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COSTS OF SEXUAL ADVERTISING IN THE LEKKING JACKSON'S WIDOWBIRD[1]

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Abstract. Costs of two sexual advertisements, a 20 cm long tail and lek display, were investigated in Jackson's Widowbird (*Euplectes jacksoni*). Although leks were frequently disturbed by approaching raptors, no predation was recorded. Judging from counts of growth bars, the nuptial tail completes growth in five weeks, and its final length seems to depend equally on growth time and growth rate. A cost of tail formation is inferred from a lower index of body condition (relative body mass) among males in late compared to early stages of tail growth, and from frequent fault bars (translucent bars due to reduced deposition of keratin) in tail feathers. The number and size of faults were larger in the proximal (last formed) half of feathers, and the frequency of faults increased with both feather length and growth rate. A physiological cost of lek attendance and display was indicated by lower condition among full grown courtholders compared to floaters. In two of four seasons, this was also supported by a decline in condition as a function of how long after lek initiation a male was captured. Among all measured males, full grown tail length was positively related to body condition. In a smaller sample of behaviorally observed males this relationship was obscured, while condition instead was negatively related to display rate and lek attendance. Aerodynamic costs of the tail are discussed, as are the possible roles of tail plumes and display as advertisers of male quality.

Key words: Sexual selection; physiological costs; mass loss; tail formation; lek; Euplectes jacksoni.

INTRODUCTION

Models of sexual selection through female choice all assume a viability cost that opposes and eventually prevents further evolution of the preferred male ornament (Kirkpatrick 1992; M. Andersson, in press). While the mate choice explanation of secondary sex traits has been extensively treated both theoretically and empirically (M. Andersson, in press), the balancing forces of natural selection have been less studied. This is unfortunate for at least two reasons.

First, differences among species in costs and constraints might in part explain the bewildering taxonomic diversity in type and degree of sexual advertising (Price et al. 1987). Second, costs of sexual signals is a central theme in the debated issue of secondary sex traits as indicators of male quality (Zahavi 1975, M. Andersson 1982, Pomiankowski 1988). Relationships between ornament expressions and male viability are therefore of interest, even if not providing strong tests of indicator versus Fisher models of sexual selection (Balmford and Read 1991).

Information about the type of costs imposed on producing and carrying a morphological ornament, or on performing a display, is crucial. Of the variety of identified or suggested constraints, the two major categories are physiological costs and increased exposure to predation (Burk 1982; Ryan et al. 1982; Endler 1983; Halliday 1987; M. Andersson, in press).

Among archetypical examples of sexual selec-

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tion are lekking birds. Males in these species are emancipated from resource defense and parental duties, and invest heavily in sexual advertising through some complex display, in most cases, an exquisitely adorned plumage. Females mostly seem free to choose among the males (but see Trail 1985, Beehler and Foster 1988), and the typically strong skews in male mating success suggest female preferences for certain phenotypes. Although other factors are likely to contribute to the unanimity of female choice on leks, such as site preferences and choice copying (Gibson et al. 1991), phenotypic cues for mate choice have in recent years been identified in a number of lek species (Balmford and Read 1991, Wiley 1991). In most cases, however, the constraints that restrict male ornament expression or display performance remain to be clarified. A notable exception is Sage Grouse (*Centrocercus urophasianus*), in which physiological costs of the strut display have been demonstrated in detail (Vehrencamp et al. 1989), whereas predation generally did not seem to limit individual male performance (Bradbury et al. 1989). Similar results have been reported for great snipe (*Gallinago media*) (Höglund et al. 1992).

