assigning M/D nodes as M or D depending on their inferred ancestor. After all nodes had been reconstructed as monomorphic or dimorphic, we tallied the number of transitions between the two states.

If change has been frequent, parsimony is likely to produce a gross underestimate of the number of changes. For example, in the extreme case of a change in state at every speciation event, parsimony will result in a construction with no change below sister pairs at the tips of the tree. Therefore, we used the maximum likelihood method of Pagel (1994) to directly estimate frequency of change. The method obtains those probabilities of change from monomorphic to dimorphic and from dimorphic to monomorphic that maximize the probability of the observed states at the tips of the tree. The main assumption is that the probability of change per unit branch length is constant throughout the tree. We assumed that the Sibley-Ahlquist tree and associated branch lengths were a given parameter. Branch-lengths were mea-

sured with a ruler. We used all 594 tips in the phylogeny as input, so that when several species for one genus were separately placed on the tree they were treated separately. There were 26 tips for which we were unable to identify plumage state of the species or genus. For these tips we bounded the estimates by running the program assuming these tips were all monomorphic and in other runs by assuming them to be all dimorphic. There also were 22 tips where Sibley and Ahlquist list a genus name, and the genus contains both monomorphic and dimorphic species. We ran the program in three ways, assigning the tips to be monomorphic, dimorphic, or to consist of two species, one of which is dimorphic and the other monomorphic. In the latter case, the two species were separated by a branch with the same length as that separating their genus from their sister genus. The branch length separating the node joining these two species from the sister genus was assigned a length of zero. Because the Pagel program requires a fully resolved tree, all branch lengths of zero (including those resulting from polytomies on the tree) were reassigned a small value (i.e. 0.1, where branch length varies up to 58 mm). The program estimates transition rates between the two states. We used formulae in Pagel (1994) to convert these rates into estimates of the probability that a species in one state would be in the other state 1 million years later. Branch length was converted into time following the passerine calibration used by Sibley and Ahlquist (1990).

RESULTS

Patterns within genera.—Monomorphism to dimorphism (and vice versa) transitions have occurred frequently; 130 passerine genera contain both monomorphic and dimorphic species, implying at least 130 transitions (Fig. 1). Among the 304 passerine genera with five or more species, 46% are entirely monomorphic, 22% are entirely dimorphic, and 32% contain at least one monomorphic and one dimorphic species. These 32% directly reflect at least one transition, and they imply that transitions between monomorphism and dimorphism are frequent.

Patterns between genera.—Using parsimony, we found a minimum of 11 cases of an inferred monomorphic-to-dimorphic transition along internal branches of the Sibley/Ahlquist tree, and 9 cases of an inferred dimorphic-to-monomorphic transition.

Maximum likelihood estimates.—The estimate of the probability that a monomorphic species would be dimorphic after 1 million years varied from 1.1 to 1.6%, depending on how unknown tip species were coded (see Methods). The estimate of the probability that a dimorphic species would be monomorphic after 1 million years varied from 3.4 to 4.4%. These estimates are confounded by many uncertainties, but they are consistent with the within-genera patterns in indicating a moderately high rate of change.

Asymmetrical evolutionary rates.—Our analyses imply that change between states of monomorphism and dimorphism is sufficiently "easy" and not ultimately constrained. It is of interest to ask whether dimorphism evolves into monomorphism at a different rate than vice versa. Using the parsimony method, 227 ancestral nodes were reconstructed as monomorphic, with 11 (4.8%) subsequent monomorphic-to-dimorphic transitions, and 136 nodes were reconstructed as dimorphic, with 9 (6.6%) subsequent dimorphic-to-monomorphic transitions. This gives an estimated per-lineage transition rate from dimorphism to monomorphism $1.4\times$ higher than the converse (the term lineage means the line connecting an ancestral species with one of its descendants). The difference is not significant ($\chi^2 = 0.2$, df = 1, $P > 0.05$).

