

Morph-dependent resource acquisition and fitness in a polymorphic bird

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Abstract Understanding genetic colour polymorphism has proved a major challenge, both in terms of the underlying genetic mechanisms and the evolutionarily forces maintaining such genetic variation. In this context, genetic differences in aggression or competitive-related traits may covary with the expression of alternative phenotypes, and affect the evolutionary stability and maintenance of colour polymorphisms. Genetic red and black head-colour morphs of the Gouldian finch (*Erythrura gouldiae*) co-occur in temporally and geographically stable frequencies in sympatric populations. Gouldian finches are obligate cavity-nesters with highly specific preferences for nest-site morphometry that directly affect reproductive success. Because intra- and interspecific competition for high quality nest-sites is prevalent, and fitness is directly related to nest-site quality, we investigated the relative access (and consequences for reproductive success) of alternative morphs to this critical limiting resource in the wild. Red males defended higher quality nest-sites, and overcame greater levels of nest-site competition against conspecifics and superior heterospecific competitors than black males. Red-headed males also produced more fledglings (especially with red-headed females) than black-headed males, independent of nest-site quality. Finally, the independent (positive) effect of nest-site quality on reproductive success was confirmed. Such competitive asymmetries are important to relative selection among coexisting morphs, and are likely to contribute to the maintenance of alternative sympatric colour-morphs in wild populations.

Keywords Colour polymorphism · Male competition · Alternative reproductive strategies · Gouldian finch

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Introduction

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. Consequently, much of the interest in polymorphic systems centers on understanding the potential adaptive value of displaying alternative phenotypes (e.g. Fisher 1930; Gross 1996; Galeotti et al. 2003; Roulin 2004), especially because discrete morphs may also vary in aspects other than appearance, such as behaviour and physiology. Such multi-trait differences mean that competing morphs may maximize their fitness by adopting different tactics (reviewed in Oliveira et al. 2008). For example, polymorphisms in male behaviour and life history are found in a number of taxa where territorial and/or highly aggressive morphs typically compete with sneaky and/or non-territorial morphs for access to mates (e.g. Kallioinen et al. 1995; Lank et al. 1995; Sinervo and Lively 1996; Sinervo and Clobert 2003; Tuttle 2003).

Here we examine the morph-specific fitness consequences of competition for nesting sites in the genetic colour polymorphic Gouldian finch (*Erythrura gouldiae*), an endangered grassfinch endemic to northern tropical Australia. Individuals of both sexes display one of three head-colour morphs, which unusually among birds (Galeotti et al. 2003; Roulin 2004), naturally coexist at relatively stable frequencies in sympatric populations: black (ca. 70 %), red (ca. 30 %) and yellow (<0.01 %) (Gilby et al. 2009). The head colour polymorphism is determined by two genes (one autosomal and one sex-linked), which stimulate or suppress the deposition of melanin (black) and carotenoid (yellow and red) pigments (Southern 1945; Pryke and Griffith 2009a). The dynamics of the sex-linked gene result in a lower relative frequency of red-headed females in the population compared to red-headed males (as the heterogametic sex, females require only one copy of the melanin-producing gene to produce a black-headed phenotype while males require two). Given the fact that individuals pairing non-assortatively with respect to head colour are likely to suffer reduced reproductive success due to genetic incompatibility (Pryke and Griffith 2009a), the reduced frequency of compatible mates for red-headed males (i.e. red-headed females) in the population may confer a fitness disadvantage.

Studies using captive populations have demonstrated several differences in behaviour related to the expression of genetic head-colour in this species. For example, red individuals are intrinsically more aggressive (Pryke 2009), out-competing black and yellow individuals for access to food (Pryke and Griffith 2006; Pryke 2007) and higher quality nest-sites (Pryke and Griffith 2009b). In the wild, as obligate cavity-nesters, Gouldian finches must acquire and defend natural tree cavities in order to reproduce. The species has highly specialised nest-site requirements, and suitable cavities are limited in the environment (Brazill-Boast et al. 2010). Gouldian finches must also compete with ecologically similar and sympatric long-tailed finches (*Poephila acuticauda*), a competitively dominant species that has highly overlapping nest-site requirements (Brazill-Boast et al. 2010, 2011). Similar to most cavity-nesting systems, the outcome of direct intra- and interspecific competition for nest-sites will be contingent on relative competitive ability (Ingold 1984; Newton 1994; Aitken and Martin 2008). For Gouldian finches, this predominantly involves males because of their role in prospecting for and defending nest-sites (Pryke and Griffith 2009b; Brazill-Boast et al. 2011).

