

Patterns of morphological variation in two sexually dimorphic bird species with different tail shapes

ARNAUD GRÉGOIRE^{1,2*}, MHAIRI L. MCFARLANE^{1,3}, BRUNO FAIVRE⁴, MATTHEW R. EVANS³ and MICHAEL I. CHERRY¹

¹Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa

²Centre d'Ecologie Fonctionnelle et Evolutive, UMR CNRS 5175, 1919 route de Mende, 34293 Montpellier, France

³Centre for Ecology and Conservation Biology, School of Biosciences, University of Exeter, Cornwall Campus, Penryn, Cornwall TR10 9EZ, UK

⁴Equipe Ecologie Evolutive, UMR CNRS 5561, Université de Bourgogne, France

Received 3 March 2006; accepted for publication 10 August 2006

Many studies have focused on tail ornamentation in birds, but not all tail shapes have been studied in depth. Graduated and pin tails have received less attention than forked tails, despite being more likely, in terms of aerodynamic theory, to be honest signals. We report morphological variation in live specimens of two sexually dimorphic passerines from the same site with different tail shapes: graduated (Cape sugarbird *Promerops cafer*) and pin (orange-breasted sunbird *Antobaphes violacea*). Coefficients of variation (CVs) were calculated for all morphological traits, both non-ornamental (range 1.91–5.72) and ornamental (range 5.83–21.71). Males and females did not differ in CV for any non-ornamental trait. Ornamental traits in males of both species were significantly more variable than all non-ornamental traits. Cape sugarbird ornamental traits were significantly more variable than those of orange-breasted sunbirds. The high levels of variation in graduated tails relative to pintails suggest that these traits have been driven mainly by sexual selection. In contrast, both constraining natural and multiple ornament selection could be responsible for the relatively low levels of variation in pintails. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 91, 437–443.

ADDITIONAL KEYWORDS: aerodynamics – graduated tail – multiple ornaments – natural selection – pin tail – sexual selection – wild populations.

INTRODUCTION

Secondary sexual characters such as extravagant tails and plumage coloration in birds have been shown to be important in mate choice and intraspecific competition (Andersson, 1982; Pryke & Andersson, 2002), and males with the most elaborate traits generally are more successful in attracting mates (Evans & Hatchwell, 1992a), holding resources (Andersson, 1992; Evans & Hatchwell, 1992b; Pryke, Andersson & Lawes, 2001), and survival (Nolan, Hill & Stoehr, 1998; Evans, 2003). However, in several cases, ornamental traits have also been shown to impose costs on

the bearer in terms of their development and transport (Balmford, Thomas & Jones, 2000; Evans & Hatchwell, 1992b; Balmford *et al.*, 1993). In terms of the handicap theory (Zahavi, 1975), such traits are therefore generally assumed to provide reliable viability cues to conspecifics because only high quality individuals are able to withstand the costs of trait elaboration (Cotton, Fowler & Pomiankowski, 2004). The evolution of ornamental traits is expected to be driven by sexual selection until the benefits in terms of resource holding and mating success are outweighed by reductions in survival.

Many tail shapes exist in birds (Fitzpatrick, 1997), all associated with some degree of aerodynamic cost. A gradient exists from the less costly forms (i.e. forked tails) to more costly ones (i.e. graduated), with pintails

*Corresponding author. E-mail: arnaud.gregoire@cefe.cnrs.fr

being intermediate in terms of their impact on drag and lift (Balmford *et al.*, 1993). The initial development of the cheapest forms of tail elongation (both forked tails and pintails) could have been driven by Fisherian and natural selection processes (Balmford *et al.*, 1993; Norberg, 1994). This has been demonstrated experimentally in barn swallows, *Hirundo rustica* (Evans, 1998; Hedenstrom & Møller, 1999). As elongation of graduated tails is so much more costly than in other tail shapes, this is likely to represent a more honest signal of quality. Pryke & Andersson (2002) found that artificially elongating the graduated tails of male red-shouldered widowbirds, *Euplectes axillaries*, resulted in an increase in mating success. In comparison to forked and graduated tails, relatively little work has centred on the aerodynamics and selection pressures acting upon pintails, although see also Evans & Hatchwell (1992a).

