

## Colourful characters: head colour reflects personality in a social bird, the Gouldian finch, *Erythrura gouldiae*

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Remarkable diversity in behaviour and morphology (phenotypes) are often observed within a species; this diversity can be understood in terms of individuals maximizing their fitness. Based on evidence from studies linking different phenotypes to individual behaviours we hypothesize that discrete colour polymorphism can reflect personality. We tested for such a relationship in a social bird, the Gouldian finch, which shows two major head-colour morphs: red and black. Forty birds of differing head colours were used in five controlled laboratory tests. We found that three of the five tests were repeatable over time, and that bird performance in these tests differed with respect to head colour. Specifically: (1) pairs of red-headed birds were more aggressive than pairs of black-headed birds; (2) black-headed birds approached and touched a novel object quicker than red-headed birds (they were bolder); (3) black-headed birds returned to feed faster following the presentation of a false predator (they were less risk-averse); (4) boldness was positively correlated with risk taking (within the whole sample, within the red-headed birds and trending in the black-headed birds). Together, our results are consistent with our hypothesis that colour polymorphism could be indicative of consistent behavioural differences, and we make a number of predictions about how we expect this to function as a signal in competitive and cooperative (social) contexts.

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The emergence and persistence of morphological variability such as discrete colour phenotypes is understood in terms of individuals maximizing their fitness (Roulin 2004); if differently coloured individuals accrue advantages but also incur some disadvantages, then differently coloured individuals can derive similar fitness under frequency dependent or disruptive selection (reviewed in Galeotti et al. 2003 and Roulin 2004). 'Personality' describes the observation that individuals of the same species of similar age, size and sex differ consistently in their behaviour across time and contexts (Koolhaas et al. 1999; Sih et al. 2004; Reale et al. 2007). Different personality traits often correlate with one another (Sih et al. 2004) and can be heritable (Drent et al. 2003; van Oers et al. 2004). Like morphological variability, the emergence and persistence of this behavioural variability is also understood in terms of individuals maximizing short- or long-term fitness (Wolf et al. 2007).

It is currently unknown whether discrete colour polymorphism and personality are related. However, many studies show a link between colour polymorphism and individual behaviours. For example, discrete colour morphs have been found to differ in levels

of aggression (Lake Victoria cichlid fish, *Pundamilia*, Dijkstra et al. 2009), sexual behaviour (South American live-bearing fish, *Poecilia parae*, Hurtado-Gonzales et al. 2010) and antipredator responses (ornate tree lizard, *Urosaurus ornatus*, Thaker et al. 2009). Indeed, melanin-based colour differences have already been found to reflect personality in eastern Hermann's tortoises, *Eurotestudo boettgeri*, in which dark males were found to be more aggressive and bolder (Mafli et al. 2011). It can therefore be hypothesized that different colour morphs (in nonmelanin-based systems) can be indicative of different personalities. This may be maintained by correlational selection, whereby selection favours a particular combination of traits, be they morphological or behavioural (Brodie 1992). For example, in the garter snake *Thamnophis ordinoides* survivorship was predicted by a combination of 'stripedness' and escape behaviour: individuals with high values of one trait coupled with low values of the other trait had the highest probability of survival (Brodie 1992).

In a social context, associating with conspecifics of certain personalities can have wide-ranging effects. For example, groups of guppies, *Poecilia reticulata* (Dyer et al. 2009), and sticklebacks, *Gasterosteus aculeatus* (Harcourt et al. 2009), composed of individuals that differ in 'boldness scores' have been shown to forage more effectively than groups of individuals of similar boldness, and

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*Anelosimus studiosus* spiders that show aggressive asocial and docile social phenotypes exhibit increased fitness in mixed-phenotype colonies (Pruitt & Riechert 2011). Given the potential benefit to assorting positively or negatively according to personality types, and the assumption that colour polymorphisms are maintained because they represent some inherent difference in the way individuals behave, could colour polymorphism act as a signal of personality?

