Socially Mediated Trade-Offs between Aggression and Parental Effort in Competing Color Morphs

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ABSTRACT: Individuals often face trade-offs between investment in parental care and alternative investments of time, energy, and resources into other life-history components, such as dominance, attractiveness, and health. Selection is thought to promote the optimal balance between the costs and the benefits of these conflicting activities by favoring individuals that adopt different tactics to maximize their overall evolutionary fitness in different environments. To test this, we experimentally manipulate both aggression (i.e., competitive environment) and parental effort (i.e., brood size) in red and black morphs of the Gouldian finch (*Erythrura gouldiae*). Although aggressive red males provide parental effort comparable to that of black males in environments where competition is low, irrespective of their relative brood size, they severely reduce or abandon parental investment in highly competitive environments. In contrast, nonaggressive black males are largely unaffected by the competitive environment and instead adaptively adjust their provisioning effort to the relative demands of their brood. Consequently, in highly competitive environments, although dominant red males defend higher-quality nest sites, they produce fewer and lower-quality offspring (in terms of mass and immunocompetence) than black males do. These opposing effects of frequency-dependent competitive environments on red and black males underlie their differential trade-offs between the costs and the benefits of aggression and parental effort.

Keywords: dominance, Gouldian finch, life-history trade-offs, parental care, polymorphism.

Introduction

Animals typically face trade-offs between the demands of conflicting activities. When a trade-off is present, multiple beneficial traits cannot be maximized simultaneously, at least in the short term, and theory predicts that selection will favor the optimal combination of traits within the constraints imposed by the trade-off (Stearns 1991; Roff 2002; Roff and Fairburn 2007). As a direct result of trade-offs between conflicting activities, some species have evolved multiple life-history strategies, whereby different individuals adopt different tactics in an attempt to maximize their fitness (e.g., Gross 1996; Lank 2002). Individual solutions to life-history trade-offs can be highly variable and often depend on the individual condition and the tactics used by others in the population (i.e., conditional and mixed strategies; Gross 1996). In a few species, however, alternative reproductive strategies underlying life-history trade-offs are discrete and genetically fixed. For such polymorphisms to be evolutionarily stable, a mechanism must exist for the alternative forms to gain equal fitness benefits over evolutionary time (Maynard Smith 1982). In a wide range of taxa, alternative strategies are often maintained through density- and frequency-dependent selection, where an individual's fitness is largely dependent on the local social environment it experiences. Examples include mammals (Mappes et al. 2008), lizards (Sinervo and Lively 1996; Sinervo et al. 2000; Svensson et al. 2001; Vercken et al. 2007), fish (Ryan et al. 1992), and insects (Borash et al. 1998; Svensson et al. 2005; Van Gossum et al. 2005).

One of the most common alternative strategies involves dominance-related activities, where highly aggressive and nonaggressive morphs trade off investment in aggression with other behavioral and life-history traits, such as mate defense (Sinervo and Lively 1996) and sneaking behaviors (Martin and Taborsky 1997; Emlen 2000). In species with biparental care, such as birds and fish, variation in the provision of parental care provides an additional but important component of fitness, especially in socially monogamous species (Clutton-Brock 1991). Trade-offs with parental effort may be particularly important because investment into aggression and parental care often overlaps in time (Sargent and Gross 1985; Wingfield et al. 1987; Ketterson and Nolan 1992). Furthermore, these may be directly mediated, at least in part, by physiological mechanisms, such as elevated levels of the steroid hormone testosterone in birds, which may simultaneously promote aggressive behaviors while suppressing parental activities (e.g., Wingfield et al. 1987; Ketterson et al. 1992; Adkins-Regan 2005). Most studies reporting life-history trade-offs between the relative investment into aggression and pa-

rental effort have reported correlations between an individual's aggressive response and its provisioning effort (Badyaev and Hill 2002; Tuttle 2003; McGlothlin et al. 2007). The few studies that have experimentally investigated such trade-offs have done so by manipulating only a single aspect, such as the level of testosterone or the expression of dominance-related traits (e.g., Ketterson et al. 1992; Qvarnström et al. 2000; Stoehr and Hill 2000). Although these studies have successfully demonstrated an adaptive adjustment between these competing life-history components, to fully understand the evolution of optimal strategies in reproductive trade-offs, we must also consider the simultaneous investment costs and benefits of both behaviors.

Here we experimentally manipulate both the competitive environment and the parental effort in red and black head-color morphs of the Gouldian finch (*Erythrura gouldiae*), a socially monogamous passerine restricted to small, isolated populations in northern tropical Australia. Head color in this species is genetically determined (Southern 1945), and both sexes can be separated into red and black morphs on the basis of the color of the facial mask. The Gouldian finch is unusual in that both red and black morphs appear to coexist at relatively stable frequencies, both temporally and spatially, throughout their geographic range (Franklin and Dostine 2000): black birds (~70% males, ~80% females) outnumber red birds (~30% males, ~20% females). In both captive and wild populations, females and males prefer to mate assortatively by head color (Pryke and Griffith 2007), presumably because postzygotic genetic incompatibilities between the morphs lead to high offspring mortality in mixed-morph pairs (Pryke and Griffith 2009*b*).

