

TAIL ORNAMENTATION, SIZE DIMORPHISM AND WING LENGTH IN THE GENUS *EUPLECTES* (PLOCEINAE)

STAFFAN ANDERSSON¹ AND MALTE ANDERSSON

Department of Zoology, University of Göteborg, Medicinaregatan 18 S-413 90 Göteborg, Sweden

ABSTRACT.—Sexual wing dimorphism in relation to tail ornaments and body size was studied in the strikingly sexually dimorphic widowbirds and bishops (*Euplectes*) of the African tropics. Seven widowbirds grow long tails, varying from 7 cm in Fan-tailed Widowbird (*E. axillaris*) to 0.5 m in the Long-tailed Widowbird (*E. progne*). Aerodynamic drag increases with tail length, and adaptations to compensate for this cost might be expected (e.g. increasing wing length), a prediction that was supported among the widowbirds. After controlling for overall size dimorphism (estimated by tarsus length), 70% of the variation in residual wing dimorphism among the widowbirds was explained by tail dimorphism. Bishops were more dimorphic in wing length than expected, which may be related to their slow display flight. The results suggest caution in using wing length alone for interspecific comparisons of sexual size dimorphism. Based on tarsus length, the lekking *E. jacksoni* is more size dimorphic than the average of its congeners, in contrast to what has been concluded in previous studies based on wing length. Received 13 May 1993, accepted 2 July 1993.

SEXUALLY SELECTED characters, such as the elongated tails or the exaggerated displays of some birds, are expected to evolve until their mating advantages are balanced by costs (Fisher 1930), like predation or physiological constraints (Harvey and Bradbury 1991, Andersson 1994). At this dynamic equilibrium, morphological or behavioral adaptations that reduce the costs (hence, improve survival and allow further exaggeration of the trait) can be expected to evolve.

Two such indirect effects of sexual selection on avian morphology have recently been reported. Hedenström and Möller (1992) used aerodynamic theory to predict morphological adaptations to the demands of song flight. Consistent with their predictions, they found greater sexual dimorphism in wing span and wing area in eight passerines with song flight than in related species without this (supposedly sexually selected) behavior. Evans and Thomas (1992) estimated the aerodynamic costs of elongated tails in three species of sunbirds (*Nectarinia* spp). An increased tail area was shown to affect the aerodynamics in several ways, but most importantly increase the drag on the bird, which is a major component of flight cost (Norberg 1990). This cost should be particularly strong for birds with graduated tail ornaments (i.e. in

which all rectrices are elongated) compared to pin tails and fork tails (Balmford et al. 1993). As predicted based on higher energy costs of flight, sunbirds with experimentally elongated tails spent less time flying than controls (Evans and Hatchwell 1992). Based on a correlation between wing length and tail length in one of the species (*Nectarinia johnstoni*), Evans and Hatchwell (1992) suggested that the sunbirds compensate for the energetic costs of a long tail by increasing wing span.

Likewise, intraspecific relationships between ornamental tail length and wing length have been found in the Long-tailed Widowbird (*Euplectes progne*; Craig 1989) and Jackson's Widowbird (*E. jacksoni*; Andersson 1992a), suggesting similar compensations for the cost of carrying long tails. In particular, the exceptionally long wings of the Long-tailed Widowbird have made it an outlier in comparative studies of sexual size dimorphism based on wing length (Payne 1984)

In this paper, we investigate the possibility that sexual dimorphism in wing length in eight widowbird species is a sexually selected adaptation to compensate for the aerodynamic costs of tail ornamentation. We also discuss the relationship between sexual size dimorphism estimated from wing-length data and that estimated from tarsus length, and the relationship between size dimorphism and body size. Sexual selection and, hence, sexual dimorphism are believed to be particularly strong in lek mating

¹ Present address: Department of Biology 0116, University of California at San Diego, La Jolla, California 92093, USA.

systems, but the comparative evidence is inconclusive, and exceptions abound (Payne 1984, Höglund 1989, Trail 1990, Oakes 1992). For example, the only lek breeder in this genus, Jackson's Widowbird, was reported as no more size dimorphic than its resource-defense polygynous congeners (Payne 1984, Höglund 1989, Oakes 1992). These comparisons were based on wing lengths, and we discuss the validity of these conclusions and the new patterns that emerge from using tarsus lengths instead.

