Experimental evidence for female choice and energetic costs of male tail elongation in red-collared widowbirds

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The black nuptial plumage of the highly polygynous male red-collared widowbird (*Euplectes ardens*) comprises a red carotenoid-based collar patch and a long graduated tail (*c*. 22 cm). Tail length was the strongest predictor of male mating success in a previous selection analysis, motivating this experimental test of the relative importance of tail plumes in male contest competition and female choice. Males were assigned to either a short (12.5 cm) or control (20 cm) tail manipulation prior to territory establishment. Male contest competition was unaffected by the tail treatments as the shortened- and control-tailed males were equally successful in acquiring territories of similar size and quality. In contrast, however, although the longer-tailed control males spent less time in flight and courtship displays, they attracted significantly more prospecting and nearly three times as many nesting females to their territories compared to the short-tailed males. In further support of tail length as the primary mate choice cue, none of the other measured and potential female cues (e.g. body size, collar colorimetrics, territorial behaviours or territory quality) influenced male reproductive success. In addition to potentially increasing detectability ('signal efficacy'), the long tail is also a likely indicator of male quality ('signal content'). Despite the higher activities of short-tailed males, control-tailed males showed a steeper decline in condition (relative body mass) during the breeding season. Furthermore, both short- and control-tailed residents lost more condition than did the short- and control-treated floaters (males not establishing territories), suggesting an interaction between tail length and the costs of territory acquisition, defence and courtship displays. These results confirm the role of mate choice and honest quality advertising as the main selection pressures behind elongated tails in widowbirds.   © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **86**, 35–43.

ADDITIONAL KEYWORDS: *Euplectes ardens* – male quality – mate choice – sexual selection – tail length.

INTRODUCTION

Extravagant tail plumes of male birds have played a pivotal role in the study of sexual selection (reviewed in M. Andersson, 1994; Ligon, 1999). There is now experimental evidence from six avian species that females prefer longer-tailed males (Andersson, 1982; Møller, 1988; Barnard, 1990; Smith & Montgomerie, 1991; Andersson, 1992a; Evans & Hatchwell, 1992; Pryke & Andersson, 2002). However, few of these studies have directly examined the relative effects of male contest competition and female choice in contributing to the increase in mating success. For example, elongated tails may function primarily in contests among males for territories and access to females (e.g. Savalli, 1994; Rintamäki *et al*., 2001).

The elaborate tails of male widowbirds (genus *Euplectes*) have been the focus of three experimental studies of sexual selection; long tails function in mate choice in the long-tailed (*E. progne*; Andersson, 1982) and Jackson's widowbirds (*E. jacksoni*; Andersson, 1992a) but are suggested to function in territorial competition in yellow-shouldered widowbirds (*E. macrourus*; Savalli, 1994). In the red-collared widowbird (*E. ardens*), a previous selection analysis found that male mating success (number of nesting females) was strongly related to tail length, which explained 47% of the variance in mating success (Pryke, Andersson & Lawes, 2001a). However, despite the multivariate control of several other traits, the relationship (as in all correlational studies) might have arisen via an

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unmeasured variable, or by some behaviour, morphology or aspect of territory quality over which males compete (M. Andersson, 1994; Berglund, Bisazza & Pilastro, 1996). In this study, we experimentally investigate the relative importance of tail length in male contest competition and female choice by manipulating male tail length (within natural variation) prior to territory establishment, when male competition is probably most intense, and monitoring subsequent female attraction.

Red-collared widowbirds are small (*c.* 20 g), sexually and seasonally dimorphic weaverbirds of African grasslands and savannas. Apart from a red carotenoid-based collar (throat) patch, nuptial males are black with a graduated tail about 22 cm long. Females and non-breeding males are streaked yellowish-brown and lack the elongated tail. During the breeding season the polygynous males establish exclusive breeding territories in open grasslands. From these territories, males display to visiting females in a slow, smooth flight with their long tails prominently displayed; the shorter central rectrices are depressed to produce a deep keel, expanding the tail in the vertical plane similar to a rudder. Males provide no resources for females other than potential nesting locations on their territories, and the female alone performs all nest building, incubation and nestling feeding.

