

SEXUAL SELECTION OF MULTIPLE HANDICAPS IN THE RED-COLLARED WIDOWBIRD: FEMALE CHOICE OF TAIL LENGTH BUT NOT CAROTENOID DISPLAY

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Abstract.—Although sexual selection through female choice explains exaggerated male ornaments in many species, the evolution of the multicomponent nature of most sexual displays remains poorly understood. Theoretical models suggest that handicap signaling should converge on a single most informative quality indicator, whereas additional signals are more likely to be arbitrary Fisherian traits, amplifiers, or exploitations of receiver psychology. Male nuptial plumage in the highly polygynous red-collared widowbird (*Euplectes ardens*) comprises two of the commonly advocated quality advertisements (handicaps) in birds: a long graduated tail and red carotenoid coloration. Here we use multivariate selection analysis to investigate female choice in relation to male tail length, color (reflectance) of the collar, other aspects of morphology, ectoparasite load, display rate, and territory quality. The order and total number of active nests obtained are used as measures of male reproductive success. We demonstrate a strong female preference and net sexual selection for long tails, but marginal or no effects of color, morphology, or territory quality. Tail length explained 47% of male reproductive success, an unusually strong fitness effect of natural ornament variation. Fluctuating tail asymmetry was unrelated to tail length, and had no impact on mating success. For the red collar, there was negative net selection on collar area, presumably via its negative relationship with tail length. None of the color variables (hue, chroma, and brightness) had significant selection differentials, but a partial effect (selection gradient) of chroma might represent a color preference when tail length is controlled for. We suggest that the red collar functions in male agonistic interactions, which has been strongly supported by subsequent work. Thus, female choice targets only one handicap, extreme tail elongation, disregarding or even selecting against the carotenoid display. We discuss whether long tails might be better indicators of genetic quality than carotenoid pigmentation. As regards the evolution of multiple ornaments, we propose that multiple handicap signaling is stable not because of multiple messages but because of multiple receivers, in this case females and males.

Key words.—Carotenoid coloration, *Euplectes ardens*, female choice, handicaps, long tails, multiple ornaments, sexual selection.

Received January 4, 2001. Accepted March 26, 2001.

The extreme diversity in design and expression of epigamic traits, among species as well as among multiple ornaments within species, remains largely unexplained. Many sexual displays are examples of multicomponent signaling (Rowe 1999), with exaggeration of several distinct signals even within a given modality (e.g., visual, acoustic). Sexual selection theory, particularly the handicap principle (Zahavi 1975) of costly and thus reliable (honest) quality advertisements proposes that ornamental signals are exaggerated to a point where viability costs balance the mating advantage (M. Andersson 1994). However, it is not clear why so many species have multiple ornaments (Møller and Pomiankowski 1993), especially because honest advertising is theoretically expected to reinforce a single most informative signal at the expense of others (Schluter and Price 1993; Johnstone 1996). Although multiple signals may include arbitrary Fisherian traits, amplifiers, and the exploitation of receiver sensory capabilities (e.g., Iwasa and Pomiankowski 1994; Rowe and Guilford 1999), the coexistence of handicaps (the redundant, or back-up, signal hypotheses; Møller and Pomiankowski 1993; Johnstone 1996) remains a contentious issue.

In avian ornamental plumage three types of visual signals are often proposed as sexually selected quality advertisements: (1) ontogenetically or aerodynamically costly tail elongation (Balmford et al. 1993; S. Andersson 1994; Norberg 1995); (2) bilateral symmetry as an indicator of developmental homeostasis (Parsons 1990; Møller and Höglund

1991); and (3) red carotenoid coloration revealing nutritional status or immune stress (Olson and Owens 1998; Hill 1999). We investigate the coexistence of all of these advocated handicap signals in a wild population of red-collared widowbirds, *Euplectes ardens*.

The long tails of breeding male widowbirds are well-known examples of costly traits (S. Andersson 1994; Norberg 1995) selected by female choice in two species (*Euplectes progne*, Andersson 1982; *E. jacksoni*, Andersson 1989, 1992), but suggested to function in male-male competition in a third (*E. macrourus*, Savalli 1994). Savalli (1993) and Craig and Villet (1998), in contrast, propose that the extreme tail ornament variation in *Euplectes* spp. (from almost no elongation to about 50 cm) can be attributed to a model of genetic drift. To help resolve these contrasting views, we examined the exaggerated tail ornamentation of another, largely unstudied, widowbird species. Most *Euplectes* spp. have conspicuous yellow or red color patches on their wings or body (Craig 1980), based on carotenoid pigments (Kritzler 1943; S. Andersson, unpubl. data), which because of their dependence on diet and health have become prime examples of honest quality advertisements (Hill 1999). Contrary to the intensely studied, and in some ways very similar, North American redwinged blackbird, *Agelaius phoeniceus* (Searcy and Yasukawa 1995), the signal functions of widowbird coloration have not been examined before. In addition, very few studies of carotenoid color variation use objective color quantifica-

tion (Endler 1990; Bennett et al. 1994). A third independent signal of male quality in the red-collared widowbird may be the symmetry of the long tail feathers, which are conspicuously spread in perch displays. Fluctuating asymmetry (FA) of bilateral traits may indicate epigenetic stress (Parsons 1990; Møller and Höglund 1991); however, a recent study in red-collared widowbirds does not support this putative signal function (Goddard and Lawes 2000).

In addition to the potential quality advertisements above, female choice of breeding situation might target a variety of other male phenotypic traits or territory characteristics. For example, females may be choosing males on the basis of body size, dominance, display behavior, territory size, or territory quality. In *Euplectes* (and related Ploceinae), in particular, male-built nest frames (cock's nests) are an important display feature (Crook 1964; Craig 1980; Andersson 1991), the number and quality of which might be subject to female choice (Collias and Victoria 1978; Craig 1982; Andersson 1991; Savalli 1994; Friedl and Klump 1999).

In this paper we use multivariate selection analysis (Lande and Arnold 1983) to investigate the strength of female choice and net sexual selection on the multiple ornaments and other phenotypic and territory characteristics. The potential for honest quality advertisement is tested by analyzing the relationships between ornamental traits and body condition and between trait expression and symmetry. Finally, we discuss the results in relation to hypotheses for the evolution of multicomponent sexual signals in birds.