The lekking Jackson's Widowbird (*Euplectes jacksoni*) is a granivorous weaverbird (Ploceinae) of East African highlands. Males, in black nuptial plumage with a 20 cm long tail, construct individual display courts on lek in open grassland and attract the drab females by a jump display (Van Someren 1946). In this paper I compile field data from a study of mate choice and sexual dimorphism in this species (Andersson 1989, 1991, 1992, 1993) to assess costs of two components of male sexual advertisement: growth and possession of the long tail plumes, and investment of lek attendance and display. Predation risks are considered from observed predator disturbance at the leks, and physiological costs are investigated by relating male body condition to stages of tail growth, lekking status (courtholder or floater), and number of days spent lekking. Examination of collected tail feathers further reveals growth rate and stress during the nuptial molt. I also discuss aerodynamic costs of the tail, and consider the possibility that secondary sex traits in Jackson's Widowbird advertise male phenotypic quality.

MATERIALS AND METHODS

Data were collected during 1984–1990 in Naro Moru district (0°9′S, 36°58′E) in central Kenya. Field seasons lasted from late November to early February, and data were collected during each season except 1988–1989. The general methods of capturing, measuring, and observation are described elsewhere (Andersson 1989, 1993), and I include here only what is relevant to this paper.

All the measured males were in nuptial plumage (black body feathering, and elongated black rectrices), but in different stages of tail growth. Morphometric measurements were always taken by the author. Tarsus length (between the extreme bending points at toes and heel) was measured to the nearest 0.1 mm with calipers. Tail length was measured with a ruler to the nearest 0.5 cm, and the number of blood quills was counted. From 43 full grown males in the 1987–1988 and 1989–1990 seasons I also collected one of the central pair of long rectrices and examined its length, weight, growth bars, and fault bars. Growth bars are alternating dark and light bands across the feather (slight differences in optical properties, but clearly visible at certain angles), apparently due to differences in the material laid down during night and day (Wood 1950). Each pair of bands thus constitutes a 24-hr growth period (Grubb 1989), and the bands consequently reveal the number of days a feather has been growing. Fault bars were examined with respect to number, location (proximal or distal half of feather), and five size classes (1–5). Fault bars are translucent bands caused by defective formation of barbules (i.e., reduced deposition of keratin), and likely to be a result of some form of physiological stress (Riddle 1908, Michener and Michener 1938), although the proximate mechanism is unresolved (King and Murphy 1984).

For body mass, the birds were weighed with a Pesola spring balance to the nearest 0.2 g. Body mass increases significantly during the day (Andersson 1989) and was therefore corrected by using the residuals from a linear regression of body mass on capture time (06:00–18:00 hrs) and setting all individuals to a 06:00 hrs "corrected body mass." Body condition was calculated as the residual from a linear regression of log ("corrected body mass") versus 3 × log (tarsus length), and converted back to grams by subtracting exp(fitted value) from "corrected body mass." A skeletally fixed trait such as tarsus length should be the most adequate univariate measure of body size (Freeman and Jackson 1990), preferable to wing length which is variable and itself likely to be influenced by the nutritional status one aims to estimate (Pehrsson 1987). The log-transformations were used to remove the underlying effects of the different dimensionality of mass (volume) and tarsus (length).

Only males in full nuptial body plumage (black body feathering except for a few light brown feathers on the belly) were included. Depending on the stage of tail growth, males were assigned to three categories: "growing" (at least 10 of the 12 rectrices with blood quills), "fresh" (1–6 blood quills; i.e., less than half of the rectrices, and thereby considered to be just about to complete tail growth), and "ready" (no blood quills, i.e., tail fully grown since an unknown number of days). Eleven males (too few to include as a fourth category) with 7–9 blood quills were omitted from the categorization to achieve a less arbitrary division between "growing" and "fresh." Males were considered to be "courtholders" if they were captured at a display court, or "floaters" if they were captured elsewhere (day or night roosts) and not subsequently recorded at a lek (see Andersson 1993).