Most models of sexual selection assume that viability costs oppose and eventually prevent further elaboration of a sexually selected character (Grafen, 1990; M. Andersson, 1994). Nevertheless, such balancing forces of natural selection have received less attention (for exceptions see e.g. Nur & Hasson, 1984; Höglund & Sheldon, 1998), despite their ability to provide an indication of the relative strength of the selection pressures on elaborate ornaments, such as bird tails (Fitzpatrick, 1998). Aerodynamic theory suggests that only the proximal part of the tail (until the point of maximum continuous width) is aerodynamically functional and that any extension beyond the widest part of the tail increases drag but not lift (Balmford, Thomas & Jones, 1993; Thomas, 1993) causing an increase in the power required for flight (Norberg, 1995). Graduated tails (all rectrices elongated), such as those displayed by red-collared widowbirds, are predicted to have particularly high flight costs compared to other tail ornaments (Balmford *et al.*, 1993) since such tails contribute significantly to the drag of the bird (Evans & Thomas, 1992; Thomas & Balmford, 1995).

These aerodynamic costs, together with the large costs of producing and maintaining elongated tails (e.g. Evans, 1991; S. Andersson, 1994), may ensure that this signal reflects male quality (Grafen, 1990; M. Andersson, 1994; Johnstone, 1995). Thus, if long tails are costly for males to display, the cost is expected to rise with increased tail length and decrease if tail length is reduced. In this study we investigate whether tail ornaments 'handicap' red-collared widowbird males by assessing changes in condition of manipulated males throughout the breeding season, as well as differences between territory holders and floaters (non-territorial males) in the population.

METHODS

This experiment was undertaken between early December 2001 and March 2002 on a red-collared widowbird population in the eastern KwaZulu-Natal midlands of South Africa (29°35′S, 30°04′E). The study site is composed of open grasslands, savannah and marshlands, isolated from other habitable areas for widowbirds by forestry and agricultural fields. Widowbirds were mist-netted at communal night roosts and ringed with an aluminium ring and three unique colour bands (excluding orange and red bands).

MORPHOMETRIC DATA

At capture, wing chord, culmen and tarsus length were measured to the nearest 0.1 mm. Since these three body measurements were correlated, the first component (explaining 79.5% of the variance) from a principal components analysis (PCA) was used to extract an independent measure of body size. Each tail feather was measured to the nearest 0.1 mm and the number of blood quills (i.e. still growing) counted. Birds were also weighed to the nearest 0.1 g at manipulation and later on at recapture (after territory establishment). An index of body condition was computed as the residuals of a linear regression of log(body mass) on 3*log(tarsus length). Collar size was calculated as the product of the maximum length and the average of three width measures of the throat patch (to the nearest 0.1 mm) when holding the head in a normal position. Since many males were caught and measured multiple times, repeatabilities were calculated to assess their reliability. All measurements were highly repeatable (wing: $F_{87,149} = 23.76$, $r = 0.92$; culmen: $F_{87,149} = 31.93$, $r = 0.93$; tarsus: $F_{87,149} = 35.76$, $r = 0.94$; total tail length: $F_{87,149} = 25.02$, $r = 0.92$; collar size: $F_{87,149} = 14.18$, $r = 0.86$; for all $P < 0.001$).

REFLECTANCE SPECTROMETRY AND COLORIMETRICS

Objective colour measurements (reflectance) of the red collar were taken using a S2000 diode-array spectrometer (Ocean Optics) with illumination from an HL2000 halogen light source. Using the C-spec software (Ancal Inc.), we took five consecutive scans (removing the probe between each) from the centre of the throat patch, and in relation to a WS-2 white standard

scanned prior to scanning each individual. The three main perceptual dimensions of colour signals (brightness, hue and chroma) were computed from the raw spectral reflectance data, and then averaged for each individual, since the five spectra measurements per individual were highly repeatable for all colour variables ($F_{119,481} = 41.52$, $r = 0.89$, $P < 0.001$). Brightness (overall intensity; $R_{350-700}$) was calculated as the reflectance over the 350–700 nm range. Hue (spectral position or 'redness'; λR_{50}) was computed as the wavelength halfway between that of the minimum and the maximum reflectance. Using λR_{50} as the individual segment divider, we calculated chroma (spectral purity; C_{R50}) as $R_{350-\lambda R50} - R_{\lambda R50-700} / R_{350-700}$. A detailed description of the colour measurements and analyses can be found in Pryke *et al*. (2001a).

