

Fiery red heads: female dominance among head color morphs in the Gouldian finch

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Although the evolution of genetic color polymorphisms has received much theoretical interest, few empirical studies have investigated the adaptive function of alternative color morphs. Furthermore, most studies have focused almost exclusively on the evolution and adaptive expression of male coloration, leaving the role of conspicuous female coloration largely unknown. Using the color polymorphic Gouldian finch (*Erythrura gouldiae*), this study experimentally tests the status signaling function of head color (red, yellow, and black) among the 3 female color morphs. In standardized dominance contests between unfamiliar females of different head colors, red-headed females dominated both black- and yellow-headed females. During contests between the morphs, red-headed females passively displaced black- and yellow-headed opponents, whereas interactions between red-headed dyads were particularly aggressive and more frequent than interactions within dyads of the other color morphs. This effect of red dominance further persisted when head color was experimentally altered; red-manipulated females (of the other morphs) dominated both black- and yellow-headed females, whereas blackened red-headed females were dominated by naturally red-headed birds. Together with similar dominance-related differences among male morphs, these results suggest that the 3 color morphs may display alternative strategies in dominance behavior. *Key words:* color polymorphism, female dominance, Gouldian finch, plumage coloration, status signaling. [*Behav Ecol* 18:621–627 (2007)]

Evolution tends to promote a single optimum male and female phenotype for each species. In a few species, however, evolution has instead resulted in extreme phenotypic diversity, where individuals within a sex display a number of discrete and heritable phenotypes. The persistence of such genetically determined polymorphism presents a major challenge to evolutionary theory because directional (normalizing) selection on a strongly heritable trait should eliminate conspicuous variation and instead lead to monomorphism (Fisher 1930). Consequently, much of the interest in polymorphic systems centers on understanding the potential adaptive value of displaying alternative phenotypes (e.g., Fisher 1930; O'Donald 1983; Gross 1996; Sinervo and Lively 1996), especially because discrete morphs may also vary in aspects other than appearance, such as behavior, physiology, and reproductive success. Such multitrait differences are often promoted by alternative behavioral strategies, where competing morphs may maximize their fitness by adopting different tactics (reviewed in Gross 1996). For example, polymorphisms in male behavior and life history are found in a number of taxa where territorial and/or highly aggressive morphs typically compete with sneaky and/or nonterritorial morphs for access to mates (e.g., Gross 1982, 1985; Lank et al. 1995; Sinervo and Lively 1996).

In birds, plumage coloration is an often striking example of genetically determined polymorphism (Galeotti et al. 2003; Roulin 2004). Although sexual selection is commonly invoked as a major selective force maintaining variable plumage coloration in birds (Hill and McGraw 2006), and despite the well-established dominance or status function of male coloration (Senar 2006), recent comparative studies suggest that avian color polymorphisms are more often determined by ecologi-

cal factors (e.g., population size; Fowle and Krüger 2003), individual recognition (Dale et al. 2001), and disruptive selection favoring alternate morphs in different habitats or environmental conditions (Galeotti et al. 2003; Galeotti and Rubolini 2004). Nevertheless, empirical studies are limited, and it remains largely unclear how such discrete color variation is maintained across individuals within a species (reviewed in Roulin 2004). Furthermore, although the vast majority of color studies have focused exclusively on the adaptive expression of male coloration (Hill and McGraw 2006), much less is known about why females of some species display similar conspicuous coloration (Amundsen and Pärn 2006). Traditionally female coloration was simply assumed to be a nonfunctional by-product, or correlated response, of selection for coloration in males (Lande 1980; Hill 1993). However, more recent evidence suggests that female coloration is not severely constrained by selection on males and that female coloration can be maintained via contest competition and mate choice (reviewed in Amundsen and Pärn 2006), the same functional explanations often proposed for male coloration. Nevertheless, failure to identify a functional role for female coloration has often led to skepticism that such coloration is adaptive. For instance, a number of studies on female coloration have found no evidence for a status signaling function (Fugle and Rothstein 1985; Muma and Weatherhead 1989, 1991; Zuk et al. 1998; but see Holberton et al. 1989; Swaddle and Witter 1995). However, most of these studies have focused on species in which females display drab plumage, rather than on color traits which are expressed in both sexes or are specific to females alone. One exception is found in the color polymorphic white-throated sparrow (*Zonotrichia albicollis*) where both males and females display 2 color morphs; tan and white (Tuttle 2003). In this system, white females are the most aggressive on breeding territories (Kopachena and Falls 1993) and during spring migration (Ficken et al. 1978), although tan females are more dominant in winter flocks (Watt et al. 1984). Together, these somewhat paradoxical results for female dominance, along with the general scarcity of

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rigorous (and experimental) tests of female coloration in most avian studies, have left the role of female coloration in resolving dominance conflicts unclear.