Data stem from five breeding seasons, eight different leks, two day roosts, and two night roosts, but no individuals are included more than once in the analysis. I pooled data across sites and years, as these factors did not show significant effects on the variation in body condition, neither in courtholders nor in floaters (one-factor analysis of variance (ANOVA), "courtholders": season effect, $F_{5,139} = 0.71$, $P = 0.61$; lek effect, $F_{7,139} = 1.31$, $P = 0.25$; "floaters": season effect, $F_{5,121} = 2.25$, $P = 0.054$; capture site effect, $F_{3,121} = 1.1$, $P = 0.35$).

Analyses of variance and linear regressions were used where residuals were approximately normal with homoscedastic variances. For bivariate relationships where no direction of causality was implied, or in situations where assumptions required for parametric tests were violated, I used Spearman rank correlation. Statistic software used were SuperANOVA and StatViewII (Abacus Concepts, Berkeley).

RESULTS

PREDATION

Predation on displaying males seemed low. The only apparent case was the remnants of a plucked and eaten male at one of the leks in the 1989–1990 season. During a total of 244 hr of lek observation (seven leks; 177 males) throughout the study, not a single predation attempt was recorded. This is not due to lack of potential predators; the males were frequently disturbed by approaching raptors. In 1989–1990 when I kept a record of predators, approaching raptors scared off at least one (usually all) of the males 80 times in 88 hr of observation, i.e., almost once an hour. The raptors were mainly wintering male Montagu's Harriers *Circus pygargus* (62 cases). Remaining observations include nine unidentified *Circus* females, four male Pallid Harriers *C. macrourus,* four Lesser Kestrels *Falco naumanni,* and one Black-shouldered Kite *Elanus caeruleus.* There was often one or more raptors within eyesight from a lek; apart from the species above, Eastern Chanting Goshawks *Melierax poliopterus,* Augur Buzzards *Buteo augur* and Longcrested Eagles *Lophaetus occipitalis* roamed the area. Larger raptors (mainly *Aquila rapax* and *nipalensis*) also scared the displaying males but they seem unlikely to ever attack a small passerine.

PHYSIOLOGICAL COSTS

A comparison of body condition (relative body mass; see Materials and Methods) of floating and courtholding males through the different stages of tail growth suggests some "physiological cost" (used onwards as broad term referring to the depletion of body reserves) of both the tail ornament and the lek behavior. The result is summarized in Figure 1, and was tested with a two-factor ANOVA, with lekking status (floater or courtholder) and growth stage as factors. Status by itself had no effect on body condition ($F_{1,256} = 1.22$, $P = 0.27$), whereas there were significant effects of growth stage ($F_{2,256} = 4.3$, $P = 0.014$) and the interaction term status × stage ($F_{2,256} = 3.26$, $P = 0.040$).

Tail ornament. Body condition of floaters as well as of courtholders seems to decline during tail growth (Fig. 1); for both categories, males with almost completed tails ("fresh") had lower condition than males still in full tail growth ("growing"). Analyzed for all males with at least one blood quill, body condition decreased significantly with decreasing number of blood quills ($r_s = 0.20$, $n = 130$, $P = 0.024$). Floaters and courtholders contributed about equally to this pooled relationship (floaters, $r_s = 0.19$, $n = 70$, $P = 0.11$; courtholders, $r_s = 0.22$, $n = 60$, $P = 0.09$). The decline might represent a depletion of body reserves during growth of tail feathers, and this is also supported by a few within-season recaptures (all floaters). Three males that had no blood quills when first caught were recaptured

