

(ISBN: 0-943610-40-0)

SEXUAL SELECTION,
LEK AND ARENA BEHAVIOR,
AND SEXUAL SIZE DIMORPHISM
IN BIRDS

BY

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Museum of Zoology and Division of Biological Sciences
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ORNITHOLOGICAL MONOGRAPHS NO. 33

PUBLISHED BY

THE AMERICAN ORNITHOLOGISTS' UNION
WASHINGTON, D.C.

1984

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ORNITHOLOGICAL MONOGRAPHS

This series, published by the American Ornithologists' Union, has been established for major papers too long for inclusion in the Union's journal, *The Auk*. Publication has been made possible through the generosity of the late Mrs. Carll Tucker and the Marcia Brady Tucker Foundation, Inc.

Correspondence concerning manuscripts for publication in the series should be addressed to the Editor, Dr. Mercedes S. Foster, USFWS/NHB-378, National Museum of Natural History, Washington, D.C. 20560.

Copies of *Ornithological Monographs* may be ordered from the Assistant to the Treasurer of the AOU, Frank R. Moore, Department of Biology, University of Southern Mississippi, Southern Station Box 5018, Hattiesburg, Mississippi 39406. (See price list on back and inside back covers.)

Ornithological Monographs, No. 33, viii + 52 pp.

Editor of AOU Monographs, Mercedes S. Foster

Special Reviewers for this issue, Bruce Beehler, Division of Birds, National Museum of Natural History, Washington, D.C., and an anonymous referee

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First received, 3 December 1982; accepted, 25 March 1983; final revision completed, 30 July 1983

Issued March 15, 1984.

Price \$8.00 prepaid (\$6.50 to AOU members).

Library of Congress Catalogue Card Number 84-70355

Printed by the Allen Press, Inc., Lawrence, Kansas 66044

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ISBN: 0-943610-40-0

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INTRODUCTION

Charles Darwin (1871) introduced the concept of sexual selection with illustrations of birds that display in leks. He viewed sexual selection as a process of evolutionary change that is distinct from natural selection insofar as it explains the evolution of characters useful in attracting females for sex, rather than in simply surviving. As Darwin and others (Selander 1972; Williams 1975; Maynard Smith 1978; Andersson 1982a) have noted, sexual selection may work in two ways. The first is by means of direct social competition among males for positions in a mating area or a social unit, and the second involves active female choice of one male over another, independent of the competitive interactions among the males. The first is called intrasexual selection; the second is intersexual selection. Darwin drew attention to the elaborate male plumages and songs of birds as an effect of sexual selection, and wondered whether the sexual dimorphism of birds was the result of males fighting or of females perceiving "beauty" in the plumage of the males. The bright plumages of the male birds of paradise and the large size of male grouse may well be evolutionary results of sexual selection.

As Darwin's concept of sexual selection was developed from considering the lekking birds, it seems appropriate to examine the process and consequences of sexual selection by contrasting birds that lek with birds that have other mating systems. We can compare birds with lekking and arena behavior with birds with territorial-polygynous mating systems, and with monogamous birds. If sexual selection is prominent in lekking birds, then we should be able to evaluate the intensity of sexual selection in various birds and to find a more intense level of sexual selection in the birds that lek. We should also account for the mechanisms and consequences of behavior and morphology of the sexes by the sexual selection model.

Sexual selection theory can be tested by comparing the variance among individuals in mating and breeding success in species groups that have different mating systems. I test the following questions here. Are males in lekking and other arena species subject to more intense sexual selection than are males in monogamous species? Are males in lekking and polygynous species under more intense sexual selection than are females? Do males in the lekking and arena species compete among themselves by direct fighting, including both physical combat and aggressive displays, rather than by alternative mating strategies? Does male competition explain the success of males in attracting females? Are the evolutionary results of sexual selection in sexual size dimorphism more pronounced in lekking birds than in their nonlekking relatives? The prediction of sexual selection theory (in particular the concept of competitive interactions among males) in each case is "yes." This study is a test of these predictions of sexual selection.

LEKS AND ARENAS

The main features of social behavior in such well-studied lekking bird species as Black Grouse (*Tetrao tetrix*) (Kruijt et al. 1972) have led to a general definition of a lek. A lek is a mating system in which (1) several males display at arenas, (2) males provide no significant resources to the females, (3) females choose among the local males (they are not herded or mated by force by any one male), and (4) males take no part in parental care (Bradbury 1977, 1981). In typical lekking

birds, the males display in close proximity to each other on a traditional display ground where they compete for certain central positions and for females. Females visit the leks and mate with certain males, but form no long-term social bonds. The females alone rear the young away from the lek; male involvement in breeding ends with copulation.

The variety of male spacing patterns in birds that have no pair bonds and no paternal care appears to form a continuum (Oring 1982). In some species males displaying on arenas lack visual contact but may maintain auditory contact, as in the "exploded arenas" of some grouse, birds of paradise, bowerbirds, lyrebirds, and parasitic finches (Gilliard 1963, 1969; Lack 1968; Hjorth 1970; Payne and Payne 1977; Lill 1979; Cooper and Forshaw 1979). In some other species (notably in some manakins), two males rather than one display on each arena (D. W. Snow 1963, 1977; Sick 1967; Foster 1977; Schwartz and Snow 1978). In the Village Indigobird (*Vidua chalybeata*), a brood parasitic finch, males display on dispersed sites, and females visit and behaviorally sample or test all the males within an area of 5 to 10 km² (Payne and Payne 1977; Payne 1981). Although males are spaced on individual display sites or "call-sites," they maintain social contact through the visits of breeding females and neighboring males. The scale of spatial dispersion in lekking and arena birds thus ranges from tight clusters of males on individual display territories tightly grouped into leks, to males on individual arenas dispersed on a broader scale and tied together only by infrequent social interactions.

The terms "lek" and "arena" have been used in various ways. Gilliard (1963, 1969) described the social organization of birds of paradise and bowerbirds without using the term "lek." He recognized a continuum of spacing systems in displaying males. In some birds, males display only a few meters apart in direct visual, auditory, and social contact with each other, but in others the contact is only social. Gilliard (1963) used the term "arena" to refer to the collective sites used by a local population. While the spacing among birds on a common display ground may differ from that of birds on isolated display grounds, the social organization was viewed as a behavioral unit. On the other hand, Lack (1968) and D. W. Snow (1977) used the term "lek" to refer to the local group of displaying males, and the oxymoron "dispersed lek" to refer to the spacing of the males when their individual display sites are not close together. Gilliard's "exploded arena" refers to the total spatial organization of a population in which males that may interact over a breeding season each have a separate display ground. Here, I consider an "exploded arena" to be the same kind of collective as a "dispersed lek." An exploded arena differs from a social system in which males are territorial in that the areas between the display sites are not defended, and a female tends not to restrict her movements to the territory of a single male. Males generally defend the display sites or display territories against other males regardless of how close their nearest neighbors may be.

In the present work I use the term "lek" in a broad sense, corresponding to the arena and exploded arena of Gilliard, and I use the term "display site" to refer to the site of an individual male. Because "arena" has been used both as a collective (Gilliard 1963, 1969) and as a display site (e.g., Snow 1982), I qualify "arena" as an "exploded arena" or an "individual arena" in the text as needed. Arenas often

involve spatial grouping of individual display sites on communal or group leks, but need not do so.

INTENSITY OF SEXUAL SELECTION: PRIZES FOR THE WINNERS IN DIFFERENT MATING SYSTEMS

METHODS: ESTIMATING THE INTENSITY OF SEXUAL SELECTION

The intensity of sexual selection can be estimated from the variation in the breeding success among individual males in a population. The intensity of sexual selection is limited by the variation in individual mating or breeding success much as the rate of natural selection is limited by the variance in the overall success of individuals in Fisher's (1958) "fundamental theorem of natural selection." The degree to which individuals vary in success sets limits on how rapidly selection can occur, assuming that genetic differences are associated with differences in success. Thus, "intensity" refers to "limiting rate," the upper limit of which is set by the variance in success (Crow 1958; Fisher 1958; Wade and Arnold 1980).

Measures of variation that may be used are the ranges in number of offspring per individual (Neel and Chagnon 1968; Trivers 1972), the mean number of mates per male (Clutton-Brock and Harvey 1977; Alexander et al. 1979), the variance in number of matings or offspring (Bateman 1948; Payne and Payne 1977; Payne 1979a), the coefficient of variation, *c.v.*, in the number of matings or offspring (Payne and Payne 1977), the information statistic of evenness, *J*, of the number of matings or young (Payne and Payne 1977; Pielou 1977), and skewness, *G*, of the number of matings or young (Sokal and Rohlf 1969; Payne and Payne 1977).

Which indices of variation are best suited for comparison? Insofar as selection theory, as developed by Fisher (1958), is described in terms of variance, then mean-square variance (or a term incorporating variance) seems appropriate for comparing the intensity of selection in populations. Variance is the most easily tested statistic between sexes and among populations of the same species (Bateman 1948; Payne 1979a; *F*-test for homogeneity of variances) if the variances are adjusted for comparison of populations with different means. Coefficients of variation (*c.v.* = standard deviation/mean) of two populations incorporate variance (square root of variance being standard deviation, *s.d.*) and can be compared directly by *t*-tests using transformations of nonnormal distributions for statistical inference (Sokal and Braumann 1980). Large samples are required for statistical inferences about higher moment values such as skewness. The available population samples of individual breeding success in birds are too small for such comparisons. The properties of the evenness statistic *J* have not been explored in relation to population biology theory, although empirically, the values of *J* are closely correlated with those of *c.v.* (Payne and Payne 1977). Ranges and means of success are of little value for comparative studies when different populations and species have different means, and furthermore, the ranges and means do not indicate the statistical distribution of success within a population.

Wade and Arnold (1980) suggested use of an index of sexual selection, I_m , the ratio of the variance in the number of mates per male to the square of the mean number of mates. They also used an index I_s which is I_m times the square of the

sex ratio. Here I prefer I_m , insofar as the primary sex ratio is generally 1:1 in wild birds (Fiala 1981; Burley 1982). Although local sex ratios may differ from 1:1 in older cohorts, this is due to differential mortality and dispersal. Moreover, for a population-genetics model we should account for mating success at least from birth through the age of first breeding, and this is implicit in the present model where we assume a 1:1 primary sex ratio. The intensity of sexual selection may vary with age. I also here generalize Wade and Arnold's model (which was expressed in terms of number of mates) to the number of matings and the number of offspring of each male. Wade and Arnold based their model on an earlier population genetics index of the intensity of selection, "the ratio of the variance in progeny number to the square of the mean number" (Crow 1958). The index I_m is conceptually equivalent to and functionally is approximately the square of my earlier c.v. (Payne and Payne 1977).

Life history evolution theory predicts a compromise between male parental care of the young and sexual advertisement for additional females (Williams 1975; Maynard Smith 1978). In lekking birds and other arena birds, the male is not involved with the young after he mates, whereas in many polygynous and monogamous birds, the male provides parental care. Field observations indicate that paternal care is more common in monogamous birds than in polygynous birds (Verner and Willson 1969). By definition, sexual selection does not occur after the termination of paternal care. A male that provides parental care to his young may do so at the expense of attracting another female, so his parental behavior affects his sexual success. A male that does not care for his young, however, or that has completed his period of care for the breeding season, can be scored for success at the time when he has completed his contribution to the young. Young may die later, and this will affect a male's genetic contributions over generations, but this post-care mortality falls outside the domain of male care and beyond the domain of sexual selection. The intensity of sexual selection in males should be estimated at a comparable point in the breeding cycle in lekking birds, polygynous birds, and monogamous birds, at the termination of male parental care.

Other indices of sexual selection have been derived (Wade and Arnold 1980). It is possible, in principle, to separate as components of sexual selection male behavior, female choice, variance in quality among females, and the population sex ratio. In addition, with intensive field work, lifetime breeding success can be determined (Clutton-Brock et al. 1982). The lifetime success of individuals in leaving surviving offspring may vary with the condition of the adults after a breeding effort and with their long-term survival. This variance falls partly outside the domain of sexual selection theory. Also, adult survival within bird species appears to be independent of breeding effort (De Steven 1980; Högstedt 1981; Smith 1981). It should also be recalled that evolutionary rates are time functions, not generation functions. Offspring born in earlier years of an adult's life contribute more to selection rates than do offspring born later, because of compound interest. As the data for these additional components are usually not available from field studies of birds, and the survival and reproductive components of variance are largely independent both in theory and in the available field evidence, I use the simplest index, I_m .

In summary, the index of sexual selection, I_m , is adapted from a theoretical population genetics model. I use it to estimate potential rates of selection, assuming a heritable component of the difference in breeding success.

IS SEXUAL SELECTION IN MALES RELATED TO THE MATING SYSTEM?

To test whether the intensity of sexual selection in lekking birds is higher than in other birds, I compared the variation in breeding success among species with different mating systems. An earlier comparison showed that lekking birds were more variable in individual male success than were territorial polygynous species, and these varied more than species with exclusive monogamous pairs (Payne and Payne 1977). Data on mating or breeding success are now available for a few additional species and populations (Table 1).

I consider all species for which data on individual success in mating and breeding to the time of the termination of male parental care were available. Postfledging survival was not available. The sample is restricted to populations in which the mean male success was at least 1. All known individual males in the local population are included, whether or not they bred; in most species this involved all territorial males.

The unpublished data are from my field studies (Indigo Buntings, *Passerina cyanea*), or those (sometimes published in part) for which the observers made available their records (pers. comm.) of individual birds (Bank Swallows, *Riparia riparia*, Hoogland and Sherman 1976; Tree Swallows, *Tachycineta bicolor*, De Steven 1980; House Wrens, *Troglodytes aedon*, S. C. Kendeigh; Darwin's Cactus Finch, *Geospiza fortis*, and Darwin's Medium Ground Finch, *G. scandens*, T. D. Price, in press).

Breeding success in male promiscuous birds is highly variable. I_m was greater than 1.0 in all populations, and evenness J was low, ranging up to 0.70 (Table 2).

Males of 11 species of typical clumped or dispersed lekking birds all had I_m values greater than 1.0 (Table 2). In each case, success was determined from the copulations seen on the lek. Lekking birds for which individual breeding successes of the males on a lek have been recorded include four species of grouse of the Old and New World forests and prairies (Sage Grouse, *Centrocercus urophasianus*, Lumsden 1968; Wiley 1973; Prairie Chicken, *Tympanuchus cupido*, Robel 1966; Black Grouse, Koivisto 1965; Kruijt and Hogan 1967; De Vos 1983; and Capercaillie, *Tetrao urogallus*, Müller 1979), two northern calidrine waders (the arctic Buff-breasted Sandpiper, *Tryngites subruficollis*, S. G. Pruett-Jones, pers. comm.; and the Palearctic Ruff *Philomachus pugnax*, Selous 1906–07; Bancke and Meezenburg 1958), two manakins in the New World tropics (the White-bearded Manakin, *Manacus manacus*, Lill 1974a; and the Golden-headed Manakin, *Pipra erythrocephala*, Lill 1976), two birds of montane New Guinea (Lawes' Six-wired Bird of Paradise, *Parotia lawesii*, S. G. Pruett-Jones, pers. comm.; and Lesser Bird of Paradise, *Paradisaea minor*, Beehler, in press), and a brood parasitic African finch (Village Indigobird, Payne and Payne 1977). I_m varied more than twofold among some populations of the same species, so the range of values of I_m appears to be generally more appropriate for comparison than any particular value.

