Colour bands, dominance, and body mass regulation in male zebra finches (*Taeniopygia guttata*)

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SUMMARY

The arbitrary assignment of different coloured leg bands to zebra finches (*Taeniopygia guttata*) has profound effects on mate preference, reproductive success, mortality rates, parental investment and sex ratio. Choice chamber experiments indicate that the effect is mediated by altered attractiveness to members of the opposite sex. Effects on intrasexual dominance are more equivocal. We present two experiments which demonstrate significant effects of band colour on behavioural dominance (red banded birds are dominant to light green) and the resulting diurnal pattern of gain in mass, fat, and seeds stored in the crop. Consistent with the literature on dominance and strategic regulation of body mass in other species, subordinate (green-banded) birds maintain higher fat reserves at dawn, but dominant (red-banded) birds show the highest overall daily mass gains. The lack of obvious effects of band colour on dominance in previous studies may lie in the degree to which food can be monopolized by particular individuals.

1. INTRODUCTION

Zebra finches are monogamous, sexually dimorphic birds that have long been a model species in both studies of sexual selection and of the ontogeny of sexual preferences (references in Zann 1996; Collins & ten Cate 1996). Much of the research has focused on how visual preferences are acquired, and the fitness consequences of such preferences once they have developed (ten Cate & Bateson 1988; Laland 1994; Collins & ten Cate 1996; Zann 1996). Strikingly, even artificial ornaments can have profound influences on individuals' life history traits, including the quality of mate obtained, extra-pair copulation activity, reproductive success, the sex ratio of offspring, the level of parental care, and mortality (Burley 1981, 1985*a*, 1986*b*, 1988*a*; Burley *et al.* 1994; Price & Burley 1994; Zann 1994, 1996). These effects are thought to be mediated through effects on the perceived attractiveness of sexual partners, with males and females both showing specific colour preferences for ornaments on members of the opposite sex. For example, Burley *et al.* (1982) found that female zebra finches preferred males wearing red plastic leg bands over orange-banded or unbanded birds, and disliked males with light green leg bands. Such colour preferences might be arbitrary, or a redirection of a natural preference for the red colour of males' bills, which may signal quality, reproductive status, or simply differentiate males from females or heterospecifics (Burley 1986*a*; Burley & Coopersmith 1987; Burley *et al.* 1992). However, whilst some effects of bill or band colour have

been replicated (Burley 1986*a*, 1988*b*; De Kogel & Prijs 1996; Hunt *et al.* 1997), others have not (e.g. Ratcliffe & Boag 1987; Sullivan 1994; Houtman 1992; Collins *et al.* 1994; Weisman *et al.* 1994; Vos 1995), so the generality and importance of such colour preferences remain controversial (review by Collins & ten Cate 1996).

Less attention has been paid to the effect of band colour on male–male interactions in zebra finches, although effects of bill colour are known to exist (e.g. Immelman 1962; Burley & Coopersmith 1987; Vos 1995). Collins & ten Cate (1996), in their review of the literature, suggest that differences in the opportunity for males to interact, or for females to observe male–male interactions, may lie behind the lack of agreement between experimental paradigms (although there are other possible reasons; Bennett *et al.* 1994; Collins & ten Cate 1996; Hunt *et al.* 1997). Certainly, coloured artificial ornaments have been shown to affect intrasexual agonistic behaviour in other species (Brodsky 1988; Hagan & Reed 1988; Metz & Weatherhead 1991, 1993), and Burley (1985*b*) indicates that red bands appear threatening to other male zebra finches. Other studies have failed to find an effect of coloured ornaments on dominance interactions (e.g. Beletsky & Orians 1989; Cristol *et al.* 1992; Holder & Montgomerie 1993; Hannon & Eason 1995), including an aviary experiment on breeding zebra finches (Ratcliffe & Boag 1987). In this paper, we directly test for effects of colour banding on male–male interactions. Furthermore, we relate colour band-induced changes in dominance status to predictions about the optimal feeding and fat storage strategy of individuals (Ekman & Lilliendahl 1993; Witter & Cuthill 1993; Witter & Swaddle 1995; Cuthill & Houston 1997).

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In the short term, subordinates will be displaced from food sources, but should adjust daily routines to this increased unpredictability, and store higher fat reserves at dawn to buffer themselves against any shortfall (McNamara & Houston 1990; Houston & McNamara 1993; Houston *et al.* 1993; McNamara *et al.* 1994).

