Behavioral Ecology

The official journal of the ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2015), 26(3), 900–908. doi:10.1093/beheco/arv030

Original Article

Boldness–exploration behavioral syndrome: interfamily variability and repeatability of personality traits in the young of the convict cichlid (*Amatitlania siquia*)

Geoffrey P.F. Mazué,[a,b] François-Xavier Dechaume-Moncharmont,[b] and Jean-Guy J. Godin[a]
[a]Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada and [b]Équipe Ecologie Évolutive, UMR CNRS 6282 Biogéosciences, Université de Bourgogne, 6 boulevard Gabriel, 21000 Dijon, France

Received 6 January 2015; revised 18 February 2015; accepted 26 February 2015; Advance Access publication 3 April 2015.

In recent years, considerable research interest in behavioral ecology has focused on characterizing and understanding individual differences in behavior that are consistent over time and across contexts, termed animal "personalities," and correlations between various behaviors across contexts, termed behavioral syndromes. Although there is some evidence that differences in personality among individuals within populations can be genetically based and adaptive, when and how individual personality differences emerge in a population is not well understood, but of considerable general interest. Here, using juveniles of the convict cichlid (*Amatitlania siquia*) as a model system, we investigated in the laboratory whether individuals consistently differ in their personalities and whether behavioral syndromes are apparent at an early developmental stage and, if so, whether distinct personality traits are heritable. Under standardized laboratory conditions and using sibling analysis, we quantified interindividual differences in their boldness behavior under potential predation threat and their exploratory activity in a novel environment, 2 ecologically important behaviors, as our focal personality traits and estimated their respective repeatability and heritability. We report for the first time consistent (repeatable) and heritable individual differences in boldness and exploratory behaviors, and a boldness–exploration behavioral syndrome, in young convict cichlids. Bolder fish were more exploratory than relatively timid ones. These results provide novel evidence for the emergence in early life history of consistent individual differences in personality traits and behavioral syndromes in this species and suggest that genetic variation for boldness and exploratory behaviors, and thus potential for selection on these traits, exists in our study population.

Key words: **behavioral syndrome, boldness, exploration, heritability, juvenile cichlid fish, personality, repeatability.**

INTRODUCTION

Variation in biological traits is pervasive in natural populations and necessary for the action of selection and thus evolution (Freeman and Herron 2007). An enduring challenge has been to understand how variation in traits that are under selection is maintained in the wild (Freeman and Herron 2007). Over the past decade, there has been a surge of interest in behavioral ecology focusing on understanding the mechanisms generating and maintaining consistent individual differences in behavior, termed animal "personalities," and correlations between various behaviors across contexts, termed behavioral syndromes, within and among populations (Dall et al. 2004, 2012; Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziemba 2004). Animal personalities have been most commonly characterized along 5 behavioral axes, namely, shyness–boldness, exploration–avoidance, activity, aggressiveness, and sociability (Réale et al. 2007).

Empirical studies have shown that animal personalities and behavioral syndromes covary with ecological conditions, depend on the state of the individual, and can be maintained by frequency-dependent selection (Dall et al. 2004, 2012; Sih and Bell 2008; Garamszegi et al. 2012; Wolf and Weissing 2012; Sih et al. 2015). For example, individual boldness and aggressiveness in fishes are often positively correlated (i.e., constitute a behavioral syndrome), but the structure and strength of this syndrome covaries with the prevailing predation regime (e.g., Huntingford 1976; Dingemanse et al. 2007; Brydges et al. 2008; Archard and Braithwaite 2011). Direct viability selection from fish predators can lead to the

---

Address correspondence to J.-G.J. Godin. E-mail: jgodin@carleton.ca.

emergence of a positive correlation between boldness and aggression among survivors in a population, when none existed prior to predation, as shown experimentally in the three-spined stickleback, *Gasterosteus aculeatus* (Bell and Sih 2007).

Personality studies in both the field and laboratory have demonstrated that interindividual variation in behavior contributes to variation in individual fitness, which in turn allows for evolutionary changes through natural selection (Freeman and Herron 2007), and that individual personalities can be adaptive (Dingemanse and Réale 2005; Smith and Blumstein 2008). When and how individual personality differences emerge in a population is thus of considerable interest but not well understood (Stamps and Groothuis 2010; Sih et al. 2015). Four general mechanisms have been proposed: nongenetic inheritance of personality, genetic inheritance of personality, gene–environment interactions (reaction norms) shaping the development of personality, and positive feedbacks between individual state and behavior. First, nongenetic inheritance involves environmental transmission of behavioral traits through parental effects, such as parental care (Reddon 2012). Experimental studies have shown that offspring personality can be explained by the personality of their parents, suggesting the presence of a parent–offspring transmission of personality traits (e.g., Dingemanse et al. 2003; Schuett et al. 2013). Second, some studies have revealed evidence for a genetic-based transmission of various personality traits, with moderate to high estimates of heritability (Stirling et al. 2002; van Oers et al. 2005; Réale et al. 2007; Dochtermann et al. 2015). Third, an individual's personality can be shaped over time as the result of interactions between its genotype and environmental conditions it encounters as it develops (Stamps and Groothuis 2010). Fourth, variation in state among individuals and positive feedbacks between state and behavior (among-individual covariance between state and behavior) can potentially lead to adaptive personalities (Wolf and Weissing 2012; Sih et al. 2015).

In the current study, we investigated under standardized laboratory conditions whether individuals consistently differ in their personalities and whether behavioral syndromes are apparent at an early developmental stage and, if so, whether distinct personality traits are heritable. As personality is defined as repeatable among-individual variation in behavior (Dall et al. 2004; Réale et al. 2007; Dochtermann et al. 2015) and repeatability is linked to quantitative genetics (Boake 1989), obtaining repeatability estimates for personality traits can provide insights into their heritability (Dochtermann et al. 2015). If genetically based, personality differences among individuals may have important evolutionary implications (Sih, Bell, Johnson, and Ziemba 2004; Dall et al. 2012; Dochtermann et al. 2015). Here, we used the convict cichlid fish (*Amatitlania siquia*) as our model study system. Although adult convict cichlids differ consistently in their parental behavior (Budaev et al. 1999), we do not yet know whether young convict cichlids show consistent (repeatable) and heritable differences in behavioral personality traits at the time of independence from parental care. We quantified interindividual differences in their boldness behavior toward a predation threat and exploratory activity in a novel environment, 2 ecologically important behaviors, as our focal personality traits and estimated their respective heritability by analyzing behavioral variation within and among families (i.e., sibling analysis).

