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Colour polymorphic Gouldian finches avoid complex backgrounds but prefer simple camouflage colours over white backgrounds

Katarina Perkovic^{1,2} & Claudia Mettke-Hofmann^{2*}

¹Faculty of Science, Department of Biology, University of Zagreb, Rooseveltov trg 6, 10000 Zagreb, Croatia

²School of Natural Sciences & Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool, L3 3AF, United Kingdom;

* Corresponding author: C.C.Mettke-Hofmann@ljmu.ac.uk; +44 (0)151 231 2247

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Abstract:

Many animals blend in well with their environment known as camouflage which is a successful predator avoidance strategy. However, captive environments often do not allow for camouflage and may result in stress and reduced welfare. We investigated whether colour polymorphic Gouldian finches use background matching or complex backgrounds as a camouflage strategy. Birds were tested in unfamiliar cages with half of the cage with one background and the other half with another background. The time spent in front of each background was measured. The first experiment compared a simple green background versus a complex patterned background consisting of red, green and black shapes, whereas the second experiment compared a simple green background against a white background which is often used in cages. Backgrounds were swapped after 10 days to control for site preferences (phase 1 and 2). In both experiments all birds clearly preferred the simple green background. Diverting habituation processes were observed in the second experiment with black-headed birds visiting the white background more during phase 1 than phase 2, whereas the opposite was the case for the red-headed birds. In the first experiment, preference for open habitats may have interfered with optimal background matching. The second experiment showed that white backgrounds are aversive for the birds. Different habituation speeds are consistent with differences in exploration and risk-taking between the head colour morphs. The results show that 2D background colours are a simple but effective enrichment to increase welfare in birds.

Keywords: Background matching; Camouflage; Welfare; Bird; 2D

1. Introduction

Animal welfare is a major concern when keeping animals in captivity. Environmental enrichment plays an important part to improve welfare and promote natural behaviour (Matheson et al., 2008; Newberry, 1995; Robbins and Margulis, 2016). In birds, specifically song birds, enrichment often comprises foraging substrates, water baths, natural branches and area of cover (Bateson and Feenders, 2010). Most of these enrichments aim to increase natural behaviours and reduce stereotypical behaviours. However, another important aspect of welfare is how safe an animal feels in its environment. While many bird species are extremely colourful, their plumage is well adapted to their natural environment and birds often 'hide in plain sight' by using colours and patterns that match their environment making them difficult to detect for potential predators (Kjernsmo and Merilaita, 2012). This kind of behaviour is an adaptation to natural environments (Endler, 1978), and based on the assumptions that natural behaviour improves welfare of captive animals (Bateson and Feenders, 2010; Engerbetson, 2006; Matheson et al., 2008), providing the animal with a background that supports camouflage might play an important role as a form of enrichment and to reduce stress.

Blending in with the environment is known as background matching or crypsis, and occurs throughout the animal kingdom (Endler, 1978). A colour pattern is considered cryptic if it approximates those of the background in size distribution, colour frequencies, brightness or contrast and geometry (if the prey is normally seen only in a particular orientation) and resembles a random sample of the background (Endler, 1978). Background matching has been shown to be a predator avoidance strategy (Johnsson and Kjällman-Eriksson, 2008; Morgans and Ord, 2013). The importance of background matching in captivity has been investigated in European cuttlefish (*Sepia officinalis*). Juveniles often injure themselves when startled and Tonkins et al. (2015) investigated the effect of background on thigmotaxis and stress behaviour. They tested plain, bare plastic tanks against four types of enriched tanks (gravel, sand, synthetic seaweed, and photographs of gravel). When simulating cleaning routines, cuttlefish displayed more thigmotaxis and stress behaviours in bare tanks than in enriched tanks. Interestingly, cuttlefish preferred photographs of gravel over actual gravel possibly due to gravel being too fine for cuttlefish to hide or burry in (Tonkins et al., 2015). The study suggested that 2D backgrounds can be used as a substitute for actual substrate as they do reduce negative behaviours, and as such improve welfare of captive animals. Similarly, the African Clawed Frog (*Xenopus laevis*) which is known to use cryptic colouration as a defence mechanism preferred natural and ecologically relevant black background over non-relevant white background (Holmes et al., 2016). Moreover, corticosterone release, occurrence of atypical behaviour and weight loss was higher in frogs with white backgrounds. The study concluded that tank background colour is an important aspect of welfare in captive African Clawed Frogs (Holmes et al., 2016).

The hypothesis that background matching reduces the risk of detection by visual predators has recently been challenged by an alternative hypothesis. Merilaita (2003) suggested that information processing in predators is reduced in complex habitats resulting in lower detection of prey irrespective of their camouflage with the respective environment. Support for this hypothesis comes from least killifish (*Heterandria formosa*) who preferred complex backgrounds over matching ones in some contexts including predation (Kjernsmo and Merilaita, 2012), blue tits (*Cyanistes caeruleus*) who indeed needed longer to find artificial prey on a complex background (Dimitrova and Merilaita, 2010) and a similar study comparing detectability of artificial prey by birds and humans (Xiao and Cuthill, 2016).