MATERIALS AND METHODS

Study Species

The red-collared widowbird, *E. ardens*, is a polygynous, granivorous weaverbird (subfamily Ploceinae) of shrubby grassland and bush clearings in eastern and southern Africa. Like other widowbirds, males molt into nuptial plumage prior to the breeding season (October to April; Emlen 1957; Skead 1965). Male nuptial plumage is black except for a crescent-shaped red collar on the chest. Males also grow a long, graduated tail (~ 22 cm). Male plumage is in striking contrast to the drab brown plumage and short tail ($\bar{x} \pm \text{SD} = 44 \pm 24$ mm, $n = 241$) of females and nonbreeding males. There is also a sexual size dimorphism (male tarsus: $\bar{x} \pm \text{SD} = 24.07 \pm 0.57$ mm, $n = 209$; female: $\bar{x} \pm \text{SD} = 21.88 \pm 0.66$ mm, $n = 249$; t -test = 37.8, $df = 207$, $P < 0.001$), but it is the least pronounced sexual size dimorphism among the widowbirds (Andersson and Andersson 1994; Craig and Villet 1998).

Males establish and defend relatively large ($\bar{x} \pm \text{SD} = 0.44 \pm 0.29$ ha, $n = 43$, range = 0.14–1.51 ha) and exclusive breeding territories from conspecifics and other *Euplectes* intruders (Emlen 1957). Male competition to acquire and maintain territories is high as judged by a large population of floaters (males in nuptial plumage that do not establish territories) that frequently intrude onto occupied territories to attract females (Pryke et al., in press). Both sexes feed away from the breeding territories (Craig 1980; pers. obs.). The females visit male territories solely to secure mating opportunities and nest sites. During courtship the males display their long prominent tail in a slow smooth flight with ex-

aggerated wing-beats. During this display the central rectrices are depressed and keeled to form an inverted sickle shape, and the head feathers are erected in a hood. The male circles a visiting female, landing near her with tail askew and wings outspread while uttering a characteristic hissing sound. The female may either fly off or stay in the displaying male's territory, but she usually moves away from the male. The display is repeated to a female until she retreats or solicits copulation.

After the main rains the males construct several very simple cock's nests ($\bar{x} \pm \text{SD} = 13.1 \pm 4.73$ nests, $n = 43$ territories, range = 3–22) by producing a loose structure of a few intertwined grass blades between upright plant stalks (Skead 1965; pers. obs.). Interestingly, females rarely use the nest frames and rather build fresh nests close by or elsewhere on the territory (S. R. Pryke, unpubl. data). Red-collared widowbirds build a typical *Euplectes* nest that is semiclosed with a side entrance and woven from fresh grass in dense grass or leafy shrub close to the ground ($\bar{x} \pm \text{SD} = 45.5 \pm 15.7$ cm above the ground, $n = 144$, range = 16–88 cm). Male parental care has not been recorded in this species.

A population of red-collared widowbirds was studied in the Hilton district, KwaZulu Natal Province, South Africa (29°43'S, 30°17'E; elevation ~ 1100 m) between December 1999 and April 2000. The study area is a mosaic of reed-filled marshes and open grasslands (dominated by *Paspalum dilatatum* and *Eragrostis curvula*) interspersed with shrubs.

Morphometric Data

All widowbirds were mist-netted either on their territories or at communal night roosts nearby and were uniquely color-banded. Red color bands were not used, because they might influence male attractiveness (e.g., Burley 1988; Metz and Weatherhead 1991). Right and left tarsus and culmen were measured to the nearest 0.1 mm and wing length to the nearest 0.5 mm. The three linear dimensions of body size (tarsus, culmen, and wing) were highly intercorrelated, so the first component derived from a principal components analysis (PCA), which explained 68.8% of the variance, was used as a measure of body size. Body mass was measured to the nearest 0.5 g (50 g Pesola spring-balance). Although male body mass might change temporally throughout the day due to differences in crop contents, there was no relationship between body mass and the time of capture in this sample ($r_s = 0.17$, $n = 185$, $P = 0.27$).

Using tarsus length, which is one of the most reliable univariate measures of skeletal size in birds (Freeman and Jackson 1990), we computed a body condition index as the residuals from a linear regression of log(body mass) on $3 \times \log(\text{tarsus length})$ (S. Andersson 1994). Ectoparasite load (e.g., lice, ticks, and mites) on tail and wing feathers was scored from zero to three (none to heavy load).

All tail feathers were measured with a ruler to the nearest 0.1 mm from the point of insertion (base of the tail) to the tip of the feather. Total tail length was estimated from the longest rectrix (i.e., feather number 2). The number of tail feathers with blood quills (i.e., still growing) was counted. Missing, growing, and damaged feathers were excluded from the subsequent analyses. Tail asymmetry was calculated as

the absolute difference between the length of the left (L) and right (R) characters (e.g., each pair of rectrices in the tail; Palmer and Strobeck 1986; Møller and Höglund 1991). A mean fluctuating asymmetry (FA) value was calculated for tail length as the mean of the absolute differences between each pair of rectrices. Birds with broken, missing, or growing feathers were excluded from the FA analyses.

Collar patch size was measured using calipers to the nearest 0.1 mm by taking the maximum horizontal measure (width) and three vertical (height) measures along the patch. Collar width and length were significantly correlated ($r_s = 0.82$, $n = 125$, $P < 0.0001$) and collar area was calculated as the product of the width and the average height.

Because many individuals were recaptured, repeatabilities (Lessells and Boag 1987) were calculated for each of the morphological characters, and these were all highly significant ($r_s = 0.81$ – 0.96 , $n = 57$, $P < 0.001$).

Reflectance Spectrometry and Colorimetrics

Spectral reflectance (at ± 2 nm resolution) from the red collar was measured using a PS1000 spectrometer (Ocean Optics, Inc., Dunedin, FL), HL2000 halogen light source, WS-2 white reference, a fibre-optic reflectance probe (Avantes, Eerbeek, Netherlands), and C-spec software (Ancal, Inc., Las Vegas, NV). The probe was fitted with a matte black tube that shielded out external light and standardized the measuring distance. The probe was held (not pressed) against the plumage, scanning the direct (specular) reflectance from a 4-mm wide spot. Preceded by a reference scan for each individual, five consecutive scans (removing the probe between each) were taken from the center of the collar patch. Colorimetric analyses were made over the 350–700 nm spectral range. Although bird vision usually extends down to about 320 nm (Burkhardt 1989), UV/VIS measurements of captive birds and museum specimens have confirmed that the flat, weak reflectance below 400 nm continues down to 300 nm. Consequently, the contribution of the unmeasured 320–350-nm segment to the signal variation should be minimal.