The convict cichlid is a socially monogamous, substrate-brooding fish that provides extended biparental care to its offspring (Keenleyside 1991; Wisenden and Keenleyside 1994; Wisenden 1995). Parental care includes both parents actively guarding their mobile brood of young within their breeding territory and chasing potential fish predators away from the vicinity of their brood. In nature, young convict cichlids become free swimming within 1 week of hatching and gradually become more active as they forage on the substrate at increasing distances away from their parents. They become independent of their parents and gradually disperse from their natal territory once they reach about 10–12 mm in standard body length (i.e., approximately 6 weeks posthatching; Wisenden 1994). Independence from parental care and dispersal from natal to novel habitats are potentially risky and costly events in an animal's life (Bonte et al. 2012), owing importantly to increased exposure to predators (Lima and Dill 1990; Bonte et al. 2012). This is certainly the case for young convict cichlids in the wild; dependent young that are not protected by one or both parents suffer very high rates of mortality to predation (Wisenden and Keenleyside 1994), and young that move increasing distances from their family unit are increasingly less likely to return to the safety of their family and are thus highly vulnerable to predation (Lee-Jenkins et al. 2014). Therefore, there is strong selection from predators in particular for the evolution of behaviors that maximize survivorship in the early life-history stages of the convict cichlid. We thus presumed that the 2 personality traits under investigation here (i.e., boldness and exploratory tendency) are essential to the early life-history ecology of the convict cichlid and expected that consistent interindividual variation in the expression of these 2 traits would be apparent in the young of this species and that they would be intercorrelated (i.e., form a behavioral syndrome) and heritable.

The boldness–shyness continuum is one of the major personality axes in animals, including fishes (e.g., Wilson et al. 1993; Wilson and Godin 2009; Toms et al. 2010). Boldness and exploratory activity are commonly positively intercorrelated, thus forming a behavioral syndrome, in fishes (e.g., Fraser et al. 2001; Wilson and Godin 2009; Cote, Fogarty, et al. 2010; Wisenden et al. 2011) and in birds (e.g., Verbeek et al. 1994; van Oers et al. 2004), and both behaviors are heritable (reviewed by van Oers et al. 2005) and implicated in dispersal (Cote, Clobert, et al. 2010). For example, natal dispersal distance in the great tit (*Parus major*) is positively correlated with exploratory behavior, with disperser individuals being faster explorers of novel environments than locally born individuals (Dingemanse et al. 2003). Similarly, in the invasive mosquitofish (*Gambusia affinis*), boldness, exploration tendency, and activity are positively intercorrelated (Cote, Fogarty, et al. 2010), and individual boldness is a good predictor of distance moved (i.e., exploration) within a natural stream in the killifish (*Rivulus hartii*) (Fraser et al. 2001). In juvenile convict cichlids, exploratory behavior and predator-escape behavior have been shown to be correlated, with individuals that are fast to explore a novel environment are slower to respond to a predator attack, suggesting that the way an individual explores a novel environment might affect its survival (Jones and Godin 2010). Moreover, predator inspection behavior, which is widely used as a behavioral measure of individual boldness in animals (Dugatkin and Godin 1992), can deter predator pursuit and attack (Godin and Davis 1995) and bias mate choice (Godin and Dugatkin 1996; Schuett et al. 2010).

METHODS

Subjects and holding conditions

We obtained our experimental subjects from the spawning of mated pairs of convict cichlids in our laboratory. These adult cichlids were outbred and descendants of wild convict cichlids collected in the

Río Cabuyo, Costa Rica. Mated pairs were housed in separate identical aquaria (67.5 L) filled with aged, dechlorinated, and continuously filtered tap water that was maintained at 24–27 °C. Each aquarium contained a gravel substratum, an artificial plant for refuge, and a clay flower pot as a spawning site. The aquaria were illuminated overhead with fluorescent tubes on a 13:11 h light:dark cycle and were visually isolated from each other with opaque screens. Adult fish were fed ad libitum with frozen brine shrimp (Hikari™ Bio-Pure Brine Shrimp) and pelleted food (Hikari™ Cichlid Floating Pellets) once daily. A total of 14 breeding pairs of adults were available to produce our experimental families.

We monitored breeding aquaria daily for reproductive events. Once spawned eggs hatched in a breeding aquarium, the newly hatched young (= "fry") remained in the aquarium with their parents until used in our behavioral tests (see below) and were fed ad libitum twice daily with live brine shrimp nauplii (*Artemia franciscana*) or commercial dry flake food (Nutrafin™, Rolf C. Hagen, Inc., Montréal, Canada). Once the fry in any given family reached about 1 cm in standard length, when they generally become independent of parental care in nature (Wisenden 1994), a group of 10–15 siblings were removed from the home parental aquarium and placed together in a randomly selected smaller holding aquarium (40 × 20 × 25 cm; *L* × *W* × *H*). All of the family holding aquaria were identical so as to minimize potential environmental effects on behavior; each aquarium contained a gravel substratum, was filled with aged, continuously filtered, and oxygenated dechlorinated tap water maintained at 24–25 °C by an immersion heater, and illuminated overhead with fluorescent lighting on a 13:11 h light:dark cycle. The family holding aquaria were randomly placed side-by-side on 2 staging shelves, one above the other. The families were similarly fed ad libitum twice daily with brine shrimp nauplii or dry flake food, as they were previously in their home parental aquaria, until used in our experimental tests when the juveniles were 23.2 ± 3.8 mm (mean ± SD, standard length) and approximately 8–12 weeks of age.

We tested a total of 167 fish originating from 14 full-sib families, with the number of siblings per family ranging from 6 to 15. All subjects were juveniles and thus could not be sexed. We assumed no sex bias in our study as no sex difference was noted in the repeatability of behaviors for juveniles of vertebrate species in general (Bell et al. 2009).

Experimental protocol

To quantify the repeatability of boldness (B) and exploration (E) behaviors separately, we tested individual focal fish twice, with 2 days separating repeated tests, for either behavior. Repeatability is a measure of the within-individual consistency of a trait over time and is obtained from repeated measures on the same individuals (Boake 1989; Nakagawa and Schielzeth 2010). We chose to repeatedly test each behavior (B and E) twice because of the constraints of our experimental design and to minimize stress on the fish and because Bell et al. (2009) found no evidence that repeatability estimates depend on the number of repeated observations per test individual (but see Wolak et al. 2012).

Each focal fish thus required 4 days to test, with 1 test carried out per day. The order of the boldness and exploration tests was randomized among all test fish, with half of the individuals assigned to the sequential pattern of tests B1-E1-B2-E2 and the other half to the opposite pattern E1-B1-E2-B2. The sequential order of tests assigned to each focal fish did not affect their boldness behavior (linear model, $F_{1,129} = 0.196$, $P = 0.659$) or exploration tendency (linear model, $F_{1,138} = 2.146$, $P = 0.145$). The day before a behavioral test, each focal fish was isolated from its sibling in their family holding aquarium by placing it in a 480-mL transparent, perforated, floating plastic cup attached to one side of the aquarium. This procedure allowed the focal fish to continue viewing and smelling its siblings swimming freely in the aquarium and minimized stress associated with handling prior to the test. All fish in the family holding aquaria were fed twice during any trial day: early in the morning (before the onset of testing) and at the end of the day (following testing). All behavioral observations were made by the same person so as to avoid interobserver variation, and the scoring of behavioral traits for each focal fish between repeated tests was done blindly of the scores obtained on the preceding tests.