The widowbirds (formerly *Coliuspasser*) together with the bishops form the genus *Euplectes*, a group of 16 small (13–45 g) granivorous weaverbirds (subfamily Ploceinae) of the African tropics (Delacour and Edmond-Blanc 1933, Hall and Moreau 1970). All species are similar in general biology and behavior (Craig 1980) and, obviously, closely related as hybridization occurs in captivity (Colahan and Craig 1981). All *Euplectes* are strikingly sexually dimorphic in plumage. Breeding males have black body plumage with patches of bright red, yellow, or white. The male bishops are the most brilliantly colored and have a short tail, while male widowbirds replace the tail feathers during the pre-breeding molt, and grow graduated ornamental tails of various lengths. Females are in most cases noticeably smaller, streaky buff or brown, and difficult to distinguish in the field. Non-breeding males resemble the females but in some species retain part of the nuptial coloration on rump or wings.

Habitat preferences range from reed beds and savanna with sparse bushes through to open grassland, and probably all species are polygynous (Craig 1980). Except in the lek-breeding Jackson's Widowbird, males defend nesting territories and participate to some extent in nest building, but not (or very rarely) in incubation or feeding.

The tail ornaments vary greatly in size, from the slightly elongated 7-cm tail in the male Fan-tailed Widowbird (*E. axillaris*) to the 50-cm plumes trailing behind the male Long-tailed Widowbird—more than four times his body length and one of the most extreme avian adornments. For the Long-tailed Widowbird (Andersson 1982) and the lekking Jackson's Widowbird (20-cm tail; Andersson 1989, 1992b) there is evidence that tail length is a cue used by females in mate choice. It seems reasonable to assume that the long tails of male widowbirds generally are sexually selected, probably

through female choice, but in some cases may also function as agonistic signals. The long tails are of the graduated type that should handicap flight considerably (Balmford et al. 1993). In this paper we test the prediction that adaptations to reduce such costs have evolved in the widowbirds.

METHODS

Table 1 gives the biometric data used for each species. Data were obtained by S.A. primarily from the collection of bird skins in the National Museums of Kenya, Nairobi, and (for *E. hartlaubi psammocromius*) in the British Museum of Natural History, Tring. Specimens that could not unequivocally be assigned by sex or species were excluded. As some samples, particularly of females, were very small or equivocal (uncertain sexing and/or species identification), we included data from the literature (Maclean 1988, Craig 1989). For tarsus and tail length of *albonotatus* and *macrourus*, MacLean (1988) did not give sample sizes. Measurements of *afer* and *fransiscanus* were provided by A. J. F. K. Craig. The smallest samples included are for *gierowii* females (2), and *macrourus* males (4) and females (4). All other samples are larger than five. Due to lack of data, three species (Golden-backed Bishop [*E. aureus*], Fire-fronted Bishop [*E. diadematus*] and Red Bishop [*E. orix*]) were excluded from the analysis. Most *Euplectes* are widespread in Africa and some have geographically isolated populations and subspecies (Hall and Moreau 1970, Mackworth-Praed and Grant 1985). When applicable, the full names of the subspecies included in this analysis are given in Table 1. For one species, the Long-tailed Widowbird, there were large sample sizes for more than one of the geographically isolated populations in Craig (1989), of which we randomly selected one (*E. progné delamerei*) by throwing a die. However, we also made sure that inclusion of any of the other two did not significantly affect the results. The scientific and common names used follow Sibley and Monroe (1990).

On the museum skins, tarsus length was measured with calipers as the distance from the middle of the intertarsal joint to the distal edge of the last complete tarsal scale (i.e. before the toes begin). Wing (chord) length was measured with a ruler as the distance between the bend of the wing and the tip of the longest primary. The dry wing chords of the museum skins could not be flattened against the ruler to the extent that is common practice when measuring live birds (Svensson 1975), producing a slight underestimate (1–2 mm) of absolute wing length, but not affecting the sexual dimorphism as the sexes were treated equally. For tail length a thin ruler was positioned under the upper tail coverts such that it stopped at the base of the feathers, thus providing a measurement of distance from there to the tip of the longest rectrix.