Breeding success has been determined for only one nonpairing bird with an exploded arena, the Village Indigobird. This species is a brood parasite that leaves its eggs in the care of a foster species. It lays more eggs than related finch species with a life style of parental care (Payne 1977). The variance and I_m of individual breeding success is like that in the communal lekking species, indicating that the

TABLE 1
FREQUENCY DISTRIBUTIONS OF THE SEASONAL BREEDING SUCCESS OF INDIVIDUAL MALES

Species	Male mating success and reproductive success*											Comments	Source	
	0	1	2	3	4	5	6	7	8	9	10			>10 ^b
A: Males display on arena, form no pair bond, and do not care for young (matings/male)														
<i>Centrocercus urophasianus</i>	14	5	2	1	1	0	0	1				2 (13, 15)		Lumsden 1968
<i>Centrocercus urophasianus</i>	21	2	0	3	0	2						2 (25, 41)		Wiley 1973
<i>Tetrao tetrix</i>	3	1	0	0	0	0	1					1 (17)	arena 1	Koivisto 1965
<i>Tetrao tetrix</i>	5	1	0	1	0	1	0	1	0	1		1 (15)	arena 2	Kruijt and Hogan 1967
<i>Tetrao tetrix</i>	5	4	1	2	1	1	1					1 (15)	1975	Kruijt and Hogan 1967
<i>Tetrao tetrix</i>	5	0	0	0	0	1	2	0	0	1		1 (22)		De Vos 1983
<i>Tetrao urogallus</i>	3	0	1	0	0	0	0	1				1 (21)		Müller 1979
<i>Tympanuchus cupido</i>	6	0	1	0	0	0	1					1 (21)		Robel 1966
<i>Tryngites subruficollis</i>	14	2	3	1	1	0	0	1				1 (19)		S. G. Pruett-Jones et al., pers comm.
<i>Philomachus pugnax</i>	16	0	1	0	1	1	0	1	0	0	1	1 (19)		Selous 1906-1907
<i>Philomachus pugnax</i>	6	1	2	1								5 (11, 13, 14, 17, 19)		Bancke and Meeseburg 1958
<i>Manacus manacus</i>	9	0	0	1	0	0	0	1				1 (18)		Lill 1974a
<i>Pipra erythrocephala</i>	3	1	2	2								5 (12, 14, 14, 14, 22)	lek 2	Lill 1976
<i>Pipra erythrocephala</i>	6	1	2	1	0	0	1	0	1	0	1	3 (13, 15, 18)	lek 4	Lill 1976
<i>Parotia lawesii</i>	7	4	1	1	1	0	0	0	0	1				S. G. Pruett-Jones, pers. comm.
<i>Paradisaea minor</i>	6	1										1 (25)		B. Beehler, pers. comm.
<i>Vidua chalybeata</i>	5	3	1	0	0	0	0	1				1 (19)	junction	Payne and Payne 1977
<i>Vidua chalybeata</i>	10	2	1	0	0	0	0	0	0	0	1		cowpie	Payne and Payne 1977
B: Polygynous, males sometimes care for young (fledglings/male)														
<i>Agelaius phoeniceus</i>	49	0	1	3	5	1	0	2					1975	Payne 1979a; Wade and Arnold 1980
<i>Agelaius phoeniceus</i>	64	0	1	2	1	3	1	3				2 (11, 11)	1977	Payne 1979a; Wade and Arnold 1980
<i>Cistothorus palustris</i>	6	2	1	2	6	4	2	2						Verner 1965

TABLE 1
CONTINUED

Species	Male mating success and reproductive success*										Comments	Source				
	0	1	2	3	4	5	6	7	8	9			10	>10 ^b		
<i>Spiza americana</i>	10	2	1	7	13	4	2	0	3	0	3	0	3	8 (11, 11, 11, 12, 14, 19, 21, 22)	area D	J. L. Zimmerman 1966, 1982, pers. comm.
	C: Monogamous, males and females care for young (fledglings/male)															
<i>Lagopus lagopus</i>	1	4	8	7	11	13	10	11	5	3	1				lowland	Jenkins et al. 1963
<i>Lagopus lagopus</i>	6	3	5	5	6	13	8	11	8	4	3				highland	Jenkins et al. 1963
<i>Empidonax virescens</i>	2	1	4	9	2	4	2	0	1							Walkinshaw 1966
<i>Riparia riparia</i>	3	1	1	6	6	14	1									Hoogland and Sherman 1976; P. W. Sherman, pers. comm.
<i>Troglodytes aedon</i>	21	1	3	14	15	27	22	9	4	1	5		8 (11, 11, 11, 11, 12, 13, 13, 14)	outfield	S. C. Kendeigh, pers. comm.	
<i>Troglodytes aedon</i>	4	0	1	0	1	4	2							hillcrest	S. C. Kendeigh, pers. comm.	
<i>Tachycineta bicolor</i>	0	2	0	3	15	21	21	2								D. DeSteven 1980, pers. comm.
<i>Protonotaria citrea</i>	1	0	0	3	1	4	0	2								Walkinshaw 1953
<i>Passerina cyanea</i>	18	0	7	16	4	0	2	2							1980	R. B. Payne, pers. obs.
<i>Passerina cyanea</i>	17	4	6	18	7	3	2								1981	R. B. Payne, pers. obs.
<i>Spizella pusilla</i>	8	2	4	11	9	8	5	6	0	3	0	1 (11)				Walkinshaw 1978
<i>Melospiza melodia</i>	1	0	2	3	4	1	1	2	0	0	1					Nice 1937
<i>Geospiza fortis</i>	65	4	7	28	27	7	4	0							1981	Price, in press
<i>Geospiza scandens</i>	43	5	11	24	12	2	0	1							1981	Price, in press

* Entries are the number of individuals observed to have the number of matings or fledglings indicated. Reproductive success is scored as the number of matings observed in the lekking birds (A), and as the number of young that leave the nest in birds with some paternal care (B and C), reflecting the data available. Additional details of each population are summarized in "Comments," Table 2.

^b Numbers in parentheses indicate the number of matings or fledglings for each male that had more than 10.

TABLE 2
 VARIATION IN BREEDING SUCCESS OF MALES^a

Species	N males	Mating success		I_m^c	J^d	Comments ^e
		Mean	Variance ^b			
A. Males display on arena, form no pair bond, and do not care for young						
<i>Centrocercus urophasianus</i>	26	1.96	14.65	3.81	.61	4
<i>Centrocercus urophasianus</i>	30	2.90	73.54	8.74	.33	4
<i>Tetrao tetrix</i>	6	4.00	45.97	2.87	.40	4
<i>Tetrao tetrix</i>	10	2.50	11.35	1.82	.62	4
<i>Tetrao tetrix</i>	15	2.33	14.59	2.69	.53	4
<i>Tetrao tetrix</i>	9	2.89	11.43	1.37	.62	4
<i>Tetrao urogallus</i>	5	4.80	74.56	3.24	.09	4, 5
<i>Tympanuchus cupido</i>	9	3.33	49.25	6.72	.35	4
<i>Tryngites subruficollis</i>	22	1.00	3.00	3.00	.60	6, 7
<i>Philomachus pugnax</i>	22	2.14	21.36	4.66	.51	4
<i>Philomachus pugnax</i>	15	5.47	47.01	1.57	.70	4
<i>Manacus manacus</i>	12	2.33	28.79	5.30	.35	4
<i>Pipra erythrocephala</i>	13	6.69	50.83	1.14	.41	4
<i>Pipra erythrocephala</i>	16	5.25	39.56	1.44	.44	4
<i>Parotia lawesii</i>	15	1.47	5.45	2.52	.64	4
<i>Paradisaea minor</i>	8	3.25	67.69	6.41	.08	4
<i>Vidua chalybeata</i>	11	2.82	29.97	3.77	.48	4
<i>Vidua chalybeata</i>	14	1.00	7.08	7.08	.34	4
B. Polygynous, males sometimes care for young						
<i>Agelaius phoeniceus</i>	61	.82	3.22	4.79	.47	8, 9
<i>Agelaius phoeniceus</i>	77	.99	6.09	6.21	.56	8, 9
<i>Cistothorus palustris</i>	25	3.76	11.27	.80	.87	8, 13
<i>Spiza americana</i>	53	1.58	4.70	2.44	.76	8
C. Monogamous, males and females care for young						
<i>Lagopus lagopus</i>	74	4.92	5.02	.21	.96	14
<i>Lagopus lagopus</i>	72	5.17	7.36	.28	.97	15
<i>Empidonax virescens</i>	25	3.36	3.49	.31	.88	6
<i>Riparia riparia</i>	32	3.78	2.61	.18	.95	10
<i>Troglodytes aedon</i>	130	4.82	9.86	.42	.95	8, 11
<i>Troglodytes aedon</i>	12	3.16	6.52	.65	.82	8, 12
<i>Tachycineta bicolor</i>	64	4.94	1.39	.06	.99	8
<i>Protonotaria citrea</i>	11	4.27	3.63	.20	.94	8
<i>Passerina cyanea</i>	49	2.12	3.78	.79	.70	8, 16
<i>Passerina cyanea</i>	57	2.19	3.07	.64	.90	8, 17
<i>Spizella pusilla</i>	57	4.02	6.89	.43	.93	8
<i>Melospiza melodia</i>	15	4.27	6.07	.33	.93	8
<i>Geospiza fortis</i>	142	1.89	3.59	1.04	.87	8
<i>Geospiza scandens</i>	98	1.67	2.89	1.04	.78	8

^a Statistics are based on the data in Table 1.

^b Variance values for promiscuous birds in group A, Table 20, of Payne and Payne (1977) had misplaced decimals. Values were recalculated for the present study.

^c I_m is an index of sexual selection for males (m). $I_m = \text{variance}/\text{mean}^2$.

^d $J = H'/H_{\text{max}}$, where $H' = \sum -p_i \ln p_i$ and H' is the sample diversity, p_i is the proportion of total matings or breeding success by an individual with i success, $\ln p_i$ is the natural logarithm of p_i , and s is the number of individual males. H_{max} is the maximum diversity possible in the population if all individuals had equal success ($H_{\text{max}} = \ln s$). J is an index of evenness (Payne and Payne 1977; Pielou 1977).

^e Numbers indicate the following, 4: success = number of matings observed; 5: small, declining population observed for 15 years; 6: success = number of individual females mated per day; 7: estimate based on maximum number of males and minimum number of females; 8: number of young fledged/season/male; 9: data include all adults and local first-year males. For data on adults only see Payne (1979a) and Wade and Arnold (1980); 10: success = survival of young to day 10, colony no. 16; 11: Hillcrest population; 12: Outfield population; 13: Seattle populations only, two years; 14: Lowlands—1960, size of fledged broods; 15: Highlands—1960, size of fledged broods; 16: George Reserve—1980, only those birds present for 10+ days that mated with at least one female and only if fledging success was determined for all nests; 17: George Reserve—1981, criteria as in 16.

biological consequences of variance in mating success and the degree of sexual selection are similar in an exploded arena bird and in birds with group lek displays. Buff-breasted Sandpipers have an intermediate spacing pattern with large individual display grounds in a loose lek (Myers 1979). The spacing of male Lawes' Six-wired Birds of Paradise in New Guinea varies, with some in leks and others on isolated, outlying individual display arenas (S. G. Pruett-Jones, pers. comm.).

Seasonal breeding success has been determined for several northern temperate region birds that are usually monogamous. Populations in which females were individually marked and the number of fledglings for each bird was determined for a season were included. The estimated intensities of sexual selection in monogamous species were lower than those for nonmonogamous birds. I_m for most monogamous birds was less than 1.0, and J was 0.70 or more in all populations. The difference in the estimated intensity of sexual selection in males is clear, as there was barely any overlap between lekking birds and monogamous birds in either index (Table 2).

The intensities of sexual selection in polygynous birds in which females nest on the territories and use the resources of their mates are intermediate. Red-winged Blackbirds (*Agelaius phoeniceus*), in which most breeding males have more than one female, are highly variable. First-year birds comprised more than half the color-banded males. Most were seen only once, and none remained and established territories. First-year males occasionally drop in flight over a marsh and may copulate by taking nonsoliciting females by surprise (Payne 1979a). The apparent male bias in sex ratio may reflect the greater mobility of these young males through the breeding population. I_m is also greater than 1.0 in the Dickcissel (*Spiza americana*), in which a high proportion of males are polygynous (Zimmerman 1966, 1982). Indigo Buntings are usually monogamous, but about 15 percent of all mated males have an additional female in the same season, sometimes simultaneously with the first (Payne 1982a). Variance in breeding success of these males is intermediate between the more promiscuous icterids and the more monogamous flycatchers, warblers, and emberizid sparrows.

Breeding success varies among male Darwin's finches, *Geospiza fortis* and *G. scandens*, because of variation in the adult sex ratio. Males survive better than females in years of drought. By 1978, for example, 85 percent of the birds banded by Boag and Grant (1981) in 1976 had died, and males were several times more numerous than females. Success in females, all of whom were mated, was much less variable (cf. Tables 3, 4). The results indicate intense sexual selection in a monogamous population with a highly uneven sex ratio (Price, in press).

The data show that males in lekking and arena species are more variable in mating success than are monogamous birds and are more variable than birds with low levels of polygyny (10 to 20 percent of breeding males with two or more females). The variation shows greatly different success among local males, so the lekking birds and other arena birds, as predicted, are subject to more intense sexual selection.

COMPARISON OF SEXUAL SELECTION IN THE TWO SEXES

Sexual selection theory predicts that males are generally under more intense sexual selection than females. Comparisons of the observed variance in male and female breeding success, however, are few (Trivers 1972; Payne and Payne 1977;

TABLE 3
 FREQUENCY DISTRIBUTIONS OF THE SEASONAL BREEDING SUCCESS OF INDIVIDUAL FEMALES

Species	Female reproductive success											Comments ^b	Reference	
	Number of young fledged/female													
	0	1	2	3	4	5	6	7	8	9	10	>10 ^a		
<i>Vidua chalybeata</i>	2	1	7	3	5	1	1							Payne 1977
<i>Troglodytes aedon</i>	19	1	3	14	14	33	23	12	2	3	3	5	(11, 11, 11, 12, 13)	12 S. C. Kendcigh, pers. comm.
<i>Cisticorhor palustris</i>	5	2	0	3	8	3	0	2	2	1				13 Verner 1965
<i>Agelaius phoeniceus</i>	14	0	2	6	7									1975 Payne 1979a; Wade and Arnold 1980
<i>Agelaius phoeniceus</i>	13	3	7	9	8									1977 Payne 1979a; Wade and Arnold 1980
<i>Passerina cyanea</i>	29	2	14	20	5	0	2	1						16 R. B. Payne, pers. obs.
<i>Passerina cyanea</i>	32	8	10	19	6	2	1							17 R. B. Payne, pers. obs.
<i>Geospiza fortis</i>	2	3	5	20	24	8	6							1981 Price, in press
<i>Geospiza scandens</i>	1	4	10	26	14	2	1							1981 Price, in press

^a Numbers in parentheses indicate the number of fledglings for each female fledging more than 10 young.

^b Numbered comments refer to those listed in footnote e, Table 2. Others indicate year studied.

TABLE 4
 VARIATION IN BREEDING SUCCESS OF FEMALES^a

Species	N	Mean	Variance	I_f^b	J^c
<i>Vidua chalybeata</i>	20	2.75	2.40	.31 +	.62 +
<i>Troglodytes aedon</i>	132	4.72	7.73 -	.42 -	.95 =
<i>Cistothorus palustris</i>	26	3.73	7.08 +	1.90 -	.90 +
<i>Agelaius phoeniceus</i>	29	1.72	3.14 +	1.06 +	.80 +
<i>Agelaius phoeniceus</i>	40	1.90	2.45 +	.67 +	.88 +
<i>Passerina cyanea</i>	73	1.77	2.93 +	.94 -	.71 -
<i>Passerina cyanea</i>	78	1.60	2.61 +	1.02 +	.86 +
<i>Geospiza fortis</i>	68	1.67	1.80 +	.14 +	.98 +
<i>Geospiza scandens</i>	58	3.00	1.17 +	.13 +	.97 +

^a + indicates males more variable than females, - indicates males less variable than females, = indicates no difference, and a blank indicates no basis for comparison (different sample populations and techniques). Data on mating success in males listed in Table 2. Mating success of females is the observed number of fledglings, except for *V. chalybeata* for which it is numbers of eggs ovulated/10 days.

^b I_f is an index of sexual selection for females (f). $I_f = \text{variance}/\text{mean}^2$.

^c As in footnote d, Table 2.

Payne 1979a). More data are needed, especially for arena birds and polygynous birds.

Males are significantly more variable in breeding success (number of young reared to fledging) than are females in the Red-winged Blackbird (Payne 1979a). Some males have several females and several broods in a breeding season. Other males (nearly all the first-year males and half of the local adults) have none. Females generally leave either no young or fledge a complete brood. In the population I studied, predators and inclement weather were more frequent causes of mortality than was starvation. Most males are unsuccessful, whereas a few males leave many young. Payoff stakes are high for the males. In contrast the payoff is low and more nearly equal for the females, who provide nearly all the parental care.

Information available on variation in the breeding success of female birds is summarized in Tables 3 and 4. The number of young reared to independence has not been determined in any lek birds, and the only data available for variation in females in an exploded arena bird are for a parasitic finch. The index of sexual selection in females, I_f , is the ratio of the variance in the number of offspring per individual female to the square of the mean individual success (Wade and Arnold 1980). Data (Table 4) for the usually monogamous species show a lower intensity of selection in females (I_f) than in males (I_m). In some, the difference is statistically significant. In the exceptions, females sometimes switch mates within a season, and the birds practice both polygyny and polyandry (Verner 1965; Payne 1983a, b; S. C. Kendeigh, pers. comm.).

The difference between the sexes in the variance of breeding success supports the hypothesis that sexual selection is greater in males than in females. This difference in the sexes in the variance of breeding success has apparently led to the evolution of bright male plumages, costly displays, elaborate songs, and other behaviors in males who actively compete for breeding females (Fisher 1958; Maynard Smith 1978; Payne 1979b, 1983a).

Darwin supposed that sexual selection would be more intense in the nonmonog-

amous birds, and the estimated I_m values are indeed greater in these birds. There may be an advantage to males in attracting the early-breeding females even in monogamous birds (Darwin 1871; Fisher 1958), and sexual selection may account for the bright plumages in some of these as well. The monogamous species with the lowest I_m and the highest J in breeding success are hole-nesting, single-brooded, monomorphic songbirds. The next lowest variation in breeding success is in passerines that are sometimes double- or triple-brooded. In nonmonogamous birds, variance in breeding success is associated with the number of mates and matings, with some males having several mates and others having no mates.