This study experimentally tests the status signaling role of female coloration in the color polymorphic Gouldian finch (*Erythrura gouldiae*), a bird exhibiting 3 naturally co-occurring head color morphs in both sexes (black, red, and yellow). The genetics of this head color polymorphism are well resolved (Brush and Seifried 1968) and determined by the interaction of 2 genes (one sex linked and one autosomal), which results in 3 completely discrete phenotypic morphs. At the autosomal locus, 2 alleles control carotenoid color expression; the dominant allele is responsible for the red-headed morph, whereas the recessive allele produces the yellow-headed phenotype. 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 (Southern 1945; Murray 1963). A truly discrete polymorphism such as this is extremely rare in birds because most color polymorphic species studied to date (e.g., O'Donald 1983; Roulin 1999; Dale 2000; Krüger et al. 2001) display continuous, or at least overlapping, variation in genetically determined phenotypic color/pattern expression, where intermediates are often unable to be reliably assigned to a specific phenotypic color/pattern morph. Furthermore, the 3 color morphs of the Gouldian finch naturally coexist together in wild populations; estimates suggest that the black-headed morphs are the most common (ca. 70%), red headed moderately common (ca. 30%), and yellow headed extremely rare (<0.1%; Brush and Seifried 1968; Franklin and Dostine 2000). In both wild and captive populations, these socially monogamous finches tend to mate assortatively with respect to head color (Pryke and Griffith 2007). Male mate choice plays a particularly important role in maintaining assortative mating, with males of all 3 color morphs preferring females of their own morph type (Pryke and Griffith 2007). Yet, although females exhibit consistent and repeatable preferences for particular color morphs, overall, females do not discriminate assortatively.

The head color polymorphism in males is further associated with behavioral differences in dominance: red-headed males are the most aggressive and persistently dominate both black- and yellow-headed males, whereas yellow-headed males are particularly subordinate, and black-headed males are of intermediate status (Pryke and Griffith 2006). To test for a similar status function of the color polymorphism in females, 3 dominance experiments were performed, each using unfamiliar birds staged in contests with females of the same color morph, females of different color morphs, or female morphs with experimentally manipulated head coloration.

METHODS

Female dominance was assessed using wild-type captive birds ($n = 197$) sourced from a large number of aviculturists throughout Australia. All birds were fitted with a single numbered white plastic band to minimize potential color band effects on color communication. Birds from each locality were housed in groups of 6–12 individuals in separate sex and morph aviaries (2.1 m³), visually isolated from each other.

Before the experiments began, standard morphometrics of wing chord length (0.5 mm), beak, tarsus, and tail length (0.1 mm) were taken. As these 4 body size traits were intercorrelated, a principal component (PC) analysis was run to extract an independent body size measurement. The first components (PC1) described 66.8% of the variation and were positively weighted for each trait (0.73 tarsus, 0.67 beak, 0.78 wing, and 0.85 tail). After the first molt from the dull green–brown

juvenile plumage (<1 year), birds can no longer be accurately aged. For these experiments, both adult birds (>2 year old) and first year breeders (birds that molted from juvenile to adult plumage in the housing aviaries) were randomly used.

Spectral reflectance of the red, yellow, and black of the 3 head morphs, as well as the ultraviolet (UV)/blue head band, UV/violet chest patch, yellow belly, and green rump, was objectively measured using a USB2000 spectrometer (Ocean Optics, Dunedin, FL), with illumination from a xenon light source (Ocean Optics PX-2). Three consecutive scans (lifting and replacing the probe between scans) were taken with a fiber-optic probe from the center of each patch and in relation to a WS-2 white standard scanned prior to each individual. From the raw spectral reflectance data, the 3 main dimensions of color signals (spectral location, intensity, and purity) were computed and then averaged for each individual. Brightness (spectral intensity) was estimated by $R_{320-700}$, the sum of reflectance from 320 to 700 nm. Hue (spectral location) was estimated by $\lambda(R_{50})$, 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, overall chroma (spectral purity) was calculated as C_{R50} as $(R_{320-\lambda(R50)} - R_{\lambda(R50)-700}) / R_{320-700}$. To specifically address the contribution of UV to the blue- and violet-colored patches, we also included a measure of UV chroma, calculated as the relative reflectance ratio of UV to total reflectance ($R_{320-400} / R_{320-700}$). Further details on the methods used to collect and analyze reflectance are described in Pryke and Griffith (2006).

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 colored leg band for identification (bright pink, white, or green). All trials lasted for 20 min to determine whether females were able to rapidly assess the competitive ability of their opponent primarily on the basis of plumage variation. In each trial, a female from one cage was tested against a randomly chosen, unfamiliar female from another cage (i.e., birds from a different locality that had never been in contact previously). Most birds were used in each of the 3 experiments (see below; mean \pm standard deviation [SD] = 2.63 ± 0.58 number of experiments per bird; range: 1–3; $n = 540$ experimental trials) but never more than once against the same opponent, and each dyad was unique.