Demonstration of effects of colour bands on male dominance interactions may therefore not only help resolve an important controversy in the mate choice literature (Collins & ten Cate 1996), but could provide a powerful experimental tool in linking immediate consequences of a signal to daily routines of behaviour and energy allocation.

2. METHODS

(a) General

All birds were outbred, wild-type, sexually experienced adult males, aged approximately two years, housed in five single-sex groups prior to the experiment. All holding and experimental rooms were lit by daylight-mimicking fluorescent tubes to ensure colour rendition similar to that in the field (Bennett *et al.* 1996). Standard fluorescent and incandescent lighting is weak in emission of UV wavelengths compared to natural daylight (Wysecki & Stiles 1982), a factor that has demonstrable effects on visual signalling in this species (Bennett *et al.* 1996; Hunt *et al.* 1997). Birds were initially ringed on each leg with a numbered orange leg-band (supplied by A. C. Hughes, Middlesex, UK), and had no previous experience of any other band colours. A remotely activated video camera (Sony Hi-8), mounted in front of the experimental cage(s), was used to monitor behaviour. Body masses were measured to the nearest 0.1 g on an electronic balance and the visible fat stored in the intrafurcular groove was scored on a subjective six-point scale (Helms & Drury 1960). Fat deposition in small birds is sufficiently rapid that changes can be seen over the course of a day (e.g. Helms & Drury 1960; Rogers & Rogers 1990; Gosler 1996). As long as precautions are made to score visible fat blind, this index provides a reasonably reliable non-invasive measure of total fat reserves (e.g. Rogers 1991; Meijer *et al.* 1994; Scott *et al.* 1995); Meijer *et al.* (1996) showed that visible fat score explains 89% of individual variation in chemically extracted fat in zebra finches. The numbers of seeds in the crop were also counted by gently blowing apart the feathers around the neck and throat (Meijer *et al.* 1996). This non-invasive subjective score explains 90% of the variation in actual seed mass in the crop (Meijer *et al.* 1996). In experiment 1, one person removed birds from the cages and removed the colour bands, before passing the birds to another person who assessed fat and crop scores (blind to band colour). In experiment 2, although bands were not removed, fat and crop scoring were performed by two persons blind to the experimental hypothesis. All birds were also carefully checked for feather loss, reddening of the skin, or any injuries resulting from agonistic interactions, and were monitored after the experiment for any long-term adverse effects; there were none. Wherever several types of behaviour or morphological variables are analysed within the one experiment, the quoted significance levels have been adjusted using the Dunn-Sidak 'Bonferroni' method (Sokal & Rohlf 1995, p. 239) such that the experiment-wise significance level is maintained at 0.05 (two-tailed).

(b) Experiment 1

Experiment 1 investigated short-term effects of band colour on dominance and mass gain over the course of a day. At 09.00 h each day, approximately 1 h after dawn, a quartet of males was selected from different holding cages such that all four birds were unfamiliar with each other. The birds were weighed, fat- and crop-scored, and had their numbered identification rings removed. They were then randomly allocated red, orange, light green, or no bands. Banded birds wore one band of the allocated colour on each leg. The quartet was placed in a single cage (1.0 m × 0.4 m × 0.3 m), in an isolated room, with a single feeder and water dispenser, each of which allowed access to only one bird at a time. The video was activated for 30 min at each of 10.00, 13.00 and 16.00 h. The trial ended at 16.30 h, at which time the colour bands were removed and the birds were re-measured, before being returned to their original holding cages. Birds had a further 3 h of feeding time before lights-out. There were eight replicate trials using a total of 32 males.

Videos were analysed for time and duration of feeds, the number of times the target bird displaced another from the feeder ('displacer' in table 1), the number of times it was displaced ('displaced' in table 1), the number of times it pecked other birds, and the number of times it was pecked. Data could not be normalized, so analysis was by Friedman non-parametric repeated-measures analysis of variance (ANOVA) (Siegel & Castellan 1988).

(c) Experiment 2

Experiment 2 investigated longer-term influences of band colour on dominance and body mass over a three-week period. Twenty-four males were selected from five separate housing cages. Birds were ranked by body mass, and pairs allocated by rank order so that pair-members were (i) of similar mass (greatest disparity 0.3 g), and (ii) from different stocks, and hence unfamiliar. Pairs were then randomly allocated to 12 cages (1.0 m × 0.4 m × 0.3 m), maintained on a 9 h light:15 h dark photoperiod at a temperature of $25 \pm 2^\circ\text{C}$. Water was available throughout *ad libitum*, and food (commercial bird seed) from 45 min after lights-on to 60 min before lights-out; this ensured that no pairs could feed when others were being weighed (see below) or otherwise disturbed. Each cage had a single feeder and water dispenser which allowed access to only one bird at a time. All cages were cleaned when food was removed, to ensure no spilled seeds were available.

