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SPECIES RICHNESS COVARIES WITH MATING SYSTEM IN BIRDS

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ABSTRACT.—Many studies have sought to identify traits that influence the relative number of species in related taxa. We examined whether species richness was associated with social mating system in birds. Taxa with promiscuous mating systems tended to be more species-rich than their nonpromiscuous sister taxa. This association was statistically significant when examined with tests that take into account the magnitudes of paired contrasts. The results do not arise from covariation between mating system and body size. We discuss these findings in the context of the hypothesis that sexual selection promotes speciation. *Received 16 February 1995, accepted 25 April 1995.*

AMONG THE MOST important questions in evolutionary biology are those concerned with factors affecting speciation. Many traits have been proposed as key innovations or adaptive breakthroughs responsible for the diversification of particular taxa, but empirical tests of such hypotheses have proven methodologically difficult (see Raikow 1986, Slowinski and Guyer 1993). Tests of association in comparative studies must be based on samples reflecting independent derivations of the trait of interest across a series of taxa whose historical relationships can be reconstructed (Felsenstein 1985, Harvey and Pagel 1991, Guyer and Slowinski 1993, Slowinski and Guyer 1993). Traits for which effects on relative species numbers have been analyzed in this manner include phytophagy in insects (Mitter et al. 1988), breadth of oviposition sites in insects (Zeh et al. 1989), and viviparity in fishes (Lydeard 1993). All of these are traits at the level of individual organisms. In our study, we examined species richness in relation to a population-level trait, social mating system.

It has long been recognized that closely related species often differ most strikingly in their secondary sexual characteristics (Darwin 1871). For example, within groups of birds as diverse as grouse, hummingbirds, and birds of paradise, the males of many species show striking variation in coloration and ornamentation, whereas the females are relatively uniform in appearance. Such variation among males often provides criteria for species' boundaries according to the phylogenetic species concept (Cracraft 1983, McKitrick and Zink 1988). Moreover, these traits are inferred to function in premating reproductive isolation under the biological species concept (Mayr 1942, 1963). Clearly, any force tending to accelerate evolutionary changes in secondary sexual characters would hasten the rate at which allopatric populations achieved species rank under both the phylogenetic and biological species concepts.

Sexual selection is recognized as a process that can lead to the rapid modification of a variety of characters, particularly those involved in mating preferences (Fisher 1930; Kaneshiro 1980, 1989; Lande 1981, 1982; Kirkpatrick 1982; Kaneshiro and Giddings 1987; Lande and Kirkpatrick 1988). In fact, the mutually reinforcing elaboration of mating preferences and secondary sexual characters during "run-away" sexual selection implies that this process could be very effective in producing the differentiation necessary for the development of major morphological differences, and even premating reproductive barriers, between populations (Kaneshiro 1980; Lande 1981, 1982; West-Eberhard 1983; Wu 1985; Lande and Kirkpatrick 1988).

Although there is this theoretical justification for predicting a relationship between the action of sexual selection and the process of speciation, the methodological difficulties involved in testing such a prediction are not trivial. Precise data regarding sexual-selection gradients (Lande and

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Arnold 1983) are known for very few natural populations, and past rates of speciation are difficult or impossible to reconstruct. Nevertheless, one can approach the hypothesis indirectly by choosing conservative indicators of the variables of interest. For example, although it is now clear that sexual selection can occur in species exhibiting a wide variety of social mating systems (Birkhead and Møller 1992), sexual selection generally will be stronger in species exhibiting promiscuous mating systems than in species with nonpromiscuous mating systems (Arnold and Duvall 1994). Promiscuity thus may be an indicator of relatively intense sexual selection.

Similarly, for the purposes of the test described here, the number of extant species (species richness) that we observe in a given taxon is a conservative estimator of past rates of speciation in that taxon. Because species richness is actually the net difference between speciation and extinction events over a given period of time, one must be careful not to mistake the effect of reduced extinction rates with that of increased speciation rates, and vice versa. We must examine the likely effects of sexual selection on both processes. There is some reason to believe that sexual selection increases the likelihood of extinction through its ability to reduce the mean fitness of a population (Fisher 1930, McLain 1993). Conversely, there is no indication that sexual selection reduces extinction rates. Therefore, a positive relationship between the intensity of sexual selection and species richness is most reasonably interpreted as a reflection of increased rates of speciation.