To be useful as signals, ornamental traits must vary enough to allow discrimination between individuals (Darwin, 1859; Evans & Barnard, 1995), and must vary more than those which are naturally selected. Heritable genetic variation in secondary sexual traits can be maintained by environmental variability (Hamilton & Zuk, 1982; Evans, 1991). Conversely, if secondary sexual traits are constrained by natural selection, the variance of such traits should be equivalent to that of presumably naturally selected morphological features, such as skeletal anatomy. Empirical studies have investigated how ornaments vary phenotypically, and how this variation compares with that of naturally selected traits (Alatalo, 1988). However, previous studies have generally been conducted on museum skins (Alatalo, 1988; Fitzpatrick, 1997; Cuervo & Møller, 1999; Cuervo & Møller, 2001), with relatively few studies being performed in live individuals (Evans & Barnard, 1995; Pryke *et al.*, 2001).

In the present study, we present data from live individuals from two species of socially monogamous, necivorous birds from natural, wild populations at the same site. Orange-breasted sunbirds, *Anthobaphes violacea* (Linnaeus), and Cape sugarbirds, *Promerops cafer* (Linnaeus), have elaborate tails which are expected to be aerodynamically suboptimal (*sensu* Balmford *et al.*, 1993) and are therefore likely to be sexually rather than naturally selected. Cape sugarbirds are sexually dimorphic in tail length: both sexes have graduated tails but the length in males is approximately two-fold greater than that observed in females. Males also have an enlarged bulge on their sixth primary, termed a palette, thought to be used during display flights to generate sound. Both sexes are brown with yellow undertail coverts (Fry, Keith & Urban, 2000). Orange-breasted sunbirds are sexually dimorphic in tail length and plumage colour. Fry *et al.*

(2000) described male orange-breasted sunbird tails as graduated although, according to the definition of Fitzpatrick (1997), the tail is in fact the pintail type: the central two rectrices of the main tail are less than seven-eighths of the central pin feathers. Males also have a metallic green head and a purple breastband, yellow pectoral tufts and an orange breast, whereas females lack pintails and are a dull olive green (Fry *et al.*, 2000). The main aim of the present study was to evaluate which traits can be expected to be the target of sexual selection. We first compared the coefficient of variation (CV) between sexes. Then, we compared CVs between maximum (i.e. ornamental) tail length and other morphological traits for males within each species. Finally, we compared the CVs of tail length between species to evaluate the relative intensity of sexual selection in each species.

MATERIAL AND METHODS

Birds were captured using mistnets in Jonkershoek Nature Reserve (18°58'E, 33°60'S) outside Stellenbosch, South Africa, in the Jonkershoek valley, 10 930 ha, which consists of natural mountain fynbos and indigenous forest patches (Fraser, 1989). Birds were captured between February and July 2004 during the breeding season of both species. Each individual was fitted with a numbered aluminium ring and a unique combination of plastic colour rings. Head plus bill length, and bill and tarsus length, were measured to the nearest 0.1 mm using callipers. Wing length (maximum chord) and the maximum length of the central two tail feathers were measured to the nearest 0.5 mm, using metal rulers. In sunbirds, both the longest two feathers of the main tail in both sexes (hereafter referred to as 'main tail'), and the two pin feathers in males were measured (hereafter referred to as 'maximum tail'). In Cape sugarbirds, palette width was also measured using a metal ruler. This corresponds to the distance from the base of the notch at the distal end of the feather, to the point at which overall feather width returned to normal, parallel to the feather shaft. Body mass was measured to the nearest 0.5 g using a PESOLA spring balance.