Head color is also correlated with different behavioral and physiological traits (Pryke and Griffith 2006; Pryke et al. 2007). Red males are highly sensitive to changes in the competitive environment, especially toward the relative frequency of their own aggressive morph, exhibiting highly elevated testosterone and corticosterone levels in socially competitive environments (Pryke et al. 2007). This higher aggression of red males is advantageous during dominance interactions, where red males aggressively dominate black males (Pryke and Griffith 2006), and thus may be particularly advantageous in wild populations because of the intense intra- and interspecific competition for limited nest cavities (J. Brazil-Boast, S. R. Pryke, and S. C. Griffith, unpublished manuscript). In contrast, in highly competitive environments (i.e., where there are high frequencies of red birds), the nonaggressive black males reduce their levels of circulating testosterone and thus follow a more passive strategy that buffers them against social stresses (Pryke et al. 2007) but may also prevent them from acquiring limited or high-quality resources.

By simultaneously manipulating the relative frequency of aggressive red birds (i.e., manipulating aggression) and experimentally altering brood size to the lower and upper population limits (i.e., manipulating parental effort), we tested the optimal investment strategies between aggression and parental effort in both red and black morphs. Furthermore, we assessed how the relative trade-off and investment strategy adopted by individuals under a range of different social environments affected offspring survival and health.

Methods

Experiments were run during March–September in 2006 and 2007 at the Save the Gouldian Fund Research Facility in Martinsville, Australia. Wild-type Gouldian finches used in these experiments were naive (virgin) birds of the same age (all in their first year of adult plumage) from our large captive-bred colony (Pryke and Griffith 2009*b*). All birds were banded with a unique combination of color bands and were measured with standard methods before the experiments (see Pryke and Griffith 2006; Pryke et al. 2007). Body size was estimated using the first principal component (PC1) of a principal components analysis, which explained 74.1% and 78.3% of the variation in wing, tail, tarsus, and bill length for females and males, respectively.

Gouldian finches are obligate cavity nesters and are unable to build their own freestanding nests. For these breeding experiments, birds were given artificial nest boxes, which were constructed to mimic the deep and narrow tree hollows used by birds in the wild. The rectangular nesting chamber was built of plywood (20 cm high × 10 cm wide), to which a long (14 cm) and narrow (6 cm) entrance tunnel (i.e., PVC pipe lined with sand) was affixed. Fine grass used for lining the nest was regularly supplied. Throughout the duration of the experiments, each nest was checked daily and progress recorded.

Manipulating and Measuring Aggression

To manipulate the competitive environment, 20 unfamiliar birds (i.e., 10 males and 10 females) were introduced into a large, unfamiliar aviary (15 m long × 5.5 m wide × 3.8 m high) and were allowed to breed. Two replicates of five different social environments were created by altering the relative frequency of red and black birds in each of the five populations (red/black: 0/20, 6/14, 10/10, 14/6, and 0/20). Although the density of birds in each population was similar to that observed in wild populations (i.e., birds typically breed in adjacent trees), the extreme range in morph frequencies was specifically chosen to manipulate the level of aggression—that is, from low-aggression (100% black) to high-aggression (100% red) populations. Equal numbers of

head colors from each sex were used, and, in line with previous results (Pryke and Griffith 2007), most birds paired assortatively with respect to head color (81.2%). Since genetic incompatibilities between color morphs result in high offspring mortality (Pryke and Griffith 2009b) and females adaptively adjust their relative investment accordingly (Pryke and Griffith 2009a), we included only assortative breeding pairs ($n = 42$ red, $n = 38$ black) to maintain a standardized context. To further compare the relative effects of the social environment on parental behaviors and offspring condition, we also assortatively paired 40 males and 40 females (20 red pairs and 20 black pairs) in single, visually isolated cages (2.1 m^3) and allowed them to breed in the absence of social interactions.

In each environment, dominance was inferred from three different competitive contests. First, birds were encouraged to compete for access to high-quality nest boxes. Gouldian finches characteristically attack from above and will not aggressively displace their opponents from a vertically lower (subordinate) position. As a consequence, dominant males occupy and defend the highest perch or nest box (Evans and Fidler 2005; Pryke and Griffith 2006). For this experiment, 12 nest boxes were equally spaced (1 m apart) along an ascending gradient, from lowest (0.5 m from the ground) to highest (3.5 m), in each aviary. Nest boxes were checked daily, and the time to occupation (i.e., nest building) and the relative position of the nest box were recorded.

