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## SEXUAL SELECTION, MATING SYSTEMS, AND THE EVOLUTION OF AVIAN ACOUSTICAL DISPLAYS

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In 1872 Darwin noted that males in species with polygynous mating systems have more highly developed secondary sexual characters than their monogamous counterparts and that the highly developed weaponry common in polygynous species could be associated with more intense male competition for mates in these species. More difficult for him to explain, however, was the evolution of extremely dimorphic traits in polygynous species, such as plumes and vocalizations, that had no obvious direct function in male combat. Recent developments in sexual-selection theory have provided a framework for understanding how these traits evolve (Fisher 1930; Bateman 1948; Trivers 1972). Trivers (1972) proposed that females use male sexual displays as cues for assessing the quality of prospective mates as sperm donors. Following this suggestion, a variety of models has proposed that the evolution of extreme male display features is based on assessment by females (Alexander 1975; Zahavi 1975; Halliday 1978; Borgia 1979; Thornhill 1980; Andersson 1982; Hamilton and Zuk 1982).

Fisher (1930) offered a different model, the "runaway process," suggesting that male display characters evolve through the development of a genetic correlation between female choice and the character in males chosen by females. In this model, unlike the assessment models, females gain no direct benefits from choosing males with elaborate displays, and it has been suggested that choice for these characters might evolve even if their effect outside the context of sexual selection is to lower the fitness of females who choose males with elaborate displays (Lande 1981; Kirkpatrick 1982; Arnold 1983; O'Donald 1983). The assessment and runaway models have led to conflicting views about the functional significance of display; yet there have been few tests attempting to resolve these differences.

Despite a great deal of interest in avian vocalizations, sexual-selection theory, and avian mating systems (Wittenberger 1981; Catchpole 1982), the relationship between song structure and how it is shaped by sexual selection is poorly understood. Kroodsma (1977) found a positive correlation between the degree of polygyny and the size of the song repertoire in North America wrens (Troglodytidae). The opposite pattern has been found in European warblers (*Acrocephalus*; Catchpole 1980) and European buntings (*Emberiza*; Catchpole and McGregor 1985).

Farabaugh (1982) showed that vocal duetting occurred exclusively in monogamous species. In no case, however, has there been a general survey of the relationship between bird songs and mating systems; the question of how sexual selection affects the evolution of bird song remains to be examined in detail.

In this paper, we consider the application of sexual-selection theory to the evolution of acoustical displays in polygynous species in which males make no material contribution to the young (hereafter referred to as NMC polygyny). In these species male display characters appear to reach extremes. Following Trivers (1972), we assume that the conditions and requirements for mate selection by females differ vastly between species with monogamous and NMC-polygynous mating systems and that this should give rise to different patterns of courtship display. Since avian monogamy is typically associated with biparental care, females should evolve to assess such characters as male territory quality and male experience that affect the male's material contribution to offspring. In NMC-polygynous species males have no role in rearing offspring; thus, female choice should be directed toward optimizing the payoffs from her short association with a mate (e.g., assessing the quality of a male as a potential sire for her offspring). To the extent that females in NMC-polygynous mating systems use similar mechanisms for assessing the quality of their mates as sires (i.e., a general mechanism of assessing male courtship displays in order to facilitate mate choice), we predict convergence in the types of courtship calls used by males. If assessment has had an important role in the evolution of male displays, then we predict specifically that male acoustical courtship displays in NMC-polygynous species should be qualitatively different from those in monogamous species, and that there is convergence among NMC-polygynous species.

Assessment and runaway models of sexual selection make somewhat divergent predictions about the nature of acoustical courtship display in NMC-polygynous species. Fisher (1930) suggested that display characters elaborated by the runaway process start off as characters having functional significance in sexual display but in another context (e.g., species recognition). This should lead to a pattern in which displays of NMC-polygynous and monogamous species are qualitatively similar, but displays of polygynous species are elaborated versions (e.g., are given at increased amplitude). In addition, his model does not predict convergence in call characters among NMC-polygynous species. Kirkpatrick (1982, 1985, 1986) suggested that male display characters are totally arbitrary. This leads to predictions that there are no systematic differences between the calls of NMC-polygynous species and those of their monogamous counterparts, and that there is no convergence in the characteristics of calls among NMC-polygynous species. Thus, the assessment and runaway models predict distinctive patterns for the evolution of exaggerated display.

Here we compare acoustical displays from birds in nine families having polygynous and monogamous species. Male acoustical displays of monogamous and polygynous species were analyzed for a variety of vocal and nonvocal characters involved in sexual displays. The results of these comparisons were used to determine if there are systematic differences in courtship displays associated with the mating system and if there are convergences in display patterns among

independently derived NMC-polygynous species. These results are then used to evaluate models for the evolution of extreme sexual display.

#### METHODS

We analyzed vocal recordings from 158 avian species in 9 families: Cotingidae (cotingas), Paradisaeidae (birds of paradise), Phasianidae (pheasants, grouse, quail), Pipridae (manakins), Ploceidae (weavers, sparrows), Psittacidae (parrots), Ptilonorhynchidae (bowerbirds), Pycnonotidae (bulbuls), and Scolopacidae (sandpipers). Each family contains monogamous and polygynous mating systems. Polygynous mating systems include resource-based polygyny and NMC polygyny (see above); the latter mating system includes exploded arenas (Gilliard 1963) and leks. The availability of vocal recordings determined the choice of species, which are listed in the Appendix. The Library of Natural Sounds (Cornell University) was the major source of recordings. Acoustical measures for several scolopacids were taken from published field studies (*Gallinago media*, Ferdinand 1966; other scolopacid species, Cramp and Simmons 1983).