Dominance was inferred from staged contests using 2 different competitive contexts (Pryke and Griffith 2006). In the first context, birds were placed in standardized dyadic contests for access to limited food (see Pryke et al. 2002). To standardize hunger and maximize the motivation of individuals to compete for resources during trials, all food was removed from the housing aviary compartments the previous evening. Experiments were conducted in the first 5 h after sunrise. Two females 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 10 min ($n = 390$ trials) except for 2 dyads that did not feed for the duration of the trial and were excluded from the analyses. During the trials, the nature and outcome of all aggressive interactions were recorded 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., nonthreatening approach). The individual that retained control of the food dish following an interaction was considered the winner of that interaction, and those winning the majority of interactions within a trial (greater than 75%) were considered the overall winners of the trial (Pryke et al. 2002; Pryke and Griffith 2006). Three ties were recorded, which along with 9 other dyads, where dominance could not be easily assigned, were excluded from subsequent analyses.

In the second context, a linear dominance hierarchy was created by forcing birds to occupy their relative dominance position on an ascending ladder perch. Male Gouldian finches 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 (Pryke and Griffith 2006). To test whether a similar dominance hierarchy exists among females, a vertical hierarchy was created by positioning a 3-rung wooden ladder 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 unfavorable perch). Using 3 unfamiliar birds, the 20-min trials were conducted between 13 and 18 h. During the trials, the amount of time each contestant spent on each of the different ladder rungs was recorded (for further details, see Pryke and Griffith 2006).

Using these 2 different competitive contexts and 3 different experiments, a total of 540 dominance trials were performed from December 2005 to February 2006. In the first experiment, contests were staged between females of the 3 different head morphs ($n = 60$ red-headed, 60 black-headed, and 60 yellow-headed females). In dyadic contests over competition for food, a total of 180 trials were performed, whereas in the triadic dominance hierarchy experiments, a total of 60 trials were run. In the second experiment, contests were staged between females of the same head color ($n = 60$ red-headed, 60 black-headed, and 60 yellow-headed females: dyadic contests = 90 trials; triadic contests = 30 trials). In the last experiment, in order to isolate the effect of the head color signal in dominance from the female's behavior, dyadic contests were performed using birds whose head color had been experimentally manipulated. In each of the 9 experimental dyads, 30 trials were performed using unique dyads of unfamiliar females (total of 180 trials). In this experiment, experimental birds had their head color either reddened ($n = 90$) or blackened ($n = 90$) before being staged in contests with a natural colored control bird (see Figure 3 for details on the tested dyads). To temporarily remove the carotenoid-based head colors, the head masks of red-headed females were completely blackened by massaging black pigment into the feathers (B100; Copic Too Marker Products, Tokyo, Japan), following the protocol outlined in Pryke et al. 2002. To further isolate the effect of red headedness in dyadic contests, the head color of yellow-headed birds was temporarily reddened (Copic R29) to conceal their natural color. This red treatment provided a good match to the longwave "red" of red-headed birds (see also Pryke and Griffith 2006). All natural colored control birds were similarly manipulated, but with a transparent pen (Copic 0 colorless). This control treatment had no detectable affect on the resulting color or spectral reflectance of the head plumage (including UV, which is absent or minimal in the black, red, and yellow head plumage). After a trial, the manipulated color patches were carefully removed from the birds (with ethanol) to prevent familiarization with the treatments before returning them to their housing cages. Black-headed birds were not color treated, as they were re-

quired for future experiments (this color change would have involved permanently bleaching the feathers).

Statistical analyses

Outcomes from all experiments were initially performed using linear mixed models (in GenStat 7.1.0; 2003, The Numerical Algorithms Group Ltd, Oxford, UK). Linear mixed models are algorithms of generalized linear models (GLMs), except that they also allow random components to be fitted; random components in this case take into consideration the use of the same bird in more than one trial or experiment (e.g., red- and yellow-headed females were used in more than one of the experimental head-manipulation dyads). A significant random term suggests that individual responses will affect the outcome of dominance interactions (i.e., variation within individuals is significantly greater than the variation between individuals). However, because the random terms (individuals) in the tested models had a negative component of variance (indicating that it explained none of the variance in the model), they were dropped and an equivalent linear model was conducted instead. Using the most parsimonious model (i.e., GLM) is appropriate when random terms have nonsignificant effects; although the results from the GLMs did not differ qualitatively from their mixed model equivalent.

Because of the structure of the experiments and data, it was necessary to fit 3 different GLMs. In the first model, to test what factors determine dominance in dyadic contests over food, winning success (0/1) was fitted as the response in a GLM with a binomial error structure and a logit link function. In the second model, the outcomes of triadic contests for relative position in the dominance hierarchy were modeled using a logarithmic link function and Poisson distribution (because the data were not normally distributed). Similarly, the third model substituted interaction type (i.e., proportion of active and passive supplants) as the response variable in GLM, which was fitted with a logarithmic link function and a Poisson distribution.