Beginning three days after allocation to single-sex pairs, two cages per day were switched to phase 1 of the experiment. The staggered entry of birds to the experiment was so that all birds could be videotaped on day 1 of treatment. Treatment consisted of removal of the orange leg bands at lights-on, then random allocation of red bands to one member of the pair and light green bands to the other. Each bird wore one band on each leg. Birds retained these bands throughout phase 1, which lasted ten days. At the end of this period, at dawn, bands were swapped between pair members such that the bird wearing red bands received green, and vice versa. Birds retained these band colours for the duration of phase 2 of the experiment (which lasted ten days), after which colour bands were removed and birds returned to their original housing cages.

Twice a day, within 45 min of 'dawn' and 'dusk', all birds were weighed, fat- and crop-scored as described in (a) above. Cages were always selected in the same order, but within

Table 1. *Behaviour and mass changes in experiment 1*

(Median frequencies of different types of behaviour from video analysis and median gains in mass, fat, and crop scores over the day. S is from Friedman's non-parametric two-way ANOVA. p -values displayed are unadjusted for multiple testing, but asterisks indicate significance (* $p < 0.05$, ** $p < 0.01$) after adjusting such that the experiment-wise error rate is maintained at 0.05; see main text.)

variable	band colour				S	p
	red	orange	unbanded	green		
displacer	0.9	0.8	0.9	0.1	10.90	0.013*
displaced	0.2	1.2	0.0	0.8	10.02	0.019
pecks by	2.8	6.1	2.3	2.6	2.20	0.532
pecks at	4.6	3.8	9.9	3.1	3.65	0.302
no. of feeds	2.0	3.1	2.3	2.0	0.75	0.861
time feeding (s)	57.4	63.4	105.1	49.6	0.95	0.813
Δ mass (g)	-0.2	0.1	0.0	0.0	3.40	0.335
Δ fat	0.8	-0.2	0.0	-0.9	13.86	0.003**
Δ crop (seeds)	3.2	5.3	5.3	9.4	1.78	0.620

cages, birds were selected haphazardly. The time difference between measurement of the two birds was only a couple of minutes, and *post hoc* analysis showed no bias in selection of one colour before the other. On entry to phase 1, when birds first received red or green bands, pairs of cages were videotaped for 90 min within 4 h of dawn. The first half of the day was chosen because data from experiment 1 had indicated that high levels of feeding and interactions occur at this time. Videos were analysed for time and duration of feeds, displacements from feeder or perches, and direct pecking of one bird by the other. Data were not normally distributed, so analysis was conducted using Wilcoxon matched-pairs signed-ranks tests; quoted sample sizes are the number of untied ranks for the test, although data were collected for all 12 pairs.

Untransformed body mass and square-root-transformed crop scores yielded normally distributed residuals when subjected to repeated-measures ANOVA (SPSS Inc. 1988). The experimental unit was the cage ($n = 12$) with within-subjects factors treatment (red or green band), phase (1 or 2) and day within phase. Day has ten levels when analysing dusk values, but only nine for variables measured at dawn; this is because dawn on day 1 of the experiment occurs prior to any experience of the band treatments. While fat score is a rank-order variable, its residuals from ANOVA were normally distributed, and other morphometric studies have shown that it is approximately linearly related to chemically extracted body fat (Rogers 1991; Krementz & Pendleton 1990). As a safeguard against the validity of this assumption, non-parametric tests were also performed on the mean fat scores across days 1–10 of each experimental phase.

3. RESULTS

(a) Experiment 1

Video records showed significant differences in the frequency with which birds displaced each other from the feeder (table 1). *Post hoc* analysis (Siegel & Castellan 1988) showed that green-banded birds displaced other individuals significantly less than any other colour, with red, orange, and unbanded birds making similar numbers of displacements. There was a close-to-significant difference in the frequency with which different colours were displaced (adjusted

$p = 0.056$), with the trend being for green- and orange-banded birds to be displaced more often than red-banded and unbanded birds. If we take the difference between these two variables (displacer minus displaced) as a measure of dominance, then red-banded and unbanded birds were dominant over green- and orange-banded birds (Friedman's $S = 12.07$, $p = 0.007$; *post hoc* tests $R = U > G = O$). There were no hints of differences in feeding or aggressive pecking behaviour (all $p > 0.6$; table 1).