Background matching camouflages an organism to only a specific microhabitat. However, animals often use different microhabitats to which they will be matched to different degrees. Organisms can respond in two ways to this challenge: they will either closely match one of the microhabitats or find some form of compromise by loosely matching both or more microhabitats (Sherratt et al., 2016). Several experiments have been conducted to investigate which of the two responses is more protective. In an experiment conducted by Dimitrova and Merilaita (2009), blue tits predated on cryptic artificial prey items with different patterns (small, intermediate, large) set against two different backgrounds (small and large patterned). Intermediate patterned prey had a slightly higher chance of survival than matching patterns. Sherratt et al. (2016) used virtual prey searched for by human predators and allowed the prey to evolve (any undetected prey would automatically replicate) under alternating light-dark backgrounds. Prey rapidly evolved to match one or the other background. Sherratt et al. (2016) suggested that very dissimilar backgrounds favour specialisation (as found in their simulation), whereas more similar backgrounds may favour intermediate morphs (as in the blue tit experiment). This is especially important for species inhabiting two or more habitats and species with variable activity patterns.

Interestingly, species occurring in several habitats often show colour polymorphism (Galeotti et al., 2003). Colour polymorphism is the coexistence in one interbreeding population of two or more sharply distinct and genetically determined forms, the least abundant of which is present in numbers too great to be due to solely recurrent mutation and is a widespread phenomenon across the animal kingdom (Galeotti et al., 2003). Colour polymorphism has been linked to different background-matching abilities (Sowersby et al., 2015) and has been shown to reduce predation (Karpestam et al., 2016). For example, the red devil (*Amphilophus labiatus*) is a polymorphic cichlid fish occurring in two morphs - gold and dark (Sowersby et al. 2015). While the dark morph is much more abundant in nature, the gold morph is genetically and behaviourally dominant and shows higher growth rate. However, the black morph was better able to match different backgrounds than the gold morph (Sowersby et al., 2015) which may reduce risk of predation, and might explain why certain colour morphs might be less abundant in nature despite having some apparent advantages.

In this study we tested background preferences in the colour polymorphic Gouldian Finch (*Erythrura gouldiae*) which is an endemic songbird to Australia and categorised as near-threatened by BirdLife International (2016) and as endangered by the Australian Government (EPBC 2018) with an estimated population size of less than 2,500 individuals. Despite its rarity in the wild it is one of the most abundant birds kept by breeders and private keepers (Nicolai and Steinbacher, 2001) due to its incredibly colourful plumage with a green back, purple breast, yellow underparts and different head colours in both sexes. Much like the red devil, the Gouldian finch has a genetically dominant red-headed morph and recessive black-headed morph which is more abundant than the red-headed morph (70% vs 30%) and a very rare yellow-headed morph (<1 %; Brush and Seifried, 1968). While red-headed birds are more aggressive and dominate black-headed birds (Pryke, 2007; Pryke and Griffith, 2006), the latter are more explorative and take greater risk in dangerous situations (Williams et al., 2012). The aims of this study were to test whether Gouldian finches a) use background-matching as a form of camouflage and whether b) red-headed and black-headed morphs have different preferences. We specifically tested for complex background matching as this reduces predation irrespective of the degree of camouflage (Dimitrova and Merilaita, 2014) but also tested for background matching in general. We also considered whether the two head colours responded differently to the backgrounds over the course of the experiment (habituation). This latter was

included as red-headed birds are more cautious in unfamiliar situations than black-headed birds (Mettke-Hofmann, 2012; Williams et al., 2012) which may affect engagement with different complexity (experiment 1).

2. Materials and methods

2.1. *Study species*

The Gouldian Finch is a colourful song bird of the family Estrildidae found in northern Australia, ranging from the northern region of the Northern Territory to the Kimberley region of Western Australia with a few records from Cape York Peninsula and north-west Queensland (BirdLife International, 2016). It inhabits open tropical savannah woodland and feeds on annual grasses such as *Sorghum* sp. during the dry season and perennial grasses during the wet season (Weier et al. 2017). All birds in captivity outside of Australia derive from wild stocks imported before the import ban in 1960 (Franklin et al., 1999).

For this study 24 captive bred birds purchased from different breeders were used. We had equal numbers of black-headed and red-headed birds in both sexes (six black-headed and six red-headed birds, each) with ages ranging from two to five years. Birds were kept in mixed sex and age groups of six birds in holding cages (1 m x 1.2 m x 0.8m; H x L x W). All birds were familiar with each other due to mixing birds in other experiments when testing for personality (King et al., 2015; Mettke-Hofmann, 2012; Williams et al. 2012). Holding cages contained natural twigs, perches, food (Blattner Amadine Zucht Spezial, Blattner Astrilden Spezial, bird grit from Blattner Heimtierfutter, Ermengerst, Germany and eggshells) and water ad lib (incl. water bath). Cage walls and ceiling were all wire mesh but adjacent cages were separated by white wooden dividers and the rear of the cage faced a white wall. Cages were arranged along the side of the walls allowing the birds to see each other.

For the experiment groups of four newly assembled individuals were moved into experimental cages (1 m x 1.2 m x 0.7 m) for two weeks. Cages were arranged in the middle of the experimental room in two rows with the rear side of the cages in the two rows facing each other. Experimental cages consisted of two perches; one left and one right of the cage and two feeders (with the same food as in the holding cages) in the middle of the front of the cage (see Fig. 1) and drinkers next to them. Three walls were made of wood, whereas the front and ceiling were wire mesh. Overall, four experimental cages were available for parallel testing of 16 birds. This resulted in two sets of testing, the first set with four groups and the second set with two groups which followed directly after the first set was finished. The arrangement allowed having groups back-to-back to the opposite cage rather than one group without a group on the rear side which could have resulted in biases towards the side closer to the other birds. Birds could hear each other but not see each other. Within each group birds were matched for sex to avoid formation of breeding pairs. The six groups of birds differed in their composition. For each sex, we had one purely black-headed group, one purely red-headed group, and one mixed head colour group (two birds of each head colour). Birds were individually colour banded for identification.

