

Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch

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Recent sexual selection studies on the evolution of bird colouration have mainly focused on signals with a high level of condition-dependent variation, with much less attention given to colour traits whose expression is genetically controlled. Here, we experimentally tested the relative importance of a genetic colour polymorphism in determining male dominance in the Gouldian finch (*Erythrura gouldiae*), a species displaying three completely discrete but naturally co-occurring genetically inherited phenotypes; yellow-, red- (carotenoid) and black-headed (melanin) morphs. First, in staged dominance contests between unfamiliar birds of different head morphs, red-headed males dominated black-headed males, both of which dominated the yellow-headed birds. Second, within morphs, the intensity and size of the strongly ultraviolet-blue collar determined the outcome of these contests, and among the red-headed males, redder males dominated less chromatic birds. Lastly, when the dominance signal of red-headed birds was experimentally destabilized (i.e. blackened or reddened), naturally red-headed morphs continued to dominate both the black- and yellow-headed morphs. Together, these results suggest that intrinsic dominance-related behavioural differences between the three colour morphs, which are likely to influence the relative fitness of each morph, contribute to the complex selective patterns maintaining these three discrete phenotypes in relatively stable frequencies in wild populations.

Keywords: colour polymorphism; Gouldian finch; male competition; status signalling; melanin; carotenoids

1. INTRODUCTION

The evolution of colour traits through the process of sexual selection has been an intense area of research in past decades (e.g. Hill & McGraw 2006). This work, however, has focused almost exclusively on continuously distributed condition-dependent traits, typically characterized by high levels of variance across a population, with the most attractive individuals displaying the highest levels of colour expression, or the ornament of the largest size. For example, the black badge of the house sparrow (*Passer domesticus*) varies in size along a continuum from the smallest to the largest badge (Griffith *et al.* 1999), and the plumage of the house finch (*Carpodacus mexicanus*) varies along a colour gradient from straw yellow to bright red (Hill 1991), with this colour variation strongly related to the condition of individuals at the time of signal production (e.g. Hill 1991, 1992; Griffith 2000). By contrast, very few studies have investigated the adaptive function of colour traits that are under genetic control, and where genetic variation in a population causes discontinuous phenotypic variation in colouration. The co-occurrence of discrete colour phenotypes (morphs) within a population (i.e. genetic colour polymorphism), implies a selective balance between the alternative morphs, both enjoying some advantage but also suffering some disadvantage. Thus, contrary to condition-dependent traits, different colour variants signal alternative

strategies to cope with a number of various factors (e.g. environmental, behavioural), such that differently coloured individuals derive similar fitness under frequency dependent (e.g. Sinervo & Lively 1996; Losey *et al.* 1997) or disruptive selection (reviewed in Galeotti *et al.* 2003; Roulin 2004). In effect, colour morphs can be viewed as phenotypic genetic markers and thus provide a particularly appropriate system for testing explanations for the evolution of colour signals.

Alternative behavioural strategies have long been recognized as an important mechanism promoting plumage colour polymorphism (Fisher 1930; Roulin 2004). The display of alternative colour morphs may for instance alter success in dominance and aggressive interactions (Kallioinen *et al.* 1995; Lank *et al.* 1995; Sinervo & Lively 1996; Sinervo & Zamudio 2001). For example, in the lek-breeding ruff (*Philomachus pugnax*), dominance is a heritable behaviour associated with plumage colour polymorphism, dark males being aggressive and white males adopting a sneaky strategy to mate with females (Lank *et al.* 1995; Widemo 1998). Similarly, in the side-blotched lizard (*Uta stansburiana*), males display one of three alternative throat colour morphs (orange, blue and yellow), each with an associated territorial behaviour (Sinervo & Lively 1996; Sinervo & Clobert 2003); orange males are super-dominant and defend large territories, blue-throated males defend small territories, while the sneaking yellow males do not defend territories. Yet, while the mechanisms favouring the

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persistence of colour polymorphisms within natural populations have a long history of investigation (Fisher 1930; Roulin 2004), empirical evidence for the selective pressures acting on different colour morphs have proved elusive.