Second, to quantify aggression at the nest, birds were presented with red and black taxidermic mounts (made from skins of adult Gouldian finches) during the intense chick-feeding period (nestling ages 10 and 14 days old). Between 0600 and 0900 hours, a model was placed 20 cm from the nest while both parents were away from the nest. Within 2 min of the parents' return to the nest, we counted the number of times the male and female attacked the model, flew by it, or hovered near it. On the basis of these aggressive behaviors, males and females were assigned an aggression score (1–6; from lowest to highest) similar to those used in other studies of nest defense (e.g., Hakkarainen et al. 1998; Duckworth 2006): (1) no aggressive reaction, (2) minimal response (one to three flybys and/or hovering) and no overt aggressive behavior (zero attacks), (3) moderate response (more than three flybys and/or hovering) and no overt aggressive behavior (zero attacks), (4) moderate aggressive behavior (one to three physical attacks), (5) highly aggressive behavior (three to six attacks), and (6) extremely highly aggressive behavior (more than six attacks). Males and females did not always return to the nest together (57.4%); in these cases, the model was left until both parents had seen it. All males were exposed to the models, but six females did not return during the model presentations (and were excluded from

the analyses). Red and black models were both presented to each nest (separated by 4 days) but in random order; the order of model presentation did not affect male ($F_{1,75} = 1.89$, $P = .17$) or female ($F_{1,69} = 0.24$, $P = .62$) aggressive behavior.

Finally, the relative time that birds spent in dominance and aggressive interactions was quantified daily at the central food station (Pryke and Griffith 2006; Pryke et al. 2007). Between 0530 and 1030 hours, all interactions between color-banded birds were recorded with a video camera during their intense provisioning period (nestling ages 10–14 days; see below). Interactions at the feeder varied from active (e.g., threat displays, displacements, and physical attacks) to passive supplants in which a bird simply fled when approached by an opponent (i.e., nonthreatening approach). The number of interactions and the relative time spent in aggressive interactions for individuals were highly correlated for both males ($r = 0.94$, $n = 76$, $P < .001$) and females ($r = 0.85$, $n = 72$, $P < .001$); thus, only the time spent in aggressive interactions was included in the subsequent analyses.

Manipulating and Measuring Parental Care

Of the 84 assortative breeding attempts in social environments, 76 resulted in successfully hatched broods (seven red and one black nest failed). One to two days after the chicks hatched (mean ± SE = 1.2 ± 0.4 days), we created broods of reduced size (fewer than two nestlings, compared to the original clutch size) and enlarged size (more than two nestlings, compared to the original clutch size) by partially exchanging randomly chosen nestlings between nests of the same hatching date and a similar clutch size (irrespective of morph or social environment). After the manipulation, both enlarged ($n = 38$; $n = 22$ red, $n = 16$ black) and reduced ($n = 38$; $n = 20$ red, $n = 18$ black) nests contained the parents' own and foster nestlings, and the manipulated brood sizes remained within the range of natural variation observed in this species (two to nine nestlings per brood). This manipulation allowed us to assess the investment of the parents in response to an elevated or reduced food demand of the brood and the interaction between the competitive environment and the parental effort. To further quantify parental effort in the absence of social interactions, the brood sizes of 20 red pairs and 20 black pairs of birds breeding in complete isolation were also enlarged ($n = 8$ red, $n = 12$ black) or reduced ($n = 12$ red, $n = 8$ black). For brood size manipulations, the original clutch size did not differ significantly between morphs ($F_{1,115} = 0.81$, $P = .34$) or social environments ($F_{5,109} = 2.66$, $P = .11$; morph × social environment: $F_{5,109} = 1.91$, $P = .17$). After the manipulation, the brood size was significantly larger in enlarged

than in reduced broods ($F_{1,115} = 129.3$, $P < .001$), but it did not differ significantly between the morphs ($F_{1,115} = 0.22$, $P = .63$) or social environments ($F_{5,109} = 0.15$, $P = .69$; morph × social environment: $F_{5,109} = 0.41$, $P = .52$).

Parental provisioning rates were quantified using a remote monitoring system that recorded all visits to the nest (Magrath and Elgar 1997). Individual birds within the different populations were identified by uniquely coded passive integrated transponder tags (Trovan, Aalten, the Netherlands), which were glued to their color bands. These transponders are small (11 mm × 2 mm) passive devices that emit a unique identification code when in close proximity to powered antennae. Antennae (i.e., powered wire coils) with a 4-cm detection range were placed centrally (i.e., 7 cm from the nest entrance) around the outside of the entrance tunnel to the nest. Two pairs of infrared sensors positioned 4 cm apart (less than the length of a bird) on either side of the antennae were used to detect the direction of the bird's movement (i.e., into or out of the nest). The antennae were activated (at 1-s intervals) when either of the two infrared beams was interrupted. For the analyses, parental visits were quantified only when both beams were interrupted, to exclude any incomplete movements or visits by birds (e.g., a bird moves from inside the nest toward the entrance and then back to the nest). In addition, only nest visits that resulted in feeding (>10 s; 98.7% of all recordings) were included in the analyses. For each nest, the visitation rate was averaged across a 72-h period starting at 0530 hours on day 10 (nestling ages 10–14 days), which coincides with the period when nestling food demand is the highest.

