**ORIGINAL PAPER**

# Predictors of individual variation in reversal learning performance in three-spined sticklebacks

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## Abstract

Behavioral flexibility is a type of phenotypic plasticity that can influence how animals cope with environmental change and is often measured with a reversal learning paradigm. The goal of this study was to understand why individuals differ in behavioral flexibility, and whether individual differences in behavioral flexibility fit the predictions of coping styles theory. We tested whether individual variation in flexibility correlates with response to novelty (response to a novel object), boldness (emergence into a novel environment), and behavioral persistence (response to a barrier), and tested for trade-offs between how quickly individuals learn an initial discrimination and flexibility. We compare results when reversal learning performance is measured during an early step of reversal learning (e.g. the number of errors during the first reversal session) to when reversal learning performance is measured by time to criterion. Individuals that made fewer mistakes during an early step of reversal learning spent more time away from the novel object, were less bold, less persistent, and performed worse during initial discrimination learning. In contrast, time to criterion was not correlated with any of the behaviors measured. This result highlights the utility of dissecting the steps of reversal learning to better understand variation in behavioral flexibility. Altogether, this study suggests that individuals differ in flexibility because flexibility is a key ingredient to their overall integrated strategy for coping with environmental challenges.

**Keywords** Animal cognition · Three-spined stickleback · Animal personality · Reversal learning · Flexibility · Persistence · Individual differences

## Introduction

As concerns rise about how human-induced rapid environmental change will impact global biodiversity and ecosystem stability, there is increasing interest in identifying the traits that allow some organisms to respond adaptively and thrive in a changing environment, such as behavioral flexibility (Sih et al. 2011; Wright et al. 2010; Wong and Candolin 2015). Behavioral flexibility is a type of phenotypic

plasticity that can influence how animals cope with environmental change. While the term "behavioral flexibility" has been used to refer to a wide range of phenomena, including problem-solving and innovation (Audet and Lefebvre 2017; Reader and Laland 2003), one aspect of flexibility particularly relevant to responding to changing environments is the ability of animals to switch away from old behavior patterns that were previously beneficial, but no longer are fruitful (Stamps 2016). For example, behaviorally flexible animals might be better able to search for new food sources when previous sources become scarce or dangerous (Dill 1983). Additionally, flexibility can improve fitness if it allows individuals to identify novel opportunities to gain access to mates (Shine et al. 2005a, b), or to plastically respond to predation threats in adaptive ways (Lima 2009). Animals that are sensitive to changes in outcomes related to their environment, and phenotypically plastic enough to respond adaptively to those changes, are predicted to excel in moderately variable environments. However, sensitivity to environmental cues might be costly in more stable environments

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(e.g., reduced foraging efficiency) and thus variation in flexibility may be maintained over temporal and/or spatial scales (Wolf et al. 2008). Behavioral flexibility is often moderately repeatable (Cauchoix et al. 2018) and heritable (Laughlin et al. 2011; Sorato et al. 2018; but see Sauce et al. 2018). Therefore flexibility has the potential to influence evolutionary outcomes (Foster and Sih 2013; Ghalambor et al. 2007; West-Eberhard 2003).

Behavioral flexibility is often measured using reversal learning paradigms in which animals are trained to discriminate between two or more variations of a cue (e.g., color) by associating one particular cue (e.g. the color blue) with a reward (e.g. food). After a predetermined number of trials or after the subject has reached a predetermined criterion, the reward is paired with another variation of the cue on subsequent trials and reversal learning performance (behavioral flexibility) is often assessed by the number of trials or sessions that are required to reach a predetermined criterion for learning the new association. There is often extensive variation in reversal learning performance among individuals of the same species (e.g., birds: Bebus et al. 2016; Tello-Ramos et al. 2019; fish: Bensky et al. 2017; Lucon-Xiccato and Bisazza 2014; invertebrates: Chandra et al. 2001; Liedtke and Schneider 2014; mammals: Guenther et al. 2014; Mazza et al. 2018; reptiles: Carazo et al. 2014). However, the factors driving and maintaining variation in flexibility among individuals are still unclear (den Ouden et al. 2013; Izquierdo et al. 2017).

Considering that there are multiple steps of the reversal learning process, dissecting it into multiple components might help to clarify the causes of variation in flexibility (Chow et al. 2017; Federspiel et al. 2017). During reversal learning, the animal first has to stop following the previously rewarded response, and then the animal must learn to follow the new association (Boulougouris et al. 2008). It is likely that there is individual variation in processes influencing the separate steps; therefore overall reversal learning performance could reflect multiple, non-mutually exclusive causes. If this is the case, then it should be easier to explain individual variation during one of the steps of reversal learning compared to overall reversal learning performance, i.e. because statistical noise accumulates across the various steps.