Despite their generally diverse and brilliant colouration, the occurrence of a genetically based discontinuous colour polymorphism is extremely rare in birds (Galeotti *et al.* 2003; Roulin 2004), particularly among passerines (0.9%), the focal avian family in most studies on avian colouration. Furthermore, the phenotypic colour expression of most genetically controlled colour polymorphic birds studied to date is not completely discrete, instead varying continuously along a colour or environmental gradient, or at least overlapping in colour expression/pattern to some extent (for example, red-billed queleas, *Quelea quelea*: Dale 2000; ruffs, *Philomachus pugnax*: Lank 2002; tawny owls, *Strix aluco*: Roulin *et al.* 2003; common buzzards, *Buteo buteo*: Krüger *et al.* 2001). However, an ideal avian species for investigating the selective pressures maintaining a completely discrete genetically determined colour polymorphism is the Gouldian finch (*Erythrura gouldiae*), a bird exhibiting three heritable and naturally co-occurring head morphs—black, yellow and red in both sexes. This head colour polymorphism is determined by two genes (one autosomal and one sex-linked), which stimulate or suppress the production of melanin (black) and carotenoid (yellow and red) pigments (Southern 1945; Brush & Seifried 1968). At the autosomal locus, a dominant allele is responsible for the red-headed phenotype through the production of red carotenoid pigments, while the recessive allele produces yellow carotenoid pigments (i.e. in place of the red carotenoids), producing the yellow-headed morph (Brush & Seifried 1968). At the sex-linked locus, recessive alleles produce eumelanin (black melanin), which masks the effects of the carotenoids responsible for red/yellow headedness and produces the black-headed morph (Brush & Seifried 1968). Unusually, these head morphs naturally coexist together in wild populations.

In addition to the dramatic head polymorphism, Gouldian finches are also arguably one of the most brightly coloured passerines; displaying a black and white tail, deep blue rump, bright green wings and back, yellow belly, violet–purple breast, and a brilliant azure–blue collar bordering the head mask (figure 1). These traits are all expressed with continuous variation across a population (and morphs), typical of standard sexually selected ornamental traits in other species. Sexual dimorphism in these socially monogamous finches is pronounced with females displaying considerably duller and less chromatic plumage (S. R. Pryke & S. C. Griffith 2005, unpublished data) and shorter pintail feathers (21.7% shorter; $F_{1,256} = 172.73$, $p < 0.001$). To test the function of the head colour polymorphism as well as the multiple sexually dichromatic ornaments in dominance interactions, three standardized experiments were performed, using unfamiliar birds staged in contests with: (i) males of different head morphs, (ii) males of the same morph, and (iii) males with experimentally manipulated head colours (i.e. blackened and reddened). Since social dominance is an important determinant of male mating success, with dominant males typically preventing subordinates from breeding (Evans & Fidler 2005), any signal

trait that increases the efficiency (or decreases the cost) of frequent dominance contests should be favoured by sexual selection.

2. MATERIAL AND METHODS

Male dominance was assessed using captive birds ($n = 153$) sourced from a large number of wild-type aviculturists throughout Australia. All birds were fitted with a single numbered white plastic band to minimize potential colour band effects on colour communication. Birds from each locality were housed in groups of 8–12 individuals in separate sex and morph aviaries (2.1 m³), visually isolated from each other. Within the holding cages the potential for dominant males to monopolize food resources was minimized by placing multiple food dishes within each cage.

Prior to the experiments, standard measurements of flattened wing chord (0.5 mm), culmen, tarsus, tail and tail pin feather length (0.1 mm) were taken. Since patch size, independently or together with colour, may affect dominance (Marchetti 1998; Pryke *et al.* 2002) the size of the prominent coloured patches used in male aggressive displays (see §3) were measured. The violet chest patch was quantified (0.1 mm) by the maximum breadth (horizontal to the head), and height (vertical to the head) of the patch while holding the head in a standard position, and the width of the blue collar was measured at the mid-point of the throat and back of the head. The patch measurements were all highly repeatable (all males re-measured at a later stage; $n = 153$; repeatabilities: violet breadth, $r = 0.88$; violet depth, $r = 0.93$; head blue, $r = 0.88$, throat blue, $r = 0.84$; $p < 0.001$ for all). After the first moult from the dull green–brown juvenile plumage (less than 1 year), birds can no longer be accurately aged. For these experiments, we randomly used both adult birds (greater than 2 year old) and first year breeders (birds which moulted from juvenile to adult plumage in our housing aviaries). Spectral reflectance of the red, yellow and black of the three head morphs, as well as the blue head band, violet chest patch, yellow belly and green rump, were objectively measured using a USB2000 spectrometer (Ocean Optics, Dunedin, USA) with illumination from a xenon light source (Ocean Optics PX-2). Three consecutive scans (removing the probe between each) from the centre of each patch were taken with a fibre-optic reflectance probe and in relation to a WS-2 white standard scanned prior to each individual.