Here, we present the first systematic study investigating this potential link using a highly social bird, the Gouldian finch, as a model system. Both male and female Gouldian finches have extremely colourful plumage and exhibit two main head-colour morphs, red and black, found at a sympatric stable 3:7 ratio in wild populations, in addition to a rare yellow-headed morph (Brush & Seifried 1968; Gilby et al. 2009). In its natural habitat the Gouldian finch lives in open, subtropical woodland of northern Australia, where the birds nest in loose colonies and forage mainly on grass seeds (Dostine et al. 2001), forming mobile flocks (of mixed morph) of between 10 and 400 individuals outside the breeding season (O'Malley 2006). Studies in captivity have shown that red-headed (RH) birds are more aggressive than black-headed (BH) birds (Pryke 2007; Pryke & Griffith 2006) and that females show a preference for RH males over other head colours (Pryke & Griffith 2007). In addition, RH males have, on average, higher testosterone and corticosterone levels than BH males when in a socially challenging situation (several RH males together; Pryke et al. 2007). Although these traits seem to be linked to head colour, it has not been shown that these and other traits are correlated within an individual, forming a behavioural syndrome and thus indicating that head colours reflect personality traits (rather than independent behaviours). In our study, we investigated whether several behavioural traits that are often part of personality types relate to head colour, and whether these traits are correlated, in order to test the hypothesis that colour polymorphism signals personality.

By definition, personality relates to individual variability in behaviours that are consistent over time and across contexts (Koolhaas et al. 1999; Reale et al. 2007; Sih et al. 2004). We therefore first tested whether Gouldian finch behaviour was repeatable over time using a number of behavioural tests (those of the 'big five' that are also found in animals; Gosling & John 1999). For those behaviours that were repeatable over time, we proceeded to test the hypothesis that distinct colour morphs are indicative of different personalities, and we tested a number of predictions. Given that previous experimental work has shown that RH birds are dominant over BH birds in both males (Pryke & Griffith 2006) and females (Pryke 2007), we tested the prediction that pairs of BH birds exhibit lower levels of aggression than pairs of RH birds (prediction 1). How head colour might relate to other personality traits is less clear; we might expect RH birds to take more risks and be bolder and more explorative than BH birds, as aggression is often positively correlated to these traits (Sih et al. 2004) (prediction 2a). However, RH birds could take less risk, be shyer and be less explorative than BH birds for at least two reasons (prediction 2b): first, RH birds might be more conspicuous to predators than BH birds (Gotmark & Olsson 1997); second, in a social foraging context, if RH birds are more aggressive, then it might pay (in terms of immediate foraging return) for BH birds to take more risks (Koivula et al. 1994) and also be bolder and more explorative to find resources before the dominant RH birds. We tested these predictions by measuring bird responses in five tests. We tested levels of aggression in pairs of birds of the same head colour, as the behaviour of animals in mixed-colour groups does not always translate to other group compositions (Dijkstra et al. 2009), and any differences in levels of aggression among mixed-colour dyads could be due to variability in how individuals detect and respond to opponents of differing head colour (Barton & Hill 2005; Hill & Barton

2005). We tested risk taking in individual birds using a predator-stimulus test (van Oers et al. 2004) and an object neophobia test (Mettke-Hofmann et al. 2002). We tested exploration (boldness) in individual birds using a spatial neophilia (Mettke-Hofmann et al. 2009) and an object neophilia test (Mettke-Hofmann et al. 2002).

## METHODS

### Study Subjects

Forty Gouldian finches obtained from 13 private breeders were used. All were wild type and parent reared. Birds ranged in age from 1 to 5 years (information derived from closed rings and breeder information), and birds were placed into two age categories: juvenile (12 of those born in 2010) and adult (28 of those born before 2010). Tarsus length (an indicator of body size, measured using callipers) ranged from 12.91 cm to 15.84 cm, and there were 19 males (12 RH; seven BH) and 21 females (11 RH; 10 BH). Birds were housed together in three 100 × 200 cm and 200 cm high 'free-flight enclosures' in mixed head colours and sexes for at least 2 months prior to them participating in experiments. They were fed Amadinen-Zucht Spezial (seed mixture for Gouldians from Blattner Heimtierfutter, Ermengerst, Germany), canary and millet seed, grit, eggshells and water ad libitum from food hoppers, bowls and water dispensers. Once a week they were given millet spray and supplemented with minerals and vitamins (Nekton MSA and Nekton S). Birds were provided with a full spectrum light source with a cycle of 13:11 (light:dark), and kept at a temperature of approximately 24 °C. Birds were used for further behavioural observations after the experiments were finished.

