



Carotenoid-based epaulettes reveal male competitive ability: experiments with resident and floater red-shouldered widowbirds

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Many birds display carotenoid-based ornaments, which are typically considered to be honest indicators of individual health and condition. Experimental work on male red-shouldered widowbirds, *Euplectes axillaris*, has demonstrated a function of the carotenoid-based epaulettes in male contests and territory acquisition. Using two experiments, we investigated whether the natural variation in this colour signal reveals male competitive ability. Males with larger and redder (more longwave) epaulettes established territories to the exclusion of males with smaller and less red signals, which formed a large population of 'floaters'. In an experiment in which we removed 42 resident males, these floaters rapidly filled up vacant territories. Among removed birds held in captivity, residents strongly dominated floaters in dyadic contests over access to an easily monopolized feeder (i.e. outside the context of territory defence). Only epaulette size predicted the outcome of these male contests. In addition, when competitors were experimentally given similar epaulette signals (removed or painted red to the average population size), the males were involved in more aggressive interactions than during unmanipulated contests, but residents continued to outcompete floaters. On release (after 8 days) to the breeding grounds, most residents (88%) rapidly reclaimed their territories from replacements. Combined, these results suggest that some intrinsic 'resource-holding potential', associated with the variation in epaulette signal, is primarily responsible for residents dominating nonresidents.

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In many birds, territorial competition among males results in some individuals being excluded from territories and thus from breeding. Such 'floaters' often remain in the area, frequently intrude on to occupied territories (Arcese 1987; Stutchbury 1991) and rapidly fill vacant territories when residents are removed (Krebs 1982; Shutler & Weatherhead 1991). Although territory owners tend to win all conflicts with intruders (Rohwer 1982), it is unclear why residents dominate nonterritory holders, especially without escalated contests to settle disputes. A number of hypotheses have been proposed to explain this asymmetry between owners and floaters (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Maynard Smith 1982). First, residents may have a competitive advantage over floaters (i.e. have higher resource-holding potential), for example through body size or condition that explains their consistent success in contests and fights (Riechert 1998). Second, unrelated to asymmetries in fighting ability, the territory may be of greater value to the owner than to the intruder (value

asymmetry hypothesis; Beletsky & Orians 1989; Tobias 1997), perhaps because the resident has greater knowledge of the territory (Getty 1987; Stamps 1987) and neighbours (Beletsky & Orians 1987), and therefore invests more in territorial contests. Finally, arbitrary conventions (uncorrelated asymmetry hypothesis) may be used to settle contests, so that the resident wins conflicts simply because he is resident (Davies 1978; Rohwer 1982).

The relative importance of these ideas in determining territorial status (i.e. owner–floater asymmetries) is unclear. For example, results from the well-studied red-winged blackbirds, *Agelaius phoeniceus*, fail to show any consistent differences between resident and floater males. Some studies support the resource-holding potential hypothesis, since males with retained or larger epaulettes repel floaters more successfully (Peek 1972; Røskaft & Rohwer 1987) or have greater success in staged contests in captivity (Searcy 1979; Eckert & Weatherhead 1987). However, most of the more recent work suggests that competitive asymmetries are of secondary importance (e.g. Shutler & Weatherhead 1991, 1992; Beletsky & Orians 1993). Other studies propose that occupancy time is crucial to create perceived value asymmetries (Beletsky & Orians 1989; Shutler & Weatherhead 1991), and some

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suggest that arbitrary ownership conventions best explain territorial status (Shutler & Weatherhead 1992). We investigated the relative role of these hypotheses in determining the territorial and floating status of male red-shouldered widowbirds, *Euplectes axillaris*.

Male red-shouldered widowbirds defend exclusive breeding territories in grasslands fringing wetland and riverine areas in central and southern Africa. Like all widowbirds, they are highly polygynous, with females providing all parental care. Red-shouldered widowbirds are seasonally and sexually dimorphic; females and non-breeding males are streaked brown, whereas breeding males are black with carotenoid-based red epaulettes (lesser wing coverts). Experiments on captive birds suggest that the red epaulettes function as status signals; experimentally reddened males dominated orange-treated, control and blackened (no epaulette) males in dyadic contests over limited food (Pryke & Andersson 2003). Similarly, in the field, males with experimentally enlarged epaulette signals successfully established territories and received fewer aggressive intrusions from conspecifics than males with blackened or reduced signals (Pryke & Andersson 2003). These experiments suggest that the carotenoid-based epaulettes, like the red chest patch in the related red-collared widowbird, *E. ardens* (Pryke et al. 2001a, 2002), function in male competition for territories and in settling contests. The production of carotenoid-based plumage at the onset of the breeding season may depend on access to limited carotenoid pigments, present nutritional condition, parasite load and competing physiological functions during moult (Lozano 1994; Olson & Owens 1998; Hill 1999). The expression of carotenoid-based plumage coloration is thought to incur high production costs and may reflect the health and condition of males. We investigated whether asymmetries in epaulette size and colour between males have any effects on the outcome of contests, and thus might be regarded as honest signals of fighting ability.

