Male tail length, sexual display intensity and female sexual response in a parasitic African finch

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Abstract. Aviary experiments on the effect of tail length of males on the sexual response of females were carried out with a promiscuous, parasitic finch, the shaft-tailed whydah, *Vidua regia*. Oestradiol-treated females, presented with two males of widely differing tail lengths, performed copulation-solicitation displays to males with lengthened tails in preference to normal-tailed controls, and to controls in preference to males with shortened tails. Yet although males were always visually isolated from each other, individuals displayed and vocalized significantly more when their tails were longer than that of the other male, and less when their tails were shorter. Females presented with a long-tailed decoy and a short-tailed live male solicited neither, but spent significantly more time with the live male.

Vertebrates that are both promiscuous and parasitic lend themselves especially well to experiments on the role of sexual selection in the elaboration of male phenotypic traits. Males of such species have no postcoital investment in offspring provisioning or defence, factors important in many species with paternal care (Searcy 1982); prospecting females may therefore be minimally influenced by male-defended resources and paternal ability, and maximally influenced by male phenotype. Also, male and female brood parasites have an unusually similar, and minimal, input into reproduction. Maternal investment is limited to egg production and deposition in a suitable host nest, while male investment ceases at mating. While the seasonal costs of egg production for female brood parasites should be high, due to the greater numbers of eggs produced (Payne 1977; Scott & Ankney 1983), the per-offspring parental investment of female parasites is much less than that of nesting females, and more equal to that of their copulation partners.

These parental investment ratios should strongly influence mating systems and the basis of mate choice (Trivers 1972; Burley 1977), since reproductive discretion or 'coyness' is correlated with relative parental effort. Yet empirical studies of sexual selection in vertebrates normally use species in which only one sex, usually the female, has an extensive post-fertilization investment. Of the few mate choice studies in which parental investment is more equal, most involve monogamous species with biparental care (e.g. Burley 1977, 1981; Burley

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& Moran 1979; ten Cate & Mug 1984). The relatively low and even reproductive effort in brood parasites may, therefore, provide an unusual counterpoint to our understanding of sexual selection in parental species.

To analyse sexual responses of females to variation in an exaggerated male ornament, I manipulated tail length in a promiscuous, brood-parasitic finch, the shaft-tailed whydah, *Vidua regia*, in carefully controlled aviary conditions. Reproductively active males weigh about 15 g and have elongated, spatulate tails ($\bar{X} = 235$ mm, coefficient of variation $= 5\cdot7\%$, $N = 12$) which are more than twice as long as the body; females and immature males weigh about 13 g and have sparrow-like plumage. Territorial males occupy dispersed call-sites which are visited by females, floater males and other call-site owners (see Payne & Payne 1977; Barnard 1989 for congeners).

METHODS

Maintenance and Treatment of Subjects

I conducted 44 mate-choice trials in March–April 1986, during the height of the local breeding season, in an outdoor aviary ($6\cdot0 \times 2\cdot8 \times 2\cdot2$ m) set in *Acacia* savanna breeding habitat. Four breeding males and four adult females were trapped from call-sites 12–18 km from the aviary. As I could not obtain birds known to be unrelated and unfamiliar with each other from distant points outside the study area, I attempted to standardize the degree of likely familiarity by trapping all the birds from the

same 8-km stretch of road. Female and male shaft-tailed whydahs visit call-sites within a home range of several square kilometres (Barnard 1989, see also Payne & Payne 1977; Shaw 1984; Barnard & Markus 1989), so it is possible that individuals in the trials had encountered each other before. However, this would not introduce any systematic bias in the randomized design of the trials, and indeed no female preference for individual males was found (see Results).

Females were housed together in a holding aviary (1·3 × 0·6 × 0·6 m), and males were housed singly in visually isolated, identical experimental cages (1·1 × 0·8 × 0·8 m) in the main aviary. During the experiments, the two males not involved in any one trial were held singly in a quiet building. The birds were continually supplied with fresh water, millet, green inflorescences of preferred grasses, termites and ground cuttlebone. All were acclimated for 17–29 days before the trials began and adapted quickly to captivity. Colour bands were removed for the duration of the experiments.

Females received subcutaneous silicone-tubing implants of 17-β-oestradiol (12 mm long, inner diameter 1·6 mm, outer diameter 2·3 mm) along the flank 5 days before trials commenced, following Searcy (1984). On each trial day, males were randomly allocated to one of four treatment groups: tail-lengthened, tail-shortened, and two sham-treated (cut and reglued) controls. One control bird was used in the day's trials while the other was rested. Each male's tail was altered daily, but due to random allocation some males experienced certain treatments more frequently than others and were involved in more trials. Manipulation procedures followed Andersson (1982a; see also Møller 1988). Shortening modified tail length to 125 mm (46–48% decrease), sham treatment to 232 mm (0–3% decrease) and lengthening to 330 mm (38–42% increase). Males were visually isolated at all times.