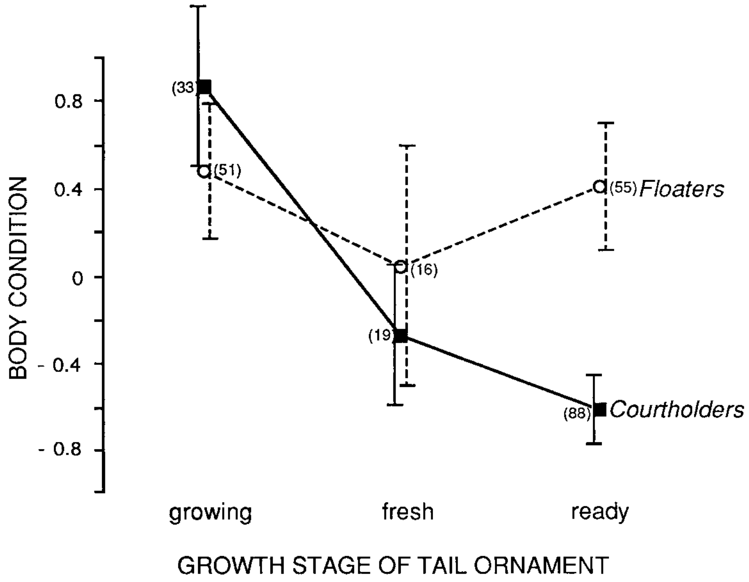

FIGURE 1. Body condition (see text) for courtholders and floaters (lekking status) in different stages of tail growth. "Growing" = 10–12 blood quills in tail, "fresh" = 1–6 bl.q., and "ready" = 0 bl.q. Standard error bars are given for each subgroup, with sample sizes in parentheses. Two-factor ANOVA: Lekking status, $F_{1,256}$ = 1.22, $P = 0.27$; growth stage, $F_{2,245} = 4.3$, $P = 0.014$; interaction term status × stage, $F_{2,256} = 3.26$, $P = 0.040$.

7–10 days later, and had lost little or no body mass (+2.5 g, −0.5 g, −1.1 g, respectively). In contrast, three males with rectrices still growing when first caught had lost more weight at recapture (−4.3 g, −3.1 g, −1.5 g, respectively).

Based on the analysis of the full-grown tail feathers collected from 43 "ready" or "fresh" males, the tail seems to be formed during four to six weeks (number of growth bars: $\bar{x} \pm$ SD 37 ± 4, range 28–47, $n = 43$), with an average daily rate (length divided by number of growth bars) of 5.1 ± 0.4 mm (range 4.2–6.5, $n = 43$). To pursue the proximate sources of tail variation, I regressed feather length on number of growth days and daily growth rate. The two factors were of similar importance (multiple regression, $F_{2,40} = 635$, $P < 0.001$, $R^2 = 0.97$, standardized β = 1.46 and 1.23, respectively). Males thus seem to vary both in duration and rate of tail growth. As these were males with full-grown tails for which I cannot estimate date of tail completion, the variation in date when tail growth began is not known. However, the simultaneous occurrence of semi-grown and full-grown tails along with the rather small differences in growth rate suggests that males differ markedly in the timing of the onset of growth.

The physiological mechanism causing fault bars in feathers, and the nature of the stress they might represent, are unresolved issues (see King and Murphy 1984), and the following results should be viewed with caution. However, the numerous and large fault bars (conspicuous perforations perpendicular to the rachis, the largest being more than a millimeter wide and running across the entire vane) is such a striking feature of the Jackson Widowbird rectrices that they seem inevitable to include in this context. With much variation among individuals, there were about 40 fault bars of varying sizes on the tail feathers ($\bar{x}$ ± SD: 38 ± 19, range 9–78, $n = 43$), or two per cm (2.0 ± 1.0, $n = 43$). The "stress," or whatever factor is causing them, seems to increase from early to late stages of tail growth, as the proximal half of the feathers had more frequent faults than the distal half (2.4 ± 1.0, and 1.5 ± 1.2 faults cm^{-1}, respectively, pairwise t-test, $t_{42} = 5.2$, $P < 0.001$). The difference in fault area (sum of size scores) was even larger (proximal half 3.8 ± 2.3; distal half 2.0 ± 1.7; pairwise t-test, $t_{42} = 6.5$, $P < 0.001$). This corroborates the low body condition found in males about to complete tail growth (Fig. 1).