Two methods were used to identify the social context in which the sexual displays of each species were recorded. We define *courtship displays* as those displays that are typically directed at a female; male *advertising displays* are long-range displays that typically are not directed at a particular female. Only courtship and advertising displays were analyzed. For 122 of the species, the social context could be accurately determined because data sheets or comments from the researchers who recorded the displays were available. For the remaining species, published field studies provided a basis for inference of behavioral context from the display sample. Any recording for which the context could not be determined was excluded from the analysis. It should be noted that in several species males produce a single display or group of displays used both for courting and for advertising. These were excluded from comparisons of courtship and advertising displays.

In order to quantify differences among species, we measured the highest frequency (Hz) and lowest frequency (Hz) of each vocalization at a standardized level of input, using a Spectral Dynamics Corporation Digital Signal Analyzer (model SD350). From these measures, a frequency range (lowest frequency of a sound subtracted from its highest frequency) was calculated for each sound analyzed. The minimum analysis resolution was 25 Hz.

Recordings were scored subjectively for discreteness. Vocalizations that sounded relatively pure in tone with a high proportion of discrete sounds were scored as "tonal," and vocalizations that sounded harsh with many broadband sounds were scored as "noisy." We further divided the sounds into specific, descriptive sound categories. Tonal sounds (narrow frequency ranges) included whistles, trills, musical phrases, and simple repeated notes. Noisy sounds included clicks, buzzes, harsh slurs, scratches, booming, and nonvocal sounds. Frequency-range values were calculated from the sample data after these categories were defined and after all samples had been analyzed. The categories are defined below.

*Whistles* are pure, tonelike sounds, with or without frequency modulation (mean frequency range  $1275 \pm 240$  Hz).

*Trills* are series of similar notes repeated at a rate of 10–30 per s (mean frequency range  $1452 \pm 370$  Hz).

*Musical phrases* are two or more different notes uttered in stereotypic groups, with highly tonal quality (mean frequency range  $1389 \pm 234$  Hz).

*Simple repeated notes* are single discrete sounds given singly, often repeated at intervals (mean frequency range  $1676 \pm 295$  Hz).

*Clicks* are brief ( $< 0.10$  s) harsh sounds, given either singly or in bursts of sounds (mean frequency range  $5477 \pm 996$  Hz).

*Harsh slurs* are noisy, frequency-modulated phrases; they often sound metallic or machinelike (mean frequency range  $4264 \pm 738$  Hz).

*Buzzes* are series of similar harsh sounds repeated at a rate of more than 30 per s (mean frequency range  $4456 \pm 625$  Hz).

*Scratches* are single growllike sounds (mean frequency range  $5097 \pm 615$  Hz).

*Booming sounds* are very loud low-frequency sounds, usually given as a continuous noise for several seconds (mean frequency range  $3225 \pm 1363$  Hz).

*Nonvocal sounds* are harsh sounds produced by nonvocal structures, such as wings, and incorporated into the vocal display (mean frequency range  $4812 \pm 1150$  Hz).

For each species the following sound measurements were obtained: the total number of distinct sounds used during the acoustical display; the frequency of occurrence of each sound class; the highest and lowest frequency of each sound; the frequency range of each sound; the mean frequency range of each class; and the overall average range of sound frequencies used by each species (the total of all sound-class frequency ranges divided by the number of classes). For each species, 1 to 22 individuals were sampled ( $\bar{X} = 3.18$ ).

Multivariate ANOVA tests, Spearman rank correlations ( $r_s$ ), Kruskal-Wallis tests (chi-square approximation), sign tests, and combined-probability tests were used for statistical comparisons (Sokal and Rohlf 1969; Helwig and Council 1982). For ANOVA tests, plots of data and residuals were used to test for normality and equality of variances. Where needed, appropriate transformations were made (Draper and Smith 1966). Means are expressed as  $\bar{X} \pm$  one standard error.

## RESULTS

The significant differences among the display characters used by male birds are affected by the type of mating system and by phylogenetic relationship. When we compared means for display traits for each mating system while controlling for the effect of relatedness among species, we found that males from NMC-polygynous species used significantly more clicks, buzzes, scratches, booms, nonvocal sounds, and “noisy” vocalizations in their courtship displays than did males of monogamous species (table 1). Moreover, the average range of sound frequencies produced by NMC-polygynous males was significantly greater than those used by monogamous males. NMC-polygynous males also used a greater variety of sounds in their courtship displays, whereas monogamous males used significantly more whistles and tonal sounds.