Coping styles theory provides a useful framework for understanding variation in behavioral plasticity (Dingemanse et al. 2010; Jolles et al. 2019) and flexibility (Carere and Locurto 2011; Coppens et al. 2010; Sih and Del Giudice 2012). According to coping styles theory, individuals differ along a suite of correlated physiological and behavioral traits related to how they respond to environmental challenges, including changes in environmental cues (Koolhaas et al. 1999, 2010). Flexible individuals are more reactive; they are relatively cautious, sensitive to changes in their environment

and faster to respond to changes in the environment compared to bolder, proactive individuals that consistently display less of a stress response (Coppens et al. 2010). Therefore coping styles theory makes several predictions about how individual differences in behavior might be related to variation in behavioral flexibility.

First, flexible and reactive individuals are predicted to respond differently to novelty (e.g., greater neophobia) and to changes in the environment (e.g., greater change in behavior in response to cue changes) relative to proactive individuals, a prediction with some empirical support (e.g., Bebus et al. 2016; Benus et al. 1990; Bolhuis et al. 2004; de Lourdres Ruiz-Gomez et al. 2011). Reactive individuals may benefit from being more attuned to changes in environmental cues and more attentive to unexpected outcomes (Aron and Aron 1997; Aron et al. 2012; Chudasama et al. 2003; Schoenbaum et al. 2009).

Second, coping styles theory predicts that behavioral flexibility is related to behavioral persistence. In particular, reactive individuals are predicted to be faster to inhibit a response that has been previously rewarded once that response is no longer rewarded, and therefore faster to explore alternative behavioral patterns that may be more successful (Izquierdo and Jentsch 2012; Roberts and Wallis 2000). In contrast, persistent individuals become routinized and perseverate because they fail to inhibit the previously learned association.

Finally, coping styles theory predicts that flexibility is related to variation along the shy-bold continuum, such that proactive individuals are expected to be relatively bold. Bolder individuals are expected to quickly learn novel associations, perhaps because they are more willing to take risks to explore new environments, increasing opportunities to gain new information, but are also predicted to quickly establish routinized behavioral patterns and therefore be less flexible (Carere and Locurto 2011; Dougherty and Guillette 2018; Griffin et al. 2015; Sih and Del Giudice 2012). As a result, coping styles theory proposes that behavioral flexibility trades-off with initial learning of a completely novel task. This tradeoff could be a key contributor to the maintenance of variation in behavioral flexibility within natural populations (Bebus et al. 2016; Koolhaas et al. 1999; Sih and Del Giudice 2012). Alternatively, behavioral flexibility as assessed by reversal learning performance might reflect general learning ability; some individuals perform better than others across learning tasks generally, which could lead to positive correlations between initial and reversal learning (Galsworthy et al. 2002; Head et al. 1998; Matzel et al. 2003).

Results of studies examining the predictions of coping styles theory in the context of behavior and learning (including flexibility) have been mixed (Dougherty and Guillette 2018). While a number of studies find patterns consistent

with coping styles theory (e.g., Bebus et al. 2016; Guillette et al. 2011), others find no correlations or even the opposite of the predicted pattern, e.g. positive correlations between boldness and flexibility (e.g., Bensky et al. 2017; Guido et al. 2017; Guillette et al. 2015). Part of the problem could be that reversal learning performance is measured in different ways in the literature. While several studies on behavioral flexibility focus on how long it takes animals to learn a novel association with the previously unrewarded cue (i.e., the cumulative result of multiple steps comprising the reversal learning process) (e.g., Guenther et al. 2014; Guillette et al. 2011, 2015; Mazza et al. 2018; Tebbich et al. 2012), other studies focus on the immediate response to the change in contingencies (e.g., Bolhuis et al. 2004; Zidar et al. 2017). Thus more work is needed to identify how the timing of performance measures and other moderating factors (e.g., sex: Carazo et al. 2014; Dougherty and Guillette 2018; Titulaer et al. 2012), influence the behavioral × cognition patterns observed.

The goal of this study was to understand why individuals differ in behavioral flexibility, and whether individual differences in behavioral flexibility fit the predictions of coping styles theory in three-spined stickleback, an important model for examining natural intra-specific variation in behavior, including behavioral flexibility (Bensky et al. 2017; Rystrom et al. 2019). We tested the hypothesis that individuals that are more behaviorally flexible are more neophobic, less bold, less behaviorally persistent and perform worse during initial learning. We explicitly compare results when reversal learning performance is measured during an early step of reversal learning (e.g. the number of errors during the first reversal session) to when reversal learning performance is measured by time to criterion.

## Materials and methods

### Subjects and housing

In May of 2016, adult sticklebacks were collected from Putah Creek, CA and transported to the University of Illinois Urbana-Champaign where they were housed in $53 \times 33 \times 24$ cm (37.85L) tanks in groups of ten to fifteen individuals. Fish were housed in 20 degrees Celsius water and on a summer (16L: 8D) photoperiod. A recirculating flow-through system consisting of a series of particulate, biological, and UV filters (Aquaneering, San Diego, USA) was used to clean the water. 10% of the water volume in the tanks was replaced each day. While housed in groups, the fish were fed a mixed diet consisting of frozen bloodworm, frozen brine shrimp, and frozen mysis shrimp ad lib each day.

