Coloration reflects behavioural types in the convict cichlid, *Amatitlania siquia*

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Interindividual behavioural differences, consistent over time and across situations, are frequently related to differences in reproductive success, susceptibility to disease and competitive ability. The behavioural phenotype of a conspecific is likely to affect the outcome of a social interaction, so an individual must be able to accurately assess behavioural phenotypes in order to optimize behavioural responses during mate choice, cooperative relationships and agonistic interactions. However, behavioural assessment based on dyadic interactions in different contexts can be costly because it may require significant time, increase the risk of predation and often necessitates special cognitive abilities. Different colour cues are associated with different life history strategies in many species, so coloration might also correlate with behavioural phenotype. Thus, conspecifics could use coloration as a single cue for the mediation of social interactions. We investigated the relationship between personality and coloration in the monogamous, biparental convict cichlid. This species has black melanin-based stripes with interindividual variation in the intensity of these stripes. In addition, females have bright orange spots on their abdomens. Using repeatable measures of boldness, exploration and aggressiveness, we were able to define a behavioural syndrome and quantified the behavioural type of each individual. Behavioural types were predicted by colour traits. In particular, proactive individuals (more aggressive, bolder and quicker to resume behaviour after being startled) were more likely to be dark and, among females, have smaller orange areas. Our results support the hypothesis that coloration in the convict cichlid is related to personality. Thus, coloration could play an important role in mediating social interactions, allowing a quick and reliable assessment of conspecifics' behavioural types.

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The ability of individuals to assess the behavioural and physiological status of conspecifics is important in mediating social interactions and maintaining social cohesion. In many contexts, individuals do not interact randomly; instead, behavioural phenotype affects the type, number and strength of interactions within populations (Krause, James, & Croft, 2010; Schürch, Rothenberger, & Heg, 2010). Consistent individual behavioural differences over time and across situations are defined as personality. They often correlate with one another, generating behavioural syndromes (Sih, Bell, & Johnson, 2004), and this is likely to have fitness consequences (Dall, Houston, & McNamara, 2004; Smith & Blumstein, 2008) because it affects how individuals associate and interact. Pike, Samanta, Lindström, and Royle (2008) showed that boldness within fish shoals of the three-spined stickleback, *Gasterosteus*

aculeatus, affected the frequency and distribution of interactions. In networks of bold fish, individuals tend to move randomly within the group, with no preferential interactions. By contrast, in networks of shy fish, individuals tend to form a small number of social bonds with one or more conspecifics with which they have the most interactions, and there are limited movements within the shoal. Information gathering thus depends on the behavioural types of individuals within a group. Wilson, Krause, Herbert-Read, and Ward (2014) recently demonstrated the influence of behavioural type on the mutualistic interactions between the cleaner fish, *Labroides dimidiatus*, and its client, in that explorative, bolder and more active fish were more likely to cheat and travelled greater distances from their station. Finally, behavioural types are expected to have significant effects on mating decisions in birds and fish, because individuals prefer mates with similar exploratory behaviours (Schuett, Godin, & Dall, 2011) or they actively avoid aggressive partners (Dzieweczynski, Russell, Forrette, & Mannion, 2014). Assortative mating for behaviour can also reduce the conflict between partners and lead to better reproductive success (Ariyomo & Watt,

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2012, 2013; Schuett, Dall, & Royle, 2011; Schuett, Godin, et al., 2011; Spoon, Millam, & Owings, 2007).

In this context of nonrandom social association, individuals may benefit from quick access to reliable information about conspecifics' behavioural types because this may optimize decision making for selecting and choosing a sexual partner of high quality, developing and maintaining cooperative relationships and reducing injury during agonistic interactions. However, direct personality assessment is likely to be time consuming and risky (Candolin, 2003) because it requires social encounters in many different situations (under predation risk, in conspecific contests, in novel environments, in response to social and nonsocial disturbances, etc.). Moreover, gathering such information from different sources (the environment, conspecifics, oneself) and/or multiple cues (behaviour, morphology, vocalizations) can be cognitively challenging (Bateson & Healy, 2005; Fawcett, Boogert, & Lefebvre, 2011; Galipaud, Bollache, Oughadou, & Dechaume-Moncharmont, 2015). For example, in animal contests, an individual is commonly expected to engage in conflict only if there is a reasonable chance of success. Assessment of opponents may require complex cognitive abilities, but some researchers have proposed simpler processes (Elwood & Arnott, 2012; Fawcett & Mowles, 2013).

Here, we suggest that individuals can perform the apparently complex assessment of behavioural types by the use of single cues that are reliable and easy to reach. Coloration is known to be a key cue for social communication. In fact, coloration covaries with many physiological and morphological traits, and the costs associated with production, maintenance and display support the reliability of colour cues in signalling traits such as body condition, good genes, parasite resistance and immunocompetence (Roulin, 2004). Because colour morphs can also be associated with life history strategies, so differently coloured individuals may have different behavioural types. Individuals could therefore use coloration in intra- and intersexual interactions to assess conspecifics' behavioural traits, such as aggressiveness, ability to defend a territory, parental abilities and tendency to take risks. In fact, several studies of wild vertebrates have reported that dark pigmentation may be related to social status, sexual activity, stress response or boldness (Da Silva et al., 2013; Korzan, Robison, Zhao, & Fernald, 2008; Mafli, Wakamatsu, & Roulin, 2011; Mateos-Gonzalez & Senar, 2012; Van den Brink, Henry, Wakamatsu, & Roulin, 2012). Recent evidence indicates that the activity of the melanocortin system can be locally regulated and coordinated across organs by neuroendocrine communication. This supports the idea that pleiotropic effects of the key regulators of melanogenesis (hormones, cytokines and neuropeptides) might be responsible for the widespread association of melanin-based coloration with behavioural traits (Ducrest, Keller, & Roulin, 2008).