Furthermore, the length of the feather was pos-

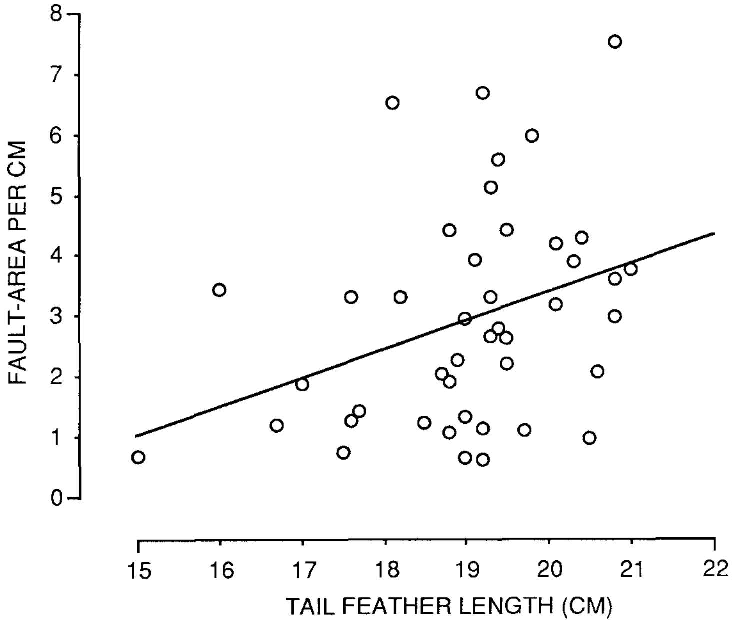

FIGURE 2. The fault-area per cm in tail feather (the sum of size scores [1–5] of fault bars, divided by the length of the feather) plotted against feather length for 43 different males. $r_s = 0.37$, $P = 0.016$. Linear regression; $y = 0.47x - 6.0$, $F_{1,41} = 5.5$, $P = 0.024$, $R^2 = 0.12$.

itively correlated with the number of faults per cm ($r_s = 0.33$, $n = 43$, $P = 0.034$), and somewhat more so with fault-area per cm (Fig. 2; $r_s = 0.37$, $n = 43$, $P = 0.016$), suggesting that the total stress experienced during the formation of a tail feather increases non-linearly with its length. The specific weight of feathers (g cm^{-1}) was positively related to both feather length ($r_s = 0.42$, $n = 43$, $P = 0.006$) and growth rate ($r_s = 0.48$, $n = 43$, $P = 0.002$); i.e., there was no trade-off between tail length and "tail quality." Despite their increased number and size of fault bars, long tail feathers thus represent a larger investment, at least in terms of the amount of material laid down by the male.

Given the likely physiological costs of tail growth and display, these characters might be indicators of any aspect of the male phenotype that improves his ability to invest in sexual advertisement. Some of the results are interesting in this respect. Full-grown tail length was positively correlated with male body condition (the weight of feathers is negligible in this respect; about 0.004 g per cm). This pattern was true for courtholders ($r_s = 0.30$, $n = 88$, $P = 0.005$) as well as floaters ($r_s = 0.30$, $n = 55$, $P = 0.03$), and when the two groups were pooled ($r_s = 0.26$, $n = 143$, $P = 0.002$).

Lek attendance and display. Among "ready" males (i.e., full grown since an unknown number of days), floaters and courtholders differ in body condition (Fig. 1), although the absolute difference is small (about 1 g in residual body mass). It appears that floaters recover their initial condition, whereas the condition of courtholders continues to decline after tail growth is completed. This might be due to the demands from lek attendance and display. Such a display cost is further supported by decrease in body condition with time spent lekking. For each season (or lek, in case the two leks in a season were not simultaneous in time), I regressed male body condition (excluding tail-growing males to avoid the confounding cost of ornament production; see above) on number of days passed (at capture) since the estimated starting date of the lek.