Objective indices of the three main dimensions of color signals, spectral intensity, location, and purity (Hailman 1977) were computed from the five scans and averaged for each individual. From 5-nm segmented average spectra in the range 380–700 nm, we also computed coefficients in the uniform human CIE Lab color space (International Commission on Illumination 1971) for 10 degree observer and the D65 (daylight) illuminant. These were used to confirm that our objective measures strongly predicted the intended colorimetric in human color vision, and thereby probably a corresponding signal dimension in avian color space. Three color variables were derived. Brightness (spectral intensity) was estimated by $R_{350-700}$, the sum of reflectance from 350–700 nm. Hue (spectral location, here referred to as redness) was estimated as $\lambda(R50)$, the wavelength at which reflectance is halfway between its minimum (R_{\min}) and its maximum (R_{\max}). $\lambda(R50)$ explained 75% of human-perceived hue variation (linear regression: CIE h_{ab} vs. $\lambda[R50]$, $F_{1,126} = 445.8$, $P < 0.001$, $r^2 = 77.9\%$). Chroma (spectral purity) has a more complex dependence on several reflectance shape aspects, such as slope height and steepness. A general way to capture

this variation is to use the difference between two spectral segments (which ideally should correspond to cone absorbance spectra when these are known), divided by the total reflectance (see Endler 1990). To avoid a fixed arbitrary segment, which confounds chroma with hue variation, we used individual $\lambda(R50)$ as the segment divider, and computed C_{R50} as $[R_{350-\lambda(R50)} - R_{\lambda(R50)-700}]/R_{350-700}$. Like the hue measure, C_{R50} strongly predicted the corresponding variation in human color space, explaining 88% of the CIE Lab chroma measure (linear regression: CIE C_{ab} vs. C_{R50} , $F_{1,126} = 893.6$, $P < 0.0001$, $r^2 = 89\%$).

After thus mathematically disentangling three perceptually relevant aspects of reflectance variation, the three signal dimensions remained significantly correlated (hue and chroma, $r = 0.33$, $n = 127$, $P < 0.001$; hue and brightness, $r_s = -0.53$, $n = 127$, $P < 0.001$; brightness and chroma, $r_s = -0.52$, $n = 127$, $P < 0.001$). These are expected relationships in pigment colors (subtractive reflectance), however, because absorbance (i.e., pigment concentration) by necessity increases chroma at the expense of brightness, and also (unless the slope of the absorbance cut-off is vertical) shifts the hue (S. Andersson, unpubl. data). Uncorrelated measures of reflectance variation can be obtained by, for example, PCA (Endler 1990; Cuthill et al. 1999), which by definition creates uncorrelated, orthogonal, variance axes. However, this also complicates the interpretation in terms of color perception compared to segment-based measures. For example, although PC1 typically captures brightness variation, PC2 and PC3 are not easily interpreted in terms of hue and chroma (Grill and Rush 2000). In addition, when tested on the present data, PCA scores explained less of the corresponding CIE Lab measures than the above variables did (S. Andersson, unpubl. data).

Behavioral Observations

Each resident male was observed daily between dawn and dusk when the males defended their breeding territories. A random-number table was used to determine the order in which males were observed. All activities and their durations were continuously recorded on a dictaphone with time given to the nearest five seconds. Male display rates were extracted for analysis. Display rate was calculated as the total time a male spent in courtship display divided by the time (in minutes) he was present during the territory observations. As female visitation rate is likely to affect display intensity and a higher display rate contribute to female attraction, a correction for female movement should be made (e.g., Gibson and Bradbury 1985). However, the red-collared widowbird males display to all eclipse (brown) birds of both their own and other species (Craig 1980; S. R. Pryke, unpubl. data), and therefore it was not always possible to determine whether the displays were directed toward the female red-collared widowbirds. But this cause and effect problem is unlikely to substantially affect the results, because males perform their courtship displays irrespective of female proximity (S. R. Pryke, unpubl. data).

Territory Characteristics

Territorial males restricted their activities to a well-defined area, did not allow other males to trespass the boundaries,

and actively defended the territory from other males (i.e., aggressive displays, chasing, parallel flight displays and direct attacks). Territory boundaries were mapped from direct observations of individually marked males and defined using the convex polygon method (Odum and Kuenzler 1955). The map of the territories was digitized, and ArcView Ver. 3.0 (ESRI 1996) was used to estimate territory area.

To ensure that no male replacement had taken place, the presence of a male on a territory was monitored weekly throughout the study. Only one male lost his territory two weeks before nesting began. Territory size and locality was updated every three weeks. Differences in territory size between updates were so slight that area parameters were not significantly altered (estimated change in area: $\bar{x} \pm SD = 0.052 \pm 0.021$ ha, $n = 43$; paired t -test: $t = 0.76$, ns).

The mean foliage density and height within each territory was estimated as an indirect measure of the suitability of vegetation for nesting. Foliage height (maximum plant height) and density (on a rank scale from zero to 10) was measured at fixed sampling points situated 20 m apart on 50-m transects across the entire study area. Vegetation measurements were taken at two-week intervals and averaged across both the territories and the nesting season.

Nest locations were marked with a small numbered flag and plotted onto the territory maps. Nests were inspected every third day until the nest was abandoned, nestlings had fledged, or the nest was lost to predators.

Male Reproductive Success

Neither the small clutch size ($\bar{x} \pm SD = 2.7 \pm 0.63$ eggs, $n = 93$, range = 2–4 eggs) nor the low fledging success due to 70% predation (S. R. Pryke, unpubl. data) were suitable measures of male fitness. In this study we are concerned with selection resulting from female choice, thus we used two measures of male reproductive success that are directly influenced by female mating preferences: (1) the number of active nests; and (2) the clutch initiation date (pairing order).

Active nests were those nests containing eggs or nestlings. The number of active nests on a male's territory is likely to be a strong indication of female mating preferences in this system, unless they are counteracted (rather than inflated) by genetic extrapair copulation mate choice. Extrapair copulation frequency is unknown in this species, but is relatively low in the related polygynous red bishop (*E. orix*), where the number of nestlings sired is strongly related to the number of nests (Friedl and Klump 1999). In addition, females obtain little more than genes from their social mate choice, so it is unlikely that their criteria for extrapair copulation mate choice should be different.

The clutch initiation date was the date of the first egg that a female laid in the breeding season. The average date for all nests within a male's territory was calculated as the estimate of pairing order. The date of first breeding in birds may greatly affect the probability of offspring surviving to adulthood (e.g., Norris 1993). There may, therefore, be a fitness component of sexual selection on male traits, if males with larger trait values tend to mate with early breeding females. In all nests visited during laying, only one egg per day was added to the clutch. If a nest with a completely

hatched brood was found, clutch initiation date was calculated by subtracting the average incubation period ($\bar{x} \pm SD = 13.3 \pm 0.5$ days, $n = 19$, range = 13–14 days) and the appropriate number of days for egg laying from the day of hatching. Clutches preyed upon or abandoned during the incubation period were excluded.