MALE COMPETITION AND FEMALE CHOICE OF MATES: MODES OF SEXUAL SELECTION AND ALTERNATIVE MATING STRATEGIES OF MALES

Is sexual selection brought about directly by females choosing as mates the males with the elaborate characters, or by the competitive success of males? In the second case, females may cue on those characters, such as apparent size, voice, and vigor, that the males themselves use in their aggressive displays. If so, it would be difficult to determine whether female choice is independent of male competition. Darwin's concept of female choice implies a perceptual behavior by females that is to some extent independent of the interactions among males. He stated (Darwin 1871:735) that "beauty is sometimes more important than success in battle." Females may prefer males with elaborate plumages or large size, and this preference, itself, may lead to a runaway process of sexual selection (Fisher 1958). The process requires genetic variance or heritability both in male characters and in female preference (Maynard Smith 1978; Lande 1980). The genetic process of sexual selection may also involve males that are aggressive or not according to local social conditions, or males that have fixed alternative mating behaviors as a frequency-dependent genetic alternative mating strategy within a population (Krebs and Davies 1981).

How would females evolve such a preference in the first place? Perhaps females first evolve a sensitivity to the differences among competing males and respond more to males with the larger apparent size or more brilliant patches of feathers that the males themselves use as aggressive signals. Although at first these cues may guide the females to the competitively successful males, the females may retain the bias even when the characters no longer are valid cues to competitive competence, as after genetic fixation. "Beauty" in the form of bright colors in plumage or on bare skin might advertise a male's health, and so might be useful to females in assessing genetic quality (Hamilton and Zuk 1982). Genetic drift and correlated genetic responses in the two sexes may also be involved in the origins of female choice (Lande 1980; Kirkpatrick 1982). Explaining the origin and the maintenance of male characters that attract females is difficult, particularly where the characters used by females in choosing mates are not of direct survival benefit.

METHODS

In the remainder of this paper I discuss sexual size dimorphism as it is related to male competition in birds with different mating systems. In this section I

attempt to determine whether or not the mating success of males in lekking birds is related to their competitive abilities in fighting and aggressive display, and whether alternative nonaggressive mating strategies are important. Published descriptions of breeding behavior are not standardized for birds in general. However, a survey of the behavior of the lekking and arena birds should establish whether the males generally are aggressive in the context and form of display in mating. To test whether male mating "strategies" (Krebs and Davies 1981) involve fighting and ritualized combat or alternative behavior patterns, I reviewed published descriptions of the behavior of breeding males in lekking and arena birds.

COMPETITIVE MALES

In some lekking and other promiscuous arena birds, females may choose the males that are the most successful in intermale competitive aggression. In certain species the males give aggressive-like displays to females, displays similar to the ones they give to their competitive male neighbors. The females may then use the displays of aggressiveness to assess the quality of males as mates. Aggressive male courtship displays have been remarked upon in several groups of arena birds. Many grouse approach the female with body crouched, wings exposed, and a rapid run. This behavior resembles the actions directed toward other males on their display territories (Hjorth 1970). The displays of lekking Ruff and Great Snipe (*Gallinago media*) are directed mainly towards other males, not females. The same apparently aggressive postures may be used toward a female when she arrives at a lek (Hogan-Warburg 1966; Lemnell 1978). Anna's Hummingbirds (*Calypte anna*) begin their courtship of females with an aggressive display dive like that given to intruding males (Stiles 1982). Male Satin Bowerbirds (*Ptilonorhynchus violaceus*) give a fluff-hunch posture toward visiting females, much as they do toward visiting rival males (Vellenga 1970; Rowley 1974). Indigobirds fly toward and hover over a female with the same behavior sequence used in driving away an intruding male (Payne and Payne 1977).

Aggressive behaviors are commonly ritualized into the courtship displays of both polygynists and pair-forming monogamists as well as into those of lekking birds. I predict from sexual selection theory that courtship displays should be more aggressive in those species with the most intense sexual selection, to the extent that females choose mates by their aggressive, competitive performance. Females of some lekking birds and arena birds, then, may mate with the male that has been the most successful in conflict with other males. Male social dominance appears to come first, with females mating with the winners. Social dominance among males and its relationship to mating success are suspected, but not well known, in several groups, including the grouse, Ruff, several manakins, cotingids, birds of paradise, and parasitic finches (Hogan-Warburg 1966; Wiley 1973; Foster 1977, 1981; Payne and Payne 1977; D. W. Snow 1977, 1982; LeCroy 1981). Courtship displays in certain other lekking birds do not appear to be aggressive (for example, the "maypole" slide of some manakins, Snow 1963, 1976; Lill 1974a, b). As males in better physical condition may be more successful in competition, the males may be displaying their condition to assessing females. We need to determine the degree to which the early courtship displays of male birds in species with different kinds of mating systems are aggressive.

ALTERNATIVE MATING STRATEGIES

In arena species, are males that are not aggressive or that do not display nevertheless successful in mating? Alternative mating strategies within a species are well known in certain insects (Blum and Blum 1979; Thornhill 1979) and fish (Loiselle and Barlow 1978; Dominey 1980; Gross 1982), but are only uncommonly mentioned in birds (Krebs and Davies 1981).

Lekking Ruffs are the only birds known to have apparently genetically-determined differences in sexual behavior. Certain males are not aggressive like the displaying males in the lek, and they court females away from a lekking ground, visit several lek arenas, and remain around the edge of a lek as "satellites" (Hogan-Warburg 1966; van Rhijn 1973). These satellite males and the aggressive males have similar plumages, except that most satellites have a whitish neck ruff and head tufts. They sometimes mate with females visiting the lekking grounds. The fact that they are different in plumage suggests that their behavior also may represent a genetic morph. Adult males can develop female-like plumage in captivity (Stonor 1937), but are not known to do so under field conditions.

The occurrence of non-displaying males near active leks suggests alternative mating styles in a few other species. Male grouse (Black Grouse; Sharp-tailed Grouse, *Tympanuchus phasianellus*) sometimes attract a female and copulate away from a lek (Hjorth 1970; Kruijt et al. 1972; Sexton 1979). In *Paradisaea* birds of paradise, males in "immature" or "female-like" plumage display like the plumed males and on occasion mate with females visiting a lek (Wallace 1869; LeCroy et al. 1980). Female-like male riflebirds (*Ptiloris victoriae*) sometimes display to a female near an adult male on an arena (Schodde 1979). Female-like plumages are known in some other birds of paradise (Gilliard 1969) and in a few other lekking birds such as manakins (Snow 1963; Sick 1967) and the arena bellbirds, *Procnias* (D. W. Snow 1973a). Female- or immature-plumaged male manakins sometimes display in leks, sometimes away, and may or may not have large testes (Sick 1967; D. W. Snow 1977). Young male Satin Bowerbirds are in female-like plumage for the first few years of life. They visit the arenas, where they are attacked by the older resident male, probably because they are a sexual threat (Vellenga 1970, 1980b).

The plumages of these subadult males lack the bright colors of the lekking males, and so lack the signals that elicit attack by the resident males (e.g., Rohwer et al. 1980). The aggressive behavior of adult Satin Bowerbirds toward their younger visitors at the arena, however, casts doubt on the predictiveness of this female mimicry hypothesis insofar as young males lack the plumage colors of the resident adults, yet are vigorously attacked. The scarcity to date of observations of mating by males in subadult plumage suggests that the alternative strategies are not important, in general, and that the elaborate bright colors and large sizes of male lek birds are often an evolutionary result of social competition.

Forced copulations are known for several waterfowl (McKinney and Stolen 1982), but unsolicited copulations are uncommon, generally, in birds and have rarely been seen in lekking birds (Payne 1980). Another male behavior is interference with a displaying resident male at his site (Foster 1981, 1983). These spoilers may mate with the female after a disturbance, but more often the behavior may just harass the local resident. Interactions between intruders and residents

are aggressive and may be important in the spacing of males at leks (Foster 1981, 1983).

How do females choose one male over another? Critical questions include whether females use heritable male traits and whether individual strategies of female choice may have equal adaptive value. To date, studies of mate choice have not shown that the variance in mating success among males is in large part explained by size, position in the lek, aggressive behavior, or individual differences in display. Bradbury and Gibson (1983:134) comment that "no one has yet identified the critical cues used by females in making choices within a given lek." Further field observations and experiments are needed to test hypotheses about mate choice in lekking and pair-forming birds.

SEXUAL DIMORPHISM AND SEXUAL SELECTION

Sexual selection may explain the differences in the form and behavior of males and females. Darwin (1871) suggested that the bright colors and ornaments of birds were mainly the results of sexual selection rather than natural selection. Of the birds illustrated (Darwin 1871, Vol. 2:42–202), six were lekking or arena birds, and two others (hummingbirds), probably so, two were polygynous pheasants, and one was a polyandrous painted snipe. Of the feathers illustrated, two were from lekking birds, two were from monogamous snipe, and seven were from polygynous birds (mainly of one pheasant thought to lek; Davison 1981b). Although lekking birds figured prominently in Darwin's account of sexual selection, he developed his argument in large part independently of the mating systems. At the time, the mating systems were known for few species of birds. Several birds with "leks" in Darwin's account were believed to be polygamists, but "leks" also were described for monogamous birds with regular display sites (Darwin 1871, Vol. 2:101). Darwin (1871, Vol. 1:270) suggested "... that with birds there often exists a close relation between polygamy and the development of strongly-marked sexual differences." It can hardly be a coincidence that some of the most prominent sexual differences in structure occur in birds with lekking and arena mating systems.

Because the intensity of sexual selection, as estimated from the variance in breeding success, is higher in lekking species than in other birds, it seems likely that sexual selection may have led to a greater elaboration of male size and color in lekking birds. If sexual selection is more intense in birds with no male parental care and no pair bond, then these birds may have a greater degree of sexual dimorphism. The direction and intensity of sexual dimorphism may indicate the form of sexual selection. If sexual selection is effected largely through combative competition among males, the males should be relatively larger in the polygynous and lekking species. This prediction associates size with success in male-male combat. Large size often may be associated with success in battle. Because the potential gain in breeding success is so much higher in promiscuous species than in monogamous species, fighting and large size of males would be expected to figure prominently in the promiscuous and polygynous species. The resulting benefits of combat in mating are not so highly different among males in a monogamous species. Thus, males should be larger in body size, relative to females, in the nonmonogamous species.

Many instances have been noted of sexual dimorphism in plumage color (Gil-

liard 1963, 1969; Verner and Willson 1969) and body size (Selander 1972; Pitelka et al. 1974; Wiley 1974) in relation to the mating system. Moreover, there appears to be a diversity of patterns of covariance in size and color of the sexes in different avian families. If sexual selection is effected largely through female choice, then no particular reason exists to expect males to be larger than females. Females might choose smaller males for agility, or brighter males for "beauty," rather than larger males for success in combat.

Of course, costs or risks may attend males using an aggressive mating strategy. However, little direct evidence exists of predation or disease being greater in more colorful birds (Baker and Parker 1979; Hamilton and Zuk 1982). In contrast, there is considerable direct observational evidence of social competition and combat among birds in territorial and, especially, in some lekking species (Hjorth 1970; Jones 1981). Larger individuals are more successful in establishing social dominance in some species (Baker and Fox 1978a; Birkhead 1981; Petrie 1983), but not in others (Searcy 1979b, c; Price, in press). No lek or other arena birds are known in which the larger males are more successful in social competition or in mating success. Male body size was correlated with the number of mates in a sylviid warbler (Bibby 1982) and in a polygynous icterid (Yasukawa 1981). Size was not correlated with mating success in other populations of the same icterid (Searcy 1979a; R. B. Payne, pers. obs.), in two lekking manakins (Lill 1974a, 1976), in a parasitic finch with an exploded arena (Payne and Payne 1977), or in a usually monogamous finch (Payne 1982a). In the sometimes polyandrous Moorhen (*Gallinula chloropus*), a species in which females are more aggressive than males, large females mated with males in better energetic (body fat) condition and initiated more nesting attempts in a season (Petrie 1983). Females may choose large males in a population of *Geospiza scandens* (Price, in press). Differential survival in relation to size has been found in some birds (Johnston 1967; Johnston et al. 1972; Baker and Fox 1978a, b; Johnson et al. 1980; Boag and Grant 1981; Grant and Price 1981; Johnston and Fleischer 1981; Price, in press), though not in others (Searcy 1979a, b, d, e). Furthermore, body size is known to be heritable within some species (Boag and Grant 1978; Smith and Dhondt 1980; Grant and Price 1981; Van Noordwijk et al. 1980), so size is subject to genetic selection.

These few observations of size-related differences in male success and the heritability of size are generally consistent with the hypothesis that large body size in males has evolved under competitive sexual selection. The existing variability among closely related species in size and sexual dimorphism in relation to mating system allows a more direct test of the hypothesis that sexual dimorphism is an evolutionary response to sexual selection.

METHODS

Sexual selection theory predicts that the variance in reproductive success (and so the intensity of sexual selection) should be a prominent factor determining the sex-specific differences in behavior and morphology. Because lekking species are under more intense sexual selection than species with polygynous or monogamous pair bonds, the theory predicts that males and females should be most different in the lekking taxa. Other sources of differences between the sexes can also be compared to determine whether the mating system is the principal factor asso-

ciated with sex differences in general. To eliminate phylogenetic factors, or at least to limit their effect, I restrict comparisons to those within a family, or to related families in cases where mating systems do not vary within a family. To take into account food and habitat as primary influences on sexual dimorphism, I discuss briefly the ecology of the birds. Although quantitative details are not available in many instances to test how ecological factors may influence sexual dimorphism, the comparisons allow us to see whether these elements loom larger than the intensity of sexual selection in determining the degree of sexual dimorphism in birds. We lack data to derive intensities of sexual selection in most species for which the mating system is known, so I generalize the results given earlier to assume that lekking birds tend to be under greater sexual selection than nonlekking birds as a whole. Finally, although sexual size dimorphism is the most readily quantified result of sexual selection on behavior and morphology, I also mention any trends that are apparent for other morphological features (such as plumage color) and behavior, including song, to be associated with the mating system and so with the intensity of sexual selection.

I compared sexual dimorphism in body size for all families of birds in which lekking or arena behavior is known in at least one species. Measurements (means, or midranges where means were not available) were taken from published descriptions and unpublished data. Wing length is considered an overall indicator of size, at least among species within the same family and so of similar proportions. Size is more readily compared than color, and wing length data are more readily available than body weight for comparisons among species. Wing length is correlated with body weight among related species (e.g., Sigurjónsdóttir 1981; Snow 1982). The results are shown graphically with female size plotted as an independent variable (Figs. 1–12). Females are perhaps closer to an ecologically optimal size for exploiting their niches than are males, who may shift their food niches when they are larger than their females. Although female size may vary in response to sexual selection for male size, due simply to similar effects of genes on males and females (Maynard Smith 1978; Lande 1980), female size is the standard to use in judging sexual dimorphism. By Darwin's reasoning, among the polygynous and arena birds, males are the more selected sex in sexual selection, and it is in their difference from females that the effects of sexual selection are seen.

The results are graphed to illustrate the relationships between sexual size dimorphism, body size, and mating systems. Statistical descriptions and inferences are used sparingly because of small sample sizes (most families do not have large numbers of species with lekking, exploded arena, and monogamous mating systems) and because both body size and mating systems are associated with certain genera within a family. Closely related species in most cases are similar in size, mating system, and sexual size dimorphism. Moreover the shapes of birds differ somewhat among certain genera. As an example, short-winged birds in which the males are modified for short-range flight display tend to appear less sexually dimorphic with wing length than with body weight as a size criterion. From a phylogenetic viewpoint, congeneric species are not independent samples for testing association of dimorphism with mating systems. Characters may be shared due to common descent rather than to independent evolution of adaptations for the mating system (Clutton-Brock and Harvey 1977).

COMPARISON OF SEXUAL SIZE DIMORPHISM AND MATING SYSTEMS

Tetraonidae.—Ptarmigan (*Lagopus* spp.) form pairs and are dispersed on territories, some woodland grouse (*Bonasa*) display on solitary, dispersed sites, and others—mainly grouse species of open country—display in leks (de Vos 1979). Behavior has been described by Hjorth (1970), de Vos (1979), and others, and sexual dimorphism by Wiley (1974). In the monogamous species, breeding females feed and nest on male territories and use male vigilance for detection of predators, whereas breeding females of promiscuous species do not (Wittenberger 1978).

The largest grouse (Sage Grouse; Capercaillie; Black-billed Capercaillie, *Tetrao parvirostris*) are the most dimorphic (Fig. 1) and display on leks (Wiley 1973; Andreev 1979; Cramp 1980; Jones 1981). In lekking species, sexual dimorphism increases with female body size. Wiley (1974:211) pointed out, using body weight, that “the promiscuous species are larger as well as more dimorphic.” He attributed the large size in males to a presumed long time required for growth to maturity (although males reach adult body size in their first year, Moss 1980), and suggested that sexual differences in maturation rates might in part explain the promiscuous mating systems in these birds. A more direct view is that the longer time to maturity is an effect of sexual selection (Wittenberger 1978). Both sexual size dimorphism and female body size are greater in lekking grouse species than in nonlekking and monogamous grouse species—a pattern in other families as well.