The taxonomic treatment may be interpreted as indicating a higher rate of transition from dimorphism to monomorphism than the converse. The plot of the proportion of genera containing both monomorphic and dimorphic species against number of species in the genus rises from zero (as it must when there is only one species in the genus) to 45% for those genera containing many species (Fig. 1). The increase in mixed genera appears to be more at the expense of dimorphic than of monomorphic genera (Fig. 1). The unweighted regression slope of the seven points in Figure 1 for monomorphic genera is $\beta = -0.03 \pm$ SE of 0.006. For dimorphic genera the slope is steeper, i.e. $\beta = -0.05 \pm 0.007$. The steeper slope for the dimorphic genera appears to be mainly because the very speciose genera (those with >15 species) rarely consist entirely of dimorphic species. We used a test to compare the numbers of one-species genera that are monomorphic or dimorphic (269 vs. 170) with the numbers of genera containing >15 species that are either all monomorphic or all dimorphic (32 vs. 9). Relatively more of the speciose genera are monomorphic ($\chi^2 = 3.8$, df = 1, $P < 0.05$). One explanation for this result is that dimorphic species are quite likely to give rise to a monomorphic descendant (and thus the genus of which the species is a member becomes classified as

"mixed" rather than purely dimorphic). If this occurs, then speciose genera should more often be mixed or pure monomorphic than they should be dimorphic, at least when these speciose genera are contrasted with those containing few species.

The maximum likelihood method estimates give a rate of change from dimorphism to monomorphism approximately $3\times$ higher than the rate from monomorphism to dimorphism, but we cannot easily assess the statistical significance of this result, given a variety of different sources of error. The parsimony, likelihood, and taxonomic treatments all are consistent with there being a higher per-lineage rate of transition from dimorphism to monomorphism than the converse, but at least two alternative explanations exist. First, the taxonomy method relies on classifications of dimorphic species to genera being based on the same criteria as the classification of monomorphic species to genera. Second, and more generally, our interpretation depends on the assumption that the expected per-lineage transition rate is a constant. It is easy to come up with scenarios where transition rates have varied in different parts of the tree so that the rate of change from dimorphism to monomorphism is not higher in one part of the tree than in any other part. For example, some groups could have stayed monomorphic with no transitions between either state, while others could have rapidly changed between the two states, with equal probability. When averaged across all lineages, the rate of change from dimorphism to monomorphism will be higher than the converse. Because scenarios such as these are based on *a posteriori* inspection of those groups currently monomorphic, they cannot be rejected with statistical methods.

DISCUSSION

Our most striking result is that sexual dimorphism and monomorphism have evolved repeatedly one from the other. We have identified 130 cases of transitions between monomorphism and dimorphism based on the number of genera containing both a monomorphic and a dimorphic species, and 20 deeper in the phylogeny, giving a total of 150 cases altogether. This is expected to be a minimum estimate of the actual number of times that the dimorphism/monomorphism transitions have oc-

curred. When traits evolve frequently there is a tendency for parsimony to grossly underestimate the frequencies of change lower down the tree, and parsimonious estimates place much of the change in the tips of the tree, as is seen here. Accordingly, we used an alternative assumption that the probability of change throughout the tree has been constant, but we placed no restriction on how large that change has been. Under this assumption, estimated probabilities of transitions between states range from 0.01 to 0.04 per species per million years.

Among passerines, females are never obviously brighter-plumaged than males. The transition between dimorphism and monomorphism can result from male evolution (i.e. a bright plumage is gained during the evolution of dimorphism from monomorphism, or lost during the evolution of monomorphism from dimorphism). Alternatively, the transition can be due to female evolution (i.e. a bright plumage is gained during the evolution of monomorphism from dimorphism, and lost during the evolution of dimorphism from monomorphism; Björklund 1991, Irwin 1994).

We have not attempted to classify monomorphic species as dull or bright because of the obvious subjectivity in such classifications. For example, very bright birds may appear cryptic in their natural backgrounds. However, comparisons of dimorphic and monomorphic populations within a single species can be used to unequivocally identify monomorphic populations as relatively dull (like the female of the dimorphic population) or bright (like the male of the dimorphic population). In an important paper, Peterson (1996) surveyed geographic variation in sexual dimorphism within species and superspecies groups. Within the passerines, Peterson lists 36 species or superspecies that have both monomorphic-dull and dimorphic populations, 27 species or superspecies that have both monomorphic-bright and dimorphic populations, and two species or superspecies that have monomorphic-bright, monomorphic-dull, and dimorphic populations (Peterson also lists many additional examples of geographic variation in the degree of dimorphism). Cases of sexual dimorphism evolving within species can be used to determine directions of evolution (by comparing the monomorphic with the dimorphic population). Among those species showing geographic variation in dimorphism, monomorphic-dull populations are about as

frequent as monomorphic-bright populations, implying that female change drives the evolution of sexual dimorphism about as often as does male change (Peterson 1996).