Only measurements obtained from adult birds with fully grown, undamaged tail feathers and palettes were included in this study. The distributions of every trait were not significantly different from a normal distribution, but all were log₁₀-transformed to a standardized scale. Body mass was cubic-root-transformed to allow comparison with linear traits (Evans & Barnard, 1995). The CV, controlling for sample size, was estimated for each trait (Sokal & Rohlf, 1981). As the transformed variables did not usually reach the condition of normality, a *Z*-statistic was used to compare the difference between the coefficients of variation

(Zar, 1996). This test was used to compare: (1) the CV of each morphological trait between sexes within each species; (2) CVs in males of each species, contrasting ornamental trait CV with the other morphological CVs; and (3) the CV of maximum tail length between males of the two species. We quantified the repeatability of the measurements for the various traits by estimating the percentage measurement errors (ME%) using a model II analysis of variance (Bailey & Byrnes, 1990) between capture events, for birds captured twice. Finally, the acceptance level was adjusted using a sequential Bonferroni correction (Sokal & Rohlf, 1981) to take into account the multiple, and non-independent, comparisons.

RESULTS

Data from 75 Cape sugarbirds (36 males and 39 females), and 89 orange-breasted sunbirds (42 males and 47 females), were analysed. All traits measured, non-ornamental and ornamental, are presented in Figure 1. CVs were in the range 1.91–21.71. For both species, CVs did not differ significantly between sexes in most of the non-ornamental traits: body mass, head plus bill length, tarsus length, and wing length

(Table 1). In Cape sugarbirds, maximum tail length was significantly and considerably more variable in males than in females (Table 1).

Maximum tail length in Cape sugarbirds was considerably more variable than other morphological measurements (all contrasts $P < 0.0001$) apart from palette width ($P = 1.00$, Table 2). For orange-breasted sunbirds, maximum tail length was significantly more variable than all of the other traits (all $P < 0.001$) except main tail length (Table 2). The variance of maximum tail length in male Cape sugarbirds was significantly higher than that observed in male orange-breasted sunbirds ($Z = 7.04$, $P < 0.0001$).

DISCUSSION

CVs IN MALES: IS MAXIMUM TAIL LENGTH A SEXUALLY-SELECTED TRAIT?

Overall, our results are quantitatively similar to those obtained by Evans & Barnard (1995) for scarlet-tufted malachite sunbirds, and to those of Pryke *et al.* (2001a) for male red-collared widowbirds. Our results showed that, for most of the traits, the CVs are of a similar magnitude in both sexes. This suggests that most of the non-ornamental traits are