To control for sex effects only females were tested in this study. Sixty females were randomly selected from the group tanks to participate in this study. Females were reproductively mature but were not gravid during the experiment (average length = 48.9 mm, length standard deviation = 4.7 mm, average mass = 1.54 g, mass standard deviation = 0.38 g). Once a female started the experiment, she was housed individually in a $36 \times 33 \times 24$ cm (26.5 L) tank. The tank bottom was divided into thirds, and the floor of the outer two-thirds was lined with gravel. A plastic plant was placed at the center of the middle third of the tank. Individuals had visual access to fish in adjacent tanks between testing trials. Once an individual started the experiment it was only fed during experimental trials (see below for details) in order to maintain motivation.

### Experimental overview

To test how individual differences in behavior and initial learning correlate with behavioral flexibility, we measured response to a novel object, boldness, behavioral persistence, and discrimination learning performance in the same individual sticklebacks in a fixed order of assays. While it is plausible that the animals' experience in one assay could influence its behavior in the next assay (order effects), we assume that the extent of carryover was the same for all of the individuals (Bell 2013).

For details of each part of the experiment refer to the sections below; here we describe the general timeline. The day following transfer to individual tanks, individuals were fed once daily in their home tank until they met the criterion demonstrating they were motivated to consistently and quickly eat ("Initial motivation"). The morning after criterion for Initial motivation was met, a single novel object trial was administered in the individual's home tank to measure its response to a novel object being placed in their tank ("Novel object task").

Later that same day (~ 3–4 h later), the subject went through the first training session for the barrier detour task ("Barrier detour task pretraining"). Training and all the remaining measures took place in a separate designated tank. This tank was the same dimensions as the individuals' home tanks. One major difference was that it did not contain gravel, which helped differentiate the testing environment from the individual's home tank, improved visibility for the experimenters and increased the salience of key objects (i.e., food rewards and discrimination objects). Barrier detour task training entailed repeated trials in which an individual could emerge from a shelter to get a food reward in the middle of the tank. From the fish's perspective, the tank was initially novel and potentially dangerous during the first session; therefore we interpret emergence time during the first session (4 trials) as

a measure of boldness. Individuals received one session of barrier detour task training a day until they met criterion. The following day, we measured how the individual responded to a barrier placed between the shelter and the food reward, blocking the previously trained search pattern ("Barrier detour task"). We interpret an individual's behavioral response to the barrier as a measure of behavioral persistence.

The day after the barrier detour task, training for discrimination learning began ("Initial and reversal learning"). Individuals received one session a day. First, the individual was trained to search two possible locations for a food reward. Once criterion was met, initial discrimination training sessions began the following day, where individuals were trained to choose a blue cup over a yellow cup for a food reward. Once the performance criterion for initial learning was met, the reversal learning phase began the next day and the yellow cup was now rewarded. Individuals completed the experiment once they reached the performance criterion for the reversal learning phase.

To minimize observer effects for all stages of the different behavioral and training assays, a mirror was positioned at a 45° angle above the tank. This allowed the experimenters to observe all trials from a top down view of the individual with minimal disruption. For both the novel object assay and barrier trials, a camcorder (JVC Everio HD Hard Dish Camcorder Model No: GZ-HD40U) was used to record a top down view of the trial via the mirror positioned above the tank.

## Initial motivation

Food motivation and personality can influence both participation in cognitive tasks and performance (van Horik and Madden 2016; van Horik et al. 2017). To ensure that individuals were acclimated to their home tanks and displayed relatively equal food motivation to one another before beginning the experiment, we measured how quickly individuals ate during feeding trials. Once a day, the plastic plant was removed from the tank, and plastic blinders were used to block all sides of the tank. A glass petri dish (60 W × 15H mm; Corning Inc, Corning, USA) was then placed in the center of the tank with 10 bloodworms placed inside and the foraging behavior of the individual was recorded for 10 min. Once the individual ate, the plant was returned to the tank and the blinders were removed. We inferred that an individual was acclimated and motivated after the individual ate at least 8 out of 10 worms within 10 min on three consecutive days (range 3–10 days until fish met criterion, mean: 3.92 days, sd 1.72 days); the individual was tested in the novel object task the following morning.

## Novel object task

The purpose of this assay was to assess individual differences in response to the presence of a novel object in their home environment. A circular blind was used to corral the individual into the middle third of the tank, where the individual was undisturbed for 5 min. While the individual was in the blind, a perforated tank divider was then placed to block the individual from accessing the back part of the tank, which was out of the camera's view, during the trial. A novel object (toy plastic lion (10L x 7H cm; TERRA by Battat, Montreal, Canada)) was placed into either the left or right third of the tank at random (Fig. 1a). This object was selected as it was never seen by the fish previously, the shape is presumed to have no evolutionary relevance, and the colors were neutral.