However, melanin-based coloration is only one colour cue associated with behaviour in vertebrates. Many birds and fish display carotenoid-based ornaments; these also covary with behavioural traits and are typically considered to be honest indicators with functions in both sexual and social contexts (Sefc, Brown, & Clotfelter, 2014). For example, colourful birds are more aggressive in competitive contests for access to territory and mates (Pryke & Andersson, 2003; Pryke & Griffith, 2006), and there is a preference for colourful individuals and the same morph type as mates (Godin & Dugatkin, 1996; Pryke & Griffith, 2007). In cichlid fish, recent studies showed that carotenoid-based coloration is positively related to mating success and social dominance (Sefc et al., 2014 for review). If colour traits match an individual's behavioural type, then they can convey reliable information to conspecifics, such as social status, aggressiveness and parental abilities, and thereby mediate social interactions between individuals over access to resources, mate choice or social encounters.

In the present study we investigated the relationship between consistent interindividual behavioural differences and coloration differences in the convict cichlid (formerly known as *Amatitlania nigrofasciata*). In this monogamous, highly aggressive species, reproductive success depends on the ability to provide high-quality parental care, to establish, maintain and defend a territory with a mate and to access resources during the nonbreeding season (Godin & Rangeley, 1992; Keenleyside, Bailey, Young, & Robilliard, 1990). Individuals may thus benefit from acquiring reliable information about behavioural types of competitors, so they only escalate conflict when the risk of injury is low, and about potential partners. The streaked appearance of the species, with individual variation in intensity of the grey and black stripes (due to variation in the deposition of grey-black eumelanin pigment), is likely to be involved in signalling. In addition, females develop a unique and conspicuous orange ventral coloration. Such reversed sexual dimorphism only occurs in a few species, but recent studies support the idea that conspicuous female traits might be sexually selected as well (Amundsen, 2000). In particular, female coloration might convey information about individual quality and thus be associated with female competiveness or ability to monopolize a territory, but might also be sexually selected by males. The study of Beeching, Gross, Bretz, and Hariatis (1998) supported the idea that female coloration plays an important role in dominance, because female cichlids expressed more agonistic behaviour towards more brightly coloured female stimuli. However, some recent findings indicate that males prefer colourful females of the cichlid *Pelvicachromis taeniatus* (Baldauf, Bakker, Kullmann, & Thünken, 2011) and of two-spotted gobies, *Gobiusculus flavescens* (Amundsen & Forsgren, 2001), and these results are consistent with the hypothesis that female ornamentation is sexually selected. Here, we quantified a series of traits commonly used to measure personality of vertebrates in social and nonsocial situations, and assessed the correlations of these traits. We then summarized the traits in individual behavioural types (as in Sih et al., 2004), and investigated the extent to which variation in coloration among individuals was associated with behavioural type.

METHODS

Study Animals and Laboratory Conditions

Male and female convict cichlids (mean standard length ± SE and range [minimum–maximum]: 9.3 ± 2.5 cm, 7.7–11.7 cm in males, 6.5 ± 1.4 cm, 5.6–7.5 cm in females; mean body mass ± SE: 15.5 ± 1.1 g in males, 6.2 ± 0.3 g in females) were selected from different rearing groups of our breeding population maintained in the university's animal facility. These fish are descendants of aquarium fish obtained from wholesalers. All fish were housed in same-sex tanks (52.5–96 litres), with six fish per tank, at 25 ± 1 °C, under a 12:12 h light:dark cycle. The fish were fed daily with Cichlid XL flakes (Tetra, Germany). Four to five days before the start of the behavioural tests, a single fish was placed in a 20-litre tank (40 × 20 cm and 25 cm high). Each tank was equipped with a PVC tube as shelter, an air stone and gravel substrate. To prevent food dispersion throughout the tank, a feeding area (10 × 20 cm) located on the surface of the water was delimited in the front of the tank with an opaque partition. Visual isolation was achieved by separation of tanks with opaque plastic dividers.

Personality Tests

We assessed personality in 21 male and 18 female convict cichlids using four behavioural tests. The exploration test and startle response test were conducted for each focal fish within a day in January and February 2013, and the test order was randomized between days. Boldness towards a novel food and aggression were tested over 2 days in April and May 2013. For each individual, each test was repeated 1 week later for assessment of behavioural repeatability. Subsequent to the four personality tests, the standard lengths of the fish were measured to the nearest 0.1 cm.