Individual variation in relative dominance and aggression may explain not only the difference between breeding or not, but for species with specialized nest-site preferences, such as Gouldian finches (Brazill-Boast et al. 2010), the quality of the nest-site they acquire (Aitken and Martin 2008). Nest-site quality has consistently been shown to predict reproductive fitness in cavity-nesting birds (e.g. Johnson and Searcy 1993; Goodenough et al. 2008), including Gouldian finches (Pryke and Griffith 2009b; Brazill-Boast et al. 2012). Here we investigate morph-specific competitive ability and relative access to high quality nest-sites in a wild Gouldian finch population. We use both a known predictor of nest-site quality (cavity characteristics; Brazill-Boast et al. 2010) and a proxy (levels of nest-site competition) to determine whether red-headed individuals (specifically males) have access to higher quality nest-sites and whether this access translates into increased reproductive fitness. If red-headed males do receive fitness benefits from acquiring higher-quality nest-sites, this may balance the predicted effects of an increased likelihood of mating with an incompatible (black-headed) female. There is strong evidence for these mechanisms from captive studies, however, their effects in the wild have yet to be assessed. This study aims to elucidate the role of differential resource acquisition in maintaining sympatric head-colour morphs in natural populations.

Methods

Study site

All data were collected between February and August 2007–2010, to coincide with the Gouldian finch breeding season. The study sites consisted of a 108.7 ha area of Gouldian finch breeding habitat in the eastern Kimberley, Western Australia (S15°34', E128°09') (see Brazill-Boast et al. 2010 for details). The site was provisioned with custom-designed nest-boxes; which were constructed using natural hollowed branches (collected in the local area) to closely resemble natural cavities (and thus the variation in nest-box quality was similar to the variation in quality of the natural cavities; Brazill-Boast et al. 2012). Over the 4 years, the study sites were provisioned with a total of 800 boxes, and 129 Gouldian finches and 342 long-tailed finch pairs initiated nests in the custom-designed boxes (58.9 % of all nest-boxes used). Despite the habitat being supplemented with additional nest-sites, intra- and interspecific competition was prevalent across the study site (Brazill-Boast et al. 2011). This is supported by the relatively high occurrence of nest evictions (25 Gouldian finch nests taken over by Long-tailed finches; 31 % of all nest failures).

Nest-site monitoring

All nest-boxes in the study area were marked and mapped, and were checked at least once every 7–10 days for signs of nest initiation (nest-building or eggs). Once a nest had been initiated, it was checked every 2–3 days to record hatching date. Following hatching, nest-boxes were checked every 2–4 days. Parents were caught at the nest using a hand net and given a numbered aluminum leg band and a unique combination of three coloured plastic leg bands. To determine the morph frequencies of birds within the population (i.e. random sample including non-breeding birds), individuals were also caught using mist-nets placed at waterholes surrounding (<5 km) the breeding sites every 1–2 weeks during the season.

Because the yellow morph is very rare (<0.01 % of natural populations; only 2 yellow birds bred during the 4 years), they were excluded from all further analyses.

Video recording

Video cameras were used to record behaviour (see Brazill-Boast et al. 2011 for details) during daylight hours (06h00–16h00) (mean \pm SE = 26.8 ± 1.1 h/nest). Recording took place when nestlings were 10–13 days old, which coincides with the age when parental activity is the highest (Pryke and Griffith 2009b). Nestlings typically fledge (leave the nest) when 22–29 days old.

