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Received 6 August 1985, 12 October 1985

ABSTRACT: Among North American passerine birds, species that are sexually monomorphic in coloration have, on average, more named subspecies than do species that are sexually dimorphic. This finding is consistent with the hypothesis that group selection, acting more strongly on the greater between-population variance in species in which much geographic variation has been noted, has counteracted the evolution of costly sexually selected ornamentation. Some other reasons for expecting an association between the numbers of named subspecies and the degree of sexual dimorphism lead to a predicted relationship opposite the one observed.

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The belief that natural selection would favor group advantageous, but individually disadvantageous, traits has been out of favor among evolutionary biologists since the group selection mechanism advocated by Wynne-Edwards (1962) was shown to be ineffective relative to individual selection except under extremely unlikely conditions (reviewed by Maynard Smith 1976; but see Wilson 1980 for a different mechanism and view of group selection). If group selection is ever an effective force in evolution, it may be that it is observable and testable only when not countered nor augmented by individual selection. A convincing demonstration of group selection might have to rest on the knowledge that individual selection is neutral with respect to the trait(s) in question.

One class of traits that is expected to be neutral with respect to individual selection after rapidly reaching equilibria (in the sense that a particular equilibrium is neither disturbed nor maintained by individual selection) are the sexually selected adornments that serve to attract mates ("epigamic" characters of Huxley 1938). Fisher (1958) described a mechanism by which such sexual selection would progress, showing that, once started, selection for male ornamentation and for female preference of more extreme ornamentation would increase geometrically ("runaway sexual selection") until checked by opposing selection for male survivorship. Recent analyses of the process (Lande 1981; Kirkpatrick 1982) have shown that the equilibrium achieved when sexual selection and other components of natural selection reach a balance is a neutrally stable one: Once a population is displaced from one equilibrium point it will rapidly evolve to a new equilibrium in a direction determined by the displacement. Thus, after reaching an initial equilibrium, the fate of sexually selected traits in a population will be subject to "even the very weak forces of genetic drift, mutation pressure, or pleiotropy" (Kirkpatrick 1982) ... or even group selection.

Sexually dimorphic traits may also be maintained by forces other than mate preference, making epigamic selection difficult to demonstrate in many cases. The horns and antlers of many artiodactyls and the large size of male pinnipeds may be important in male-male competition for access to mates, the other side of sexual selection discussed by Darwin (1871). Intersexual niche partitioning appears to result from the larger size of female raptors (Storer 1966) and from bill size dimorphism in woodpeckers (Selander 1972). Finally, sexual dimorphism may arise as a nonadaptive pleiotropic effect of other sex-differentiating traits. Relative to size and structure differences, however, the bright coloration of many birds is much less likely to evolve for adaptive functions other than the attraction of

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Evolutionary Theory 7: 173-177 (December, 1985)

The editors thank two referees for help in evaluating this paper.

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mates. (Though once coloration evolves as an intersexual attractant, it may function as a signal to same-sex competitors as well [Fisher 1958; Wolf and Stiles 1970; Smith 1972]).

Sexual color dimorphism in birds increases the likelihood of predation (Selander 1972) and perhaps requires an increased energetic cost of plumage production, especially if the breeding plumage requires more frequent molts or an altered timing of molting. In polygamous species, increased mortality of the displaying sex would have an effect on population productivity only if severe, or if the visual adornments were not fully suppressed in the other sex. In monogamous species, the vast majority of birds, the loss of individuals of either sex for the sake of epigamic competition would reduce population fitness. Sexual dimorphism in color is, then, a costly sexually selected trait, at least in monogamous populations, the evolution of which might be reversed by group selection.

Group selection acts on interpopulation variance, which in turn is determined by effective population size, mutation rate, migration rate, and the action of other selective forces, all of which are difficult to estimate. For birds, however, an indication of the interpopulational variance is available in the proliferation of subspecies named by ornithologists. Although many of the named subspecies probably represent geographic variation in one or a few characters, rather than concordant variation in a suite of traits (Wilson and Brown 1953), the numbers of named subspecies should, to a first approximation, indicate the relative amounts of interpopulation variation within biological species.