After 5 min, the blind was removed and we recorded the individual in the tank for 15 min. We focused on the animals' immediate response to the novel object and measured the time it took the individual to orient towards the novel object (i.e., nose pointed directly towards the novel object), the time it took the individual to approach the novel object (i.e., head within one body length of the novel object), the time the individual spent within the third of the tank that contained the novel object, as well as the time the individual spent both within this third and oriented towards the novel object for 5 min. Upon completion of the task, the novel object and the tank divider were removed, the plant was returned to the tank, and the blinders were removed.

## Barrier detour task pretraining

Training for the barrier detour task started the afternoon the novel object task was administered (~ 3–4 h afterwards). The purpose of the barrier detour task was to assess individual differences in behavioral persistence. Individuals were first trained to follow a simple direct search pattern in order to obtain a food reward. Training trials helped to establish that food motivation was relatively equal among the individuals even within a novel tank environment, as well as establish the prepotent response of leaving a shelter to directly approach and eat a food reward. During early trials individuals often explored the tank before approaching the food, but they became consistently more direct during subsequent trials. Once an individual consistently followed the direct search pattern across multiple trials, the individual's response to a transparent barrier that made a direct approach no longer productive was recorded.

Individuals were trained for one session per day until the training criterion was met (see below), and each session comprised of four trials. To begin the session, the individual was gently transferred with a white cup from their home tank to an opaque shelter that was then placed into
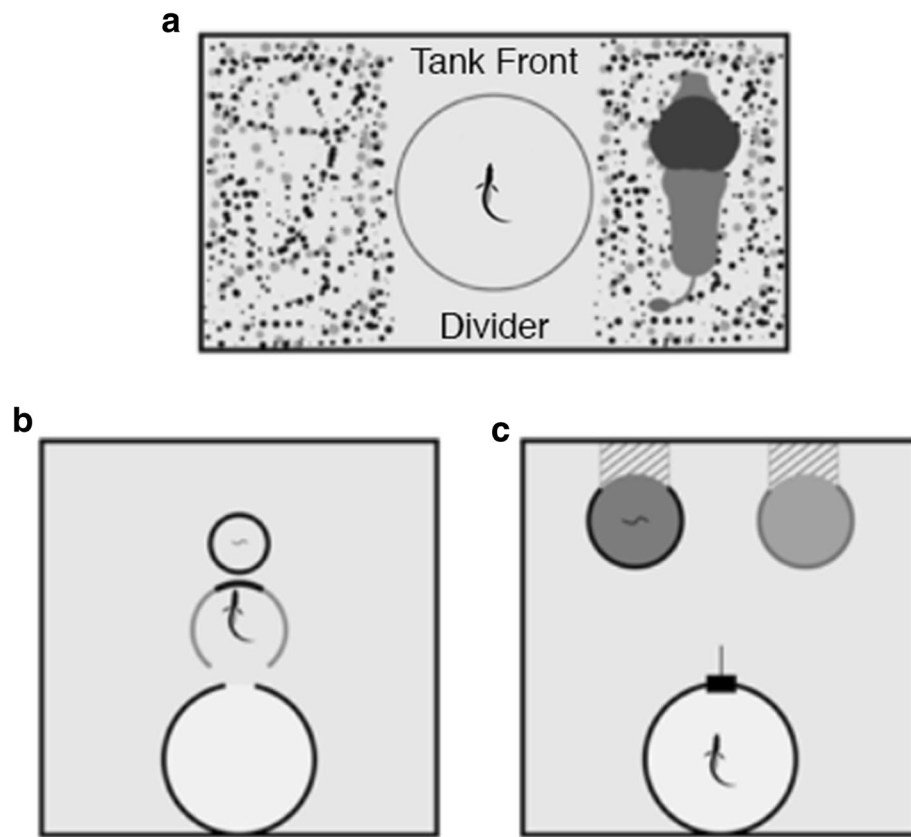
Fig. 1 Visual description of the tanks used for behavioral observations (not to scale). **a** The novel object task (top–down camera view). An individual was placed in a circular blind in the center third of the home tank. A novel object (toy lion) was then placed at one end of the tank. A perforated tank divider blocked the back portion of the tank to keep the fish in camera frame. After 5 min, the blind was removed and the individual's behavior was monitored. **b** The barrier detour task. Fish were trained to find food upon leaving a shelter. Then, a transparent barrier was placed between the shelter and the food. Upon emerging from the starting shelter, the individual's interaction with the transparent barrier was recorded. The black region of the barrier denotes the "barrier apex". **c** The color discrimination task. The individual began each trial in the starting shelter. Once the cork was removed and the individual emerged from the shelter, the fish's behavior was observed. In particular, we noted whether the fish entered the choice zone (indicated by stripes) of the blue or yellow cup while orienting towards the chosen cup