We first tested whether breeding territories are a limiting resource by removing territory owners prior to breeding and monitoring the subsequent replacements. To address whether residents are superior competitors to floaters, we compared ornamental, morphological and colorimetric characteristics between owners and floaters. In addition, we staged dyadic contests over access to a feeder in captivity to eliminate confounding or extrinsic differences in competitive ability (e.g. site dominance by which residents always evict intruders) and identified the traits associated with winning. Finally, to determine whether the epaulette variation honestly signals male competitive ability, owners and floaters were given equal epaulette signals (in terms of size and colour) and paired in contests over food. The results from these experiments should allow further insight into the evolution and dynamics of visual signals used in contest settlement in this group.

METHODS

We conducted this study during December 2001 and January 2002 on a breeding population of red-shouldered

widowbirds in the eastern KwaZulu-Natal Midlands of South Africa (29°35'S, 30°04'E). Males defended territories in a series of marsh and grassland sites (which were isolated by forests and agricultural fields) within the large wetland study area. We captured the males in mist nets and marked them with a unique combination of three colour bands (excluding red and orange) and a numbered aluminium leg band. We measured flattened wing chord (to the nearest 0.5 mm), tail, culmen and tarsus length (to the nearest 0.1 mm). We weighed the birds (to the nearest 0.5 g using a Pesola spring balance) and estimated an index of body condition by the residuals from the linear regression of $\log(\text{body mass})$ on $3 \times \log(\text{tarsus length})$. Epaulette size (area of red coloration) was calculated from the maximum length and the average of three width measurements (to the nearest 0.1 mm).

Objective colour measurements of the red epaulette were obtained with an S2000 diode-array spectrometer (Ocean Optics Inc., Dunedin, U.S.A.) with illumination from an HL2000 halogen light source. Using the C-spec software (Ancal Inc., Las Vegas, U.S.A.), we took five consecutive scans (lifting and replacing the probe between scans) from the centre of the epaulette with a fibre optic reflectance probe (4 mm measuring diameter), and in relation to a WS-2 white standard scanned before we scanned each individual. Three main objective colour indices, spectral intensity, position and purity, 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 ($r=0.89$, $F_{117,471}=110.41$, $P<0.001$; Lessells & Boag 1987). 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 its minimum (R_{\min}) and maximum (R_{\max}) reflectance. Using λR_{50} as the individual segment divider, we calculated chroma (spectral purity; $C_{R_{50}}$) as $R_{350-\lambda R_{50}} - R_{\lambda R_{50}-700} / R_{350-700}$. A detailed description of the colour measurements and analyses can be found in Pryke et al. (2001b).

We captured all territorial males in the same area and monitored their identity and activity daily for 2 weeks before the removal experiments. Territory boundaries did not overlap and were identified as the outer boundaries of displays and aggressive interactions with neighbours. We calculated territory area from these boundary points using ArcView (version 3.1, 1996, ESRI, Redlands, U.S.A.). To assess habitat quality of the territories, we measured mean vegetation type (the average number of different types of vegetation) and vegetation density (expressed as a percentage) every 2 weeks at fixed sampling points situated at 20-m intervals across the area and averaged across the breeding season (Pryke et al. 2001b).