TABLE 1

MULTIVARIATE ANOVA FOR MATING SYSTEM AND FAMILY EFFECTS ON COURTSHIP DISPLAYS:  
MONOGAMY AND NMC POLYGyny

VARIABLE	MATING SYSTEM			FAMILY		
	<i>F</i> *	<i>P</i>	HSD Test*	<i>F</i> †	<i>P</i>	HSD Test†
No. of whistles	5.25	0.024	‡	2.38	0.002	pheasants
No. of musical phrases	0.42	NS	NS	1.92	NS	NS
No. of trills	0.18	NS	NS	0.93	NS	NS
No. of simple notes	0.21	NS	NS	1.68	NS	NS
No. of clicks	9.47	0.003	§	2.14	NS	NS
No. of harsh slurs	2.62	NS	NS	2.83	0.007	bowerbirds
No. of buzzes	11.41	0.001	§	3.68	0.001	bowerbirds
No. of scratches	15.53	0.001	§	10.60	0.001	bowerbirds, birds-of-paradise
No. of booms	7.27	0.008	§	2.14	NS	NS
No. of nonvocal sounds	15.13	0.001	§	3.06	0.004	pheasants
No. of tonal sounds	4.55	0.035	‡	2.11	NS	NS
No. of noisy sounds	45.71	0.001	§	1.54	NS	NS
Total no. of display sounds	15.18	0.001	§	3.64	0.001	bowerbirds
Average frequency range of all sounds	22.34	0.001	§	2.12	NS	NS

NOTE.—NS, not significant.

\* Mating-system effects: *df* = 1, *N* = 103. Overall  $F_{14,80} = 4.83$  ( $P < 0.001$ ). HSD test = Tukey's studentized range test for differences among mating-system means ( $\alpha = 0.05$ ).

† Family effects: *df* = 8, *N* = 103. Overall  $F_{112,626} = 2.34$  ( $P < 0.001$ ). HSD test = Tukey's studentized range test for difference among family means ( $\alpha = 0.05$ ). Each family noted uses significantly more of the sound class than do other families.

‡ Sound class is more common in monogamous species.

§ Species in NMC-polygynous mating systems use the sound class more frequently than do monogamous species.

In order to test for family effects, we compared the means for courtship display traits for each family while controlling for the effects of mating system (table 1). For several variables (whistles, harsh slurs, buzzes, scratches, nonvocal sounds, and the total number of display sounds), family effects were significant, and for each of these variables, at least one family differed significantly from the others. Grouse (Phasianidae) used significantly greater numbers of whistles and nonvocal sounds than did all the other families. Bowerbirds (Ptilonorhynchidae) produced greater numbers of harsh slurs and buzzes, and birds of paradise (Paradisaeidae) used significantly more scratches in their courtship displays. Bowerbirds used the largest number of sound classes in their courtship displays, differing significantly from all other families in this regard. The average range of sound frequencies produced in each family did not differ.

To investigate within-family effects of mating systems on courtship displays, we classified each family on the basis of the relative importance of particular sound characters in monogamous species and NMC-polygynous species. We then compared these results among families to determine if there was a tendency for particular sound characters to be expressed more often in NMC-polygynous or

TABLE 2  
EFFECT OF MATING SYSTEM ON THE USE OF SOUND CHARACTERS, BY FAMILY

SOUND CHARACTER	FAMILY*								SIGN TEST ( <i>P</i> )†
	Coting- idae	Paradis- aeidae	Phasi- anidae	Pipridae	Ploce- idae	Psit- tacidae	Ptilono- rhynchidae	Pycno- notidae	Scolo- pacidae
No. of whistles	-	-	-	+	-	-	+	-	0.981
No. of musical phrases	-	+	-	-	-	0	+	-	0.965
No. of trills	-	0	0	+	+	0	+	0	0.500
No. of simple notes	+	+	-	+	+	-	-	+	0.254
No. of clicks	+	+	+	+	+	0	+	0	0.062
No. of harsh slurs	0	+	0	+	-	0	+	0	0.188
No. of buzzes	0	+	0	+	0	0	+	0	0.312
No. of scratches	+	+	+	+	0	+	+	0	0.016
No. of booms	+	0	+	0	0	+	0	0	0.125
No. of nonvocal sounds	0	0	+	+	0	+	0	0	0.125
No. of tonal sounds	-	+	-	-	same	-	+	same	0.938
No. of noisy sounds	+	+	+	+	+	+	+	0	0.004
Total no. of display sounds	-	+	+	+	+	+	+	same	0.035
Average frequency range	+	+	+	+	+	+	+	+	0.002

\* Within-family comparisons (courtship displays only). +, NMC-polygynous species use the sound class more often than do monogamous species; -, sound class more common in monogamous species; 0, sound class not produced within family; same, no difference among mating systems.

† Combined probability tests: for the first 10 variables,  $\chi^2 = 32.16$ ,  $P = 0.040$ ,  $df = 20$ ; for all 14 variables,  $\chi^2 = 62.49$ ,  $P < 0.001$ ,  $df = 28$ .