In each model, all potential explanatory terms, combinations, and 2-way interactions were tested, including effects such as body size (PC1), body mass, colorimetrics, head morph, leg band color, individual, manipulation, age, previous dominance success, housing location, 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 best-fitting and most parsimonious model, second-order Akaike's information criterion (AIC_C) was calculated for each model (i.e., AIC_C balances the fit of the model against the number of parameters used in the model). AIC_C weights, which indicate the probability that the model is the best among the tested models, were used to effectively compare different models (Burnham and Anderson 2002). Because all models tested had an AIC_C weight of at least 84% compared with other potential models, for simplicity, only the final models are presented.

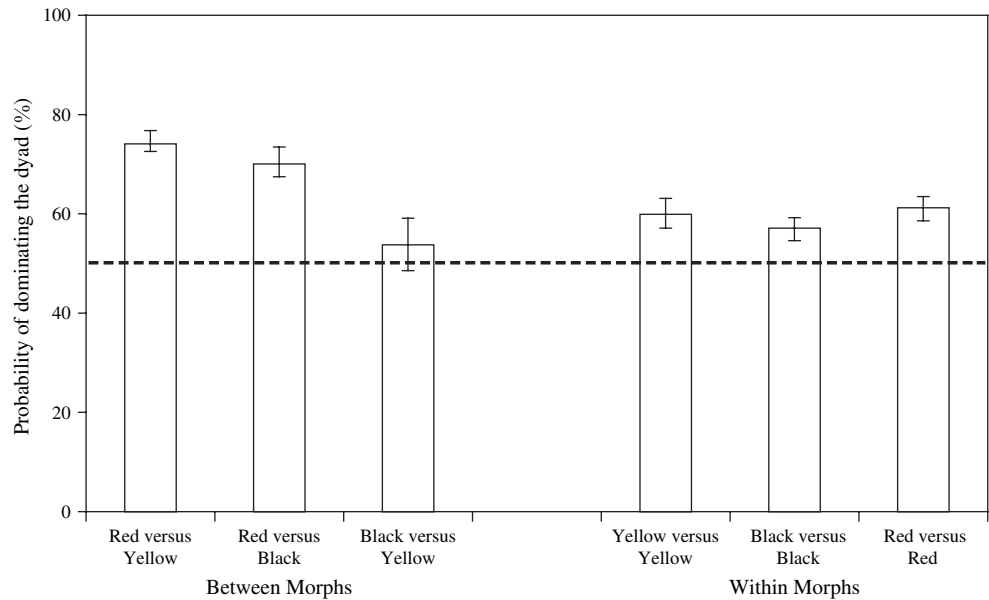
RESULTS

Dominance between female color morphs

In competition for food, female head color was the only factor significantly affecting the outcome of the dyadic contests ($\chi^2 = 16.24$, degrees of freedom [df] = 176, $P < 0.001$). In particular, red-headed females dominated both black- ($t = 3.29$, $P < 0.001$) and yellow-headed birds ($t = 3.69$, $P < 0.001$), whereas black- and yellow-headed females had relatively equal probabilities of dominating each other ($t = 1.47$,

Figure 1

For between-morph experiments, the probability (%) of a female color morph (listed first) dominating her opponent (listed second) of a different head color morph. For within-morph experiments, the probability of a larger female (PC1) dominating her smaller opponent (of the same morph type). Probabilities are generated from the coefficients of the best-fit GLM for the win/loss outcome of the contests (GLM: probability = $e^{(\text{coefficient})}/[1 + e^{(\text{coefficient})}]$). The errors bars represent the 95% confidence intervals (CIs), calculated from the standard errors of the coefficients (upper CI = coefficient + $[2 \times \text{SE}]$; lower CI = coefficient - $[2 \times \text{SE}]$). The dashed line indicates where the 2 females have an equal likelihood (i.e., 50%) of dominating the dyad.



$P = 0.14$; Figure 1). None of the other potential interacting factors, including body size (PC1), body mass, and colorimetrics (see Methods for full list of tested variables) had any effect on the outcome of dominance. Similarly, when competing in the triadic dominance hierarchy, female head color was the only factor influencing possession of the dominant position ($\chi^2 = 10.91$, $df = 59$, $P < 0.001$); red-headed females persistently dominating the top perch in the linear hierarchy compared with black- ($t = 2.73$, $P = 0.006$) and yellow-headed females ($t = 3.85$, $P < 0.001$), the latter of which did not differ significantly ($t = 1.51$, $P = 0.13$).

The morph color of competing females also affected the type of interaction (active or passive) used to settle contests between the 3 color morphs ($\chi^2 = 22.30$, $df = 176$, $P < 0.001$). Most supplants between yellow- and black-headed females were active (57.8%; Figure 2), with females often actively displacing their competitors (e.g., pecking or flying at them). In comparison, fewer active supplants were recorded in contests with red-headed birds, where losing black- (28.5%; $t = 5.82$, $P < 0.001$) or yellow-headed birds (18.3%; $t = 9.61$, $P < 0.001$) were more likely to passively move away from the feeder or perch at the approach of the red-headed female.