Resident males ($N=42$) were captured on their territories or at communal night roosts and removed for the aviary experiments and to create vacancies, thereby allowing the settlement of nonterritorial replacement males. To minimize effects of prior acquaintance, we captured nonterritorial males ($N=34$) at night roosts at a different site in the area. As most territory owners were

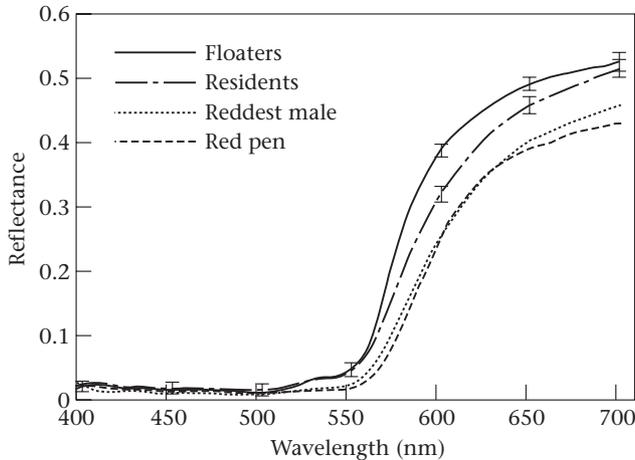


Figure 1. Reflectance spectra ($\bar{X} \pm SE$) of the red carotenoid-based epaulettes of male red-shouldered widowbird floaters ($N=65$) and residents ($N=53$). The manipulated epaulettes were painted with red pens, which were selected to correspond closely to the 'reddest' male in the population ($N=310$).

banded, we assumed that unbanded males ($N=11$) and colour-banded males not known to hold a territory in the area ($N=23$) were floaters. All birds were captured within a 2-day period.

Territorial and floater groups were housed separately in four outside aviaries (1.5×2.7 m and 2.2 m high), which were visually isolated from each other, at the University of Natal, Pietermaritzburg, South Africa. Birds were provided with numerous water and food dishes (mixed wild bird seed, dehusked sunflower seeds and vitamins) and allowed 3 days to habituate before the experiments. For the first experiment we paired owners and floaters to identify any relation between male dominance and ornamental, morphological or behavioural characteristics. In the second experiment (2 days later), we manipulated birds (by either removing or reddening the epaulette) to evaluate whether males given equal epaulette signals had a similar probability of dominating the dyad. To remove the epaulette signal, we completely blackened the red plumage with black Copic pens (Black B100; Too Marker Products Inc., Tokyo, Japan). To increase the signal, we manipulated epaulettes to the average population size ($\bar{X} \pm SD = 233 \pm 51$ mm², $N=315$) by colouring them red with red Copic pens (Cadmium red R27; Too Marker Products, Tokyo, Japan) to conceal the natural colour. This red pen provided the best match to the natural variation in plumage reflectance and corresponded to the upper limit of hue or redness in the population ($\lambda_{R_{50}} = 599.2$ nm, $N=310$; Pryke & Andersson 2003). Once an experiment was completed, we removed the treatments from the birds (with alcohol) to prevent familiarization with the manipulations before returning them to their housing aviaries. The birds in the paired contests were always matched with respect to their original territorial status (i.e. resident versus floater), but within these limits males were assigned to contests randomly (i.e. without reference to their morphology) in each experiment and all dyads were unique.

Experiments were conducted during the first 5 h of daylight in a neutral cage that was visually isolated from all other birds. Trials lasted for 15 min to determine whether males were able to assess one another rapidly primarily on the plumage signals. We determined dominance in each dyad by recording the winner and loser in encounters over a restricted food bowl. Because the outcome of conflicts may be influenced by the relative hunger of contestants (Andersson & Åhlund 1991), we removed all food the night before trials. During the trial, we recorded the nature and outcome of all aggressive interactions and supplants, which varied from active (e.g. threat displays, displacements and physical attacks) to passive (e.g. nonthreatening approaches). No males were injured in any of the trials, and all physical attacks resulted in the loser fleeing the interaction to the safety of a shelter or perch. Males controlling the feeder after an interaction were considered the winners of the interaction, and those winning the majority of interactions within a trial were considered to be the overall winners. Data on the bird feeding first and those dominating the trials were extracted for analyses.

The morning after the completion of the last experiments (8 days after capture), all 76 experimental birds were returned to the study area and released at their communal night roost. We observed all territories to determine whether the initial residents evicted replacements and reclaimed their original or other territories in the area. These evictions included passive displacements, aggressive chases (the pursuit of an opponent, sometimes over many territories) and occasional fights ($N=2$) where physical contact was made (e.g. pecking or biting the opponent); no injuries to males were observed.