the back-center of the testing tank and the individual was allowed to acclimate for 3 min. The shelter had a circular opening (2.5 cm diameter) in the side that was positioned towards the center of the tank. At the start of the trials a rubber cork blocked the opening. A glass petri dish with a single bloodworm was placed in the center of the test tank (~ 7 cm from the entrance of the shelter). To start the trial, the observer removed the cork from the opening of the shelter and the latency for the individual to emerge from the shelter and to eat the worm was recorded. If the individual ate the reward, the observer gently scooped up the individual and placed the individual back into the shelter in preparation for the next trial. Between trials individuals were allowed to reacclimate to the shelter for 3 min. If the individual did not emerge from the shelter within 10 min after the cork was pulled, or eat within 5 min after emergence, the observer recorded the maximum times for these behaviors. The food reward was then removed, and the individual gently poured

out of the shelter if necessary by tipping the shelter so the individual was forced to exit from the side opening. After approximately 1 min, the individual was scooped back up into the shelter for the next trial. After the fourth trial of the day the individual was returned to its home tank.

Emergence time from a refuge into a novel environment is often interpreted as a measure of boldness (Wilson and Godin 2009); therefore we recorded the time it took each individual to emerge from the refuge on their first four training trials and used the average of those measures as a proxy for boldness.

To control for any motivational and personality differences that could impact task participation, training continued until the criterion was reached. In order to move on to the barrier detour task, the individual had to emerge from the shelter within 10 min and directly approach and eat the food reward within 5 s on 3 out of the 4 trials. The one failed attempt could not be on the fourth trial. This criterion

was used to ensure that the individual would be motivated throughout the four trials; three individuals did not meet this criterion and were omitted from the study (range for individuals that completed pre-training: 1–5 days until fish met criterion, mean 1.34 days, sd 0.92 days).

## Barrier detour task

After reaching the pretraining criterion, the individual moved on to the barrier detour task the following day. The barrier detour task session also consisted of four trials. In order to reinforce the direct search pattern, the first three trials were exactly the same as the training trials. On the fourth trial a transparent semi-circular barrier was placed between the shelter and food reward (Fig. 1b). The opening into the barrier was positioned directly in front of the entrance to the shelter. After removing the cork the individual was allowed 30 min to emerge from the shelter, navigate around the barrier and eat the food reward. All of the individuals ate within 30 min, but there was individual variation in how long individuals persisted on the old search pattern before attempting an alternative approach. An individual that followed the prepotent search pattern established during training would enter the barrier space and hit the barrier at its nearest point to the food reward, hereafter referred to as the "barrier apex" (2 cm arc at the center of the barrier). We interpret greater time spent at the "barrier apex" as persistence with the prepotent response, or low inhibitory control (Bray et al. 2014; Guillette et al. 2015; Juszczak and Miller 2016; Kabadayi et al. 2018). We recorded the duration of the first bout at the "apex" (a bout was defined as repeated contact with the barrier apex where there was no break in contact for longer than 5 s), total time at the apex and the latency to move away from the apex to swim around the ends of the barrier. Upon completion of the fourth trial, the individual was returned to its home tank.

## Color discrimination learning and reversal

Pretraining for discrimination learning began the day following the barrier detour task and occurred in the same tank that was used for the barrier detour task. Individuals were first trained to search two possible locations for a food reward; they were trained to emerge from the same shelter used for the barrier detour task and search two colorless cups. The shelter was placed in the center of the back wall of the tank and the two cups were positioned next to one another at the front center of the tank. Each cup had a 2 cm portion of their sides removed to allow access into the cups. Each cup had a petri dish inside with five blood worms. The food was accessible in one cup while in the other cup the food was made inaccessible by wrapping the opening of the dish in tape. Holes were punctured into the tape so that food scent cues were available from both cups. Also, tape rimmed the edge of the dish in the cup with accessible food, so cues from the tape could not be used as a discriminatory stimulus. Individuals received two trials a day. The rewarded cup was on each side once and the first location was pseudo-randomized so that the first cup location was never the same more than two days in a row. Individuals met criterion once they readily ate on both trials on two consecutive days (range 2–6 days; mean 2.41 days, sd 0.91 days). One individual was expelled at this stage due to lack of motivation.

We measured individual differences in initial (phase 1) and reversal learning (phase 2) performance using a two-way discrimination task, as in Bensky et al. 2017. Individuals received one session a day; each session consisted of ten trials. During the discrimination trials, a blue and yellow cup were presented, and one of the cups had a petri dish with accessible food while the other cup had food in a petri dish that was inaccessible due to tape covering the dish. Again tape was present on each dish and holes in the tape allowed for food chemical cues from the inaccessible cup, so these odor cues could not be used for discrimination. The side that was rewarded during each trial was pseudo-randomized for each individual according to the following two rules: (1) half of the trials were rewarded on each side, and (2) a single side could not be rewarded more than two trials in a row. At the beginning of the trial, the shelter was opened and the individual was allowed to emerge on its own to explore the tank. The openings of the cups were faced towards the front of the tank (away from the starting shelter), and the individual's choice was determined based on which of the choice zones it entered first while orienting towards the center of the corresponding cup (Fig. 1c). Importantly, even if an individual was incorrect on its first choice it was given 5 min to find the correct cup and eat the food. This way the association between cup color and reward could be made on each trial. Between trials, individuals were gently transferred back into the starting shelter and given 3 min to rest. Each individual received all 10 trials of a session before another individual was trained. Previous studies have found no color bias between blue and yellow in this population (Bensky and Bell 2018). All individuals were initially trained to associate the blue cup with a food reward until that individual reached the training criterion for the first phase, which was two consecutive sessions of choosing the correct cup on at least 8 out of 10 trials. If an individual did not emerge from the shelter within 10 min, or make a choice within 5 min of emerging, the trial was considered a "Balk" and the trial was run again. If an individual balked three times in a session the session was suspended and we attempted to complete the session the following day. Individuals were suspended from the study if they balked on three trials for consecutive sessions. Three individuals were expelled during this initial training stage due to lack of motivation.