Colour-banding produced significant differences in the amount of fat accumulated over the day (table 1). *Post hoc* analysis (Siegel & Castellan 1988) indicated that red-banded birds gained more fat than all others, orange-banded and unbanded birds gained similar amounts, and green-banded birds gained less than all others; indeed they lost fat. There were no differences in mass gain or numbers of seeds stored in the crop (table 1). The fact that both the latter variables showed a trend in the opposite direction to that of fat ($R < O = U < G$), might suggest that red-banded birds fed more in the early part of the day, and hence had converted food to fat reserves by dusk, whereas green-banded birds fed later in the day. The videotapes recorded too few feeding events in each portion of the day to be able to test this directly, but the long-term data from experiment 2 also address this point.

(b) Experiment 2

Video analysis revealed that red-banded birds displaced green-banded birds significantly more than vice versa (mean displacements by red-banded birds 7.08, green-banded birds 1.58; $W = 53.0$, $n = 10$, adjusted $p = 0.043$). The trend for pecking was similar but not significant (red-banded birds 5.33, green-banded birds 0.67; $W = 23.0$, $n = 7$, adjusted $p = 0.480$). There were no detectable differences in the number of feeds (red-banded birds 43.0, green-banded birds 55.9; $W = 17.5$, $n = 12$, adjusted $p = 0.341$) or total feeding time (red-banded birds 316.0 s, green-banded birds 348.0 s; $W = 27.5$, $n = 12$, adjusted $p = 0.860$).

Green-banded birds maintained higher body masses at dawn than red-banded birds (treatment $F_{1,11} = 30.25$, adjusted $p = 0.001$; figure 1a). The difference emerged rapidly both at the start of phase 1, and on swapping the colours over in phase 2, as interaction terms are not significant (treatment $\times$ phase $F_{1,11} = 0.39$, adjusted $p = 0.980$; treatment $\times$ day $F_{8,88} = 2.16$, adjusted $p = 0.176$; treatment $\times$ phase $\times$ day $F_{8,88} = 1.95$, adjusted $p = 0.274$). Dawn fat scores mirror this pattern, with green-banded birds having greater fat at dawn than red-banded birds (treatment $F_{1,11} = 30.25$, adjusted $p < 0.001$; figure 1c). A significant treatment $\times$ phase $\times$ day interaction ($F_{8,88} = 2.86$, adjusted $p = 0.035$) is due to a slight lag in fat levels changing after bands were swapped at the start of phase 2 (figure 1c). Dawn crop scores were zero under all conditions.

Dusk masses show the reverse pattern to those at dawn, with red-banded birds being heavier than green-banded birds (treatment $F_{1,11} = 13.07$, adjusted $p = 0.020$; figure 1a). This is true for both phases (treatment $\times$ phase $F_{1,11} = 0.14$, adjusted $p = 0.988$; treatment $\times$ phase $\times$ day $F_{9,99} = 0.81$, adjusted $p = 0.990$). A significant treatment $\times$ day interaction ($F_{9,99} = 3.21$, adjusted $p = 0.010$) results from a 1–2 day

lag in treatment effects appearing at the start of each phase (figure 1a). On day 1 after swapping rings at the start of phase 2, birds that have newly received green bands have much lower masses by dusk (figure 1a). In statistical terms, dusk fat shows the same effect as mass, with red-banded birds fatter than green-banded birds (treatment $F_{1,11} = 13.81$, adjusted $p = 0.015$; figure 1d), and no significant interaction terms (treatment $\times$ phase $F_{1,11} = 8.84$, adjusted $p = 0.063$; treatment $\times$ day $F_{9,99} = 2.45$, adjusted $p = 0.073$; treatment $\times$ phase $\times$ day $F_{9,99} = 0.87$, adjusted $p = 0.982$). The apparent, but not significant, reversal of the effect of band treatment between phases 1 and 2 (figure 1d) is perhaps attributable to the fact that birds receiving green bands happened to have higher dusk fat scores before the experiment started (figure 1d, day 0 means). Differences between these birds are reduced by the addition of colour bands in phase 1, and enhanced when the colours are swapped in phase 2.