Selection Analysis

To estimate net intersexual selection on male ornaments and related traits and to identify the direct and indirect effects of female choice, we used standardized multivariate selection analysis (Lande and Arnold 1983; Arnold and Wade 1984). Fitness measures were transformed to relative male fitness by dividing the estimate of male reproductive success by the population mean (Lande and Arnold 1983). All included independent variables were standardized (mean = 0, variance = 1) before analyses. Standardizing removes the effects of differential scaling and therefore allows a comparison (in standard deviation units) of the relative importance of each variable (Gibson 1987).

Directional selection differentials were calculated as the covariances between relative mating success and the standardized male characters. Selection differentials estimate the net selection (combined direct and indirect effects via correlated traits) acting on a trait by measuring the relative strength of bivariate relationships between each trait and relative reproductive success (Gibson 1987). Selection gradients were calculated as partial linear regression coefficients (β) from multiple regression of relative fitness to the standardized value of the trait. Selection gradients quantify the strength of selection acting on a trait independently of variation in the other characters included in the regression model (Lande and Arnold 1983). With mating success as a dependent fitness measure, selection gradients thus identify the probable cues used in mate choice (Andersson 1989).

Because regression residuals were approximately normal with homoscedastic variance, significance tests were based on Pearson correlation coefficients for selection differentials and ANOVA for selection gradients. In multivariate regression strong correlations among the independent variables (multicollinearity) can lead to an overestimation of the standard errors of the regression coefficients, reducing the power of the analysis (Mitchell-Olds and Shaw 1987). To assess the influence of multicollinearity on the results, a PCA correlation matrix of the standardized variables in each regression was examined. Condition numbers (square root of the ratio of the largest eigenvalue to the smallest) below 10 are generally considered acceptable (Fry 1993). The condition numbers from all selection gradients were less than four, indicating that the correlations among the variables were not sufficiently high to adversely affect the significance tests.

RESULTS

Variation in Male Traits

Female choice of males depends on sufficient intrapopulation variation for females to visually perceive differences between male characteristics. Coefficients of variation (CV) were calculated to compare variability within the territorial

TABLE 1. Means (\bar{x}), standard deviations (SD), and coefficients of variation (CV) for measured variables in male red-collared widowbirds (*Euplectes ardens*).

Male variable	\bar{x}	SD	CV	<i>n</i>
Culmen (mm)	14.2	0.38	2.66	43
Tarsus (mm)	24.7	0.32	1.31	43
Wing (mm)	77.3	1.26	1.63	43
Body mass (g)	21.6	1.16	5.36	43
Collar area (mm ²)	282.1	23.57	8.35	43
Tail length (mm)	213.5	35.91	16.85	43
Mean absolute tail asymmetry	5.5	3.21	58.76	43
Ectoparasites (0–3)	1.3	0.29	22.67	43
Collar brightness ($R_{350-700}$)	80.9	26.16	32.35	33
Collar hue ($\lambda[R50]$)	581.2	13.27	2.28	33
Collar chroma (C_{R50})	0.6	0.09	15.81	33
Grass density (%)	61.6	18.37	29.20	43
Territory area (ha)	0.4	0.27	62.12	43
Number of cock's nests	13.1	4.73	36.16	43
Display rate (displays/min)	0.4	0.24	58.62	43

male characters (Table 1). Body size traits exhibited CVs of 1.3% to 5.4% and were comparable with those of other studies of avian intrapopulation morphological variation (e.g., Alatalo et al. 1988; Barnard 1991; Evans and Barnard 1995). However, territory characteristics and other potentially sexually selected characters were considerably more variable, fitting the expectations for a highly dimorphic and polygynous species (Alatalo et al. 1988). Such high variation may provide potential cues for mate choice. Interestingly, variation in tail length (about 17%) was substantially higher than those of congeners: 6.0–9.4% in the longtailed widowbird, *E. progne* (Andersson 1982; Craig 1989); 12.5% in Jackson's widowbird, *E. jacksoni* (Andersson 1993); and 5–8% in the yellow-shouldered widowbird, *E. macrourus* (Savalli 1994).

Color Variation

The red, crescent-shaped collar patch was highly variable in both size (area) and color. The CV for collar area within the population was 17% ($\bar{x} \pm SD = 233.9 \pm 41.9$ mm², $n = 126$), which was the same magnitude as tail length. CVs of the three colorimetrics (brightness, hue, and chroma) were also substantial but are difficult to interpret without comparable data from other species. Reflectance variation among the territorial males is illustrated in Figure 1 by the average reflectance and two extreme males with respect to $\lambda(R50)$ (hue). In addition to this variation, territorial males differed from males that did not establish a territory (at least not in the study area), by having larger and redder collar patches, suggesting that these traits are intrasexually selected signals in competition over territories (S. Andersson, S. R. Pryke, J. Örnborg, M. J. Lawes, and M. Andersson, unpubl. data).

Fluctuating Asymmetry

Tail asymmetry was normally distributed (DN = 0.19, $n = 126$, $P = 0.68$) and mean values did not deviate from zero ($t = 1.87$, $n = 126$, $P = 0.43$) demonstrating that this trait meets the criteria for exhibiting FA (Palmer and Strobeck 1986). The degree of FA was not correlated with tail length ($F_{1,126} = 0.08$, $P = 0.48$, $R^2 = 0.08\%$) and males with longer

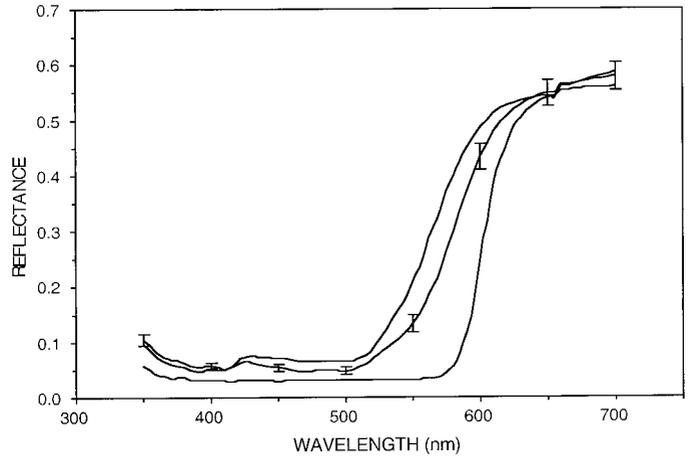


FIG. 1. Average reflectance (with standard error bars at 50 nm intervals) of the red collar patch for the 43 territorial males. The range of the hue ($\lambda[R50]$) variation is indicated by the reflectances with the most shortwave and the most longwave $\lambda(R50)$ values, respectively.

tails did not demonstrate lower levels of asymmetry as predicted by the FA hypothesis (Møller 1990). In addition, no significant second-order polynomial relationship existed between tail size and FA ($F_{1,126} = 1.06$, $P = 0.79$, $R^2 = 0.06\%$), and therefore the relationship between tail size and asymmetry is not described by stabilizing selection (i.e., U-shaped function).