TABLE 3  
P VALUES FOR COMPARISONS OF POLYGYNOUS MATING SYSTEMS AND EFFECTS OF  
CONTEXT ON ACOUSTICAL DISPLAYS

VARIABLE	EXPLODED ARENA vs. LEKS		RESOURCE POLYGYNY vs. MONOGAMY	COURTSHIP vs. ADVERTISING	
	Courtship*	Advertising†	Courtship‡	All§	NMC POLYGYNY
No. of whistles	NS	NS	NS	0.045	NS
No. of musical phrases	NS	NS	NS	NS	NS
No. of trills	NS	NS	NS	NS	0.043
No. of simple notes	NS	NS	NS	NS	NS
No. of clicks	0.006	0.001	NS	NS	NS
No. of harsh slurs	NS	NS	NS	0.046	NS
No. of buzzes	0.030	NS	0.001	0.040	0.008
No. of scratches	NS	NS	NS	NS	NS
No. of booms	NS	NS	NS	NS	NS
No. of nonvocal sounds	NS	NS	0.001	0.047	0.055
No. of tonal sounds	NS	NS	NS	0.057	NS
No. of noisy sounds	NS	0.047	0.001	NS	0.022
Total no. of display sounds	NS	NS	0.026	0.005	0.004
Average frequency range of all sounds	NS	NS	0.003	NS	NS

NOTE.—Tests are Kruskal-Wallis chi-square approximations for differences among means. NS, not significant.

\* For each test,  $df = 1$ ,  $N = 47$ . Significant results indicate that the sound class is more common in exploded-arena species.

† For each test,  $df = 1$ ,  $N = 47$ . Significant results indicate that the sound class is more common in exploded-arena species.

‡ For each test,  $df = 1$ ,  $N = 62$ ; significant results indicate that the sound class is more common in resource-based polygynous species than in monogamous species.

§ All mating systems included. Species with indistinguishable courtship and advertising displays excluded. For each test,  $df = 1$ ,  $N = 93$ . Significant results indicate that the sound character is more common in courtship than in advertising displays.

|| Only NMC-polygynous species included. Species with indistinguishable courtship and advertising displays excluded. For each test,  $df = 1$ ,  $N = 50$ . Significant results indicate that the sound character is more common in courtship displays.

monogamous species (table 2). Within these families, males in NMC mating systems used significantly greater numbers of clicks, scratches, and noisy sounds than did monogamous males and also produced sounds of greater frequency range. The results of this analysis confirm the results described above: the type of mating system significantly affects display sounds, and NMC-polygynous species tend to use noisier courtship displays. This result is recurrent across families in widely different taxa.

The several different types of polygyny can be compared to produce a more-detailed analysis of factors affecting display characteristics. When males from lekking species are compared with males from exploded-arena species (table 3), the numbers of clicks and buzzes used in courtship differ significantly. Males on exploded arenas produce greater numbers of these sounds than do males in leks. The lack of numerous differences among NMC-polygynous species is also evident



when their advertising displays are compared (table 3): males on exploded arenas produce greater numbers of clicks and noisy sounds during advertising than do males in leks.

We also tested for differences in the courtship displays of monogamous and resource-based polygynous mating systems (table 3). Males from resource-based polygynous species produce greater numbers of buzzes, nonvocal sounds, and noisy sounds during courtship than do monogamous species and also use greater frequency ranges and a larger number of sound classes. However, the courtship displays of resource-based and NMC-polygynous males do not differ significantly (for 14 variables compared, mean  $\chi^2 = 0.48$ , 1 df,  $P > 0.50$ ; Kruskal-Wallis test).

To examine the effect of behavioral context on sexual displays, we compared mean display characters for courtship and advertising displays. Several sounds are more commonly associated with courtship than with advertising displays (table 3; note that in the following analyses we excluded those species in which males do not produce clearly distinguishable courtship and advertising displays). During courtship, males in all mating systems use significantly greater numbers of whistles, harsh slurs, buzzes, nonvocal sounds, and tonal sounds than they do during advertisement, and also produce larger total numbers of display sounds. Significant differences in the context of display are also evident when only NMC-polygynous species are analyzed: courtships among these species are more likely than advertising displays to feature trills, buzzes, nonvocal sounds, noisy sounds, and greater total numbers of display sounds.

#### DISCUSSION

We have shown that in nine avian families male courtship displays from species with NMC-polygynous mating systems systematically differ from those of monogamous species in the same family. The NMC-polygynous species converge toward harsh-sounding vocalizations in their courtship displays, as opposed to the typically melodic displays of monogamous species. These results conform best to the predictions of assessment models, as we discuss below. It is possible, however, that similarities in the calls of NMC-polygynous males occur for reasons other than the need of females to assess differences among males. Some alternative explanations are a common evolutionary origin of NMC-polygynous species, the derivation of courtship displays from convergent advertising displays, and common patterns of male competition.

##### *Common Evolutionary Origin*

It is possible that the similarities we observed in courtship calls among males in NMC-polygynous species are not a result of convergent evolution, but of the inheritance of polygyny and associated display behavior from a common ancestor. There is, however, good reason to doubt that common ancestry is the cause of the observed convergences. Monogamy is, by far, the most common mating system among birds (99% of species; Gilliard 1963). The near universality of monogamy suggests that the relatively rare NMC-polygynous species occurring in each family have evolved independently from monogamous ancestors. It seems rea-

sonable to assume that the display characters of those ancestors are similar to display characters in monogamous species extant within that family today. Our comparisons involve birds of four different orders, suggesting no close relationships among these groups. Within the passerines, the only order with multiple families in our comparisons, cotingas and manakins are most probably close relatives and it is possible that polygyny in these families has a common evolutionary origin (Sick 1967; Snow 1973). It is, however, unlikely that a common origin exists for polygyny in any of the other pairs of passerine families we studied. Bowerbirds and birds of paradise are the only other pair thought to be closely allied (Gilliard 1969; Cooper and Forshaw 1977), but recent biochemical evidence suggests a more distant relationship between these families (Sibley and Ahlquist 1986). Moreover, in both groups the monogamous species are thought to be ancestral to the polygynous species (Gilliard 1969; Schodde 1976), supporting the view that polygyny in these groups is independently derived. Thus, common evolutionary origin is not the cause of the observed similarities in male call patterns in NMC-polygynous species, and the observed patterns must be the result of convergent evolution.