2.2. Experimental set-up

Overall, two experiments were conducted, the first comparing complex vs simple backgrounds, the second comparing two simple backgrounds of different camouflage. The same birds were used in both experiments.

2.2.1. Experiment 1: Comparison of complex and simple backgrounds

For the first experiment complex and simple backgrounds were compared. Both backgrounds were new to all birds. Half of the cage (side and rear wall) was covered with the simple background, the other half with the complex background (Fig. 1). Backgrounds were printed using normal printing paper (60 cm x 40 cm) and taped to the walls (using two sheets, each). The complex background consisted of irregularly shaped red, black, and green patterns in the proportion of 1/4 red, 1/4 black and 1/2 green colour and was matched in lightness (Dimitrova and Merilaita, 2009) to the simple uniformly green background. Red and black were chosen to make the complex background equally attractive to both colour morphs, green was chosen according to the green back of all birds. Backgrounds were designed in Adobe Photoshop cs6 with #1e5a15 (green) for both backgrounds, and #ff2b19 (red) and #131313 (black) additionally for the complex background. Lightness of backgrounds was compared using Lab Colour mode in Adobe Photoshop. The simple background had a lightness of 33, whereas the complex background had a lightness of 32.75 calculated as the mean value of red, black and green lightness ($0.25 \times 59 + 0.25 \times 6 + 0.5 \times 33 = 32.75$). Position of the complex and simple background was balanced across cages and groups.



Figure 1: Cage with simple and complex patterned background.

The experiment consisted of two phases; phase 1 lasted for 10 days with data collection occurring on day 1 – 5 (Monday – Friday) and 8 – 10 (Monday – Wednesday) after which backgrounds were swapped sidewise (left-right) in each cage (phase 2) to account for any side preferences (Fig. 2). Phase 2 lasted for three days (day 10 – 12; Wednesday - Friday). Phase 1 was longer to allow the birds to get used to the new group composition and the unfamiliar room and cages. Data collection occurred for one hour each day with digital video cameras (connected to a GeoVision 1480 (Taiwan) recording system) positioned in front of the cage. Video recording commenced at 9:00 am each day, except for day 1 and day 10 (after the swap) when data collection started at 2:00 pm immediately after moving the birds into the cage. It should be noted that two recordings were done on day 10, one at 9:00 am

with the original setting and one at 2:00 pm immediately after backgrounds had been swapped (see Fig. 2).

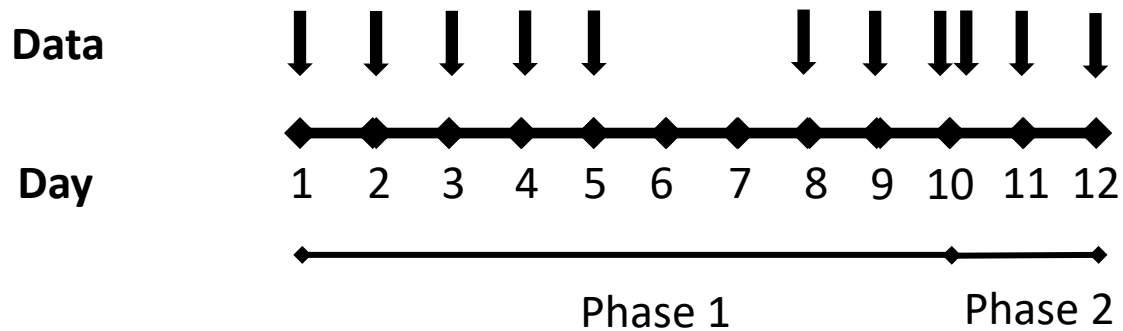


Figure 2: Timeline of experimental protocol for experiment 1

The duration of phase 1 and 2 are shown as well as days of data collection. On day 10, the last day of phase 1 was run in the morning, backgrounds were then swapped sidewise and the first day of phase 2 was run after moving the birds back into the cage in the afternoon.

2.2.2. Experiment 2: Comparison of two simple backgrounds differing in camouflage

The second experiment compared the simple green background against a plain white background to test preferences of birds between a more natural looking green colour that allows for a certain degree of camouflage and a plain white colour that is used in most cages. Both background colours were familiar to the birds, the green background from experiment 1 and the white background from the normal holding cages though exposure to the green one (2 weeks) was shorter than exposure to the white one. For the green background we used the same simple background as in the previous experiment, and the white background was a plain paper sheet.

Cages were set up the same as in the previous experiment, except that the complex background was replaced with the white one. Furthermore, phase one lasted only 9 days with data collection during phase 1 on days 1 – 4 (Monday – Thursday) and 8 – 9 (Monday – Tuesday). Phase 2 lasted three days with data collection on all days (day 9 – 11; Tuesday - Thursday). Experiments started at 9:00 am each day except for experiments done on day 1 and day 9 (after the swap) which started at 2:00 pm. During this experiment only two groups were tested each time to avoid side preferences in cages close to the wall. Groups consisted of the same birds as in experiment 1. The first groups tested were pure black-headed birds in both sexes, followed by pure red-headed birds in both sexes and one final group of mixed head colour females. We excluded the male mixed group due to a bird loss. The total number of birds used in this experiment was 20.