### Experimental Set-up

Tests were conducted in six experimental cages (80 × 120 cm and 100 cm high), which contained three perches and in which food and water were provided ad libitum. Experimental cages were arranged in pairs with a sliding door between and separated by a removable wooden partition. Six birds were moved to the individual experimental cages at a time and were allowed 4 days to habituate to their new surroundings (with a partner for the first 3 days if subjects seemed particularly anxious when entering the cage). Birds took part in experiments from 0800 hours until 1300 hours over 5 days, singularly for the risk-taking and novelty experiments, and in a pair for the aggression experiment (see below for specific experiment details). One experiment was performed per day, subjects did not have visual access to neighbours during experiments, and all experiments were recorded by digital video cameras using GeoVision 1480 for later analysis. The experimenter was absent from the room while the experiments were being conducted. Experiments complied with ethical and welfare guidelines for animals and the legal requirements of the University and the United Kingdom. In particular, holding and experimental aviaries conformed to Home Office codes of practice and were carried out in approved facilities in the University. All experiments carried out were nonregulated by the Home Office, and an Inspector's advice was sought to confirm this.

### Object Neophilia

To test object neophilia (defined as exploration in which investigation is elicited by an object's novelty; Greenberg & Mettke-Hofmann 2001) a bunch of coloured threads 12 cm long (half of birds were tested with grey threads, half brown threads), were attached with tape to a neutral position on a perch in the cage, and the latency to approach the object to within one body length

(marked as a black line on the perch) and latency to touch the object was recorded over a period of 1 h. Birds were not forced to approach, as the object was at a neutral location away from food and water. Therefore, approach and investigation was assumed to reflect interest in the object (i.e. neophilia: [Mettke-Hofmann et al. 2005](#); intrinsic neophilia: [Wood-Gush & Vestergaard 1991](#)). For analysis the mean of the two latencies was used (neophilia latency).

#### *Avoidance of Novelty*

Neophobia reactions (avoidance of novel object never seen before, associated with fear; [Greenberg & Mettke-Hofmann 2001](#)), can easily be induced by presenting a novel object close to regularly used feeders ([Coleman & Mellgren 1994](#)). To test object neophobia the feeder was removed from the experimental cage for 1 h. The same feeder was then returned to the cage but with a rectangular cork ( $5.5 \times 3.5$  cm and 2.5 cm high) fixed to the wire mesh just above the feeder (half of birds were tested with a blue cork, half a white cork). The subject's latency to return to feed with the object present was recorded and compared to a control condition in which the familiar feeder was removed for 1 h, and returned in the same state. The difference in latency to return to feed between the experiment and the control reflects the hesitancy to feed in the presence of the novel object and was thus used as a measure of object neophobia.

#### *Aggression*

Two birds matched for head colour, sex and size were moved to a new, but identical, experimental cage and habituated in their pairs for 3 days. Following 1 h of food deprivation, a small familiar semi-circular feeder was placed into the corner of the cage where only one bird could feed at a time. The number of aggressive interactions initiated between pairs over 30 min were recorded (see [Pryke & Griffith 2006](#) for a similar approach). Aggressive interactions included displacements and threat displays with an open beak. Physical interactions were infrequently observed, which were highly ritualized and short-lasting bill fights (two to three contacts). Aggressive interactions never came near any physical injury, and the receiving bird flew to another perch without being followed.