Dominance within female color morphs

In trials where females were staged in contests with contestants of the same color morph as themselves, body size (PC1) was the only factor to influence the win/loss outcome of dyadic contests, with larger females dominating smaller birds ($\chi^2 = 5.56$, $df = 87$, $P < 0.01$; Figure 1). Replacing the dominance outcome at food bowls with that from the dominance hierarchy produced a similar model, again identifying body size as the only significant predictor ($\chi^2 = 8.32$, $df = 29$, $P < 0.01$). No significant effect of any of the other predictor variables (see Methods) was found, including variation in the color of the head morphs. For example, although red-headed females dominated both black- and yellow-headed females, there was no effect of "redness" (e.g., red hue, chroma, or brightness) on the outcome of female contests in the models.

Interaction type (passive or active) did not differ within dyads of the same head morph; however, there were overall differences in the type of supplants between the 3 head color morphs ($\chi^2 = 9.92$, $df = 87$, $P = 0.002$; Figure 2). For exam-

ple, interactions between red-headed females tended to be more actively aggressive (88.6%) and more frequent than interactions among females of black- (69.1%; $t = 2.86$, $P = 0.004$) and yellow-headed morphs (64.6%; $t = 3.17$, $P = 0.002$), whereas black- and yellow-headed birds did not differ significantly ($t = 0.72$, $P = 0.45$; Figure 2).

Dominance between experimental color morphs

Experimentally altering the head color of female morphs significantly altered the outcome of dyadic contests ($\chi^2 = 8.13$, $df = 171$, $P < 0.001$; Figure 3). Although yellow-headed females are competitively subordinate in contests with the other 2 color morphs (see above), experimentally reddened yellow heads were more likely to dominate natural black heads ($t = 3.64$, $P < 0.001$), natural yellow heads ($t = 3.92$, $P < 0.001$), and had an equal probability of winning contests with natural red-headed females ($t = 0.16$, $P = 0.87$). This effect of experimental treatment was also evident among blackened red-headed females; despite their previous success in dominating black and yellow heads (see above), red heads given black masks were equally likely to dominate natural black heads ($t = 0.63$, $P = 0.53$) and yellow heads ($t = 0.79$, $P = 0.43$) but were outcompeted by natural red heads ($t = 2.75$, $P < 0.006$). No significant effect of natural head color, or any of the other potentially interacting effects, had any detectable influence on the outcome of dominance.

The color manipulations also affected the type of aggressive interactions (i.e., active or passive supplant) used to assert dominance ($\chi^2 = 5.1$, $df = 171$, $P < 0.05$). Most supplants in the reddened group were passive (68.9%), whereas the majority of supplants in the blackened group were active (72.6%; $t = 4.13$, $P < 0.001$). For example, compared with the blackened group (i.e., often displaying a reduced status signal), reddened yellow-headed birds (i.e., displaying an increased status signal) were challenged less and generally settled contests without escalating conflict.

DISCUSSION

These results demonstrate differences in dominance status and aggression between the 3 female head color morphs. In

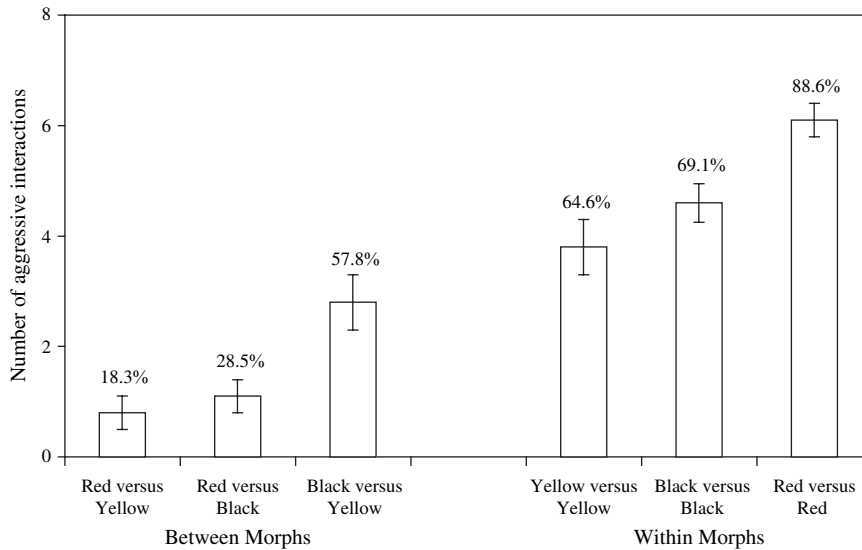


Figure 2
The average (\pm SD) number of active supplants in the dyadic contests both between and within females of the 3 head colored morphs. The percentage of active supplants (i.e., aggressive displays and/or physical displacements) in these interactions are provided above the bars. The remaining interactions involved passive supplants (i.e., feeding bird retreats when approached by an opponent).