Lacking information on the optical physiology of Gouldian finches, we computed objective reflectance parameters relevant to the opponency-based perceptual colour space (see Andersson *et al.* 1998; Pryke *et al.* 2001 for further details on colourimetrics). Brightness (spectral intensity) was estimated by $R_{320-700}$, the sum of reflectance from 320 to 700 nm. Hue (spectral location) was estimated as $\lambda(R_{50})$, the wavelength at which reflectance is halfway between its minimum (R_{\min}) and its maximum (R_{\max}). Using $\lambda(R_{50})$ as the individual segment divider, we calculated overall chroma (spectral purity: $C_{R_{50}}$ as $(R_{320-\lambda(R_{50})} - R_{\lambda(R_{50})-700})/R_{320-700}$. To specifically address the strong contribution of ultraviolet (UV) to the blue and violet coloured patches, we also included a measure of UV chroma, calculated as the relative reflectance ratio of UV to human visual light ($R_{320-400}/R_{320-700}$).

(a) Dominance experiments

All contests were staged in a neutral wire cage, visually and acoustically isolated from all other birds. Prior to the experiments, contestants were weighed (0.1 g) and randomly assigned a coloured leg band for identification (bright pink, white or green). All trials lasted for 20 min to determine whether males were able to rapidly assess the competitive ability of their opponent primarily on the basis of plumage variation. In each trial, a male from one cage was tested against a randomly chosen, unfamiliar male from another cage (i.e. birds from a different locality which had never been in contact previously). Most birds were used in each of the three experiments, but never more than once against the same opponent and each dyad was unique. Male dominance was inferred from staged contests in two different competitive contexts: (i) standardized contests over competition for food, and (ii) by creating a linear dominance hierarchy and forcing birds to occupy their relative dominance position in the vertical hierarchy (see §2c for details).

A total of 726 dominance trials were performed from January to March 2005 using these two different competitive contexts within each of the three experiments. In the first experiment, contests were staged among males of the three different morphs (dyadic: $n=60$ males, 180 trials; triadic: $n=60$ males, 60 trials). Second, contests were performed within each of the three head morphs ($n=32$ males, 96 trials). Lastly, following the experiments on natural morph colour, dyadic contests were performed using birds with experimentally manipulated head colour ($n=150$ blackened, $n=60$ reddened, 390 trials). To temporarily remove the carotenoid-based head colours, the head masks of red- and yellow-headed males were completely blackened by massaging black pigment into the feathers (B100; Copic Too Marker Products, Tokyo), starting close to the skin and working to the surface, making sure that each feather was completely marked (following Pryke *et al.* 2002). As a control, black males were treated in a similar way, with no detectable differences between natural and manipulated blackened birds. A total of 150 trials were conducted with males from each of the three different morphs who were all given a black treatment (i.e. $n=30$ for all trials between birds of original head colour: red and yellow, red and black, yellow and black, yellow and yellow, red and red). To further determine the effectiveness of the red signal, the head colour of yellow-headed birds were temporarily reddened (Copic R29) to conceal their natural colour. Red-headed birds received a similar red treatment, which provided a good match to the longwave 'red'. Reddened yellow-headed males were then pitted in contests with black ($n=30$) and treated red-headed birds ($n=30$). Following a trial, the manipulated colour patches were carefully removed from the birds (with ethanol) to prevent familiarization with the treatments before returning them to their housing cages. Since the birds used in these experiments were also involved in other concurrent and future experiments, black-headed birds were not colour treated (this would have involved bleaching the feathers; i.e. a permanent effect).

(b) Contests for limited food

In the first competitive context, males from each experiment were pitted in competition for access to a limited food resource. To standardize hunger and motivation, all food was removed from the housing aviary compartments the previous evening (at 20.00). Experiments (consisting of 20 min trials)

were run from dawn (between 05.00 and 10.00). Males were simultaneously transferred into the experimental cage (measuring $90 \times 90 \times 70$ cm), which contained perches on either side of a central feeder with visible food, but constructed so that only one bird could feed at a time. In addition, spilt food passed through the wire floor of the suspended test cage so that food remained available only at the feeder. All birds began feeding within 6 min ($n=363$), except for eight dyads that did not feed for the duration of the trial. During the trials, we recorded the nature and outcome of all aggressive interactions at the central, easily monopolized feeder. Interactions at the feeder varied from active (e.g. threat displays, displacements and physical attacks) to passive supplants where a bird simply fled when approached by its opponent (i.e. non-threatening approach). The individual that retained control of the food dish following an interaction was considered the winner of that interaction, and the individual that won the majority of the interactions (greater than 75%) was taken as the winner of that trial. Three ties were recorded, which along with two other dyads where dominance could not be easily assigned, were excluded from subsequent analyses. In all other cases, using an average of $18 (\pm 5.8)$ interactions per dyad (range: 8–62; $n=721$ dyads), birds were easily binomially classified as either winners or losers. As an alternative measure of competitive success, we also recorded the first bird to feed.