#### *Derivation from Advertisement Displays*

A potential explanation for the differences in courtship displays among monogamous males and NMC-polygynous males is that these differences arise as a result of advertising requirements in leks and exploded arenas. Unlike monogamous males, males in these NMC-polygynous mating systems do not associate closely with females except during mating and commonly use acoustical displays to advertise their location to females searching for mates. If the courtship displays of these polygynous males are derived from advertisement calls, then this phenomenon might explain the differences between the courtship displays of NMC-polygynous males and those of monogamous males.

For the majority of the species we studied, our results suggest that this derivation hypothesis may not be applicable. Among NMC-polygynous males we found significant qualitative differences between the acoustical characteristics of courtship and advertising displays. Males in NMC-polygynous species that produce distinguishable advertising and courtship displays use very different, usually noisier, sounds in their courtship than in their advertising displays. In the species that use similar courtship and advertising displays, such as the kakapo (*Strigops habroptilus*), the bellbirds (*Procnias*), and several grouse (e.g., *Tympanuchus cupido*), the advertisement-derivation hypothesis may be important, but these species are relatively rare and constitute only 11% of the NMC-polygynous species. Thus, for the majority of cases, this hypothesis fails to account for the observed convergence in patterns of courtship display.

#### *Male Competition*

The occurrence of aggressive interactions between males during sexual display is widespread in NMC-polygynous avian species and has been well documented, both in lekking species (e.g., black grouse, Koivisto 1965; greater prairie chickens, Ballard and Robel 1974; indigobirds, Payne 1973; golden-headed manakins,

Lill 1976; Guianian cocks-of-the-rock, Trail 1985; ruffs, Hogan-Warburg 1966) and, more recently, in exploded-arena species (satin bowerbirds, Borgia 1985; Borgia and Gore 1986). The commonness of male interactions at breeding sites suggests that aggressive components in courtship displays may have evolved in response to potential male interactions and are not related to female choice. Aggressive displays might be valuable in threatening individuals that might otherwise interrupt copulations; the recurrence of this problem may explain the convergence seen among NMC-polygynous species.

Such a model could be valid in the case of lekking species, in which competing males are close by; the courtship display may therefore be important for simultaneously threatening males and attracting females. However, this pattern is not expected to occur in species with exploded-arena mating systems, such as bowerbirds. In bowerbirds, male display sites are far apart, courtship calls are relatively quiet and directed at females, and courtship displays cannot be heard by males at adjacent but still distant bower sites (Borgia et al. 1985; Loffredo and Borgia 1986). In the case of satin bowerbirds, the only well-known species with an exploded-arena mating system, males not in control of a bower site occasionally attempt to interrupt copulations (Borgia 1985). However, because courtship displays are directed exclusively at females and because males chasing intruders use calls different from the courtship call, the convergence in displays among species with this type of mating system cannot be explained solely on the basis of male interactions. The apparent importance of female choice in shaping these displays suggests that a similar role may be important in the remaining NMC-polygynous species.

#### *Female Choice and Assessment Models*

The role of female choice in NMC-polygynous species may provide the best explanation for the widespread occurrence of male aggressive displays. It has been suggested that females may preferentially choose aggressive, dominant males as mates because these individuals, through their interactions with other males, may provide the best evidence of overall vigor and thus demonstrate their quality as sires (Alexander 1975; Cox and LeBoeuf 1977; Borgia 1979; Borgia et al. 1985). In these mating systems, similarities in the female use of dominance-related assessment cues may explain the widespread occurrence of aggressive male courtship displays. The noisy sounds common in these displays are often associated with aggressive behavior (Morton 1977, 1982, 1987). This relationship between behavioral context and sound structure suggests that a common functional basis for the observed convergence among NMC-polygynous-male acoustical displays may be the effect of female choice for dominant males who provide harsh, aggressive-sounding courtship displays. Detailed studies of the satin bowerbird (Loffredo and Borgia 1986) show that intraspecific differences in male courtship vocalizations can be used to judge male age and social status, supporting the view that variability in male courtship displays within NMC-polygynous species provides criteria for female mate choice.

Some sexual-selection models (Fisher 1930; Lande 1981; Kirkpatrick 1982;

Arnold 1983) predict that male sexual displays evolve through arbitrary patterns of female choice. This form of sexual selection would not be expected to produce clear patterns of male sexual display in NMC-polygynous species across different phylogenetic groups, since the specific male display characters likely to be preferred by females cannot be predicted from the models. In terms of acoustical displays, neither the types of sounds nor their intensities, being arbitrary, can be predicted. However, the pattern of male acoustical displays observed among the species we studied is clearly nonarbitrary and is convergent across phylogenetic groups. Thus, it appears that assessment models, such as the male-dominance model, may offer a more appropriate framework for predicting patterns of male display for species in which the intensity of sexual selection is likely to be high.

