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# On avian asymmetry: evidence of natural selection for symmetrical tails and wings in birds

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## SUMMARY

Fluctuating asymmetry (FA), or minor deviations from perfect bilateral symmetry in otherwise symmetrical structures, may reflect exposure to environmental or genetic stresses during trait development. Consequently, several authors have recently suggested that FA in elaborate secondary sexual characters such as the long tails of some birds could play an important role in sexual selection, perhaps by being used as a reliable signal of phenotypic quality during mate choice. Here we examine an alternative possibility: that the extent of FA in long tails and wings of birds is constrained primarily by natural selection for aerodynamic efficiency. Predictions developed from aerodynamic theory were tested by using comparative data from 63 long-tailed species. Data on FA in wing lengths confirmed that aerodynamic requirements may underlie patterns of FA in lifting surfaces: species that spend much of their time flying and those that migrate had more symmetrical wings than other birds. There was also substantial variation in the extent of tail FA. As predicted, long-tailed species with aerodynamically functional forked tails had more symmetrical outer tail feathers than those with other long tail types in which feather symmetry has less impact on flight performance. However, in common with several other recent studies, our data failed to support the predictions of the sexual selection hypothesis. In sexually dimorphic species, there was no evidence that tail asymmetry was greater in the longer-tailed sex, nor was tail FA negatively correlated with tail length. Our results therefore suggest that patterns of FA in long tails and wings may often be better understood in a context of natural rather than sexual selection.

## 1. INTRODUCTION

Fluctuating asymmetry (FA) is defined as small, random deviations from symmetry in otherwise bilaterally symmetrical traits, and can arise because individuals vary in their ability to develop both sides of their bodies identically (Van Valen 1962; Palmer & Strobeck 1986). Developmental homeostasis may be disrupted by a variety of environmental and genetic stresses, such as exposure to parasites and pollutants, a loss of heterozygosity, perhaps through inbreeding, and the breakdown of coadaptations through hybridization or invasion by new mutants (Leary & Allendorf 1986; Parsons 1990; see also Polak 1993). FA has therefore received considerable attention from geneticists and conservation biologists interested in estimating the fitness of populations (Leary & Allendorf 1986; Wayne *et al.* 1986; Jones 1987; Parsons 1990). Recently, it has been suggested that FA may also play a role in sexual selection (Møller 1991*a*, 1992*a*; Thornhill 1992*a*, *b*). Elaborate secondary sexual characters such as weapons and ornaments are sometimes costly to produce, and the costliness of these traits may

be reflected in relatively high FA values (Møller & Höglund 1991; Møller 1992*b*). Because only high-quality individuals can develop costly structures symmetrically, the degree of FA in such traits may thus constitute a reliable indicator of an individual's viability, which might be assessed during intersexual mate choice or intrasexual contests over access to mates.

To date, two principal lines of evidence support the idea that FA may be important in sexual selection. First, intraspecific analyses of several traits thought to be under directional sexual selection, including long tails and spurs in birds, and horns in beetles, show that the absolute difference between left and right values of these characters (absolute FA, or AFA) is negatively correlated with their mean value (Manning & Hartley 1991; Møller 1991*a*, 1992*b*; Møller & Höglund 1991). This is clearly consistent with the suggestion that high-quality individuals develop both symmetrical and large secondary sexual characters, and means that trait asymmetry (as well as or instead of trait size) could potentially be used for assessing mating partners or competitors. Second, in barn swallows, *Hirundo rustica*, where females prefer long-tailed mates and male tail length correlates negatively with tail AFA (Møller 1988, 1991*a*), experimental manipulations show that symmetry in the outer feathers of their forked tails confers enhanced reproductive success on males, indepen-

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dently of the effects of tail length per se (Møller 1992*a*). One explanation of this is that females have a specific preference for mates with symmetrical tails which has evolved because tail symmetry is associated with heritable variation in male viability (Møller 1992*a*).