#### *Risk Taking*

To test risk taking we used a predator-stimulus test (see [van Oers et al. 2004](#) for a similar approach). After subjects were returned to their individual cages they were habituated to the predator-stimulus apparatus (line and pulley system) for 24 h. The next morning, the subject's feeder was removed for 1 h. When the feeder was replaced, latency to feed was recorded as a control measure. After the bird had been feeding calmly for 10 s a silhouette of an avian predator was pulled up and down in front of the cage, and the bird's latency to return to the feeder and feed was recorded. The difference between the control measure and latency to feed after the predator stimulus was taken as a measure of risk-taking. Four birds (two BH females, two RH females) from our sample did not take part in this test owing to experimenter error. All birds returned to feed within 1 h after the predator stimulus and there were no short- or long-term adverse effects resulting from this experiment.

#### *Spatial neophilia*

Spatial neophilia (attraction to a novel space; [Mettke-Hofmann et al. 2009](#)) was tested by removing the wooden partition separating two adjacent cages and opening the sliding door so that the

subjects could access the adjacent temporarily empty cage (with differently arranged perches). Time spent in the novel cage was measured from first entry for 30 min to provide an indication of spatial neophilia. Birds that did not enter the novel cage within 1 h scored zero. Birds were moved to their holding aviaries after the end of this test.

#### *Repeatability of Behaviour*

Two months after the five experiments, 18 randomly selected birds (four RH males, six RH females, four BH males, four BH females) were retested in all five tests to test for consistency of behaviours. During retesting birds were presented with alternate coloured objects to account for potential habituation following the initial presentation at these two time points. Two of 18 birds (one RH male, one RH female) only completed four of the five tests (missing the repeat risk-taking experiment) owing to experimenter error.

#### *Statistical Analysis*

##### *Repeatability of tests across time and context*

Spearman rank correlation coefficients were computed in SPSS (v.17.0, 2009; SPSS Inc., Chicago, IL, U.S.A.) between reactions in the first and second set of experiments to test for consistency of the bird's reactions across time, and to test for correlations in bird responses across the tests that were found to be related to head colour (i.e. correlation of behaviour across contexts). Correlations were also conducted for same-head-colour birds to discover if the relationship was independent of head colour. As we performed multiple statistical tests (one for each of our five experiments), we used a Bonferroni-corrected *P* value of 0.01.

##### *Predictors of personality*

Predictors of personality were tested using generalized linear mixed models (GLMMs). In each of our models our response variable did not follow a normal distribution; we therefore transformed these into proportional data, and used a binomial error structure with logit-link function in all models. For the response variable transformation, each data point was divided by the maximum value recorded in order to produce a data point between 0 and 1. This allowed us to model bird responses in a GLMM framework, while still maintaining the variation in the data. Models were constructed for each personality trait found to be repeatable over time. We therefore ran three GLMMs to test predictors of aggression (model 1), object neophilia (model 2), and risk taking (model 3). Individual sex ([Mettke-Hofmann 2000a](#)), age ([Fawcett & Johnstone 2010](#)) and size ([Biro & Stamps 2008](#)) can have an effect on behaviour. In addition, whether the bird was habituated to the experimental cage with a partner could also have influenced behaviour in trials. We therefore included sex (male, female), age (adult, juvenile), tarsus length (continuous) and habituation method (with partner, without partner) as fixed effects in all our models, along with our main variable of interest, head colour (red, black). Individual bird ID was nested within breeder ID and fitted as a random effect. We present full results for each model including estimates and standard errors, and *P* values are reported from  $\chi^2$  values derived from each model. GLMMs were conducted in MLwiN (v. 2.24, 2011, Bristol University Centre for Multilevel Modelling, Bristol, U.K.).