Offspring Survival and Condition

Nestling mass, tarsus length, and immune function were measured at the end of the recorded provisioning period (nestling age 14 days). As an index of nutritional condition (Bańbura et al. 2007), the whole-blood hemoglobin concentration (g/dL) of a 20-µL blood sample was measured with a HemoCue photometer (HemoCue AB, Ängelholm, Sweden). T-cell-mediated immune responsiveness was evaluated using delayed-type hypersensitivity (DTH) tests. Each bird's right and left wing webs were injected with either phytohemagglutinin solution (PHA-P, Sigma) or sterile phosphate buffered saline (PBS), respectively, and the consequent swellings were measured with pressure-sensitive digital calipers (0.01 mm) 24 h later. The DTH index was calculated as the difference in swellings between the left wing web (control: PBS only) and the right wing web (0.2 mg PHA-P dissolved in 0.04 mL PBS); within-individual measures were highly repeatable ($r = 0.99$, $F_{119,360} = 203.4$, $P < .001$). Overall offspring survival was

calculated as the relative proportion of hatched nestlings that successfully fledged the nest (chicks ages 20–23 days).

Statistical Analyses

Data were analyzed in Genstat 9 (Rothamsted Experimental Station, Harpendon, United Kingdom) with generalized linear models with Poisson distributions and logarithmic link functions or with generalized linear mixed models with binomial error structures and logit link functions. Mixed models allow both fixed and random components to be fitted to a model: random components in this case take into consideration repeated measures of offspring (siblings) from within the same nest. The significance of explanatory terms in mixed models was assessed by their Wald statistics, which are distributed as χ^2. In all models of offspring condition and survival, nest identity and year were included and retained as random repeated subjects but did not constitute significant random components ($P > .15$). For all models, all possible effects, combinations, and interactions (two- and three-way interactions) were initially modeled. Second-order Akaike Information Criterion (AIC_C) weights were calculated for each model. The AIC_C (used for smaller sample sizes) balances the fit of the model against the number of parameters used and was used to effectively compare different models (i.e., it indicates the probability that a model is the best among the tested models). Since all models tested had an AIC_C weight of at least 85.3% compared with other potential models, for simplicity, only the final models (and significant interactions) are reported.

Results

Aggression and the Competitive Environment

Red and black birds differed significantly in several dominance traits. First, red birds defended higher-quality nest boxes; more red pairs occupied the highest nest boxes than would be expected if occupation were random with respect to nest height ($\chi^2 = 32.5$, df = 11, $P < .001$). In addition, red birds occupied nests (i.e., initiated nest building) significantly faster than black birds did ($F_{1,75} = 8.43$, $P < .001$), although there were no overall differences in clutch initiation dates between morphs ($F_{1,75} = 0.67$, $P = .49$) or social environments ($F_{4,72} = 1.11$, $P = .22$).

Second, compared with black males, red males were highly aggressive toward model presentations ($F_{1,75} = 14.32$, $P < .001$), especially toward their own morph type (morph × model morph: $F_{2,74} = 6.56$, $P < .01$; model morph: $F_{1,75} = 1.24$, $P = .27$). This effect was particularly evident in highly aggressive (red) environments (model morph × environment: $F_{4,72} = 7.93$, $P < .001$; environ-

ment: $F_{1,75} = 1.68$, $P = .19$). Similarly, although females displayed significantly lower aggression than males did (paired *t*-test: $t_{69} = 4.12$, $P = .002$), red females were more aggressive to models than black females were ($F_{1,68} = 14.32$, $P < .001$), but this aggression was independent of the social environment ($F_{1,68} = 0.14$, $P = .71$) and the color morph of the model ($F_{1,68} = 1.16$, $P = .28$).

Finally, although there were no differences between red and black females in the time spent in aggressive interactions ($F_{1,68} = 0.24$, $P = .63$), red males spent more time in aggressive interactions than black males did (table 1). In particular, the relative density of red birds had significant but opposite effects on aggression of the morphs (fig. 1). That is, as the relative density of red males increased, aggressive interactions of red males increased significantly ($t = 0.82$, $P < .001$), whereas black males tended to spend less time in aggressive interactions. Overall, there was no effect of brood size manipulations on aggressive interactions for either red or black males (fig. 1), although there was a marginally significant effect for black males with enlarged broods to reduce aggressive interactions in more competitive environments (table 1).

Parental Effort

Females rearing an experimentally enlarged brood significantly increased their provisioning rates compared with females rearing a reduced brood ($F_{1,115} = 24.72$, $P < .001$). However, parental effort was not influenced by the original clutch size ($F_{1,115} = 0.68$, $P = .41$), their partner's visitation rate ($F_{1,115} = 1.33$, $P = .19$), their social environment ($F_{4,110} = 0.19$, $P = .66$), or the female's color morph ($F_{1,115} = 1.38$, $P = .24$).