We calculated relative dimorphism as the natural

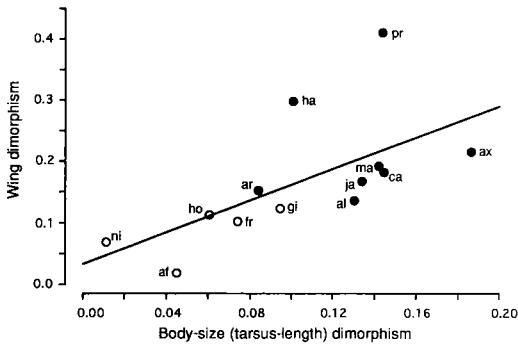


Fig. 1. Sexual dimorphism ($\ln[\text{male trait}/\text{female trait}]$) in wing length regressed on sexual dimorphism in tarsus length (indicating body size) for 13 *Euplectes* species. Bishops denoted by open and widowbirds by filled circles. First letters of species names given (see Table 1). Test of regression: $F_{1,12} = 7.1$, $P = 0.022$, $R^2 = 0.39$.

\log of [male trait/female trait] (e.g. Gaulin and Sailer 1984, Björklund 1990). As an estimate of species size we used female size (i.e. natural log of female tarsus length). The bivariate relationships were explored with linear regressions, and tested with analyses of variance and Spearman rank correlations. Unfortunately, there is no phylogeny available for *Euplectes*, which is why we treated the species as independent data points. Depending on the degree of evolutionary inertia of the investigated traits and the details of the true phylogeny, this might have unduly inflated our sample size (e.g. see Harvey and Pagel 1991), but we still find the trends worth reporting.

RESULTS AND DISCUSSION

Due to an aerodynamically functional relationship between wing span and body mass, wing-length tends to increase relative to body size within and among bird species (Norberg 1990). As expected, sexual dimorphism in wing length among the widowbirds and bishops was positively related to dimorphism in tarsus length (Fig. 1). However, the fit was not very close ($R^2 = 0.39$) and, although some of the remaining variation certainly is due to measurement errors, biased sampling, etc., other factors also seem to be involved.

This suggests that wing dimorphism might be a misleading index of sexual size dimorphism. For example, the three top-ranking species as regards to wing dimorphism (*progne*, *hartlaubii*, and *axillaris*, respectively) rank 3, 7, and 1, respectively, in size dimorphism as estimated from tarsus length. The only lekking species in

the genus, *jacksoni*, is interesting with respect to whether lek mating promotes strong sexual dimorphism. In three comparative studies (Payne 1984, Höglund 1989, Oakes 1992) with different approaches but all based on wing-length data, *jacksoni* was included as being no more dimorphic than its congeners. For example, Oakes (1992) used continuous data and compared dimorphism of lekking species with the average dimorphism of their congeners. As in his results, we found no difference in wing dimorphism between *jacksoni* and its congeners ($t_{11} = 0.03$, $P = 0.97$), but tarsus dimorphism did differ ($t_{11} = -2.2$, $P = 0.046$). Even so, it is doubtful whether this should be considered as supporting a relationship between lekking and sexual size dimorphism in this genus (*jacksoni* still only ranks 5); however, it clearly shows that the inclusion of tarsus length may yield rather different conclusions in interspecific comparisons of size dimorphism. Tarsus length may be more suitable than wing length in this respect, as it is a fixed skeletal trait and, generally, a better index of avian body size (Freeman and Jackson 1990, Björklund 1991). However, like any other univariate measure of external morphology, tarsus length should also be used with caution. A composite measure based on a number of skeletal characters would be preferable (Freeman and Jackson 1990), but it was not available in the present study. Unfortunately, skeletons are generally rarely preserved in the museum collections.