Variation in Male Reproductive Success

The distribution of 114 active nests (containing eggs or nestlings) among the 43 territorial males was highly skewed, with the most successful male recruiting nine nests (Fig. 2). Nest density (nests per territory area) was also significantly more clumped than predicted from a uniform (ideal free) distribution of nests on total available territory area ($\chi^2 = 42.62$, $df = 42$, $P < 0.001$). The second male fitness measure, clutch initiation date, deviated significantly from a Poisson distribution of random territory choice by the first females

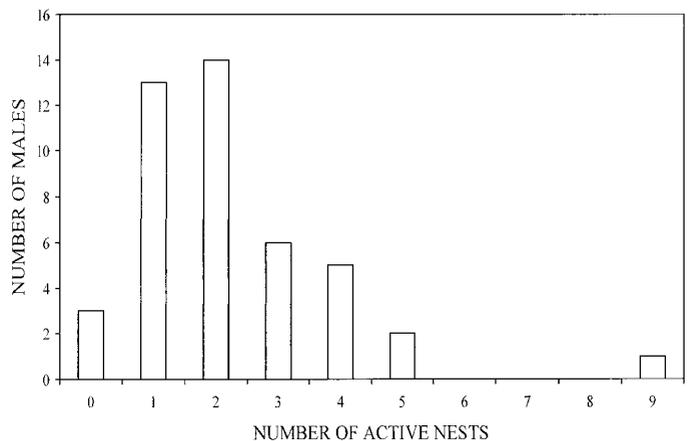


FIG. 2. Distribution of male reproductive success (number of active nests) among 43 male red-collared widowbirds.

TABLE 2. Standardized selection differentials for sexual selection on 12 traits in male red-collared widowbirds. The number of active nests and clutch initiation date were used as the relative fitness measure of mating success. Selection differentials include both the direct and indirect effects of correlated traits on male reproductive success. Probability values are based on Pearson correlation coefficients.

Male trait	Active nests			Clutch initiation date		
		<i>n</i>	<i>P</i>		<i>n</i>	<i>P</i>
Tail length	0.47	40	<0.001	0.30	40	<0.001
Collar area	-0.28	42	0.002	-0.19	42	<0.001
Body size	-0.27	43	0.03	-0.11	43	0.05
Collar chroma	0.02	33	ns	0.09	33	ns
Collar brightness	0.13	33	ns	0.08	33	ns
Collar hue	-0.20	33	ns	-0.05	33	ns
Tail asymmetry	0.08	40	ns	0.03	40	ns
Ectoparasites	0.01	43	ns	-0.01	43	ns
Territory area	-0.15	43	ns	0.04	43	ns
Grass density	0.03	43	ns	0.01	43	ns
Cock's nests	0.08	43	ns	0.02	43	ns
Display rate	0.03	43	ns	0.05	43	ns

to settle ($\chi^2 = 14.64$, $df = 42$, $P < 0.005$). The significantly skewed distributions of nests, nest density, and settlement of early females, indicate strong female choice and intersexual selection pressure.

Male Fitness Measures

Both an earlier breeding date and greater female settlement are associated with males producing more offspring. The date of initiation of breeding was a good estimate of male reproductive success because early breeding birds had higher reproductive success over the entire breeding season (total number of nestlings: $r_s = 0.63$, $n = 76$, $P < 0.001$; successful fledglings: $r_s = 0.71$, $n = 18$, $P < 0.001$). Similarly, males with more active nests on their territory had significantly more nestlings ($r_s = 0.91$, $n = 76$, $P < 0.001$) and fledglings ($r_s = 0.79$, $n = 18$, $P < 0.001$). Thus, although we use attraction of nesting females as the fitness measure to identify mate choice cues, the strong correlation to the final number of offspring confirms that female choice exerts a real selection pressure, at least within this particular breeding season.

Selection Differentials: Estimating Sexual Selection

Selection differentials (s) are the bivariate covariances between relative fitness and the male trait, representing the combined effect of direct selection and indirect selection via correlated traits. Selection differentials for both the number of active nests and clutch initiation date produced similar covariances and significance levels (Table 2). The largest significant differential for both fitness measures was found for tail length, followed by collar area and body size. This suggests strong net directional sexual selection for longer tail length and, interestingly, against male body size and the area of the red collar patch.

Selection Gradients: Identifying Cues for Female Choice

The directional selection gradients (β) estimate the partial effect of each trait on fitness, here measured by the number of active nests as fitness measure (Table 3). This analysis indicates which of the ornamental traits had the strongest direct influence on male attractiveness. To reliably test their significance, the multiple regression was recalculated for the

TABLE 3. Estimates of standardized linear (β) selection gradients for 12 traits in male red-collared widowbirds. The number of active nests and clutch initiation date were used as the measure of relative reproductive success. Due to the small sample size, the selection gradients (β_1) could not be tested; therefore a reduced model of five gradients was recalculated (β_2). Standard errors for the selection coefficients are shown in parentheses.

Male traits	Number of active nests			Clutch initiation date		
	β_1	β_2	<i>P</i>	β_1	β_2	<i>P</i>
Tail length	1.63 (± 0.38)	1.67 (± 0.36)	<0.001	0.76 (± 0.46)	0.81 (± 0.24)	<0.001
Collar chroma	0.51 (± 0.28)	0.53 (± 0.17)	0.005	0.44 (± 0.16)	0.32 (± 0.09)	0.081
Collar brightness	0.29 (± 0.21)	0.21 (± 0.16)	ns	0.21 (± 0.16)	0.18 (± 0.07)	ns
Collar hue	-0.04 (± 0.27)			-0.16 (± 0.19)		
Body size	-0.27 (± 0.19)	-0.33 (± 0.16)	ns	-0.36 (± 0.14)	-0.29 (± 0.13)	0.032
Collar area	-0.91 (± 0.62)	-0.49 (± 0.48)	0.07	-0.59 (± 0.77)	-0.36 (± 0.12)	0.009
Tail asymmetry	-0.05 (± 0.20)			-0.02 (± 0.15)		
Ectoparasites	0.11 (± 0.14)			-0.13 (± 0.22)		
Grass density	0.04 (± 0.07)			0.03 (± 0.01)		
Territory area	0.31 (± 0.20)			-0.19 (± 0.16)		
No. of cock's nests	0.07 (± 0.14)			-0.01 (± 0.11)		
Display rate	0.03 (± 0.11)			0.02 (± 0.17)		