In contrast, red and black males differed in their paternal effort (fig. 2). Red but not black males showed a progressive decrease in visitation rates with increasingly competitive environments (table 2). Although parental care did not differ between the two morphs in isolation (fig. 2), visitation rates of red males significantly decreased with increasing densities of red males ($t = 6.02$, $P <$

Table 1: Time spent in aggressive interactions by red and black males in different competitive environments and with experimentally manipulated brood sizes

|	*F*	df	*P*
Morph	30.96	1, 75	<.001
Environment	31.24	1, 75	<.001
Brood manipulation	.33	1, 75	.56
Morph × environment	13.36	4, 72	<.001
Morph × brood manipulation	.81	3, 73	.36
Morph × environment × brood manipulation	2.74	4, 72	.035

Note: Model derived from generalized linear model.
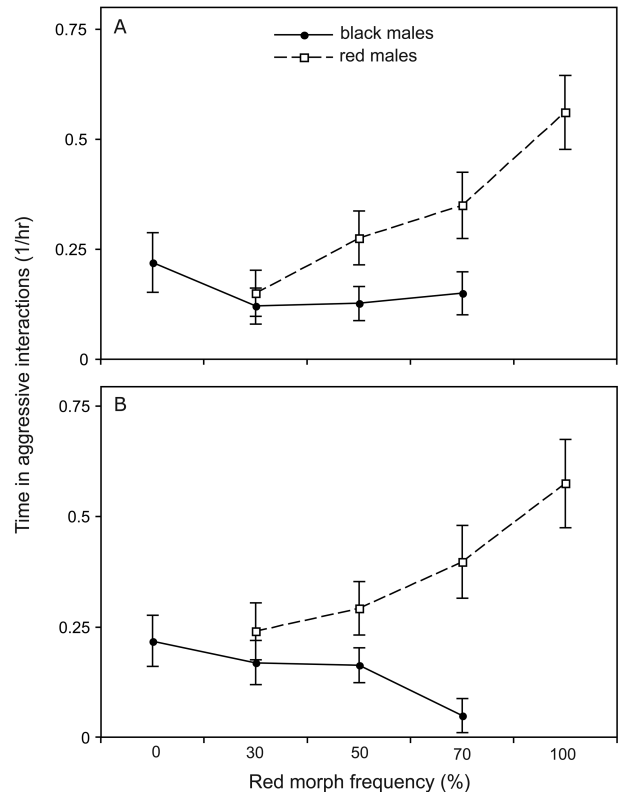
Figure 1: Proportion of time spent in aggressive interactions (h^{-1}) by red and black males in different socially competitive environments (i.e., relative red morph frequency) and with experimentally reduced (*A*) or enlarged (*B*) brood sizes. All values are presented as predicted means ($\pm$ SE) from the best-fitting generalized linear model.

.001), whereas visitation rates of black males were unaffected by the social environment ($t = 1.61$, $P = .11$). In five nests (all in the 100% red morph population), red males did not provision their nests (i.e., >10-s visits) at all during our 72-h recorded provisioning times (days 10–14).

Additionally, red and black males also differed in their responses to the brood size manipulations (table 3). While red males did not alter visitation rates between enlarged and reduced broods ($t = 1.22$, $P = .23$), black males with enlarged broods significantly increased their visitation rates compared with black males with reduced broods ($t = 9.72$, $P < .001$). These effects were independent of their original clutch size ($F_{1,115} = 0.87$, $P = .39$) or partner's visitation rate ($F_{1,115} = 0.66$, $P = .65$). Overall, parental effort differed significantly between red and black males, with black males investing more into larger broods (irrespective of their social environment), whereas red males' paternal effort was largely related to the relative social environment, irrespective of brood size (fig. 2).
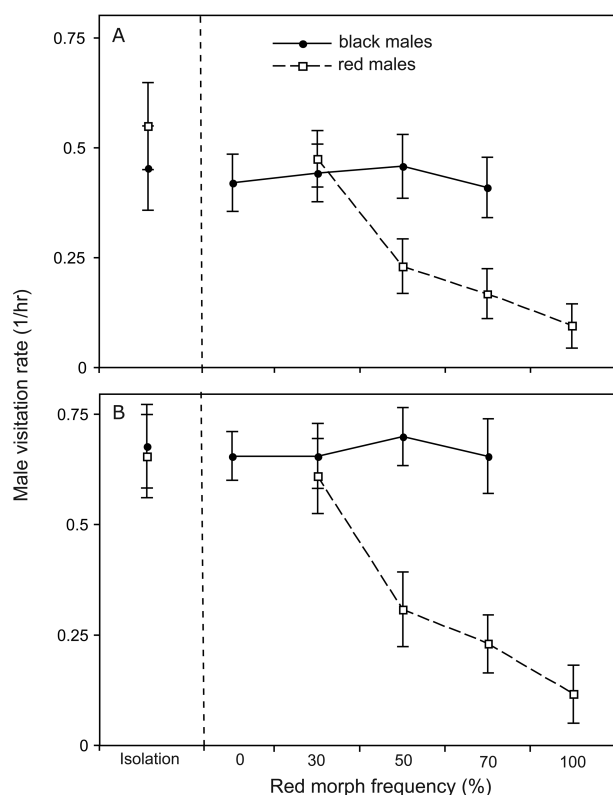
Figure 2: Proportion of time spent provisioning offspring (h^{-1}) by red and black males in varying competitive environments and with experimentally reduced (*A*) or enlarged (*B*) brood sizes. Single pairs of red and black birds also bred without social interactions in complete visual isolation ("Isolation"). All values are presented as predicted means ($\pm$ SE) from the best-fitting generalized linear model.