Quantifying boldness behavior

We used predator inspection behavior as a measure of an individual's risk-taking or boldness behavior. During an inspection visit, a focal individual cautiously approaches a putative predator at a distance in a series of brief directed approaches alternating with short stationary pauses, during which the inspector is visually fixated on the predator (Dugatkin and Godin 1992). An inspection visit is deemed to have ended when the inspector stops its directed forward movements and moves away from the putative predator. The predator inspection test is widely used to assess individual level of boldness in fishes (e.g., Dugatkin and Godin 1992; Budaev and Zworykin 2003; Toms et al. 2010; Wisenden et al. 2011).

Our test apparatus consisted of a glass aquarium (75 × 30 × 30 cm; *L* × *W* × *H*) divided into 2 areas (refuge and open zone) by an opaque partition furnished with a sliding opaque door (8 × 10 cm), which could be raised and lowered remotely using a pulley system (Figure 1a). At one end of the aquarium, a refuge area was formed using a half-circular piece of plastic centered on the door. The refuge was slightly darkened by covering its sides and top with gray cardboard to simulate a rock crevice, as used by convict cichlids in the wild (Wisenden 1995; personal observations). The bottom of both the refuge and open zone was covered with beige gravel, and the aquarium was filled with aged and aerated dechlorinated tap water (15 cm depth) maintained at 24–25 °C. A smaller glass aquarium (30 × 13 × 20 cm; *L* × *W* × H) was positioned adjacent to the opposite end of the test aquarium and held a live wolf cichlid (*Parachromis dovii*), a natural predator of the convict cichlid (Wisenden 1994). Eleven different individual predators (14.5 ± 1.2 cm) were used sequentially as a potential predatory threat to avoid predator habituation across trials. To avoid the potential learning of predator personality, each test fish was exposed to different wolf cichlid predators during each repeated behavioral tests. Post hoc analysis of the data revealed that predator identity did not affect the boldness behavior of focal fish (linear model, $F_{5,125} = 1.887$, $P = 0.101$). To facilitate the recording of horizontal distance moved in the open zone by a focal fish, we "divided" the back wall of the test aquarium into 12 equal vertical zones (numbered from 1 to 12, with 1 being the closest to the predator), each 5 cm in width. These 12 zones were used to record the minimum distance of approach to the predator for each predator inspection visit. The entire apparatus was placed behind a blind to minimize external disturbance, and fish behavior was observed from behind the blind through a small window in the blind.

As mentioned above, each focal fish was repeatedly tested for its boldness level on 2 separate occasions (Test 1 and Test 2), 2 days apart. For either test, a wolf cichlid was placed in the small predator aquarium of the apparatus the day before a trial and

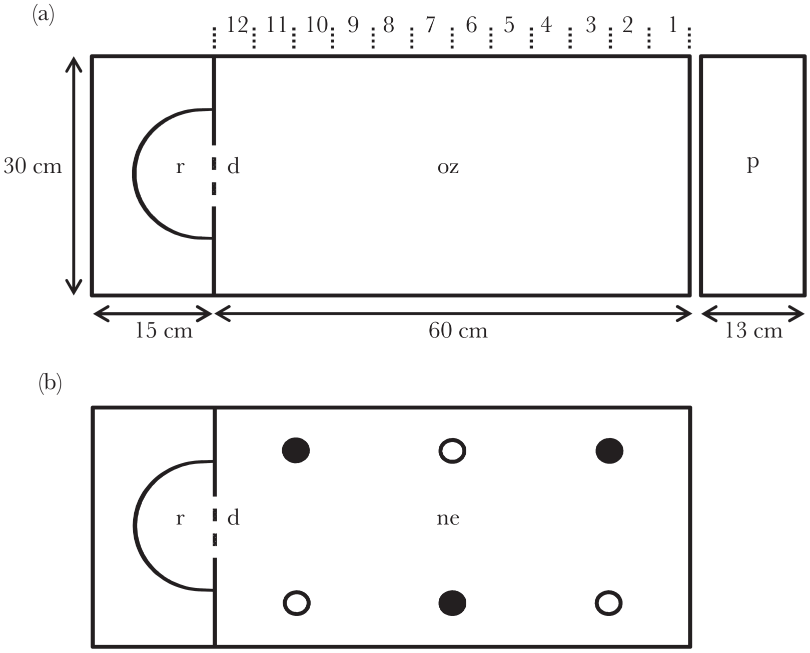

Figure 1

(a) Schematic diagram (top view) of the experimental apparatus used to assay the boldness of individual convict cichlid in the presence of a predator (r = refuge; d = sliding door; oz = open zone; p = predator aquarium). (b) Schematic diagram (top view) of the experimental apparatus used to assay the exploratory tendency of individual convict cichlids (r = refuge; d = sliding door; ne = novel environment). The filled circles symbolize the green plants used for the first measurement of exploration (Test 1), and the empty circles symbolize the red plants used for the second measurement of exploration (Test 2).

left undisturbed and unfed (to ensure high predatory motivation) overnight. For a given trial, we removed a focal fish from its family holding aquarium and placed it in the refuge of the test aquarium, with the refuge door closed. The fish was allowed to acclimatize in the refuge for 30 min without any disturbance. After this period, we raised the door remotely, allowing the focal fish to exit the refuge and enter and swim freely throughout the open zone of the test aquarium. We recorded the time elapsed between the opening of the refuge door to the focal fish exiting the refuge and entering into the open zone as "latency time to exit." The focal fish was given a maximum of 20 min from the opening of the door to exit the refuge and explore the arena. If it did not leave the refuge within this period, it was assigned a maximum latency time of 20 min and the trial was ended.

For any focal fish leaving the refuge, we recorded over the subsequent 15 min the following measures of boldness: 1) latency time to emerge from the refuge, 2) total time spent in the open zone, 3) total number of predator inspection visits, and 4) the median distance of inspection during the trial (calculated as the median of all the closest individual approach distances to the predator on each inspection visit). These behavioral measures are commonly used to assess individual boldness in fishes (e.g., Brown and Braithwaite 2004; Brown et al. 2005; Wilson and Godin 2009), as they represent exposure to predation in open habitat and risk-taking behavior in the face of a potential predation threat (Lima and Dill 1990; Dugatkin and Godin 1992; Milinski et al. 1997). We defined latency to emerge from the refuge as the total time elapsed from the moment the sliding door is raised to the focal fish completely exiting the refuge area (cf. Wilson and Godin 2009). This measure was assumed to be representative of the focal fish's willingness to leave the safety of the refuge to explore a potentially risky open habitat (the open zone). Individuals with shorter latency time were considered bolder. The total time spent in the open zone was assumed to represent the willingness of the focal fish to incur an increased risk of predation by being active in open habitat. Individuals that spent more time in the open zone were considered bolder. Given that an individual's risk of predation increases the more frequently (Lima and Dill 1990; Dugatkin and Godin 1992) and the closer it approaches a predator (Milinski et al. 1997), individuals performing more frequent inspections and approaching closer to the predator were considered bolder.