2.3. Data analysis

For both experiments, background preferences were determined by extracting a) the total time spent in front of each background (this included time spent on the perch and the feeder in front of the tested background) and b) the total time spent on each perch for each individual and day from the videos. We calculated the difference in time t (s) spent in front of each background ($t(\text{simple}) -$

$t(\text{complex})$ or $t(\text{green}) - t(\text{white})$, respectively) for each individual and day. As the two variables extracted under a) and b) were highly correlated (Spearman's correlation total time perch and feeder vs total time perch only for experiment 1, last day, phase 1: corr. coef. 0.826, $p < 0.001$, and last day phase 2: corr. coef. 0.719, $p < 0.001$) only the time spent on the perch alone was used as it avoids any food-related interference. To account for the overall different amounts of time spent on perches we calculated the proportion spent in front of each background in relation to the overall time spent on perches ($t(\text{simple}) - t(\text{complex}) / \Sigma[t(\text{simple}) + t(\text{complex})]$ and $t(\text{green}) - t(\text{white}) / \Sigma[t(\text{green}) + t(\text{white})]$).

For both experiments the following analyses were conducted. (1) We first tested exclusively for side preferences by comparing data from the last day of phase 1 with data from the first day of phase 2 (for the green-white background we used the last day of phase 2) using a General Linear Mixed Model (GLMM). The dependent variable was the difference in time spent in front of each background in phase 1 and phase 2, respectively, expressed as proportions (see above) nesting birds within cages. We used a Gamma distribution with log link function. Bird ID was used as a random factor to account for repeated testing and fixed factors were cage, phase and phase x cage. Non-significant terms were removed step-by-step starting with the least significant one. In the first experiment, the group consisting of pure red-headed males showed a side preference irrespective of the background possibly due to the cage close to the wall (GLMM $F_{11,36} = 2.010$, $p = 0.057$, cage: $F_{5,36} = 2.834$, $p = 0.029$, phase: $F_{1,36} = 3.089$, $p = 0.087$, cage x phase: $F_{5,36} = 2.644$, $p = 0.039$). This group was excluded from all subsequent analyses for experiment 1. In experiment 2, no side preferences were shown ($F_{9,27} = 1.324$, $p = 0.272$, phase: $F_{1,15} = 0.391$, $p = 0.541$, cage x phase: $F_{8,30} = 1.440$, $p = 0.221$).

(2) For the main analysis we investigated whether birds showed a preference for a particular background by comparing the time spent in front of the simple and complex (green and white for experiment 2) background on two days, the last day of phase 1 and the last day of phase 2 in both experiments. Here we used the actual time spent on each side (not the difference). As data were left skewed for the simple and white backgrounds but right skewed for the complex and green backgrounds a Wilcoxon Signed Rank test was used.

(3) Finally, we tested whether birds habituated over the testing period by comparing the last day of phase 1 with the last day of phase 2 in both experiments using GLMM. Changes in time spent in front of each background over time would indicate that birds may become less avoidant of one background with time. The dependent variable was the difference in time spent in front of each background on the last day of phase 1 and the last day of phase 2 expressed as proportions nesting birds within cages. We used a Gamma distribution with log link function. In a first model we included phase, head colour, age and sex as fixed factors. Bird ID was used as a random factor to account for repeated testing. Non-significant terms were removed step-by-step starting with the least significant one. In a second model we included the two-way interactions head colour x phase, sex x phase and age x phase. Non-significant terms were removed step-by-step starting with the least significant one.

2.4. Ethical approval

Experiments have been in accordance with The Association for the Study of Animal Behaviour (ASAB) ethical guidelines (Guidelines for the use of animals 2018) and non-invasive in nature. Experiments have been approved by the University Ethics Committee.

3. Results

3.1. First experiment: complex vs. simple green background

During both phases, all birds spent the majority of their time in front of the simple green background (Wilcoxon test: Phase 1: $z_{20}=3.771$, $p<0.001$; phase 2: $z_{20}=3.920$, $p<0.001$; Fig. 3). Time spent in front of each background did not change between phase 1 and 2 and was not affected by head colour, age, sex or any of the two-way interactions (Table 1; Fig. 4).

Table 1: Comparison of the proportion of time spent in front of each background (simple vs complex) between the last day of phase 1 (day 10) and the last day of phase 2 (day 12) in relation to head colour, age and sex (model 1) and 2-way interactions (model 2). Non-significant terms were removed in a step-wise method starting with the highest significance level.

Model	F-value	DF	P-value
Model 1			
Single variables			
Head colour, age, sex, phase	1.087	6,6	0.460
Head colour, age, sex	1.196	5,6	0.415
Head colour, sex	1.300	2,5	0.356
Sex	2.579	1,3	0.216
Model 2			
2-way interactions			
Head colour x phase, age x phase, sex x phase	1.753	11,14	0.159
Head colour x phase, age x phase	0.110	9,29	0.999
Head colour x phase	1.797	3,24	0.174