Exploration of novel environment

This test, which is commonly used in vertebrates (Forkman, Boissy, Meunier-salaün, Canali, & Jones, 2007; Jones & Godin, 2010; Réale, Reader, Sol, McDougall, & Dingemanse, 2007), followed the procedure described by Schürch and Heg (2010). The novel environment consisted of a 450-litre tank (150 × 50 cm and 60 cm high). The tank was divided into a dark compartment (40 cm wide) that was separated from the larger and brightly lit compartment by opaque plastic partitions with a sliding door. The novel environment contained a gravel substrate, two plastic plants (25 cm high) and six PVC tubes (8 cm diameter, typically used as artificial nests in breeding experiments) to provide shelters and opportunities for exploration. A fish was first transferred to the small dark compartment. After 10 min of acclimation, the door was opened and the fish was allowed to explore the bright compartment. Each fish was observed for 20 min. The locomotor activity of the fish (swimming distance) was analysed by use of automated trajectometry software (Ethovision, Noldus Information Technology, Wageningen, The Netherlands).

Feeding under risk

The test was conducted in a 52.5-litre tank (60 × 25 cm and 35 cm high). A feeding area (10 × 25 cm) on the surface of the water was delimited in one end of the tank with an opaque partition to keep floating food in that area. Immediately after we moved the fish into the tank, food was provided in the feeding area. The test started when the fish began feeding. A startle response was then induced by dropping a novel object through a PVC tube on top of the feeding area, which caused the fish to temporarily stop feeding. The time taken to resume feeding was used as a measure of the startle response. If a fish did not eat after 5 min, a maximum score of 300 s was recorded. Two different objects (a 5.7 g cat's eye glass marble and a 10.5 g brass bolt) were used in a randomized order to prevent habituation.

Food neophobia

A novel type of food was presented to the fish in the feeding area and the time needed to consume this food was recorded. If a fish did not eat after 15 min, a maximum score of 900 s was recorded. Two different novel foods (Tetra Delica Krill Shrimp Freeze Dried and a slice of cooked macaroni pasta) were used in a randomized order to avoid familiarization.

Aggressiveness

Aggressiveness is commonly used to define personality types in animals. From an ecological viewpoint, more aggressive individuals should do well in competitive situations, but a high aggression level is unsuitable where caution or care is more appropriate, such as in interactions with predators and offspring (Sih et al., 2004). Thus, an individual's aggressive display towards a conspecific is a valuable dimension of aggressiveness, but so is its motivational state (Arnott & Elwood, 2009a). To consider these two ecologically relevant traits in our study, we used the procedure developed by Arnott and Elwood (2009b). This test assesses risk-taking behaviour as the time needed to resume fighting after a stressful event. Briefly, we staged intrasexual agonistic encounters between isolated males or isolated females. Individuals were matched for body size and were not previously paired to a breeding partner. We suddenly disturbed the agonistic interactions and then determined the time taken to resume the contest. This provides a measure of the aggressive motivation of the individual, and the number of agonistic behaviours provides a measure of its aggressive display.

The opaque divider between the two visually isolated and adjacent tanks was removed and the tanks were pushed together, enabling the two fish to interact. At 2 min after the onset of agonistic interaction, we startled the focal fish by dropping a 4.95 g glass marble into the tank. The marble landed behind a narrow screen of opaque tape on the wall separating the two fish so that only the focal fish was startled. We used the same technique to subject the focal fish to a second startle 15 min later, but only if the focal fish resumed the contest within 15 min. Following each interaction, the opaque dividers were replaced to isolate fish again, and 4 h later the original pairs were retested in the same manner, but with the previously non startled fish now designated as the focal fish. For the second trial, performed 1 week later, two new sex-matched fish were used and the fish initially assigned as the startled fish in the first test was assigned as the stimulus fish in the second test. Thus the aggressive behaviour of each fish was unaffected by its response to a specific opponent or by asymmetry in its prior experience.

For each interaction, we recorded the time following the marble drop to resumption of agonistic interactions (aggressive startle). The total number of agonistic behaviours (frontal displays and attempted bites) was also recorded and defined as aggressive displays for subsequent analyses. All interactions were recorded using a CCD camcorder (Professional 21 Series, The Imaging Source, Bremen, Germany) equipped with a CCTV lens (2.8-12MM, F1.3, Computar, Commack, NY, U.S.A.).

Colour Measurements

After the behavioural tests, fish were again housed in same-sex tanks. Then, digital and spectrometric measurements were performed 1–2 weeks after the last personality trial to prevent interference of the repeated personality tests with the colour measurements.

Imaging procedure

Each fish was introduced into a photographic tank (12 × 24 cm and 33 cm high) in which all walls except the front one were white and opaque. After 10 min of acclimation, 20 min videos were recorded using a camera (D7000, Nikon). The tank was illuminated with an 18 W fluorescent tube. Pure black and pure white references for colour calibration were provided by black and white plastic-coated, fully immersible colour reference cards (Kaavie GC-2 Pocket Size White Balance & Gray Cards) that were placed on the back wall of the tank. Frames of the left and right sides of the fish were then randomly selected every 5 min during the 20 min video when the individual was swimming in a plane parallel to the camera lens. Paleness was quantified in males and females. We first converted each colour photograph into 8-bit greyscale (Appendix Fig. A1a). Then, we outlined the entire body of the fish without the transparent fins. We extracted the mean grey value for the pure black (G_{black}) and pure white (G_{white}) reference cards and the entire fish selection (G_{fish}) using ImageJ software (Schneider, Rasband, & Eliceiri, 2012). A paleness index (PI) was computed as (G_{black} − G_{fish})/(G_{black} − G_{white}). PI ranges from 0 to 1, with 0 indicating pure black and 1 pure white. Repeated measurements were consistent

(intraclass correlation coefficient: males: $r = 0.88$, 95% confidence interval, $CI = 0.80-0.96$; females: $r = 0.62$, 95% $CI = 0.40-0.84$), so the 10 values were averaged for each individual.