Sexual size dimorphism in many animals increases with body size (Andersson 1994). However, there was no such trend in *Euplectes*, or in bishops or widows treated separately (tarsus dimorphism vs. $\ln[\text{female tarsus length}]$: bishops, $r_s = 0.50$, $n = 5$, $P = 0.32$; widows, $r_s = -0.04$, $n = 8$, $P = 0.92$; all, $r_s = 0.37$, $n = 13$, $P = 0.20$).

All else being equal, the cost of flying should increase with the length (and hence area) of the tail, and males might through adaptation have countered this cost by increased wing span (Evans and Thomas 1992). A simple test of this prediction is to regress the residual wing dimorphism from Figure 1 on the sexual dimorphism in tail length (Fig. 2). The regression for all species (line a in Fig. 2) is significant but does not explain more than one-half of the variation ($R^2 = 0.51$), mainly because the bishops showed stronger wing dimorphism than would be expected from their short tails. The heavy dependence of the regression on two species,

TABLE 1. Wing, tarsus, and tail lengths (mm) of males and females (*n* in parentheses), and degrees of sexual dimorphism ($\ln[\text{male trait}/\text{female trait}]$) for 13 *Euplectes* species

Code	Euplectes species	Wing				Tarsus				Tail				Dimor- phism	Source
		Male		Female		Male		Female		Male		Female			
		Dimor- phism	Female	Male	Dimor- phism	Female	Male	Dimor- phism	Female	Male	Dimor- phism	Female			
af	<i>E. afer</i> (Yellow-crowned Bishop)	0.018	56 (11)	18.0 (42)	0.045	17.2 (11)	34 (42)	0.030	33 (11)	A. J. F. K. Craig (pers comm.)					
al	<i>E. a. albonotatus</i> (White-winged Widowbird)	0.135	66 (6)	20.5	0.130	18.0	78	0.614	42	MacLean (1988)					
ar	<i>E. ardens laticauda</i> (Red-naped Widowbird)	0.151	77 (16)	23.7 (16)	0.084	21.8 (14)	156 (16)	1.065	54 (14)	Nairbo museum					
ax	<i>E. a. axillaris</i> (Fan-tailed Widowbird)	0.214	88 (14)	23.5 (10)	0.187	19.5 (6)	68 (10)	0.494	42 (6)	MacLean (1988)					
ca	<i>E. capensis xanthomelas</i> (Yellow-rumped Widowbird)	0.185	76 (15)	64 (8)	0.145	22.1 (8)	59 (15)	0.225	47 (8)	Nairobi museum					
fr	<i>E. franciscanus</i> (Orange Bishop)	0.102	62 (94)	56 (65)	0.074	18.3 (65)	36 (94)	0.087	33 (65)	A. J. F. K. Craig (pers comm.)					
gi	<i>E. gierowii ansorgei</i> (Black Bishop)	0.122	87 (6)	77 (2)	0.094	27.0 (2)	65 (6)	0.214	52 (2)	Nairobi museum					
ha	<i>E. hartlaubi psammocromius</i> (Buff-shouldered Widowbird)	0.298	109 (12)	81 (7)	0.101	22.2 (7)	204 (12)	1.534	44 (7)	British museum, Tring					
ho	<i>E. hordeacea</i> (Black-winged Bishop)	0.112	74 (11)	66 (8)	0.061	22.1 (8)	44 (11)	0.157	38 (8)	Nairobi museum					
ja	<i>E. jacksoni</i> (Jackson's Widowbird)	0.166	89 (7)	75 (6)	0.134	26.7 (6)	177 (6)	1.307	48 (6)	Nairobi museum					
ma	<i>E. m. macrourus</i> (Yellow-shouldered Widowbird)	0.186	82 (4)	68 (4)	0.143	19.5	112	0.791	51	MacLean (1988)					
ni	<i>E. nigroventris</i> (Zanzibar Bishop)	0.069	58 (10)	54 (6)	0.011	19.2 (6)	30 (9)	-0.049	32 (6)	Nairobi museum					
pr	<i>E. progne delameri</i> (Long-tailed Widowbird)	0.409	139 (33)	93 (10)	0.144	26.0 (10)	510 (33)	2.098	63 (10)	Craig (1989)					