In the two larger samples with much variation in capture dates, the regression slopes were significantly negative; i.e., body condition declined over time (Tharua lek 1985–1986: $F_{1,23} = 5.2$, $P = 0.033$, $R^2 = 0.19$; Gatarakwa and Nobel leks 1989–1990: $F_{1,32} = 16.2$, $P < 0.001$, $R^2 = 0.34$).

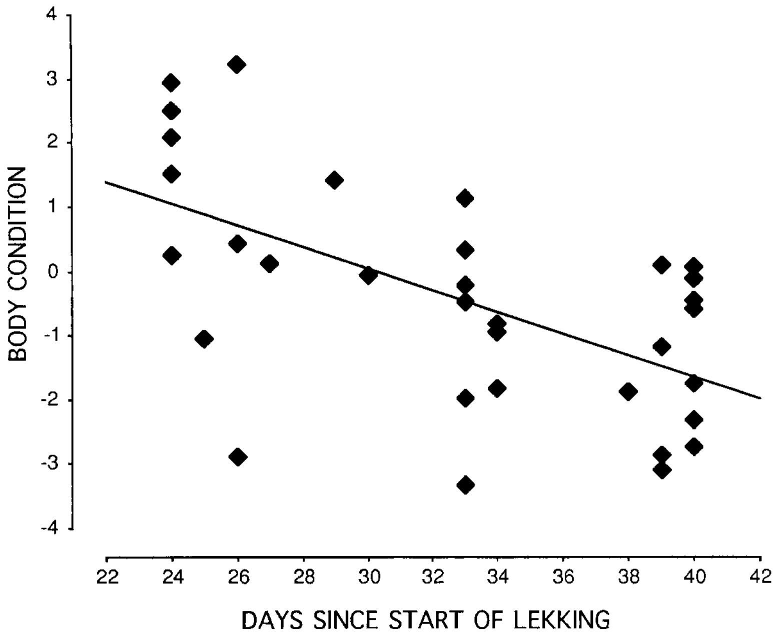

FIGURE 3. Body condition of different males (excluding "growing" males; see text) captured in the 1989–1990 season at two neighboring and simultaneous leks, as a function of the number of days passed since start of the lek. Linear regression: $y = -0.17x + 5.08$, $F_{1,32} = 16.2$, $P < 0.001$, $R^2 = 0.34$.

The relationship for 1989–1990 is depicted in Figure 3. Slope coefficients for the two seasons were −0.19 and −0.17, respectively, denoting a decrease of about 0.18 g residual body mass per day. Extrapolated to a peak display period of three weeks (a low estimate) this would constitute a weight loss of 3.8 g or 9% of the average adult male body mass (43 g).

In three cases (NM1 and NM2 leks in 1984–1985, K2 in 1985–1986, and Sth in 1986–1987), sample sizes of "ready" or "fresh" males were rather small (n = 14, 13, 12, respectively) and there were no significant changes in condition with time (linear regressions; F-tests, P = 0.81, 0.99, 0.51, respectively; slopes [standardized β] = 0.07, 0.004, 0.21, respectively). Lek M18 (1986–1987) were omitted as the few captures of "ready" or "fresh" males (n = 8) were concentrated on two subsequent days.

For behaviorally observed males, I investigated the relationship between body condition and display effort. Before pooling data across leks, the variables were transformed to standard scores for each lek (mean zero and unit variance). For the 26 observed males at the leks that showed a condition decline over time, I controlled for the decline by using the residuals from the regressions of condition vs. days since lek starts as a time-corrected measure of condition. This condition measure correlated negatively with both lek attendance ($r_s = -0.55$, $n = 26$, $P = 0.006$) and display rate ($r_s = -0.40$, $n = 26$, $P = 0.048$). Among males from the remaining leks there was no significant relationship between condition and display effort.