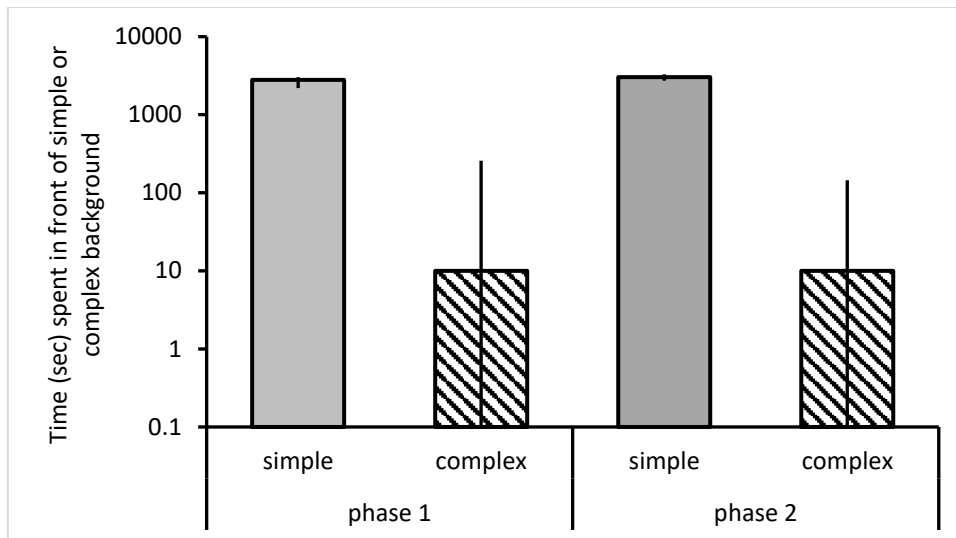


Figure 3: Median and quartiles of time (sec) spent in front of the simple (grey bars) or complex (hatched bars) background during the last day of phase 1 (day 10) and the last day of phase 2 (day 12). Attention is drawn to the logarithmic scale on the y-axis.

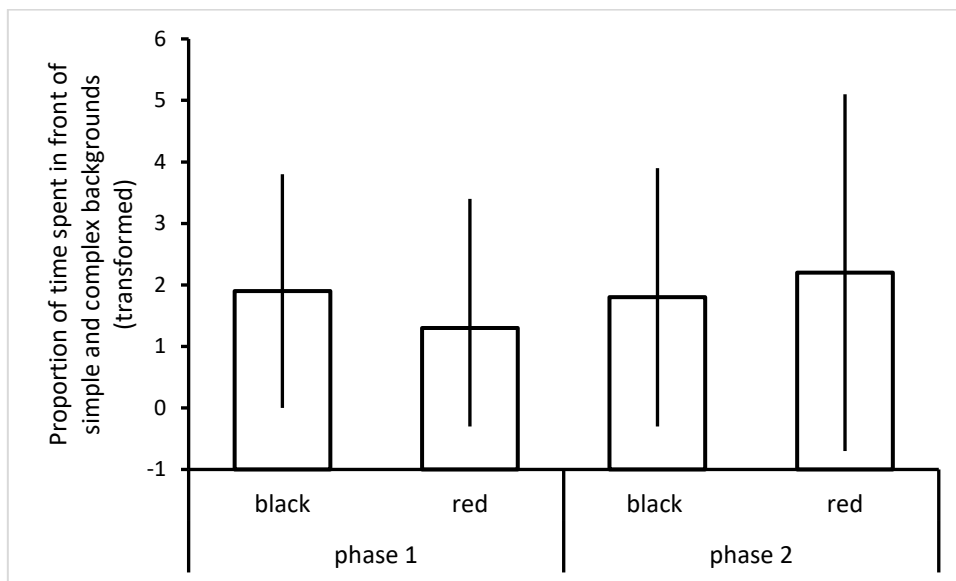


Figure 4: Mean \pm SE proportion of time spent in front of the simple or complex background during the last day of phase 1 (day 10) and the last day of phase 2 (day 12) for black-headed and red-headed birds. Proportions are log transformed with higher values representing a greater proportion of time spent in front of the simple background.

3.2. Second experiment: green vs plain white background

In both phases, all birds clearly preferred the green background over the white one (Wilcoxon test: Phase 1: $z_{20} = -2.242$, $p = 0.025$; phase 2: $z_{20} = -3.360$, $p = 0.001$; Fig. 5). However, birds showed some change in time spent in front of each background from phase 1 to phase 2. The best model included the interaction head colour \times phase (Table 2). While spending most of the time in front of the green background, the black-headed birds ventured longer in front of the white background during phase 1

as compared to phase 2, whereas the red-headed birds showed the opposite with moving to the white background more often during phase 2 as compared to phase 1 (Fig. 6).

Table 2: Comparison of the proportion of time spent in front of each background (green vs white) between the last day of phase 1 (day 9) and the last day of phase 2 (day 11) in relation to head colour, age and sex (model 1) and 2-way interactions (model 2). Non-significant terms were removed in a step-wise method starting with the highest significance level. Bold: final model

Model	F-value	DF	P-value
Model 1			
Single variables			
Head colour, age, sex, phase	1.175	6,15	0.372
Head colour, sex, phase	2.323	3,18	0.110
Head colour, sex	3.419	2,17	0.057
Head colour	3.732	1,5	0.113
Model 2			
2-way interactions			
Head colour x phase, age x phase, sex x phase	1.521	11,16	0.215
Head colour x phase, sex x phase	2.821	5,21	0.043
Head colour x phase	3.732	3,12	0.043