(c) Contests in a dominance hierarchy

In a second competitive context, a linear dominance hierarchy was created by forcing birds to occupy their relative dominance position on an ascending ladder perch. Male Gouldian finches characteristically attack from above and will not aggressively displace their opponents from a vertically lower (subordinate) position. As a consequence, dominant males typically occupy and defend the highest perch, nest box or position in an aviary (Evans & Fidler 2005). For these experiments, a three-rung wooden ladder was positioned at a 45° angle to the wire cage, with each rung 25 cm from the other, and constructed such that only one bird could occupy each level of the perch. To encourage birds to take a position on our hierarchy ladder, no other perches were available in the cage, and the cage floor consisted of wire mesh (i.e. an unfavourable perch). The 20 min trials were conducted between 13.00 and 18.00, using different birds and combinations to those used in the morning feeding trials. During the trials we recorded the nature and outcome of all aggressive interactions (e.g. passive or active) and the amount of time each contestant spent on each of the different ladder rungs.

(d) Analyses and statistics

Generalized linear models (GLM) were used to evaluate the relative contribution of a number of potential interacting effects on the outcome of the dominance contests. For dyadic contests over food, the binary (win/loss) outcomes from each dyad were modelled as the Bernoulli dependent variables with a logit link function (GENSTAT 7.1.0. VSN, 2003). In triadic and hierarchy contests, the outcomes were modelled using a logarithmic link function and Poisson distribution since the data were not normally distributed. All models were generated incorporating all possible combinations of the measured effects and their interactions (e.g. body size measurements, body mass, tail length, colourimetrics (i.e.



Figure 1. The three head morphs (yellow, red and black) of male Gouldian finches. (Photograph by Sarah R. Pryke.)

head morph, green, yellow, blue and violet patch), patch sizes, manipulation, leg band colour, beak tip colour, individual status, previous dominance success, age, housing locality, trial number, date and time). The significance of these predictor variables was tested by the change in deviance of the different models using a chi-square approximation. To objectively select the most parsimonious model, we used Akaike's information criterion (AIC), which balances the fit of the model against the number of parameters used in the model. The model with the lowest AIC value (and a difference of at least two AIC units from the other models) is accepted as the model best fitting the data (Anderson & Burham 2001).

3. RESULTS

(a) *Dominance among head morphs*

The best-fitting GLM of the binary (win/loss food dominance) dyadic experiments for the 90 trials among males of different morphs (red, black and yellow) identified head morph as the only significant predictor of contest outcome (AIC=109.7 and a weight of 88% compared to other models; $\chi^2_{89} = 8.48$, $p < 0.001$): red-headed males were more likely to defeat yellow-headed birds ($t = 7.75$, $p < 0.001$) and black-headed birds ($t = 4.56$, $p < 0.001$), whereas black males had a higher, but not significant, probability of dominating yellow-headed males ($t = 1.52$, $p = 0.13$; probabilities for the outcome of overall trials are provided in figure 2). The dominance of red-headed birds was further evident by the outcome of the triadic experiments (AIC=21.4 and a weight of 69% compared to other models; $\chi^2_{59} = 10.75$, $p < 0.001$); red-headed males dominated black males ($t = 3.67$, $p < 0.001$) who in turn dominated yellow-headed males ($t = 2.6$, $p = 0.001$). Furthermore, substituting the relative dominance position of the birds in the linear dominance hierarchy produced a weaker, but qualitatively similar, model (AIC=44.2 and a weight of 61% compared to other models; $\chi^2_{89} = 6.88$, $p < 0.001$).

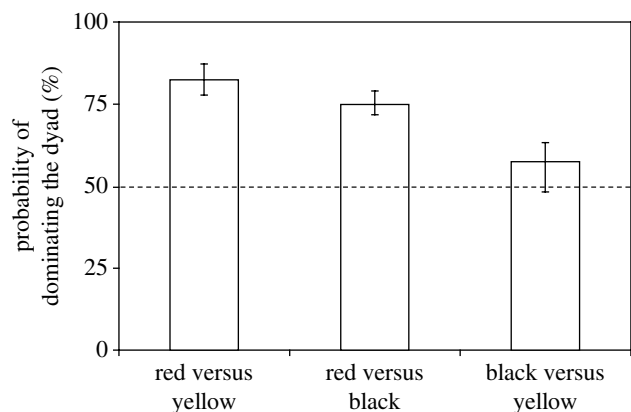


Figure 2. Within a dyad, the probability (%) of the male morph (listed first on the bottom axis) dominating his opponent (mentioned second). Probabilities are generated from the coefficients of the best-fit generalized linear model (GLM: $\text{probability} = e^{(\text{coefficient})} / (1 + e^{(\text{coefficient})})$) for the win/loss outcome of the contests. The errors bars represent the 95% confidence intervals, calculated from the standard errors of the coefficients (upper CI = coefficient + $(2 \times \text{s.e.})$; lower CI = coefficient - $(2 \times \text{s.e.})$). The dashed line indicates where the two males have an equal likelihood (i.e. 50%) of dominating the dyad.