Little difference in sexual dimorphism is evident between the pair-forming Hazel Grouse (*Bonasa bonasia*) and the congeneric Ruffed Grouse (*B. umbella*). Female Hazel Grouse have a small activity range before laying and may form pairs. Ruffed Grouse females visit several males in succession before mating and rear their young alone, away from the males’ drumming sites (Hjorth 1970; Boag 1976; Cramp 1980; Oring 1982). Spruce Grouse (*Dendragapus canadensis*) may have either a monogamous or an exploded arena system insofar as females may visit and compare the solitary males at their display sites, yet not use their areas as resource territories. Females spend most of their time away from the display territories of the males. The dispersion of these woodland grouse may vary, and their activity clustering may be due as much to common habitat selection as to social attraction (Oring 1982). The social interactions among males and between the sexes are not yet known in sufficient detail to ascertain whether the woodland grouse of North America have exploded arenas.

The extreme in size dimorphism in grouse is the Capercaillie in which the average male weighs more than twice what the average female weighs (Wiley 1974). Large size appears to be costly to the males. Males must grow twice as fast as females to reach normal size by the end of their first summer, and the sex ratio of chicks favors females, especially in small broods (i.e., when food may be most scarce; Wegge 1980). The sex ratio of older birds also is biased against males (Moss 1980). The advantage of large size in males in the breeding season apparently is realized in competition among males. Males fight over display territories and females (Moss 1980; Jones 1981). The observations that females mate mainly with the male that defeats neighboring males in combat and accompany him off his lek territory even when another male temporarily fills in his place, suggest that hens prefer the best fighters. If size confers an advantage in fighting, then intrasexual selection among males may have favored big cocks (Moss 1980). This

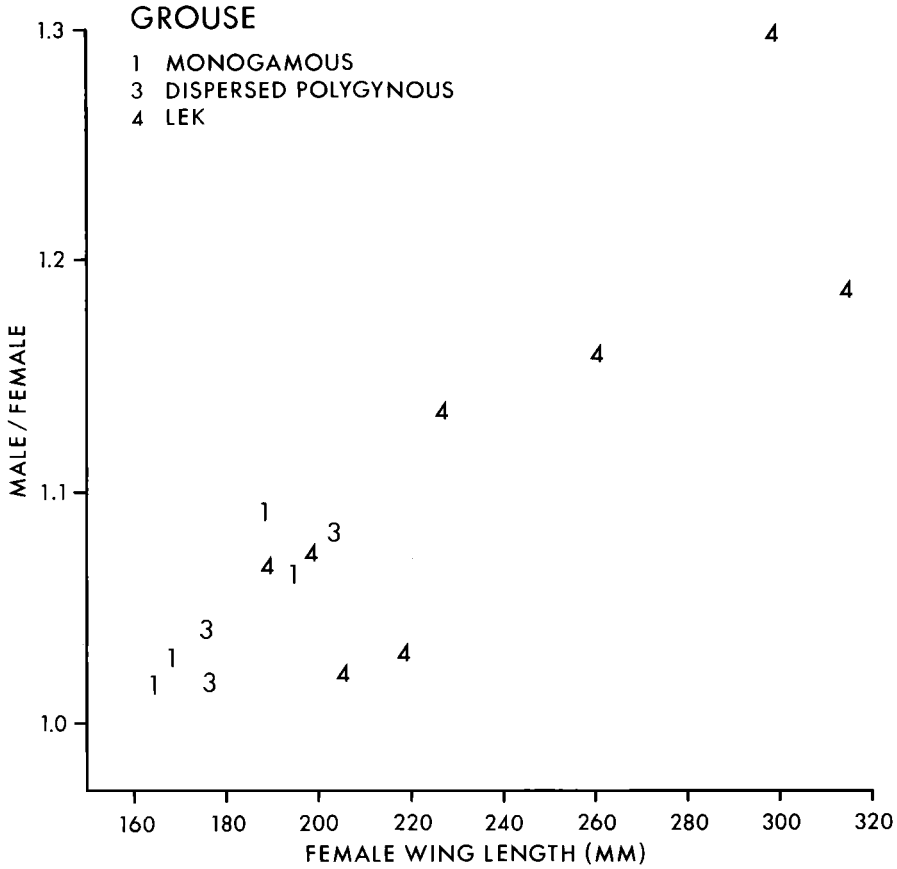


FIG. 1. Sexual size dimorphism in grouse (Tetraonidae) in relation to female size and to the mating system. Note the greater sexual dimorphism in size and the greater female body size in the lekking species, and the least dimorphism in the monogamous species. (Measurements taken from Ridgway and Friedmann 1946; Cramp 1980; and for *Tetrao parvirostris* only, from Cheng et al. 1978.)

observation is the best evidence in any bird of sexual selection operating in opposition to natural selection.

Phasianidae.—Among the Phasianidae, a lek mating system has been suggested for the Great Argus Pheasant, *Argusianus argus*, which has been a model for comparison of leks in some other birds (Gilliard 1963; Merton 1975). It is uncertain, however, whether these birds in fact have exploded arenas. Males are large and wait in ambush for large invertebrate food items (Davison 1981a). Females move about. Whether they visit and compare different males, as in other exploded arena birds, or nest on a male's territory, has not been determined. Nor is it known whether different males have highly differing mating successes (Davison 1981b).

Comparison of sexual size dimorphism among phasianids with and without paternal care indicates that those without paternal care are more dimorphic than

those with paternal care (Sigurjónsdóttir 1981). As paternal care is associated with monogamy, in general, the comparison is probably of mating systems. The promiscuous and polygynous species, therefore, apparently are more dimorphic than the monogamous species. Sexual size dimorphism is also positively associated with color dimorphism of the sexes (Sigurjónsdóttir 1981).

Aggressive behavior in males is well known in the phasianids. Darwin (1871, Vol. 2:44–46) noted the greater development of spurs on the legs of males, and the fighting behavior and resulting scars of battle and death of the combatants.

Otididae.—Bustards are large, omnivorous, open country ground-birds of the Old World. The social organization and mating systems of most species are poorly known. Lekking behavior is well known in Great Bustard (*Otis tarda*; Gewalt 1954; Cramp 1980). The large Kori Bustard (*O. kori*) is apparently monogamous (Jackson 1938a; Hanby 1982; R. Liversidge, pers. comm.). Most bustards are thought to be monogamous, but some have harems (Great Indian Bustard, *Choriotis nigricaps*), and others (Lesser Florican, *Sypheotides indica*) are promiscuous (Ali and Ripley 1969). Paternal care is found in Houbara (*Chlamydotis undulata*) in which the male remains with the female and brood (Cramp 1980).

Bustards are sexually dimorphic in size, with males larger than females in all but two species (Fig. 2). In the smallest, the Lesser Florican, and in Bengal Florican (*Eupodotis bengalensis*), males are smaller than females. Both species are promiscuous and display on dispersed arenas, and the males provide no parental care (Ali and Ripley 1969).

Lesser Florican males display on arenas, usually within sight and sound of other males. Males jump into the air, call loudly, and parachute back onto the ground (Dharmakumarsinhji 1950). The aerial displays of these bustards are not unlike those of some larger African species (Black Korhaan, *Eupodotis afra*; Black-bellied Korhaan, *E. melanogaster*), that form pairs during the nesting season (McLachlan and Liversidge 1978). Among these three species, which are sexually dimorphic in plumage, the small arena-displaying *S. indica* has reversed size dimorphism, the intermediate-sized *E. afra* is monomorphic, and in the larger *E. melanogaster* the males are larger than the females. It is not known whether size or mating system accounts for the reversed size dimorphism in *S. indica*; either could do so. However, the reversed sexual dimorphism of a larger promiscuous arena species, the Bengal Florican, suggests that the evolution of size dimorphism is a result of the mating system.

The larger species of bustards are more dimorphic than the smaller ones (Fig. 2). The two most size-dimorphic species are the harem-polygynous Great Indian Bustard (Dharmakumarsinhji 1962; Ali and Ripley 1969) and the lekking Great Bustard. The association of size dimorphism and body size in monogamous bustards suggests that sexual size dimorphism is explained by size as well as by the mating system.

Scolopacidae.—The calidrine sandpipers exhibit a wide array of mating systems and modes of parental care. Most are monogamous with both parents caring for the precocial young, some are serially or synchronously polygynous, and three species have leks with no male parental care. Pitelka et al. (1974) and Myers (1981a, b) reviewed mating systems and sexual dimorphism in these sandpipers, and the present data are taken from their reviews.

The best-known lekking sandpiper is the Ruff. Males gather in leks on individual

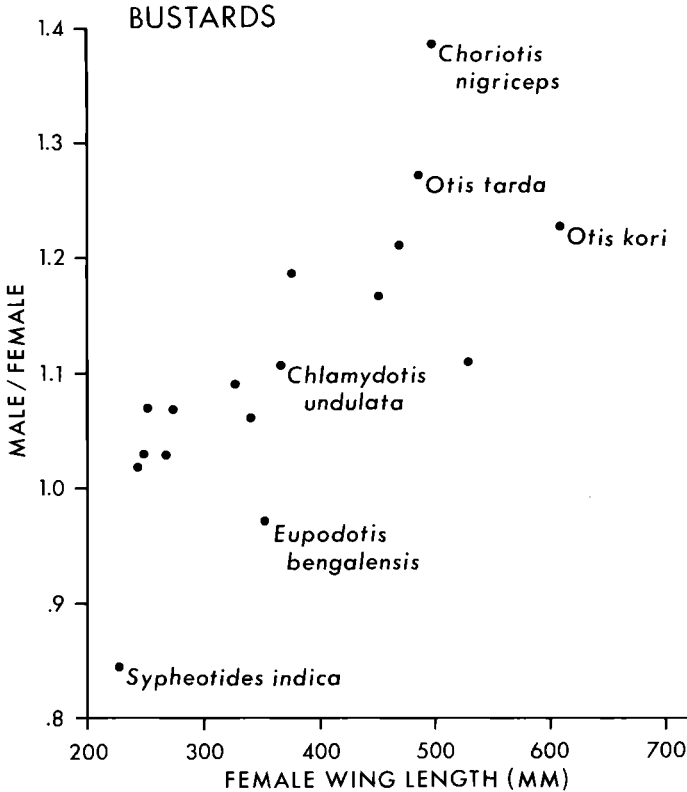


FIG. 2. Sexual size dimorphism in bustards (Otididae) in relation to female size. *Otis tarda* leks, *Choriotis nigriceps* is polygynous with "harems" of 3–5 females; *Sypheotides indica* and *Eupodotis bengalensis* are apparently promiscuous, dispersed arena displayers with no pair bond; *Chlamydotis undulata* is monogamous with male parental care. The others as far as is known are monogamous. (Measurements taken from Baker 1921; Bannerman 1931; Ali and Ripley 1969; McLachlan and Liverside 1978; Cramp 1980.)

arenas that are several meters apart and display aggressively toward each other. Females visit the lek grounds and mate usually with a centrally-located male. Males are visually individualistic in the size and markings of the neck ruff and head tufts. The satellite males do not interact aggressively with the lekking males, but lekking males are aggressive towards them. The only males to get large numbers of matings are the central, aggressive males in the lek (Hogan-Warburg 1966; van Rhijn 1973, pers. comm.). Pectoral Sandpipers (*Calidris melanotos*) display in leks of varying density (Pitelka 1959). Buff-breasted Sandpipers also display and mate in leks, with males more dispersed than in the Ruff (Myers 1979).

Sexual dimorphism is greater in the three lekking species than in the other calidridines, and greater in polygynous than in monogamous species (Fig. 3). Polygynous mating systems are known for Temminck's Stint (*Calidris temminckii*), Little Stint (*C. minuta*), Sanderling (*C. alba*), White-rumped Sandpiper (*C. fusicollis*), Curlew Sandpiper (*C. ferruginea*), and Sharp-tailed Sandpiper (*C. acuminata*) (Pitelka et al. 1974; Flint and Tomkovich 1982). Among lekking species,

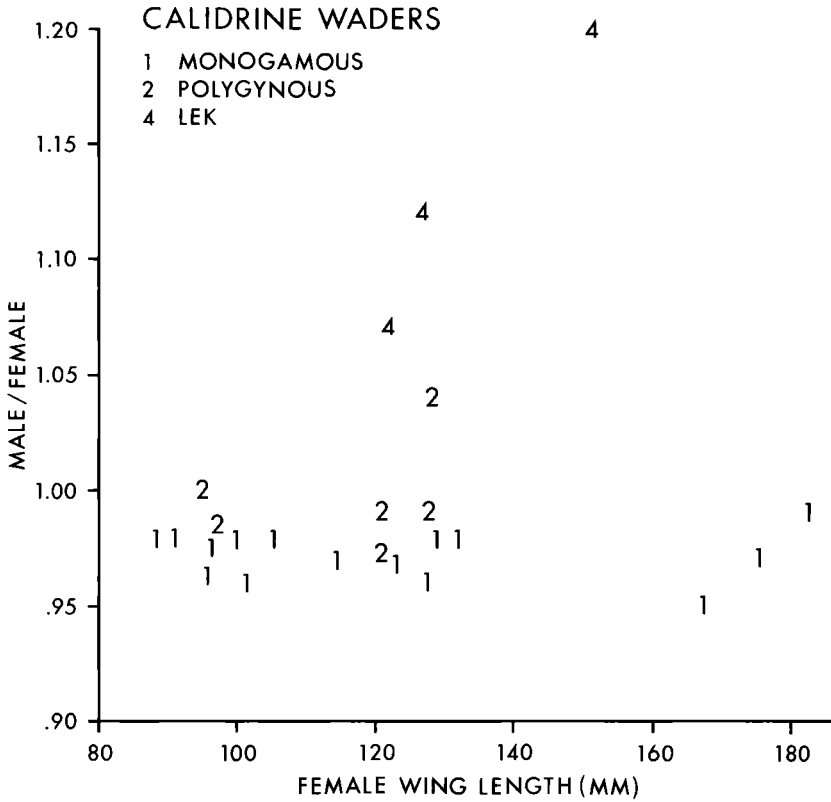


FIG. 3. Sexual size dimorphism in calidrine sandpipers (Scolopacidae) in relation to female size and to the mating system. (Measurements and mating systems taken from Pitelka et al. 1974; Myers 1981a.)

the larger species are the more dimorphic. Sexual plumage dimorphism is pronounced only in the Ruff. Body size is known to be associated with mating success in two monogamous species, Least Sandpiper (*Calidris minutilla*) and Stilt Sandpiper (*C. himantopus*). In each, the males average smaller in size than the females. Among new pairs, large females, small males, and pairs with the greatest sexual size dimorphism tend to nest earliest (Jehl 1970). The observations suggest that sexual size dimorphism has evolved directly by way of sexual selection in these species. In nonmonogamous sandpipers as well as monogamous species in which only one sex cares for the young, the nonparental sex migrates earlier than the parent giving care to the young, and these species also migrate farther. Migration and wintering distances both are associated with sexual dimorphism in size (Myers 1981a). Adult males and females migrate to the same wintering latitude (Myers 1981b). Among the interrelated variables in this complex, the most consistent association of sexual dimorphism appears to be with mating system (Myers 1981a).

Lekking behavior is also known in snipe and woodcock. Great Snipe (*Gallinago media*) display in leks, and in contrast to most snipe, their displays are primarily terrestrial. Displays are directed mainly to other males. The only aerial component

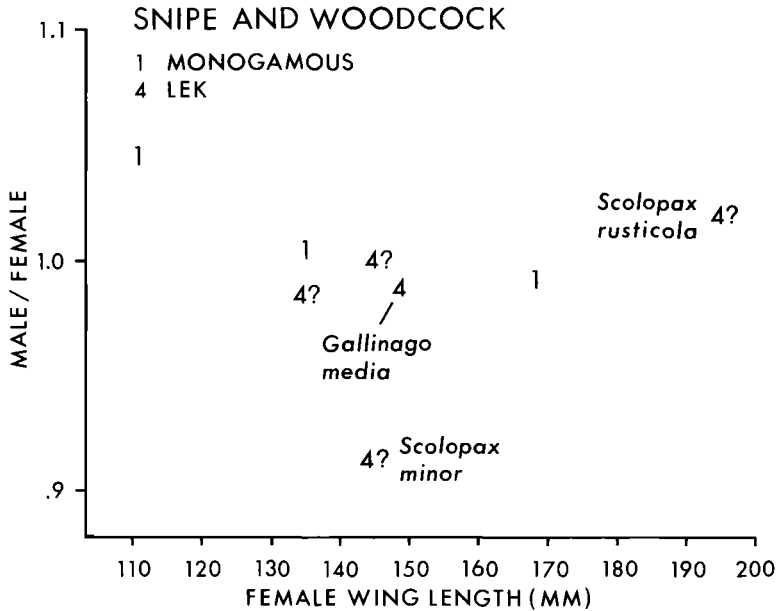


FIG. 4. Sexual size dimorphism in woodcock and snipe (Scolopacidae) in relation to female size and mating system. (Measurements taken from Prater et al. 1977.)

of the display is a midnight flight over the lekking grounds (Tuck 1972; Lemnell 1978; Avery and Sherwood 1982). Painted Snipe (*G. stenura*) and perhaps Forest Snipe (*G. megala*) display in mass mating flights or "toks," which may be aerial leks (Tuck 1972; Sutton 1981). In contrast to typical lekking species, *G. media* and *G. stenura* may have male parental care (Tuck 1972). Other Holarctic snipe are thought to be monogamous, and they have elaborate aerial displays (Tuck 1972).