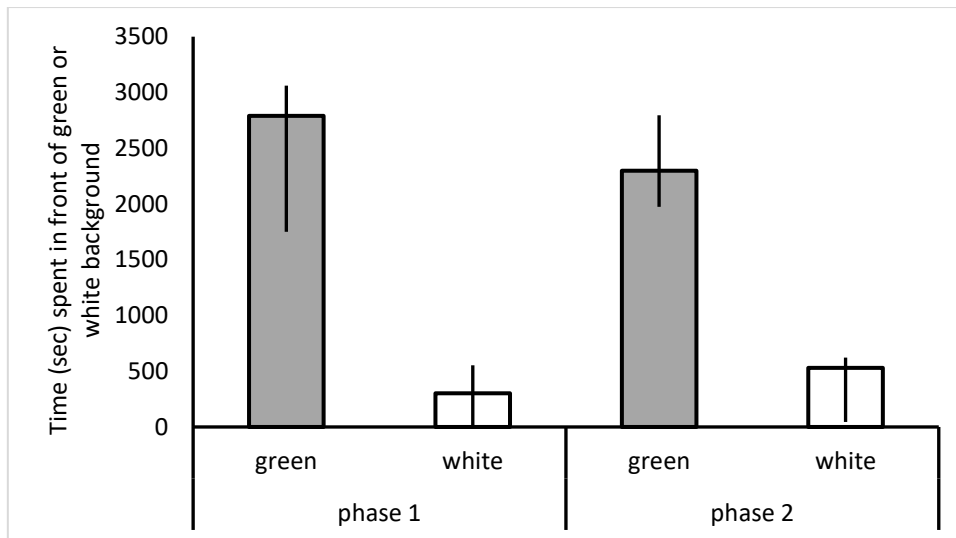


Figure 5: Median and quartiles of time (sec) spent in front of the green (grey bars) or white background during the last day of phase 1 (day 9) and the last day of phase 2 (day 11). Attention is drawn to the logarithmic scale on the y-axis.

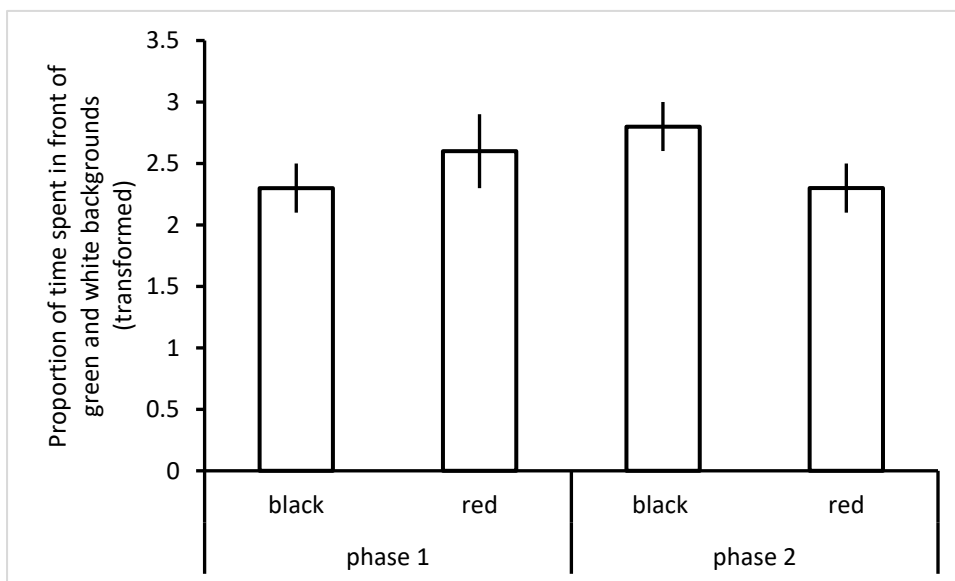


Figure 6: Mean \pm SE proportion of time spent in front of the green or white background during the last day of phase 1 (day 9) and the last day of phase 2 (day 11) for black-headed and red-headed birds. Proportions are log transformed with higher values representing a greater proportion of time spent in front of the green background.

4. Discussion

The Gouldian finches showed clear background preferences; in experiment 1 the birds preferred the simple green background over the more complex one and in experiment 2 they again preferred the green over the white background. In the latter experiment, head colour affected habituation with black-headed birds spending more time in front of the white background during phase 1 than phase

2, whereas red-headed birds gradually increased their time spent in front of the white background from phase 1 to phase 2.

The first experiment specifically tested whether Gouldian finches prefer complex backgrounds over simple ones as a means of camouflage (Dimitrova and Merilaita, 2014; Xiao and Cuthill, 2016). This was clearly not the case as the birds spent the majority of their time in front of the simple green background. This is surprising as at least for the human eye the birds were much more difficult to see in front of the complex background. The complex background was not only more complex but also matched the colours of the Gouldian finch better than the simple green background. Both should have made this background more attractive to the Gouldian finch; the better match in colours in support of the camouflage hypotheses (Endler, 1978) and the overall complexity in support of information processing constraints (Merilaita et al., 2017). With respect to the camouflage hypothesis, the complex background may not have been a perfect match in terms of colour spectrum, frequency and geometry of colours necessary for background matching (Endler, 1978). The main predators of Gouldian finches in the wild are avian predators on adults (Hatton, 2013) and reptiles such as snakes and goannas on nestlings (Tiedemann, 1996). Birds have tetrachromatic colour vision (Cuthill et al., 1999) and perceive colours differently than humans, including the ability to see in the ultraviolet range (UV; Cuthill et al., 1999). While the Gouldian finch's plumage only contains UV in the small turquoise band behind the neck (Pryke and Griffith, 2006) which may be negligible for our study, our printed colours may have deviated considerably from the birds' colours making them more conspicuous than for our eye. However, this would not be an issue with respect to the information processing hypothesis as other studies have shown that complex backgrounds are preferred over matching backgrounds (Kjernsmo and Merilaita, 2012). The same study found background matching only in the presence of predators but not in their absence (Kjernsmo and Merilaita, 2012). This could be the case in the Gouldian finches and follow-up studies should simulate predator threats to see whether preferences change.