The prediction that avian taxa with mating systems indicative of intense sexual selection have greater numbers of species than do their sister taxa with other mating systems has not been tested rigorously. Nevertheless, several empirical studies have yielded results relevant to hypotheses linking sexual selection and speciation. For example, Pierotti and Annett (1993) reported that avian families exhibiting nonmonogamous mating systems and sexual dimorphism were more species-rich than families exhibiting monogamous mating systems and sexual monomorphism. This result is consistent with the prediction described above, but the method employed to compare average numbers of species per family across groups of families, treating each family as independent, was not intended to distinguish between purely biological patterns and taxonomic artifacts. Barraclough et al. (1995) reported a significant relationship between sexual dichromatism and species richness in passerine birds. To the extent that dichromatism reflects the intensity of sexual selection, this result also is consistent with the hypothesis linking sexual selection and speciation. In a study of the relationship between lek mating systems and sexual dimorphism in birds, Höglund (1989) presented results suggesting that lek-breeding, sexually dimorphic taxa were relatively species-rich. Nevertheless, he did not state this result explicitly nor discuss it in the context of a hypothesis linking species richness to mating systems.

Ryan (1986) reported that three successive transitions in the neuroanatomy of anuran amphibians coincided with increases in species richness. The changes in neuroanatomy were associated with increases in the range of frequencies over which females were sensitive to the mating calls of males, and Ryan attributed the increased species richness to accelerated rates of speciation via divergence in mating calls. His results are consistent with the hypothesis that differentiation of traits associated with mate choice promotes speciation, but the data do not permit a general statistical test.

METHODS

To identify phylogenetic contrasts in the intensity of sexual selection, we compared taxa with promiscuous mating systems with taxa exhibiting other (mostly monogamous) mating systems. For our purposes, we defined promiscuity as a mating system in which there is no lasting social pair bond and males do not provide parental care or resources critical to female reproduction. We also included species having non-resource-based polygyny with no male parental care (e.g. some Anatidae). First, we identified all cases of avian mating systems known to meet these criteria (see Appendix). Next, we sought phylogenies that identified the sister taxa of monophyletic taxa having promiscuous mating systems. We rejected cases in which phylogenetic relationships could not be reconstructed within groups that were polymorphic with respect to mating system. For instance, many members of the Phasianidae are promiscuous, but their phylogenetic relationships are ambiguous (Johnsgard 1986, 1988). Similarly, one species in the genus *Andropadus* (family Pycnonotidae) is promiscuous, but its relationships with its congeners are unknown.

In each case where the sister taxon was uniformly nonpromiscuous, we compared the numbers of species in the two sister taxa. We examined whether the species richness of the promiscuous taxon exceeded that of its sister taxon more frequently than expected by chance, using three statistical tests: a sign test, a Wilcoxon signed-ranks test, and a bootstrap randomization test. All tests were one-tailed because of the *a priori* prediction that the association between mating system and species number would be positive. In one case, where two sources implied different phylogenetic relationships for a given promiscuous taxon, the results of the alternative scenarios were analyzed separately. In determining the number of species in each taxon, we followed Sibley and Monroe (1990). A major difficulty arises in a phylogenetic comparison of species richness because most published phylogenies do not include every species of the ingroup. Unless stated otherwise, we assumed that higher taxa treated in this manner were monophyletic.

Body size covaries with mating system in some groups of birds (Webster 1992). To control for the possible confounding effects of body size, we tested for an association between body size and mating system, and for an association between body size and species richness for the taxa in our sample. The sign tests employed in this part of the analysis were two-tailed because any association, positive or negative, involving body size would be relevant to our analysis of mating systems and species richness. We calculated a mean body mass for each taxon by averaging across all species for which data representing males and females (or birds not identified to sex) were available in Dunning (1993). For the exceptionally species-rich families Apodidae and Trochilidae, we selected a single species from each genus and calculated an average value from these for each family. In this case, the representative species from each genus was either the first one listed for which the sample size was at least 10 individuals, or the one with the largest sample if all species were represented by fewer than 10 individuals.

RESULTS

Promiscuity or polygyny with no paternal care was identified in 14 families: Megapodiidae, Phasianidae, Anatidae, Psittacidae, Trochilidae, Otididae, Scolopacidae, Tyrannidae (Tyranninae, Cotinginae, Piprinae), Menuridae, Ptilonorhynchidae, Corvidae (Paradisaeini), Pycnonotidae, Passeridae (Ploceinae, Estrildinae), and Fringillidae (Icterini). Adequate phylogenetic data (allowing direct comparisons of sister taxa with different mating systems) were available for promiscuous taxa in nine of these groups: Megapodiidae, Tetraoninae, Anatidae, Trochilidae, Tyrannidae (Cotinginae, Piprinae), Menuridae, Ptilonorhynchidae, Paradisaeini, and Icterini.