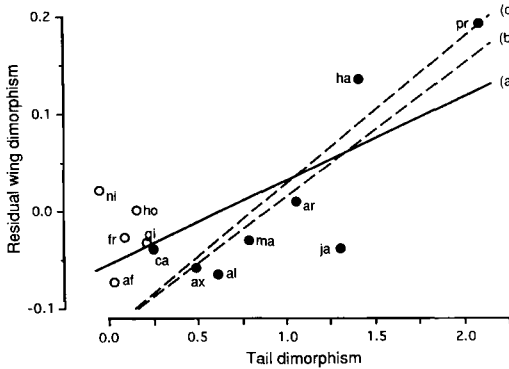


Fig. 2. Residual sexual dimorphism in wing length (from regression on body size dimorphism; Fig. 1) plotted against sexual dimorphism in (nuptial) tail length. Separate regression lines refer to: (a) all species; (b) the "subgenus" of widowbirds (filled circles); and (c) widowbirds with flight display (i.e. excluding *jacksoni*). First letters of species names given (see Table 1). Tests of regressions: (a) $F_{1,12} = 11.3$, $P = 0.006$, $R^2 = 0.51$; (b) $F_{1,7} = 15.1$, $P = 0.008$, $R^2 = 0.72$; (c) $F_{1,6} = 34.2$, $P = 0.002$, $R^2 = 0.87$.

hartlaubi and *progne*, is evident in Figure 2 and from the nonsignificant rank correlation ($r_s = 0.29$, $P = 0.31$).

Restricting the relationship to the widowbirds (among which males of all species but *capensis* have elongated nuptial tails), the relationship is stronger (line b in Fig. 2) with 72% of residual wing dimorphism being explained by tail dimorphism. The rank correlation bordered on significance in spite of the small sample ($r_s = 0.71$, $P = 0.059$). This is consistent with the prediction that widowbird males have evolved longer wings (thereby increasing wing area and decreasing wing loading) to compensate for the cost of the long tail. Even if this interpretation turns out to be correct, however, it does not explain the relatively long wings of most male bishops, and the shorter than expected wings of *jacksoni*.

Apart from elongated tails, another likely selection pressure on nuptial wing morphology is the type and extent of flight display. Hedeström and Möller (1992) gave a detailed account of the influence of various morphological traits, including wing span, on different aspects of passerine song flight. Among other things they predicted that if flapping-flight endurance is important, selection should favor increased wing span. The nature of the flight display and the strength of sexual selection for display fea-

tures in most species of *Euplectes* has not been documented in enough detail for even a tentative ranking of the aerodynamic demands on morphology, but a few intriguing observations are worth noting. First, all bishops (including the presumed widowbird *capensis*, also called the Yellow Bishop) seem to perform some version of a "bumble flight" (Craig 1980); the colored feathers of the back are "erected into a great brilliant puff as the birds drone slowly across their territories on rapidly and noisily vibrating wings" (Emlen 1957). The costs of forward flight increase dramatically when speed decreases from normal transport towards slow flight and hovering (Norberg 1990). Decreased wing loading through longer and broader wings is a common morphological adaptation to slow flight (Norberg 1990), for example in many harriers (*Circus* spp.) with slow search flights. The slow bumble flight, thus, may be one reason for the cluster of bishops at a residual wing dimorphism similar to the medium-tailed widowbird species (Fig. 2). It would be particularly suggestive if the flight display of *nigroventris* is either more laborious or performed more frequently than those of the other bishops and, conversely, if the opposite were true for *afer*.

The shorter than expected wings of *jacksoni* may be related to the lack of a flight display in this species. As earlier suggested, the longer wings in nuptial compared to subadult males could be a morphological adaptation to the cost of the jump display (Andersson 1993) and the cost of carrying the tail in transport flight. However, the costs of the slow display flight in, for example, the similarly sized *progne*, might be a stronger selection pressure on wing span. In any case, when we restricted the analysis to include only display-flying widowbirds (line c in Fig. 2), the proportion of variance explained was 87%.

