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Sexual selection and taxonomic diversity in passerine birds

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SUMMARY

Many authors have suggested that sexual selection by female choice may increase the speciation rate and hence generate taxonomic diversity. Using sister taxa comparisons, we find a significant positive correlation between the proportion of sexually dichromatic species within taxa of passerine birds, and the number of species in those taxa. Theory predicts this result if sexual dichromatism in passerines has evolved through the action of female choice.

1. INTRODUCTION

Ever since Darwin, it has been suggested that sexual selection by female choice might increase the rate of reproductive divergence between populations and thereby increase the diversity of a clade (Darwin 1871; Carson 1978, 1986; Lande 1981, 1982; West-Eberhard 1983; Dominey 1984; Schluter & Price 1993). Specifically, if there is divergence of the expression of female preference and male preferred trait between populations within a species, and the expression of male trait and female preference are correlated within populations, then there will be assortative mating within populations, and reproductive isolation may develop. This theory has been addressed in the framework of the two major models for the evolution of female choice, namely the Fisher process and handicap theory (Lande 1981, 1982; Schluter & Price 1993).

A few experiments have shown evidence for this mechanism of assortative divergence in mating preferences. For example, Houde & Endler (1990) found that the preference of female guppies for male coloration varies between natural populations, and that the expression of the female preference is correlated with the expression of the male trait within populations. Also, Baker & Baker (1990) found assortative mating within two semispecies of bunting, *Passerina cyanea* and *P. amoena*, with respect to female preference for both plumage and vocal displays in males (although see Hill (1994) for a negative result within populations of house finch).

Examples consistent with the idea that sexual selection promotes increased clade size include birds of paradise (West-Eberhard 1983), Hawaiian *Drosophila* (Carson 1978, 1986), and the cichlid fishes of the African Great Lakes (Dominey 1984). All these groups show high levels of intersexual selection, and many closely related species apparently differ only in the secondary sexual characters of males. However, a listing of such cases does not constitute a test of the hypothesis.

One way to test the hypothesis is to seek a correlation

between the strength of sexual selection and the degree of clade diversity across a range of clades which constitute a monophyletic group. Specifically, if we compare sister taxa in which the species of one taxon have females with stronger mating preferences than species in the other taxon, then the former should be more speciose, all other things being equal. This approach controls for the confounding effect of taxon age on present day diversity, and there are likely to be fewer possible confounding variables when closely related taxa are compared (Mitter *et al.* 1988; Zeh *et al.* 1989). However, such comparisons of diversity require large groups with published phylogenies which are complete at the taxonomic level of interest. Here we use Sibley & Ahlquist's DNA-DNA hybridization phylogeny of bird tribes, currently the most comprehensive molecular phylogeny of a higher taxonomic group (Sibley & Ahlquist 1990). Within their phylogeny, we have examined passerines, which constitute a large, discrete clade.

We use sexual dichromatism, the difference in colour between males and females, as an indirect measure of sexual selection, to test whether sexual selection and taxonomic diversity are correlated in passerine birds. For more than a hundred years, the prevailing view has been that intersexual selection is responsible for plumage dichromatism (Darwin 1871; Andersson 1994), counter-balanced by the associated mortality costs of increased dimorphism (Promislow *et al.* 1992; but see Owens & Bennett 1994). Also, with a small number of exceptions, species can be scored easily and unambiguously as dichromatic or not.

2. METHODS

A range of field guides was chosen to represent all the biogeographic regions (Mackworth-Praed 1952-1972; Falla *et al.* 1970; Meyere de Schaunsee 1970; Pizzey 1980; Farrand 1983; Beehler *et al.* 1986; Ali & Ripley 1987; Pratt *et al.* 1987; Cramp 1988-1993; Stiles & Skutch 1989; Mackinnon & Phillipps 1993). The species in the field guides constitute a sample of species from each of Sibley & Ahlquist's tribes. All species of passerines within these guides were scored for