Another reason for preferring the simple background could be that the patterning was relatively large and when mounted to the wall appeared very unsettled. The birds may have preferred the calmer background. Alternatively, Gouldian finches live in simple open savannah habitats (Weier et al., 2017) and the simple green background may match this habitat type better. This is an interesting point as habitat structure may have interacted with optimal camouflage. Whether Gouldian finches do not use complex backgrounds as camouflage or whether the unsettled patterning kept them away has to be investigated in future experiments.

Finally, Gouldian finches have a very colourful plumage. Halperin et al. (2017) found in lizards that mobile foragers have a dazzled pattern to impair detection during movement, whereas less mobile foragers have a camouflage pattern. While colourful, Gouldian finches are very calm birds and rarely move when sitting in a tree (own observation by C. M.-H. in the wild) and also our captive birds spent extended periods of time sitting at the same location. Therefore, it seems Gouldian finches try to camouflage while perching rather than to conceal their movement.

The second experiment tested more specifically between typical white backgrounds used in animal housing and a more camouflaging green background. This time the birds clearly chose the camouflage option. This may indicate a preference for the more matching background which would be in support of the camouflage hypothesis (Endler, 1978). Alternatively, it may indicate avoidance of the white

background. Birds may have felt exposed on the white background. As the birds knew the white background for longer than the green background it is unlikely that they were afraid of it due to lower familiarity. Background matching is a natural predator avoidance strategy (Johnsson and Kjällman-Eriksson, 2008; Morgans and Ord, 2013) and preventing this natural behaviour may affect welfare. We did not measure stress levels but future studies should consider this to get a better understanding about the importance of background on wellbeing. However, the few other studies about camouflage showed an effect on welfare in European cuttlefish and African clawed frogs (Tonkins et al., 2015; Holmes et al., 2016). A camouflaging background also links to other visual enrichment such as being able to see other animals (Newberry, 1995). Changing background colour is an easy enrichment that does not take up any space and should be considered for other bird species. However, it should be kept in mind that actual 3D background (real perches and leaves) considering complexity and texture may be more effective than colour alone (Tonkins et al., 2015).

Interestingly, the black-headed and red-headed birds showed different habituation reactions from phase 1 to phase 2. While all preferred the green background throughout the experiment, the black-headed birds spent more time in front of the white background during phase 1 than during phase 2. In contrast, the red-headed birds showed the opposite and spent more time in front of the white background during phase 2 as compared to phase 1. Black-headed Gouldian finches have been shown to be more explorative and risk-taking than red-headed birds (Mettke-Hofmann, 2012; Williams et al., 2012). Red-headed birds are more conspicuous and may avoid being exposed more than black-headed birds to reduce predation (Mettke-Hofmann, 2012). Our findings are consistent with this. While both background colours were known to the birds, the experiment was done in a different room with differently arranged cages (birds could only hear each other but not see each other) than the holding conditions. The part with the white background might have been perceived as more threatening and the birds spent most of the time in front of the safe green background. However, the higher risk-taking propensity in black-headed birds may have resulted in more excursions to the more threatening white background already during the first phase, whereas the red-headed birds did so only during the second phase when they had more settled down. This shows that the two head colour morphs habituated at different speeds and that this process of full familiarisation can take at least two weeks.

In summary, both head colour morphs preferred a simple green background over a complex patterned one but more research is needed to confirm this. When having the choice between plain green or white backgrounds all birds preferred the more camouflaging green background over the possibly more frightening white background. However, the risk-taking and explorative black-headed birds visited the white background more during phase 1 as compared to phase 2, whereas the opposite was the case for the red-headed birds. This indicates faster habituation to the white background in black-headed birds. Future research should test different patterns, particular in size.

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6. References

- Bateson, M., Feenders, G., 2010. The Use of Passerine Bird Species in Laboratory Research Implications of Basic Biology for Husbandry and Welfare. *ILAR J.* 51, 394-408.
- BirdLife International, 2016. *Erythrura gouldiae*. The IUCN Red List of Threatened Species 2013: e.T22719744A48152068. <http://dx.doi.org/10.2305/IUCN.UK.2013-2.RLTS.T22719744A48152068.en> Last accessed 15/02/2018.
- Brush, A.H., Seifried, H., 1968. Pigmentation and Feather Structure in Genetic Variants of the Gouldian Finch, *Poephila gouldiae*. *Auk* 85, 416-430.
- Cuthill, I.C., Bennett, A.T.D., Partridge, J.C., Maier, E.J., 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. *Am. Nat.* 160, 183-200.
- Dimitrova, M., Merilaita, S., 2009. Prey concealment: visual background complexity and prey contrast distribution. *Behav. Ecol.* 21, 176-181.
- Dimitrova, M., Merilaita, S., 2010. Prey concealment: visual background complexity and prey contrast distribution. *Behav. Ecol.* 21, 176-181.
- Dimitrova, M., Merilaita, S., 2014. Hide and seek: properties of prey and background patterns affect prey detection by blue tits. *Behav. Ecol.* 25, 402-408.
- Endler, J.A., 1978. A predator's view of animal color patterns. *Evol. Biol.* 11, 319-364.
- Engebretson, M., 2006. The welfare and suitability of parrots as companion animals: a review. *Anim. Welf.* 15, 263-276.
- EPBC, 2018. Environment Protection and Biodiversity Conservation Act. Species profile and threat database. Gouldian finch. http://www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=413 . Last accessed 19/02/2018.
- Franklin, D.C., Burbidge, A.H., Destine, P.L., 1999. The harvest of wild birds for aviculture: an historical perspective on finch trapping in the Kimberley with special emphasis on the Gouldian Finch. *Austr. Zool.* 31, 92-109.
- Galeotti, P., Rubolini, D., Dunn, P.O., Fasola, M., 2003. Colour polymorphism in birds: causes and functions. *J. Evol. Biol.* 16, 635-646.
- Guidelines for the use of animals, 2018. Guidelines for the treatment of animals in behavioural research and teaching. *Anim. Behav.* 135, I-X.
- Halperin, T., Carmel, L., Hawlena, D., 2017. Movement correlates of lizards' dorsal pigmentation patterns. *Func. Ecol.* 31, 370-376.
- Hatton, L., 2013. Predation as a mechanism maintaining polymorphism: Evidence for disruptive selection in the Gouldian finch. MPhil Thesis Macquarie Univ.
- Holmes A.M., Emmans, C.J., Jones, N., Coleman, R., Smith, T.E., Hosie, C.A., 2016. Impact of tank background on the welfare of the African clawed frog, *Xenopus laevis* (Daudin). *Appl. Anim. Behav. Sci.* 185, 131-136.