From the video data, two behaviours were scored for analysis. (1) Parental visitation: a visit was defined where a parent was observed to spend more than 30 s inside the nest (analysis of video data from a subset of nests ($n = 10$ [183 visits]) monitored with nest-box cameras demonstrated that these visits resulted in feeding, concurring with observations in captivity; Pryke and Griffith 2009b). All visits within the recording period were documented, allowing for the calculation of parental visitation rate, between-visit interval, and proportional share of visits. Adults are sexually dichromatic (males express brighter head colours and UV plumage on the collar), therefore sexes could be identified visually. (2) Intrusion by conspecific and heterospecific (long-tailed finch) competitors: the total number of non-parent individuals entering the nest for any period of time.

Nest-site quality

Gouldian finches select nest-sites non-randomly, using the variation in four main aspects of cavity morphometry to assess quality (Brazill-Boast et al. 2010): entrance thickness, fragility (qualitative score 1–5), cavity type (external in a protruding branch or internal in a main stem), and cavity structure (whether tissue surrounding the cavity is dead or alive). Principal Components Analysis (PCA) was used to reduce these four variables to one component (PC1) that explained 76 % of the variation in all potential nest-sites (see Brazill-Boast et al. 2010). A PC1 score (with eigenvectors: fragility = 0.913, thickness = 0.912, intrusion = 0.247, dead/live = -0.573) was then used as an index of nest-site quality, which could be assigned to every available nest-box. An identical index was previously found to predict reproductive success at this study site (Brazill-Boast et al. 2012).

Reproductive success

To quantify relative reproductive success, we used clutch initiation date, clutch size and the total number of offspring fledging the nest. Clutch initiation date was the date of the first egg that was laid in the breeding season. In all nests visited during egg laying, only one egg per day was added to the clutch. If a nest with a completely hatched brood was found, clutch initiation date was calculated by subtracting the average incubation period (mean \pm SE = 13.3 ± 0.5 days) and the appropriate number of days for egg laying from the day of hatching. Nests were checked when offspring were 18 days of age (just prior to fledging); no further nest checks were made after this time because of the likelihood of force-fledging chicks from the nest.

For fitness comparisons, red and black males were separated into assortative (bred with female of same head-colour) and disassortative pairs (bred with female of different head-colour). This was to control for postzygotic genetic incompatibilities between interbreeding morphs, which results in severe offspring mortality (Pryke and Griffith 2009a), independent of other behavioural factors (e.g. competitive ability and parental care: Pryke and Griffith 2009b; Pryke and Griffith 2010).

Statistical analyses

Data were analyzed in GENSTAT 9 (Rothamsted Experimental Station, Harpendon, UK) using Generalized Linear Models (GLM). To test for morph-specific differences in nest-site quality, male morph was included in the model as a fixed effect (using a Gaussian distribution), and cavity morphometry (i.e. entrance thickness, fragility, cavity type and cavity structure) were also entered as fixed effects to determine which aspect best predicts nest-site quality (modelled with a Gaussian distribution). Similarly, male morph was also included as a fixed effect for tests of intrusion rates (nest-site quality included as a fixed effect) and parental visitation rates (recording date included as a fixed effect), with these models based on a Poisson distribution and a logarithmic link function. To analyse clutch initiation date, clutch size and fledging survival (total number of fledglings), we included male morph, morph pair and nest-site quality as fixed effects in all models (using a Poisson distribution). All data were checked for overdispersion (but all scale parameters were ca. 1). Year was included and retained as a fixed effect in all models, but did not constitute a significant component in any model ($P > 0.19$). Means are reported with standard errors throughout.

Results

Colour morph ratios

In the random sample of birds caught in the local population over 4 years, red morph individuals comprised 19 % of the overall population (Table 1). There was a male-biased sex ratio in the overall population (1.7 male:1 female) and within the red colour morph (5.2 male:1 female), but not the black morph. Red males comprised 34.4 % of all breeding males ($n = 107$; 65.6 % black males), significantly over-representing their 25.8 % frequency in the general male population ($\chi^2 = 6.43$, $P = 0.01$).