sexual dichromatism, using 1 for dichromatic and 0 for monochromatic. In a few cases the differences between male and female are slight, creating ambiguity. These species comprise 5 of the sample, and our results are not sensitive to how they are scored: we have arbitrarily chosen to present the results of the analysis which scores them as 0.5. The species scores were used to construct a measure of the dichromatism of a tribe in two ways. A quantitative measure is simply the proportion of dichromatic species in the tribe: the sum of the species scores divided by the number of species. A qualitative measure is constructed by labelling tribes 'dichromatic' or 'monochromatic', depending on whether or not their proportion of dichromatic species is above a threshold value. Tribal dichromatism scores and the sample size of species scored are shown in the appendix. Larger tribes tended to have a smaller proportion of species represented in our sample, but there is no significant relation across tribes between sexual dichromatism and the proportion of species sampled.

For each test, all sister tribe pairs were identified from the tree in which one tribe had a higher sexual dichromatism measure than the other. Nodes in which there is no difference between sister tribes provide no information concerning the hypothesis that sexual dichromatism is correlated with taxonomic diversity. Sister taxa comparisons at levels higher than the tribe also provide information relevant to the hypothesis. Higher nodes were included when all the tribes on one side were more dichromatic than all the tribes on the other. This excludes higher nodes for which definition of the more and less sexually dichromatic branch is ambiguous: we prefer a conservative test of the hypothesis to one which requires additional assumptions about phylogenetic weightings. The tests described below were also performed solely on sister tribes to allow for the possibility that the level of nodes in the tree could affect the results; the smaller number of comparisons for this analysis reduces the power of the test.

The number of species in each taxon is from Sibley & Monroe (1990). Because none of the nodes used had sister taxa with equal diversity, each node either has the more dichromatic branch more diverse (consistent with the sexual selection hypothesis), or the less dichromatic branch more diverse (contrary to the hypothesis). Under the null hypothesis, we should not expect a significant deviation from an equal number of nodes falling into each case. The nodes were subjected to a paired sign test, and a randomization test (see table legends for details) for an association between sexual dichromatism and taxonomic diversity. The randomization test takes account of the magnitude of the diversity difference between nodes, in addition to the sign of the difference. As it is the diversity difference between branches that concerns us here, and not the absolute diversity in both branches, these tests were performed on the proportion of diversity on each branch and not on absolute diversity. The hypothesis calls for a one-tailed test, and we report one-tailed probabilities.

Recognizing that the phylogeny is not perfect, the tests were repeated including only those nodes which are defined within the error estimates of the DNA-DNA hybridization method. Cracraft (1987) performed an independent analysis on the data used by Sibley & Ahlquist (1990), and concluded that, in his opinion, 'internodal distances of 1.0 °C or greater will probably be distinct'. We use this as a criterion for defining more reliable nodes.

3. RESULTS

31% of species sampled were sexually dichromatic. Table 1 shows the results of the analysis using the

Table 1. *The association between diversity and dichromatism using the qualitative measure of taxon dichromatism*

(A taxon is labelled dichromatic if, for example, more than 40% of its species are dichromatic. It is labelled monochromatic if the fraction of dichromatic species is below the threshold. Sister taxa which differ in dichromatism are then investigated for an association between dichromatism and diversity. The diversity of each taxon is quantified as the proportion of the total number of species in the taxon pair which belongs to each taxon. Two statistical tests were then used to assess the significance of the observed associations: the sign test and a randomization test for matched pairs (see Siegel 1956). We report one-tailed probabilities throughout.)

thresholds	positive nodes		sign test	randomization test
	number	%		
All nodes				
0.0	12/15	80	0.02	0.003
0.2	14/18	78	0.02	0.01
0.4	16/20	80	0.01	0.03
0.6	10/14	71	0.09	0.09
Sister tribe comparisons only				
0.0	8/10	80	0.06	0.02
0.2	10/12	83	0.02	0.02
0.4	9/12	75	0.07	0.15
0.6	6/9	67	0.25	0.25

qualitative measure of diversity, for various choices of the threshold proportion of dichromatic species required to label a tribe 'dichromatic'. Table 2 shows the results of the analysis using the quantitative measure of the dichromatism of the tribe. The results in tables 1 and 2 reveal a positive association between dichromatism and diversity: there are more nodes in support of the sexual selection hypothesis than against it in every analysis. About 75% of nodes support the hypothesis whether the comparisons are restricted to sister taxa or whether they also include higher nodes. In the former case, the significance of the results are inevitably lowered because fewer comparisons are used.