competition for both food and top position in a dominance hierarchy, red-headed females dominated both black- and yellow-headed phenotypes. The experimental head treatments further emphasized the strength and efficiency of the red signal as an agonistic signal in conflict resolution. For example, yellow-headed females manipulated to resemble red-headed birds dominated black-headed birds, whereas blackened red-headed birds were outcompeted by naturally red-headed females (i.e., reversal of dominance status). The use of the red signal as a traditional status signal is further evident by contestants avoiding conflicts with opponents displaying red signals: black- and yellow-headed birds would rarely challenge red-headed birds. In contrast, dyads of red-headed birds initiated more aggressive interactions (i.e., active supplants), suggesting that neither individual considered herself inferior and did not show submissive or avoidance behaviors to end the conflicts. Similarly, other studies of status signaling, albeit among males, have shown that dominant birds with similar colored or sized patches are more likely to initiate conflicts (Senar 2006). Consequently, the aggressive response of individuals may be mediated through their perception of their opponent's dominance status, as signaled through the red head.

In line with these findings, red-headed Gouldian finch males are also competitively dominant, whereas black-headed birds are of intermediate status and yellow-headed males are subordinate (Pryke and Griffith 2006). Male aggression, however, appears to be intrinsically linked to the expression of red-headed coloration. By experimentally destabilizing (i.e., blackening) the dominance signal of red-headed males, naturally red-headed males continued to dominate both black- and yellow-headed males by initiating more, and sustaining longer, aggressive interactions (Pryke and Griffith 2006). Among female morphs, there was no evidence that red-headed females were intrinsically more aggressive than the other 2 color morphs. Although negative results may simply arise because of insufficient statistical power, the large sample size of competing females used in these experiments had an approximately 90% chance of detecting an aggressive response from red-headed females (i.e., a large effect size; Cohen 1992) and was also identical to the sample size used to demonstrate intrinsic differences among males. Differences in overt aggression were further evident in conflict resolution between the sexes. In settling conflicts, males would initiate physical fights (i.e., grappling with beaks and claws) more often (17% of interactions) than females (2%). Furthermore,

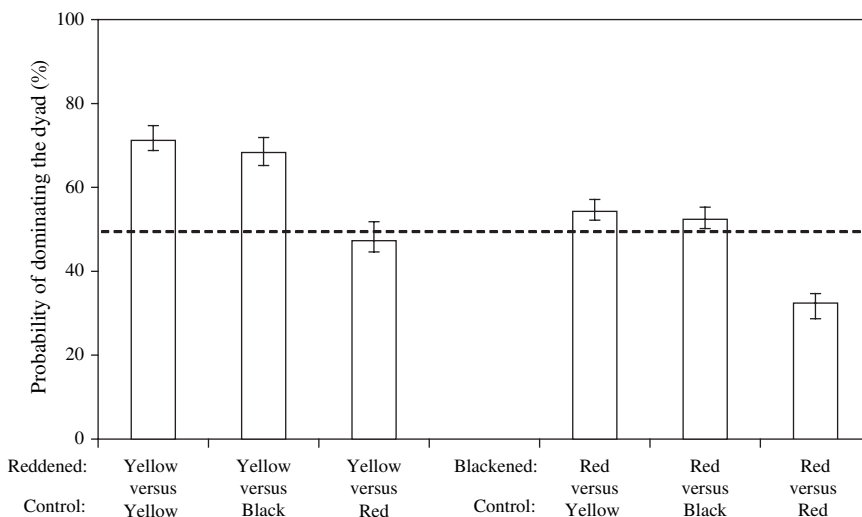


Figure 3
The probability (%) of the color-manipulated female (reddened or blackened) dominating her natural colored (control) opponent. Within the experimentally reddened, blackened, and control groups, the natural head color for the manipulated birds are provided below the bars. Probabilities are calculated from the GLM best fitting the data (see Methods and Figure 1 for details) with error bars for the 95% confidence intervals of the coefficient. The dashed line indicates where the 2 females have an equal chance (i.e., 50%) of dominating the dyad.

although the proportion of interactions won through aggressive displacement was similar between the sexes (60.2% males; 54.5% females), overall, the average number of active supplants in trials differed between males (mean \pm SD = 9.2 ± 1.5 active supplants per trial) and females (3.6 ± 0.8).

At present, the underlying cause linking dominance to the female red-headed color morph is unknown, although there are a few possibilities. Although speculative, one potential explanation is that because of the highly aggressive nature of red-headed males (Pryke and Griffith 2006), there may be some intimidation value associated with the red-headed signal. Perhaps, females simply generalize and avoid conflicts with red-headed females because they view red coloration as a general signal of aggression and competitive dominance (e.g., Hill and Barton 2005), rather than because red-headed females are aggressive per se. Another possibility is that the observed differences in competitive abilities among the morphs may be under hormonal control, especially because androgens can also be important in mediating aggression and dominance in female birds (Harding 1983; Wingfield 1994). An additional explanation, potentially influenced by hormones, is that behavioral differences in dominance may be a result of pleiotropic interactions and linkage between the genes controlling elevated levels of dominance and aggression and the expression of red headedness. Alternatively, the observed red-headed aggression may be environmentally influenced by sexual imprinting on the parental phenotypes (e.g., red-headed offspring are produced from at least one red-headed parent).