Nest-site quality

Red males successfully acquired nest-sites of higher quality than black males ($F_{1,106} = 3.81$, $P = 0.03$; Fig. 1a). With respect to specific cavity characteristics, nest-sites occupied by red males had thicker entrances ($F_{1,106} = 6.09$, $P = 0.002$) and were more robust ($F_{1,106} = 9.96$, $P < 0.001$) than those occupied by black males.

Intrusion rates were significantly higher at better quality nest-sites ($F_{1,38} = 5.31$, $P = 0.03$), and at nests occupied by red males, controlling for the effects of nest-site quality ($F_{1,38} = 6.02$, $P = 0.02$). However, the interaction was not significant (male morph \times nest-site quality: $F_{1,38} = 0.98$, $P = 0.11$). High-quality nest-sites defended by red

Table 1 Estimated morph frequencies for both population and sex, based on a sample of adults caught at waterholes within the larger breeding areas

Sex	Morph	<i>n</i>	Population (%)	Sex (%)
Male	Black	89	46.59	74.2
Male	Red	31	16.2	25.8
Female	Black	65	32.4	91.5
Female	Red	6	4.7	8.5

males received more than twice as many intrusions than nests occupied by black males (Fig. 1b). Long-tailed finches intruded into red male nests 2.8 times more than into black males' nests ($F_{1,38} = 5.26$, $P = 0.02$), and red males also received more conspecific intruders than black males ($F_{1,38} = 4.11$, $P = 0.03$).

Parental care

Parental care was equally shared between the sexes (male feeding rate/female feeding rate = 1.00 ± 0.09). There were no differences between male morphs in provisioning rates, measured as either between-visit interval ($F_{1,30} = 0.52$, $P = 0.61$), average daily feeding rate ($F_{1,30} = 0.25$, $P = 0.81$), or proportional share of the breeding pair's visits ($F_{1,30} = 0.10$, $P = 0.92$). Furthermore, none of these measures of male parental care were affected by total (conspecifics + heterospecifics) nest intrusion rate (between-feed interval: $F_{1,30} = 0.04$, $P = 0.85$; daily feeding rate: $F_{1,30} = 0.10$, $P = 0.76$; proportional share: $F_{1,30} = 1.26$, $P = 0.27$).

Reproductive success

There was no difference in clutch initiation date between red (56 ± 6.3 days) and black males (63 ± 4.2 days; $F_{1,106} = 0.22$, $P = 0.64$), irrespective of whether they were in

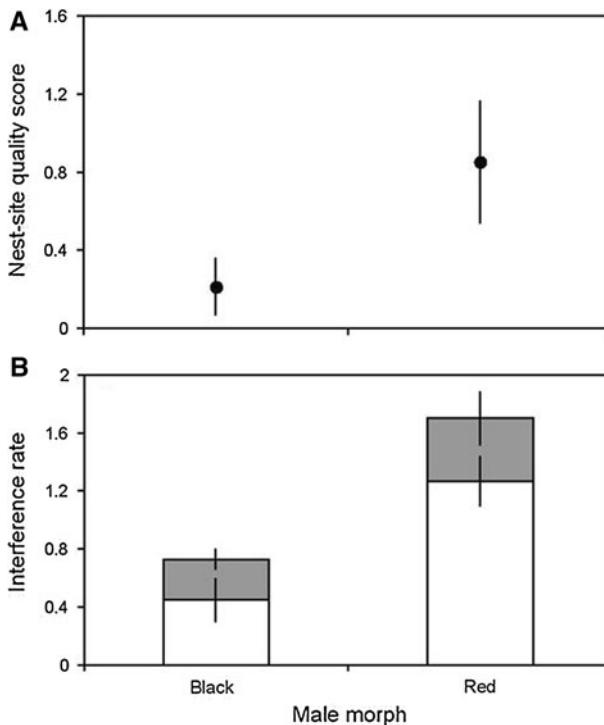


Fig. 1 **a** Average (\pm SE) nest-site quality score (PC1) for Gouldian finch nests occupied by black ($n = 70$) versus red ($n = 37$) morph males. **b** Average (\pm SE) interference rate by long-tailed (empty bars) and conspecific Gouldian finches (grey bars) (bars represent cumulative interference; i.e. total bar height = total interference) at nests occupied by black and red morph males