Only six of the nodes are defined within the error limits of DNA-DNA hybridization calculated by Cracraft (1987). All of these supported the hypothesis (sign test, $p = 0.016$ randomization test, $p = 0.016$). This test used the quantitative measure of dichromatism accepting any difference between sister taxa as significant, to include all the nodes.

4. DISCUSSION

Our results show a positive correlation between the prevalence of sexual dichromatism and taxonomic species diversity in passerine birds. The layered analysis shows that this result is not sensitive to the method of deriving tribal dichromatism from species scores. The main assumption underlying the result is our choice of phylogeny. Restriction of the analysis to those nodes which are sufficiently well defined within the errors of DNA-DNA hybridization revealed stronger support for the hypothesis, despite relying on a sample size of only six nodes.

Table 2. *The association between diversity and dichromatism using the quantitative measure of taxon dichromatism*

(This analysis was carried out on the whole data set and on various subsets, each subset constructed according to the criterion that the difference in dichromatism between sister taxa has to be greater than a specified amount for that comparison to be included in the analysis. The reason for carrying out this layered analysis is as follows. If there is only a small difference in the dichromatism scores of two taxa, it is quite possible that the direction of the difference is an accident of sampling (recall that not all species of passerines have been scored). The greater the difference, the greater our confidence that the difference really is in the observed direction. If we include all comparisons, including ones with very small differences, we risk swamping any signal that might exist with noise. But as we demand greater differences, the number of comparisons available to us declines. Because there is no way, *a priori*, to decide on a difference level which would be optimal for detecting any relation that might exist, we have tried several levels, rather in the manner of turning a radio dial.)

difference in dichromatism between sister taxa which is accepted as significant	positive nodes		sign test	randomization test
	number	%		
All nodes				
> 0.0	20/31	65	0.08	0.04
> 0.2	19/25	76	0.01	0.02
> 0.4	11/15	73	0.06	0.09
sister tribe comparisons only				
> 0.0	13/20	65	0.13	0.05
> 0.2	12/15	80	0.02	0.03
> 0.4	6/9	67	0.25	0.28

For this pattern to be explicable by the hypothesis that sexual selection by female choice has promoted cladogenesis, it is required that sexual dichromatism evolved through the action of female choice. Because of the problems of performing manipulation experiments, the cause of sexual dichromatism in birds is still unresolved (Butcher & Rohwer 1988; Andersson 1994), and so we cannot rule out the possibility that sexual dichromatism has evolved in response to processes other than female choice. There is evidence that plumage functions as an intrasexual signalling trait in some species of passerine (Marchetti 1993; Møller 1988). Although it has been suggested that intrasexual signalling traits may also increase divergence between populations (West-Eberhard 1983), this scenario has weaker theoretical basis than divergence by female choice, and it has never been modelled explicitly.

If male plumage has evolved as a species recognition trait (Alatalo *et al.* 1994), then we might expect a correlation between sexual dichromatism and diversity, if selection for species recognition is more intense in taxa with a greater number of closely related species. Some authors advise that both species recognition and the traditional process of female choice are viewed as special cases of a more general process of female choice

(Wilson 1991; Ryan 1993), and so species recognition should not be viewed as an alternative hypothesis. However, the two hypotheses are mechanistically different, and in extreme cases the direction of causality between sexual signalling and speciation is reversed. Future work is required to determine the relative contribution of within-species female choice and species recognition to the evolution of sexual dichromatism in birds.