TAIL MANIPULATIONS

One hundred and twenty males were manipulated prior to territory establishment. Males were sequentially assigned to either the short or control tail group (Table 1). Tails were not elongated because pre-experimental trials (by gluing on additional feather lengths) showed that this treatment dramatically altered the characteristic keeled appearance (i.e. resembling an inverted sickle) of the tails in courtship displays: birds could no longer successfully depress their tails into a deep keel. Red-collared widowbirds have graduated tails with rectrices of unequal length (i.e. the second rectrix is the longest while the innermost feather is the shortest). Therefore, in order to maintain the graduated appearance of tails and allow males to characteristically keel their tails, we cut each rectrix to correspond to the minimum or the mean (minus 2 cm) of the natural variation. In other words, the short tail group (maximum tail length = 12.5 cm; $N = 60$) had each tail feather shortened to the lower limits of the natural population variation for that feather (see details for each tail feather in Table 1). Controls were shortened to a maximum length of 20 cm (2 cm below the population mean of 22 cm; Pryke *et al*., 2001a), so that naturally short-tailed males could also randomly be included in the experiment (Table 1). Pre-treatment (natural) tail lengths did not differ between the treatment groups (for all 12 tail rectrices: $F_{12,108} = 0.83$, $P = 0.17$).

TERRITORY CHARACTERISTICS

Territorial males defend large, well-defined territories (mean territory size $\pm$ SD = 0.47 ± 0.31 ha, $N = 134$, range = 0.1–1.6 ha) that are either isolated or contiguous with other territories within the grasslands (for further details see Pryke, Lawes & Andersson, 2001b, 2002). Residents actively (and often viciously) defend their territories from other males (Pryke *et al*., 2001b), and territory borders were identified as the outer boundaries of displays and aggressive interactions (i.e. aggressive displays, chasing, parallel flight displays and directed attacks). Territories were mapped from direct observations and defined using the minimum convex polygon method. The maps were digitized and ArcView (ESRI, 1996) used to estimate territory area. Territory maps were updated every week, although differences between the updates were so slight that area parameters were unaltered (i.e. birds defended well-defined territories: mean $\pm$ SD change in area over 14 weeks = 0.02 ± 0.02 ha, $N = 91$ territories; $F_{13,1170} = 0.93$, $P = 0.52$).

Although a variety of territory characteristics may influence female mate choice (e.g. Eckert & Weatherhead, 1987; Aebischer *et al*., 1996), vegetation type is the most obvious and striking difference between the territories used by red-collared widowbirds in this study. Males provide females with only gametes, since females ignore the simple male-constructed initial nest rings ('cock's nests') and instead build their own

Table 1. Mean $\pm$ SD tail feather length (cm) for the natural variation in the population and for the experimental tail treatments prior to and post manipulation. Rectrix 1 refers to the average (of the left and right) outermost tail feathers while rectrix 6 is the average length of the innermost tail feathers

Rectrix	Natural variation	N	Short-tailed ($N = 60$)		Control-tailed ($N = 60$)	
			Before	After	Before	After
1	19.2 ± 3.6	175	17.3 ± 3.1	11.5 ± 0.2	19.4 ± 3.3	18.0 ± 0.1
2	23.7 ± 3.8	179	23.2 ± 3.4	12.5 ± 0.3	22.9 ± 4.2	20.0 ± 0.2
3	20.9 ± 3.4	164	21.5 ± 2.8	12.0 ± 0.2	21.8 ± 3.6	19.1 ± 0.2
4	18.8 ± 3.2	166	17.7 ± 2.5	10.1 ± 0.1	19.1 ± 3.1	17.5 ± 0.1
5	14.4 ± 2.9	158	14.8 ± 2.5	9.4 ± 0.1	14.1 ± 2.6	13.0 ± 0.1
6	9.8 ± 1.5	172	8.9 ± 1.7	8.4 ± 0.1	9.2 ± 1.1	9.5 ± 0.1
Maximum	23.7 ± 3.6	198	23.2 ± 3.4	12.5 ± 0.2	22.9 ± 4.2	20.0 ± 0.2

nests on the territory (Pryke *et al.*, 2001a). Therefore, nest site availability is likely to be the most important territory characteristic. To measure habitat quality and assess nesting suitability, we measured the number of different vegetation types, mean density (expressed as percentage) and vegetation height (m) within each territory. Vegetation measurements were taken fortnightly at fixed sampling points situated 20 m apart on 50 on transects across the study area and averaged for the nesting season.