However, consideration of the aerodynamic properties of long forked tails suggests an alternative interpretation of these experimental results. Application of lifting surface theory shows that the lift generated by birds' tails is proportional to the square of their maximum continuous span; any area distal to the point of maximum width adds drag (in proportion to area), but not lift (Thomas 1993). From an aerodynamic perspective, the optimal shape for a tail is therefore triangular when spread, which in turn means that it is forked when closed (Thomas 1993; Balmford *et al.* 1993*a*). But although a forked tail can generate the maximum lift for a given drag, it has a major disadvantage: it is particularly vulnerable to asymmetric damage of its exposed outer feathers. Such asymmetry considerably reduces the lift that the tail generates, and also results in an asymmetric distribution of lift, greatly impairing a bird's manoeuvrability (Balmford & Thomas 1992; Thomas 1993; see also Møller 1991*b*). Given the substantial impact of asymmetry on flight performance, we would argue that FA in forked tails might be limited principally by natural rather than sexual selection. Moreover, in so far as the ability of male swallows to obtain mates is affected by tail asymmetry, this may be because of its general consequences for flight efficiency, rather than because of a specific, evolved female preference for symmetrical mates per se (Balmford & Thomas 1992).

In this paper we broaden the scope of this question, and examine the relative roles of sexual selection and natural selection for aerodynamic efficiency in explaining patterns of tail asymmetry in a large sample of long-tailed species. We present morphometric data obtained from more than 1100 museum skins to test a series of predictions generated by these competing hypotheses.

## 2. PREDICTIONS

The principal aerodynamic function of birds' tails as well as their wings is to generate lift (Thomas 1993). Lateral asymmetry in these lifting surfaces can cause both a loss of lift, and an asymmetric distribution of lift, with large associated yawing and rolling forces and a substantial reduction in manoeuvrability (Balmford & Thomas 1992; Thomas 1993). Thus natural selection should act to minimize FA in tails and wings, but we predict that the strength of such counterselection (and hence the extent of FA) should vary with both flight behaviour and tail shape, as follows.

1. Birds clearly vary in the extent to which they rely on flight. For instance, some species are largely terrestrial, whereas others spend a considerable proportion of their time flying and depend on aerial agility to obtain their food. Similarly, birds vary in whether they engage in costly long-distance migration flights. Thus if natural selection for aerodynamic efficiency does in general constrain the extent of FA in avian

lifting surfaces, then asymmetry in wing length should decrease as flight importance increases, and wing FA should be lower in migratory than in non-migratory species. Clearly, in interspecific comparisons such as these, FA values must be standardized to account for species differences in wing and tail size by calculating relative FA (RFA, defined as the absolute difference in left and right measurements divided by their mean value).

2. Long tails of birds can be classified into three basic types (figure 1*a*; Balmford *et al.* 1993*a*; see Thomas (1993) for a discussion of the optimization of tail morphology). In long graduated tails, many feathers are elongated beyond the point of maximum tail width, but the central feathers are longer than any others. In pintails, only the central feathers are elongated. Clearly, in both of these tail types, the outer