Our data set comprised 14 comparisons, as detailed in Table 1. One of these, comparison 14, involved a group (*Quiscalus* grackles) for which two available phylogenies differed in the reconstruction of sister-group relationships (Lanyon unpubl. data, Björklund 1991). Including comparison 14a, the number of species in the promiscuous taxon was higher than that of its nonpromiscuous sister group in eight cases, equal in four cases, and lower in two cases. Including comparison 14b, the number of species in the promiscuous taxon was higher than that of its nonpromiscuous sister group in seven cases, equal in five cases, and lower in two cases. Simple sign tests performed on these data were not statistically significant ($P = 0.055$ including 14a, and $P = 0.090$ using 14b). When variation in the magnitudes of differences among the paired contrasts were taken into account, the results were significant for the analyses involving comparison 14a, but not for those involving comparison 14b (Table 2).

No association between mating system and body size was evident, as species in the promiscuous taxon had a larger mean body mass in 5 of 12 cases (two-tailed sign test, $P = 0.774$). Species richness and body size also were not associated; species in the more species-rich taxon were larger in 3 of 10 cases (two-tailed sign test, $P = 0.344$).

DISCUSSION

A hypothesis as general and historically long-lived as the one linking sexual selection with speciation deserves careful empirical consideration. Because the temporal scale over which such a relationship must be observed precludes experimental testing, we must resort to comparative techniques, despite their vulnerability to the difficulties inherent in reconstructing historical patterns of phylogenetic differentiation and mating system evolution. Furthermore, limitations in our knowledge of variation in the intensity of sexual selection, and in our ability to infer past rates of speciation, require that we approach the issue in terms of the relationship between mating systems and species richness.

Clearly, the comparisons we use in our study are vulnerable to errors in phylogenetic reconstruction. Any such error would tend to distort the inferred pattern of evolutionary transitions between mating systems and would make a

TABLE 1. Species richness of promiscuous taxa and their nonpromiscuous sister taxa.

	Promiscuous taxon	No. of species	Nonpromiscuous taxon	No. of species	Sign[a]	Ratio[b]	Source of phylogeny[c]
1	*Aepypodius, Alectura*	3	Other Megapodiidae	16	–	0.158	Brom 1990
2	*Bonasa bonasia*	1	Other *Bonasa*	2	–	0.333	Johnsgard 1983
3	*Cairina*	2	*Pteronetta*	1	+	0.667	Livezey 1991
4	*Anas penelope, A. americana*	2	*Anas sibilatrix*	1	+	0.667	Livezey 1991
5	*Anas chlorotis*	1	*Anas aucklandica*	1	=	0.500	Livezey 1991
6	*Anas puna*	1	*Anas versicolor*	1	=	0.500	Livezey 1991
7	Trochilidae	319	Apodidae	103	+	0.756	Sibley and Ahlquist 1990
8	*Machaeropterus regulus, M. pyrocephalus*	2	*Machaeropterus deliciosus*	1	+	0.667	Prum 1992
9	*Tijuca atra*	1	*Tijuca condita*	1	=	0.500	Sibley and Monroe 1990
10	*Menura*	2	*Atrichornis*	2	=	0.500	Sibley and Ahlquist 1990
11	Other Ptilonorhynchidae	16	*Ailuroedus*	4	+	0.800	Sibley and Ahlquist 1990
12	Other Paradisaeini	33	*Manucodia*	5	+	0.868	Sibley and Ahlquist 1990
13	*Molothrus*	5	*Curaeus*	2	+	0.714	Freeman 1990
14a	*Quiscalus mexicanus, Q. major*	2	*Quiscalus niger*	1	+	0.667	Lanyon unpubl. data
14b	*Quiscalus major*	1	*Quiscalus niger*	1	=	0.500	Björklund 1991

[a] Sign of difference when number of nonpromiscuous species subtracted from number of promiscuous species.

[b] Number of promiscuous divided by sum of number of promiscuous species and number of nonpromiscuous species.

[c] Sources for mating system data listed in Appendix; species tallies from Sibley and Monroe (1990).

TABLE 2. Statistical analysis of comparisons of species numbers across sister taxa with different mating systems.

Data set	Sign test	Wilcoxon signed-ranks test		Bootstrap
	P	Z	P	P
Using comparison 14a	0.055	−1.704	0.044	0.046
Using comparison 14b	0.090	−1.554	0.060	0.067

comparison of species richness meaningless. Similarly, our ignorance of the historical intensities of sexual selection forces us to oversimplify our treatment of the putative causal factor. Although sexual selection can operate in any mating system, the absence of more direct evidence requires that we employ gross categorizations of mating systems to recognize groups that are likely to have differed historically in intensity of sexual selection. This oversimplification implies that, even if our reconstruction of changes in mating system were perfect, our comparisons almost certainly would overlook instances of relatively intense sexual selection in groups with monogamous or mildly polygynous mating systems. We emphasize that this source of error would tend to reduce, rather than exaggerate, the degree of contrast in sexual selection actually tested in our comparisons.