Trial Procedures

In each trial, a randomly selected female was introduced for 100 min into the main aviary with a pair of separately caged males. I watched the trials with binoculars from a darkened hide 14·5 m away. Female solicitations were scored (Shaw 1984) for classification of trials as 'choice' or 'no-choice' situations. Criteria for determining a choice were particularly strict. A female had to solicit copulation

from one of two perches immediately adjacent to a male; activity on 'neutral' perches was disregarded. Simple association with a male was not considered conclusive. One female was removed when she had not responded to oestradiol treatment; her data were omitted from the analyses.

To measure sexual display and other activity during trials, I spot-sampled behaviour of the test female and two test males at 1-min intervals (Altmann 1974). Cumulative scores for aggressive flights, sexual displays, vocalizations and neutral activities (perching, preening, feeding, roosting) were compared for males within a trial. During analysis, birds were known only by a number to minimize any unconscious bias.

RESULTS

Female Choice and Tail Length

Of the 44 trials (Table I), females solicited a single male in 54·5% (single-choice trials), both males in 9·1% (dual-choice trials) and neither male in 36·4% (no-choice trials). In single-choice trials, taking trials as independent data points for the moment, females always chose the longer-tailed male ($\chi^2 = 22·04$, $df = 1$, $P < 0·0001$). It is, however, more prudent to regard individual females as sampling units. The expected cell values for individual females are too small to treat statistically, but the results in any case are extremely clearcut (Table I). When a single choice was made, the longer-tailed male was always chosen. Furthermore, in each trial in which a female solicited both males (dual choice), the longer-tailed male was always solicited first and more frequently. Each female followed this general pattern, although a single female (female AB18350) was involved in all four dual-choice trials. Females showed neither 'side preference' for male position in the aviary (chi-squared tests; NS) nor a preference for individual males (NS), and of course both male position and tail treatment were fully randomized. Therefore, tail length appeared to have a strong influence on female solicitation patterns, and supernormal tails were preferred to controls of normal length (cf. Andersson 1982a; Møller 1988).

Tail Length and Display Intensity

However, these results are more complex than they might seem. Males given longer tails were significantly more vocal and active in sexual and

Table I. Individual female sexual responses to males with manipulated tail lengths in mate-choice trials

		Choice for			
Female	Total no. of trials	Longer-tailed male	Shorter-tailed male	Neither male	Both males
AB18350	14	6	0	4	4
AB18354	14	11	0	3	0
AB18355	12	7	0	5	0
AA88882*	4	0	0	4	0
Total	44	24	0	16	4

*Removed from subsequent experiments due to lack of sexual behaviour; data omitted from analyses.
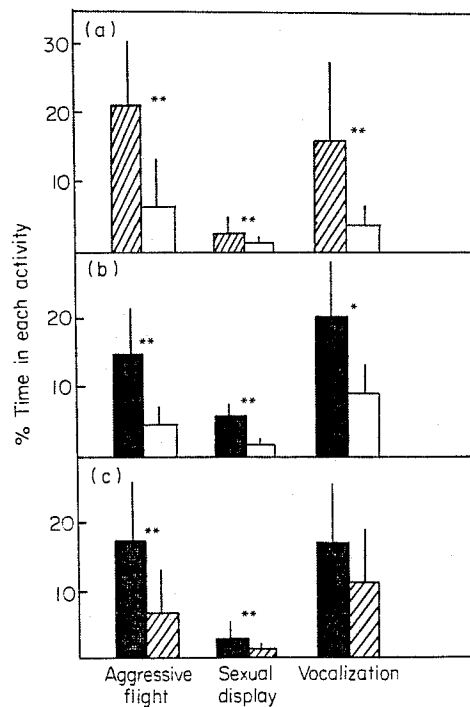

Figure 1. Aggressive flight, sexual display and vocal activity of experimental male shaft-tailed whydahs of different tail lengths. (a) Control versus tail-shortened; (b) tail-lengthened versus tail-shortened; (c) tail-lengthened versus control. ▨: Control; ■: tail-lengthened; ☐: tail-shortened. $*P < 0.01$; $**P < 0.005$, Wilcoxon two-sample rank tests (normal approximation with continuity correction of 0.5).

aggressive display than the other, shorter-tailed male (Fig. 1). This was true even though males were visually isolated and tail treatments changed daily. Taking males individually (Table II), three of four males were more aggressive when they had a longer tail than the unseen other male, and all males displayed sexually and vocalized more at these times. When shorter-tailed relative to the other male, males became subdued, spending more time perching, preening and even roosting. The behaviour of longer-tailed males was thus characterized by more sexual display, aggression, vocalization and overall activity.