However, although feeding order identified head morph as the only significant predictor (AIC=120.6 and a weight of 71% compared to other models; $\chi^2_{89} = 5.28$, $p < 0.001$), the effect was in the opposite direction; in the majority of trials, yellow-headed males were the first to feed ($t = 2.09$, $p = 0.04$). Since feeding order was unrelated to both overall dominance ($r = 0.08$, $n = 348$, $p = 0.45$) and the total time spent feeding ($r = 0.17$, $n = 348$, $p = 0.11$), feeding order is unlikely to be a relevant predictor of dominance in Gouldian finches. In addition to affecting the overall outcome of dominance interactions, head morph also affected the type of interaction and displacement (i.e. active or passive) within the three morphs

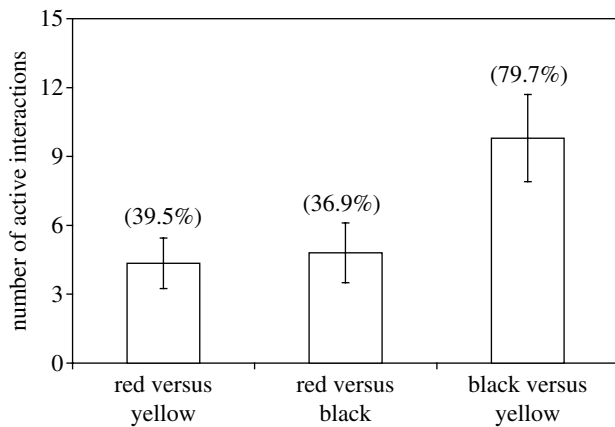


Figure 3. The average (\pm s.d.) number of active aggressive interactions in the dyadic contests among males of the three different coloured morphs. The percentage of active supplants (i.e. aggressive displays and/or physical displacements) in these interactions are provided above the bars. The remaining interactions involved passive supplants (i.e. feeding bird retreats when approached by an opponent).

(GLM with interaction type as the response variable: AIC=87.9 and a weight of 69% compared to other models; $\chi^2_{179} = 30.87$, $p < 0.001$). For example, interactions between yellow- and black-headed birds tended to be more active and aggressive (79.7%) than those between either red- and yellow-headed birds (39.5%; $t = 5.08$, $p < 0.001$) or between red- and black-headed birds (36.9%; $t = 3.61$, $p < 0.001$), where the losing bird would typically move away from the feeder at the approach of the red bird (figure 3).

(b) Dominance within head morphs

The GLM best explaining the win/loss outcome of the 48 trials involving males of the same head morphs (AIC=100.86 and a weight of 72% compared to other models; $\chi^2_{47} = 4.39$, $p = 0.003$) included a dominant effect of UV blue collar chroma ($t = 3.38$, $p < 0.001$), a significant but weaker effect of head blue collar size ($t = 1.94$, $p = 0.05$), and a positive, but not significant, effect of violet UV chroma ($t = 1.71$, $p = 0.09$). In addition, within the red-headed male dyads, redder males dominated less chromatic opponents (interaction between morph \times chroma: $t = 2.17$, $p < 0.03$). Replacing the dominance outcome at food bowls with that from the dominance hierarchy produced a similar but slightly weaker model (AIC=84.78 and a weight of 67% compared to other models; $\chi^2_{47} = 3.22$, $p = 0.007$) identifying both the UV chroma ($t = 2.47$, $p = 0.001$) and size ($t = 2.26$, $p = 0.02$) of the blue head patch as significant predictors.

Although, there were no differences in interaction type within dyads of the same head morph, there were significant behavioural differences among the three head morph dyads (i.e. between the red, black and yellow dyads; AIC=361.29 and a weight of 84% compared to other models; $\chi^2_{47} = 15.59$, $p < 0.001$). Red-headed dyads had both more active (86.7%) and more frequent interactions than the black- (61.5%; $t = 2.81$, $p = 0.005$) and yellow-headed birds (56.8%; $t = 3.61$, $p < 0.001$), the latter of which did not differ ($t = 1.55$, $p = 0.12$). Red-headed dyads also initiated aggressive conflicts earlier than either the black- (Mann-Whitney U -test: $z = 4.76$, $n = 32$, $p < 0.001$) or yellow-headed dyads ($z = 4.18$, $n = 32$,

$p < 0.001$), and black-headed dyads were quicker to interact than yellow-headed dyads ($z = 2.93$, $n = 32$, $p = 0.003$).