Quantifying exploratory behavior

Following Jones and Godin (2010), we used the novel environment test to quantify exploratory behavior. Our test apparatus (Figure 1b) consisted of a glass aquarium (75 × 30 × 30 cm; $L \times W \times H$) divided into 2 areas (refuge and open zone) by an opaque white Plexiglas partition furnished with a sliding opaque door, similar to the aquarium used in the boldness test. The bottom of both the refuge and open zone was covered with beige gravel, and the aquarium was filled with aged and aerated dechlorinated tap water (17 cm depth) maintained at 24–25 °C. The back and other side (furthest from the refuge) of the open zone were covered with light plastic sheets to minimize external disturbance and to provide a uniform background. The novel environment to be explored by the focal fish was the open zone, which contained 3 plastic aquatic plants anchored into the substrate as landmarks. These plants differed in their color and spatial arrangement between repeated Tests 1 and 2: green plants were positioned in a particular triangular arrangement for Test 1, and red plants were positioned in the opposite arrangement for Test 2 (Figure 1b), so as to mitigate potential habituation to the environment between repeated tests (Jones and Godin 2010).

As for the boldness test above, each focal fish was repeatedly tested for its exploratory tendency on 2 separate occasions (Test 1 and Test 2), 2 days apart. For either test, we removed a focal fish from its family holding aquarium and placed it in the refuge of the test aquarium, with the refuge door closed. The fish was allowed to acclimatize in the refuge for 30 min without any disturbance. After this period, we raised the sliding door remotely, allowing the focal fish to exit the refuge and enter and explore the open zone of the test aquarium (i.e., the novel environment), and recorded the time elapsed for the focal fish to exit the refuge. The focal fish was given a maximum of 20 min from the opening of the door to exit the refuge and explore the arena. If it did not leave the refuge within this period, it was assigned a maximum latency time of 20 min and the trial was ended. If the fish entered the open zone, then its behavior was filmed with a HD video camera (SONY Handycam HDR-PJ380) positioned 1 m in front center of the aquarium.

For any focal fish leaving the refuge, we recorded over the subsequent 10 min the following measures of exploratory behavior using video playback and a grid of 18 equal-sized squares (3 rows of 6) juxtaposed on the front pane of the aquarium as visualized on a large computer monitor to facilitate the recording of the area explored by the focal fish, following Jones and Godin (2010). From the analysis of the video clips, we quantified the following measures of exploration: 1) latency time to emerge from the refuge, 2) total time spent in the novel environment, 3) total number of squares on the grid traversed, and 4) the proportion of the novel environment visited (using the number of squares traversed at least once). Although the latency time to emerge from a refuge and the total time spent in an open habitat were similarly quantified in our boldness assay, these 2 behaviors can also be used as measures of the willingness to leave a safe area (refuge) to explore a novel (and potentially risky) open environment (e.g., Lima and Dill 1990; Magnhagen 2007). Individuals with long latency time and (or) short time spent in the open zone were considered to be "slow" explorers, being reluctant to actively explore a novel environment compared with "fast" explorers. The number of grid squares traversed by the focal fish was assumed to be representative of the total linear distance swum and its general activity during habitat exploration. The number of squares (out of 18) traversed at least once was taken as a proxy for the proportion of the environment explored by the fish.

Statistical analyses

All statistical analyses were performed using R (R Core Team 2014). First, we estimated separately the repeatability of each behavioral trait constituting boldness and exploration. Repeatability is the fraction of observed behavioral variation that is due to differences between individuals (Boake 1989) and corresponds to personality variation among individuals (Dochtermann et al. 2015). The particular statistical function used depended on the statistical distribution of the data. The "Rpt" function was used for normal distributions (Nakagawa and Schielzeth 2010), and the "epi.CCC" function from package epiR (Stevenson 2014) was used for negative binomial distributions (Carrasco and Jover 2005; Carrasco 2010). In cases where the data did not follow any particular distribution, repeatability was estimated using the nonparametric Spearman's rank correlation test, which assesses repeatability as the individual consistency of ranked data between repeated tests within the entire data set. Bootstrapped 95% confidence intervals were computed from 1000 bootstraps to assess the significance of repeatability estimates (R) from 0 (Nakagawa and Cuthill 2007). Each focal fish was given a mean value [(Test 1 value + Test 2 value)/2] for each behavioral trait that was significantly repeatable. Any individual fish that did not exhibit one of the above behavioral traits on either one or both of the 2 tests was assigned NA as a mean value and excluded from the data set for that particular behavioral trait. Mean values of repeatable behavioral traits were used in subsequent analyses. The Spearman rank correlation test was used to characterize the relationships among these behavioral traits and thus to identify potential behavioral syndromes. The significance level was adjusted for each test using the Benjamini–Hochberg procedure for multiple tests to minimize any inflated chance of Type 1 error (Benjamini and Hochberg 1995).

Second, using principal component analysis (PCA), a composite behavioral score along each of the 2 personality axes of interest (i.e., boldness and exploration) was calculated for each focal fish. More specifically, standardized values of repeatable behavioral traits within each context (boldness and exploration) that collectively explained the largest proportion of the observed variation in the data set were collapsed into first principal component (PC1) scores (Table 1). Two PCAs were run separately for boldness and exploration. Any potential behavioral syndrome (correlation) between PC1 scores for boldness and exploration was ascertained using the Pearson correlation test.

Lastly, the narrow-sense heritability (h^2) of boldness and exploration behaviors was estimated separately using their corresponding PC1 scores. Following Hoffmann and Parsons (1988), we used the intraclass correlation coefficient (t) obtained from a full-sib family analysis, which was calculated using the variance components obtained from a 1-way Anova of the PC1 scores computed using the "ICC" package (Wolak et al. 2012). The standard error interval (SE(t)) of the intraclass correlation coefficient was calculated following Becker (1984) as: $\mathrm{SE}(t)=\sqrt{2(1-t)^2[1+(k-1)t]^2/(k(k-1)(n-1))}$, where n is the number of families and k the average

Table 1

Repeatability estimates (*R*) of behavioral traits across 2 repeated tests (48 h apart) for the boldness and exploration contexts

Context	Behavioral trait	*R*	95% CI
Boldness	Latency time to emerge from the refuge	**0.302**[c]	0.152, 0.448
	Total number of predator inspections	**0.329**[b]	0.183, 0.460
	Distance of inspection	**0.283**[b]	0.118, 0.432
	Total time spent in the open zone	**0.285**[c]	0.129, 0.448
	Mean	**0.300**	
Exploration	Latency time to emerge from the refuge	**0.332**[c]	0.169, 0.468
	Total time spent in the novel environment	**0.355**[c]	0.196, 0.499
	Total number of squares on the grid traversed	0.154[c]	−0.018, 0.311
	Proportion of the novel environment visited	**0.270**[a]	0.106, 0.421
	Mean	**0.313***	

Boldface numbers are statistically significant ($P < 0.05$). Repeatability was estimated using the Rpt function (a), the epi.CCC function (b), or the nonparametric Spearman's rank correlation test (c), depending on the statistical distribution of the data. See Methods for further details.