BEHAVIOURAL OBSERVATIONS

Territorial males were randomly observed weekly during the morning peak of activity (04:30–09:00) for 15 min throughout the breeding season. All activities and their durations were continuously recorded (timed to the nearest 5 sec). For analyses, we extracted data on the time spent active on the territory, the intrusion rate by floaters and neighbours, the number and duration of agonistic encounters, the time spent in directed (i.e. tail folded) and display (i.e. tail keeled) flight, and the frequency of female visits. To control for temporal and seasonal differences in behavioural activities between males, we used observations commencing from the first day of territory establishment until the fledging of the last chick (mean ± SD = 13.9 ± 0.6 weeks, $N = 91$ males).

MALE REPRODUCTIVE SUCCESS

Throughout the study, territories were searched daily for nests, and then rechecked every third day until abandoned, predated or successfully fledged. Genetic parentage could not be assigned to offspring because of the high negative effects of predation and environmental influences on nest survival (80%; also 73–98% in congeners, e.g. Craig, 1982; Andersson, 1992b). Therefore, we used the number of active nests (containing eggs or nestlings) on a territory as a measure of male fitness (see Pryke *et al.*, 2001a). In both this study and in previous seasons, males attracting more nesting females to their territories also produced significantly higher numbers of nestlings ($r_s = 0.83$, $N = 126, P < 0.001$) and successful fledglings ($r_s = 0.92$, $N = 49$, $P < 0.001$). Therefore, the number of active nests on a male's territory is likely to be a good indication of male reproductive success, unless counteracted (rather than under- or overestimated) by extrapair copulation (EPC) mate choice. EPC frequency is unknown in this species, but since females obtain little more than genes from males, it appears unlikely that their criteria for genetic mate choice would be different from their social mate choice. Furthermore, given the high degree of social polygyny observed (up

to nine nesting females), males with only a few nesting females on their territories would have to achieve numerous EPCs with females nesting on very popular territories (while enduring very few themselves) to eliminate the observed reproductive skew.

STATISTICAL ANALYSES

To prevent inflating comparison-wise errors, multiple analysis of variance (MANOVA) models were used to determine whether tail-treated males (short and control) differed in morphological and colorimetric traits, and to test the effects of the tail manipulations on territorial characteristics, behavioural activities and male attraction. Using male status (i.e. resident or floater) and reproductive success (number of active nests) as the dependent variables, we also tested whether tail manipulations and male traits affected territory establishment and mate attraction, respectively. Wilks' λ (likelihood ratio criterion) tests the overall significance of the treatments on male characteristics and behaviour. If the result is significant, the univariate *F*-tests are consulted to ascertain which of the factors causes the overall significant effects. For analyses where the assumptions of parametric tests were violated, Spearman rank correlations were used.

RESULTS

TAIL MANIPULATIONS AND TERRITORY ESTABLISHMENT

The tail manipulations had no effect on territory establishment, as 48/60 short-tailed and 43/60 control-tailed males established territories in the area (Table 2). Similarly, there were no differences between the treatment groups in morphological (initial tail length, body size [PC1], initial body condition) or features of the carotenoid colour signal (collar size, brightness, chroma or hue) that could potentially influence territory acquisition (Table 3). The tail manipulations were also unimportant in determining the size of the territories defended by residents as well as territory quality (vegetation type, density and height; Table 3). The only traits affecting territorial establishment were collar size and redness (hue): territorial males had significantly redder ($P < 0.001$) and slightly larger ($P = 0.001$) collars than non-territorial (floaters) males (Table 2), as has been previously demonstrated in other populations (Pryke *et al.*, 2001b; Andersson *et al.*, 2002).

TAIL MANIPULATIONS AND MALE BEHAVIOUR

The tail manipulations had no confounding effects on territorial defence behaviours; there were no differences in the time spent on territories, intrusion rates,

Table 2. Effects of the tail manipulations on territory acquisition, and the variation (mean ± SD) in morphological and colorimetric traits between residents (establishing territories) and floaters (non-territorial males). Univariate F-values and significance levels are derived from a MANOVA (Wilks' $\lambda = 0.68$, $F_{8,111} = 6.45$, $P < 0.001$)