(c) Dominance among experimental head morphs

The best-fitting GLM explaining the outcome of contests with manipulated males (reddened and blackened; 390 trials) identified the same model for both response variables; dominating the food bowl (AIC=225.7 and a weight of 77% compared to other models; $\chi^2_{179} = 17.94$, $p < 0.001$) and top position in the hierarchy (AIC=228.9 and a weight of 68% compared to other models; $\chi^2_{179} = 18.51$, $p < 0.001$). This model identified natural head morph as the only significant predictor of contest outcome; red-headed males were more likely to defeat yellow-headed birds ($t = 3.51$, $p < 0.001$), and to a lesser extent, black-headed males ($t = 2.10$, $p = 0.03$), although manipulated yellow- and black-headed males were equally likely to dominate the dyad ($t = 1.87$, $p = 0.26$; figure 4). There was no effect of experimental manipulation on the outcome of dominance, and thus, despite the treatments, naturally red-headed males remained dominant. Furthermore, none of the other potentially interacting effects (see §2 for list) had any effect on the outcome of these contests. Although, the colour treatments did not affect the outcome of contests, they did influence the type of aggressive interactions (i.e. active or passive supplant) used to settle disputes. Replacing interaction type as the response variable in the model (AIC=221.6, $\chi^2_{359} = 108.16$, $p < 0.001$) produced a strong effect of experimental manipulation ($t = 11.97$, $p < 0.001$). This was because most supplants in the experimentally reddened group were passive (79.4%), whereas the majority of supplants in the black-treated groups were active (71.3%). For example, reddened yellow-headed birds were less aggressive (28.3% active supplants), yet they successfully dominated black-headed birds (see figure 4). In contrast, naturally red-headed males given a blackened treatment were particularly aggressive in displacing their opponents (interaction between colour treatment and pre-manipulation head colour: $t = 7.03$, $p < 0.001$). Furthermore, there was a significant difference between the treatments in assessment time prior to conflicts; males in the blackened dyads initiated aggressive interactions faster than those in the reddened group (Mann-Whitney U -tests: $z = -10.77$, $n = 300$, 60 , $p < 0.001$).

4. DISCUSSION

These results demonstrate the aggressive dominance of red-headed males in contests over both food and relative position in a dominance hierarchy. In dominance trials, red-headed morphs dominated both black-, and particularly yellow-headed phenotypes. The head manipulation experiments further demonstrated that contest outcome was not determined solely by the red plumage signal, since naturally red-headed males consistently dominated other morphs, even when the red signal was blackened, suggesting that red-headed males are intrinsically more aggressive. For example, in both experiments with naturally red-headed males and also when red-headed males were experimentally blackened (i.e. aggressive red signal is destabilized), red-headed birds strongly

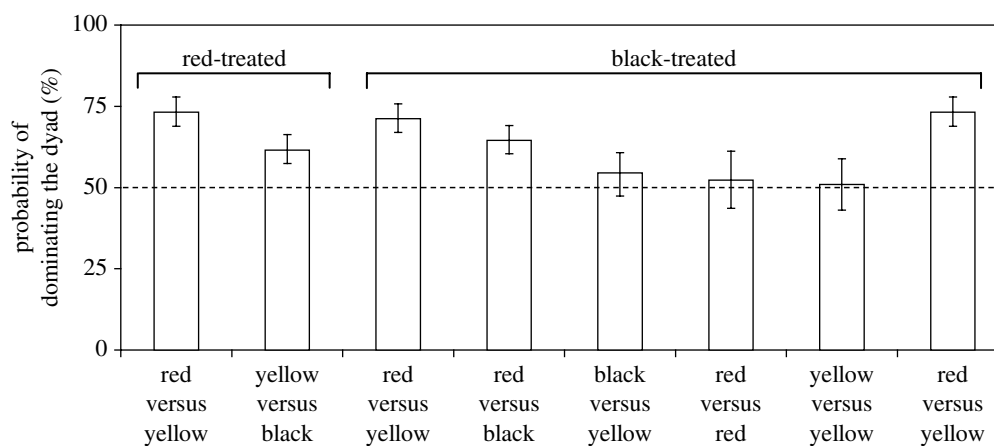


Figure 4. The probability (%) of the colour treated male (listed first) dominating his colour treated opponent (mentioned second). Probabilities are calculated from the GLM best fitting the data (see §2 and figure 2 for details) with error bars for the 95% confidence intervals of the coefficient. The dashed line indicates where the two males have an equal chance (i.e. 50%) of dominating the dyad.

dominated their contestants by initiating more, and sustaining longer, aggressive interactions (i.e. active supplants). Similarly, the intrinsic nature of the highly aggressive red-headed males is further evident when birds are placed in large mixed-morph populations for breeding; red-headed males not only aggressively dominated the favoured nest boxes (i.e. higher ones), but also appear to be more susceptible to the stresses invoked by these housing conditions and breeding (S. R. Pryke & S. C. Griffith 2005, unpublished data). Potentially, differences in pleiotropic interactions, linkage between the genes for the expression of the red carotenoids and elevated levels of aggression, or perhaps simply differences in hormonal levels (e.g. testosterone) are responsible for the observed differences in competitive ability (and stress) among the three morphs. At this early stage, however, these ideas remain speculative.