*The mean R value for exploration was calculated using only the 2 significantly repeatable behavioral traits (i.e., total time in the novel environment and proportion of novel environment visited) that were used to calculate individual PC1 scores for exploration, which in turn were used to estimate the heritability of this behavior (see Results for details).

number of individuals per family. Heritability (h^2) was then calculated as $h^2 = 2/(1/t - 1/2)$, and the corresponding standard error as $\mathrm{SE}(h^2) = 2\mathrm{SE}(t)/[1-(t/2)]^2$. Because not all individuals exited the refuge in a given test, the heritability estimate for boldness was calculated from a subset of 131 individuals (n = 14, k = 9.33) and the heritability estimate for exploration was calculated from a subset of 140 individuals (n = 14, k = 9.93).

Ethical note

This study was approved by the Institutional Animal Care Committee (protocol #101549) at Carleton University and thus meets the guidelines for the care and use of research animals of the Animal Behavior Society and of the Canadian Council on Animal Care and thus the laws of Canada.

RESULTS

Repeatability of behavior

All 4 of our behavioral measures of boldness, and 3 out of the 4 measures of exploratory behavior, were significantly repeatable (Table 1). Calculated repeatability estimates (R) for boldness and exploration averaged 0.300 and 0.313, respectively (Table 1). Individual juvenile convict cichlids were therefore consistent in their boldness and exploratory behaviors across time (i.e., between repeated Tests 1 and 2) in the current study.

Behavioral correlations

Fish that were fast at emerging from the refuge (i.e., exhibiting short latency time to exit) in the boldness context were also fast to emerge from the refuge in the exploration context (Spearman's rank correlation coefficient: r_s = 0.558, n = 167, P < 0.0001; Table 2), and individuals that spent longer periods of time in the open zone of the test arena in the boldness context also spent more time in the novel environment in the exploration context (Spearman's rank correlation coefficient: r_s = 0.223, n = 167, P = 0.011; Table 2). Fish that emerged faster from refuge tended to spend more time in an open habitat, inspected a potential predatory threat more frequently, and spent more time exploring a novel environment and explored a larger proportion of that environment (Table 2). In general, the willingness of juvenile convict cichlids to emerge from the safety of a refuge and to spend increasing time in open habitat (potentially exposed to predators) is positively correlated across behavioral contexts, and individuals that were greater risk takers (as measured by latency to emerge from a refuge) were also more exploratory.

Behavioral syndrome (across-context correlation)

Because measures of behavioral traits were significantly repeatable (Table 1) and intercorrelated within contexts (Table 2), they were reduced in number and collapsed into a single composite measure for both boldness and exploration separately using PCA. All 4 of the behavioral measures of boldness (Table 1) were entered into a PCA for boldness, whereas only 2 of the 4 behavioral measures of exploration (namely, total time spent in the novel environment and the proportion of the novel environment explored, Table 1) were entered into a PCA for exploration. For the exploration context, the total number of squares on the grid traversed by focal fish was excluded from the exploration PCA because it was not repeatable (Table 1), and latency time to emerge from the refuge in exploration (although repeatable) was similarly excluded from the exploration PCA because it was highly correlated with the latency time to emerge from refuge in the boldness context (Table 2), suggesting that these 2 variables represent the same behavior which perhaps best reflects risk-taking behavior in the boldness context.

Both PCAs yielded PC1 scores with eigenvalues larger than 1. The PC1 scores for boldness and exploration explained 41.06% and 78.36% of the total variance observed, respectively (Table 3). Boldness and exploration PC1 scores were significantly positively

Table 2

Spearman's rank correlation coefficients (r_s) for measures of boldness (b) and exploration (e) obtained for each of the 2 repeated tests for juvenile convict cichlids

Behavioral trait 1	Behavioral trait 2	r_s	P value
Latency time to emerge (b)	Number of predator inspections (b)	**−0.195**	**0.025**
Latency time to emerge (b)	Distance of inspection (b)	−0.136	0.122
Latency time to emerge (b)	Time spent in the open zone (b)	−0.136	0.104
Latency time to emerge (b)	Latency time to emerge (e)	**0.558**	**4.79×10^{-15}***
Latency time to emerge (b)	Time spent in the novel environment (e)	**−0.413**	**3.94×10^{-7}***
Latency time to emerge (b)	Proportion of novel environment visited (e)	**−0.253**	**2.59×10^{-3}***
Number of predator inspections (b)	Distance of inspection (b)	−0.078	0.374
Number of predator inspections (b)	Time spent in the open zone (b)	**0.442**	**1.26×10^{-7}***
Number of predator inspections (b)	Latency time to emerge (e)	−0.055	0.532
Number of predator inspections (b)	Time spent in the novel environment (e)	0.139	0.137
Number of predator inspections (b)	Proportion of novel environment visited (e)	0.160	0.086
Distance of inspection (b)	Time spent in the open zone (b)	**−0.359**	**2.61×10^{-5}***
Distance of inspection (b)	Latency time to emerge (e)	0.027	0.757
Distance of inspection (b)	Time spent in the novel environment (e)	0.065	0.487
Distance of inspection (b)	Proportion of novel environment visited (e)	−0.029	0.754
Time spent in the open zone (b)	Latency time to emerge (e)	**−0.181**	**0.030**
Time spent in the open zone (b)	Time spent in the novel environment (e)	**0.223**	**0.011***
Time spent in the open zone (b)	Proportion of novel environment visited (e)	0.157	0.075
Latency time to emerge (e)	Time spent in the novel environment (e)	**−0.331**	**6.44×10^{-5}***
Latency time to emerge (e)	Proportion of novel environment visited (e)	**−0.288**	**5.69×10^{-4}***
Time spent in novel environment (e)	Proportion of novel environment visited (e)	**0.561**	**5.79×10^{-13}***

Boldface numbers are statistically significant (P < 0.05). Correlation coefficients that remained significant after correction with the Benjamini–Hochberg procedure are identified with an asterisk.