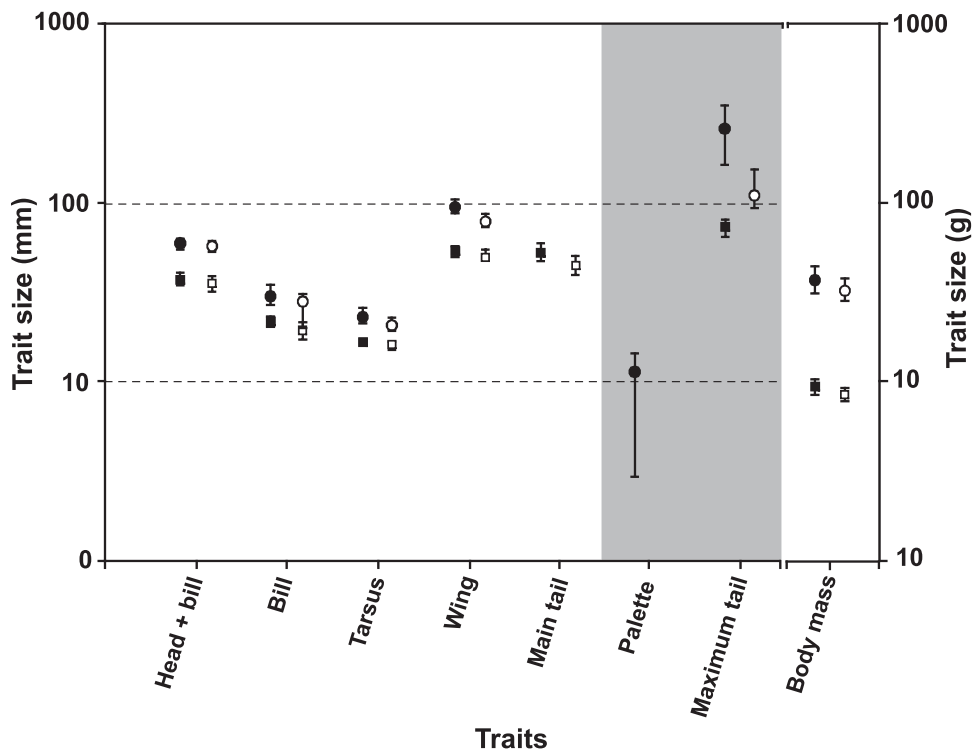


Figure 1. Variability of the various morphological traits in the Cape sugarbird and orange-breasted sunbird (ornamental traits are placed in the grey part of the figure). Median, minimum, and maximum values are shown. Circles represent Cape sugarbirds and squares represent orange-breasted sunbirds; filled symbols indicate a male and unfilled symbols indicate a female.

Table 1. Comparison of coefficients of variation (CV) of morphological traits between males and females within each species

	Non-ornamental traits						Ornamental traits									
	Body mass		Head + bill length		Bill length		Tarsus length		Wing length		Main tail length		Palette width		Maximum tail length	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Cape sugarbird																
<i>N</i>	36	37	35	35	35	38	35	38	34	38	38	35	32	35	32	35
CV (%)†	2.43‡	2.84‡	2.43	2.58	5.53	7.98	3.98	3.02	3.02	3.36	3.02	21.71	21.69	11.54	21.69	11.54
<i>Z</i>	-0.93		-0.35		-2.13		1.41		-0.62		3.44					
<i>P</i>	0.35		0.73		0.03		0.16		0.54		< 0.001*					
Measurement errors (%)	23.88		15.42		55.04		20.20		2.08		11.60					
Orange breasted sunbird																
<i>N</i>	41	47	42	47	42	46	42	47	42	47	26	44	39	44	39	44
CV (%)†	1.91‡	1.97‡	3.13	3.75	3.45	4.38	2.39	2.92	2.86	2.86	5.72	4.62	5.83	4.62	5.83	4.62
<i>Z</i>	-0.22		-1.17		-1.54		-1.30		-0.01		1.20					
<i>P</i>	0.83		0.24		0.12		0.19		0.99		0.23					
Measurement errors (%)	41.35		15.21		57.31		13.42		6.03		8.42					

Comparisons still significant after Bonferroni correction are indicated by an asterisk.

†CV corrected for sample size (Sokal & Rohlf, 1981).

‡CV calculated using cubic-root-transformed data.

Table 2. Comparison of coefficients of variation of all traits with maximum tail length for males within each species

	Body mass	Head + bill length	Bill length	Tarsus length	Wing length	Main tail length	Palette width
Cape sugarbird							
Z	9.50	9.32	6.83	8.00	8.63		< -0.01
P	< 0.0001*	< 0.0001*	< 0.0001*	< 0.0001*	< 0.0001*		1.00
Orange-breasted sunbird							
Z	6.40	3.81	3.23	5.32	4.34	0.10	
P	< 0.0001*	0.0001*	0.001*	< 0.0001*	< 0.0001*	0.92	

Comparisons still significant after Bonferroni correction are indicated by an asterisk.

subject to the same selective pressures, namely those mainly related to natural selection (Alatalo, 1988). Fitzpatrick (1997) suggested that a CV > 4 may be an indicator of sexual selection acting on tail length. Our key finding was that the ornamental traits were significantly more variable than most of the other traits in males of both species (all CVs > 4; Table 1). This suggests that these traits might be under the influence of sexual selection rather than natural selection alone (Evans & Barnard, 1995; Cuervo & Møller, 1999; Pryke *et al.*, 2001). Alternatively, high levels of variation may be expected in traits unrelated to fitness (and therefore not subjected to directional selection), and remain unconstrained by natural selection (Fitzpatrick, 1997). This appears to be unlikely because both pin and graduated tails are expected to be aerodynamically suboptimal regardless of their overall length (Balmford *et al.*, 1993; Norberg, 1995). Finally, high levels of variability in ornamental traits could be the result of higher measurement errors on these traits. However, the results indicate the reverse pattern, with a lower measurement error in these traits.