The main conclusion that transitions between alternative states have occurred quite commonly is unlikely to have been greatly affected by errors of classification. Although genera may not always represent monophyletic groups, many species' pairs that differ in state clearly are close relatives of one another (e.g. the monomorphic Tree Sparrow [*Passer montanus*] vs. the dimorphic House Sparrow [*Passer domesticus*]). Similarly, at among genera, the monomorphic, dimorphic, and mixed genera are interspersed across the tips of the Sibley-Ahlquist phylogeny. Errors in the topology are most likely to affect nearby groups, and they make little difference to the inference that transitions between monomorphism and dimorphism have been quite common. Peterson's (1996) documentation of the large numbers of species that show geographical variation in degree of dimorphism strengthens the conclusion that dimorphism can evolve readily.

The ease with which monomorphism (or dimorphism) can evolve suggests that genetic constraints are not strong. Dimorphism can evolve only if genetic variation is sex-limited, and sex-limitation may arise from two causes. First, mutations may occur on the sex chromosome. Dosage compensation appears not to occur in birds (Baverstock et al., 1982), so these mutations will automatically be expressed differently in males and females. Such sex-linked mutations are known from chickens (Hutt 1949). Second, some autosomal genes may be subject to sex-limited expression (Fisher 1958, Lande 1980). For example the expression of some colors in the male is dependent either on the presence of testosterone or the absence of estrogen (Witschi 1961, Owens and Short 1995). Selection to change coloration in one sex will then eventually lead to the evolution of dimorphism, although the process may be very slow (Lande 1980).

One way that dimorphism may evolve rapidly is if selection acts to change other sex-limited traits (such as levels of testosterone) that have pleiotropic effects on color or pattern. Color will evolve as a correlated response, and all changes will be restricted to one sex. For example, some dimorphic bird species exhibit delayed plumage maturation, whereby in the early part of their life males resemble females and only later acquire a characteristic adult plumage (Rohwer et al. 1980). In these species, relatively early breeding easily could result in the loss of the distinctive adult male plumage, and hence monomorphism (Lawton and Lawton 1988). This explanation applies to the loss of distinctive male plumages, but not to the gain of bright plumages by the female.

There appears to be little absolute prohibition on the evolution of sexual dimorphism. Nevertheless a high genetic correlation between the sexes could restrict the evolution of dimorphism. First, direct selection on males for increased coloration can cause the females to become brighter as a correlated response. Brightness in females, and hence monomorphism, subsequently could be maintained by newly arising selection pressures on females, such as male choice (Hill 1993, Jones and Hunter 1993, Wynn and Price 1993), nonbreeding social interactions (West-Eberhard 1983, Irwin 1994), or sexual selection involving female competition and/or mimicry of the opposite sex (Trail 1990). Second, if sexual selection pressures are nonspecific, and traits such as male song or courtship are equally suitable alternatives, then traits with the high sex-limited genetic variance may be the most likely to invade and become established in the population. Once one male trait has become established, other traits may be less likely to spread (Lande 1981, Höglund 1989, Schluter and Price 1993).

When averaged across the whole tree, the per-lineage rate of transition from dimorphism to monomorphism apparently is higher than the converse, and monomorphic species are more frequent than dimorphic species. Barraclough et al. (1995) use the Sibley/Ahlquist tree to show that speciation rates are higher in clades with a higher frequency of dimorphic species, and they suggest that this is a result of sexual selection promoting both dimorphism and speciation. Therefore, differential speciation rates might lead to an increase in dimorphic species, which could be opposed by the higher rate of evolution from dimorphism to monomorphism. Alternatively, some groups may tend to remain monomorphic with low speciation rates, whereas other groups are sexually selected and have both high speciation rates and a high frequency of transitions between monomorphism and dimorphism. Within the latter groups, transition rates from dimorphism to monomorphism need

not differ from transition rates from monomorphism to dimorphism. These alternatives are best examined by comparing groups that differ in the frequency of dimorphic species, and their resolution awaits a clearer understanding of selection pressures that maintain monomorphism and dimorphism in different groups.

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