Male trait	Residents ($N = 91$)	Floaters ($N = 29$)	F	P
Manipulation	43 control, 48 short	17 control, 12 short	0.40	0.53
Natural tail length (mm)	221.96 ± 36.82	239.42 ± 55.46	1.01	0.32
Body size (PC1)	0.03 ± 1.05	-0.11 ± 0.81	0.54	0.48
Body condition	0.00 ± 0.03	-0.00 ± 0.02	0.06	0.79
Collar brightness ($R_{350-700}$)	223.53 ± 55.24	243.99 ± 43.54	2.73	0.11
Collar chroma (C_{R50})	0.68 ± 0.05	0.68 ± 0.06	0.35	0.55
Collar size (mm^2)	254.43 ± 40.62	191.87 ± 57.11	10.26	0.001
Collar hue (λ_{R50})	588.68 ± 14.87	558.09 ± 15.35	47.89	< 0.001

Table 3. Comparison of male morphology and colorimetrics (MANOVA: Wilks' $\lambda = 0.93$, $F_{7,112} = 1.69$, $P = 0.13$), territorial (Wilks' $\lambda = 0.97$, $F_{5,85} = 0.58$, $P = 0.71$) and behavioural characteristics (Wilks' $\lambda = 0.74$, $F_{6,86} = 6.03$, $P < 0.01$), and male attraction (Wilks' $\lambda = 0.29$, $F_{2,88} = 104.88$, $P < 0.0001$) between short- and control-tailed males. Univariate F-values and significance levels are derived from the MANOVAs

	Short-tailed $N = 60$	Control-tailed $N = 60$	$F_{1,118}$	P
MORPHOLOGY AND COLORIMETRICS				
Natural tail length (mm)	224.71 ± 47.21	219.11 ± 39.81	0.17	0.67
Body size (PC1)	0.04 ± 1.02	0.01 ± 0.97	0.88	0.56
Body condition (residual index)	0.01 ± 0.04	-0.00 ± 0.03	1.30	0.14
Collar size (mm^2)	233.94 ± 46.1	229.53 ± 55.87	0.52	0.47
Collar brightness ($R_{350-700}$)	229.04 ± 48.3	231.91 ± 56.48	2.54	0.11
Collar chroma (C_{R50})	0.67 ± 0.05	0.68 ± 0.06	2.11	0.14
Collar hue (λ_{R50})	564.42 ± 16.76	567.93 ± 18.34	1.16	0.28
TERRITORY CHARACTERISTICS	$N = 47$	$N = 44$	$F_{1,89}$	P
Territory size (ha)	0.49 ± 0.18	0.51 ± 0.26	2.25	0.14
Number of cock's nests	9.39 ± 5.39	10.98 ± 4.77	2.21	0.13
Number of vegetation types	4.57 ± 1.48	4.56 ± 1.59	0.03	0.78
Vegetation density (%)	56.81 ± 15.12	56.52 ± 5.49	0.04	0.74
Vegetation height (m)	1.63 ± 8.15	1.52 ± 8.31	1.24	0.17
BEHAVIOURAL CHARACTERISTICS	$N = 47$	$N = 44$	$F_{1,89}$	P
Time on territories (min^{-1})	0.79 ± 0.17	0.77 ± 0.15	0.23	0.62
Intrusion rates (min^{-1})	0.63 ± 0.21	0.60 ± 0.23	0.36	0.55
Encounter rates (min^{-1})	0.15 ± 0.28	0.12 ± 0.21	0.31	0.57
Encounter durations (s)	13.68 ± 8.19	14.27 ± 9.08	0.16	0.69
Time in directed flight (min^{-1})	0.32 ± 0.23	0.19 ± 0.16	9.48	0.002
Time in display (min^{-1})	0.44 ± 0.16	0.23 ± 0.22	16.60	< 0.001
MALE ATTRACTION	$N = 47$	$N = 44$	$F_{1,89}$	P
Number of active nests	2.73 ± 0.89	0.65 ± 0.67	156.42	< 0.001
Female visitation rate (min^{-1})	0.31 ± 0.19	0.09 ± 0.13	44.85	0.002