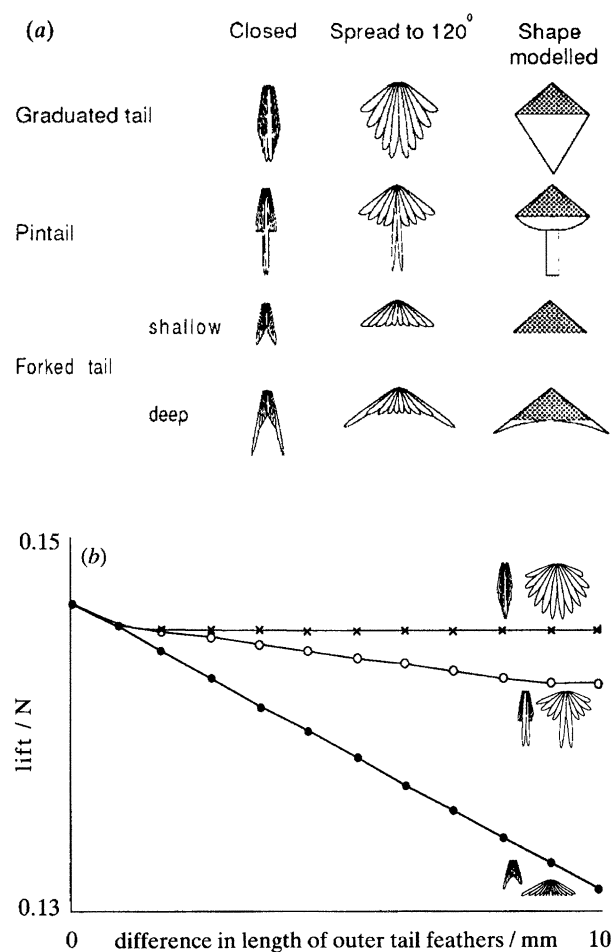


Figure 1. (*a*) Different types of long tails, giving their shapes when closed, and when spread as they would be to generate lift. The right-hand diagrams show the shapes used in aerodynamic analyses (Balmford *et al.* 1993*a*; Thomas 1993), with the aerodynamically functional, lift-generating portion of each tail shown as a stippled triangle. (*b*) Loss of lift as a function of increasing asymmetry in outer tail feathers, derived from a lifting surface model of tail aerodynamics (Thomas 1993). The plot gives results for a graduated tail (top), pintail (middle) and forked tail (bottom). All tails have outer rectrices 100 mm long, an apex spreading angle of 120°, and an angle of incidence to the local flow direction of 10°. Precise details of the curves depend on the exact shapes used in the model, but the qualitative differences between tail types hold across a broad array of conditions.

feathers contribute to the triangular, aerodynamically functional part of the spread tail (see figure 1*a*). Nevertheless, asymmetry in these feathers will have only a slight effect on the lift generated by the tail, because the presence of many, more central feathers of similar length means that the outermost feathers contribute relatively little to the maximum width of the spread tail (figure 1*b*; see also Balmford & Thomas 1992). In contrast, in long forked tails, the outer feathers are longer than more central feathers, so that asymmetry in the outermost feathers results in a substantial decrease in maximum tail width and thus considerable loss of lift (figure 1*b*). Aerodynamic considerations therefore lead us to predict that RFA in the outermost feathers of long tails should vary with tail shape, and should be higher in species with long graduated tails or pintails than in species with long forked tails. (Note that it is more difficult to predict how the FA of the longest tail feathers varies with tail shape, as these occur in different positions on different tail types, and so vary not only in their aerodynamic significance, but also in their susceptibility to asymmetric damage).

3. It is also possible to subdivide long forked tails according to how deeply forked they are. As fork depth (the ratio of the longest: shortest feathers) increases, it becomes increasingly likely that the distal tips of the outermost feathers of a forked tail project beyond the maximum width of the tail, even when it is fully spread (figure 1*a*). Any asymmetry outside the lifting surface of a tail is of relatively little aerodynamic consequence because it has no effect on the distribution of lift, which is by far the most important force generated by the tail (Thomas 1993). We therefore predict that natural selection for symmetrical outer feathers should be relatively weak in the case of deep forks, and that the extent of RFA in the outermost feathers of long forked tails should increase with increasing fork depth.

In contrast, the hypothesis that asymmetry in long tails is used as a cue in intersexual mate choice or in intrasexual contests makes the following predictions (Møller 1991*a*, 1992*b*; Møller & Höglund 1991).

4. Because the full expression of elaborate sexually selected traits is likely to be extremely costly, the degree of FA in such structures may be greater than in naturally selected traits. Thus in birds with sexually selected long tails (in practice probably most long-tailed species except those that use their tails as props, or have shallow forks (Balmford *et al.* 1993*a*; Thomas 1993)), RFA in the longest tail feathers should be greater in the longer-tailed sex than in the other sex.

5. If FA in elaborate secondary sexual characters reliably reveals phenotypic quality, and only high-quality individuals develop such traits fully, then in the longer-tailed sex of long-tailed species, tail AFA should be negatively correlated with tail length.

### 3. METHODS

We tested these predictions by measuring museum skins of 63 different long-tailed species. For each species, we measured body length, left and right wing length, and the lengths of the left and right outermost and innermost tail feathers, on up to

ten males ( $\bar{x} = 9.37$ ) and ten females ( $\bar{x} = 8.78$ ) in full breeding plumage. We avoided including specimens in moult by rejecting any skins with fragments of blood quills, or with worn feathers opposite fresh feathers. Species were not included in analyses if we measured less than five specimens of the relevant sex. Measurements were made to within 0.1 mm by using vernier callipers (if  $< 100$  mm), or using a metal rule to within 1 mm (if  $> 100$  mm). We checked the repeatability of our measures by measuring all traits twice on ten male and ten female specimens of *Hirundo rustica*, selected at random. The repeatability of each measurement (calculated as  $r_1$ , the intraclass correlation coefficient; see Zar 1984) was consistently high: repeatability estimates for different traits varied from  $0.775 \pm 0.092$  to  $0.999 \pm 0.001$  (corresponding values for  $F_{1,19}$  ranged from 7.9 to 1552.2; all  $F$ -values were significant at two-tailed  $p < 0.0001$ ). Thus our measurements were accurate enough to assess subtle patterns of variation in asymmetry among the species sampled.