If the true phylogeny of *Euplectes* had been known and controlled for in the above regressions, the sample sizes (i.e. independent evolutionary events) might have been smaller, perhaps making the relationships statistically nonsignificant. No phylogeny for this genus is available. Hall and Moreau (1970) suggested a number of "superspecies" (e.g. *hartlaubi* and *progne* as one, and *macrourus* and *albonotatus* as another). However, they based this on similarities in male nuptial plumage such as tail length, and controlling for this phylogeny would by definition deflate our data. For example, *progne*

and *hartlaubi psammocromius* might then have long wings and tails because their recent ancestor evolved these traits (i.e. making it one and not two independent associations of the two traits). On the other hand, within both the superspecies pairs—*hartlaubi/progne* and *macrourus/albonotatus*—the positive relationship between wing and tail dimorphism is supported.

Another alternative interpretation of the relationship between tail and wing dimorphism is that it results from a genetic correlation between different aspects of plumage growth (i.e. that selection for longer male tails produces a [nonadaptive] increase in male wing length). Taking it one step further, the entire variation in tail and wing length might be attributed to genetic drift. This possibility could not be refuted by Savalli (1993), who applied the test by Turelli et al. (1988) to *Euplectes* tail lengths. It seems, however, unlikely that drift alone can explain the tenfold range in *Euplectes* tail lengths.

In sum, much of the interspecific variation in widowbird wing length seems to be the result of sexually selected adaptations to compensate for costs incurred by tail ornamentation. As a consequence, wing lengths may give misleading estimates of sexual dimorphism in overall body size among widowbirds and bishops. This might apply also to other avian groups with aerodynamically handicapping displays or ornaments.

ACKNOWLEDGMENTS

We thank the staff at the Nairobi Museum's Ornithology Department, and the British Museum of Natural History (Tring) for access to the collections of bird skins, Mats-Ola Larsson for practical help, and A. Balmford and two anonymous reviewers for valuable comments on the manuscript. A. J. F. K. Craig commented on an earlier version of this manuscript, and also provided measurements for *E. afer* and *fransiscanus*. Financial support to S.A. came from the Ernst Collianders, Hierta-Retzius, Kungl. och Hvitfeldtska, and J. A. Wahlbergs foundations, Wenner-Gren Center, and the Royal Society of Arts and Sciences in Gothenburg. M.A. was supported by the Swedish Natural Sciences Research Council.