We proceeded similarly to obtain paleness values for the black stripes (dark index, DI) and the background field (bright index, BI). Contrast was then computed as $(DI - BI)/(DI + BI)$. Because PI correlated with DI and BI (see Appendix Fig. A2 for details), we only retained the paleness index and contrast for subsequent analyses.

The orange body area was also quantified in females (Appendix Fig. A1b). We first enhanced the contrast of the images to highlight the orange patches, which were then automatically selected using CS3 Photoshop (Adobe, CA, U.S.A.). Relative orange area was computed as a percentage of the entire body area using ImageJ. As these values were consistent over repeated measures (intraclass correlation coefficient: $r = 0.52$, 95% $CI = 0.28-0.76$), the 10 values were averaged for each individual.

Spectrometric measurements

We used a hand-held Ocean Optics Jaz spectrometer (Ocean Optics Inc., Dunedin, FL, U.S.A.) with a deuterium–tungsten halogen light source to measure reflectance values for wavelengths between 400 and 725 nm (65 ms integration time; average of 10 readings per recording; boxcar average of five points around each point). Each fish was anaesthetized with eugenol (Sigma-Aldrich) and placed on its right side on a nonreflective black background while submerged in water. Reflectance was measured with a fibre-optic radiance probe angled $45°$ above the surface of the body, and five measurements were taken from the most brightly coloured orange patch (usually under the pectoral fin) of each female to calculate repeatability. White standards were generated from a white balance card (Kaavie) submerged in water and dark standards were generated by closing the shutter of the spectrometer. Spectra Suite version 2.0.162 (Ocean Optics Inc.) was used to visualize and store reflectance data files. Hue and brightness were computed from the raw spectral reflectance data. Brightness was calculated as the total area under the spectral curve from 400 to 725 nm (Hill & McGraw, 2006). Hue was computed as the wavelength halfway between the minimum and maximum reflectance (Bolund, Schielzeth, & Forstmeier, 2007). As these values were consistent over the repeated measures (intraclass correlation coefficient: brightness: $r = 0.92$, 95% $CI = 0.66-0.99$; hue: $r = 0.65$, 95% $CI = 0.44-0.85$), the five values were averaged for each individual.

Statistical Analysis

All statistical analyses used R 3.0 Software (R Core Team, 2014). Repeatability of behavioural measures was assessed following the recommendations of Nakagawa and Schielzeth (2010). When the data had a negative binomial distribution, we calculated the concordance correlation coefficient (CCC) and 95% CI with the epiR package (Stevenson, 2014). When the data followed a nonstandard distribution, we relied on measurement of repeatability based on rank, and behavioural consistency over time was assessed by

Spearman rank correlation coefficients. The fish only rarely consumed the slice of macaroni pasta in the test for food neophobia, so we were unable to test repeatability of this behavioural response. However, the behavioural response to novelty is known to be consistent over time in cichlids (Chervet, Zöttl, Schürch, Taborsky, & Heg, 2011; Jones & Godin, 2010). Thus, food neophobia was used in subsequent analyses focusing solely on the time needed to consume krill. We then analysed the correlation between personality traits to test for the presence of a behavioural syndrome. We performed multiple correlation analysis using the Hmisc package (Harrell, 2014) with the procedure of Benjamini and Hochberg (1995), which is similar to Bonferroni's correction but also reduces type II errors by controlling for false discovery rate (Verhoeven, Simonsen, & McIntyre, 2005). A principal component analysis (PCA) was then performed on all correlated traits involved in the behavioural syndrome, to reduce it to a personality score (David, Auclair, & Cézilly, 2011; Mazué, Dechaume-Moncharmont, & Godin, 2015). Finally, we investigated the extent to which variation in colour traits was associated with behavioural types by calculation of Spearman rank correlations between personality scores and colour measurements.

Ethical Note

Animal care and all experimental procedures were approved by the University of Burgundy Ethical Committee (approval number 0413). There were no lesions or mortalities associated with the experimental procedures. After the experiments were completed, all fish were maintained at the animal facility in same-sex tanks for subsequent experiments.

RESULTS

Repeatability and Correlates of Behavioural Responses

The swimming distance during exploration of a novel environment and the time taken to resume feeding under risk were both consistent over time ($P = 0.029$ and $P = 0.008$, respectively; Table 1). We tested aggressiveness by measuring the time needed to resume an agonistic interaction and the frequency of agonistic behaviours, with each score averaged per individual over two startles. The frequency of aggressive displays was consistent over time (Table 1), but the repeatability of the aggressive startle was not significant (Table 1). However, due to its relevance in assessing aggressive levels in animals (see Methods) and given that the effect sizes were rather high, we included this trait in the subsequent analyses.