Palette width in Cape sugarbirds is not significantly less variable than tail length. This could indicate that tail length and palette width may both have a role in signalling. In contrast to tail length, palette width is unlikely to introduce a significant cost in either development or carriage during normal flight. Thus, this trait could be relatively unconstrained by natural selection, and be non-adaptive (*sensu* Fitzpatrick, 1997). However, male Cape sugarbirds engage in frequent wing-clapping display flights throughout the breeding season, the precise role of which is not known (Skead, 1967). Very few studies actually relate the sounds produced to morphological features (but see Miller & Inouye, 1983; Bostwick & Prum, 2003) and, to our knowledge, none show that variation in the size or shape of such traits exists and is related to the audibility or quality of sound produced. Although the high levels of variation in Cape sugarbird palette width are strongly suggestive of a sexually selective origin, care-

ful experimentation should demonstrate the role of the palette in intraspecific interactions.

The CV of orange-breasted sunbird main tail did not differ significantly from that of pintail length. These results could be explained by a genetic correlation between these traits. Genetic correlations, arising from pleiotropy and genetic linkage disequilibrium, measure the degree to which different traits share the same genetic basis (Lande, 1979; Merilä & Sheldon, 2001) and have been shown in 12 avian species (Merilä & Sheldon, 2001). Such a correlation might limit the evolution of the sexually-selected trait because of the multivariate evolution of the various feathers of the tail (Lynch, 1999).

COMPARISON OF CVs FOR MAXIMUM TAIL LENGTH BETWEEN SPECIES

The CV of male maximum tail length in Cape sugarbirds was significantly higher than that in orange-breasted sunbirds. This suggests that the balance between natural and sexual selection acting on maximum tail length differs between these species. On the one hand, more intense sexual selection may act upon the Cape sugarbird ornament. On the other, it could be that natural selection is stronger in orange-breasted sunbirds. Orange-breasted sunbird pintail length may be less variable than Cape sugarbird tail length because it is more tightly constrained by natural selection acting on its role in flight performance. It is interesting to consider the body size of the species studied with regard to their tail morphologies. The amount of power available for flight is related to body size, with smaller birds being limited by the mass of flight muscles. Tail morphology is therefore limited by the power available for flight. Evans (2004) investigated the role of body size in limiting tail morphology and showed that small birds such as wrens, *Troglodytes troglodytes*, would be unable to fly with elongated or ornamentally shaped tails. In contrast, larger birds such as pigeons, *Columba livia*, have more power available and could therefore evolve

a greater variety of tail morphologies. Male orange-breasted sunbirds are smaller than Cape sugarbirds (Fig. 1). Tail elaboration in orange-breasted sunbirds is therefore likely to be more constrained by their flight muscle mass. They are unlikely to be able to evolve either longer pintails or more costly graduated tails. This low potential for sexual selection to act could thus explain the low levels of variation observed for this species. In contrast, the larger Cape sugarbirds have more flight muscle mass and can therefore sustain the most costly form of tail elongation. Sexual selection may have been able to drive trait elaboration to a greater extent in Cape sugarbirds, resulting in higher levels of variation than in orange-breasted sunbirds.