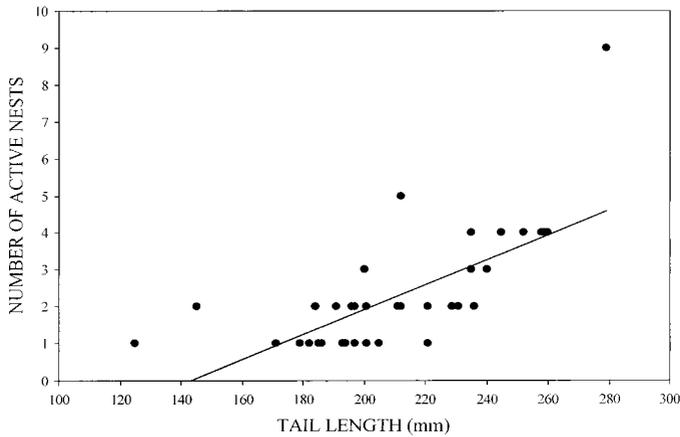


FIG. 3. Mating success (the total number of active nests) plotted against tail length ($y = 0.038x - 4.84$; $F_{1,40} = 17.3$, $r^2 = 47.4\%$, $P < 0.001$).

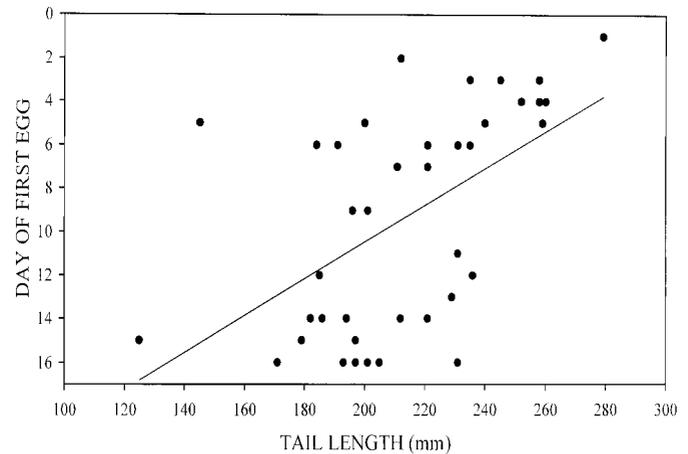


FIG. 4. Average clutch initiation date plotted against tail length ($y = -0.085x + 27.32$; $F_{1,40} = 9.3$, $r^2 = 30.0\%$, $P = 0.0003$). Day 1 represents the first egg of the nesting season (15 January 2000).

five strongest gradients. The selection of the five variables in the reduced model was based on both a backward and forward stepwise regression to determine the amount of explained variance (R^2) that was removed or added, respectively, by each variable. The reduced model was highly significant ($P < 0.001$) and increased the variance accounted for in the model by 4% (to 62%).

As suspected from the strong bivariate relationship between tail length and fitness (Table 2, Fig. 3), tail length remained the most important male trait when other traits were held constant. Over 47% of the variance in male fitness (number of nests) was accounted for by tail length alone (Fig. 3). The standardized selection gradient of 1.67 for this trait was approximately three times greater than the next largest, and indicate that an increase in tail length of one standard deviation was associated with a 167% increase in relative fitness.

There was also a significant selection gradient on collar chroma (spectral purity). This suggests that, when tail length and other traits are held constant, females show a preference for more vividly colored (but not necessarily redder) male collars, but that this partial effect is counteracted so that there is no net selection on collar chroma or any other color parameters (Table 2). A nearly significant ($P = 0.07$) negative direct effect of collar area (Table 3), combined with an indirect effect through its negative relationship with tail length (S. Andersson, S. R. Pryke, J. Örnberg, M. J. Lawes, and M. Andersson, unpubl. data), seem to be the primary reasons for the significantly negative net selection on collar area (Table 2). When we repeated the preceding analysis with clutch initiation date as the dependent variable, results were similar (Table 3). The same five traits were identified as the most important factors and used in the reduced model (decreasing R^2 from 58% to 51% in the model). In addition to the predominant effect of tail length ($R^2 = 30\%$, Fig. 4), the weak negative selection gradients for collar area and body size were significant, whereas the effect of collar chroma was not ($P = 0.08$).

We conclude that, unless there is some highly correlated trait that we have failed to measure, tail length is the pre-

dominant cue for female choice in red-collared widowbirds, explaining close to 50% of the number of nesting females a male attracts to his territory.

Male Characters and Body Condition

To determine whether the variation in tail length was explained by differences in body condition, the tail length of all full-grown males (no blood quills) captured in the area (including 50 males that were not observed to hold a territory) were regressed onto the body condition index. The significantly positive slope (Fig. 5) indicates an increase in tail length of about 4 cm from the lowest to the highest body condition estimate. There was also a just significant relationship between body condition and collar area ($F_{1,89} = 4.0$, $P = 0.049$, $r^2 = 2.5\%$), but not with other signaling traits.

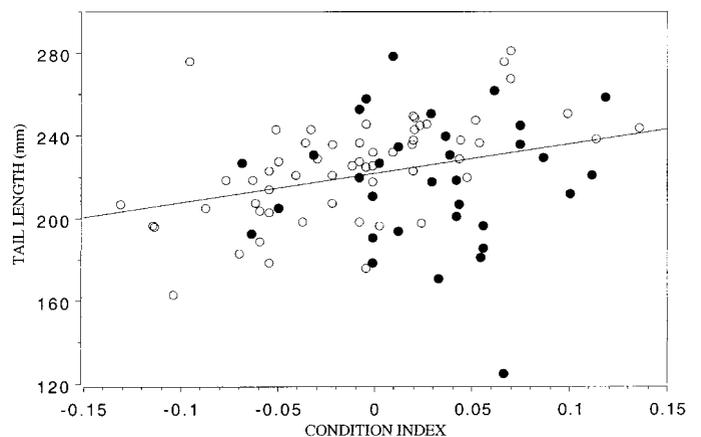


FIG. 5. Linear regression of full-grown tail length (no blood quills) on an index of body condition (residual body mass; see Materials and Methods; $F_{1,90} = 8.49$, $r^2 = 7.9\%$, $P = 0.004$). The sample includes territory-holding males from the selection analysis (filled circles) as well as males captured in the area but not found to hold a territory (open circles).