or the number or duration of aggressive encounters between the treatment groups (Table 3). However, short-tailed males tended to spend more time in flight (excluding male-male chases; $P = 0.002$) and courtship displays ($P < 0.001$) relative to control-tailed males (Table 3). Thus, males given short tails spent proportionately more time active on their territories and displaying to visiting females.
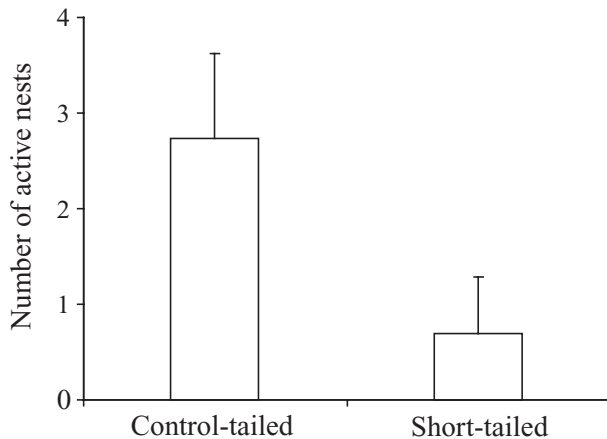
Figure 1. Mean (± SD) number of actively nesting females (i.e. male reproductive success) attracted by the control-tailed ($N = 43$) and short-tailed ($N = 48$) males. See Table 3 for significance values.

Figure 2. Linear regression of full-grown tail length (cm) on a body condition index (relative body mass) ($F_{1,98} = 31.34$, $P < 0.001$, $R^2 = 21.2\%$) at the onset of the breeding season (prior to territory establishment).

TAIL MANIPULATIONS AND FEMALE CHOICE

The distribution of the 187 active nests (i.e. male reproductive success) was highly skewed between the treatment groups, with the longer-tailed control males attracting nearly three times as many nesting females as the short-tailed males ($P < 0.001$; Table 3 and Fig. 1). Furthermore, despite the lower display rates of control-tailed males (see above and Table 3), they also attracted significantly more prospecting females to their territories ($P = 0.002$; Table 3). There was no evidence that territory quality (MANOVA: Wilks' $\lambda = 0.77$, $F_{20,272} = 1.09$, $P = 0.35$), behaviour (Wilks' $\lambda = 0.61$, $F_{24,283} = 1.05$, $P = 0.11$) or any other aspect of male morphology and colorimetrics (Wilks' $\lambda = 0.64$, $F_{28,289} = 0.32$, $P = 0.13$) influenced male reproductive success (see Table 3 for list of variables tested). Instead, female red-collared widowbirds seemed attracted to longer-tailed males.

TAIL MANIPULATIONS AND BODY CONDITION

For a biologically relevant index of individual condition, body condition was calculated from the residuals of log(body mass) on 3*log(tarsus length). However, to avoid the potential problems of using residuals in further analyses, and to confirm the relevance of our body condition measure, we also calculated ANCOVAs (with tarsus length as the added covariate) for the relevant tests; in every case these analyses produced similar results (see below).

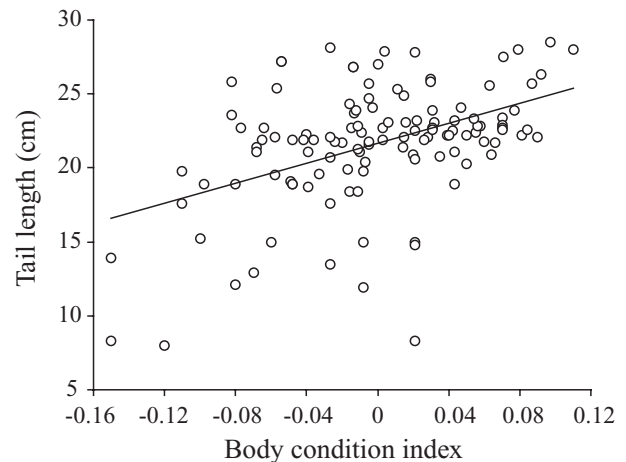As in previous studies (Pryke *et al.*, 2001a; Andersson *et al.*, 2002), full-grown tail length (no blood quills) was significantly positively related to male condition ($F_{1,98} = 31.34$, $P < 0.001$, $R^2 = 21.2$), with an increase in tail length of about 7 cm from the lowest to the highest condition estimate (Fig. 2).