LITERATURE CITED

- ANDERSSON, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature* 299: 818-820.
- ANDERSSON, M. 1994. Sexual selection. Princeton Univ. Press, Princeton, New Jersey. In press.
- ANDERSSON, S. 1989. Sexual selection and cues for female choice in leks of Jackson's Widowbird *Euplectes jacksoni*. *Behav. Ecol. Sociobiol.* 25:403-410.
- ANDERSSON, S. 1992a. Lek mating and sexual selection in Jackson's Widowbird (*Euplectes jacksoni*). Ph.D. dissertation, Univ. Göteborg, Göteborg, Sweden.
- ANDERSSON, S. 1992b. Female preference for long tails in lekking Jackson's Widowbirds: Experimental evidence. *Anim. Behav.* 43:379-388.
- ANDERSSON, S. 1993. Sexual dimorphism and modes of sexual selection in lekking Jackson's Widowbirds *Euplectes jacksoni*. *Biol. J. Linn. Soc.* 49:1-17.
- BALMFORD, A., A. L. R. THOMAS, AND I. L. JONES. 1993. Aerodynamics and the evolution of long tails in birds. *Nature* 361:628-631.
- BJÖRKLUND, M. 1990. A phylogenetic interpretation of sexual dimorphism in body size and ornament in relation to mating systems in birds. *J. Evol. Biol.* 3:171-183.
- BJÖRKLUND, M. 1991. Patterns of morphological variation among cardueline finches (Fringillidae: Carduelinae). *Biol. J. Linn. Soc.* 43:239-248.
- COLAHAN, B. D., AND A. J. F. K. CRAIG. 1981. *Euplectes* hybrids. *Ostrich* 52:58-59.
- CRAIG, A. J. F. K. 1980. Behaviour and evolution in the genus *Euplectes*. *J. Ornithol.* 121:144-161.
- CRAIG, A. J. F. K. 1989. Tail length and sexual selection in the polygynous Longtailed Widow (*Euplectes progne*): A cautionary tale. *S. Afr. J. Sci.* 85: 523-524.
- DELACOUR, J., AND F. EDMOND-BLANC. 1933. Monographie des veuves (Revision des genres *Euplectes* et *Vidua*). *Oiseau Rev. Fr. Ornithol.* 3:519-562, 687-726.
- EMLEN, J. T., JR. 1957. Display and mate selection in the whydahs and bishop birds. *Ostrich* 28:202-213.
- EVANS, M. R., AND B. J. HATCHWELL. 1992. An experimental study of male adornment in the Scarlet-tufted Malachite Sunbird: II The role of the elongated tail in mate choice and experimental evidence for a handicap. *Behav. Ecol. Sociobiol.* 29:421-427.
- EVANS, M. R., AND A. L. R. THOMAS. 1992. The aerodynamic and mechanical effects of elongated tails in the Scarlet-tufted Malachite Sunbird: Measuring the cost of a handicap. *Anim. Behav.* 43:337-347.
- FISHER, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.
- FREEMAN, S., AND W. M. JACKSON. 1990. Univariate metrics are not adequate to measure avian body size. *Auk* 107:69-74.
- GAULIN, S. J. C., AND L. D. SAILER. 1984. Sexual dimorphism in weight among the primates: The relative impacts of allometry and sexual selection. *Int. J. Primatol.* 5:515-535.
- HALL, B. P., AND R. E. MOREAU. 1970. An atlas of

- speciation in African passerine birds. British Museum of Natural History, London.
- HARVEY, P. H., AND J. W. BRADBURY. 1991. Sexual selection. Pages 199–233 in *Behavioural ecology: An evolutionary approach* (J. R. Krebs and N. B. Davies, Eds.). Blackwell, Oxford.
- HARVEY, P. H., AND M. D. PAGEL. 1991. *The comparative method in evolutionary biology*. Oxford Univ. Press, Oxford.
- HEDENSTRÖM, A., AND A. P. MÖLLER. 1992. Morphological adaptations to song flight in passerine birds: A comparative study. *Proc. R. Soc. Lond. B. Biol. Sci.* 247:183–187.
- HÖGLUND, J. 1989. Size and plumage dimorphism in lek-breeding birds: A comparative analysis. *Am. Nat.* 134:72–87.
- MACKWORTH-PRAED, C. W., AND C. H. B. GRANT. 1985. *Birds of eastern and north-eastern Africa*. Longmans, London.
- MACLEAN, G. L. 1988. *Roberts' birds of southern Africa*. New Holland Publishers, London.
- NORBERG, U. M. 1990. *Vertebrate flight*. Springer-Verlag, Berlin.
- OAKES, E. J. 1992. Lekking and the evolution of sexual dimorphism in birds: Comparative approaches. *Am. Nat.* 140:665–684.
- PAYNE, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithol. Monogr.* 33.
- SAVALLI, U. M. 1993. An application of the neutral model to the evolution of tail length in the genus *Euplectes* (Aves, Ploceidae). *Evolution* 47:696–699.
- SIBLEY, C. G., AND B. L. MONROE, JR. 1990. *Distribution and taxonomy of the birds of the world*. Yale Univ. Press, New Haven, Connecticut.
- SVENSSON, L. 1975. *Identification guide to European passerines*. Naturhistoriska Riksmuseet, Stockholm.
- TRAIL, P. W. 1990. Why should lek-breeders be monomorphic? *Evolution* 44:1837–1852.
- TURELLI, M., J. H. GILLESPIE, AND R. LANDE. 1988. Rate tests for selection on quantitative characters during macroevolution and microevolution. *Evolution* 42:1085–1089.