For each specimen we then calculated tail length (mean of longest left and right tail feathers) and AFA and RFA in wing length and outer and inner tail feather length. We also calculated relative tail length (tail length/body length). This is an appropriate technique for taking account of overall size differences between birds because comparative analyses controlling for phylogeny show that the length of lifting surfaces increases approximately isometrically with body length (Norberg 1990), and we have shown elsewhere that relative tail length does not increase with body length in either males or females of long-tailed species (Balmford *et al.* 1993*b*).

Our sample included one species (judged from illustrations in fieldguides to be that with the greatest relative tail length) from each of 50 long-tailed families. Because they were from different families, these species were then treated as independent points in subsequent tests of predictions 1, 2, 4 and 5 (see Harvey & Pagel 1991). Each species was classified according to the tail shape of the longer-tailed sex, and categorized according to 'flight importance' and whether or not it migrated by three experienced ornithologists blind to the tail length data. Flight importance categories were: (i) almost entirely terrestrial; (ii) largely terrestrial and feeding while clambering, but flying between food patches; (iii) resting often but relying on aerial manoeuvrability to obtain food; and (iv) largely aerial and feeding on the wing.

Lastly, to test prediction 3 by using Felsenstein's pairwise comparative method (Felsenstein 1985), our sample also included eight pairs of species from different families with long forked tails. The males of one species from each pair had a relatively deep fork, whereas males of the other species had a shallower fork. Pairs of species were roughly matched for male body size and relative tail length, but were otherwise selected at random.

### 4. RESULTS

#### (a) General patterns

Wings and inner and outer tail feathers all exhibited fluctuating asymmetry in our sample, as binomial tests on each species revealed that left-minus-right trait values did not differ significantly from zero (at two-tailed  $p < 0.05$ ).

The wings of long-tailed species were generally more symmetrical than their tails. Thus RFA values for wings were consistently lower than those for outer and inner tail feathers, for both males and females (Wilcoxon signed-ranks tests comparing wing and outer tail feather RFA, for males:  $z_{\text{corr}} = 5.83$ ,  $n = 48$  species pairs



Table 1. *Patterns of fluctuating asymmetry in tail and wing length in long-tailed birds*

(One species *Sylvioorthorhynchus desmursii*, has been omitted because of consistently small sample size. M, migratory; N, non-migratory.)