Body condition declined during the season; recaptured resident males had lower condition at the end than at the beginning of the season ($F_{1,65} = 64.84$, $P < 0.001$, $R^2 = 51.1\%$). This temporal difference was also evident between the manipulation groups for both body condition ($F_{1,63} = 12.63$, $P < 0.001$; manipulation by condition interaction; $F_{1,63} = 9.75$, $P < 0.001$) and body mass (ANCOVA with tarsus length as a covariate: $F_{1,62} = 8.08$, $P < 0.001$; manipulation by body mass interaction; $F_{1,62} = 5.17$, $P < 0.001$). Before specifically testing the effects of tail manipulation on body condition, the condition estimates were recalculated for each group to obtain standardized and comparable measures. This condition measure was tested in an ANCOVA (with time since territory establishment as the covariate) and indicated that control-tailed males lost more condition during the season than short-tailed males (manipulation: $F_{1,63} = 78.76$, $P < 0.001$; condition: $F_{1,63} = 21.79$, $P < 0.001$; manipulation by condition interaction; $F_{1,63} = 5.11$, $P = 0.04$; Fig. 3). Similarly, substituting body mass (with tarsus length as the primary covariate) in the above analysis showed a similar decline in condition of short-tailed males (manipulation: $F_{1,62} = 67.74$, $P < 0.001$; mass: $F_{1,62} = 17.24$, $P < 0.001$; manipulation by mass interaction; $F_{1,62} = 5.57$, $P = 0.03$).

In addition, recaptured floaters ($N = 22$) seemed to be in better condition than residents ($N = 66$; ANCOVA [with time since manipulation as the covariate]: territorial status: $F_{1,87} = 5.37$, $P = 0.05$;
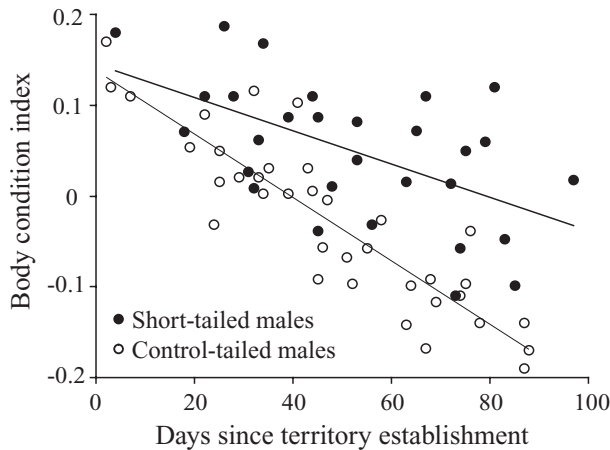
Figure 3. Body condition (relative body mass) of recaptured resident males during the breeding season as a function of the number of days since they established territories (overall: $F_{1,65} = 64.84$, $P < 0.001$, $R^2 = 51.1\%$). Body condition declined over the season in both short-tailed ($y = 0.14–0.002x$, $F_{1,27} = 15.79$, $P < 0.001$, $R^2 = 37.8\%$) and control-tailed ($y = 0.13–0.030x$, $F_{1,35} = 28.34$, $P < 0.001$, $R^2 = 68.2\%$) territory owners but was steeper in control-tailed males (see text for details on significance tests).

condition: $F_{1,87} = 8.92$, $P = 0.03$; territorial status by condition interaction; $F_{1,87} = 4.16$, $P = 0.02$). Likewise, the same result remained when condition was substituted with body mass (controlling for tarsus length) (ANCOVA: territorial status: $F_{1,86} = 12.61$, $P < 0.001$; mass: $F_{1,86} = 9.81$, $P = 0.05$; territorial status by mass interaction; $F_{1,86} = 2.87$, $P = 0.01$).

Due to the small sample size of recaptured control-tailed floaters ($N = 7$), the effect of manipulation could not be modelled in the ANCOVA. However, using the residuals from this ANCOVA model (i.e. after controlling for temporal effects), short- and control-tailed floaters tended to maintain better condition than short- and control-tailed residents, respectively (short-tailed: $z = 2.79$, $N = 7,43$, $P = 0.03$; control-tailed: $z = 3.02$, $N = 15,48$, $P = 0.01$). Furthermore, resident male condition (i.e. residuals from the ANCOVA model above) correlated negatively with both territorial defence activities ($r_s = –0.39$, $N = 66$, $P < 0.005$) and display rates ($r_s = –0.71$, $N = 66$, $P < 0.001$). This suggests that the condition difference may be due to the larger depletion of body reserves through the increased costs of territory acquisition, defence and courtship displays in resident males.