Table 3

PCA loadings of within-context behavioral trait variables used to generate principal component scores (PC1) to assess across-context correlations in boldness and exploration in juvenile convict cichlids

Context	Behavioral trait	PCA loading
Boldness	Latency time to emerge from the refuge	0.056
	Total number of predator inspections	0.310
	Distance of inspection	0.173
	Total time spent in the open zone	0.461
	Eigen value	1.64
	% variation explained	41.06
Exploration	Total time spent in the novel environment	0.500
	Proportion of the novel environment visited	0.500
	Eigen value	1.57
	% variation explained	78.36

correlated (Pearson correlation, $r = 0.22$, $n = 116$, $P = 0.019$; Figure 2) and thus comprised an across-context behavioral syndrome, suggesting that individual fish that were bolder in the face of a predation threat were also more exploratory.

Heritability of behavior

Calculated heritability estimates ($h^2 \pm$ SE) for boldness and exploration behaviors, as expressed by their respective individual PC1 scores, were 0.37 ± 0.21 and 0.30 ± 0.19, respectively.

DISCUSSION

We demonstrated for the first time consistent (repeatable) and heritable individual differences in boldness and exploratory behaviors, and a boldness–exploration behavioral syndrome, in juvenile convict cichlids. Across contexts, the willingness of individuals to take risks (i.e., approaching a predator) and their tendency to explore a novel environment were significantly positively correlated, such that bolder fish were more exploratory than relatively timid ones. These novel results provide compelling evidence for the emergence in early life history of consistent individual differences in personality traits and behavioral syndromes (sensu Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziemba 2004; Sih and Bell 2008) in this species. In comparison, personality differences in exploratory and boldness behaviors were observed as early as 9–18 weeks of age in the great tit (Verbeek et al. 1994) and 4–6 months of age in the three-spined stickleback (Dzieweczynski and Crovo 2011). Notwithstanding these and a few other related studies showing that personality can arise early in life, the ontogenetic timing of the appearance of distinct individual personality traits and behavioral syndromes in nonhuman animals has not been comprehensively addressed and warrants more attention (Stamps and Groothuis 2010).

The average repeatability estimates (*R*) obtained for boldness and exploration behavioral traits in juvenile convict cichlids are well within the range of the majority of repeatability estimates, and close to the average of 0.37, for various behaviors in species representing diverse taxa, as revealed by a recent meta-analysis (Bell et al. 2009). Based on a very limited number of studies available to date, there is no evidence that the repeatability of behavior in juveniles and adults of the same species differ (Bell et al. 2009). Therefore, how repeatability of behavior changes during development and the comparison of the repeatability of behavior between juveniles and adults within the same species are important and relatively unexplored questions with no obvious predictions about the direction of the effects (Bell et al. 2009; Stamps and Groothuis 2010).

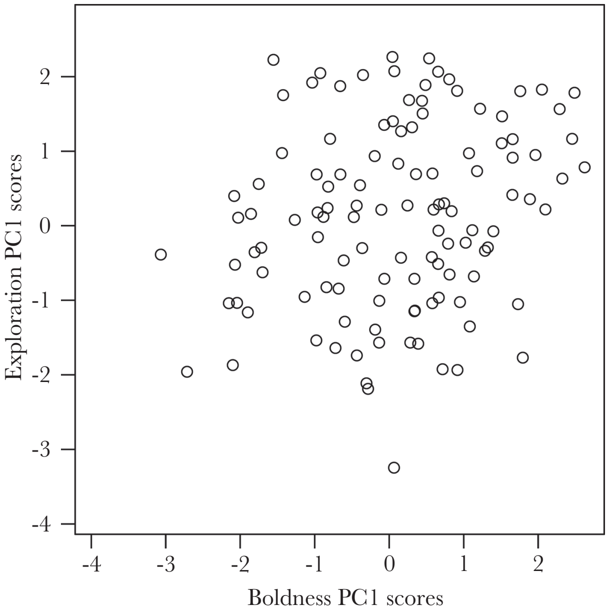

Figure 2

The relationship between the first principal component (PC1) scores of boldness and exploration behaviors in individual juvenile convict cichlids ($n = 116$). Boldness and exploratory tendency increase from left to right along each axis, respectively.

In addition to being consistent over time, boldness and exploration behaviors in juvenile convict cichlids were also heritable, with calculated heritability estimates (h^2) of 0.37 and 0.30, respectively. Although the magnitude of these estimates seem moderate, they are greater than most heritability estimates for personality traits in freshwater fishes in general (range = 0.011–0.353) (e.g., Bell 2005; Dingemanse et al. 2009) and also greater than mean heritability estimates for sexually selected behavioral traits (mean = 0.28, Prokuda and Roff 2014) and other behavioral traits such as foraging, aggression, antipredation, and mating (mean = 0.14, Dochtermann et al. 2015) in species from diverse taxa. However, despite our best efforts to minimize environmental effects by rearing fish families in similar aquaria and conditions, our calculated heritability estimates must be interpreted cautiously because our experimental fish were not raised from hatching in a "common-garden" environment and consequently we cannot exclude the possibility of some environmental effect and (or) nongenetic parental effects on offspring personality traits (cf. Reddon 2012; Schuett et al. 2013). When both repeatability (*R*) and heritability (h^2) are estimated from the same data, the ratio of these 2 estimates (h^2/R) can be considered an estimate of the *heritability of personality* (Dochtermann et al. 2015). *Heritability of personality* refers strictly to the proportion of observed personality variation attributable to additive genetic variance, whereas *narrow-sense heritability* estimates the proportion of total phenotypic variation attributable to additive genetic variation (Dochtermann et al. 2015). Because our repeatability and heritability estimates for boldness and exploration behaviors for convict cichlid young were obtained from different types of data (i.e., composite PC1 scores for heritability estimates vs. measures of multiple behavioral traits characterizing boldness and exploration behaviors, respectively, for repeatability estimates), it was not appropriate for us to calculate heritability of personality estimates using the aforementioned ratio. Notwithstanding these limitations, our comparatively high heritability estimates nonetheless suggest that some genetic variation for boldness and exploratory behaviors, and thus potential for selection on these traits (cf. Stirling et al. 2002; Freeman and Herron 2007), exists in the Río Cabuyo population of convict cichlids and provide support for the hypothesis of a genetic-based transmission of personality from parents to offspring.

We also report novel evidence for a phenotypic link between boldness and exploration (i.e., a boldness–exploration syndrome) in juvenile convict cichlids; such a syndrome has also been observed in other species (e.g., van Oers et al. 2004; Wilson and Godin 2009; Cote, Fogarty, et al. 2010; Wisenden et al. 2011). Additionally, Jones and Godin (2010) previously observed a exploration–antipredator behavioral syndrome in juvenile convict cichlids originating from the same Costa Rican population as ours. They found that more exploratory individuals were slower to respond to (i.e., escape from) an attacking predator, and thus may be at a greater risk of predation, compared with less exploratory ones. Because of their phenotypic (and possibly genotypic) linkage, selection on exploratory behavior could produce indirect correlational selection on boldness and antipredator behaviors or vice versa (cf. Sih, Bell, and Johnson 2004; Sih, Bell, Johnson, and Ziemba 2004), which interestingly could have important implications for ecological dispersal within a species as exploration, boldness, and antipredator behaviors are important in dispersal (e.g., Fraser et al. 2001; Cote, Fogarty, et al. 2010; Bonte et al. 2012).