Feeding startle response correlated positively with food neophobia, which correlated positively with aggressive startle (Fig. 1). Aggressive display correlated negatively with aggressive startle (Fig. 1). There were no other significant relationships between the five behavioural traits ($-0.35 < r_S < 0.29$, $P > 0.081$). Thus, we performed a PCA on all traits except exploration, which was excluded from the behavioural syndrome due to its lack of correlation with

Table 1
Consistency over time in the behavioural responses of 21 male and 18 female convict cichlids

Personality test	Exploration	Feeding under risk	Aggressiveness[a]	
Behavioural response	Swimming distance/standard length	Feeding startle (s)	Aggressive startle (s)	Frequency of aggressive display
All fish	0.46[−0.04;0.77]	0.45[0.14;0.69]	0.24[−0.12;0.60]	0.48[0.23;0.72]
Males	0.33 [−0.24;0.74]	0.42[0.02;0.70]	0.29[−0.18;0.75]	0.51[0.18;0.74]
Females	0.31[−0.17;0.71]	0.42[−0.14;0.85]	0.28[−0.46;0.86]	0.48[-0.07;0.81]

Repeatability was assessed by concordance correlation coefficients and 95% confidence intervals (in brackets) for the aggressive display. Spearman rank correlations were used for analysis of all other behavioural responses, and 95% confidence intervals (in brackets) were computed by bootstrapping.

[a] The frequency of aggressive display was calculated as the total number of agonistic behaviours divided by the time spent in agonistic interaction.
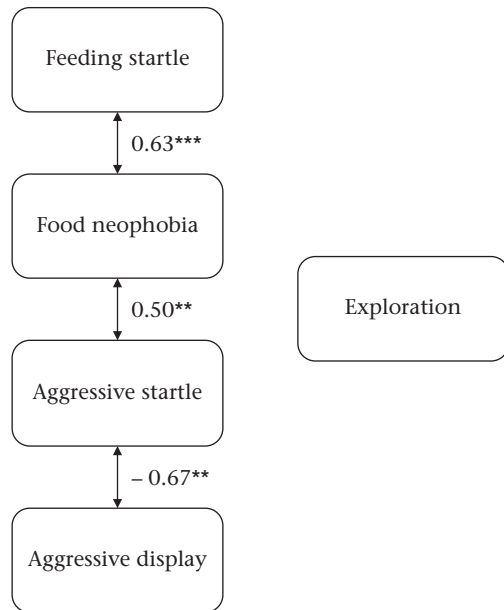
Figure 1. Correlation between personality traits defining the behavioural syndrome in our convict cichlids. Spearman correlation coefficients are indicated next to each link. $**P < 0.01$; $***P < 0.001$ after Benjamini and Hochberg (1995) correction (see Methods).

other traits (David et al., 2011; Mazué et al., 2015). The purpose of the PCA was to reduce individual personality to a single value, hereafter called the personality score.

Personality Score

The first two principal components (PC1 and PC2) of the PCA explained 79% of the variance (Table 2). PC1 correlated with the four personality traits, in that individuals with lower PC1 values were quicker to resume feeding after the startle, bolder and more aggressive. For all subsequent analyses, we therefore used the personality scores derived from PC1; we defined individuals with low scores as proactive and individuals with high scores as reactive (Réale et al., 2007; Sih et al., 2004).

Correlation Between Personality and Coloration

There was a positive correlation between personality score and paleness index (PI). Thus, proactive fish were darker (smaller PI) than reactive fish (Spearman rank correlation: $r_S = 0.40$, $N = 34$, $P = 0.020$; Fig. 2a, b). There was a similar correlation between personality score and the relative orange area on females, in that proactive females had smaller coloured areas ($r_S = 0.60$, $N = 13$, $P = 0.034$; Fig. 2c). In addition, there was a negative correlation between personality score and contrast, in that proactive fish had greater contrast than reactive fish (Spearman rank correlation: $r_S = -0.48$, $N = 34$, $P = 0.004$; Appendix Fig. A3). There were no

Table 2
Component loadings of personality traits observed from principal components analysis

Personality trait	PC1	PC2	PC3
Feeding startle	0.51	−0.50	−0.41
Food neophobia	0.56	−0.40	0.24
Aggressive startle	0.51	0.45	0.62
Aggressive display	−0.40	−0.63	0.62
Percentage of variance explained	48.2	30.8	12.4
Eigenvalue	1.93	1.23	0.49

significant correlations between personality score and brightness ($r_S = -0.21$, $N = 34$, $P = 0.48$) or hue ($r_S = 0.11$, $N = 34$, $P = 0.71$).

DISCUSSION

The relationships of some personality traits, except exploration, enabled us to define a behavioural syndrome in convict cichlids. In addition, behavioural types were predicted by colour traits: proactive individuals (more aggressive, bolder and quicker to resume behaviour after a startle) were darker, and proactive females had a smaller relative orange area. Our results support the hypothesis that colour traits are related to personality and therefore could play an important role in mediating social interactions, allowing a quick and reliable assessment of conspecifics' behavioural types.

The correlation between behavioural type and coloration cues possibly relies on some physiological basis. The melanocortin system is known to be involved in the stress response, so darker individuals should be less sensitive to stressful factors (see Ducrest et al., 2008 for a review; but see O'Connor, Metcalfe, & Taylor, 1999 and Ligon, 2014 for contrasting results in species that become darker as a submissive signal). Our finding that darker individuals had faster startle responses is thus consistent with previous studies of vertebrates. However, the association of coloration with stress is not limited to the melanocortin system. Animals derive carotenoids solely from the diet, and these compounds have important physiological functions (as antioxidants, increasing the immune response, vitamin A precursor and glucocorticoid hormones) and also serve as pigments. Thus, there may be a trade-off, in which allocation of carotenoids for one function would reduce allocation to other functions (Svensson & Wong, 2011). For instance, increased stress during a period of parental care and nest defence might necessitate reallocation of integument carotenoids to immune or antioxidant functions. This leads to the hypothesis that only high-quality females can express bright orange carotenoid-based ventral coloration and cope with stressors.