We used multiple logistic regression models to identify the relative effects of male traits in determining territorial status (i.e. resident or floater), and stepwise discriminant function analysis to classify males as either residents or floaters, using morphological and colorimetric measures. Since we were unable to capture all marked resident and floater males for the dominance experiments, sample sizes for male trait measurements are larger than those in the contest experiments. We analysed the outcomes of dyadic contests with generalized linear models (GLM) with binomial errors and logit links (GenStat 5, 2000, VSN International Ltd, Oxford, U.K.). For these analyses we used the win/loss outcomes of dyadic contests as the Bernoulli dependent variable and modelled all possible effects and combinations using body size, body condition, tail length, epaulette size and colorimetrics, territorial status, individual status, epaulette treatments, housing locality and treatment time. We tested the significance of these predictor variables by the change in deviance of the different models using a chi-square approximation, and the models best fitting the data were objectively selected using Akaike's information criterion (AIC; Anderson & Burnham 2001). Statistical analyses are two tailed and means are given \pm SDs.

Permission to collect and house the widowbirds was granted by KwaZulu-Natal Wildlife Services and all work was approved by the University of Natal's Animal Ethics Committee.

RESULTS

Territory Removals

Once residents were experimentally removed, nonterritorial males rapidly replaced them. Of the 42 vacant territories, 34 were occupied on the day of removal and eight by the next morning. However, the new occupants rarely occupied the entire territory ($N=3$), because the areas were often shared by more than one replacement ($N=28$ territories; 1.64 ± 0.91 replacement males per vacant territory) or neighbours expanded their territories ($N=11$ territories; three of these reoccupied territories were completely shared by neighbouring males). Subsequently, territories of the replacement males were significantly smaller than the original vacated territory (initial territory size: 0.17 ± 0.05 ha; replacement territory size: 0.08 ± 0.07 ; paired t test: $t_{39}=12.38$, $P<0.001$) but of similar habitat quality (vegetation type of initial residents: 4.26 ± 0.35 ; replacements: 4.01 ± 0.31 ; $t_{39}=0.67$, $P=0.49$; vegetation density of initial residents: $68.51 \pm 5.32\%$; replacements: $62.17 \pm 5.97\%$; $t_{39}=0.85$, $P=0.27$). Thus, the experimental removals suggest that a considerable proportion of males are floaters in this population, since territory owners were promptly replaced after their removal.

Male Traits and Territorial Status

As the three body size traits (tarsus, wing and culmen) were intercorrelated, we ran a principal components analysis (PCA) to extract an independent body size measure. The first components (PC1) described 65.4% of the variation and were positively weighted for each trait (0.86 tarsus, 0.69 culmen, 0.90 wing). Although this plumage ornament seems likely to be allometrically related to wing length and thereby body size, neither of these measures predicted epaulette size (wing length: $F_{1,118}=2.64$, $R^2=0.32$, $P=0.12$; body size: $F_{1,118}=0.16$, $R^2=0.002$, $P=0.68$). There was, however, a positive relation between epaulette size and redness (Fig. 2).

Of 118 marked males in this experiment, 65 (55.1%) did not acquire a territory at the onset of the breeding season. Among these nonterritorial males (apart from 34 used for the contest experiments), 17 obtained experimentally vacated territories, but in the subsequent analyses were still defined as 'floaters' since they were physically and colorimetrically indistinguishable from the other males in this category (ANOVA: for all measurements: $F_{1,64}=0.48-1.82$, $P>0.1$; Fig. 2).

Only epaulette size and hue differed significantly between floaters and residents (Table 1). Territorial males displayed larger (35% larger; Fig. 2) and redder (through a 7-nm more longwave hue; Fig. 1) epaulettes than floaters. In a stepwise, multiple logistic regression to predict owner-floater status ($\chi^2_2=58.1$, $N=118$, $P<0.001$, $R^2=0.88$), males were more likely to obtain a territory when they displayed larger ($\chi^2_2=28.4$, $P<0.001$) and redder epaulettes ($\chi^2_2=6.1$, $P=0.01$). However, the tendency of males to cluster in two epaulette signal categories (Fig. 2) suggested that a confounding discrete variable, notably