## **RESULTS**

#### *Repeatability of Traits*

Scores for subjects that were tested again after 2 months were found to be repeatable for aggression (Spearman rank correlation:

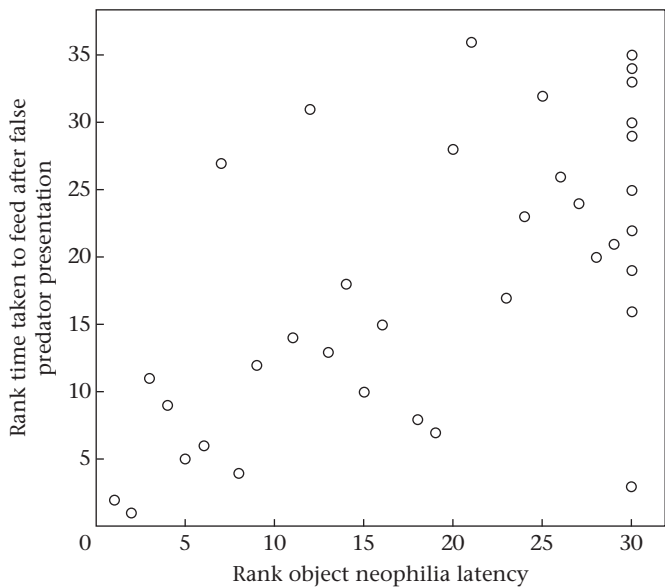
$r_s = 0.754$ ,  $N = 18$ ,  $P < 0.001$ ), object neophilia ( $r_s = 0.843$ ,  $N = 18$ ,  $P < 0.001$ ) and risk taking ( $r_s = 0.674$ ,  $N = 16$ ,  $P = 0.004$ ). Spatial neophilia and object neophobia were not highly repeatable over time after a Bonferroni correction (spatial neophilia:  $r_s = 0.520$ ,  $N = 18$ ,  $P = 0.027$ ; object neophobia  $r_s = 0.321$ ,  $N = 18$ ,  $P = 0.243$ ). Given that we expected head colour to be indicative of behavioural responses that are repeatable (predictable) we did not test whether spatial neophilia, or object neophobia scores were predicted by head colour (below).

Correlations Across Traits

Individual risk-taking behaviour was positively correlated with object neophilia across all birds ( $r_s = 0.601$ ,  $N = 36$ ,  $P < 0.001$ ; Fig. 1) and within the RH birds ( $r_s = 0.554$ ,  $N = 21$ ,  $P = 0.009$ ), and the same trend was present within BH birds after Bonferroni correction ( $r_s = 0.561$ ,  $N = 15$ ,  $P = 0.029$ ). Object neophilia scores and aggression, and aggression and risk taking did not show a significant correlation ( $r_s = 0.076$ ,  $N = 40$ ,  $P = 0.640$ ;  $r_s = 0.072$ ,  $N = 36$ ,  $P = 0.678$ , respectively).

Head Colour as a Signal of Personality?

Head colour predicted behavioural responses of birds in all of the measures that were found to be repeatable. Birds in BH dyads initiated fewer aggressive interactions than those in RH dyads, in support of our first prediction (aggression test: Table 1, Fig. 2). Compared with RH birds, BH birds also approached and contacted a novel object sooner (object neophilia test: Table 2, Fig. 3a), and were faster to return to the feeder after a startle (risk-taking test: Table 3, Fig. 3b) in support of prediction 2b. In addition to an effect of head colour, we also found sex to influence the response of birds in our novel object test: males were faster than females at approaching and contacting the novel object (object neophilia test: Table 2). Other predictors (sex, age, tarsus length and habituation method) had no effect on the personality traits tested.