family	species	flight importance category	migration	tail shape	male wing RFA	female wing RFA	tail FA in longer-tail sex	
							outer feather RFA	$r_s$ (n) between longest feather AFA and tail length <sup>b</sup>
Phaethontidae	<i>Phaethon lepturus</i>	4	N	P	0.007	—	0.026 <sup>a</sup>	0.10 (5)
Fregatidae	<i>Fregata minor</i>	4	N	F	0.016	—	0.020	−0.50 (5)
Accipitridae	<i>Chelictinia ricourii</i>	3	M	F	0.006	0.005	0.010	—
Phasianidae	<i>Argusianus argus</i>	1	N	G	0.024	0.015	0.037	0.30 (10)
Jacanidae	<i>Hydrophasianus chirurgus</i>	1	N	P	0.021	0.009	0.021 <sup>a</sup>	−0.30 (8)
Stercorariidae	<i>Stercorarius longicaudus</i>	4	M	P	0.014	0.009	—	−0.36 (10)
Laridae	<i>Sterna paradisaea</i>	4	M	F	0.006	0.005	0.022	−0.24 (10)
Loriidae	<i>Chamosyna papou</i>	2	N	P	0.021	0.014	0.034	0.61 (7)
Psittacidae	<i>Polytelis longicauda</i>	2	N	P	0.016	0.013	0.017	−0.09 (10)
Musophagidae	<i>Corythaëola cristata</i>	2	N	G	0.006	0.010	0.024	0.01 (9)
Cuculidae	<i>Rhopodytes viridirostris</i>	2	M	G	0.009	0.020	0.016 <sup>a</sup>	0.22 (8)
Caprimulgidae	<i>Uropsalis lyra</i>	3	N	F	0.009	—	0.016	0.27 (10)
Hemiprocniidae	<i>Hemiprocne mystacea</i>	3	N	F	0.006	0.009	0.011 <sup>a</sup>	0.40 (10)
Trochilidae	<i>Trochilus polytmus</i>	3	N	F	0.013	0.014	0.018	−0.25 (10)
Coliidae	<i>Colius macrourus</i>	2	N	G	0.010	0.008	0.058	0.69 (10) <sup>c</sup>
Trogonidae	<i>Pharomachrus mocinno</i>	3	N	P	0.008	0.008	0.019	0.15 (10)
Alcedinidae	<i>Tanyptera sylvia</i>	3	N	P	0.010	0.015	0.018	0.28 (10)
Momotidae	<i>Baryphthengus ruficapillus</i>	3	N	G	0.007	0.010	0.025	0.11 (10)
Meropidae	<i>Merops orientalis</i>	3	M	P	0.012	0.007	0.006 <sup>a</sup>	−0.13 (10)
Coraciidae	<i>Coracias abyssinnica</i>	3	M	F	0.006	0.006	0.027	—
Brachypteracidae	<i>Uratornis chimaera</i>	1	N	G	0.007	0.010	0.025	—
Bucerotidae	<i>Berenicornis albirostris</i>	2	N	G	0.023	0.008	0.021	0.37 (10)
Eurylaimidae	<i>Psarisomus dalhousiae</i>	3	N	G	0.007	0.013	0.015 <sup>a</sup>	−0.23 (10)
Galbulidae	<i>Galbula dea</i>	3	N	G	0.012	—	0.027	−0.35 (5)
Tyrannidae	<i>Alecturus risorius</i>	3	M	P	0.011	0.008	0.022	0.17 (10)
Pipridae	<i>Chiroxiphia linearis</i>	2	N	P	0.011	0.006	0.012	−0.19 (10)
Cotingidae	<i>Phibalura flavirostris</i>	3	N	F	0.011	0.007	0.009	—
Hirundinidae	<i>Hirundo atrocaeruleus</i>	4	M	F	0.003	0.006	0.018	0.42 (10)
Motacillidae	<i>Motacilla clara</i>	2	M	F	0.006	0.009	0.014 <sup>a</sup>	—
Laniidae	<i>Corvinella melanoleuca</i>	3	M	G	0.009	0.006	0.016 <sup>a</sup>	0.01 (9)
Ptilogonatidae	<i>Ptilogonys caudata</i>	3	N	P	0.006	0.006	0.039	−0.35 (9)
Mimidae	<i>Mimus longicaudus</i>	2	N	G	0.007	0.010	0.009	−0.65 (10) <sup>c</sup>
Timaliidae	<i>Heterophasia picaoides</i>	2	N	G	0.012	0.011	0.024	0.17 (10)
Sylviidae	<i>Prinia crinigera</i>	2	N	G	0.011	0.021	0.025	0.40 (10)
Muscicapidae	<i>Copsychus malabaricus</i>	3	M	G	0.010	0.015	0.016	0.25 (10)
Maluridae	<i>Stipiturus malachurus</i>	2	N	G	0.023	0.026	0.032	−0.09 (10)
Monarchidae	<i>Terpsiphone paradisii</i>	3	N	P	0.006	0.006	0.007	−0.14 (10)
Aegithalidae	<i>Aegithalos caudatus</i>	2	N	G	0.009	0.008	0.027	−0.17 (10)
Nectariniidae	<i>Nectarinia johnstonii</i>	3	N	P	0.007	0.007	0.015	0.04 (10)
Menuridae	<i>Menura novaehollandiae</i>	1	N	G	0.022	—	0.030	0.11 (7)
Meliphagidae	<i>Promerops caffer</i>	2	N	G	0.018	—	0.023	0.04 (9)
Emberizidae	<i>Emberizoides herbicola</i>	2	N	G	0.012	0.015	0.018	0.43 (10)
Fringillidae	<i>Uragus sibiricus</i>	2	M	F	0.010	0.014	0.005	—
Estrildidae	<i>Uraeginthus granatinus</i>	2	N	G	0.005	0.013	0.014	−0.04 (10)
Ploceidae	<i>Vidua paradisaea</i>	2	N	P	0.016	0.007	0.040	0.06 (10)
Sturnidae	<i>Lamprotornis caudatus</i>	2	N	G	0.011	0.011	0.026	0.41 (10)
Dicruridae	<i>Dicrurus remifer</i>	3	N	F	0.009	0.008	0.016	0.17 (10)
Paradisaeidae	<i>Astrapia mayeri</i>	2	N	P	0.010	0.003	0.036	−0.60 (6)
Corvidae	<i>Crypsirina temia</i>	2	N	G	0.007	0.006	0.017	−0.45 (10)