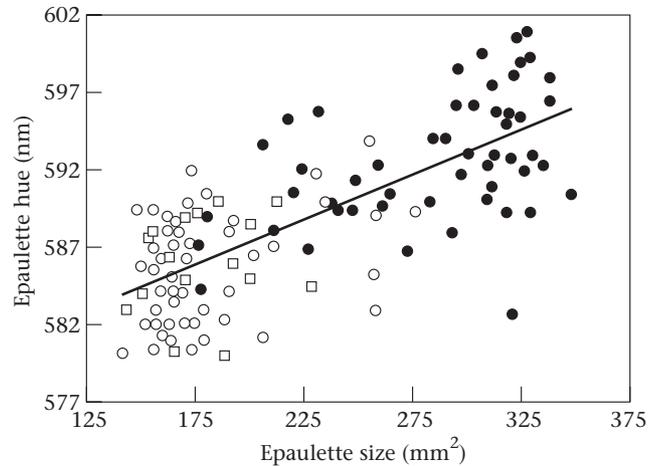


Figure 2. Relation between epaulette size (mm^2) and colour (hue; λR_{50}) for floaters (\circ ; including replacements, \square) and residents (\bullet) in the population ($F_{1,118}=37.52$, $R^2=0.35$, $P<0.001$; epaulette hue= 0.041 (epaulette size)+ 578.37); floaters: $F_{1,65}=7.53$, $R^2=0.16$, $P=0.01$; resident males: $F_{1,53}=10.16$, $R^2=0.31$, $P<0.001$.

male age (which we had no direct means of measuring), might be the main effect on territorial status. To investigate this possibility, we first used a stepwise discriminant function analysis to show that floaters and residents were significantly clustered based on physical and colorimetric variables (Wilks' lambda= 0.26 , $F_{1,117}=213.49$, $P<0.001$), again with a dominant effect of epaulette size ($F_{1,118}=127.64$, $P<0.001$) and a significant but weaker effect of epaulette hue ($F_{1,118}=6.71$, $P=0.01$). To explore a potential age effect, we then replaced the continuous epaulette size and hue variables with a discrete 'dummy age' variable obtained from the discriminant analysis. This also produced a significant logistic regression model ($\chi^2_1=69.4$, $N=118$, $P<0.001$) but explained less of the variation ($R^2=0.57$). Because of the extreme collinearity between the 'dummy age' and epaulette measures, they could not be included in the same model. Thus, although this is highly circular (since the 'dummy age' variable was assigned from the continuous traits against which its effect was compared), it seems at least that the epaulette variation had the strongest independent effect on male status as resident or floater. We consider further aspects of a potentially confounding age effect in the Discussion.

Territorial males with larger and redder epaulettes may also have gained better-quality territories. Among residents, males with larger epaulettes defended larger territories ($F_{1,53}=34.02$, $R^2=0.18$, $P<0.001$); however, there was no significant effect of any other male trait (Table 1) on the territory characteristics (e.g. territory size, habitat type, vegetation density) in the multiple regression models (P values all >0.1). Furthermore, territory quality seemed to be a poor predictor of male quality, since there was no association between the rank orders of the competitive abilities of the residents and their replacements (Spearman rank correlations: for all traits: $r_s<0.1$, $N=17$, $P>0.1$).

In a multiple stepwise regression model to determine whether male traits (Table 1) predicted male condition,

Table 1. Male territorial status (resident/floater) in relation to male traits

Male trait	Floater	Residents	$F_{1,118}$	P
Body size (PC1)	-0.11±1.09	0.08±0.91	0.66	0.42
Body condition*	-0.01±0.07	0.02±0.03	0.53	0.47
Tail length (mm)	76.57±3.63	71.85±2.88	1.25	0.28
Epaulette size (mm ²)	163.98±16.59	289.46±40.69	284.33	<0.001
Epaulette hue (λ_{R50})	584.16±3.18	591.09±4.09	65.47	0.001
Epaulette chroma (C_{R50})	0.69±0.06	0.69±0.10	0.05	0.94
Epaulette brightness ($R_{350-700}$)	195.83±30.16	187.73±32.34	1.56	0.21

Variation ($\bar{X}\pm SD$) in ornamental, morphological and colorimetric traits between floater ($N=65$) and resident ($N=53$) males. F and P values are derived from one-way ANOVAs.

*Condition was estimated as the residuals from the regression of body mass on tarsus length (see Methods).

only epaulette size was positively related to body condition (standardized estimate $\beta=0.36$, $F_{1,118}=9.27$, $R^2=0.39$, $P<0.001$). However, this effect was apparent only among territory owners (ANCOVA: body condition: $F_{1,118}=10.65$, $P=0.002$; territory status: $F_{1,118}=5.31$, $P=0.02$; body condition \times territorial status interaction: $F_{1,118}=3.01$, $P=0.09$; standardized linear regressions: residents: $\beta=0.31$, $F_{1,53}=11.03$, $P<0.01$; floaters: $\beta=0.09$, $F_{1,65}=1.91$, $P=0.16$), which suggests that larger epaulettes may indicate current body condition among residents but not among floaters.