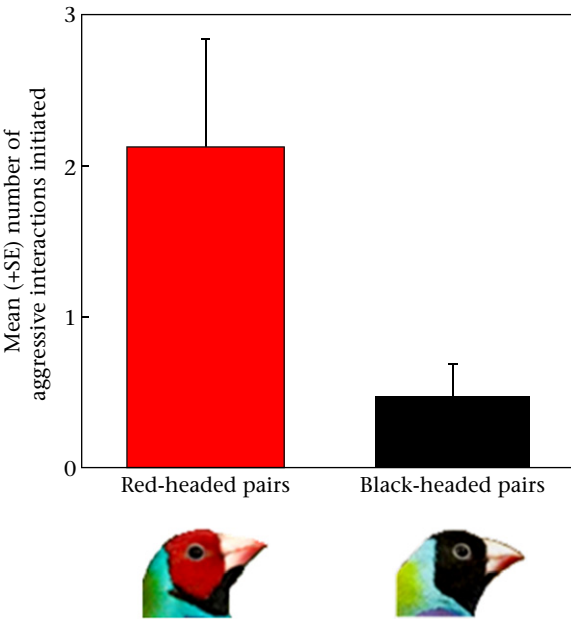
**Figure 1.** Correlation between object neophilia latency (time, s, to approach and touch a novel object) and difference between the time (s) taken to return to a familiar feeder and feed after a false predator has been presented and a control condition (no predator).

**Table 1**  
Model results for the GLMM to test whether head colour predicted scores for aggression

Model term	Estimate (SE)	df	P
Head colour		1	0.001
Red	2.017 (0.624)		
Black	0.000 (0.000)		
Sex		1	0.235
Female	0.482 (0.406)		
Male	0.000 (0.000)		
Age		1	0.521
Juvenile	−0.430 (0.673)		
Adult	0.000 (0.000)		
Habituation		1	0.131
With partner	0.933 (0.618)		
Without partner	0.000 (0.000)		
Tarsus length	−0.007 (0.334)	1	0.975
Intercept	−3.900 (4.982)		
Individual identity and breeder ID (random term)	2.428 (0.782)		

DISCUSSION

We found individual variability in Gouldian finch responses in each of our behavioural tests, and consistency in bird responses in our tests of aggression, risk taking and object neophilia. Neither object neophobia nor spatial neophilia were found to be consistent over time. With respect to the latter, the room was identical in both tests and birds may have habituated to the novel environment, which is a well-known phenomenon in animals (Mettke-Hofmann 2000b). Similarly, the novel object only differed in colour but not in shape and size and generalization processes may have occurred, rendering the object as not entirely novel (Christensen et al. 2011). The behaviour of individuals in our risk-taking trials positively correlated with their behaviour in another context (object neophilia) and this was also present within RH birds and a trend in BH birds. Together, these findings indicate variability in behaviours across individuals and consistency within individuals, and therefore are consistent with important characteristics of personality traits (Koolhaas et al. 1999; Reale et al. 2007; Sih et al. 2004).



**Figure 2.** Head colour of the Gouldian finch in relation to mean + SE number of aggressive interactions initiated by individuals when paired with same-head-colour birds.



**Table 2**

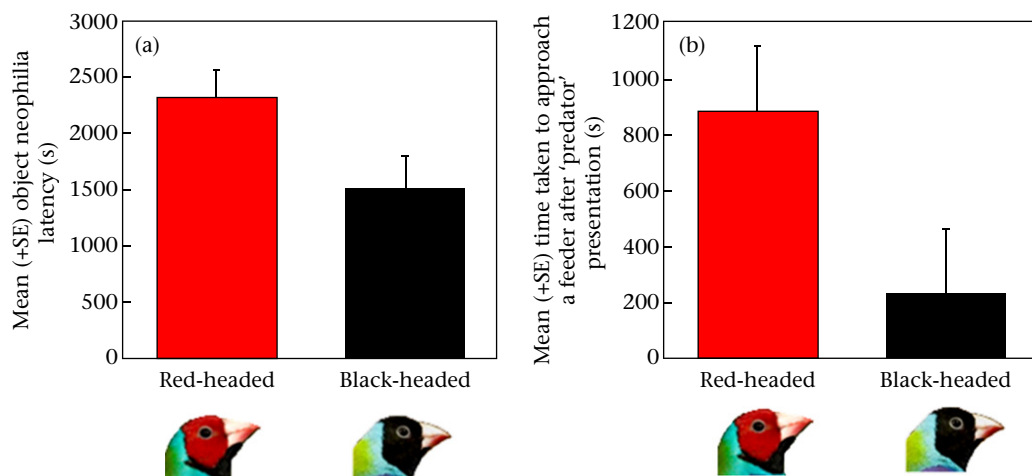
Model results for the GLMM to test whether head colour predicted scores for object neophilia