4. DISCUSSION

The effects of colour bands on dominance interactions between male zebra finches is similar to the

Figure 1. Daily changes in (a) dawn and dusk mass (both plotted on same figure), (b) dusk crop score, (c) dawn fat score and (d) dusk fat score, in experiment 2. Solid squares are means ($\pm$ s.e.) for red-banded birds, open squares represent light green-banded birds. Symbols for day 0 are means over the days (three or more) prior to the experiment. Band treatments were swapped after day 10, such that red-banded males (solid squares) on days 11–20 are the same individuals as the green-banded males (open squares) on days 1–10, and vice versa.

effects on male attractiveness demonstrated by Burley *et al.* (1982). In experiments 1 and 2, red-banded males displaced green-banded males more than vice versa. In experiment 2 it is not possible to tell whether this is an effect of red bands, or green, or both. The fact that in experiment 1 the red-banded bird was frequently the displacer and rarely displaced, whilst the green-banded bird was rarely the displacer and frequently displaced, suggest both effects may operate. The duration of observation periods was too short to analyse whether pairwise interactions between particular colours were more common. Such data, and different experimental designs, would be necessary to partition the effects of red on dominance from those of green on subordination. The fact that direct aggression, via pecking, did not seem affected by colour bands supports Burley's (1985*b*) observation that red rings may intimidate other birds rather than enhance the aggressiveness of the wearer.

Ratcliffe & Boag (1987) found no observable effects of colour bands on male–male competition in an aviary breeding experiment. They also observed no effects on pair formation or breeding success, unlike Burley (1981, 1985*a*, 1988*a*). They attributed this to the fact that their aviaries had male-biased sex ratios, enhancing the effects of competition over choice, and their males, unlike Burley's, were not matched for other characters such as display rate or body size. Similar effects may operate in our experiments, as our birds were matched for body size. In other words, both our and Burley's experiments were designed to enhance possible effects of colour bands, effects that may be overwhelmed by other important influences on intersexual and intrasexual interactions. Notable in our experiments was the fact that food could be monopolized by one individual rather than being freely available to all. This can strongly influence the impact of dominance interactions upon fat storage (Witter & Swaddle 1995).

Subdominant great tits (*Parus major*; Gosler 1996) and willow tits (*Parus montanus*; Ekman & Lilliendahl 1993) have been shown to store more fat than dominants. Manipulations of dominance by the removal of birds from social groups also produce these changes in body mass (Ekman & Lilliendahl 1993; Witter & Swaddle 1995). This, perhaps counterintuitive, result has been interpreted as a response to a less predictable food supply, due to displacement of subdominants from feeding sites. Whether or not this is actually the causal factor is unclear (Witter & Swaddle 1995; Verhulst & Hogstad 1996; Cuthill & Houston 1997), but colour bands in our experiments produced similar changes in fat to those that would be predicted from their effects on dominance. Green-banded males had higher fat reserves and body mass at dawn, as would be expected if their ability to gain access to food early in the day was uncertain (McNamara & Houston 1990; Houston & McNamara 1993; Houston *et al.* 1993; McNamara *et al.* 1994). Dominant red-banded males can afford lower dawn reserves as they are certain of being able to monopolize resources at the start of the day. However, the higher dusk mass, fat, and crop stores of red-banded males (figure 1) are not readily explained

by such an argument. Dominant males show greater diurnal variation in mass, fat, and crop reserves (figure 1); they gain more during the day and lose more mass overnight (cf. Koivula *et al.* 1995). Direct observation was of insufficient duration to detect differences in feeding intensity. It would be valuable to investigate any differences in the diurnal pattern of feeding; one might predict that red-banded birds feed more at the start, and perhaps end, of the day, with green-banded birds relegated to other periods. The greater overnight mass loss, and daily gain to replenish it, would be consistent with higher energetic expenditure of dominant individuals (Røskaft *et al.* 1986; Hogstad 1987; Bryant & Newton 1994; see discussion in Witter & Swaddle 1995). Without direct measurement of metabolic rates, the relative impact on energy regulation of dominance-related expenditure versus differential access to food must remain speculation (see discussion in Witter & Swaddle 1995; Cuthill & Houston 1997).

Collins & ten Cate (1996) suggested that the reason why the red band/bill preference of females has been found in some studies and not others may lie in differences in the potential for male–male or male–female interactions. In Burley *et al.*'s (1982) experiment, females were pre-exposed to males before entering the choice chamber. They thus had the opportunity to observe male dominance interactions which, from our results, would themselves have been influenced by colour banding. Females may associate red with dominance-related behaviours and green with subdominance. Whether this is alone sufficient to explain female colour preferences is doubted by Collins & ten Cate (1996), but the relative importance of recently observed male–male competition versus prior sexual imprinting remains to be determined. What is certain is that the sometimes subtle, sometimes large, influences of colour banding on zebra finch behaviour continues to be a powerful tool for investigating intersexual and intrasexual interactions, and their influence on life history decisions.

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