MULTIPLE ORNAMENTS

The low levels of variation in orange-breasted sunbird pintail length relative to those of Cape sugarbirds could also be related to the possibility of sexual selection acting on coloration as well as tail ornaments in orange-breasted sunbirds. Male orange-breasted sunbirds, in addition to having pintails, are brightly coloured, with yellow pectoral tufts and an orange breast. These plumage areas are carotenoid-rich (B. Faivre, unpubl. data) and are therefore likely to be costly signals (Olson & Owens, 1998). It could be that these features play an important role in signalling: the pectoral tufts are known to play a role in both inter- and intrasexual signalling in this species (Broekhuysen, 1963). It has been demonstrated in other species that females can select a male on a suite of characteristics. For example, Jawor *et al.* (2003) showed that northern cardinals, *Cardinalis cardinalis*, mate assortatively on the basis of both plumage and bill colour. In other systems, each ornament has a different function. For example, in scarlet-tufted malachite sunbirds, males use red pectoral tufts in male–male competition for territories, but females select males on the basis of their pintail length (Evans & Hatchwell, 1992a; Evans & Hatchwell, 1992b). Multiple ornament systems such as these can be maintained through the multiple receiver hypothesis (Andersson *et al.*, 2002), where different signals are directed at different receivers. A more careful analysis of male orange-breasted sunbird plumage characteristics, such as pectoral tuft length and colour intensity, would be necessary to investigate whether this species conforms to this idea. This study highlights that species with pin or graduated tails (i.e. shapes which have generally been overlooked) represent promising biological models to evaluate the evolution and maintenance of secondary sexual characters as well as multiple ornament selection.

ACKNOWLEDGEMENTS

We are grateful to R. Gaigher and other volunteers for their valuable help in the field. Birds were captured and ringed under permit no. 177/2003 from Cape Nature, whom we thank also for giving us permission to work in Jonkershoek. This study was supported by a postdoctoral fellowship from the National Research Foundation of South Africa (to AG), a Leverhulme Trust Study Abroad Studentship (to MLM), and an international science cooperation grant from the CNRS/NRF (to MIC/BF), and the University of Stellenbosch (to MIC).

REFERENCES

- Alatalo RV. 1988.** Patterns of variation in tail ornament size in birds. *Biological Journal of the Linnean Society* **34**: 363–374.
- Andersson M. 1982.** Female choice selects for extreme tail length in a widowbird. *Nature* **299**: 818–820.
- Andersson S. 1992.** Female preference for long tails in lekking Jackson's widowbirds: experimental evidence. *Animal Behaviour* **43**: 379–388.
- Andersson S, Pryke SR, Ornborg J, Lawes MJ, Andersson M. 2002.** Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *American Naturalist* **160**: 683–691.
- Bailey RC, Byrnes J. 1990.** A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. *Systematic Zoology* **39**: 124–130.
- Balmford A, Lewis MJ, Brooke MD, Thomas ALR, Johnson CN. 2000.** Experimental analyses of sexual and natural selection on short tails in a polygynous warbler. *Proceedings of the Royal Society of London Series B, Biological Sciences* **267**: 1121–1128.
- Balmford A, Thomas ALR, Jones IL. 1993.** Aerodynamics and the evolution of long tails in birds. *Nature* **361**: 628–631.
- Bostwick KS, Prum RO. 2003.** High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves). *Journal of Experimental Biology* **206**: 3693–3706.
- Broekhuysen GJ. 1963.** The breeding biology of the Orange-breasted sunbird *Anthobaphes violacea* (Linnaeus). *Ostrich* **34**: 187–234.
- Cotton S, Fowler K, Pomiankowski A. 2004.** Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis? *Proceedings of the Royal Society of London Series B, Biological Sciences* **271**: 771–783.
- Cuervo JJ, Møller AP. 1999.** Phenotypic variation and fluctuating asymmetry in sexually dimorphic feather ornaments in relations to sex and mating system. *Biological Journal of the Linnean Society* **68**: 505–529.
- Cuervo JJ, Møller AP. 2001.** Components of phenotypic variation in avian ornamental and non-ornamental feathers. *Evolutionary Ecology* **15**: 53–72.