Model term	Estimate (SE)	df	P
Head colour		1	0.008
Red	1.515 (0.567)		
Black	0.000 (0.000)		
Sex		1	0.006
Female	1.036 (0.380)		
Male	0.000 (0.000)		
Age		1	0.638
Juvenile	−0.338 (0.718)		
Adult	0.000 (0.000)		
Habituation		1	0.542
With partner	−0.302 (0.495)		
Without partner	0.000 (0.000)		
Tarsus length	−0.137 (0.365)	1	0.707
Intercept	0.954 (5.434)		
Individual identity and breeder ID (random term)	3.507 (0.930)		

In line with previous work (Pryke 2007; Pryke & Griffith 2006), and in support of our first prediction, we found that RH birds were more aggressive than BH birds, initiating more agonistic interactions than BH birds when tested in same head-colour pairs. This result is unsurprising, as red coloration is associated with aggressive behaviour in fish (Dijkstra et al. 2009), birds (Pryke et al. 2001), reptiles (Healey et al. 2007) nonhuman primates (Setchell & Wickings 2005) and humans (Barton & Hill 2005; Hill & Barton 2005), and the addition of red stimuli can increase social dominance of zebra finches, *Taeniopygia guttata* (Cuthill et al. 1997). We found that BH birds took more risks and were bolder than RH birds, in support of prediction 2b. Specifically, BH birds returned to a feeder following the presentation of a false predator faster than RH birds did (risk-taking test) and approached and touched a novel object quicker than RH birds did (object neophilia test). The fact that risk taking/boldness and aggression do not go hand in hand may at first appear puzzling, and suggests that the aggression-boldness syndrome may not be universal (as hypothesized by Wolf et al. 2007). Indeed, our result that aggression and boldness/risk taking is decoupled is in contrast to results found in many other studies (Sih et al. 2004), including melanin-based polymorphic systems (Mafli et al. 2011). We expect this difference to be explained by both the specific morphology of aggressive birds (red heads) and the social and ecological environment that this species is exposed to, which is discussed below.

In terms of morphology, red coloration has been found to be conspicuous against natural backgrounds (Gotmark & Olsson 1997), and more conspicuous birds have been found to suffer higher predation rates (Galeotti et al. 2003). Thus, selection could favour more conspicuous RH birds taking fewer risks. There is some empirical evidence for this in the wild: in Iberian rock lizards, *Iberolacerta monticola*, the more conspicuous males fled to a refuge more often with the approach of a predator, and stayed in the refuge for longer than their less conspicuous male conspecifics (Cabido et al. 2009). Similarly, in a study on 10 parrot species, the less conspicuous sex explored a novel object sooner than the more conspicuous sex (Mettke-Hofmann 2000b). In our study, not only were BH birds bolder to approach a novel object but also took greater risks after the encounter with a false predator silhouette. Moreover, these two behavioural traits were correlated with each other (in the entire sample, within the RH birds and trending within BH birds), indicating that, irrespective of the head colour, they form a behavioural syndrome. This implies that there is not only selection on boldness and risk taking in relation to head colour but that there is also selection on specific combinations of these behavioural traits within an individual. It may be that only this specific combination of boldness and risk taking within an individual results in similar fitness of the colour morphs. Our results, therefore, demonstrate that head colour could signal personality.