As with all comparative tests, we cannot rule out the possibility that our observation is a result of both sexual dichromatism and species diversity being correlated with an unknown confounding variable. However, we know of no such 'third variable' for our sample. In addition, it has been suggested that taxonomists might tend to recognize more species in groups that are sexually dichromatic. This would occur only if interspecific variation of male plumage in sexually dichromatic groups is greater than interspecific plumage variation in monochromatic groups, because only then does male plumage provide extra information on which to split such groups. If this effect occurs, our interpretation would be that diversity of male plumage expression is correlated with sexual selection, but that this may or may not lead to true species divergence. However, there is probably ample variation in female plumage characteristics between species in the sexually dichromatic groups to suggest that these species would still be recognized on the basis of female characters alone, and hence we believe that our result relates to true species diversity.

5. CONCLUSIONS

There is a positive correlation between the number of species in passerine tribes and the proportion of species in those tribes which are sexually dichromatic. This finding is consistent with, and predicted by, the long standing hypothesis that sexual selection by female choice can increase the speciation rate of a group. Allowing for the role of alternative processes in the evolution of sexual dichromatism, our conclusion is that taxonomic diversity is correlated with the prevalence of sexual signals in passerine birds.

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APPENDIX 1

sister tribes	number of species	proportion of dichromatic species	number of species sampled
Pittidae	31	0.58	13
Eurylaimidae	14	0.19	8
Cotinginae	69	0.67	57
Piprinae	52	0.75	48
Tityrini	20	0.71	12
Schffornithini	3	0.00	3
Rhinocryptidae	28	0.19	27
Conopophagidae	8	0.88	6
Ptilonorhyncidae	20	0.64	14
Menuridae	4	0.00	4 ^a
Acanthizini	35	0.00	24
Sericornithini	26	0.14	14
Pachycephalini/ falcunculini	54	0.38	34 ^a
Mohouini	3	0.00	3
Vangini	58	0.66	31
Malaconotini	48	0.38	39
Monarchini	98	0.46	44
Dicrurini	24	0.00	15
Oriolini	111	0.68	51
Artamini	24	0.08	20
Ptilogonotini	4	1.00	4
Bombycillini	3	0.00	3
Saxicolini	155	0.55	38
Muscicapini	115	0.56	40
Sturnini	114	0.29	44
Mimini	34	0.00	14
Troglodytinae	75	0.00	48
Polioptilinae	15	0.45	11
Sylivini	22	0.30	14
Chamaeini	1	0.00	1
Estrildini	140	0.38	133
Viduini	15	1.00	4
Melanocharatini	6	0.60	5
Toxorhamphini	4	0.00	4

APPENDIX 1 (*cont*)

sister tribes	number of species	proportion of dichromatic species	number of species sampled
Nectariniini	123	0.78	68
Dicaeini	44	0.64	17
Carduelini	136	0.78	73
Drepanidini	30	0.38	20
Icterini	97	0.53	50
Cardinalini	42	0.68	19

^a These taxa are named as higher groups in the classification presented in Sibley & Alquist (1990), but the UPGMA phylogeny does not support the subdivision of these taxa into two tribes. We treat them as tribes.

APPENDIX 2

higher sister taxa	number of species	proportion of dichromatic species	number of species sampled
Formicariidae	56	0.00	28
Conopophagidae/ Rhinocryptidae	36	0.34	33

Malurinae	18	1.00	11
Amytornithinae	8	0.26	8
Dasyornithinae/ Acanthizinae	64	0.06	41
Pardalotinae	4	0.50	4
Malaconotinae	106	0.53	70
Aegithinae	4	0.00	4
Paradisaeini/ Artamini/Oriolini	180	0.61	109
Corvini	117	0.00	71
Oriolini/Artamini	135	0.57	0.71
Paradisaeini	45	0.74	38
Muscicapinae	270	0.56	78
Turdinae	179	0.30	72
Ploceinae/ Estrildinae	272	0.64	190
Prunellinae	13	0.00	6
Nectariniinae	167	0.74	85
Promeropinae	2	0.00	2
Carduelini/ Drepanidini	166	0.71	93
Fringillini	3	1.00	3
Thraupini/ Cardinalini/ Icterini	552	0.53	207
Parulini	115	0.22	57