Finally, if both lek attendance and display are costly, and if there were little or no variation in male quality, one might expect a trade-off between the two aspects of display effort; for example, males with high display output might leave the lek more often and for longer periods to recover lost reserves. The case was instead the opposite, as attendance and display rate (standardized with respect to lek) were positively correlated ($r_s = 0.42$, $n = 50$, $P = 0.003$). Because display rate was calculated over total observation time, there could still be a finer tuned trade-off, so that males displaying at high rates when present at their courts showed low attendance. But when I replaced (total) display rate with rate per minute present, the correlation remained positive, though not significant ($r_s = 0.22$, $n = 50$, $P = 0.13$). The most vigorous displayers seemed to be the most tenacious attenders.

DISCUSSION

I do not know for which of the listed raptors a widowbird is a potential meal, but the fear of such small species as the Black-shouldered Kite suggests that the lekking males run some risk of being killed at the lek. Harriers were the most frequent causes of disturbance, and a pallid harrier has been observed capturing a female or juvenile longtailed widowbird from a flock (Malte Andersson, pers. comm.). An aposematic function of the nuptial plumage (e.g., Baker and Parker 1979) is largely refuted by the postnuptial molt back to the brown, female-like plumage. In sum, predator harassment definitely affected lek activity, but apparently is not an important limiting factor for male ornamentation or display.

The case is stronger for physiological constraints, although the results are indirect. Ideally, body condition and energy expenditure, along with tail growth and performance, should have been measured repeatedly for a number of males to allow direct assessments of individual costs (e.g., Vehrencamp et al. 1989). As my recaptures were few, I have instead investigated single-occasion measures of condition in relation to indices of male investments, such as stage of tail growth, current status as courtholder or floater, time spent lekking, and subsequent display activity. The results may thus be influenced by unidentified and correlated factors affecting the differences between males. On the other hand, one might also view the trends as robust because they emerged in spite of males being sampled only once.

Costs of the long tail. The declining body condition during completion of the tail suggests a physiological constraint on plumage adornment. Molt and feather formation is believed to be physiologically demanding. For example, feather production alone (thermoregulatory costs removed) increased oxygen consumption by 13% in molting cowbirds (Lustick 1970). Pre-breeding formation of elongated tail ornaments seems likely to be stressful. This is suggested by seasonal variation in tail length in relation to food supply (Evans 1991), correlations between tail length and age (and hence experience and probably phenotypic condition) over several years (Smith 1965, Manning 1987), and stronger fluctuating asymmetry, indicative of developmental stress, in tail ornaments compared to non-ornamental tails of conspecific females and males of related species (Möller and Höglund 1991).

The Jackson's Widowbird tail feathers grow at a rate of five mm per day, which is more than the approximately three mm per day that seems to be normal for small passerines (Newton 1967, Ginn and Melville 1983, Murphy and King 1984). Although the causes and implications of the thin fault lines found in the rectrices of other bird species are unclear (King and Murphy 1984), the frequency and conspicuous size of the fault bars in Jackson's Widowbird tails seem hard to interpret other than as reflecting some cost of the rapid growth. The concentration of faults to the last formed half of the tail agrees with the decline in body condition towards the end of tail growth. This could not be explained by deteriorating food conditions; food becomes more plentiful as the grass ripens towards the later part of the breeding season. But it is an open question whether the increased stress should be interpreted as resulting mainly from feather growth alone, from carrying the tail in flight (see below), or from the onset of lek activity somewhere halfway through tail formation. In any case, the positive relationships between frequency of fault bars and both growth rate and final tail feather length might reflect a physiological cost strong enough to explain part of the variation in this secondary sex character.

Evans and Thomas (1992) showed that the narrow tail streamers of some sunbird species roughly double the tail area and thereby contribute between a half and three percent (depending on flight speed) of the total drag on the bird. Overcoming drag is the major cost of normal flight (increasing at higher speeds), and this tail ornament was estimated to increase energy consumption during flight by between one and five percent. The graduated tail of Jackson's Widowbird should handicap flight considerably more. All rectrices are elongated, producing a long (21 cm) and wide (at least 2.5 cm when folded) lateral surface. Even with a minimum approximation of a flat plate, the increase in area compared to the six-cm, folded, non-ornamental tail must be at least fivefold, and strongly increase its contribution to drag. The loss of maneuverability must likewise be large, and it is in fact striking how straight the nuptial males fly compared to females and subadult males. An aerodynamic cost of carrying a long tail is also supported by a positive correlation between sexual dimorphism in wing length and tail length in the genus *Euplectes* (S. Andersson and M. Andersson, in press).