<sup>a</sup> Female is the longer-tailed sex.  
<sup>b</sup> This excludes species with shallow forks.  
<sup>c</sup>  $p < 0.05$  (one-tailed).

with non-zero differences, two-tailed  $p < 0.0001$ ; for females,  $z_{\text{corr}} = 5.14$ ,  $n = 42$  species pairs, two-tailed  $p < 0.0001$ ; comparing wing and inner tail feather RFA, for males:  $z_{\text{corr}} = 3.59$ ,  $n = 46$  species pairs, two-tailed

$p < 0.001$ ; for females,  $z_{\text{corr}} = 3.72$ ,  $n = 40$  species pairs, two-tailed  $p < 0.001$ ). This result is consistent with the idea that the extent of FA in lifting surfaces is constrained primarily by natural selection for efficient

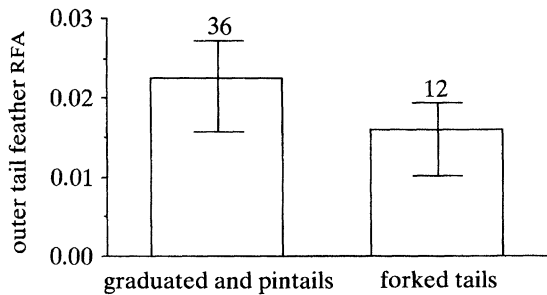


Figure 2. Relative fluctuating asymmetry in the outer tail feathers of species with long graduated and pintails, and species with long forked tails. The plot shows median values and interquartile ranges, and numbers indicate sample sizes.

flight, because aerodynamic theory demonstrates that a given level of RFA in wing length impairs flight far more than the same degree of RFA in tail length (A. L. R. Thomas, unpublished observations).

(b) Testing predictions

Analyses of interspecific variation in wing asymmetry revealed that the extent of FA in lifting surfaces varied as predicted with the importance of aerodynamic efficiency (see table 1; in these and all other tests of predictions, we cite one-tailed  $p$ -values because the predictions are unidirectional). When flight importance categories were pooled (because there were very few taxa from categories 1 and 4), we found that males of relatively terrestrial species (categories 1 and 2) exhibited consistently higher relative FA in wing length than did males of more aerial species (categories 3 and 4; Mann-Whitney U-test:  $z_{\text{corr}} = 2.41$ ,  $n_1 = 25$ , median RFA = 0.011;  $n_2 = 24$ , median RFA = 0.009; one-tailed  $p < 0.01$ ; table 1). This pattern was repeated for females ( $z_{\text{corr}} = 2.52$ ,  $n_1 = 23$ , median RFA = 0.011;  $n_2 = 20$ , median RFA = 0.008; one-tailed  $p < 0.01$ ; table 1). Similarly, species that rely on flight to migrate tended to have more symmetrical wings than non-migrant species, although this result was not significant for females (for males:  $z_{\text{corr}} = 1.71$ ,  $n_1 = 12$  migrant

species, median RFA = 0.009;  $n_2 = 37$  non-migrants, median RFA = 0.010; one-tailed  $p < 0.05$ ; for females:  $z_{\text{corr}} = 1.44$ ,  $n_1 = 12$  migrant species, median RFA = 0.008;  $n_2 = 31$  non-migrants, median RFA = 0.010; one-tailed  $p < 0.10$ ; see table 1).

Patterns of symmetry in tail feathers also matched our aerodynamic predictions. Thus considering outer tail feather asymmetry in 48 long-tailed species, RFA was higher in birds with graduated or pintails than in species with long forked tails (Mann-Whitney U-test comparing outer tail RFA in the longer-tailed sex:  $z_{\text{corr}} = 2.40$ ,  $n_1 = 36$  species with graduated or pintails, median RFA = 0.023;  $n_2 = 12$  fork-tailed species, median RFA = 0.016; one-tailed  $p < 0.01$ ; figure 2; see table 1). Outer feather asymmetry also varied as predicted among those species with long forked tails. In the pairwise analysis, in six out of eight species pairs, RFA in outer tail feathers was greater in the species with the deeper fork than in the species with the shallower fork (Wilcoxon signed-ranks test:  $z_{\text{corr}} = 1.78$ , one-tailed  $p < 0.05$ ; table 2).