However, our study supports alternatives to the carotenoid trade-off hypothesis because proactive females (which were more aggressive, bolder and quicker to resume behaviour after the startle) had smaller orange spots. Two previous studies of cichlids that tested the carotenoid trade-off hypothesis using an immunological approach also reported results inconsistent with the trade-off hypothesis. In particular, dietary supplementation with carotenoids did not affect skin coloration and did not enhance the innate immune response in gold or barred morphs of the polychromatic Midas cichlid, *Amphilophus citrinellus* (Lin, Nieves-Puigdoller, Brown, McGraw, & Clotfelter, 2010). Similarly, in female convict cichlids, bacteria-challenged fish experienced reduced oxidative stress while simultaneously allocating more carotenoids to the integument, especially when maintained on a diet with trace levels of carotenoids (Brown, 2014). As suggested by Anderson, Wong, Fuller, Zigelsky, and Earley (2015), energy expenditure demanded by a proactive profile may cause reabsorption of carotenoids from the integument, thus reducing the orange coloration in proactive females.

Convict cichlids are highly aggressive when defending their territory and brood against intruders. Contrasting stripes are often associated with aggression in cichlid species (Barlow, 2002). The melanocortin system influences melanin-based coloration and aggressive behaviour (Ducrest et al., 2008), so coloration can accurately predict conflict outcome (Dijkstra, Seehausen, & Groothuis, 2005; Evans & Norris, 1996; Maan, Groothuis, & Wittenberg, 2001). In other words, it is likely that fish use information conveyed by coloration when deciding to engage in potentially dangerous agonistic interactions. A study of *Pundamilia* cichlids indicated that the advantage of red coloration for males disappeared and staged contests lasted longer when skin coloration
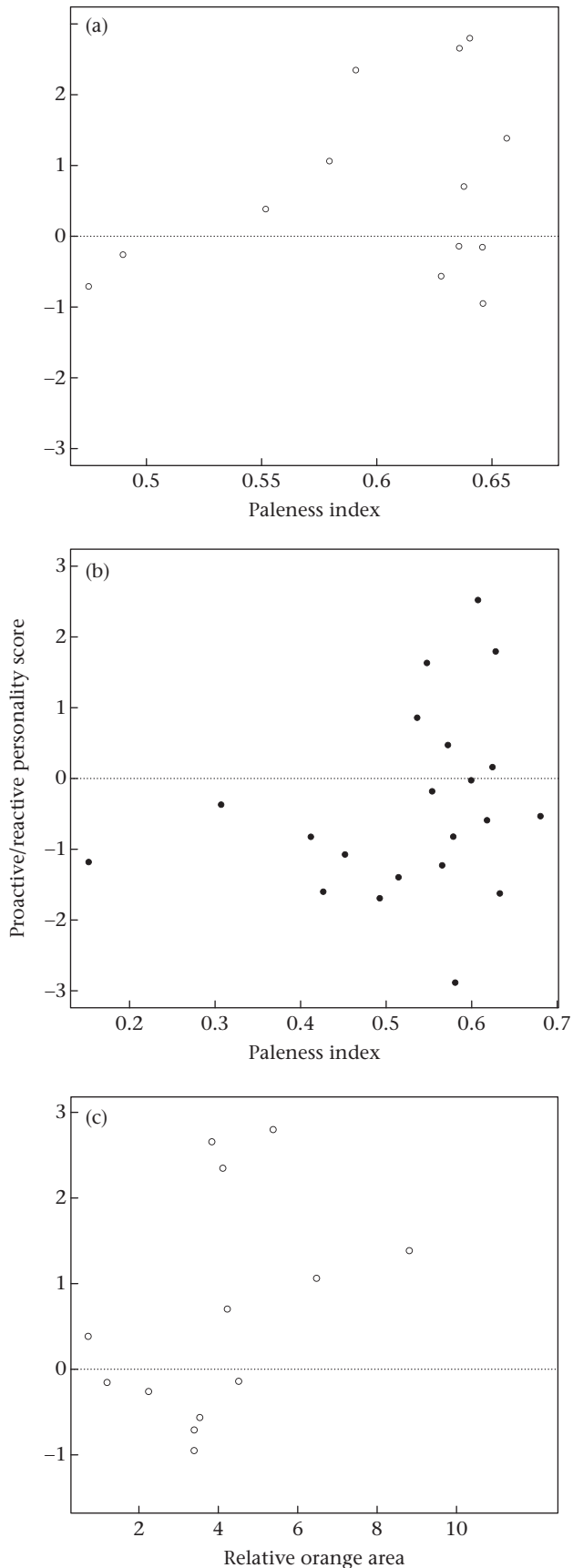
was obscured by green light; this suggests that the bright red body colour plays a role in preventing escalation during agonistic interactions (Dijkstra et al., 2005). Male cichlids *Astatotilapia burtoni* can switch between brightly coloured morphs and cryptic morphs depending on their success in aggressive encounters (Korzan et al., 2008). During agonistic interactions, such changes in coloration may reduce escalation because colour conveys information about status or fighting ability (Beeching, 1995; Hurd, 1997). In the Midas cichlid, the coloration and larger size of gold morphs inhibit aggression by grey morphs, although gold morphs themselves are not more aggressive (Barlow, 1983). In contrast, amelanistic males of the convict cichlid lack the ability to modulate coloration, and this may explain their competitive disadvantage against wild-type barred males (Reddon & Hurd, 2009).