high-quality nests ($F_{1,106} = 0.36$, $P = 0.52$) or in assortative or disassortative pairs ($F_{1,106} = 1.87$, $P = 0.17$). Similarly, there were no differences in clutch size between the morphs ($F_{1,106} = 1.62$, $P = 0.21$), between assortative or disassortative breeding pairs ($F_{1,106} = 3.52$, $P = 0.06$) or with respect to nest-site quality ($F_{1,106} = 0.85$, $P = 0.37$). However, fledging success was dependent on both male morph ($F_{1,106} = 4.91$, $P = 0.005$) and the head-colour of their female partner $F_{1,106} = 5.81$, $P = 0.01$; male morph \times morph pair: $F_{1,106} = 6.26$, $P = 0.004$; Fig. 2). Red males breeding in assortative (compatible) pairs produced more fledglings than black assortative pairs ($t = 4.07$, $P < 0.01$), and had much higher fledging success than both red ($t = 4.98$, $P < 0.01$) and black males in disassortative pairs ($t = 7.81$, $P < 0.001$), when controlling for nest-site quality (morphometry). There was no difference in fledging success between assortative black pairs and red ($t = 0.76$, $P = 0.42$), and black males ($t = 1.14$, $P = 0.11$) breeding in disassortative pairs (Fig. 2). Furthermore, fledging success was also dependent on nest-site quality ($F_{1,106} = 7.82$, $P < 0.001$); birds breeding in high quality nests had higher fledging success than birds in lower quality nests (independent of male morph). Therefore, red males defended higher-quality nest sites (especially in morph-assortative pairs) and successfully fledged more offspring than black males.

Discussion

Red males acquired nest-sites that were of higher quality than those occupied by black males. The index of quality used was based on the species' known preference for nest-site characteristics (Brazill-Boast et al. 2010), and has been shown to predict reproductive success (Brazill-Boast et al. 2012). Although very little is known about Gouldian finch behaviour in the wild, generally males appear to adopt the roles of prospecting for nest-sites and nest building. Because there were no differences in breeding latency between male morphs, and clutch initiation date was unrelated to nest-site quality, it is unlikely that morph-specific differences in acquiring high-quality nest-sites are the result of superior nest-prospecting or breeding precedence of red males. Instead, it appears that the

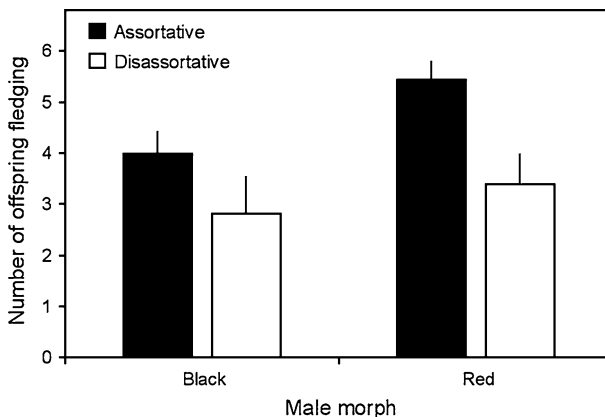


Fig. 2 Average (\pm SE) offspring fledging success (number of offspring leaving the nest) for *black* males in assortative ($n = 63$) and disassortative pairs ($n = 7$), and *red* males in assortative ($n = 8$) and disassortative pairs ($n = 29$)

alternative genetically determined head-colour morphs are associated with individual ability to compete for high quality nest-sites.