However, our analysis of asymmetry in long tails provided no support for the suggestion that tail FA is important in sexual selection. Comparing the degree of asymmetry in the longest tail feathers of the two sexes, there was no tendency for RFA to be greater in the longer-tailed sex (Wilcoxon signed-ranks test:  $z_{\text{corr}} = 1.03$ ,  $n = 39$  species, n.s.; this analysis excludes species with long but shallow forks, as such tails are less likely to be the result of sexual selection (Balmford *et al.* 1993a)). Even when this sample was further restricted to those species with very pronounced sexual dimorphism in tail length, where the mean relative tail length of males was at least twice that of females, there was no difference between the sexes in RFA of their longest tail feathers (Wilcoxon test comparing RFA in the longer- against the shorter-tailed sex:  $z_{\text{corr}} = 0.28$ ,  $n = 8$  species, n.s.; not enough specimens were available for measuring RFA in both sexes of two other highly dimorphic species).

We also found no evidence that absolute FA in longest tail feathers was consistently negatively cor-

Table 2. Outer tail feather FA in relation to fork depth in eight families with long forked tails

family	species pair	male fork depth	male outer tail feather RFA
Accipitridae	<i>Chelictinia ricourii</i>	1.93	0.010
	<i>Elanoides forficatus</i>	2.53	0.011
Laridae	<i>Sterna melanogaster</i>	2.23	0.011
	<i>Sterna paradisaea</i>	2.54	0.022
Hemiprocnidae	<i>Hemiprocne comata</i>	1.92	0.013
	<i>Hemiprocne longipennis</i>	2.20	0.007
Trochilidae	<i>Polygonymus caroli</i>	1.37	0.008
	<i>Sappho sparganura</i>	2.95	0.014
Coraciidae	<i>Coracias caudata</i>	1.64	0.012
	<i>Coracias abyssinica</i>	1.95	0.027
Tyrannidae	<i>Muscipipra vetula</i>	1.45	0.010
	<i>Gubernetes yetapa</i>	3.62	0.010
Hirundinidae	<i>Hirundo rustica</i>	2.27	0.026
	<i>Hirundo smithii</i>	2.44	0.069
Dicruridae	<i>Dicrurus caerulescens</i>	1.30	0.008
	<i>Dicrurus macrocercus</i>	1.55	0.009

related with tail length (table 1). In 43 long-tailed species (again excluding those with shallow forks), correlations between AFA and tail length in the longer-tailed sex were negative in 18 cases, and positive in 25 cases. This pattern did not differ from a random distribution ( $\chi^2 = 1.14$ , d.f. = 1, n.s.). Moreover, only two correlation coefficients (one negative and one positive) were statistically significant (at one-tailed  $p < 0.05$ ). Given the sample size of 43 species, this is exactly what one would expect from chance alone. Finally, this lack of a consistent negative association between AFA and tail length was reiterated even when the sample was further restricted to those ten species where the mean relative tail length of males was more than double that of females. Although tail length was almost certainly subject to sexual selection in these ten species, correlations between AFA and tail length were negative in only four cases and positive in six; no correlation was statistically significant (at one-tailed  $p < 0.05$ ).

## 5. DISCUSSION

Our measurements of asymmetry in the tails and wings of long-tailed birds provide evidence that natural selection for aerodynamic efficiency is an important determinant of the extent of FA in avian lifting surfaces. Each of the predictions derived from this hypothesis was supported by the comparative data set. Perhaps not surprisingly, we found that wings were more symmetrical in those bird species that rely heavily on flight. More interestingly, however, aerodynamic considerations are also capable of explaining previously unreported patterns of asymmetry in long tails. Thus birds with forked tails, and especially those with shallow forks, had particularly low FA in their outermost tail feathers. This presumably arises because of strong natural selection to minimize such asymmetry in shallow forks, where it impairs aerodynamic efficiency far more than in other tail types (figure 1*b*).

In contrast to this, our results provide no evidence to support the hypothesis that FA in long tails plays a role in sexual selection. Contrary to previous reports (Møller & Höglund 1991; see also Møller 1992*b*), we found no consistent association between sexual dimorphism in tail length and dimorphism in tail FA. Furthermore, unlike several previous authors working with fewer species, we found that the degree of symmetry in long, probably sexually selected tails was not generally related to their size (cf. Manning & Hartley 1991; Møller 1991*a*; Møller & Höglund 1991; but see below).