Nevertheless, regardless of the underlying cause linking genetically controlled colouration to male aggression in the Gouldian finch, this behaviourally linked dominance effect contributes towards further understanding the co-occurrence of the discrete morphs within populations of this species. The stable coexistence of multiple morphs within a population presents a particular challenge to evolutionary theory because only one morph should prevail unless they each entail a similar net fitness, since a genotype with higher fitness would be expected to replace a genotype with lower fitness. Alternative behavioural strategies have long been recognized as an important force in the evolution and maintenance of polymorphic traits (Fisher 1930; Roulin 2004). For example, male lek-breeding ruffs exhibit two genetically determined behavioural strategies, both related, although not exclusively, to their plumage polymorphism (Lank *et al.* 1995; Widemo 1998). In this species, independents establish territories on leks, while satellites do not attempt to hold a fixed position on the lek, rather attempting sneaky copulations with females visiting independents (Widemo 1998). The persistence of these two alternative, genetically based strategies is thought to constitute a mixed evolutionary stable strategy (ESS; Maynard Smith 1982) with identical, frequency dependent, fitness benefits to males pursuing the different strategies (Widemo 1998). However, the rate of copulations achieved on the

leks strongly favoured independents (Widemo 1998), and for a mixed ESS to be empirically supported, further work needs to account for other interacting contributions to overall fitness, such as actual paternity (Thuman & Griffith 2005). Furthermore, the plumage polymorphisms of male ruffs are not completely discrete, with the high variability in their plumage expression thought to have evolved to signal individual identity (Lank 2002).

To date, the ruff offers the only avian example of a genetically determined colour polymorphism functioning as an ESS in natural populations, and like the Gouldian finch, there are many gaps to complete before fully understanding the system. A more comprehensively worked system is the side-blotched lizard (*U. stansburiana*), in which the three heritable male colour morphs (red, orange and blue) are each associated with an alternative mating strategy and territorial behaviour; highly dominant orange males defend large territories with multiple females, sneaky yellow males do not hold territories but obtain copulations by resembling females, and blue males defend small territories usually with one female whom they mate guard intensely (Sinervo & Lively 1996; Sinervo & Clobert 2003). Since each male has a mating advantage when rare, the frequency of these alternative strategies (and hence the associated morph fitness) cycle in a type of 'rock-paper-scissors' game (Sinervo & Lively 1996; Alonzo & Sinervo 2001; Sinervo & Zamudio 2001).

Although, as yet, the interaction of other aspects of life-history and selective mechanisms in the Gouldian finch are unknown, there are some potentially interesting parallels with the side-blotched lizard. In Gouldian finches, red-headed birds dominate black-headed birds, who in turn dominate yellow-headed males. Competitively dominant red-headed males may benefit from their higher status, most likely in agonistic interactions with other males over food, nest sites and females. By contrast, yellow-headed males are particularly subordinate and their submissive behaviour may perhaps also be part of an alternative adaptive behavioural strategy. For example, yellow-headed birds may be bolder than the other morphs; typically they were the first to explore the experimental cage (a novel environment) and consequently were the

first to find the food (before been supplanted by more dominant males). However, in this particular experiment (i.e. dominance) this effect may simply be a consequence of their opponent taking a dominant position in the experimental cage, forcing them to occupy a submissive position on the bottom of the cage (where the food was positioned). Thus, while an adaptive strategy is an appealing idea, further investigations into the system are obviously needed before any conclusions can be made.

Between the highly dominant red-headed and submissive yellow-headed males, black-headed birds have an intermediate dominance status. Black-headedness is expressed by a recessive allele at the sex-linked locus, which masks the yellow/red colour determined by the autosomal gene. It is possible to distinguish the underlying yellow/red phenotype of black-headed birds by the colour of their beak tip (yellow or red). Therefore, an interesting possibility is that black-headed birds carrying the genes for red-headedness (i.e. homozygous dominant and heterozygous on the autosomal locus) are dominant, while those with yellow-headedness (i.e. homozygous recessive) are subordinate. However, beak tip colour, and thus the underlying phenotype, had no effect in any of the dominance trials, either within or among the different morphs, suggesting that black-headed birds are viewed as a separate phenotype rather than an intermediate expression between red and yellow.