There is now evidence for the evolution of adaptive personality traits, with fitness consequences, through selection in animals in the wild (Dingemanse and Réale 2005; Smith and Blumstein 2008). Known selection agents on personality traits include predation (Bell and Sih 2007) and choosy sexual partners (Godin and Dugatkin 1996; Schuett et al. 2010). However, the ecological significance of consistent and heritable differences in personality traits among juvenile convict cichlids (current study; Jones and Godin 2010) in nature is presently unknown. This species is particularly vulnerable to predators, and suffers high mortality rates to predation, in its natural habitats during early life-history stages (Wisenden 1994; Wisenden and Keenleyside 1994; Lehtonen 2008; Lee-Jenkins et al. 2014; Wisenden et al. 2015). The reproductive (nesting) success of individual adult convict cichlids in our study population (Río Cabuyo) varies considerably on a small spatial scale, and this variation is primarily attributable to spatial variation in fish predation on young (Wisenden 1994). Given such spatial variation in predation pressure within this population, it is conceivable that the expression of individual differences in boldness, exploration, and antipredator behaviors (current study; Jones and Godin 2010), particularly during the transitional period from parental care to independence and gradual dispersal away from their natal parental territory (Wisenden 1994, 1995), could influence growth and survival and generate differences in fitness among individuals. This proposition remains to be tested experimentally. Because individual convict cichlids spawn in the same riverine microhabitat in which they were born and raised (Wisenden 1994), and to the extent that personality affects fitness (Dingemanse and Réale 2005; Smith and Blumstein 2008), there may well be strong selection for heritability of personality traits, such as boldness and exploration, in young convict cichlids in the Río Cabuyo and in other stream populations of the species. As small-scale variation in nesting success and natal philopatry are relatively common in animals (e.g., Greenwood 1980; Clutton-Brock 1988; Dittman and Quinn 1996; Grabowska-Zhang et al. 2012), our findings are broadly applicable to other study systems.

In general, relatively little is known about the development of individual personalities and behavioral syndromes, and their plasticity, in wild animals (Stamps and Groothuis 2010). We believe that the convict cichlid is an ideal model system for addressing these questions and that our current study and that of Jones and Godin (2010) on juveniles of this species have made important initial contributions to such an endeavor.

FUNDING

This work was supported by a Discovery research grant (#8074-2010) from the Natural Sciences and Engineering Research Council of Canada awarded to J.-G.J.G.

We thank A.-C. Auge, H. Auld, R. Pusiak, and V. Scarponi for assistance with fish care; D. Réale, F. Rousset, M.-J. Perrot-Minnot, and J. Dhinaut for discussions on the methods for estimating heritabilities, and the editor and 2 reviewers for their constructive comments on our manuscript.

Handling editor: Bob Wong

REFERENCES

Archard GA, Braithwaite VA. 2011. Increased exposure to predators increases both exploration and activity level in *Brachyrhaphis episcopi*. J Fish Biol. 78:593–601.

Becker WA. 1984. Manual of quantitative genetics. 4th ed. Pullman (WA): Academic Enterprises.

Bell AM. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). J Evol Biol. 18:464–473.

Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. Anim Behav. 77:771–783.

Bell AM, Sih A. 2007. Exposure to predation generates personality in three-spined sticklebacks (*Gasterosteus aculeatus*). Ecol Lett. 10:828–834.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc B. 57:289–300.

Boake CRB. 1989. Repeatability: its role in evolutionary studies of mating behavior. Evol Ecol. 3:173–182.

Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehouck V, Matthysen E, Mustin K, Saastamoinen M, et al. 2012. Costs of dispersal. Biol Rev. 87:290–312.

Brown C, Braithwaite VA. 2004. Size matters: a test of boldness in eight populations of bishop, *Brachyraphis episcopi*. Anim Behav. 68:1325–1329.

Brown C, Jones F, Braithwaite VA. 2005. In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. Anim Behav. 70:1003–1009.

Brydges NM, Colegrave N, Heathcote RJ, Braithwaite VA. 2008. Habitat stability and predation pressure affect temperament behaviours in populations of three-spined sticklebacks. J Anim Ecol. 77:229–235.

Budaev SV, Zworykin DD. 2003. Habituation of predator inspection and boldness in the guppy (*Poecilia reticulata*). J Ichthyol. 43:243–246.

Budaev SV, Zworykin DD, Mochek AD. 1999. Individual differences in parental care and behaviour profile in the convict cichlid: a correlation study. Anim Behav. 58:195–202.

Carrasco JL. 2010. A generalized concordance correlation coefficient based on the variance components generalized linear mixed models for overdispersed count data. Biometrics. 66:897–904.

Carrasco JL, Jover L. 2005. Concordance correlation coefficient applied to discrete data. Stat Med. 24:4021–4034.

Clutton-Brock TH, editor. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. Chicago (IL): University of Chicago Press.

Cote J, Clobert J, Brodin T, Fogarty S, Sih A. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philos Trans R Soc B. 365:4065–4076.

Cote J, Fogarty S, Weinersmith K, Brodin T, Sih A. 2010. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). Proc R Soc B. 277:1571–1579.

Dall SRX, Bell AM, Bolnick DI, Ratnieks FL. 2012. An evolutionary ecology of individual differences. Ecol Lett. 15:1189–1198.

Dall SRX, Houston AI, McNamara JM. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecol Lett. 7:734–739.

Dingemanse NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ. 2003. Natal dispersal and personalities in great tits (*Parus major*). Proc R Soc Lond B. 270:741–747.

Dingemanse NJ, Réale D. 2005. Natural selection and animal personality. Behaviour. 142:1165–1190.

Dingemanse NJ, Van der Plas F, Wright J, Réale D, Schrama M, Roff DA, Van der Zee E, Barber I. 2009. Individual experience and evolutionary history of predation affect expression of heritable variation in fish personality and morphology. Proc R Soc B. 276:1285–1293.

Dingemanse NJ, Wright J, Kazem AJ, Thomas DK, Hickling R, Dawnay N. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. J Anim Ecol. 76:1128–1138.

Dittman A, Quinn T. 1996. Homing in Pacific salmon: mechanisms and ecological basis. J Exp Biol. 199:83–91.

Dochtermann NA, Schwab T, Sih A. 2015. The contribution of additive genetic variation to personality variation: heritability of personality. Proc R Soc B. 282:20142201.