Female Response to Tail Length versus Display Intensity

Although further time was unavailable, I sought to control male display activity in a preliminary series of four trials by presenting test females with a long-tailed, freshly mounted decoy and a short-tailed live male. The decoy had previously elicited extremely strong aggression from territorial males; from the hide it could not be distinguished from a perched, inactive male. In none of the four trials did the test female solicit copulation. However, females spent almost three times more time next to the short-tailed live male ($\chi^2 = 28.08$, $df = 1$, $P < 0.0001$). Samples were inadequate to analyse individual female responses meaningfully.

DISCUSSION

When given a long tail, male whydahs displayed and vocalized much more than the other shorter-tailed male, even though tail treatments changed daily and males never saw each other. Whether this is due to male 'self-awareness' or feedback via females is unclear, but it should be a simple matter to compare male behaviour in the absence of females. It was apparent during the test period that

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Table II. The influence of tail length on male activity during mate-choice trials

	Male			
	AB18349	AB18353	BB57149	AB18351
Sexual display	4·19± 5·51 8·37**	6·39± 6·24 17·41***	2·95± 4·45 11·90***	6·16± 5·97 4·73*
Aggressive flight	19·98±12·41 10·04**	20·24± 6·60 1·80	10·77± 8·68 7·70**	22·09± 8·67 6·82**
Vocalization	13·79±11·25 5·94*	21·76± 9·43 13·92***	16·25± 7·75 7·03**	22·89± 8·32 23·53***
Hopping	7·34± 6·02 0·29	19·83±11·19 3·63*	7·90± 7·23 1·99	9·79± 4·92 3·53
Total activity	29·26±15·21 13·00***	41·67±11·09 0·57	23·74±12·06 6·71**	37·13±14·04 17·81***
Feeding	23·11± 9·10 4·10*	18·64± 4·72 0·41	21·67± 4·69 0·36	21·22± 5·35 0·62
Perching	48·36± 6·62 0·97	42·40± 7·75 0·30	55·46± 8·01 4·15*	48·42± 6·13 4·67*
Preening	15·97± 6·39 0·28	20·80± 7·97 0·02	16·62± 6·29 2·64	16·19± 7·26 2·26
Total inactivity	66·49±12·40 7·82**	57·66± 9·14 0·43	74·52±10·11 4·57*	63·75±10·11 8·08**
df	2,13	2,21	2,21	2,17

Arscine-transformed activity scores ($\bar{X}\pm$ sd) show intra-male variation in activity during different tail treatments; univariate F-ratios indicate statistical association of activity and tail length. *$P<0.05$; **$P<0.01$; ***$P<0.001$; one-way ANOVA.

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the presence of a female was a necessary stimulus for male sexual display. In both field and aviary situations, however, males appear readily intimidated by the presence of other males, even if the latter can only be heard and not seen (P. Barnard, unpublished data).

Female whydahs in the tests directed their copulation-solicitation displays at vigorously displaying, longer-tailed males. When confronted with a live male with a shortened tail and a decoy with a lengthened tail, females solicited neither but spent significantly more time near the active, live one. Similar experiments, using males treated with testosterone or mild anaesthetic drugs, should clarify whether display activity or tail length is more important to females. However, these preliminary data suggest that sexual display activity strongly influences female solicitation patterns, as is the case in fish (Farr 1980; Thresher & Moyer 1983; Bischoff et al. 1985), spiders (Jackson 1981) and other birds (Garson et al. 1980; Bossema & Kruijt 1982; Kruijt et al. 1982; Searcy 1984; Simmons 1988). This may be due to a simple differential stimulation of females at the neuroendocrinological level (e.g. Dyson & Passmore 1988).

If there is any adaptive reason why whydah females should actively discriminate against shorter-tailed males when seeking copulations, it is simply that the tails of such males may reflect low fertility and an incomplete physiological readiness to breed. Adult male whydahs do not all acquire breeding plumage at the same time. Some males are still in prenuptial body moult well into the breeding season, belatedly growing long retrices (Barnard 1989; unpublished data). These males appear unable to control an established call-site under normal circumstances (Barnard 1989), and behave submissively in the presence of longer-tailed males. They are likely to have low (but increasing) levels of circulating hormones such as testosterone, and or smaller testes (see also Møller & Erritzøe 1988). If so, males with short tails may be discriminated against by females simply because they are not yet fully fertile.

Female parasites such as whydahs are under severe temporal constraints during the breeding season, due to problems involved in synchronizing egg laying with that of a host (Barnard & Markus 1989; P. Barnard, unpublished data). While this should not promote indiscriminate promiscuity, it

does suggest that females should be less interested, evolutionarily, in males offering abstract genetic quality than in males that can fertilize them rapidly. Intuitively we may suppose that genetic quality and overall fertility are related (Andersson 1982b, 1986), but this still awaits empirical confirmation. Both a long tail and a vigorous display do, however, indicate prime breeding condition and possibly high fertility to females (see Barnard & Markus 1989). For non-parental species I see no reason to invoke more abstract benefits.

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