Dominance Experiments

The two measures of captive dominance were consistent: the male that gained the longest access to the food dish also won the majority of aggressive interactions (96% of experiments; $r_{102}=0.92$, $P<0.001$). Subsequently, the best-fitting GLMs for the combined 102 trials (unmanipulated, blackened and reddened treatments) identified the same models for both measures (based on the lowest AIC values; see Methods). Two models fitted the data best (with a difference of less than two AIC units and weights of 86 and 88%, respectively, compared to all the other models). In the first model (time dominating food dish: AIC=182.2, $\chi^2_{102}=143.2$, $P<0.001$; aggressive interactions: AIC=231.8, $\chi^2_{102}=94.3$, $P<0.001$; Fig. 3), only the relative territorial status of individuals was a significant predictor of the outcome of contests. In the second model, initial epaulette size replaced territorial status and alone produced the best-fitting model (time dominating food dish: AIC=181.4, $\chi^2_{102}=83.1$, $P<0.001$; aggressive interaction: AIC=230.1, $\chi^2_{102}=93.6$, $P<0.001$). The identification of these two models is probably a result of the strong correlation between epaulette size and territory status (see above). Therefore, regardless of colour manipulations (i.e. unmanipulated, blackened and reddened) and other possible effects, residents, which were displaying (i.e. untreated group) or had initially (i.e. treated groups) larger epaulettes, consistently dominated floater males (Fig. 3).

The type of interactions at the food dishes also differed between residents and floaters, but interactions were not included in the models because they were recorded in only 49 trials. In 43 of these, however, the winning male

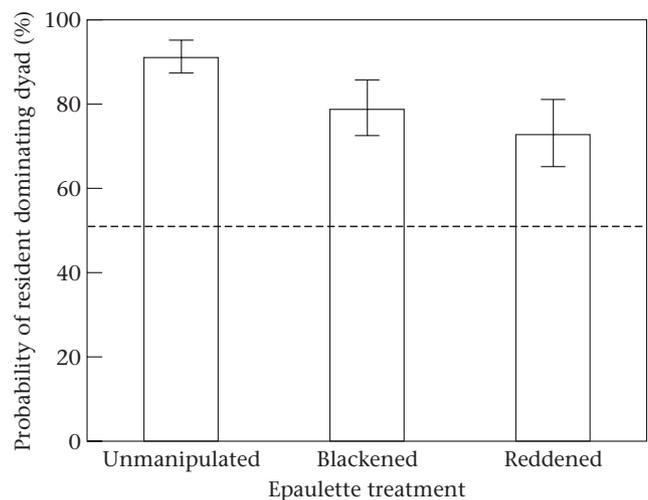


Figure 3. The probability (expressed as a percentage) of unmanipulated, blackened and red-painted residents dominating floaters within a dyad, calculated from the coefficients of the best-fit GLM for the outcome of aggressive interactions (see Results; Probability = $e^{(\text{coeff})}/[1 + e^{(\text{coeff})}]$). Error bars represent 95% confidence levels of the coefficients. The dashed line indicates where the two males have an equal probability (50%) of dominating in the dyad.

(the territory owner in 39 cases) initiated the displacement or interaction (sign test: $P<0.001$). Displacement rates of the winners were also correlated with their epaulette size (Spearman rank correlation: $r_s=0.63$, $N=49$, $P<0.001$). In addition, the type of interaction (i.e. passive or active) differed between the treatment groups (Kruskal–Wallis test: $H_{9,28,12}=23.8$, $P<0.001$). This was because most supplants in the unmanipulated group were passive (83.9%), where the floating male tended to avoid the feeder when the resident approached or was feeding. In contrast, the majority of supplants in both the blackened (91.5%) and the red-painted (79.3%) groups were active with males often physically fighting at the food bowl. The groups also differed in assessment time prior to conflicts; males in the blackened dyads initiated aggressive interactions faster than in either the reddened (Mann–Whitney U test: $U=7.62$, $N_1=28$, $N_2=12$, $P<0.001$) or untreated dyads ($U=5.31$, $N_1=28$, $N_2=9$, $P<0.001$), and dyads in the untreated group were quicker to interact

than those in the reddened group ($U=6.79$, $N_1=9$, $N_2=12$, $P<0.001$). Thus, among unmanipulated males, residents (with larger epaulettes) dominated the food dish without being challenged, and when birds received equal epaulette signals, residents aggressively won the majority of interactions with floaters.