For each bird species resident to the United States, the number of North American subspecies (minimally one for monotypic species) was obtained from the A.O.U. Check-list (1957, with 1973 and 1976 supplements). (The 1983 Sixth Edition does not list subspecies.) Species introduced in historical times may not yet have differentiated sufficiently for subspecific designation, even if the population structure is conducive to the accumulation of between-population variance; therefore, they were excluded from the analysis. Primarily Central American species whose ranges extend marginally across the Rio Grande and primarily Palearctic species that occasionally breed in western Alaska are usually represented in the U.S. (and the A.O.U. Check-list) by one subspecies, while many more subspecies are found in the main parts of their ranges; thus, such species were also excluded.

The presence or lack of sexual dimorphism in color for each species was obtained from Robbins, Bruun, Zim & Singer (1966), with other field guides consulted when there was some ambiguity. Although a continuous measure of the degree of sexual dimorphism might yield the most information, any such scale, assuming one could be derived, would be overly subjective. To avoid subjectivity, any degree of color dimorphism illustrated or described in the field guides was considered sufficient to classify a species as dimorphic. If those species that I would consider marginally dimorphic (e.g., American robin, white- and red-breasted nuthatches) had been classified as monomorphic, the conclusions below would have been strengthened.

The number of named subspecies per species varies greatly from order to order, perhaps reflecting different efforts by taxonomic splitters as much as real biological differences between major groups. Therefore, comparisons of subspecific classifications should be done within the ordinal level or lower. Only the very large order Passeriformes has sufficient monomorphic and dimorphic species to permit statistical comparison of the numbers of subspecies. (Most other orders also follow the trends described below, as does each family of passerines with more than two monomorphic species and more than two dimorphic species in North America.) Among the North American passerines the average number of named subspecies was found to be 50% greater among the monomorphic species than among the dimorphic species (mean = 3.77, SE = 0.37, N = 141 for monomorphic species; mean = 2.50, SE = 0.26, N = 103 for dimorphic species). When the frequency distributions of subspecies numbers (Fig. 1) are compared between monomorphic and dimorphic classes by Smirnov's

nonparametric test for the equality of distributions (Conover 1971), the distribution of subspecies of monomorphic species is found to be shifted significantly to the right relative to the dimorphic distribution (test statistic = .194, $P < .05$). A chi-square test also reveals significantly different distributions ($\chi^2 = 10.0$, 4 d.f., $P < .05$, lumping cells of more than four subspecies). Thus, species in which the population structure is more likely to be conducive to group selection (the ones with more subspecies) are more often monomorphic, whereas more panmictic species (indicated by fewer subspecies) on which the force of group selection would be less are more often sexually dimorphic in coloration. By using numbers of named subspecies as a measure of population differentiation, I do not mean to imply that group selective processes are acting at the subspecies level. Rather, the fragmentation of breeding populations that is necessary for group selection to act would also promote the regional and local variation that taxonomic splitters use to define subspecific taxa. Lacking detailed studies of population social structure and genetic differentiation, it is impossible to specify at what hierarchical level, from small local demes to regional races or subspecies, between-group selection might be acting.