The day after criterion was met, the individual received an additional trial with the rewarded blue cup to ensure that they were still following the initial association, and then the reversal phase began. During the reversal learning phase, the food was always placed into the yellow cup and again each individual was trained until criterion.

To measure learning performance, we recorded the number of sessions it took each individual to reach criterion (i.e., at least 8/10 trials correct on consecutive sessions). We examined both the individual's behavioral response immediately after the reversal (i.e. behavior during the first reversal trial, as well as performance across the first ten reversal trials of the first reversal session) and the time it took to acquire the new association between the yellow cup and the reward, i.e. time to criterion during the reversal phase.

All of the individuals initially searched the blue cup on the first trial of reversal learning. Roughly half of the individuals repeatedly visited the blue cup before searching the yellow cup while the other half only visited the blue cup once. Therefore, we used a binary-based score to indicate whether or not individuals persisted on the blue cup, where individuals that searched the blue cup once were scored "0" while individuals that revisited the blue cup more than once were scored "1".

## Statistical analysis

60 individuals began the experiment, and 53 completed the entire experiment. Individuals that did not complete the experiment were excluded from the analysis. Positively-skewed duration and latency variables were log-transformed to improve normality. All analysis was done using R 3.4.2 (https://www.r-project.org/). Boldness was based on the average emergence time across the four trials of the first barrier detour task session. For ease of interpretation, we multiplied the log-transformed average emergence time by negative one so that greater values indicate shorter emergence times, i.e. greater boldness. To reduce the number of variables involved for the other two behavioral assays, we performed two separate principal component analyses (PCA) on the correlation matrices of the variables measured in the novel object and barrier detour task, respectively (R Core Team 2013; package = "factoextra"; function = "prcomp"). $PC1_{novel\ object}$ explained 74.5% of the variation in four variables recorded in the response to a novel object test (Table 1a), where greater $PC1_{novel\ object}$ scores indicate longer times to orient and approach the novel object, and less time spent near and oriented towards the novel object. $PC1_{barrier}$ explained 77.2% of the variation in three variables measured in the barrier detour task (Table 1b), where greater $PC1_{barrier}$ scores indicate longer first bouts and total durations at the apex, as well as longer times to first attempt an alternative route that required moving away from the apex.

Given previous findings showing correlations between body size, behavior (e.g., emergence times: Brown and Braithwaite 2004), and learning (e.g., Amiel et al. 2014), we tested for significant associations between body length and behavior to determine whether to control for body size in downstream models. We used linear regression models to test for the effect of body size on the PC scores. Sessions to criterion and number of correct trials over the first reversal session were treated as count data; therefore generalized linear models were used to measure the effect of size on these variables. To control for overdispersion, a negative

**Table 1** Loadings on the first principle components for the (a) novel object assay, and (b) barrier detour task)

| (a) | |
| --- | --- |
| Response to a novel object (log-transformed) | $PC1_{novel\ object}$ loadings |
| | Eigenvalue: 2.98; %variance: 74.5% |
| Time to orient | 0.771 |
| Time to approach | 0.917 |
| Time spent in the zone containing the novel object (5 min) | − 0.893 |
| Time spent in the zone containing the novel object and oriented toward the novel object (5 min) | − 0.863 |
| (b) | |
| Barrier detour task (log-transformed) | $PC1_{barrier}$ loadings |
| | Eigenvalue: 2.32; %variance: 77.2% |
| First apex bout duration | 0.911 |
| Total time at apex | 0.937 |
| Time to first attempt towards barrier edge | 0.780 |

All behaviors were duration measures and were log-transformed to normalize the data prior to analysis

binomial distribution was used for these models. A logistic regression model was used for our binary persistence variable from the first reversal trial. Larger individuals took longer to reach criterion on initial learning ($\beta = -0.042$, $z = -2.153$, $p = 0.0313$, $n = 53$), but standard length was not related to any of the other variables in this study (Supplementary Table 1). Therefore, standard length was included as a covariate in models involving sessions to reach criterion on initial learning, but was not included in other models.