The mating systems of woodcock are not well understood. Both North American (*Scolopax minor*) and European (*S. rusticola*) Woodcock have aerial displays that attract females. In both, the display areas of individual males overlap considerably (Pitelka 1943; Hiron 1980). Males remain with the females only until the eggs are laid, then resume display. The aggregations of displaying male woodcock resemble leks.

Lekking snipe are no more dimorphic in size than nonlekking species (Fig. 4). Lekking *G. media* is not necessarily larger than its related monogamous congeners. In the woodcock, males are smaller than females in body weight, wing length, and bill length in *S. minor*, but males are longer-winged and shorter-billed than females in *S. rusticola* (Prater et al. 1977). Although males of the snipe species produce sound in flight with the outer tail feathers, these feathers are similar in structure in the two sexes (Tuck 1972; Rutschke 1976). Females of at least one species sometimes produce the bleating flight sounds, themselves (Tuck 1972:52). In the woodcock the outer primaries are narrow and attenuated in *S. minor* in both sexes, but are normal in both sexes in *S. rusticola*.

Plumage color is similar in the sexes in snipe and in woodcock. The lack of

sexual dichromatism may be related to the crepuscular and nocturnal display schedules, as suggested for *G. media* by Lemnell (1978); the scolopacids generally are monomorphic in plumage anyway.

Psittacidae.—The Kakapo (*Strigops habroptilus*) of New Zealand is a flightless nocturnal parrot that displays on a traditional, communal lek. Display grounds were known to the native Maoris and recently have been rediscovered by biologists. Males shape depressions in grass and place twigs and lichens in the bowl (Best 1980). Birds make paths from one display bowl to another, and to and from the mating grounds. Males display within a few meters of each other and mate with any parrot-size object that approaches (Merton 1975, 1977). The sexes are similar in plumage; males are only one percent larger than females (Forshaw 1978). Lek behavior is not associated with sexual size dimorphism in the parrots.

Trochilidae.—With a few exceptions, hummingbirds do not form pair bonds. Males sometimes defend a territory on which they feed. These feeding territories are often independent of mating and may be defended in or out of the breeding season. Most hummingbirds depend upon flowers for nectar. The spacing and flowering time of their food plants are diverse. Because of these two factors, a great diversity in social organization exists among hummingbird species, and sometimes within a single species. Males of some species hold small territories associated with a patch of flowers, whereas others that feed on highly dispersed flowering plants may hold no territory but may visit distant flowers on a daily route or "trapline." Males of certain species are territorial only while flowers are moderately abundant. When the local abundance of flowers increases to a point at which the birds would gain nothing from excluding other nectar feeders, or when it drops to a point at which the birds use more energy in excluding others than they gain in unexploited nectar sources, they abandon territoriality (Stiles 1973, 1980, 1981; Stiles and Wolf 1979).

The mating systems of hummingbirds vary. In about half of the tropical species whose mating systems have been observed, males at least occasionally display in leks (Stiles and Wolf 1979; F. G. Stiles, pers. comm.). In contrast, the North American hummingbirds do not commonly form communal leks. Polygynous or promiscuous mating is the general rule in hummingbirds; only a few species have male parental care (Wolf and Wolf 1971; Stiles and Wolf 1979).

Because some hummingbirds may congregate in response to local habitat factors such as food, but others regularly form mating aggregations or leks, it is difficult to define their spacing patterns. Copulation is infrequently seen in hummingbirds, and sightings are few even in the best-studied species (Stiles and Wolf 1979). Birds that feed on clumped territories do not necessarily breed there, and some species move locally according to rains and the phenology of flowers (Stiles 1980).

Lekking behavior varies among local populations and seasons. Males in some populations of *Phaethornis ruber* lek and in others are solitary (Nicholson 1931; B. K. Snow 1973b). Individual male *Calypte anna* may switch from defending individual food-centered territories to displaying on temporary leks and commuting to undefended food sources, according to the food supply at the time (Stiles 1973).

Lekking is apparently both an evolutionary response and an immediate behavioral response of hummingbirds to the local abundance of nectar and flowers,

particularly of epiphytes and herbs that occur in small clumps. The distribution of the food source does not explain the evolution of lekking in nectar-feeding birds in general, however. The sunbirds (Nectariniidae) of the Old World are ecological counterparts of the hummingbirds, but all are pair-forming, and none mates on leks (Skead 1967; Wolf and Wolf 1976).

More field work is necessary to test the conditions of behavioral adaptability of hummingbirds. Enough field studies have been done, however, to allow comparison, in a tentative way, of the sexual dimorphism in size in food-territorial hummingbirds and lekking hummingbirds.

Some hermit hummingbirds (Phaethorninae) display and mate in singing assemblies or leks; males sing in a bush, and females visit to mate (Snow 1968; Wiley 1971; B. K. Snow 1973a, b, 1974, 1977; Stiles and Wolf 1979). Males are larger than females in the larger species, most of which lek. Size of the lekking birds ranges from very small (*P. ruber*, mean wing length in males 34.8 mm) to rather large (for hummingbirds; *Eutoxeres aquila*, mean wing length 73.0 mm; Wetmore 1972a; E. R. Blake, pers. comm.). Size is not closely associated with dispersion, and species that are not known to lek or that lek only sometimes are intermediate in size. Species with pronounced sexual dimorphism in size include the lekking *Klais guimeti* and *Topaza pella*. Males of the smallest species are smaller than their females (Fig. 5). The most size-dimorphic hermit, *Glaucis hirsuta*, however, is territorial, does not lek, and males actively defend the nest against other hermits (B. K. Snow 1973a).

Males of the smallest territorial hummingbirds in North America are smaller than their females, and juveniles are larger than adults. In *Archilochus colubris*, *A. alexandri*, *Selasphorus rufus*, and *S. sasin*, wing length decreases more with age in males than in females (Leberman 1972; Stiles 1972; Kodric-Brown and Brown 1978; Ewald and Rohwer 1980; Baldrige 1983). Adult males acquire their shorter wings shortly before the breeding season. The decrease in wing length with age in males suggests that the small size in males is sexually selected.

It has been suggested that the trend for males to be smaller than females in the smaller hummingbirds is due to metabolic constraints on body size in the females. If the females were any smaller, they might not be able to meet the costs of egg formation (Lasiewski and Lasiewski 1967; Wolf et al. 1976). The most extreme reversed sexual dimorphism in size occurs in the small western North American *Archilochus alexandri*, *Selasphorus sasin*, *S. rufus*, and *Stellula calliope*. Individual males in these birds display apart from each other and defend territories, which may be dispersed arenas insofar as no pair bonds are formed. In these and certain other species, the males produce whistles with their wings in flight. Males may be structurally modified for sound production (Miller and Inouye 1983). Small size, a seasonal habitat, a lack of permanent display assemblies, and aerial displays are interrelated, and no evidence exists that size dimorphism is mainly an adaptation for any particular mating system in these hummingbirds.

Hummingbird species that defend food territories tend to have higher wing-loading than species that trapline their flower resources (Feinsinger and Chaplin 1975). *S. rufus* males defend richer food territories in autumn than do females, who have lower wing-loading (Kodric-Brown and Brown 1978). The aerodynamic and energetic requirements for diving displays and maintenance of interference-

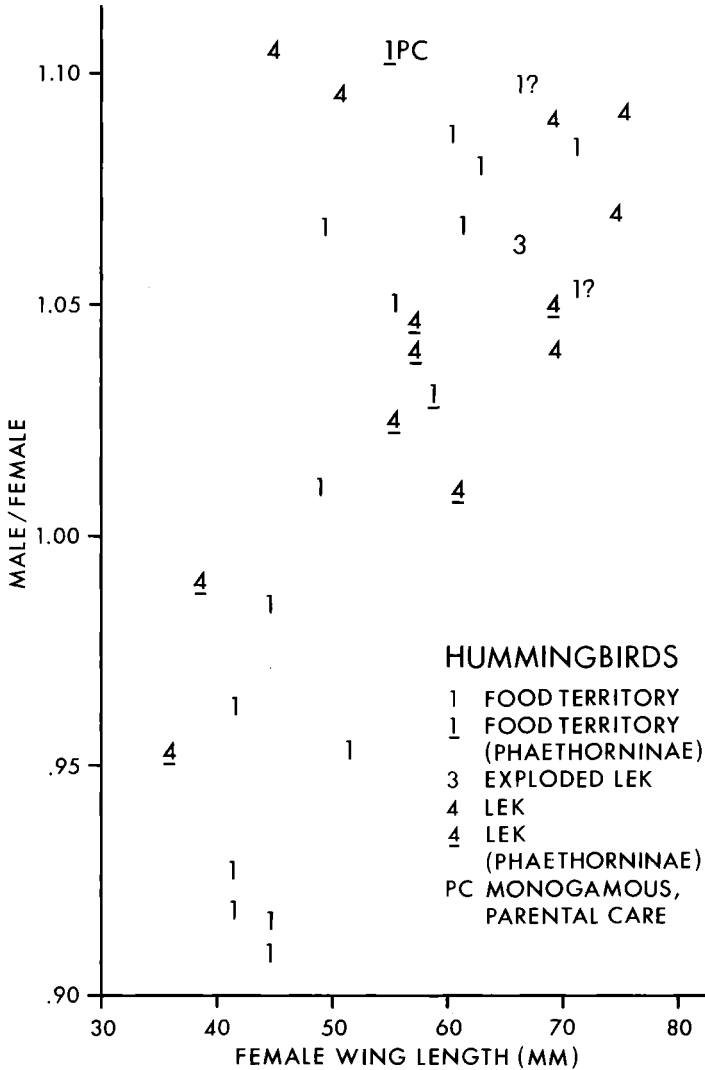


FIG. 5. Sexual size dimorphism in hummingbirds (Trochilidae) in relation to female size and mating system. (Measurements taken from Ridgway 1911; Wetmore 1972a; Wolf et al. 1972, 1976; B. K. Snow 1973a; Stiles 1973; Carpenter 1976; Kodric-Brown and Brown 1978; Stiles and Wolf 1979; and South American species from E. R. Blake, pers. comm.)

free mating territories may have selected for agile, short-winged males. In contrast, many tropical Central American hummers, especially birds in dense forest interior and second growth habitats, tend to have static displays on a perch (Stiles 1982).

Most hummingbirds other than hermits, both territorial and lekking forms, are sexually dimorphic in color. Sexes of species such as *Anthracothorax prevostii* (mating system unknown, but either food territories or exploded arenas) do not differ in size but are distinct in plumage. No hermit hummingbirds are as dimorphic in plumage color as many nonhermits, but in some (*P. guy*, *P. ruber*),

males are brighter than females. The song complexity of hummingbird species does not appear to be related to their mating system (Stiles and Wolf 1979). It is quite possible that some hummingbirds considered here to be "nonlekking" may have exploded arenas.

In general, sexual dimorphism is more closely associated with female body size than with mating system in the hummingbirds. Body size itself varies among hummingbird species in relation to their food. Small size allows the birds to use efficiently the insect-pollinated flowers that are low in nectar flow but are often locally abundant (Wolf et al. 1976; Stiles 1981, pers. comm.).

The absence of any overall trend for association of mating systems and sexual dimorphism in size may be due to the opportunistic behavior of hummingbirds (Stiles 1973). The mating system may vary within rather broad limits depending on the dispersion, richness, and defensibility of resources. Dispersion of the females rearing young is independent of the dispersion of the promiscuous males. Hummingbirds originally may have been promiscuous; in only a few kinds (e.g., *Panterpe*, *Glaucis*) are the members of a pair associated for more than a moment (B. K. Snow 1973a; F. G. Stiles, pers. comm.).

Indicatoridae.—Honey-guides are brood parasites in which neither sex provides any parental care (Friedmann 1955; Ranger 1955). Males of three African species of *Indicator* call loudly from dispersed sites located several hundred meters apart. These call-sites of the established males are the sole mating sites. Ringing studies (G. Ranger, pers. comm.) showed that both sexes of honey-guides visit widely over several square kilometers. The mating system appears to be an exploded arena. The Asiatic *I. xanthonotus* has local display sites where mating takes place. The male guards a food source (a bee nest) and allows a female to feed only if she has mated with him (Cronin and Sherman 1977). The mating system differs from an exploded arena only in that a male guards a resource that the females use. Mating systems of species in other genera of honey-guides are not known. The closest relatives of the honey-guides are woodpeckers (Picidae) and barbets (Capitonidae), all of which are mainly monogamous.

Honey-guides (*Indicator* spp.) are more sexually dimorphic in size than barbets and woodpeckers (Fig. 6). The only woodpecker (*Hemicircus canente*) within the geographic range of these honey-guides that is more dimorphic in size than an *Indicator* lives singly or in pairs and has drumming territories (Ali and Ripley 1970). In none of these groups is sexual size dimorphism related to body size.

Cotingidae.—In the cotingids, a New World tropical family, about a third of the species have leks or exploded arenas, a third live in pairs, and the mating systems of the others are not known (Snow 1982). As all eat fruit, but only some have leks or arenas, fruit-eating alone does not explain the variation in mating systems within the family, although the quality and dispersion of fruits may help to do so. In their diversity of mating systems and in the fruit-eating niche of the adults (some feed insects to their young), the cotingids parallel the birds of paradise of the Old World.

Cotingids have a wider range of body sizes than any other passerine family (Snow 1982). Much of the size variation is related to the mating system. Nearly all cotingids that lek are larger than cotingid species that form pairs (Fig. 7). The lekking Red-ruffed Fruitcrow (*Pyroderus scutatus*) and the umbrellabirds (*Cepha-*

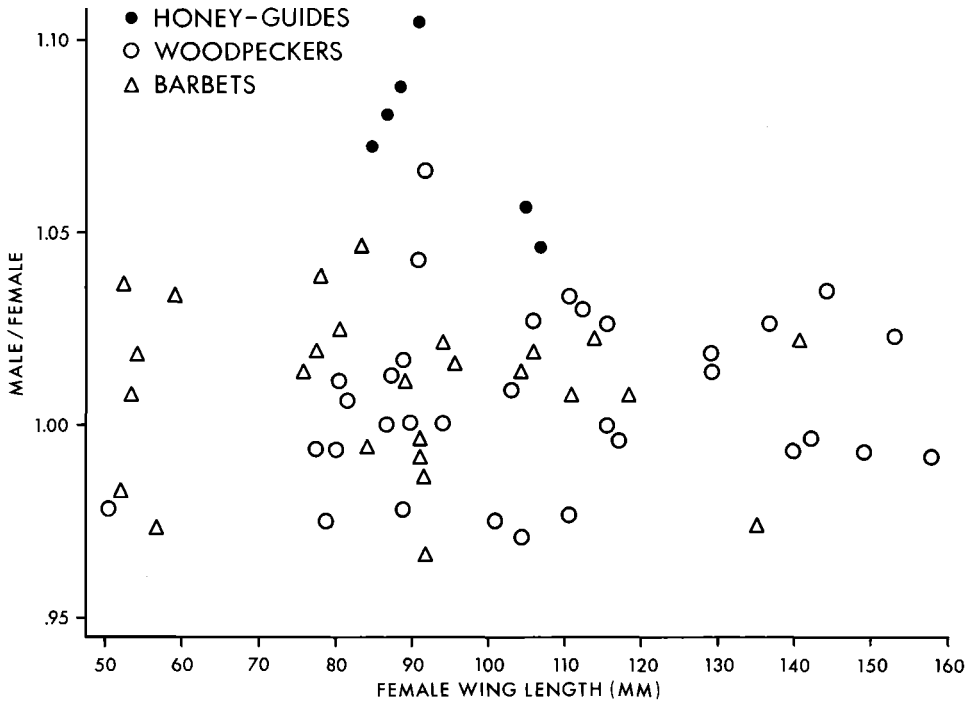


FIG. 6. Sexual size dimorphism in honey-guides (Indicatoridae), barbets (Capitonidae), and woodpeckers (Picidae) in relation to female size. The honey-guides are promiscuous brood parasites; the barbets and woodpeckers are nearly all monogamous. All species graphed are from southern Asia or Africa, the areas where the honey-guides have been studied. (Measurements taken from Bannerman 1933; Friedmann 1955, 1978; Ali and Ripley 1970; McLachlan and Liversidge 1978.)

lopterus spp.) are the largest cotingids; umbrellabirds and the middle-sized bellbirds (*Procnias* spp.) have exploded arenas. Umbrellabirds and bellbirds are more dimorphic in size than any of the group-lek species or the monogamous species.

The lekking species also tend to be more dimorphic in size than the monogamous species, but exceptions exist. The lekking pihás (*Lipaugus* spp.; including *L. unirufus*, Willis and Eisenmann 1979) are no more dimorphic than the pair-forming *Pipreola* and *Ampelion* species. The Purple-throated Fruitcrow (*Querula purpurata*) is a cooperative breeder and is as large and as sexually dimorphic in size as the average lekking cotingid. In the Red Cotinga (*Phoenicircus carnifex*), a lekking bird, males have shorter wings than females, with specialized narrow flight feathers that may be used in an active flight display, as in certain manakins. In *Cotinga maynana*, the best-observed of the blue cotinga species, males have shorter wings than females. The primaries of males in this species group are modified in form and make a noise in display flight. Females alone tend the nest, and males appear to display on exploded arenas. Body weight is related to wing length in the family, although different proportions occur among some genera (Snow 1982).