Territory Reclamation

On release (8 days after capture), 32 of the 42 prior residents successfully evicted the replacements and regained their original territories, and five initial owners took over other territories (overall 37/42 (88%) regained territories). These evictions took place rapidly: 26 on the day of release and the remaining 11 by the following morning. For take-overs, the males recovered the entire area of their original territory (paired t test: $t_{32}=0.51$, $P=0.62$) from replacements and neighbours. In contrast, none of the prior floaters acquired territories in the area.

DISCUSSION

Our results confirm the natural fitness consequences of the experimentally demonstrated agonistic signal function of the red epaulettes in territory establishment and male contests (Pryke & Andersson 2003). The variation in both epaulette size and colour were strongly related to male status as territorial or floater, which was not predicted by any other measured trait. As a consequence of this competition, a considerable population of competitively inferior floaters roam the area and promptly fill any vacant territories that become available. The rapid occupation (often within minutes or a few hours) of vacated territories suggests that these males are truly floaters rather than holders of marginal territories. Furthermore, removals were generally conducted during the mornings while territory owners were present on their territories and thus unlikely to discover and occupy a vacancy so quickly. In addition, only three territories were taken by neighbours. There is also a high intrusion rate on to territories by conspecific males when the owners are conspicuously present (Pryke & Andersson 2003), which are unlikely all to be territory owners. Furthermore, the agonistic epaulette signals of replacement males closely resembled those of known floaters, but were significantly different from the epaulettes of the original owners (Fig. 2). Therefore, a large population of floating males seems to exist, and as floaters acquired territories only by replacing (experimentally removed) residents, it is likely that competition for territories is intense.

In territorial systems where intruders are unlikely to supplant owners and fighting is costly or risky, theoretical models of contest competition suggest that signalling ownership (e.g. value or uncorrelated asymmetries) or competitive and fighting ability is likely to be advantageous (Maynard Smith 1982; Rohwer 1982; Berglund et al. 1996). In this study, the natural variation in the epaulette signal of red-shouldered widowbirds was important in resolving male conflicts. In addition to only males with larger and redder epaulettes obtaining

territories, residents with larger epaulettes also acquired larger territories. In the captive male contests, residents (with larger epaulette signals) also dominated floating males. However, the role of the epaulette signal alone in settling conflicts is difficult to interpret. Epaulettes appear to function primarily in male contests during territory establishment. Similarly, in dominance interactions between dyads (of unknown territorial status) with natural and experimentally asymmetric epaulette signals, winners, apparently wary of an augmented signal, threatened or displaced males with enhanced epaulette signals less often than those with reduced signals (Pryke & Andersson 2003). Nevertheless, our manipulation experiments suggested that contest outcome was not determined entirely by the epaulette signal, since residents consistently dominated floaters when these also had similar blackened or reddened epaulettes. The epaulette signal thus seems to indicate strongly, but not exclusively, an intrinsic competitive ability, which might derive from an unmeasured trait.

A number of such potentially confounding variables might have influenced our results. For example, although we caught males at different sites within the study area, the birds might have had prior knowledge of each other, which could have reduced the effectiveness of the signal manipulation experiments. Among unmeasured traits, age (of which we have no reliable cue) may be related to dominance as well as plumage colour, and thereby partially invalidate our conclusion that the epaulette has a status-signalling function. Since we have no visual cue to age nuptial males, even between first-year breeders and older males, we are unable to test this. Nevertheless, rather than having an independent effect on contest outcome, age seems more likely to be a part of the male quality that is honestly signalled by the epaulette, that is, the signal function remains effective but less so, or not at all, within age classes (Jackson et al. 1988). Furthermore, the carotenoid-based collar patches of red-collared widowbirds vary considerably between years, with male rank (i.e. resident or floater status) changing accordingly (S. R. Pryke, unpublished data), suggesting that age alone is not responsible for dominance status.