In our analysis, the hypothesis linking sexual selection to speciation was supported when a Wilcoxon signed-ranks test and a bootstrap simulation were applied to one version of the data set (including comparison 14a), but not when they were applied to the other version (including comparison 14b), or when a sign test was employed (Table 2). This ambiguity is probably related to our small sample size. The same proportion of positive comparisons that we report (0.8) would yield a strongly significant sign test ($P < 0.01$) if the sample size were increased to 20.

Besides sexual selection, other factors that might affect speciation include gene flow, spatial variability in natural selection, and unpredictable historical events (such as those involved in polyploidy). The last of these cannot reasonably be invoked to account for the pattern that we report, and the broad variety of taxa that we considered effectively rules out the other two factors as explanations for our results. We must also consider the possibility that our results are attributable to a covariance between an unknown factor affecting species richness and the mating systems used here to identify high levels of sexual selection. Although we are not able to rule out all such possibilities, the broad phylogenetic scope of our study would seem to make this source of confusion unlikely. Our analysis includes representatives of nine families in five orders, spanning much of the geographical and ecological variation observed among birds.

Acknowledging the limitations of our approach, we conclude that there is an association in birds between promiscuous mating systems and relative species richness that supports the hypothesis that sexual selection promotes speciation. Our study is a preliminary step toward a rigorous empirical test of an important hypothesis in evolutionary biology. We welcome reanalysis of this problem at such time when larger sets of comparisons are possible.

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APPENDIX. Avian taxa classified as promiscuous or highly polygynous (males provide no resources to their mates or young). Names of higher taxa (e.g. family or genus names by themselves) refer to all of the species included in that taxon according to Sibley and Monroe (1990).

Aepypodius and *Alectura* (Jones 1990); Phasianini (some; Johnsgard 1986); *Centrocercus, Tetrao,Tympanuchus,* and *Bonasa bonasia* (Johnsgard 1983); *Meleagris* (Campbell and Lack 1985); *Cairina* and *Aix* (Johnsgard 1978); *Anas* (all except *waigiuensis, sibilatrix, capensis, gibberifrons, castanea, aucklandica, specularis, specularioides, versicolor;* Johnsgard 1978, McKinney 1991); *Strigops* (Merton et al. 1984); Trochilidae (Skutch 1976); *Otis* (Cramp and Simmons 1980); *Gallinago media* (Cramp and Simmons 1980, Höglund and Lundberg 1987); *Tryngites* (Pruett-Jones 1988); *Philomachus* (Cramp and Simmons 1980, van Rhijn 1991); *Calidris melanotos* (Campbell and Lack 1985); *Mionectes oleagineus, M. macconnelli,* and *M. rufiventris* (Willis et al. 1978); *Phoenicircus, Tijuca atra, Lipaugus unirufus, L. vociferans, L. fuscocinereus, Pyroderus scutatus, Cephalopterus, Perissocephalus, Procnias, Rupicola* (Snow 1982); *Oxyruncus* (Stiles and Whitney 1983); *Pipra* (some; Ridgely and Tudor 1994); *Chiroxiphia* (some; Snow 1963; Foster 1977, 1981); *Corapipo gutturalis* (Davis 1949); *Manacus manacus* (Lill 1974); *M. vitellinus* (Willis and Eisenmann 1979); *Machaeropterus pyrocephalus* (Robbins 1985); *M. regulus* (Meyer de Schauensee et al. 1978); *Menura* (Campbell and Lack 1985); Ptilonorhynchidae (except *Ailuroedus;* Cooper and Forshaw 1977); Paradisaeini (except *Manucodia;* Cooper and Forshaw 1977); *Andropadus latirostris* (Brosset 1982); *Euplectes jacksoni* (Andersson 1982); *Vidua chalybeata* (Payne 1973); *V. macroura* (Shaw 1984, Alatalo et al. 1988); *V. orientalis, V. paradisaea,* and *V. obtusa* (Payne 1984, Alatalo et al. 1988); *Quiscalus major, Q. mexicanus* (Webster 1992); *Molothrus ater* (Yokel 1989); *M. aeneus* and *M. bonariensis* (Campbell and Lack 1985); *M. rufoaxillaris* (Mason 1987); *Scaphidura oryzivora* (Campbell and Lack 1985); *Psarocolius, Gymnostinops, Ocyalus,* and *Cacicus* (some; Campbell and Lack 1985, Webster 1992).