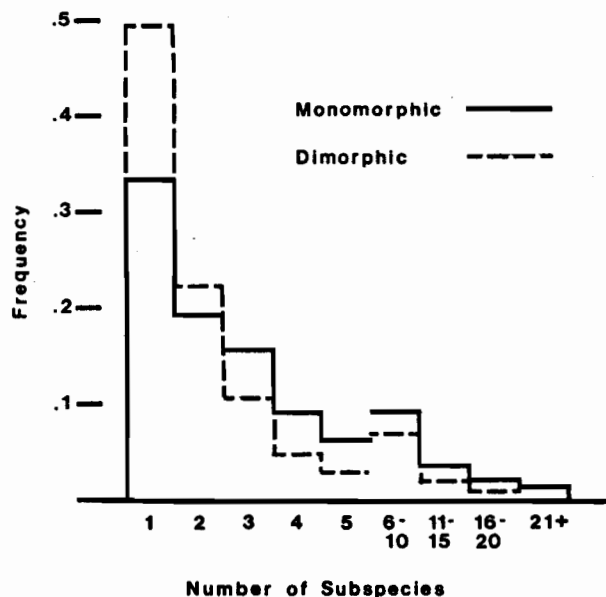


Figure 1. Frequency distributions of numbers of subspecies for 141 species of sexually monomorphic passerines and 103 species dimorphic in coloration.

Could the observed association between number of subspecies and lack of dimorphism be accounted for other than by the action of group selection eliminating costly sexual adornments? First, the trend could be a taxonomic artifact: sexually monomorphic bird species may be more finely subdivided by taxonomists than are dimorphic species. Some subspecies of birds are described primarily on the basis of variation in male coloration (e.g., northern oriole, common grackle), however, suggesting that the nomenclatural bias would be just the reverse. Second, the association may result from a cause-effect relationship opposite the one I have postulated: sexual monomorphism may promote, and dimorphism inhibit, the divergence of populations. Again, however, the potential bias would seem to run in the other direction. The conflicting costs of competing for mates often leads to intraspecific variation in sexually selected traits (Gadgil 1972; O'Donald 1974; Alcock 1979), and sexual selection of extreme ornamentation has been proposed as a mechanism by which reproductive isolation and speciation could rapidly proceed (Fisher 1958; Lande 1981).

Third, the tendency for greater sexual dimorphism in those species with less population divergence could be a spurious result of the correlation of both variables with mating system. Sexual selection is presumed to act more strongly on polygamous breeding systems, leading to a greater degree of sexual dimorphism than in monogamous species (Darwin 1871; Selander 1972), though mate preference in monogamous species may also have substantial effects (Darwin 1871; Fisher 1958; O'Donald 1980; Catchpole 1980). Would polygamy lead to reduced population subdivision (and subspeciation)? The reverse seems more likely, for variance in reproductive success reduces effective population size and thus would increase interpopulation variance. Moreover, greater genetic variance between potential mates would accompany increased population divergence. Hence, sexual selection might be expected to act most strongly on highly differentiated species, especially if it functioned to prevent hybridization with differently adapted populations or subspecies.

Finally, the class Aves is notable for the rarity of polygamy, especially among the passerines (Verner and Willson 1969; and note that a multivariate analysis factoring out an effect of mating system from the data used in this study was not possible because very few of the species are thought to be polygamous.). Thus the frequent development of elaborate visual, vocal, and behavioral mate-attracting displays in birds cannot be explained fully by theories that relate the degree of sexual selection to variance in reproductive success. Compared to other tetrapod classes, however, bird populations often are large and panmictic (Shields 1982), and thus would be subject to weaker group selective forces for muting sexually selected advertisements.

In conclusion, North American passerine species that are monomorphic have more named subspecies, on average, than do species sexually dimorphic in coloration, consistent with the hypothesis that group selection acting on interpopulation variance reduces the frequency of costly sexually selected ornamentation. Admittedly crude estimates of population structure (named subspecies within the U.S.A.) and of sexual dimorphism (all or none assessment of color dimorphism) were used in this analysis. Analytical power was sacrificed for expediency and to avoid subjective bias. Clearly, it would be desirable to compare levels of sexual dimorphism to more direct measures of interpopulation variance, such as estimates of mean genetic distance, were such data to become available. The assumption that sexual dimorphism in color results from sexual selection needs further verification. Also, the theoretical prediction that sexually selected ornamentations rapidly reach neutral equilibria between the forces of natural and sexual selection ought to be verified in the field. Still, conservative statistical tests reveal a significant trend in the data. Other connections suggested between the number of subspecies and sexual dimorphism predict a trend opposite the one observed.

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