To examine correlations among the three behavioral variables, we computed pairwise Pearson correlation coefficients. To examine the relationships among the behavioral variables and the learning measures, we used generalized linear modeling, which allowed us to take into account body length as a covariate, and incorporate binomial and negative binomial distributions where appropriate. Finally, generalized linear models were used to test for the relationship between initial and reversal learning performance. In this case, because length was correlated with initial learning, individual body length was first regressed onto time to initial criterion and the resulting residuals were then used to predict reversal learning performance.

## Results

### How are response to a novel object, boldness and persistence related to each other?

Individuals that spent more time away from the novel object (i.e. greater $PC1_{novel\ object}$) tended to also emerge slower during the early barrier training trials ($r = -0.357$, $p = 0.0087$, $n = 53$). The individuals that spent more time at the barrier apex during the barrier trial (i.e. greater $PC1_{barrier}$) emerged faster during these earlier training trials ($r = 0.374$, $p = 0.0058$, $n = 53$). There was a trend for individuals that spent more time away from the novel object to also spend less time at the barrier apex ($r = -0.263$, $p = 0.057$, $n = 53$). Therefore, persistent individuals were more bold and were faster to spend more time near the novel object.

### Do individuals differ in initial and reversal learning performance?

To confirm that individuals in this experiment learned to associate a color with a food reward, we examined how individuals performed over time. At the beginning of the experiment, individuals chose the blue and yellow cups at relatively equal frequency, consistent with the lack of a color bias in this population. Performance improved with training as individuals increasingly chose the blue cup after training began. On average, individuals reached criterion after $5.28 \pm 4.17$ sd sessions, with substantial inter-individual variation in time to reach criterion (range 2–18 sessions; Fig. 2a).

Individuals started the reversal learning phase performing significantly below chance levels (average proportion correct = 0.174, sd 0.169, $z = 4.747$, $p < 0.0001$, $n = 53$; Fig. 2b). This suggests that on average, individuals persisted on the previously rewarded association immediately after the reward location was switched. There was substantial inter-individual variation during the first step of reversal learning: some individuals always chose the previously rewarded cup for well into the second reversal session, while other individuals consistently chose the newly rewarded cup within the first couple of trials (e.g., 7/10 correct in reversal session 1).
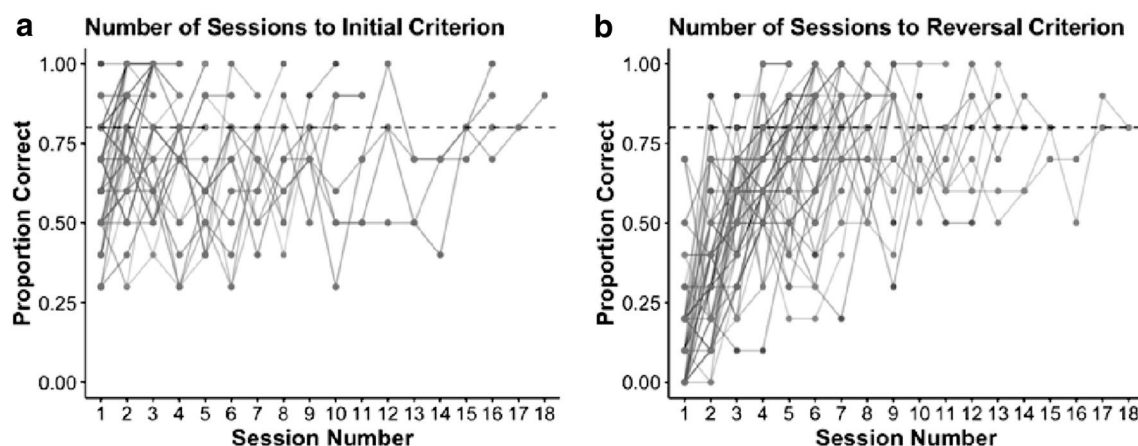


**Fig. 2** Individual learning curves from **a** initial learning, and **b** reversal learning discrimination phases. Lines represent the performance of individuals across sessions. Criterion was reached when the proportion of correct choices was greater than or equal to 0.8 (marked by horizontal dotted line) on two consecutive sessions. Note that individuals tended to perform around chance levels or better at the beginning of the initial learning phase; individuals began showing signs of improvement even within the first session. In contrast, individuals performed poorly during the first two reversal sessions as individuals tended to persist on the initially rewarded cup

Sticklebacks eventually learned to acquire a new color association. On average, individuals took $8.08 \pm 3.3$ sd sessions to reach criterion during reversal learning, again with extensive inter-individual variation in time to reach criterion during reversal learning (range 4–18 sessions).

### Is initial and reversal learning performance predicted by response to a novel object, boldness and/or persistence?

Behavior during all three behavioral assays was related to initial learning performance. Individuals that spent more time near the novel object (smaller $PC1_{novel\ object}$), were bolder (shorter emergence time), and which were more persistent (more time at the barrier apex, $PC1_{barrier}$) learned the initial discrimination faster ($PC1_{novel\ object}$: $\beta = 0.162$, $z = 3.37$, $p = 0.0007$, $n = 53$; boldness: $\beta = -0.159$, $z = -2.343$, $p = 0.0191$, $n = 53$; $PC1_{barrier}$: $\beta = -0.196$, $z = -3.732$, $p = 0.0002$, $n = 53$).