The result of the dominance experiments might also have been caused by the captive conditions. Possibly, the limited aviary space (compared with much larger territories) encouraged the birds to resolve conflicts through physical fights rather than status signalling. Alternatively, since the conflicts among the manipulated male groups were more aggressive (i.e. active supplants), compared with the numerous passive supplants among untreated males, the treated males may have adjusted their behaviour according to their opponent's response towards the perceived signal (e.g. Jackson 1991). For example, the two blackened males within a dyad may have responded to their similarly treated opponents by increasing their aggressive behaviour, forcing the opponent to respond similarly, and thus escalating the fight. The response of males to the large, red epaulettes is less clear, since opponents would be expected to avoid conflicts with males displaying enlarged signals. Perhaps initial and mutual avoidance behaviours were perceived as

equivalent high status (as displayed by the enlarged epaulette signal) in both males, which might have led to an escalated conflict. This is supported by the reddened males spending significantly longer than either the blackened or unmanipulated males in assessing each other before initiating fights. Consequently, the aggressive response of conspecifics may depend on both their opponent's and their own status as judged or perceived by their opponent's behaviour.

For the red epaulette to signal male status reliably it should be associated with costs to prevent cheating. The honesty of status signals may be controlled by life history trade-offs between signal expression and reproductive effort (Gustafsson et al. 1995; Griffith 2000), between multiple costly signals (Andersson et al. 2002), or via social control in which the signaller is frequently tested in fights with males of higher status (e.g. Rohwer & Rohwer 1978; Maynard Smith & Harper 1988; Deag & Scott 1999). In addition to a social cost of cheating (through frequent challenging), the most common explanation for honest status badges in birds (Senar 1999), the red epaulettes of male red-shouldered widowbirds may also be subject to the direct production costs associated with carotenoid pigmentation (e.g. Lozano 1994; Olson & Owens 1998; Hill 1999; Møller et al. 2000). These include limited access (foraging ability), uptake and allocation between competing physiological and immunological functions, all of which might be related to the competitive ability of rivals as well as to the quality of prospective mates. Therefore, the red epaulette may be an honest signal of male dominance status, with honesty enforced by both immediate production costs (since epaulettes are moulted just before territory establishment) and social challenging during the intense territorial competition.

Dominance in the red-shouldered widowbird is unlikely to be a primary consequence of site dominance (i.e. value or arbitrary asymmetries). As described above, when the effects of territories were controlled for (i.e. in the captive experiments), residents were dominant to floaters, even when the epaulettes were removed or made equal. This outcome may, however, be caused by the residents' perception of dominance (e.g. Jackson 1988), because of their previous success at establishing territories or winning contests (i.e. in the initial unmanipulated dyads). In other words, residents and floaters may have retained their perceived 'site dominance' status (or lack of it) even when removed from the breeding grounds. Nevertheless, this effect is likely to be minimal in the staged contests, since experimentally switching asymmetric colour signals within repeated dyads completely reversed dominance in both red-shouldered and red-collared widowbirds (Pryke et al. 2002; Pryke & Andersson 2003). Furthermore, males removed from territories and held captive for about a week were able rapidly to reclaim either their former territories or other territories from floating males.

This strongly contrasts with site-dominant territorial status in other species, for example great tits, *Parus major* (Krebs 1982), willow warblers, *Phylloscopus trochilus* (Jakobsson 1988), and red-winged blackbirds (Beletsky &

Orians 1989), where time-dependent asymmetries in territory value govern the success of replacements in defeating released owners. Thus, although previous territorial experience may contribute towards determining dominance asymmetry between resident and floater red-shouldered widowbirds, the superior fighting ability of residents, signalled by their larger epaulettes, is probably the primary determinant of territorial status. Therefore, in contrast to recent avian studies (e.g. Shutler & Weatherhead 1991, 1992; Beletsky & Orians 1993; Tobias 1997), our study suggests that resource-holding potential is primarily responsible for determining territorial status between resident and floater males.

In this study, we have shown that variation in both epaulette size and (objectively measured) redness was related to territorial success in male red-shouldered widowbirds. Males with larger epaulette signals acquired territories to the exclusion of numerous floaters. These resident birds also dominated floaters in competitive contests (both when untreated and when manipulated with similar badges), and further evicted replacement males from territories when released. Taken together, these results suggest that resident red-shouldered widowbirds are superior fighters, signalling their greater competitive ability by producing and displaying larger epaulette signals.

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