- Johnsson, J.I., Kjällman-Eriksson, K., 2008. Cryptic prey colouration increases search time in brown trout (*Salmo trutta*): effects of learning and body size. *Behav. Ecol. Sociobiol.* 62, 1613-1620.
- Karpestam, E., Merilaita, S., Forsman, A., 2016. Colour polymorphism protects prey individuals and populations against predation. *Sci. R.* 6, 22122 | DOI: 10.1038/srep22122.
- King, A.J., Williams, L.J., Mettke-Hofmann, C., 2015. The effect of social conformity on Gouldian finch personality. *Anim. Behav.* 99, 25-31.
- Kjernsmo, K., Merilaita, S., 2012. Background choice as an anti-predator strategy: the roles of background matching and visual complexity in the habitat choice of the least killifish. *Proc. R. Soc. B Lond* 279, 4192-4198.
- Matheson, S.M., Asher, L., Bateson, M., 2008. Larger, enriched cages are associated with 'optimistic' response biases in captive European starlings (*Sturnus vulgaris*). *Appl. Anim. Behav. Sci.* 109, 374-383.
- Merilaita, S., 2003. Visual background complexity facilitates the evolution of camouflage. *Evol.* 57, 1248-1254.
- Merilaita, S., Scott-Samuel, N.E., Cuthill, I.C., 2017. How camouflage works. *Phil. Trans. R. Soc. B* 372, 20160341. <http://dx.doi.org/10.1098/rstb.2016.0341>.
- Mettke-Hofmann, C. 2012. The effect of head colour and age on personality traits in a social setting. *Ethology* 118, 906-916.
- Morgans, C.L., Ord, T.J., 2013. Natural selection in novel environments: predation selects for background matching in the body colour of a land fish. *Anim. Behav.* 86, 1241-1249.
- Newberry, R.C., 1995. Environmental enrichment: Increasing the biological relevance of captive environments. *Appl. Anim. Behav. Sci.* 44, 229-243.
- Nicolai, J., Steinbacher, J., 2001. Prachtfinken: Australien, Ozeanien, Suedostasien. Ulmer publisher, Stuttgart.
- Pryke, S.R., 2007. Fiery red heads: female dominance among head color morphs in the Gouldian finch. *Behav. Ecol.* 18, 621-627.
- Pryke, S.R., Griffith, S.C., 2006. Red Dominates Black: Agonistic Signalling among Head Morphs in the Colour Polymorphic Gouldian Finch. *Biol. Sci.* 273, 949-957.
- Robbins, L., Margulis, S.W., 2016. Music for the Birds: Effects of Auditory Enrichment on Captive Bird Species. *Zoo Biol.* 35, 29-34.
- Sherratt, T.N., Pollitt, N., Wilkinson, D.M., 2006. The evolution of crypsis in replicating populations of web-based prey. *Oikos* 116, 449-460.
- Sowersby, W., Lehtonen, T.K., Wong, B.B.M., 2015. Background matching ability and the maintenance of a colour polymorphism in the red devil cichlid. *J. Evol. Biol.* 28, 395-402.
- Tiedemann, S.C., 1996. Causes of the decline of the Gouldian Finch *Erythrura gouldiae*. *Bird Cons. Int.* 6, 49-61.
- Tonkins, B.M., Tyers, A.M., Cooke, G.M., 2015. Cuttlefish in captivity: An investigation into housing and husbandry for improving welfare. *Appl. Anim. Behav. Sci.* 168, 77-83.

Weier, A., Radford, I.J., Manson, E.A., Durrans, L.J., Lawes, M.J., 2017. Frequent fires reduce the nutritional quality of *Sorghum stipoides* seed, a keystone food resource for the Gouldian finch (*Erythrura gouldiae*). *Rangeland J.* <http://dx.doi.org/10.1071/RJ16124>.

Williams L.J., King, A.J., Mettke-Hofmann, C., 2012. Colourful characters: head colour reflects personality in a social bird, the Gouldian finch, *Erythrura gouldiae*. *Animal Behav.* 84, 159-165.

Xiao, F., Cuthill, E.C., 2016. Background complexity and the detectability of camouflaged targets by birds and humans. *Proc. R. Soc. B* 283, 20161527. <http://dx.doi.org/10.1098/rspb.2016.1527>.