The association of coloration with aggressiveness in cichlids is not limited to male–male encounters. In particular, the female-specific orange ventral coloration elicits aggressive behaviours in females but not males (Beeching et al., 1998). In contrast, Anderson et al. (2015) found that females had decreased ventrolateral coloration when exposed to a greater risk of predation and agonistic interactions with heterospecifics, but this coloration was unrelated to interactions with conspecifics and mates. Despite evidence of the association of colour traits with aggressiveness or fighting ability, it appears that individuals do not always use this information to avoid potentially costly interactions (Culumber & Monks, 2014; Maan et al., 2001), unless they have access to alternative options, such as hiding or attacking another territory owner.

Convict cichlid partners both have roles in parenting, with the female providing direct care to the offspring and the male defending the territory against intruders (Keenleyside, 1991). This division of labour is not strict, because females also contribute to nest defence, particularly in the presence of large intruders (Keenleyside et al., 1990). Hence, an individual may indirectly benefit from choosing a mate based on coloration. Conspicuous colour is assessed more quickly than behavioural type, correlates with potential cooperative behaviours (Roulin, Da Silva, & Ruppli, 2012) and prevents risky interactions with an overly aggressive partner. Therefore, proactive males, which are better at defending high-quality territories, may benefit by mating with reactive females, which provide better parental care (Budaev, Zworykin, & Mochek, 1999; Roulin, Dreiss, & Kölliker, 2010). However, assortative pairing based on behavioural type may have a selective advantage over disassortative pairing if it results in better synchronization of parental care. In many monogamous species with biparental care, pairs similar in personality have greater reproductive success (great tits, *Parus major*, Both, Dingemanse, Drent, & Tinbergen, 2005; zebra finches, *Taenopygia guttata*, Schuett, Dall, et al., 2011; Steller's jays, *Cyanocitta stelleri*, Gabriel & Black, 2012). Cichlids are frequently found to mate assortatively by colour pattern in nature and under experimental conditions (see Maan & Sefc, 2013 for a review). Additional work is needed to determine whether assortative pairing for coloration in the convict cichlid reflects an underlying preference for a given behavioural type or self-referent preference (Dechaume-Moncharmont, Freychet, Motreuil, & Cézilly, 2013; Galipaud, Bollache, & Dechaume-Moncharmont, 2013).

Our findings also raise the question about the need for female convict cichlids to have two coloration systems (one based on melanins and the other on carotenoids) for communication of

Figure 2. Relationship between the paleness index in (a) female and (b) male cichlids and personality score. The index ranges from 0 to 1, with 0 indicating pure black and 1 pure white. (c) Relationship between the relative orange area in female cichlids and personality score. The personality score was derived from the first principal component (PC1) obtained through a PCA on feeding startle response, food neophobia, aggressive startle and aggressive display. Individuals with lower personality scores were defined as proactive (quicker to resume feeding after the startle, bolder and more aggressive) and individuals with higher personality scores were defined as reactive.

information about behavioural type. We suggest that these two systems are not equally involved in the different challenging contexts discussed above. Given that carotenoids must be ingested whereas melanins are synthesized from a number of precursors, the presence of carotenoid-based coloration is commonly related to foraging access. Thus, a proactive individual (fast explorer, bold and aggressive, Sih et al., 2004) is assumed to have more access to carotenoids. Beeching et al. (1998) reported that the carotenoid-based ventral coloration of female convict cichlids only plays a role in intrasexual aggression; however, this trait may also be related to mate choice in this monogamous, biparental species because behavioural types covary with parental abilities (Budaev et al., 1999). In addition, the pleiotropic effects of melanocortins reported by Ducrest et al. (2008) strongly suggest a preferential association of melanin-based coloration with aggressive behaviour. Griffith, Parker, and Olson (2006) excluded any potential heightened condition dependence of one type of pigment over the other, but the extent to which genes regulate melanin- and carotenoid-based coloration are not consistent with this statement. In particular, melanin-based coloration in birds is highly heritable, whereas the carotenoid-based coloration is phenotypically plastic and highly sensitive to environmental conditions (Roulin & Ducrest, 2013). These pigments may also have qualitative differences in their ability to act as honest signals of the qualities of the bearers. Thus, if colour traits reliably predict individual behavioural types and thereby mediate mating decisions, conflict outcomes or stress responses, then selection can proceed at two levels. Selection might act indirectly on behavioural differences via mating preference or cooperation based on coloration, and selection should also favour individuals that best perceive differences in coloration. The difference in use of colour cues can also occur because the encountered individual will not provide the same benefit as the sex, behavioural type or conditions experienced by the decision maker (Dirienzo & Hedrick, 2014). For example, proactive individuals are more impulsive and less flexible in decision making than reactive individuals (Sih & Del Giudice 2012). Thus proactive individuals may use single cues without obtaining all of the information, whereas reactive individuals may place more emphasis on quality of cues. Additional research using computer-animated images of the convict cichlid will help to test whether individuals actually use information reflected by coloration and whether it is context dependent.