What could explain these differences between our results and those of previous studies? One obvious possibility is that our failure to detect patterns of tail FA predicted by the sexual selection hypothesis represents a type II error. Differences in the lengths of left and right tail feathers are often small, so that accuracy in measuring tail FA is probably quite low (P. Barnard, personal communication). Nevertheless, we doubt that measurement error explains the present absence of results supporting the sexual selection hypothesis, because the repeatability estimates suggested that our

measurements were probably as accurate as those of other recent studies (see, for example, Møller 1992*b*). Moreover, our measures were clearly sufficiently accurate to reveal those patterns of variation in tail and wing FA predicted by aerodynamic theory.

An alternative explanation is suggested by recent data on the growth of long tail feathers in paradise whydahs *Vidua paradisaea* (P. Barnard, personal communication), in which partly grown tail feathers are relatively short and asymmetrical. Inclusion of partly moulted specimens into analyses therefore generates the predicted negative correlation between tail FA and tail length, but this relation disappears when only birds with fully grown tails are included. This result does suggest that grossly asymmetrical tails could reveal low-quality, late-moulting individuals. However, such correlations do not address the question of whether asymmetry of fully developed ornaments reveals viability differences. In most long-tailed species studied in detail, it appears that the majority of individuals have finished moulting their tail feathers when mate choice occurs, and that choice is made among birds with fully grown ornaments (Andersson 1982; Møller 1989; Evans 1991; but see Barnard 1991). Because of this, in the present study we were extremely careful to reject moulting specimens from our data set, using two observers to examine all birds. In the only published study reporting consistent negative correlations between tail FA and tail length across several species, similar techniques were used to identify birds in moult (Møller & Höglund 1991); however, all measurements and recordings were done by a single person (J. Höglund, personal communication), and it is thus possible that a few more moulting specimens were accidentally included in these analyses than in our own. Clearly, it may only be necessary to incorporate one or two such specimens per species to generate weak but consistent negative correlations between tail asymmetry and length.

Several other recent studies have also failed to find evidence that fluctuating asymmetry in secondary sexual characters is important in sexual selection. For instance, in paradise whydahs, the elaborate tail feathers of males are at least as symmetrical as non-ornamental structures such as wings and tarsi, suggesting that in this species tail FA may not reflect the costs of growing a sexual ornament (P. Barnard, personal communication). Similarly, new work has failed to uncover the predicted negative relation between AFA and trait size in an array of elaborate sexually dimorphic structures, including pectoral plumes in male sunbirds (Evans & Hatchwell 1993), horns in male Uganda kob *Kobus kob thomasi* and topi *Damaliscus lunatus* (A. Balmford, unpublished observations), long tails in both male whydahs and sunbirds (P. Barnard, personal communication; Evans & Hatchwell 1993), and facial plumes in male and female least auklets *Aethia pusilla* and crested auklets *A. cristatella* (I. L. Jones, unpublished observations). Lastly, experimental manipulations show that, in paradise whydahs, females do not prefer males with symmetrical tails (Oakes & Barnard 1993), whereas, in the scorpionfly *Panorpa japonica*, apparent female choice



for mates with symmetrical wings may in practice arise because females exhibit a preference for the pheromone of males with low FA, rather than for symmetrical wings per se (Thornhill 1992*b*).

Obviously, these results do not allow us to reject completely the hypothesis that FA in the tail feathers of birds plays a role in sexual selection in certain cases. The necessary correlations between tail elaboration and symmetry clearly do exist in a few species (Manning & Hartley 1991; Møller 1991*a*). Moreover, in swallows, by manipulating the appearance of males' tails but not their aerodynamic properties, Møller (1993) has recently provided elegant and compelling evidence of a specific female preference for males with symmetrical outer tail feathers. Nevertheless, it is evident from our results that the predictions of the sexual selection hypothesis for the role of FA are not supported in a survey of representatives from every family of long-tailed birds. Natural selection is likely to be a far more important factor influencing asymmetry in tail length. As well as being the principal selective agent driving certain forms of tail elongation in birds (Balmford *et al.* 1993*a*; Thomas 1993), the need for aerodynamic efficiency may often constrain the extent of FA seen in long tails.

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