Although, black-headed males are not socially dominant they are the most common head morph in wild populations (70%), while red-headed males are moderately common (30%) and yellow-headed males extremely rare (estimated at one in 3000–5000; Brush & Seifried 1968; Franklin & Dostine 2000). The results from this dominance experiment do not completely explain these frequencies; if dominant red-headed birds gained the greatest benefits they would be expected to be more common than the intermediate black-headed birds. However, it is unlikely that aggression and dominance alone, or in isolation, contributes to the observed morph frequencies.

How this dominance advantage translates into relative morph fitness or the maintenance of the head polymorphism is still unclear at the moment. However, the continued persistence of the black-headed morphs (and even the very rare yellow-headed morphs) suggests that any dominance advantages are countered by antagonistic selection pressures which favour these other morphs, perhaps through temporally, spatially or density-dependent natural and/or sexual selection pressures. In theory, many potential explanations have been proposed for the coexistence of colour polymorphisms within populations, however, empirical studies are limited and provide little support for one or more mechanism(s), which are known in only a few cases (see Lank 2002; Galeotti *et al.* 2003; Roulin 2004). Further studies, investigating both the presence and relative importance of other interacting selection pressures, both on different colours within and among colour morphs, are clearly needed.

In addition to further understanding the agonistic selection pressures on the three discrete colour morphs of the Gouldian finch, our study also provides some insight into the evolution of colour signals in birds. While the manipulative experiments demonstrated the intrinsic link between colour morph and male aggression, the red signal

itself also appears to function as a traditional status signal of male dominance. For example, by artificially changing the natural colour signals of male morphs (e.g. yellow-headed birds given a red treatment), we were able to completely reverse dominance status such that yellow-headed males (with experimentally reddened heads) dominated black-headed birds. This is further evidenced by contestants avoiding conflicts with opponents displaying red signals: in dyads, where males were both given reddened heads, the initial and mutual avoidance behaviours by these contestants may have resulted from the higher perceived dominance status of red-headed opponents. This is supported by the experimentally reddened dyads spending significantly longer than the experimentally blackened dyads in assessing each other before initiating fights. Consequently, the aggressive response of conspecifics to each other may be mediated through their perception of their opponent's dominance status (and aggression), as signalled through the red head colour.

Furthermore, this study also demonstrated that subtle variation in the colour quality of the genetically controlled colouration was related to success in dominance interactions. Within the red-headed morph, redder (i.e. more longwave) individuals dominated less intensely coloured opponents and therefore, at least within morphs, this signal seems to operate as a classic dominance trait, adding to the growing evidence that variation in red carotenoid-based signals may play an important dominance role in a number of species (Evans & Hatchwell 1992; Searcy & Yasukawa 1995; Pryke *et al.* 2002; Pryke & Andersson 2003a,b; Crowley & Magrath 2004). Indeed, while melanin-, rather than carotenoid-based, traits have typically been associated with dominance (reviewed in Senar 2006), it is interesting that in this species, the first time in which the signal function of the two coloured pigments can be directly compared in a meaningful way (i.e. same trait within the same species), red-headed individuals (expressing carotenoids) are dominant over black-headed birds (expressing melanins). This finding provides further support for a general dominance signal function of carotenoid-based plumage (Griffith *et al.* in press; Griffith & Pryke 2006), and interestingly, together with a number of other species (e.g. cichlids: Evans & Norris 1996; sticklebacks: Bakker & Milinski 1993; widowbirds: Pryke *et al.* 2002), and a recent study demonstrating that red affects the outcome of competitive sporting interactions in humans (Hill & Barton 2005), suggests that there may be a general intimidation value to red colouration in agonistic encounters.

Although, the relative contribution and importance of different selective pressures remains speculative at present, given the dramatic colour polymorphism and striking multi-component colouration, it appears probable that an interaction of different selective pressures maintains both the continuous (i.e. presumably condition-dependent colour patches) and discontinuous (i.e. head morphs) colouration in this species. For example, the intensity of the UV/blue collar (surrounding the head mask), the colour expression of which varies qualitatively across all morphs (see figure 1), is important in settling dominance contests within each of the three discrete head morphs, and is also a primary target in female mate

decisions (irrespective of the male or female morph; S. R. Pryke & S. C. Griffith 2005, unpublished data). Whereas the discrete head colour polymorphism may signal intrinsic genetically based behavioural characteristics, which appear to underscore a clear dominance hierarchy among males; aggressive and dominant red-headed males and subordinate yellow-headed males. These differences, in a trait likely to be under strong selection, suggest that diverse selection pressures may vary across the morphs, balancing out net morph fitness and thus explaining the persistence of the three conspicuous morphs in wild populations.

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