When true genetically determined color morphs are maintained within natural populations, such as the Gouldian finch, some mechanisms must exist to allow all competing forms to coexist. Although supporting empirical evidence is limited, a number of diverse mechanisms have been proposed, including individual recognition (Dale 2000; Dale et al. 2001), disruptive selection (Galeotti et al. 2003; Galeotti and Rubolini 2004), mate choice and nonrandom mating (Krüger et al. 2001; Tuttle 2003), and frequency-dependent selection (Gross 1991; Sinervo and Lively 1996). In polymorphic species exhibiting between-morph variation in dominance, alternative behavioral strategies (tactics) may be adopted by the different color morphs in an attempt to maximize their fitness (e.g., Lank et al. 1995; Gross 1996; Sinervo and Lively 1996). For example, alternative throat color morphs of male side-blotched lizards (*Uta stansburiana*) are each associated with an alternative dominance behavior (superdominant, territorial, and sneaker), and these alternative strategies (and thus associated morph fitness) are maintained through negative frequency dependence (Sinervo and Lively 1996).

How alternative dominance behaviors of the Gouldian finch contribute to the maintenance of the color polymorphism is unclear at present. The 3 color morphs coexist together at different frequencies where black-headed birds are the most common, yellow-headed birds extremely rare, and red headed are of intermediate status (Brush and Seifried 1968; Franklin and Dostine 2000). The low frequency of yellow-headed birds may partially be explained by their subordinate status (i.e., strongly dominated by red- and black-headed birds) (Pryke and Griffith 2006), together with mate discrimination against yellow-headed males and the observed patterns of assortative mating (Pryke and Griffith 2007). Although the moderately common red-headed birds are highly dominant (both males and females), competition among red-headed birds is more intense and aggressive than competition between alternative color morphs (Figure 2; Pryke and Griffith 2006), which could limit the frequency or densities of aggressive red-headed birds (e.g., Partridge 1983; Sinervo and Lively 1996). Potentially, together with assortative mating by head color (Pryke and Griffith 2007), this could explain

the higher densities of black-headed birds (of intermediate dominance status) in natural populations. Nevertheless, although dominance and the evolutionary forces underlying dominance behaviors may partially be responsible for maintaining the color polymorphism, it seems likely that additional selective pressures (e.g., genetic pleiotropy, predation, frequency-dependent selection) may also vary across the color morphs, balancing out net morph fitness and contributing to the maintenance of the 3 color morphs at their different frequencies. Further studies into alternative morph fitness and the role of female dominance in reproductive investment (e.g., mate choice, parental investment, and life history traits) are the next step to uncover the adaptive nature of alternative dominance behaviors.

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REFERENCES

- Amundsen T, Pärn H. 2006. Female coloration: review of functional and nonfunctional hypotheses. In: Hill GE, McGraw KJ, editors. *Bird coloration, volume 2: function and evolution*. Cambridge (MA): Harvard University Press. p. 280–348.
- Brush AH, Seifried H. 1968. Pigmentation and feather structure in genetic variants of the Gouldian finch, *Poephila gouldiae*. *Auk*. 85: 416–430.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer-Verlag. p. 488.
- Cohen J. 1992. A power primer. *Psychol Bull*. 112:155–159.
- Dale J. 2000. Ornamental plumage does not signal male quality in red-billed queleas. *Proc R Soc Lond B Biol Sci*. 267:2143–2149.
- Dale J, Lank DB, Reeve HK. 2001. Signaling individual identity versus quality: a model and case studies with ruffs, queleas, and house finches. *Am Nat*. 158:75–86.
- Ficken RW, Ficken MS, Hailman JP. 1978. Differential aggression in genetically different morphs of white-throated sparrow (*Zonotrichia albicollis*). *Z Tierpsychol*. 46:43–57.
- Fisher RA. 1930. *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Fowlie MK, Krüger O. 2003. The evolution of plumage polymorphism in birds of prey and owls: the apostatic selection hypothesis revisited. *J Evol Biol*. 16:577–583.
- Franklin DC, Dostine PL. 2000. A note on the frequency and genetics of head colour morphs in the Gouldian finch. *Emu*. 200:236–239.
- Fugle GN, Rothstein SI. 1985. Age-related and sex-related variation in size and crown plumage brightness in wintering white-crowned sparrows. *J Field Ornithol*. 56:356–368.
- Galeotti P, Rubolini D. 2004. The niche variation hypothesis and the evolution of colour polymorphism in birds: a comparative study of owls, nightjars and raptors. *Biol J Linn Soc*. 82:237–248.
- Galeotti P, Rubolini D, Dunn PO, Fasola M. 2003. Colour polymorphism in birds: causes and functions. *J Evol Biol*. 16:635–646.
- Gross MR. 1982. Sneakers, satellites and parents: polymorphic mating strategies in North American sunfishes. *Z Tierpsychol*. 60:1–26.
- Gross MR. 1985. Disruptive selection for alternative life histories in atlantic salmon. *Nature*. 313:47–48.
- Gross MR. 1991. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Philos Trans R Soc Lond B Biol Sci*. 332:59–66.
- Gross MR. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol Evol*. 11:92–98.
- Harding CF. 1983. Hormonal influences on avian aggressive behaviour. In: Savre BB, editor. *Hormone and aggressive behaviour*. New York: Plenum Press. p. 223–247.
- Hill GE. 1993. Male mate choice and the evolution of female plumage coloration in the house finch. *Evolution*. 47:1515–1525.