Most cotingids are sexually dimorphic in color. Among the lekking species, *Lipaugus*, *Perissocephalus*, and *Pyroderus* are not dimorphic in plumage or are

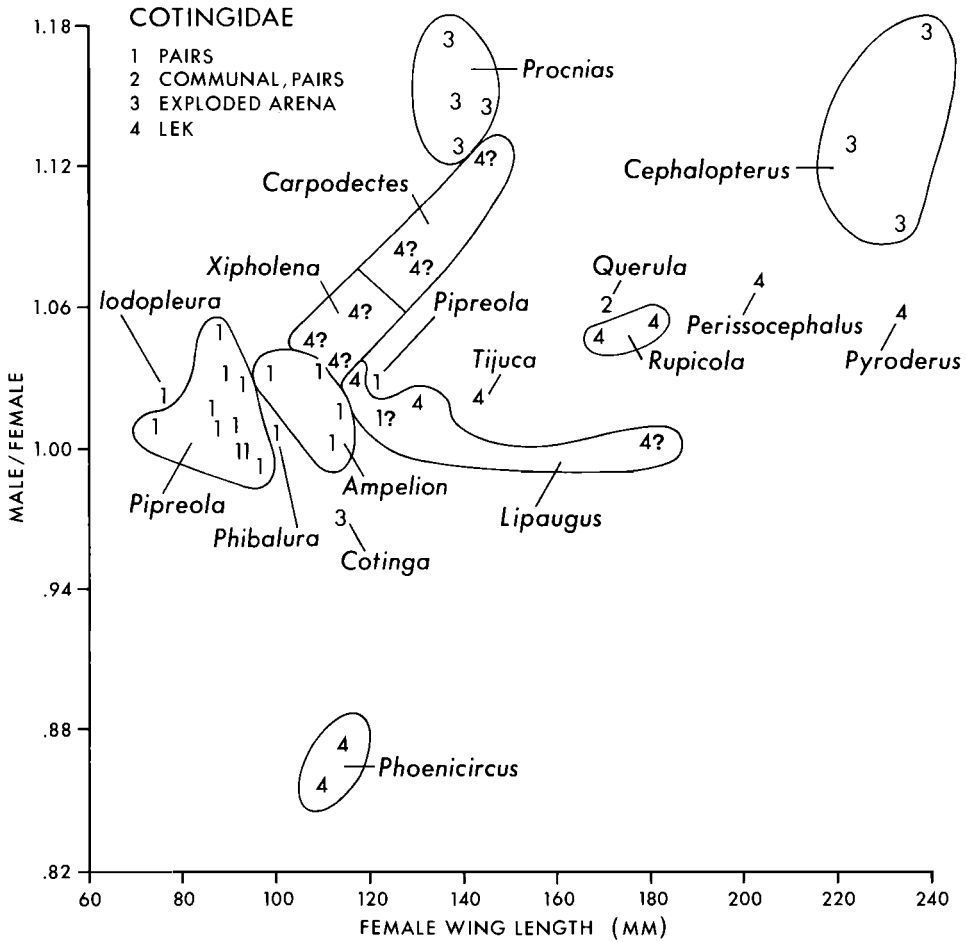


FIG. 7. Sexual size dimorphism in cotingas (Cotingidae) in relation to female size and mating system. (Measurements and mating systems taken from D. W. Snow 1973a, 1982; Willis and Eisenmann 1979.)

only slightly so, whereas others such as Cock-of-the-Rock (*Rupicola* spp.) are quite dimorphic. Pair-forming cotingids also generally are dimorphic in color (Snow 1982). Color dimorphism in cotingids generally is more obvious than the slight size dimorphism. There is no obvious trend for the lekking species to be dimorphic either in size or in color, or for these to vary together. Nevertheless, the greatest degree of sexual size dimorphism is associated with elaborate male ornamentation and showy courtship displays (Snow 1982).

Certain cotingids give loud songs. Calls of the bellbirds, which display on exploded arenas, are audible over more than 2 kilometers and are perhaps the loudest of all bird songs (D. W. Snow 1973a). Loud calls also have been noted in the lekking cotingids (*Tijuca*, *Lipaugus*, *Pyroderus*, *Cephalopterus*, *Perissocephalus*). The calls of *Lipaugus streptophorus*, which may form pairs, are not as

loud as those of the lekking species in this genus (D. W. Snow 1973b). Vocal behavior may be more closely associated with lekking than with size or color dimorphism in cotingids.

Alternative mating strategies of males are not well known in the cotingids. In Bearded Bellbirds (*Procnias averano*), satellite males sometimes perch near the calling male (Snow 1970). More detailed field studies are needed to determine the social behavior of most cotingids (Snow 1982).

Pipridae.—Manakins are small, mostly fruit-eating passerines in tropical forests and edge habitats. Not many species have been watched at the nest; none is known to have male parental care. The mating system in each is a variation on the lek theme (Sick 1959, 1967; Snow 1963). In several species, more than 20 males display in a large lek, each male on an individual court. In *Manacus manacus* and *Pipra erythrocephala*, a few males in a large lek get most of the matings (Lill 1974a, b, 1976). In *Chiroxiphia* manakins, two males often display in "pairs." The two males alternate roles in their mutual display—one gets all the matings. The subordinate male may get his turn when the dominant male loses competence or dies, and it may be to the subordinate's advantage to continue the traditional mating site, because females may visit in later years (Foster 1977, 1981; D. W. Snow 1977). *Machaeropterus regulus* and *M. pyrocephalus* display in twosomes (Sick 1967). *Pipra filicauda* also display in twosomes, with the males alternating roles (Schwartz and Snow 1978). Males in twosomes may be less aggressive than males in large leks, and D. W. Snow (1977) suggested that the dominance-subordinance roles are easily maintained, that male groups are cooperative, and that there is little male-male aggressive contest, with sexual selection resulting from female choice. Foster (1981), however, found intense aggressive interactions among male *Chiroxiphia caudata*, including physical contact. In a few manakins the males are farther apart (100 m or so) on exploded arenas (*Corapipo*, Snow 1963; *Machaeropterus deliciosus*, Willis 1966; *Pipra coronata*, *P. coeruleocapilla*, Skutch 1969; J. W. Fitzpatrick, pers. comm.; *Neopelma*, Snow 1963).

Sexual dimorphism in size in the manakins varies in relation to the body size and to the mating system (Table 5). Sexual dimorphism is related to female size (Fig. 8, Table 6; overall regression, analysis of variance, $F = 4.89$, $P < 0.02$). In the small species the males are smaller than the females; in the large species the males are larger. In the other manakins with information available on mating dispersion, the species with large numbers of males on the lek (*Manacus*, *Pipra*) tend to be smaller than species on exploded arenas (Table 6, mean wing lengths of females, $F = 11.5$, $P < 0.01$). Nevertheless, the smallest manakins display in small groups (2 to 4 males). The most size-dimorphic are *Ilicura militaris*, in which two or three males display in neighboring trees, and *Neopelma chrysocephalus*, in which males display alone. The pattern of size dimorphism does not support D. W. Snow's (1977) hypothesis that intrasexual competition among males is less in the species displaying in twosomes. That hypothesis would predict increased male size and increased size dimorphism in the species on large leks. Foster's (1981) observations of fighting in *C. caudata* also indicate intense intrasexual selection in the manakins that display in small groups. The results suggest that sexual size dimorphism may be greater in species with physical combat among lekking males.

In some manakins the males have structurally modified wings that are associated

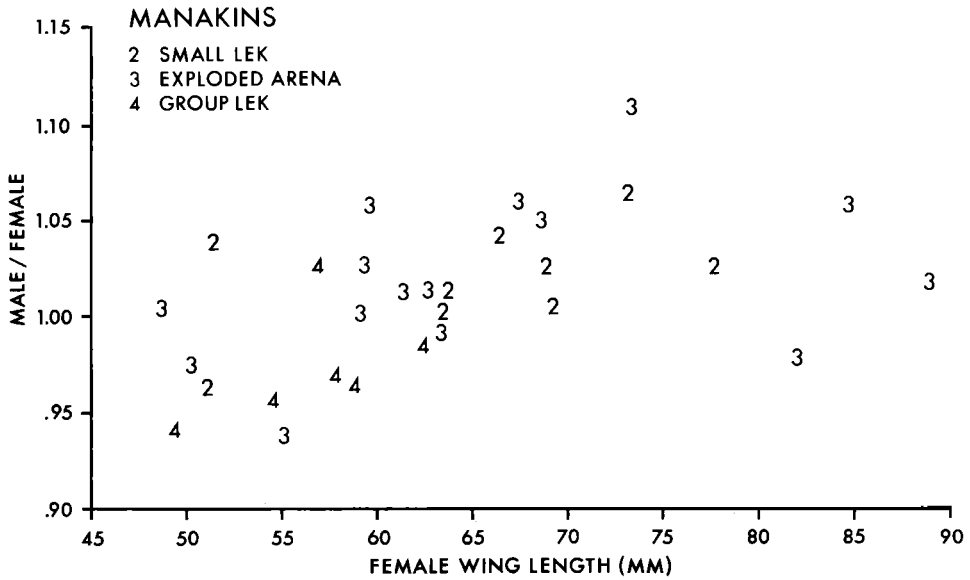


FIG. 8. Sexual size dimorphism in manakins (Pipridae) in relation to female size and male dispersion. (Measurements and arena behavior from Table 5.)

with mechanical noises in courtship (Darwin 1871; Snow 1963; Willis 1966). *Manacus manacus* has stiff, curved, narrow primaries, *Ilicura militaris* has thick shafts of the primaries, *Machaeropterus regulus* and *M. pyrocephalus* have enlarged secondary shafts, and *M. deliciosus* has the secondaries modified with highly specialized, porcupine-quill-like shafts. Female *M. manacus* have wing primaries like the males; females of the other forms have normal wing feathers. Less highly specialized, but consistently sex-associated, is the more rounded wing shape in male *Chiroxiphia linearis*. In certain manakins with a mechanical sound in display the males have no obvious morphological feather specializations (Snow 1963), and the wing feathers resemble those of the female. Structural modifications are accompanied by shortened wings, so, as in the cotingids, these must be taken into account when using wing length as a measure of size and dimorphism.

Body weights were available for both sexes in 14 species of manakins in which females were less than 20 g (Table 5). If wing length is a reliable indicator of body size, then the male : female ratio of wing length should be correlated across species with the male : female ratio of body weight. Weights of females in breeding condition (egg in duct, ovarian follicle 3 mm or larger, or "laying" indicated on specimen label) were not included, as their ovaries and oviducts would have been disproportionately large. Wing length and body weight were significantly correlated for females ($r_s = 0.620$, $P < .05$), but not for males ($r_s = 0.352$, ns). Wing length ratios were not significantly correlated with weight ratios ($r_s = 0.231$, ns) or with female body weight ($r_s = 0.312$, ns). Manakin species of different sizes and size dimorphisms cluster by genus rather than by the dispersion and number of males on a lek. The results in manakins suggest different histories of sexual

TABLE 5
SEXUAL SIZE DIMORPHISM OF MANAKINS AS INDICATED BY WING LENGTH AND BODY WEIGHT^a

Species	Mean wing length (mm)		Mean body weight (g)		Ratio M/F	M (N)	F (N)	Ratio M/F	Lok spacing ^b	Source ^c		
	M	(N)	F	(N)							M	(N)
<i>Schiffornis turdinus</i>	90.5	(13)	88.4	(9)	1.024	32.0	(9)	31.0	(4)	1.03	3	FMNH, UMMZ; USNM, AMNH (wts.)
<i>Schiffornis virescens</i>	80.6	(8)	81.8	(6)	.985	22.2	(2)				3	CM, FMNH, UMMZ, USNM; AMNH (wts.)
<i>Xenipo atronitens</i>	72.1	(10)	68.7	(10)	1.049	15.5	(2)				3	Blake; AMNH (wts.)
<i>Antilophia galeata</i>	79.8	(10)	77.8	(8)	1.026			8.6	(3)		2	UMMZ, FMNH
<i>Tyrannetes stolzmanni</i>	49.7	(10)	50.7	(10)	.980						3	CM, UMMZ, FMNH; LSU (wts.)
<i>Tyrannetes virescens</i>	49.2	(10)	48.9	(9)	1.004						3	CM, FMNH
<i>Neopelma chrysocephalum</i>	71.6	(10)	67.5	(4)	1.061						3	Blake
<i>Neopelma palliense</i>	81.0	(11)	73.1	(7)	1.108						3	CM, FMNH, USNM
<i>Heterocercus litteatus</i>	89.5	(10)	84.5	(8)	1.059						(3)	CM, FMNH, UMMZ
<i>Machaeropterus regulus</i>	50.0	(10)	52.0	(16)	.962	9.62	(15)	9.13	(13)	1.054	2	Blake, USNM; LSU (wts.)
<i>M. pyrocephalus</i>	53.6	(10)	51.5	(10)	1.040	9.33	(6)	10.3	(7)	.906	2	FMNH, UMMZ, LSU, CM; AMNH (wts.)
<i>M. deliciosus</i>	63.3	(11)	61.7	(3)	1.030			12.0	(1)		3	FMNH, UMMZ, LSU, USNM
<i>Manacus manacus</i>	52.4	(63)	54.7	(82)	.958	18.5	(93)	16.8	(106)	1.101	4	Snow and Snow 1963
<i>M.(m.) aurantiacus</i>	46.8	(13)	49.7	(9)	.942	19.5	(1)				4	Ridgway 1907; LSU (wt.)
<i>Corapipo leucorhoa</i>	59.8	(14)	59.3	(10)	1.001	10.7	(13)	12.7	(4)	.843	3	CM, FMNH, UMMZ; LSU (wts.)
<i>C. gutturalis</i>	57.1	(11)	55.9	(8)	1.002						4	CM, FMNH, UMMZ
<i>Ictinia militaris</i>	63.3	(10)	59.7	(10)	1.060						(3)	FMNH, UMMZ
<i>Chiroxiphia linearis</i>	70.6	(29)	71.1	(11)	.993	16.8	(41)	19.1	(48)	.880	2	FMNH, UMMZ; M.S. Foster (wts.)

TABLE 5
CONTINUED

Species	Mean wing length (mm)			Mean body weight (g)			Ratio M/F	(N)	Ratio M/F	(N)	Lek spacing ^b	Source ^c
	M	F	(N)	M	F	(N)						
<i>C. lanceolata</i>	71.7	70.3	(10)	1.020	24.0	(1)			2	Wetmore 1972b; LSU (wts.)		
<i>C. pareola</i>	69.3	66.5	(5)	1.033	17.4	(3)	.939		2	FMNH		
<i>C. caudata</i>	77.4	73.7	(9)	1.051		(1)			(2)	UMMZ, CM; AMNH (wt.)		
<i>Pipra pipra</i>	60.9	59.3	(5)	1.027	12.0	(10)	.855		3	Wetmore 1972b, LSU		
<i>P. coronata</i>	62.8	61.4	(6)	1.023	8.68	(103)	.924		3	CM, FMNH, UMMZ, LSU		
<i>P. coeruleocapilla</i>	53.4	55.7	(8)	.959	10.5	(6)	.850		3	CM, FMNH		
<i>P. aureola</i>	64.1	63.7	(3)	1.006	16.0	(1)			3	Blake, CM, LSU; AMNH (wt.)		
<i>P. fasciicauda</i>	64.9	63.7	(10)	1.020	16.1	(13)	1.064		2	FMNH, LSU		
<i>P. filicauda</i>	64.4	63.8	(10)	1.009	14.3	(4)	.927		2	Blake, LSU		
<i>P. mentalis</i>	56.2	58.0	(18)	.969	17.6	(8)	.993		(4)	Wetmore 1972b, LSU		
<i>P. erythrocephala</i>	56.7	58.7	(46)	.966	12.8	(223)	.908		4	Snow and Snow 1963		
<i>P. chloromeros</i>	61.5	62.5	(12)	.983	17.0	(5)	1.097		4	CM, FMNH		

^a For polytypic species, specimens measured are from the same locality or the same subspecies as those whose behavior has been studied in the field.

^b Spacing of displaying males follows Sick (1959, 1967), Snow (1963), Skutch (1969), Lill (1974a, b, 1976), and Schwartz and Snow (1978). 2 = displays by male twosomes; 3 = dispersed males not in visual contact; 4 = groups of 4 or more males with mutual displays or within sight and sound of each other. Some birds have varying or intermediate display spacing: *Chiroxiphia caudata* (here 4) sometimes display in groups of only 3 males (D. W. Snow 1977), but usually have larger leks (Foster 1981); the display itself usually involves only 2 males at a time though more than 2 may be present (M. S. Foster 1981; pers. comm.); *Ilicura militaris* (here 3) display in neighboring trees but chase each other (Sick 1959); *Pipra mentalis* (here 4) display in small leks of up to 5 males on perches within 7-40 m of each other, but some twosomes of males perch together between these display sites (Snow 1963). *Heterocercus lineatus* is tentatively designated as 2 (Sick 1959).