Brood Survival and Condition

In total, 273 (67.3%) nestlings from 76 nests successfully fledged in the five different social environments, and 202 (98.9%) nestlings fledged from 40 nests where the birds were breeding in isolation. In contrast to the similar rates of offspring survival between red and black birds breeding in isolation (fig. 3), red birds in highly competitive environments produced significantly fewer surviving offspring than black birds did (table 3).

Furthermore, while the immune responsiveness of offspring did not differ between red and black nests in isolation (fig. 4), with increasing competition red nests exhibited reduced cell-mediated responses (table 3), lower whole-blood hemoglobin concentrations (morph × environment: $\chi^2 = 19.9$, df $= 4$, $P < .001$; morph: $\chi^2 = 6.54$, df $= 1$, $P = .02$; environment: $\chi^2 = 15.21$, df $= 4$, $P < .001$), and lower body weight (morph × environment: $\chi^2 = 16.52$, df $= 4$, $P < .001$; morph: $\chi^2 = 5.18$,

df $= 1$, $P = .03$; environment: $\chi^2 = 7.21$, df $= 4$, $P = .02$) among nestlings. These effects were irrespective of the offspring's origin (foster or genetic offspring: $\chi^2 = 0.12–0.64$, df $= 1$, $P = .82–.55$) or its morph type (red or black: $\chi^2 = 0.32–0.87$, df $= 1$, $P = .71–.47$).

For the birds breeding in isolation, there were no effects of brood size manipulation on relative offspring survival for either red or black morphs (fig. 3). Similarly, there were no overall effects of brood manipulation on offspring survival and health (table 3). However, in highly competitive environments, offspring from enlarged broods and reared by red parents were less likely to survive (fig. 3), were lighter (morph × manipulation × environment: $\chi^2 = 5.39$, df $= 4$, $P = .07$), and also suffered reduced immune responses (morph × manipulation × environment: $\chi^2 = 8.73$, df $= 1$, $P = .004$). In contrast, there were no differences in offspring reared in enlarged or reduced broods by black parents (figs. 3, 4).

Discussion

Parental effort by red and black males differed in response to the social environment. While there were no differences in parental provisioning rates between the morphs when they were socially isolated, in competitive environments red males responded more aggressively to simulated intruders and spent more time in aggressive interactions, irrespective of their parental demands (i.e., brood size). In contrast, black males substantially increased their provisioning rates to meet the demands of increased brood size and were largely unaffected by the competitive environment. This divergent aggressive response reinforces the contrasting behavioral dominance strategies employed by the aggressive red and nonaggressive black males (Pryke et al. 2007) and suggests that red and black males trade off their investments in aggression and parental effort differently.

Although red males gain better access to higher-quality nest sites, their increased aggression also results in large fitness costs. In highly competitive environments, red males provide little (to no) parental care to their broods. Interestingly, although one parent is expected to partially

Table 2: Parental effort by red and black males in different competitive environments and with experimentally manipulated brood sizes

	F	df	*P*
Morph	7.88	1, 115	<.001
Environment	11.16	1, 115	<.001
Brood manipulation	34.4	1, 115	<.001
Morph × environment	30.96	4, 112	<.001
Morph × brood manipulation	19.85	4, 111	<.001

Note: Model derived from generalized linear model.

Table 3: Offspring survival and immunocompetence (delayed-type hypersensitivity index) from red and black nests reared in different competitive environments and with experimentally manipulated brood sizes

|	χ^2	df	P
Offspring survival:			
Morph	1.17	1	.24
Environment	21.17	4	<.001
Brood manipulation	.55	1	.59
Morph × environment	25.93	4	<.001
Morph × brood manipulation	.23	2	.63
Morph × environment × brood manipulation	12.43	4	.001
Offspring immunocompetence:			
Morph	8.60	1	.004
Environment	9.45	4	.002
Brood manipulation	.46	1	.64
Morph × environment	12.7	4	<.001
Morph × brood manipulation	1.04	2	.59
Morph × environment × brood manipulation	8.69	4	.004

Note: Models derived from generalized linear mixed models.