Costs of display. The jump display (stereotypically repeated leaps into the air) appears as demanding as some other avian lek displays that have been shown to push males to very high metabolic rates (Vehrencamp et al. 1989, Höglund et al. 1992). A cost of lekking in Jackson's Widowbird is implied by the lower condition of "ready" courtholders compared to floaters, and also by the decline (during two of the seasons) in condition with time since lek start. Why was this decline not detected in all cases? Possibly it is a question of smaller sample sizes and insufficient variation in capture dates. For lek Sth in 1986–1987 there was also very low display activity during the period when the males were captured, and for the Naro Moru leks in 1984–1985 there is the interesting possibility that males easily replenished weight losses as they frequently fed at an adjacent wheat field. For lek K2 in 1985–1986 there is no excuse.

At the leks where the trends were significant, the figures suggested a weight loss of 0.18 gram per day, corresponding to 9% of the body mass during the average three weeks of peak display. This is slightly more than the net weight losses of 6% during 20 days of lekking in male great snipe (Höglund et al. 1992), 5% during one to two months in sage grouse (Beck and Braun 1978), and 7% in Black Grouse males during 14 days of peak lek activity (Angelstram 1984). The pattern in Jackson's Widowbird also seems to agree with data on seasonal weight changes in some of its congeners showing a yearly weight maximum at start of breeding followed by a decline (Craig 1978).

Advertisement of male quality. The positive correlation between final tail length and condition suggests that males differ either in initial amount of body reserves, or in the slopes of their cost function ("expenditure" versus tail length), or both. Important factors could be age, parasite load, foraging skill, metabolic efficiency, etc., all of which theoretically might be related to some heritable component of fitness, which then might be the ultimate goal of the female preference. A negative relationship between length and bilateral asymmetry (reflecting stress) of tail feathers further qualifies tail length as an indicator of male viability (Möller and Höglund 1991).

The reasoning above applies also to the variation in ability to attend the lek and display, although the relationship between condition and these traits instead tended to be negative. When males were measured, tail formation was in most cases a past investment, while cost of display was a current investment, so this does not seem biologically unrealistic. Rather than suggesting a trade-off between tail length and performance, the contrasting correlation signs are likely to be sampling effects; tail length among the behaviorally studied males was not negatively correlated with lek attendance ($r_s = 0.15$, $n = 50$, $P = 0.31$) or display rate ($r_s = 0.22$, $n = 50$, $P = 0.12$).

Both tail length and performance might thus indicate male quality, as implied by Williams (1966) and then elaborated and modeled by many authors. Tail length may be an indicator of past investment in ornament growth, and display rate and attendance may indicate present metabolic expenditure. Moreover, a negative relationship between condition at capture and subsequent display rate does not necessarily mean that males share a common function relating net physiological costs to display effort. In sage grouse, the top displayers ranked lowest in condition at capture, possibly because they had been displaying for a longer time, yet they suffered the least subsequent weight loss. Vehrencamp et al. (1989) suggested that these males were efficient at recovering lost reserves, and discussed the possibility that males perform at individual optima, determined by their individual cost functions (also see Parker 1982). It is tempting to try to fit the Jackson's Widowbird data into this framework, but the results are far from this level of resolution. It is, however, easy to imagine a scenario where high quality males produce longer tails at a lower cost, and have higher display-related energy turnover. The direct measurements of male cost functions (e.g., Vehrencamp et al. 1989), as well as the identification of the key components of male quality, remains to be done.

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