Our results suggest that selection acting on monogamous males for vocal abilities has probably been quite different from selection associated with polygynous mating systems. Several lines of evidence indicate that, in monogamous species, selection for male parental care and territorial defense may have promoted the evolution of discrete sounds. Specifically, the highly tonal sounds favored by monogamous males are effective as individual recognition cues between neighboring males in territories and between the male and female of a monogamous pair (Brooks and Falls 1975). Recent work on the evolution of sound structures suggests that highly tonal sounds are favored as effective long-distance signals in territorial competition (Wiley and Richards 1978, 1982; Morton 1987). Vocal duets and antiphonal songs, often associated with pairing and male-female cooperative behaviors, commonly involve tonal sounds and are known to occur only in monogamous species, even in such highly polygynous families as Cotingidae and Phasianidae (Thorpe 1972; Farabaugh 1982). Thus, selection for communication with a mate and for territorial defense may have strongly influenced the evolution of acoustical displays in monogamous species.

Some avian mating systems combine characteristics of monogamy and NMC polygyny. In several groups, such as pheasants (e.g., *Polyplecteron*) and ploceids (*Euplectes*, *Vidua*), individual males defend territories in which several families nest and feed, with limited participation of the male in brood care. Our results show that their display vocalizations are noisier than those of monogamous species, but not different from NMC-polygynous species. Following the model presented above, the vocalizations of resource-based polygynous groups might be predicted to resemble those of monogamous birds, since both kinds of males may be under selection pressure to defend resources important for raising offspring. However, since polygynous males also attempt to maximize the number of females attracted to their territories, there may also be strong selection for male competitive abilities through aggressive displays. This type of selection may be responsible for the similarity between the calls of males in resource-based and NMC-polygynous mating systems.

The parrots (Psittacidae) provide an interesting test for our model. Few recordings exist for the courtship displays of parrots, but available data suggest that the pattern of acoustical display is consistent with that of other families. The kakapo (*Strigops habroptilus*) is the only known parrot with a leklike mating system

(Merton et al. 1984), and its acoustical displays include very loud, harsh sounds, similar to those produced by many grouse (Phasianidae). In contrast, the courtship displays of monogamous parrot species (as opposed to parrot vocalizations in other contexts) generally involve soft, highly tonal whistles and chattering notes (Forshaw 1969; Cramp and Simmons 1983). Therefore, even among parrots, which are highly divergent from other avian groups, the one species with an NMC-polygynous mating system has diverged from its monogamous ancestors in a direction that parallels NMC-polygynous species in other orders.

The suggested relationship between mating systems and the kinds of sounds used by males in sexual displays appears to have a functional basis in the particular direction of selection for maximizing male fitness in each mating system. Thus, it appears that avian display sounds are far from arbitrary in their structure and function and, rather, are structurally and functionally convergent across phylogenetic groups.

#### SUMMARY

We tested the prediction that males of polygynous species with leklike mating systems exhibit convergent acoustical displays. Acoustical displays were compared among species in nine avian families having species with monogamous and polygynous mating systems. Polygynous species were more noisy, consistently used a broader range of sound frequencies, made many nonvocal sounds, and were less melodic than their monogamous counterparts. The sounds produced by polygynous males were similar to aggressive calls. These results confirm the prediction of an evolutionary convergence in courtship sound characters among species that have independently evolved polygyny. The hypothesis that male displays are not arbitrary but have important functions emerging with the evolution of polygyny is also supported. The similarity among male displays may be a result of the female use of courtship calls to assess the dominance of prospective mates.

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# APPENDIX

## FREQUENCY RANGES FOR THE SPECIES USED IN THIS STUDY

FAMILY/SPECIES	MATING SYSTEM†	FREQUENCY RANGE (Khz)*								AVERAGE RANGE OF ALL SOUNDS	
		Whistles	Musical Phrases	Trills	Simple Notes	Clicks	Harsh Slurs	Buzzes	Scratches		Booms
COTINGIDAE											
<i>Ampelion rubrocristatus</i>	M		2.09								2.09
<i>Ampelion sclateri</i>	M		1.17								1.17
<i>Ampelion stresemanni</i>	M					8.74		3.18			5.96
<i>Carpornis cucullatus</i>	EA		1.51								1.51
<i>Cotinga nattererii</i>	EA	1.47	3.13	2.21							2.97
<i>Lipaugus unirufus</i>	EA	1.52									1.52
<i>Lipaugus vociferans</i>	L		4.01								4.01
<i>Pachyramphus aglaiae</i>	M	1.63	2.19								1.91
<i>Pachyramphus castaneus</i>	M	0.48	1.56	0.80	0.77						0.90
<i>Pachyramphus polychopterus</i>	M		0.92								0.92
<i>Pachyramphus rufus</i>	M	1.06			0.63						0.84
<i>Perissocephalus tricolor</i>	L									1.18	1.18
<i>Phoenicircus carnifex</i>	L	1.01			0.56						0.78
<i>Procnias alba</i>	EA				0.51						0.51
<i>Procnias averano</i>	EA				5.25						5.25
<i>Procnias nudicollis</i>	EA				3.96						3.96
<i>Procnias tricarunculata</i>	EA								11.50		11.50

(continued)

APPENDIX (Continued)