Dugatkin LA, Godin J-GJ. 1992. Prey approaching predators: a cost-benefit perspective. Ann Zool Fenn. 29:233–252.

Dzieweczynski TL, Crovo JA. 2011. Shyness and boldness differences across contexts in juvenile three-spined stickleback *Gasterosteus aculeatus* from an anadromous population. J Fish Biol. 79:776–788.

Fraser DF, Gilliam JF, Daley MJ, Le AN, Skalski GT. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. Am Nat. 158:124–135.

Freeman S, Herron JC. 2007. Evolutionary analysis. 4th ed. Upper Saddle River (NJ): Pearson Prentice Hall.

Garamszegi LZ, Markó G, Herczeg G. 2012. A meta-analysis of correlated behaviours with implications for behavioural syndromes: mean effect size, publication bias, phylogenetic effects and the role of mediator variables. Evol Ecol. 26:1213–1235.

Godin J-GJ, Davis SA. 1995. Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. Proc R Soc Lond B. 259:193–200.

Godin J-GJ, Dugatkin LA. 1996. Female mating preference for bold males in the guppy, *Poecilia reticulata*. Proc Natl Acad Sci USA. 93:10262–10267.

Grabowska-Zhang AM, Wilkin TA, Sheldon BC. 2012. Effects of neighbour familiarity on reproductive success in the great tit (*Parus major*). Behav Ecol. 23:322–333.

Greenwood PJ. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Anim Behav. 28:1140–1162.

Hoffmann A, Parsons P. 1988. The analysis of quantitative variation in natural populations with isofemale strains. Genet Sel Evol. 20:87–98.

Huntingford FA. 1976. The relationship between antipredator behavior and aggression among conspecifics in the three-spined stickleback. Anim Behav. 24:245–260.

Jones KA, Godin J-GJ. 2010. Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. Proc R Soc B. 277:625–632.

Keenleyside MHA. 1991. Parental care. In: Keenleyside MHA, editor. Cichlid fishes: behavior, ecology and evolution. New York: Chapman and Hall. p. 191–208.

Lee-Jenkins SSY, Jeswiet SB, Godin J-GJ. 2014. Spatial separation from family in the mobile young of a biparental fish: risks and dynamics of returning home. Naturwissenschaften. 101:11–15.

Lehtonen TK. 2008. Convict cichlids benefit from close proximity to another species of cichlid fish. Biol Lett. 4:610–612.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool. 68:619–640.

Magnhagen C. 2007. Social influence on the correlation between behaviours in young-of-the-year perch. Behav Ecol Sociobiol. 61:525–531.

Milinski M, Lüthi JH, Eggler R, Parker GA. 1997. Cooperation under predation risk: experiments on costs and benefits. Proc R Soc Lond B. 264:831–837.

Nakagawa S, Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol Rev. 82:591–605.

Nakagawa S, Schielzeth H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev. 85:935–956.

van Oers K, De Jong G, van Noordwijk AJ, Kempenaers B, Drent PJ. 2005. Contribution of genetics to the study of animal personalities: a review of case studies. Behaviour. 142:1191–1212.

van Oers K, Drent PJ, de Goede P, van Noordwijk AJ. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proc R Soc Lond B. 271:65–73.

Prokuda AY, Roff DA. 2014. The quantitative genetics of sexually selected traits, preferred traits and preference: a review and analysis of the data. J Evol Biol. 27:2283–2296.

R Core Team. 2014. R: a language and environment for statistical computing, version 3.0.3. Vienna (Austria): R Foundation for Statistical Computing [cited 2014 April 17]. Available from: http://www.R-project.org.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. Biol Rev. 82:291–318.

Reddon AR. 2012 Parental effects on animal personality. Behav Ecol. 23:242–245.

Schuett W, Dall SRX, Wilson AJ, Royle NJ. 2013. Environmental transmission of a personality trait: foster parent exploration behaviour predicts offspring exploration behaviour in zebra finches. Biol Lett. 9:1–6.

Schuett W, Tregenza T, Dall SRX. 2010. Sexual selection and animal personality. Biol Rev. 85:217–246.

Sih A, Bell AM. 2008. Insights for behavioral ecology from behavioral syndromes. Adv Study Behav. 38:227–281.

Sih A, Bell AM, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol. 19:372–378.

Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: an integrative overview. Q Rev Biol. 79:241–277.

Sih A, Mathot KJ, Moirón M, Montiglio P-O, Wolf M, Dingemanse NJ. 2015. Animal personality and state-behaviour feedbacks: a review and guide for empiricists. Trends Ecol Evol. 30:50–60.

Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. Behav Ecol. 19:448–455.

Stamps J, Groothuis TGG. 2010. The development of animal personality: relevance, concepts and perspectives. Biol Rev. 85:301–325.

Stevenson M. 2014. epiR: an R package for the analysis of epidemiological data. R package version 0.9-59 [cited 2014 August 13]. Available from: http://CRAN.R-project.org/package=epiR.

Stirling DG, Réale D, Roff DA. 2002. Selection, structure and the heritability of behaviour. J Evol Biol. 15:277–289.

Toms CN, Echevarria DJ, Jouandot DJ. 2010. A methodological review of personality-related studies in fish: focus on the shy-bold axis of behavior. Int J Comp Psychol. 23:1–25.

Verbeek MEM, Drent PJ, Wiepkema PR. 1994. Consistent individual differences in early exploratory behaviour of male great tits. Anim Behav. 48:1113–1121.

Wilson ADM, Godin J-GJ. 2009. Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. Behav Ecol. 20:231–237.

Wilson DS, Coleman K, Clark AB, Biederman L. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. J Comp Psychol. 107:250–260.

Wisenden BD. 1994. Factors affecting reproductive success in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). Can J Zool. 72:2177–2185.

Wisenden BD. 1995. Reproductive behaviour of free-ranging convict cichlids, *Cichlasoma nigrofasciatum*. Environ Biol Fish. 43:121–134.

Wisenden BD, Keenleyside MHA. 1994. The dilution effect and differential predation following brood adoption in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). Ethology. 96:203–212.

Wisenden BD, Sailer CD, Radenic SJ, Sutrisno R. 2011. Maternal inheritance and exploratory-boldness behavioural syndrome in zebrafish. Behaviour. 148:1443–1456.

Wisenden BD, Stumbo AD, Self PA, Snekser JL, McEwen DC, Wisenden PA, Keenleyside MHA, Itzkowitz M, Brisch E. 2015. Co-evolution of offspring antipredator competence and parental brood defense in convict cichlids. Hydrobiologica. 748:259–272.

Wolak ME, Fairbairn DJ, Paulsen YR. 2012. Guidelines for estimating repeatability. Methods Ecol Evol. 3:129–137.

Wolf M, Weissing FJ. 2012. Animal personalities: consequences for ecology and evolution. Trends Ecol Evol. 27:452–461.