^c Measurements and weights (wts.) from specimens in collections of CM = Carnegie Museum of Natural History; FMNH = Field Museum of Natural History; LSU = Museum of Zoology, Louisiana State University; UMMZ = University of Michigan Museum of Zoology; USNM = National Museum of Natural History. E. R. Blake measured the species indicated. J. V. Remsen and S. M. Lanyon determined body weights and certain wing lengths of the LSU specimens, and B. Farmer examined the USNM specimens. I measured the CM, FMNH, and UMMZ specimens.

TABLE 6
COVARIANCE ANALYSIS OF SEXUAL SIZE DIMORPHISM AND FEMALE WING
LENGTH IN MANAKINS^a

	Male breeding dispersion		
	Male twosomes	Exploded arena	Lek
N	9	13	6
Mean FW	66.80	61.80	56.6
SE FW	2.29	1.98	3.23
Mean SSD	1.019	1.028	.9733
Adjusted mean SSD	1.008	1.029	.9871
SE	.0097	.0077	.0119
a-constant	.932	.790	.818
b-slope	.0013	.0038	.0027
R ²	.23	.58	.39
P	ns	.01	ns

	Equality of adjusted means (SSD)		Equality of slopes	
	F-statistic	P	F-statistic	P
Twosomes-exploded arena	2.69	ns	3.37	.06
Twosomes-lek	3.63	ns	1.82	ns
Exploded arena-lek	16.3	.001	.14	ns

^a FW = female wing length in mm; SE = standard error; SSD = sexual size dimorphism (ratio of male wing length to female wing length); a and b = regression coefficients; R² = correlation coefficient; P = probability. Analysis excluded data for *Schiffornis* spp. (questionably manakins; Snow 1975).

selection within different species groups, that male body size is not summarized simply by wing length, and that small size is associated with short and maneuverable wings in the displaying males.

Plumage color dimorphism is pronounced in all manakins plotted (except in *Schiffornis*); males are brighter. Other manakins were not included because their mating systems are unknown; some are sexually alike in plumage color. In a few species of lekking, sexually dichromatic manakins, the males have elongated tail feathers. Songs are simple and unmusical in the manakins in general. The dull-olive, sexually monomorphic thrush manakins (*Schiffornis*) have loud, whistled songs, more like those of some tyrannid flycatchers (Sick 1967; Skutch 1969). They have individual male display arenas and no male parental care (Skutch 1969); no marked birds have been watched.

Tyrannidae.—Most tyrant flycatchers are monogamous. A few species lack male parental care (Skutch 1960). Ochre-bellied Flycatchers (*Mionectes oleagineus*) appear to display on dispersed arenas, calling out of sight of each other. Males are about 10 percent larger than females (Snow and Snow 1979) and have an emarginate wing; the sexes are otherwise alike in plumage. The species is no more sexually dimorphic in size, however, than the monogamous tyrannids *Elaenia flavigaster* and *Miophobus fasciatus* that live in the same area on Trinidad (Snow and Snow 1963).

In McConnell's Flycatcher (*Mionectes macconnelli*), males display 50 to 100 meters apart but sometimes "group loosely" in a lek (Willis et al. 1978). The sexes are equal in size (mean wing length in 6 males 63.6 mm, in 4 females 63.4 mm, form *M. m. amazonus*). Several other tyrannids may have arenas, as they

lack male parental care, and males do not accompany the nesting females. These include *Lophotriccus galeatus*, *Myiobius atricaudus*, *M. barbatus*, *Oncostoma cinereigulare*, *Rhynchocyclus olivaceus*, *R. brevirostris*, and *Terenotriccus erythrus*. All are monomorphic in plumage and have a male/female wing-length ratio of 1.0 to 1.1 (1.14 in *L. galeatus*). No marked populations have been watched, and the mating systems are unknown. These birds are no more dimorphic in size than monogamous tyrannids in which males take an active part in parental care (measurements from Wetmore 1972b; FMNH; UMMZ; behavior from Skutch 1960, 1969; Snow and Snow 1979).

Oxyruncidae.—The Sharpbill *Oxyruncus cristatus* is a relative of the cotingids and tyrant flycatchers. Males sing a few hundred meters apart, apparently on individual arenas. The nesting behavior is unknown (Stiles and Whitney 1983). Males are slightly larger than females and are similar in plumage (Wetmore 1972b).

Pycnonotidae.—The Yellow-whiskered Greenbul (*Andropadus latirostris*) is the only known lekking passerine in forested habitats in Africa (Brosset 1982). Males sing in groups, often remaining for many days on the lek. Solitary males sometimes sing away from the lek for a few days. Courtship behavior was seen at the leks; matings were not observed. The young are reared by one adult alone, presumably the female. Yellow-whiskered Bulbuls are dull and sexually monomorphic in plumage, and the sexes are similar in size as in the monogamous species (Brosset 1971). The other bulbuls in the same forests are also mainly dull-plumaged fruit-eaters, but they are monogamous with biparental care of the young.

Paradisaeidae.—A few species of birds of paradise are monogamous, some are polygynous with males dispersed on mating sites and providing no parental care, and others are lekking birds (Gilliard 1969; Schodde 1976; Cooper and Forshaw 1979). Fruit and insects are generally important foods for all species (Schodde 1976; Cooper and Forshaw 1979; Beehler 1983). Many species are not well known, and field studies are needed.

Males are larger than females in nearly all species regardless of the mating system (Fig. 9). Males are proportionately larger in the larger species. This trend is apparent both in the manucodes and other monogamous species and in birds with leks or exploded arenas (Table 7). Nevertheless, sexual size dimorphism is greater in the nonmonogamous birds of paradise than in the monogamous species. Birds with communal leks are more dimorphic in size than birds with exploded arenas, but the difference appears to be due to the larger size of the lekking species (Table 7).

The monogamous species are either monomorphic or dimorphic in plumage color. All the promiscuous and polygynous species are dimorphic. Elaborate male breeding plumage is found both in certain lekking species and in some exploded arena birds. Most of the latter birds (such as the riflebirds, *Ptiloris*) have male plumage with iridescent patches on an otherwise dark plumage. Lekking and exploded arena birds generally have very loud calls, but loud calls are not restricted to birds with any one mating system (LeCroy 1981). The Magnificent Riflebirds (*Ptiloris magnificus*) and several six-wired birds of paradise (*Parotia* spp.) vary in dispersion, with males solitary or in groups (Schodde 1976; Cooper and Forshaw 1979). The former was considered here to be an exploded arena species and the latter to be communal lek species.

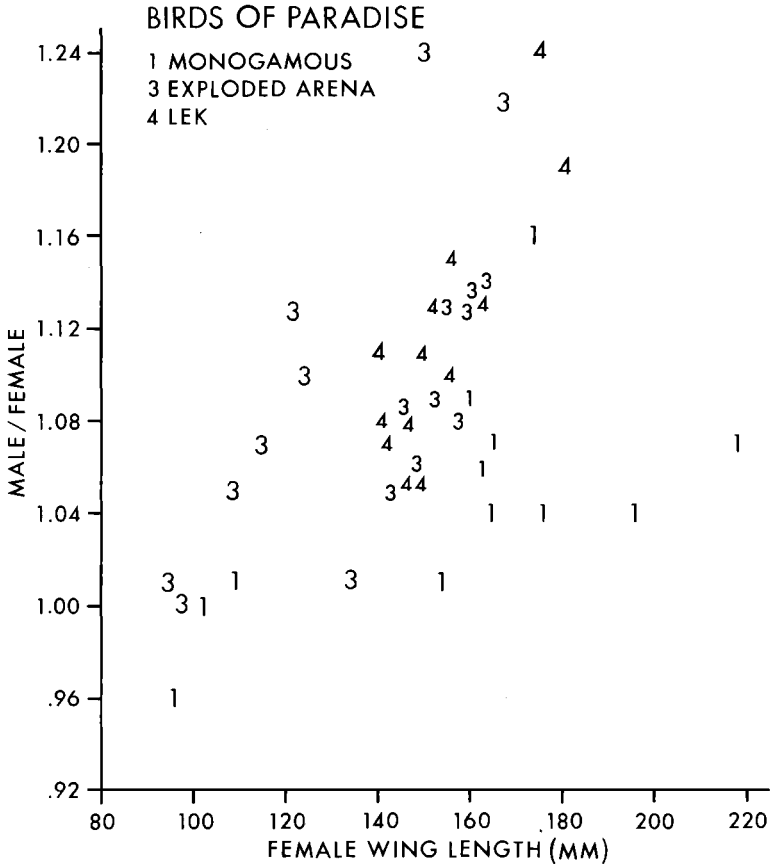


FIG. 9. Sexual size dimorphism in birds of paradise (Paradisaeidae) in relation to female size and to the mating system and social organization. (Measurements and mating system taken from Cooper and Forshaw 1979.)

Displays of ornately-plumed males in one bird of paradise, *Paradisaea decora*, appear to be directed aggressively toward other males. Supplanted males leave the group or retreat to its edge. When a female arrives, all but one of the plumed males disappear (LeCroy et al. 1980). Similar behavior has been seen in *P. raggiana*. The behavior may indicate a sociosexual deference of subordinate males to the aggressive dominant male (LeCroy 1981). Males of some species may remain in a female-like plumage for up to six years (Gilliard 1969), and female-plumaged males have been seen to mate (Wallace 1869, LeCroy et al. 1981). A male may use more than one behavioral approach to mating over its lifetime, but this has not been shown with marked birds.

Ptilonorhynchidae.—Bowerbirds include both arena birds and monogamous species with parental care by both sexes. They are mainly fruit-eaters (Cooper and Forshaw 1979). The three species of catbirds *Ailuroedus* are monogamous, and males help care for the young. The other bowerbirds do not form pairs, and the females alone rear the young. One, the Golden Bowerbird (*Prionodura new-*

TABLE 7
COVARIANCE ANALYSIS OF SEXUAL SIZE DIMORPHISM AND FEMALE WING
LENGTH IN BIRDS OF PARADISE WITH DIFFERENT MATING SYSTEMS^a

	Mating system		
	Monogamous	Exploded arena	Lek
N	12	17	13
Mean FW	156.9	137.6	153.9
SE FW	6.45	5.05	6.00
Mean SSD	1.0445	1.0936	1.1162
Adjusted mean SSD	1.0324	1.1083	1.1083
SE	.0141	.0121	.0134
a-constant	.908	.848	.541
b-slope	.00087	.0018	.0037
R ²	.41	.37	.74
P	.05	.01	.001

	Equality of means (SSD)		Equality of slopes	
	F-statistic	P	F-statistic	P
Monogamous-exploded arena	13.2	.001	1.83	ns
Monogamous-lek	13.3	.001	11.0	.001
Exploded arena-lek	21.0	.001	2.76	ns

^a As in footnote a, Table 6.

toni), was described by Gilliard (1969) and Schodde (1979) to display in a lek, with each male having a bower on an arena near other males; others have reported males to be more dispersed (A. Lill, pers. comm.). Most species maintain bowers where they court the females. The males are generally out of sight and sound of each other (e.g., Diamond 1982). In the Tooth-billed Catbird (*Scenopoeetes dentirostris*), males sometimes display within sight of each other and so may lek (Cooper and Forshaw 1979). This is the only nonmonogamous bowerbird that does not build a complex bower. In the Satin Bowerbird, males may display within 100 meters or so of each other. Females visit several neighboring males but generally mate with only one (Vellenga 1970, 1980a; G. Borgia, pers. comm.). In Macgregor's Bowerbird (*Amblyornis macgregoriae*), males are spaced evenly in suitable habitat at distances of 100 to 200 meters. The regularity of spacing suggests territories, but only the area by the bower is actively defended, and the "social dynamics" of the birds suggest an "exploded lek" (Pruett-Jones and Pruett-Jones 1982). Males interact by visiting and raiding bowers, including those of males that are not immediate neighbors. The display sites of these bowerbirds may be exploded arenas in the sense of Gilliard (1969).

Sexual dimorphism in size is no greater in the arena bowerbirds than in the monogamous species (Fig. 10). The most dimorphic species, Archbold's Bowerbird (*Archboldia papuensis*), displays singly. The serial replacement of 11 males as they were trapped over 11 days at an arena suggests that males compete for traditional mating sites (Gilliard 1969). No other display sites were found over a large area of apparently suitable habitat. This observation suggests an arena system in which the resident male courts the females visiting from a large area. The least size-dimorphic bowerbird is the Regent Bowerbird (*Sericulus chrysocephalus*),

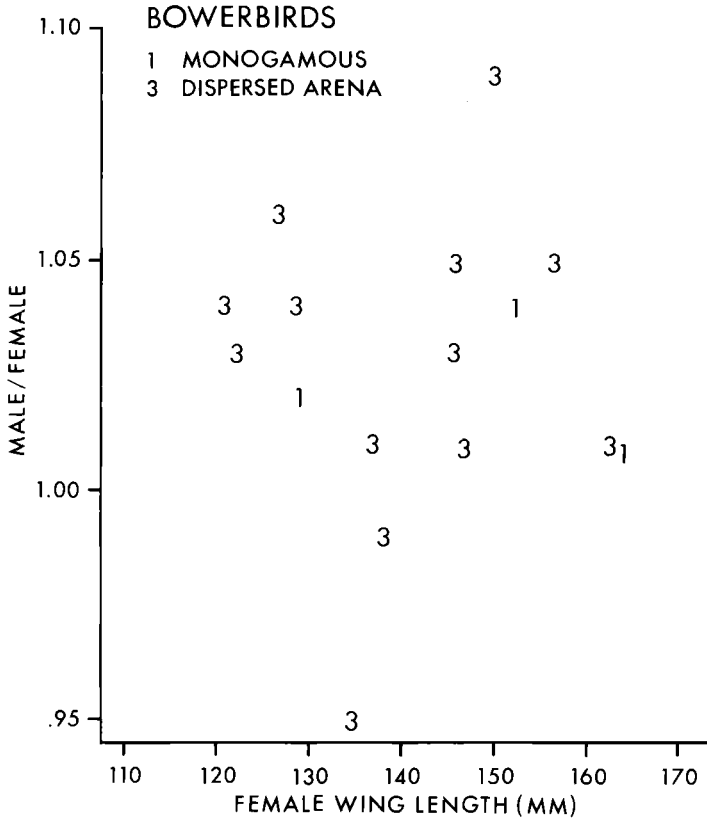


FIG. 10. Sexual size dimorphism in bowerbirds (Ptilonorhynchidae) in relation to female size and mating system. (Measurements taken from Cooper and Forshaw 1979.)

another exploded arena species. The monogamous catbirds are intermediate in size and in sexual dimorphism.

Males that build courtship bowers usually decorate the bower with particular colors that often match their plumage or eye color (Schodde 1976, 1979). Is this display of color an aggressive advertisement of successful combat over rival males? Satin Bowerbirds in aviaries kill other small blue birds for decoration of their bowers (Gilliard 1969). Wild male Satin Bowerbirds, however, decorate their arenas with yellow leaves, snail shells, and blue parrot feathers, but not with bowerbird feathers (G. Borgia, pers. comm.). In another interpretation, Diamond (1982) suggested that the displays with colored fruit at the bower of some species are derived from courtship feeding at the ancestral nest.

Several species of bowerbirds have complex songs that mimic other sounds of the forest (Gilliard 1969) and may mimic other local individuals of their own species. Local variations in song have not been studied to determine whether song neighborhoods may occur and correspond to socially interacting individuals.

Menuridae.—Although Darwin (1871) cited an assembly of displaying males, lyrebirds are now known not to form communal leks (Durrell 1966; Kenyon 1972;

Lill 1979). In *Menura novaehollandiae* the male displays alone on a large mound, showing off his glorious tail and mimicking other local forest sounds in his song. Local males tend to mimic the same sounds, suggesting that one lyrebird imitates another (Robinson 1979). Males take no part in parental care. Females nest near the male area, but their activity range may include the territories of two males, and Lill (1979) saw a female visit two males in succession. Mating is apparently promiscuous with no pair bond. Males are only slightly larger than females (mean wing length in 5 males = 289 mm, in 5 females = 274 mm; Mathews 1918–1919; FMNH; USNM). Males have an elaborate tail; females have a longish tail but lack the ornamental barbs of the male.

Ploceidae.—African weaver finches include many monogamous and polygynous species. Only one displays in a lek. More than a dozen male Jackson's Whydah (*Euplectes jacksoni*) may display within a hectare or two, each on his own defended arena beside a formed tuft of grass. Females visit the lek to mate, but build their nests off the lek area (Van Someren 1945, 1956).

Comparison of sexual size dimorphism in the related genera *Euplectes* and *Quelea* shows that all the polygynous species are dimorphic (Fig. 11). Males are proportionately larger in the larger species. The lekking *E. jacksoni* is dimorphic, but no more so than the smaller, polygynous *E. ardens*. The exceptional species is the Sakabula (*E. progne*), in which males are half again as large as females in wing length, and more than twice their weight. Male wing length appears to increase by 30 percent over the first three years (Traylor 1965). Males have a very long tail which is displayed in a slow flight over the territories. The wings may be large to provide low wing-loading which would allow the males to outfly predators, and wing length may not reflect overall body size (M. Andersson, pers. comm.). Tail length appears to attract females. Andersson (1982b) found that males whose tails were experimentally lengthened gained more new active nests with eggs or young than did control males. Males whose tails were shortened had the fewest. Tail length did not appear to affect the behavior of males, and Andersson interpreted the results as due to female choice. The male initiates nest-building on his territory but takes no part in parental care (McLachlan and Liv-ersidge 1978; Craig 1980).