In terms of the social and ecological environment, if BH birds take more risks and RH birds are more aggressive, in a foraging context this could lead to consistent differences in morph foraging tactics (Caraco & Giraldeau 1991). For instance, we know that in willow tits, *Poecile montana*, subordinate individuals feed at more risky sites because of interference by dominants at safe sites (Koivula et al. 1994), and the frequency of scrounging behaviour is known to increase with dominance rank in flocks of house sparrows (Liker & Barta 2002). Thus, for Gouldian finches, less conspicuous BH birds could increase their foraging opportunities by foraging at more risky (e.g. more exposed) sites, thereby reducing competition with more aggressive RH birds. The lower conspicuousness of the black head may make them less vulnerable to predation, favouring foraging at exposed sites. In addition, BH birds may adopt producer tactics and actively seek out new resources (as they are bolder; Caraco & Giraldeau 1991). This may be particularly important at the beginning of the wet season, when seeds are scarce and birds move around searching for patches of remaining seeds (Dostine et al. 2001). The early arrival at a food source would give the BH birds the advantage of higher food intake



**Figure 3.** Head colour of the Gouldian finch in relation to (a) mean + SE object neophilia latency and (b) mean + SE difference between the time taken to return to a familiar feeder and feed after a false predator has been presented and a control condition (no predator).

**Table 3**

Model results for the GLMM to test whether head colour predicted scores for risk-taking

Model term	Estimate (SE)	df	P
Head colour		1	0.025
Red	0.923 (0.414)		
Black	0.000 (0.000)		
Sex		1	0.974
Female	−0.001 (0.321)		
Male	0.000 (0.000)		
Age		1	0.867
Juvenile	0.074 (0.446)		
Adult	0.000 (0.000)		
Habituation		1	0.371
With partner	−0.349 (0.391)		
Without partner	0.000 (0.000)		
Tarsus length	−0.245 (0.397)	1	0.537
Intercept	2.783 (5.911)		
Individual identity and breeder ID (random term)	1.081 (0.340)		

before they are forced to move to less productive sites or more risky sites by RH birds that can use scrounger tactics and replace the less competitive BH birds (Caraco & Giraldeau 1991).

Overall, these results provide strong support for our hypothesis that head colour is an indicator of personality in the Gouldian finch, and it can be postulated that the colours are used as a signal of personality to other individuals in the social group. Indeed, in a previous study investigators experimentally reddened the usually subordinate rare yellow-headed morph males, which were subsequently able to dominate the BH birds, showing that the BH birds used the red colour as a dominance signal (Pryke & Griffith 2006). Under the foraging scenario described above, signalling of personality via head colour could therefore act to reduce the chances of escalated conflict at feeding sites, and even enhance coordination if individuals were to assort according to head colour (Dyer et al. 2009; Harcourt et al. 2009; Webster & Ward 2011).

In addition to the differences in behaviours seen with respect to head colour, we also found that males were faster at approaching and contacting a novel object than females. Sex differences in exploratory behaviour have been shown in great tits, *Parus major* (Dingemanse et al. 2003), and red-rumped parrots, *Psephotus haematonotus* (Mettke-Hofmann 2000a). These sex differences in exploratory behaviour may be explained by differing roles in mate choice and reproduction. In the Gouldian finch, the male takes the lead in nest-hole inspection, whereas the female often shows caution (Goodwin 1982), which could explain why males are more neophilic. However, as sex differences were only found in one of the traits tested, this needs to be more thoroughly explored.

Given that the Gouldian finch is a highly social species (Dostine et al. 2001), it is important to investigate what roles the head colours (and therefore personality traits) play in social situations (Webster & Ward 2011). Mixing pairs of birds of differing head colours in similar personality experiments as described in this study would ascertain the effect of another individual of differing and same head colour on the reactions. In addition, a social foraging experiment involving differing ratios of head colours would be needed to determine whether the head colours signal different roles in the social group. These ideas are being actively researched. In addition, theoretical and empirical evidence suggests that individuals that are more aggressive and take more risk have a faster 'pace of life' (e.g. mature faster or grow faster; Stamps 2007); in the Gouldian finch these traits are decoupled, providing an ideal system to explore the underlying mechanisms as we are unable to predict which head colour, for example, may mature faster. Furthermore, given that mature birds with head-colour differences

have been found to differ in their physiology (Pryke et al. 2007), this system also offers an ideal opportunity to explore the pathways between genetic variation and the expression of personality.

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