DISCUSSION

Sexual Selection and Tail Length in Widowbirds

Among the three strikingly displayed plumage ornaments in male red-collared widowbirds (tail length, tail symmetry, and the red collar), as well as other measures of male morphology and territory quality, the selection analyses singled out tail length as the most important correlate of mating success. Although the result is correlational, there are strong indications that female choice is responsible for this unusually strong sexual selection pressure. First, territory size and quality were included in the selection model but were irrelevant. Second, other results and experiments (S. R. Pryke, unpubl. ms.) show that the carotenoid collar signal, but not the tail ornament with which redness is negatively correlated (S. Andersson, S. R. Pryke, J. Örnberg, M. J. Lawes, and M. Andersson, unpubl. data), functions as an agonistic signal. Third, the agreement with mate choice experiments in other widowbirds (see below). Fourth, behavioral observations refute the function of tails in male contest competition; for example, two males without tails (lost at capture) had zero mating success (nests) but retained their territories throughout the season.

The selection on tail length was true whether total number of active nests or the order of female settlements were used as a male fitness measure. Our results thus confirm the role of sexual selection through female choice in the evolution of elaborate widowbird tails, and support the findings of a similar sexual selection analysis and a field experiment in Jackson's widowbird, *E. jacksoni* (Andersson 1989, 1992), and the pioneering experiment on longtailed widowbirds, *E. progne* (Andersson 1982). Savalli (1994), however, found that in the case of the relatively less extreme tails (~ 10 cm) of the yellow-shouldered widowbird (*E. macrourus*), there was no effect of tail length on female choice. Tail plumes instead seemed important in male-male competition, because tail-shortened males were less successful in maintaining their territories (Savalli 1994). One possible explanation is that the substantially shorter tails in this widowbird represent a phylogenetically older condition (Craig 1980), from which the more extreme widowbird tails have evolved secondarily through female choice (Berglund et al. 1996).

The idea that widowbird tails have evolved through sexual selection has been questioned from the standpoint that genetic drift is sufficient to explain the interspecific variation in tail length among the *Euplectes* (Savalli 1993; Craig and Villet 1998). For several reasons, however, it seems unlikely that the extreme ornamental variation (i.e., from almost no tail elongation in the redshouldered widow, *E. axillaris*, to the 50–60-cm long plumes of the longtailed widow) is the result of random processes. Including this study, evidence for directional sexual selection on tail length has been found in four *Euplectes* species (*E. progne*, *E. jacksoni*, *E. macrourus*, and *E. ardens*). Drift might well have played a role in the history of widowbird tail divergence, but it is reasonable to assume that sexual selection has also been at work, as it clearly is today. In addition, the neutral model here makes the implicit assumption that a major anatomical trait can drift considerably in size (in this case by an order of magnitude) unconstrained by natural selection from, for example, pro-

duction costs or hampered locomotion. The many translucent stress bars on widowbird tail feathers (S. Andersson 1994) and the laborious flight of male widows in windy conditions, suggest that costs are steep enough to only allow change through persistent directional selection, such as that arising from open-ended mating preferences. It seems likely that sexual selection has played a major role in the divergence of tail elongation within the *Euplectes*, striking different balances between sexual and natural selection in different species.

Costs of Tail Elongation

Long graduated tails are aerodynamically costly, especially in terms of the increased drag from a larger tail area (Norberg 1995; Thomas and Balmford 1995), suggesting that these tail types are reliable signals of male quality (Balmford et al. 1993). Honesty may also be imposed by the substantial physiological costs of tail growth, as has been argued for Jackson's widowbird, *E. jacksoni*, in which the rapid tail growth starts several weeks before food conditions improve (S. Andersson 1994). Frequent fault bars in rectrices (S. Andersson 1994), which are also present in red-collared widows (pers. obs.) and longtailed widows, *E. progne* (M. Andersson, pers. comm.), and the extremely variable timing of tail completion in all three species are further support for a cost of tail growth (for a detailed discussion, see S. Andersson 1994). Like in Jackson's widow (S. Andersson 1989, 1994), we found a positive relationship between full-grown tail length and body condition in red-collared widows, suggesting that females attracted to long tails also choose viable males.

Signal Content of Long Tails and Carotenoid Coloration?

A recent handicap model suggests that when several traits are honest indicators of quality, females should evolve preferences for a single ornament with the highest combination of honesty and detectability (Schluter and Price 1993). Is the strong female preference for long tails rather than carotenoid displays related to a difference in honesty between the two plumage signals? Further research into the reliability of the signal types is needed, but there are some possibilities in this case. A first possibility is simply that carotenoid pigmentation is not a costly and honest indicator in this species, as suggested for another African weaverbird, the red-billed quelea (*Quelea quelea*), in which Dale (2000) found no relation between red facial plumage and condition or reproductive success. However, bill redness was a strong predictor of male condition and has previously been found to signal dominance (Shawcross and Slater 1983), the same signal function that we argue for the carotenoid display in red-collared widowbirds (see below). In addition, compared to the quelea the carotenoid plumage display is highly variable in red-collared widowbirds (Table 1), and there is evidence for condition dependence (residual body mass) of both its size and redness in a large sample of territorial and floater males (S. Andersson, S. R. Pryke, J. Örnberg, M. J. Lawes, and M. Andersson, unpubl. data). In sum, there clearly seems to be scope for costs and honesty of carotenoid signaling in red-collared widowbirds. The question thus remains why females seem to ignore this information in their choice of nesting partner.

Another possibility is that the two ornaments differ in the quality type that they indicate. In contrast to the classic example of female house finches (*Carpodacus mexicanus*) seeking immediate resources and paternal effort (Hill 1991, 1999), good genes are more likely the primary benefit of female choice in red-collared as well as in other widowbirds with uniparental care and minimal or no resources provided by the male. An interesting possibility might then be that the good-genes benefit is larger for tail length compared to carotenoid pigmentation. This means that even if current nutrition or condition would be better predicted by collar redness, the genetic component of viability could be more strongly related to tail length, which thereby should be the target for "gene-shopping" females. Until ornament heritabilities and their genetic correlations with viability can be estimated and compared, this is of course a highly speculative explanation, but it is important to keep the distinction between direct and genetic signal content in mind. More studies of direct and indirect benefits of different handicap signals are clearly needed.

A third alternative explanation for why females focus on the long tail rather than the red collar might be its higher detectability. In contrast to the relatively small collar patch, the elongated tail plumes enlarge the visual surface of the male by two to three times, making it visible from much farther away than the red collar. To the human observer, the tail display (in flight) is easily detected from at least 100–200 m whereas the red collar is visible only in close proximity (less than 20 m; pers. obs.). Therefore, even if both plumage signals are equally reliable indicators of the same male quality, the strong female preference for exaggerated tails may relate to higher detectability and thus signal efficiency. Building on the model by Schluter and Price (1993), this implies that there is no net benefit (fitness gain minus search cost) for females to also assess the carotenoid display.