or fully compensate for the decreased provisioning by the other parent (e.g., Hegner and Wingfield 1987; Ketterson and Nolan 1992), red females did not adjust their provisioning relative to their partner's investment, even though they adaptively increased their provisioning rates according to their brood size (i.e., enlarged vs. reduced broods). Consequently, offspring reared by red parents in competitive environments, especially those reared in enlarged broods, were considerably lighter (up to 29.3%) and had reduced immunocompetence (cell-mediated immune response) compared with red broods in low-competition environments (or with black broods). Cell-mediated immune responses in nestlings have been found to predict survival probability in a number of bird species (e.g., Saino et al. 1997; Tella et al. 2000; Christe et al. 2001), presumably because they are reflective of poorer-quality offspring. Consistent with this, we found that red nests in highly competitive environments (i.e., all red morphs) successfully fledged only 48.8% (reduced broods) or 21.2% (enlarged broods) of their offspring. This contrasts with the reproductive success of black parents; irrespective of the competitive environment or brood size manipulation, black parents produced large and healthy offspring, the majority of which successfully fledged (91.2% reduced brood, 90.5% enlarged brood). Therefore, although red males have a dominance advantage over black males, at high red frequencies they compromise their reproductive fitness by heavily investing in aggression, to the detriment of parental provisioning and the quality of their offspring.
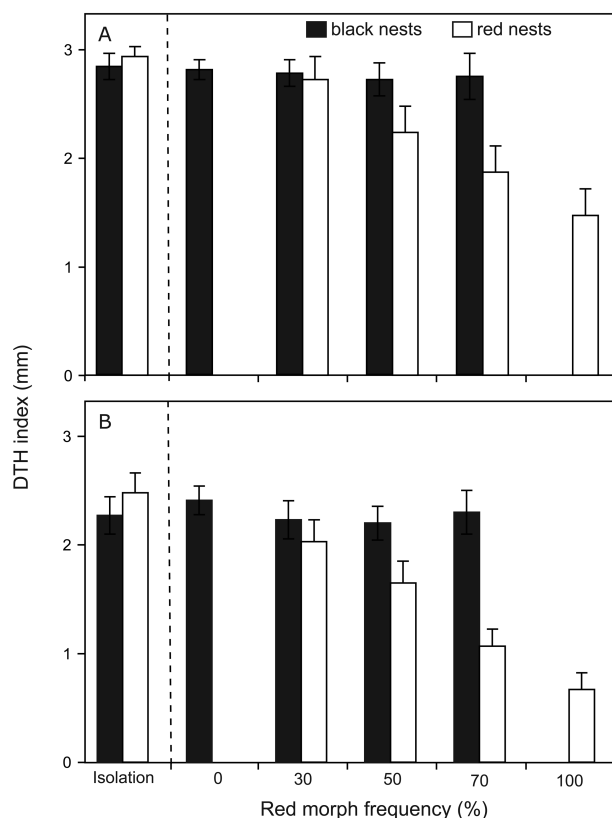
Furthermore, nonaggressive black males are also likely to suffer reproductive costs in red-dominated populations.

Although our experiment provided sufficient nest sites for all breeding pairs, in wild populations competition is intense, and up to 12 pairs will commonly compete for access to a single nest cavity (J. Brazil-Boast, S. R. Pryke, and S. C. Griffith, unpublished manuscript). Therefore, at high red frequencies, black males are unlikely to successfully acquire limited or high-quality nest sites (i.e., deep cavities with smaller entrance holes) and may be excluded from breeding altogether or may suffer high predation rates from nesting in poor-quality cavities.

Alternative strategies should be adaptive only if the benefits outweigh the costs (Maynard Smith 1982). Previous studies have shown that color morphs differ in behavior and life-history traits in a variety of taxa and that frequency- or context-dependent selection typically allows these multiple genetic forms to persist (e.g., Gross 1996; Sinervo and Lively 1996; Svensson et al. 2005; Mappes et al. 2008). Our results suggest that the alternative reproductive strategies adopted by red and black males are maintained by negative frequency-dependent selection in
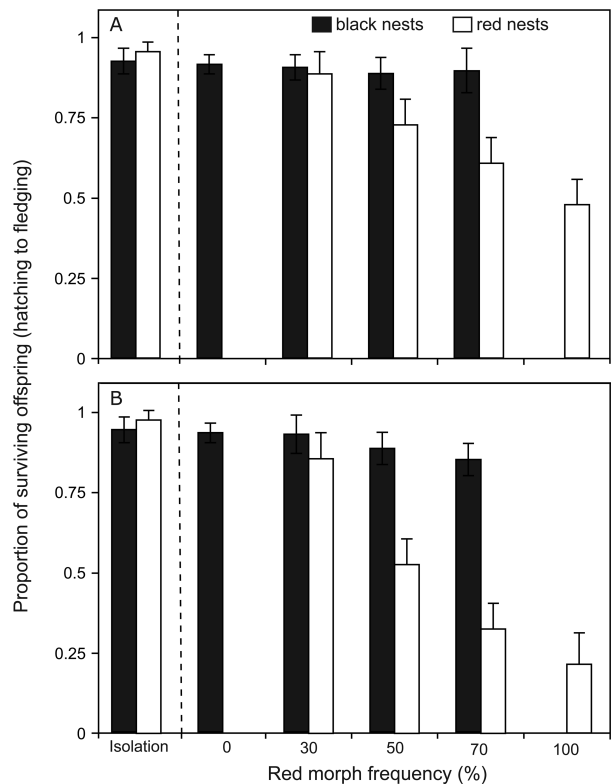
Figure 3: Proportion of offspring surviving (from hatching to fledging) from red and black nests reared in different competitive environments and in experimentally reduced (*A*) and enlarged (*B*) broods. Single pairs of red and black birds also bred in complete visual isolation ("Isolation"). All values are presented as predicted means (+SE) from the best-fitting generalized linear mixed model.