Acknowledgments

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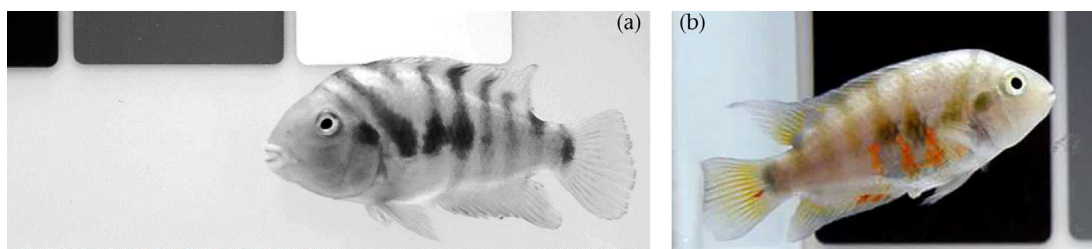
Appendix

Figure A1. Colour measurements in convict cichlids. (a) Representative image of a male cichlid after conversion to 8-bit greyscale for paleness measurements. (b) Representative image of the orange ventral coloration in a female cichlid.
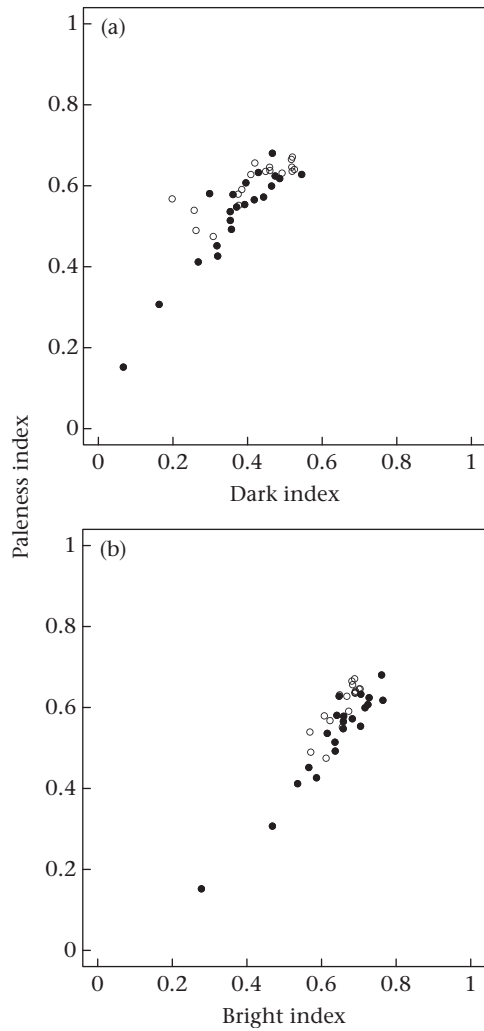
Figure A3. Contrast in male (solid dots) and female (open dots) convict cichlids. The personality score was derived from the first principal component (PC1) obtained through a PCA on feeding startle response, food neophobia, aggressive startle and aggressive display. Individuals with lower personality scores were defined as proactive (quicker to resume feeding after the startle, bolder, and more aggressive) and individuals with higher scores were defined as reactive.

Figure A2. Correlation between overall paleness index (PI) on the entire body surface and paleness index for (a) the dark stripes (dark index, DI) and (b) the background field (bright index, BI) in male (solid dots) and female (open dots) convict cichlids. The three values range from 0 (pure black) to 1 (pure white). Spearman rank correlation between overall PI and DI: $r_S = 0.85$, $N = 34$, $P < 0.001$; between overall PI and BI: $r_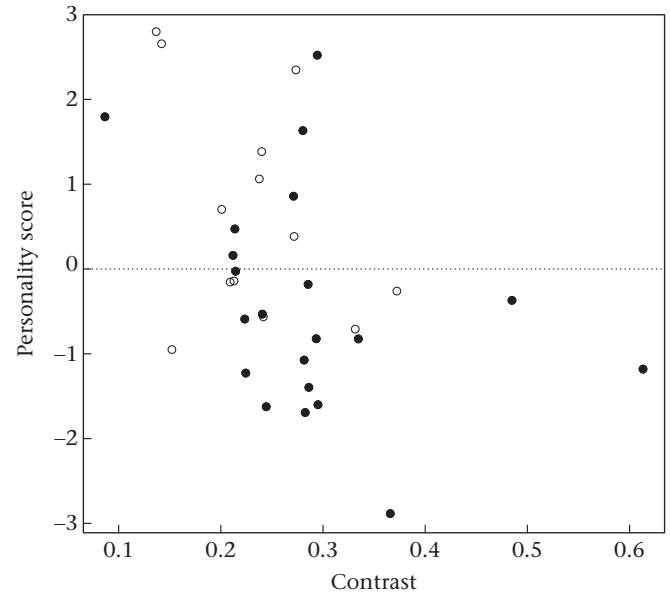S = 0.76$, $N = 34$, $P < 0.001$.