FAMILY/SPECIES	MATING SYSTEM†	FREQUENCY RANGE (Khz)*										AVERAGE RANGE OF ALL SOUNDS
		Whistles	Musical Phrases	Trills	Simple Notes	Clicks	Harsh Slurs	Buzzes	Scratches	Booms	Nonvocal Sounds	
<i>Pyroderus scutatus</i>	L									2.78		2.78
<i>Querulea purpurata</i>	M	0.47							1.44			0.96
<i>Rupicola peruviana</i>	L					5.29			2.73			4.01
<i>Rupicola rupicola</i>	L				2.13				4.32			3.22
<i>Tijuca atra</i>	EA		0.15						3.87			0.15
<i>Tityra cayana</i>	M								7.52			3.87
<i>Tityra inquisitor</i>	M											7.52
<i>Tityra semifasciata</i>	M		2.09									2.09
PARADISAEIDAE												
<i>Astrapia mayeri</i>	L				1.67							1.67
<i>Astrapia stephaniae</i>	L				5.76							5.76
<i>Cicinnurus regius</i>	EA		0.41		0.52							0.46
<i>Diphyllodes magnificus</i>	EA	4.31							4.03			4.17
<i>Drepanornis albertisii</i>	EA	1.25										1.25
<i>Drepanornis bruijii</i>	EA	0.87			1.78							1.42
<i>Epinachus fastosus</i>	EA					2.87				4.65		3.76
<i>Epinachus mayeri</i>	EA				0.33			4.63	3.96			2.78
<i>Lophorina superba</i>	EA								3.38			3.38
<i>Loria loritae</i>	M	0.11										0.11
<i>Manucodia chalybatus</i>	M				1.73							1.73





APPENDIX (Continued)

FAMILY/SPECIES	MATING SYSTEM†	FREQUENCY RANGE (Khz)*										AVERAGE RANGE OF ALL SOUNDS
		Whistles	Musical Phrases	Trills	Simple Notes	Clicks	Harsh Slurs	Buzzes	Scratches	Booms	Nonvocal Sounds	
<i>Lophortyx californicus</i>	M	0.98			4.70							2.84
<i>Lyrurus tetrix</i>	L					9.02						9.02
<i>Odontophorus speciosus</i>	M	0.69		1.72	0.74							1.05
<i>Odontophorus stellatus</i>	M	0.39										0.39
<i>Pavo cristatus</i>	P								12.36		5.24	8.80
<i>Phasianus colchicus</i>	P								10.84			10.84
<i>Polyplecteron malacense</i>	P				1.46							1.46
<i>Tetrao urogallus</i>	EA								6.97		5.91	6.35
<i>Tympanuchus cupido</i>	L	0.42				1.36				7.19	0.54	3.38
PIPIDAE												
<i>Chiroxiphia lanceolata</i>	L		0.55		1.12							0.53
<i>Chiroxiphia linearis</i>	L					12.49			9.55			11.02
<i>Chiroxiphia pareola</i>	L	2.17			1.76			5.39				3.11
<i>Corapipo gutturalis</i>	EA	0.80									6.09	3.44
<i>Machaeropterus pyrocephalus</i>	EA			1.20	0.32							0.76
<i>Machaeropterus regulus</i>	EA		1.84									1.84
<i>Manacus auranitiacus</i>	EA										5.83	5.83
<i>Manacus candei</i>	EA						4.55	1.92			4.46	3.64
<i>Manacus manacus</i>	EA							8.14	9.67			8.90

<i>Manacus vitellinus</i>	EA				6.12	6.12
<i>Neopelma aurifrons</i>	EA	2.85				2.85
<i>Neopelma chrysocephalum</i>	EA			3.31		3.31
<i>Pipra coronata</i>	EA		2.49	1.94		2.22
<i>Pipra erythrocephala</i>	EA	3.63			5.82	3.72
<i>Pipra pipra</i>	EA				3.35	3.35
<i>Piprites chloris</i>	M			0.73		0.73
<i>Schiffornis major</i>	M	1.56				1.56
<i>Schiffornis turdinus</i>	M	0.91				0.91
<i>Schiffornis virescens</i>	M	1.14				1.14
<i>Tyrannneutes stolzmanni</i>	EA	2.35				2.35
<i>Tyrannneutes virescens</i>	EA	1.07				1.07
<i>Xenopipo atronitens</i>	L			0.97		0.97
PLOCEIDAE						
<i>Dinemellia dinemelli</i>	M	1.81				1.81
<i>Euplectes ardons</i>	P	2.05		4.81	5.61	4.16
<i>Euplectes axillaris</i>	P				4.24	4.24
<i>Euplectes capensis</i>	P			3.12		3.12
<i>Euplectes jacksoni</i>	L				12.68	12.68
<i>Malimbus cassinii</i>	M	2.12				2.12
<i>Malimbus rubricollis</i>	M	1.75	1.41			1.57
<i>Montifringilla nivalis</i>	M			1.17		1.17
<i>Passer domesticus</i>	M			2.55		2.55
<i>Passer griseus</i>	M			3.51		3.51
<i>Passer montanus</i>	M			2.24		2.24
<i>Passer rutilans</i>	M			2.54		2.54
<i>Petronia xanthocollis</i>	M			2.12		2.12

(continued)

APPENDIX (Continued)