- Hill GE, McGraw KJ. 2006. Bird coloration, volume 2: function and evolution. Cambridge (MA): Harvard University Press.
- Hill RA, Barton RA. 2005. Red enhances human performance in contests. *Nature*. 435:293.
- Holberton RL, Able KP, Wingfield JC. 1989. Status signaling in Dark-eyed Juncos, *Junco hyemalis*: plumage manipulations and hormonal correlates of dominance. *Anim Behav*. 37:681–689.
- Kopachena JG, Falls JB. 1993. Aggressive performance as a behavioural correlate of plumage polymorphism in the white-throated sparrow (*Zonotrichia albicollis*). *Behaviour*. 124:249–266.
- Krüger O, Lindström K, Amos W. 2001. Maladaptive mate choice maintained by heterozygote advantage. *Evolution*. 55:1207–1214.
- Lande R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*. 34:292–305.
- Lank DB, Smith CM, Hanotte O, Burke T, Cooke F. 1995. Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. *Nature*. 378:411–415.
- Muma KE, Weatherhead PJ. 1989. Male traits expressed in females: direct or indirect selection? *Behav Ecol Sociobiol*. 25:23–31.
- Muma KE, Weatherhead PJ. 1991. Plumage variation and dominance in captive female red-winged blackbirds. *Can J Zool*. 69:49–54.
- Murray R. 1963. The genetics of the yellow-masked Gouldian finch. *Avic Mag*. 69:108–113.
- O'Donald P. 1983. The Arctic Skua: a study of the ecology and evolution of a seabird. Cambridge: Cambridge University Press.
- Partridge L. 1983. Non-random mating and offspring fitness. In: Bateson P, editor. *Mate choice*. Cambridge: Cambridge University Press. p. 227–255.
- Pryke SR, Andersson S, Lawes MJ, Piper SE. 2002. Carotenoid status signaling in captive and wild red-collared widowbirds: independent effects of badge size and color. *Behav Ecol*. 13:622–631.
- Pryke SR, Griffith SC. 2006. Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proc R Soc Lond B Biol Sci*. 273:949–957.
- Pryke SR, Griffith SC. Forthcoming 2007. The relative role of male versus female mate choice in maintaining assortative pairing among discrete colour morphs. *J Evol Biol*.
- Roulin A. 1999. Nonrandom pairing by male barn owls *Tyto alba* with respect to a female plumage trait. *Behav Ecol*. 10:688–689.
- Roulin A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biol Rev*. 79: 815–848.
- Senar JC. 2006. Chapter 3: bird coloration as an intrasexual signals of aggression and dominance. In: Hill GE, McGraw KJ, editors. *Bird coloration, volume 2: function and evolution*. Cambridge (MA): Harvard University Press. p. 87–136.
- Sinervo B, Lively CM. 1996. The rock-paper-scissors game and the evolution of alternative male reproductive strategies. *Nature*. 380: 240–243.
- Southern HN. 1945. Polymorphism in *Poephila gouldiae*. *J Genet*. 47: 51–157.
- Swaddle JP, Witter MS. 1995. Chest plumage, dominance and fluctuating asymmetry in female starlings. *Proc R Soc Lond B Biol Sci*. 260:219–223.
- Tuttle EM. 2003. Alternative reproductive strategies in the white-throated sparrow: behavioral and genetic evidence. *Behav Ecol*. 14:425–432.
- Watt DJ, Ralph CJ, Atkinson CT. 1984. The role of plumage polymorphism in dominance relationships of the white-throated sparrow. *Auk*. 101:110–120.
- Wingfield JC. 1994. Hormone-behaviour interactions and mating systems in male and female birds. In: Short RV, Balaba E, editors. *The difference between the sexes*. New York: Cambridge University Press. p. 303–330.
- Zuk M, Kim T, Robinson SI, Johnsen TS. 1998. Parasites influence social rank and morphology, but not mate choice, in female Red Junglefowl, *Gallus gallus*. *Anim Behav*. 56:493–499.