Female Preference and Fluctuating Asymmetry

In common with several other recent studies (e.g., Oakes and Barnard 1994; Evans and Barnard 1995; Kimball et al. 1997) our data failed to support the predictions of the sexual selection hypothesis of FA (Møller and Höglund 1991). Although there was strong and presumably perceivable variation in tail asymmetry (Table 1), tail FA was not under directional selection through female choice. Furthermore, asymmetry was not lower in longer tails, nor was tail symmetry related to male condition (see also Goddard and Lawes 2000). The potential reproductive benefits of producing large ornaments may surpass the costs of asymmetrical development and therefore males may attempt to maximize tail ornamentation (Goddard and Lawes 2000). In addition, recent studies have demonstrated that trait size is more responsive to stress than FA (Hunt and Simmons 1997; David et al. 1999; Woods et al. 1999; Björkstén et al. 2000), suggesting that tail length is a more reliable quality-indicator than tail FA.

Female Preference and Territory Quality

Females in many polygynous bird species choose males on the basis of their territories or a combination of male and

territory characteristics (M. Andersson 1994; Searcy and Yasukawa 1995), but there was no evidence in this study that territory quality or size affected mating success. Neither did the number of cock's nests on a male's territory predict male reproductive success, unlike other studies on related *Euplectes* (Savalli 1994; Friedl and Klump 1999; Lawes et al. 2001). The male nest building in red-collared widowbirds is restricted to a quickly produced, loosely woven ring of a few grass blades (Craig 1980; pers. obs.). Although females may inspect the nest frames, few or none are used in subsequent nesting. They might constitute necessary courtship stimuli, similar to the cavities in the display structures of the lekking *E. jacksoni* (Andersson 1991), but without any intermale variation on which female choice is based.

The Coexistence of Multiple Costly Ornaments

A question with regard to the evolution of multiple ornaments (Møller and Pomiankowski 1993) is how several handicap signals can be maintained rather than converging on a single most efficient (informative and detectable) trait (Schluter and Price 1993; Johnstone 1996). Although multiple good-genes criteria can be stable under special circumstances (Schluter and Price 1993; Johnstone 1996), these theoretical models suggests that multiple ornaments usually are not true handicaps but rather arbitrary Fisherian runaway traits, exploitations of receiver psychology (Rowe 1999) or perhaps amplifiers of a single handicap message (Hasson 1989). In accordance with this, most studies of multi-ornamented species demonstrate or suggest only one, if any, handicap mechanism (for reviews, see M. Andersson 1994; Bradbury and Vehrencamp 1998). Similarly in the red-collared widowbird, female mate choice appears almost exclusively directed at male tail length, despite the presence of another strong handicap candidate, carotenoid coloration, as well as a suite of other morphological and behavioral traits.

Our results thus do not support multiple choice criteria (redundant signal hypothesis) for combined assessment of male quality (e.g., Zuk et al. 1990a, 1992; Kodric-Brown 1993; Møller and Pomiankowski 1993) or different aspects of male quality (multiple message hypothesis; Zuk et al. 1990b; Møller and Pomiankowski 1993). Until further breeding seasons are included, we can not rule out the possibility that female choice criteria vary between years as in Marchetti (1998), but like most other mate choice studies we assume that our snapshot of sexual selection is representative.

From both field and captive dominance experiments (Pryke et al. 2001), the red carotenoid display appears to function primarily in male contest competition for territories. This is similar to the agonistic function of red epaulets in redwinged blackbirds (*A. phoeniceus*) and longtailed widowbirds, as well as the red pectoral feathers in scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*; see review by M. Andersson 1994). In this situation, multiple handicaps may result from neither the redundant signaling nor the multiple message hypotheses, but from selection by different receivers (the multiple receiver hypothesis). Separate agonistic and epigamic plumage signals have been identified in several bird species, for example, malachite sunbirds (Evans and Hatchwell 1992a,b), ring-necked pheasants (*Phasianus colchicus*; von

Schantz et al. 1989; Mateos 1998), and the yellow-browed leaf warbler (*Phylloscopus inornatus*; Marchetti 1998). With different receivers locking in to different signals, these signals do not compete over the same response and could thus be selected for efficiency (honesty \times detectability sensu Schluter and Price 1993) within their own context. They might, however, compete in terms of sender investment, as indeed seems to be the case in red-collared widowbirds (S. Andersson, S. R. Pryke, J. Örnberg, M. J. Lawes, and M. Andersson, unpubl. data). The important point, however, is that two handicap signals can coexist because they are selected by different receivers, in this instance female and male conspecifics, but it could also be, for example, different age classes, predators, or prey. The multiple receiver hypothesis is by no means a new idea for multiple ornamentation (e.g., Butcher and Rohwer 1988; M. Andersson 1994; Savalli 1995), but it has been neglected in the recent literature on multiple ornaments (e.g., Møller and Pomiankowski 1993; Johnstone 1996).

Conclusions

Despite theoretical predictions that multiple handicap signals are unlikely to be stable (Schluter and Price 1993; Iwasa and Pomiankowski 1994; Johnstone 1996), the red-collared widowbird possesses two classic quality-indicating avian ornaments, a long graduated tail and a red carotenoid display, as well as a number of other potential signal traits. We have shown that females base their mate choice almost exclusively on tail length, which explains a uniquely large proportion (47%) of the polygynous mating success of males. The red color signal is instead likely to function as an honest status signal in male contest competition (Pryke et al. 2001). We propose that the multiple receiver hypothesis, in which multiple handicaps coexist because they are selected by different receivers, might be a common explanation for multiple ornaments in birds. We have also argued that in systems like this, where females receive little or no direct benefits from choosing high-quality males, exaggerated anatomical traits such as long graduated tails might be a more reliable indicator of heritable genetic quality than carotenoid coloration. In status signaling, heritability is not an issue and signal expression (the carotenoid display in this case) need only be a phenotypically honest signal of, for example, fighting ability or (when applicable) other direct benefits such as parental investment. Studies of genetic versus phenotypic signal content of different types of ornamentation are needed.

ACKNOWLEDGMENTS

We thank Mondi Forest Ltd. and F. Blakeway for access to the study area; J. Örnberg for help in the field; and M. Andersson, M. Zuk, G. Hill, and P. Dunn for comments on the manuscript. Funding was provided by the Swedish Natural Science Research Council (to SA and M. Andersson), the South African National Research Foundation (to SRP), the University of Natal Research Foundation (to MJL), and a Swedish STINT exchange program between our two departments.

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