FAMILY/SPECIES	MATING SYSTEM†	Whistles	Musical Phrases	Trills	Simple Notes	Clicks	Harsh Slurs	FREQUENCY RANGE (Khz)*				AVERAGE RANGE OF ALL SOUNDS
								Buzzes	Scratches	Booms	Nonvocal Sounds	
<i>Plocepasser donaldsoni</i>	M				3.72		6.99					5.36
<i>Plocepasser mahali</i>	M		4.27									4.27
<i>Ploceus bicolor</i>	M						6.12					6.12
<i>Ploceus nigricollis</i>	M											3.06
<i>Ploceus ocularis</i>	M			1.88	3.06							1.88
<i>Pseudonigrita arnaudi</i>	M		1.64									1.64
<i>Vidua chalybeata</i>	EA				5.77							5.77
<i>Vidua macroura</i>	EA			2.47	6.21							4.34
PSITTACIDAE												
<i>Alisterus scapularis</i>	M	0.49							3.43			0.49
<i>Cacatua galerita</i>	M											3.43
<i>Calyptrorhynchus magnificus</i>	M								5.11			5.11
<i>Platycercus elegans</i>	M								3.56			3.56
<i>Strigops habroptilus</i>	L								4.44	0.79		2.62
PTILONORHYNCHIDAE												
<i>Ailuroedus crassirostris</i>	M				4.34				4.68			4.61
<i>Ailuroedus melanotus</i>	M				1.21							1.21
<i>Amblyornis flavifrons</i>	EA	0.80			0.45	4.08			3.74			2.27
<i>Chlamydera cerviniventris</i>	EA								7.63			7.63

<i>Chlamydera</i> <i>nuchalis</i>	EA		5.32	1.45	1.25	5.15	3.29
<i>Prionodura</i> <i>newtoniana</i>	EA				4.07	5.54	4.80
<i>Ptilonorhynchus</i> <i>violaceus</i>	EA	0.30	0.56	4.55	7.07	7.77	4.05
<i>Scenopoeetes</i> <i>dentirostris</i>	EA	1.87	0.94	4.99	4.10	5.39	2.95
PYCNONOTIDAE							
<i>Andropadus</i> <i>latirostris</i>	L		4.99				4.99
<i>Criniger calurus</i>	M	1.32					1.32
<i>Criniger finschi</i>	M		1.36				1.36
<i>Hypsipetes</i> <i>amaurotis</i>	M	3.35					3.35
<i>Hypsipetes</i> <i>charlottae</i>	M	1.09					1.09
<i>Phyllastrephus</i> <i>fischeri</i>	M		2.82				2.82
<i>Phyllastrephus</i> <i>terrestris</i>	M		3.08				3.08
<i>Pycnonotus</i> <i>barbatus</i>	M		1.90				1.90
<i>Pycnonotus</i> <i>sinensis</i>	M	1.93					1.93
SCOLOPACIDAE							
<i>Arenaria</i> <i>interpres</i> †	M		1.30				1.30
<i>Calidris alpina</i> †	M	0.50	1.58				1.58
<i>Calidris canutus</i> †	M						0.50
<i>Calidris maritima</i> †	M		2.58				2.58
<i>Calidris minuta</i> †	M		1.75				1.75
<i>Calidris minutilla</i>	M		0.82				0.82
<i>Calidris</i> <i>temminckii</i> †	M		2.80				2.80
<i>Gallinago</i> <i>gallinago</i>	M		0.76				0.76
<i>Gallinago media</i>	L		1.50	4.25			2.88

(continued)

# APPENDIX (Continued)

FAMILY/SPECIES	MATING SYSTEM†	FREQUENCY RANGE (Khz)*										AVERAGE RANGE OF ALL SOUNDS
		Whistles	Musical Phrases	Trills	Simple Notes	Clicks	Harsh Slurs	Buzzes	Scratches	Booms	Nonvocal Sounds	
<i>Gallinago nemoricola</i>	M				2.63							2.63
<i>Gallinago stenura</i> ‡	M				3.47							3.47
<i>Limicola falcinellus</i> ‡	M							3.40				3.40
<i>Limosa lapponica</i> ‡	M		2.00									2.00
<i>Micropalama himantopus</i>	M	0.32			0.73	3.60		4.73				2.03
<i>Numenius arquata</i> ‡	M	0.76										0.76
<i>Numenius phaeopus</i>	M	0.92		1.07								1.00
<i>Phalaropus fulicarius</i> ‡	P				2.95							2.95
<i>Phalaropus lobatus</i> ‡	P		2.10	1.44		3.24		5.63				3.25
<i>Scolopax minor</i>	P											3.54
<i>Tringa erythropus</i> ‡	M	1.25			0.70							0.98
<i>Tringa flavipes</i>	M		1.20	1.07								1.14
<i>Tringa glareola</i> ‡	M		1.75									1.75
<i>Tringa nebularia</i> ‡	M		0.90			3.90			2.00			2.26
<i>Tringa ochropus</i> ‡	M		2.40									2.40
<i>Tringa totanus</i> ‡	M		0.90		1.72							1.45
<i>Xenus cinereus</i> ‡	M	1.44										1.44

\* Frequency range (Khz) = highest frequency minus lowest frequency. Values are means for each sound class.

† M, monogamous; P, resource-based polygyny; EA, exploded arena; L, lek.

‡ Scolopacid species for which acoustical measures were taken from Cramp and Simmons 1983.

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