The availability of suitable nest-sites (Brazill-Boast et al. 2010) and/or prevalence of direct intra- and interspecific competition for nest-sites, appears to be limiting the reproductive success of Gouldian finches at some locations (Brazill-Boast et al. 2011). Therefore, as in many cavity-nesting systems, opportunity to breed and acquisition of a high-quality nest-site will be closely related to aggression and competitive ability (e.g. Minot and Perrins 1986; Wiebe 2003; Aitken and Martin 2008). Nests occupied by red males received more intrusions from conspecific, and especially heterospecific intruders, when controlling for nest-site quality, than nests defended by black males. This suggests that red males acquired nest-sites that were considered to be higher quality by both Gouldian and long-tailed finches. Furthermore, this implies that red males experienced (and dominated) relatively more competition than black males. Interspecific competition was particularly severe for red males, and because long-tailed finches are socially dominant competitors that typically outcompete Gouldian finches for resources (Brazill-Boast 2013), this is likely to have been especially difficult to counteract.

Sympatric genetic colour polymorphic species are often associated with different behavioural strategies (e.g. Lank et al. 1995; Sinervo and Lively 1996; Tuttle 2003), and may persist if the relative fitness returns of each strategy are generally frequency-dependent, and thus, net selection is balanced across all morphs (Fisher 1930; Roulin 2004). It is much less common, however, to observe both temporally and spatially stable differences in the relative success of fitness-related behaviours (e.g. resource acquisition) associated with morphs (but see Dijkstra et al. 2009). This is because, theoretically, the most successful morph should competitively displace all others, leading to a monomorphic system. Frequencies of red morphs in other Gouldian finch populations have been reported at 18–26 % (Franklin and Dostine 2000), in line with those reported here, and appear to have been temporally and geographically stable for at least 150 years (Gilby et al. 2009). Thus, the dominance advantage held by red over black males does not translate into increased fitness (i.e. is not reflected in population dynamics), suggesting that alternative factors are limiting the frequency of red males.

For red males, the competitive advantage and subsequent fitness benefits may be constrained by socially enforced frequency-dependence. In captivity, the competitive advantage to red males comes at a frequency-dependent cost, with red birds at experimentally high densities (50–100 % of the population) suffering high stress levels (corticosterone), reduced immune function and compromised health (Pryke et al. 2007), which together leads to increased mortality (Pryke and Griffith 2009b). Furthermore, red (but not black) males at high frequencies trade-off investment in parental care with aggressive behaviour, resulting in reduced number and quality of offspring, but at low densities (ca. 30 %) provide comparable parental care and have high reproductive success (Pryke and Griffith 2009b). Although there were no differences in paternal care between red and black males in our breeding population, this may be because red males were breeding at below-threshold density (ca. 35 %). Potentially, if the relative densities of the aggressive red morphs increased, such a frequency-dependent mechanism may limit their relative fitness.

Another important factor likely to influence reproductive fitness in Gouldian finches is mate choice. Recent studies have shown that both males and females prefer to mate assortatively with respect to morph (Pryke 2010), which seems to be explained by the fitness costs associated with genetic incompatibility in mixed-morph pairs (Pryke and Griffith 2010). Although most black birds in the wild mate assortatively, red males are largely constrained to breeding with black females (because of the limited number of red

females; see Fig. 2). In pair-wise fitness comparisons, red males in assortative pairs had the highest reproductive success (i.e. fledging success), whereas red males in disassortative pairs produced fewer offspring that successfully fledged (likely due to genetic incompatibilities), comparable to black males in low-quality nest-sites. Therefore, the low frequencies of red females in wild populations, and constraints on optimal mate preferences, suggest that the potential reproductive advantages gained by red males in defending high-quality nest-sites may in many cases be counteracted by disadvantages associated with breeding with an incompatible mate.

Although the relative selective pressures on males and females of each morph remain unknown at present, there are likely to be different costs and benefits associated with different genetically-determined behaviours, which together will contribute to the maintenance of this polymorphism. Head colour signals intrinsic, genetically based dominance which this study has associated with a direct fitness benefit; nest-site quality. However, further studies are required to disentangle environmental, demographic and genetic effects to fully understand the strength and direction of selection on these coexisting morphs in the wild.

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Ethical standards All work described here complies with current Australian laws, and was approved by the Institutional Animal Care and Ethics Committees at Macquarie University, and carried out under license from the Western Australian Department of Environment and Conservation.

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