Brood parasitic finches include the whydahs and indigobirds (*Vidua* spp.) and the Cuckoo-finch (*Anomalospiza imberbis*). Male Village Indigobirds sing on traditional call-sites located a few hundred meters apart. Females visit several singing males in rapid succession, are courted by each male in turn, then return to one male and copulate (Payne and Payne 1977). Behavior, dispersion of the call-sites, and the variance in mating success among males indicate that the social organization is an exploded arena. Similar dispersion and behavior occur in other *Vidua* species (Payne 1973, 1980, 1982b). The social organization and mating system of the Cuckoo-finch are unknown.

Sexual size dimorphism in the parasitic finches is not as great as in the polygynous species of *Euplectes* in the same size range (Figs. 11, 12). *Vidua* species are barely more dimorphic in size than most African estrildid finches. Each is larger than its foster species of estrildid.

Plumage color dimorphism in the sexes is more obviously related to the mating system. The polygynous *Euplectes* species and the parasitic *Vidua* are all sexually dimorphic in plumage. In contrast some species of the monogamous estrildids

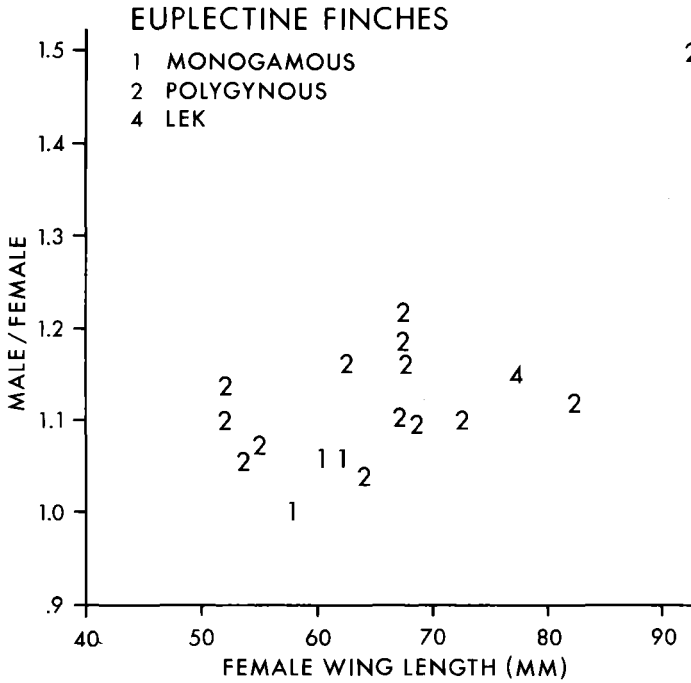


FIG. 11. Sexual size dimorphism in African quelea, weaver-finches, and bishops (Ploceidae) in relation to female size and mating systems. (Measurements taken from Jackson 1938b.)

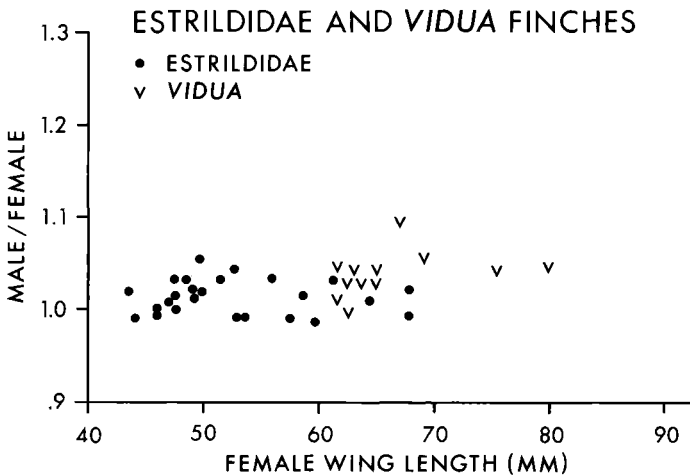


FIG. 12. Sexual size dimorphism in brood parasitic whydahs (*Vidua*, Ploceidae) and African estrildid finches (Estrildidae) in relation to body size. [Measurements of *Vidua* taken from Jackson 1938b (*V. fischeri*, *V. hypocherina*), McLachlan and Liversidge 1978 (*V. macroura*, *V. regia*), Payne 1971, 1980 (*V. obtusa*, *V. paradisaea*), Payne 1973 (*V. funerea*, *V. chalybeata*, *V. purpurascens*), and Payne 1982b (the remaining species). Estrildid measurements taken from Bannerman 1948; McLachlan and Liversidge 1978.]

TABLE 8
TRENDS IN SEXUAL SIZE DIMORPHISM, MATING SYSTEMS, AND BODY SIZE IN BIRDS^a

Taxon	SSD in monogamous species	SSD in lek species	SSD in lek species > monogamous species	SSD related to body size	Comments
Grouse	no	yes	yes	yes	
Calidridines	no	yes	yes	yes	
Snipe and woodcock	varies	varies	no	no	
Bustards	yes	yes	yes	yes	females > males in promiscuous species
Parrots	little	little	no	no	
Hummingbirds	variable	variable	no	yes	females > males in small species
Honey-guides ^b	no	yes	yes	no	
Cotingids ^c	slight	yes	yes	yes	
Manakins	none monogamous	varies	—	yes	females > males in small species
Tyrant flycatchers	slight	slight	no	not tested	
Birds of paradise	yes	yes	yes	yes	
Bowerbirds ^d	yes (some)	yes (some)	no	no	
Euplectine finches	slight	yes	yes	yes	
Viduiine and estrildid finches	no	slight	yes	no	

^a SSD = sexual size dimorphism (ratio of male wing length to female wing length).

^b Honey-guides were compared with woodpeckers and barbets.

^c Sharpbills are no more dimorphic than the smaller monogamous cotingids.

^d Lyrebirds are no more dimorphic than the monogamous bowerbirds.

are not dimorphic in plumage, though the monogamous *Quelea* species are dimorphic. Some polygynous *Euplectes* and viduine finches have elaborate male breeding plumages; the larger species have elaborate tails (Craig 1980; Payne 1980). These appear more closely associated with the form of male display (flight vs. perch) than with the mating system.

Songs have been studied in detail mainly in the exploded-arena Village Indigobird (Payne 1973, 1979b, 1980, 1982b). In most species of viduine finches, the males mimic the songs and calls of their foster parent species, and the females visit males that match their own foster parent species' songs. They have local song dialects in which the song variations of the more successful breeding males are copied by neighbors and visitors (Payne 1981, 1983a). Song structure and repertoire appear to have been shaped both by competition among males and (especially the song mimicry of the foster species) by female choice. The complex song repertoire of these promiscuous birds is consistent with the hypothesis that intense sexual selection has led to elaborate vocal behavior (Payne 1983a).

DISCUSSION

Sexual dimorphism in size varies both with mating system and with body size in birds (Table 8). Males are larger than females in the lekking and exploded arena species in most systematic families, but not in all. Insofar as the degree of sexual size dimorphism is associated with the mating system in these different families,

the results bear out the prediction of greater sex differences in species with more intense sexual selection. However, some nonlekking species also are dimorphic. The degree of sexual size dimorphism, in addition, varies directly with overall body size among species. For example, sexual dimorphism in the grouse is greatest in lekking species, but so is body size. As size and sexual size dimorphism are so closely associated, it is impossible to attribute all variation in sexual dimorphism directly to the mating system.

Certain birds give further evidence of an effect of mating system on sexual dimorphism. In the calidridines and in the piciforms (honey-guides, woodpeckers, and barbets), the promiscuous species are more dimorphic than the monogamous species even though female size is not associated with the mating system. Sexual size dimorphism most clearly is associated with mating system in the birds of paradise. In this family, sexual dimorphism increases with body size in the lekking species much more dramatically than in the monogamous species. Also, the degree of sexual dimorphism is greater in the promiscuous lekking and exploded arena species when adjusted for body size.

The association of sexual size dimorphism and female body size may result from an interaction between two evolutionary processes. First, males are larger than females due to sexual selection even in monogamous birds. Secondly, lekking and highly polygynous species are larger than in monogamous species due to a correlated response in females to genes sexually selected in the males, as suggested by Maynard Smith (1978) and Lande (1980). The concept of a correlated response updates Darwin's (1871) "principle of transference" of characters selected by sexual selection in one sex being expressed also in the other sex. In the same way, the flight feathers in certain females (snipe *Gallinago* spp., *Scolopax minor*, *Manacus manacus*) may be modified in structure like those of the male.

An ecological explanation of the association of sexual size dimorphism with body size seems unlikely because the same size trend occurs in such a variety of ecological guilds: in seed-eating finches, in fruit-eating passerines, and in omnivorous, vegetarian, and insectivorous ground birds. Where large males and small females take different foods, the shift in diet may be secondary to the selected size differences, as in primates (Clutton-Brock and Harvey 1977). In the case most strongly suggesting a primary ecological divergence of the sexes, bill morphology and feeding behavior were more sexually dimorphic in island species than in mainland species of woodpeckers (Selander 1972). Possibly the difference between the sexes on islands was related to sexual selection on males under conditions where they were not constrained by competition among related species. In general, if selection were to occur for trophic specialization outside the context of sexual selection, we should see trophic morphs with both sexes belonging to each morph, as in some fishes (Fryer and Iles 1972; Morse 1980; Kornfield et al. 1982). But in the birds, all size dimorphism is associated with sex.

In the bustards, hummingbirds, and manakins, the smallest species are "reversed" in sexual size dimorphism as the females are larger than the males, and the smallest reversed species are the most dimorphic. The same trend occurs in raptors (Snyder and Wiley 1976; Andersson and Norberg 1981), insectivorous bats (Myers 1978), and certain other mammals (Ralls 1977). Different explanations of size and sexual dimorphism may apply in these taxa. If metabolic constraints, such as those associated with egg-laying, set a physiological lower size

limit in female birds, then one would expect the size of the smallest females to coincide. However, the sizes of the smallest females range across a gradient from tiny hummingbirds and manakins to the bustards, large ground birds 100 times larger in body weight. Factors other than physiological constraints of small body size may account for reversed size dimorphism in some or all of these birds. These may include the form of the male display.

The taxa with reversed sexual size dimorphism considered here tend to be those with active aerial displays. Much as small hummingbird males may be at an advantage because of superior maneuverability, so also may the small manakins. Males are quick and agile in active display on the lek. Taxonomic groups with reversed sexual size dimorphism do not appear to have reduced aggressive behavior or alternate modes of sexual selection. Male hummingbirds on territories are aggressive, fight, and chase (Legg and Pitelka 1956; Kodric-Brown and Brown 1978), and the larger species are generally dominant and exclude the smaller species from resource-centered territories (Wolf et al. 1976). Displaying male bustards also are aggressive (Dharmakumarsinhji 1950; Gewalt 1954; Cramp 1980). The bright colors and plumage patterns in these groups suggest an evolutionary history of female choice and runaway sexual selection (Fisher 1958). Perhaps sexual selection has proceeded by way of female choice more than by way of male competition in hummingbirds and manakins.

After overall body size has been taken into account, is sexual size dimorphism in nonmonogamous birds explained by something other than sexual selection for aggressive behavior among the males? It is generally thought that large size in males of polygynous birds is the result of sexual selection for large size and that this is counterselected by a higher mortality (Selander 1972; Moss 1980). Banding recovery data of icterids show that male survival is greater than female survival in two small species, while female survival is greater in two larger species (Searcy and Yasukawa 1981). Males are larger than females in all four species. These results suggest no general tendency for males to have lower survival than females among sexually dimorphic polygynous birds. Size and survival are not consistently associated, nor is food nor habitat consistently associated with the degree of sexual dimorphism. Nevertheless, the relationship between the mating system and sexual dimorphism is consistent among these species. Therefore, it seems likely that sexual dimorphism in size is mainly the result of sexual selection.

In overview, the intensity of sexual selection (indicated by I_m) and sexual dimorphism tend to be associated in a positive manner in birds. Lekking species are more variable in male breeding success and are more sexually dimorphic in size than are monogamous birds. The lack of a closer association within families probably reflects differences in the history of sexual selection among species groups. The differences among families in the details of their sexual size dimorphism are perhaps best viewed as part of the stochastic nature of sexual selection, which may initially work on male size, color, song, or any other character, or combinations of these characters (Fisher 1958; Lande 1980; Kirkpatrick 1982).

The results are generally consistent with an hypothesis of intrasexual competition leading to sexual dimorphism in body size. This interpretation is supported by observations of sexual conflict involving physical contact as well as ritualized aggressive displays among males in lekking birds. The results also show, however, that not all variation in sexual dimorphism is explained simply in terms of this

model. Sexual dimorphism in color is not explained simply by female choice, because color may influence social competition among males as well as the sexual attraction of females to males. The residual association of color dimorphism and mating systems in birds remains to be analyzed. Insofar as sexual dimorphism in size and color are positively associated in some groups (Phasianidae), but not in others (Trochilidae, Cotingidae, Pipridae), and are not negatively associated in any, some evidence exists for independent evolution of sexual dimorphism through selection both by intrasexual competition among males and by female choice of mates.

ACKNOWLEDGMENTS

The study was supported in part by a National Science Foundation grant (BNS-8102404). For their original field data on the breeding success of individual birds I thank D. De Steven, S. C. Kendeigh, T. D. Price, P. W. Sherman, L. H. Walkinshaw, and J. L. Zimmerman. M. Crock was helpful in collating the field data on breeding success. I thank J. van Rhijn for comments on waders, R. Liversidge on bustards, F. G. Stiles and P. W. Ewald on hummingbirds, G. Ranger on honeyguides, J. W. Fitzpatrick and M. S. Foster on manakins, G. Borgia on bowerbirds, and M. Andersson on ploceids. The Field Museum of Natural History, and the Carnegie Museum, kindly permitted access to their collections. J. V. Remsen and S. M. Lanyon measured and recorded weights from specimens in the Museum of Zoology, Louisiana State University, B. Farmer measured manakins and lyrebirds in the National Museum of Natural History, and W. E. Lanyon checked specimen weights in the American Museum of Natural History. E. R. Blake provided wing measurements of certain manakins and hummingbirds. B. Beehler, J. Bradbury, T. H. Clutton-Brock, M. S. Foster, L. W. Oring, M. Pruett-Jones, S. Pruett-Jones, T. D. Price, and D. W. Snow sent manuscripts before publication. J. Hinshaw helped type the manuscript. B. Beehler, J. Bradbury, G. K. Creighton, P. W. Ewald, M. S. Foster, W. D. Hamilton, J. P. Kruijt, A. Lill, P. Myers, T. D. Price, F. G. Stiles, R. Thornhill, and M. Zuk commented on the manuscript.

SUMMARY

The intensity of sexual selection in birds that display on leks is higher than it is in monogamous species and in most polygynous species where the males provide resources or a nesting site. A population genetics model was used to estimate I_m , the potential for sexual selection among males in a population, from their variance in breeding success. I_m differed among birds with different mating systems. In lekking species, a few males accounted for most of the success, and most had none. Breeding success was more evenly distributed among males in the monogamous species. The results showed the greatest variance in success, and, thus, the greatest potential for genetic sexual selection, in males of the lekking species, and the lowest in the monogamous species.

Bird families in which one or more species breed in leks were compared to test whether sexual size dimorphism is related to the mating system. Evolutionary sexual selection involves both male-male competition and female choice. The degree to which males are larger than females in the species with intense sexual selection was used as a test of the relative importance of male competition. Males

were larger than females in most lekking species, but males were slightly larger also in monogamous species. In the birds of paradise, lekking species were more sexually dimorphic in size than in monogamous species throughout a wide range of female body sizes. In a few families (Tetraonidae, Cotingidae), female body size varied with the mating system and tended to be larger in species with intense sexual selection among males. This association may reflect a correlated genetic response in the "unselected" sex.

Although males were larger than females in most lekking and other polygynous birds, males were smaller in a few. These birds with "reversed" sexual size dimorphism included promiscuous bustards, a lekking snipe, a woodcock, small hummingbirds, small manakins, and a few cotingids. In all of these the male has an active aerial display. Apparently, male agility in display, not male fighting prowess, has been selected in these birds. In the other lekking birds, the observed size dimorphism is consistent with an hypothesis of intrasexual aggression and competition as a main route of sexual selection.

Behavioral mechanisms that underlie evolutionary sexual selection appear to involve both male-male competition and the choice of a mate by the female. In several lekking birds, female mate choice appears to be directed toward the more successful intrasexually aggressive males. Intrasexual competition may explain most instances of evolved sexual selection in lekking birds. Alternative sexual strategies, such as unsolicited copulations, female mimicry, and sociosexual parasitism by deceitful, apparently noncompetitive males, are uncommon in birds.

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