Figure 4: Cell-mediated immune responses (delayed-type hypersensitivity [DTH] index) of offspring from red and black nests reared in different competitive environments and in experimentally reduced (*A*) and enlarged (*B*) broods. Single pairs of red and black birds also bred in complete visual isolation ("Isolation"). All values are presented as predicted means (+SE) from the best-fitting generalized linear mixed model.

history traits—such as extrapair fertilizations, adult survival, and offspring viability—will also affect the optimal trade-off and, thus, the adaptive strategy adopted by red and black males.

The alternative behavioral strategies utilized by females, if any, are less clear. In line with previous findings (Pryke 2007), red females were more aggressive than black females. However, in contrast to males, red females did not adjust their relative parental effort to the competitive environment. Furthermore, since red females do not compensate for the reduced provisioning efforts of red males in competitive environments, red females also suffer reduced fitness when paired with red males in environments with high red frequency. Although it is seemingly costly for red females to breed with red males in highly competitive environments, the large fitness costs to red females of pairing with black males (Pryke and Griffith 2009*b*) or deserting the nest (and forgoing breeding) may be greater. In addition, red males are more likely to acquire access to limited nest cavities and/or higher-quality sites, thus providing opportunities to breed.

In conclusion, our results suggest that alternative reproductive strategies adopted by red and black males are maintained by genetic differences in sensitivities to the social environment. In particular, red males exhibit high behavioral plasticity in reproductive behaviors, providing substantial parental care in environments where competition is low (similar to the investment of black males) but investing heavily in aggression in highly competitive environments. Although more work is needed to gain a full understanding of the adaptive value of variation in parental effort and aggression between the morphs (and the interaction of other life-history traits), this study indicates the importance of genetic and environmental factors in shaping trade-offs between individuals.

the local social environment. Red males suffered large fitness costs in red-dominated populations but had the highest success in experimental populations with low red frequencies, similar to those observed in the wild (30% red, 70% black). Nevertheless, although red males in low-competition environments provide comparable parental effort to that of black males and successfully fledge healthy offspring (85.3% reduced brood, 89.8% enlarged brood), there were no apparent fitness advantages to red over black males in any experimental context. Since we did not test red frequencies below the natural variation (i.e., <30%), it is unknown whether red males have greater fitness advantages at lower frequencies. However, even at natural frequencies, red males are likely to have an additional dominance advantage over black males because, although they achieve similar reproductive success, they are more likely to exclude black males from nest sites. Furthermore, it is likely that differences in other behaviors and life-

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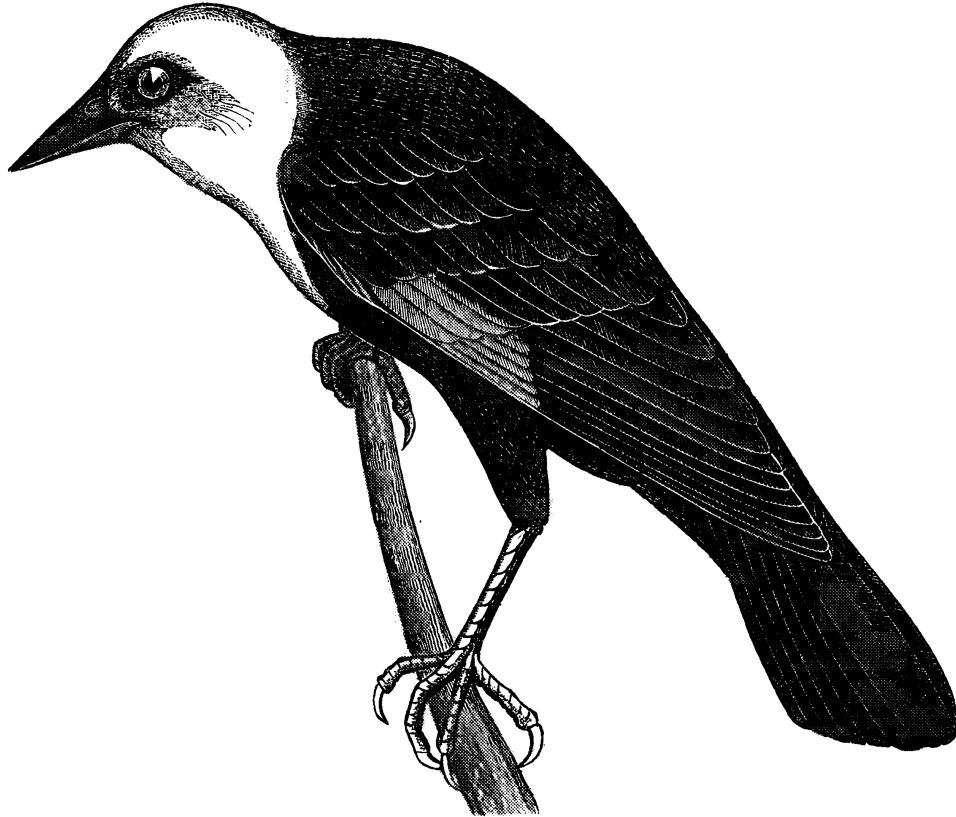
Yellow-headed blackbird *Xanthocephalus icterocephalus*, from "The Yellow-Headed Blackbird" by Dr. Elliott Coues (*American Naturalist*, 1871, 5: 195–200).