- Darwin C. 1859.** *The Origin of Species*. London: John Murray.
- Evans MR. 1991.** The size of adornments of male scarlet-tufted malachite sunbirds varies with environmental conditions, as predicted by handicap theories. *Animal Behaviour* **42**: 797–803.
- Evans MR. 1998.** Selection on swallow tail streamers. *Nature* **394**: 233–234.
- Evans MR. 2003.** Survival of male scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*) on Mount Kenya and the influence of ornamentation. *Biological Journal of the Linnean Society* **80**: 125–133.
- Evans MR. 2004.** Limits on the evolution of tail ornamentation in birds. *American Naturalist* **163**: 341–357.
- Evans MR, Barnard P. 1995.** Variable sexual ornaments in scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*) on Mount Kenya. *Biological Journal of the Linnean Society* **54**: 371–381.
- Evans MR, Hatchwell BJ. 1992a.** 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. *Behavioral Ecology and Sociobiology* **29**: 421–427.
- Evans MR, Hatchwell BJ. 1992b.** An experimental study of male adornment in the scarlet-tufted malachite sunbird. I. The role of pectoral tufts in territorial defence. *Behavioral Ecology and Sociobiology* **29**: 413–419.
- Fitzpatrick S. 1997.** Patterns of morphometric variation in birds' tails: length, shape and variability. *Biological Journal of the Linnean Society* **62**: 145–162.
- Fraser MW. 1989.** Short-term responses of birds to fire in old mountain fynbos. *Ostrich* **60**: 172–182.
- Fry CH, Keith S, Urban EK. 2000.** *The birds of Africa*, Vol. VI. London: Academic Press.
- Hamilton WD, Zuk M. 1982.** Heritable true fitness and bright birds: a role for parasites? *Science* **218**: 384–387.
- Hedenstrom A, Møller AP. 1999.** Length of tail streamers in barn swallows. *Nature* **397**: 115.
- Jawor JM, Linville SU, Beall SM, Breitwisch R. 2003.** Assortative mating by multiple ornaments in northern cardinals (*Cardinalis cardinalis*). *Behavioral Ecology* **14**: 515–520.
- Lande R. 1979.** Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* **33**: 402–416.
- Lynch M. 1999.** Estimating genetic correlations in natural populations. *Genetical Research* **74**: 255–264.
- Merilä J, Sheldon BC. 2001.** Avian quantitative genetics. *Current Ornithology* **16**: 179–255.
- Miller SJ, Inouye DW. 1983.** Roles of the wing whistle in the territorial behaviour of male broad-tailed hummingbirds. *Animal Behaviour* **31**: 689–700.
- Nolan PM, Hill GE, Stoehr AM. 1998.** Sex, size, and plumage redness predict house finch survival in an epidemic. *Proceedings of the Royal Society of London Series B, Biological Sciences* **265**: 961–965.
- Norberg RA. 1994.** Swallow tail streamer is a mechanical device for self-deflection of tail leading-edge, enhancing aerodynamic efficiency and flight manoeuvrability. *Proceedings of the Royal Society of London Series B, Biological Sciences* **257**: 227–233.
- Norberg UM. 1995.** How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology* **9**: 48–54.
- Olson VA, Owens IPF. 1998.** Costly sexual signals: are carotenoids rare, risky or required? *Trends in Ecology and Evolution* **13**: 510–514.
- Pryke SR, Andersson S. 2002.** A generalized female bias for long tails in a short-tailed widowbird. *Proceedings of the Royal Society of London Series B, Biological Sciences* **269**: 2141–2146.
- Pryke SR, Andersson S, Lawes MJ. 2001.** Sexual selection of multiple handicaps in the red-collared widowbird: female choice of tail length but not carotenoid display. *Evolution* **55**: 1452–1463.
- Skead CJ. 1967.** *The sunbirds of Southern Africa also the sugarbids, the white-eyes and the spotted creeper*. Cape Town: AA Balkema.
- Sokal RR, Rohlf FJ. 1981.** *Biometry*. New York, NY: WH Freeman and Co.
- Zahavi A. 1975.** Mate selection – a selection for a handicap. *Journal of Theoretical Biology* **53**: 205–214.
- Zar JH. 1996.** *Biostatistical analysis*. Englewood Cliffs, New Jersey Prentice Hall Inc., 144–146.