DISCUSSION

This experiment corroborates the female preference for longer-tailed males suggested by a descriptive analysis of sexual selection pressures (Pryke *et al.*, 2001a). Female mate choice was unaffected by other aspects of male morphology, colorimetrics or behaviour. Tail length might also function in male contest competition for territories that enables widowbird males to attract females (Savalli, 1994). However, in the red-collared widowbird, tail length appears unimportant in resolving territorial conflicts. First, the tail-treatments (manipulated prior to establishing territories when male competition is likely to the most severe) had no effect on territory acquisition (i.e. resident or floater status), and the size, quality and characteristics of resident male territories did not differ between the tail treatments. Second, there was no evidence that territory size, quality, or territorial behaviours affected female mate choice. Finally, a number of males without tails (lost at capture), both in this study ($N = 3$) and in previous seasons ($N = 13$), had no mating success (i.e. nests), but successfully established and defended their territories throughout the breeding seasons. Tail length thus seems unlikely to be important in male dominance. Instead, the outcome of male contests and success in territorial competition is primarily determined by the size and particularly colour ('redness') of the collar signal, which differs markedly between floater and resident males (Pryke *et al.*, 2001b, 2002; Andersson *et al.*, 2002).

The long tails of male red-collared widowbirds are prominently displayed from their territories. During the courtship flight display, the tail is expanded (spread) both laterally and vertically (by keeling the rectrices), thus considerably increasing the visual surface and making males highly detectable in their open grassland and savanna habitats, which may have been the initial advantage of tail elaboration (i.e. increasing signal efficacy; Guilford & Dawkins, 1991; Andersson, 2000). This tail display is noticeably similar and, according to a preliminary molecular phylogeny (S. Andersson & A. Johansson, unpubl. data), has probably evolved independently in the congeneric long-tailed widowbirds (*E. progne*), which depress and keel their tails in a similar way.

Simultaneously or subsequently to increasing signal efficacy, the exaggerated tail might have become an indicator of male condition and quality. The current positive relationship between tail length and body condition suggests that females attracted to males with longer tails also select more viable males. In addition, the long graduated tails should handicap flight considerably (Norberg, 1995; Thomas & Balmford, 1995) as all rectrices are elongated, producing a long (range 8–29 cm) and wide (at least 3 cm when folded) tail area, contributing considerably to aerodynamic drag (Balmford *et al.*, 1993). There may also be an energetic and physiological cost associated with larger tails, since control-tailed males (relative to

shortened ones) spent less time in general and courtship flights. This is further supported by the steeper decline in condition of control-tailed males, despite their lower display rates, compared to short-tailed males. Thus it seems unlikely that longer-tailed birds (attracting nearly three times as many females as shortened birds) are in worse condition solely because of the higher costs of attracting and interacting with more females.

Furthermore, the nature of the flight display may also influence aerodynamic and energetic costs. Compared to normal red-collared widowbird flight, in which the tail is folded and straight, courtship flights are much slower with the tail depressed to a keel. Since the costs of forward flight increase dramatically at reduced speeds (Norberg, 1990), the tail display appears to be particularly costly. Furthermore, having to constantly perform these courtship displays as well as territorial defence activities (e.g. displays, challenges and physical attacks) is likely to be demanding. Similar to the lekking Jackson's widowbird, where a physiological cost of lek attendance and display was indicated by differences between courtholders and floaters (S. Andersson, 1994), resident red-collared widowbirds have lower condition than floaters in both this and a previous study (Andersson *et al.*, 2002). Therefore, the maintenance and display of longer tails appears to handicap male red-collared widowbirds.

Finally, the nuptial moult from non-breeding plumage with short tails (4 cm) to elongated tails may also be stressful. For example, the strong trade-off between the investment in carotenoid coloration and elongated tails, suggests an allocation conflict between the production of the two ornaments (Andersson *et al.*, 2002).

This experiment confirms the epigamic signal function of long tails in red-collared widowbirds. Male tails are elaborated far beyond the optimal (naturally selected) tail length (i.e. probably the 4 cm tail length of females and non-breeding males) and impose larger costs on longer-tailed males. However, the costs of displaying exaggerated tails are balanced by the benefits of female preference for extreme tail length, suggesting that these ornaments are quality-indicating handicaps. Among the polygynous widowbirds, there is now experimental evidence from four species that tail length functions in mate choice (*E. progne*: Andersson, 1982; *E. jacksoni*: Andersson, 1992a; *E. axillaries*: Pryke & Andersson, 2002; *E. ardens*: this study), suggesting that female choice is a major selective force behind the evolution of elongated tails in male widowbirds.

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