Reversal learning performance was also correlated with response to the novel object, boldness and persistence, but this was only true when considering an early step of reversal learning, i.e. the number of mistakes made during the first session of reversal. Specifically, individuals that spent less time near the novel object and took longer to emerge from a shelter chose the correct cup more often during the first reversal session ($PC1_{novel\ object}$: $\beta = 0.234$, $z = 3.714$, $p = 0.0002$, $n = 53$, boldness: $\beta = -0.268$, $z = -2.852$, $p = 0.0044$, $n = 53$, Fig. 3; see Supplemental Table 2 for all pairwise models). Moreover, bolder individuals (emerged faster) ($\beta = 0.5882$, $z = 2.417$, $p = 0.0157$, $n = 53$, Fig. 4a) and those that were more persistent towards the barrier apex ($\beta = 0.4849$, $z = 2.265$, $p = 0.0235$, $n = 53$, Fig. 4b), were more likely to repeatedly visit the blue cup before searching the yellow cup during the first reversal trial.

In contrast, we did not detect any significant correlations between reversal time to criterion and response to the novel object, boldness and persistence ($PC1_{novel\ object}$: $\beta = -0.038$, $z = 1.173$, $p = 0.241$, $n = 53$; boldness: $\beta = 0.0503$, $z = 1.223$, $p = 0.221$, $n = 53$; $PC1_{barrier}$: $\beta = -0.043$, $z = -1.242$, $p = 0.214$, $n = 53$).

### Is initial learning performance related to flexibility?

Some animals might perform better during reversal learning because they simply perform better on all learning tasks. Alternatively, there might be a tradeoff between different forms of learning. To evaluate these possibilities, we examined correlations between measures of initial and reversal learning performance. Sessions to criterion during initial learning was not correlated with sessions to criterion during reversal learning ($\beta = -0.0217$, $z = -0.304$, $p = 0.761$, $n = 53$). However, sessions to criterion during initial learning was correlated with the first step of reversal learning: individuals that took longer to reach criterion during initial learning had higher performance (more correct trials) during the first reversal session ($\beta = 0.3308$, $z = 2.324$, $p = 0.0201$, $n = 53$, Fig. 5).

## Discussion

The goal of this study was to understand why individuals differ in behavioral flexibility, and whether individual differences in behavioral flexibility fit the predictions of coping styles theory. We predicted that we would find evidence of a suite of correlated behavioral measures from across our assays such that "proactive" individuals would be faster to approach and spend time near a novel object, faster to emerge into a novel area, and exhibit lower behavioral inhibition in response to a barrier relative to other ("reactive")

**Fig. 3** Individual differences in **a** behavioral reaction to a novel object and **b** boldness were correlated with performance during the first reversal session. Individuals that took longer to approach and spend time near and oriented to a novel object (higher $PC1_{novelobject}$, **a**) and that were slower to emerge from a shelter into a novel environment (time to emerge, **b**) chose the rewarded cup more frequently during the first reversal session
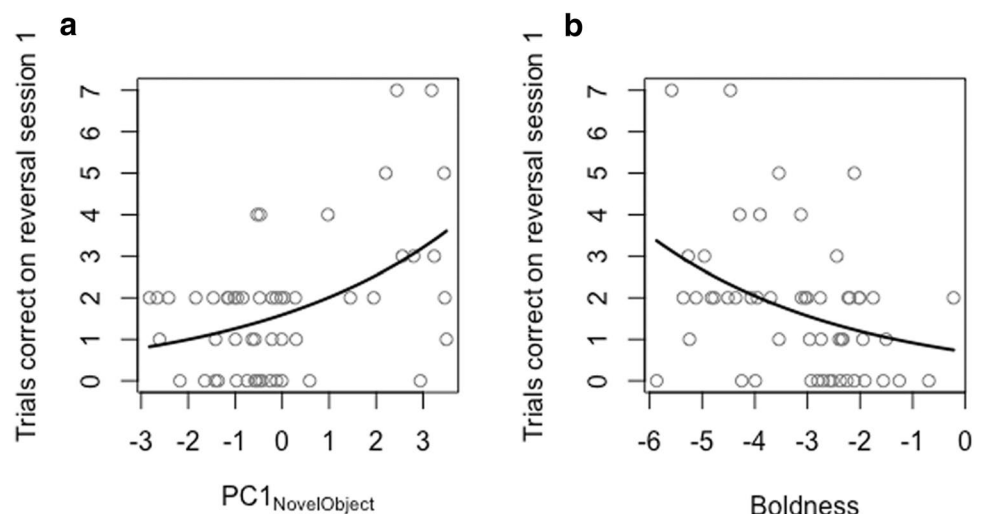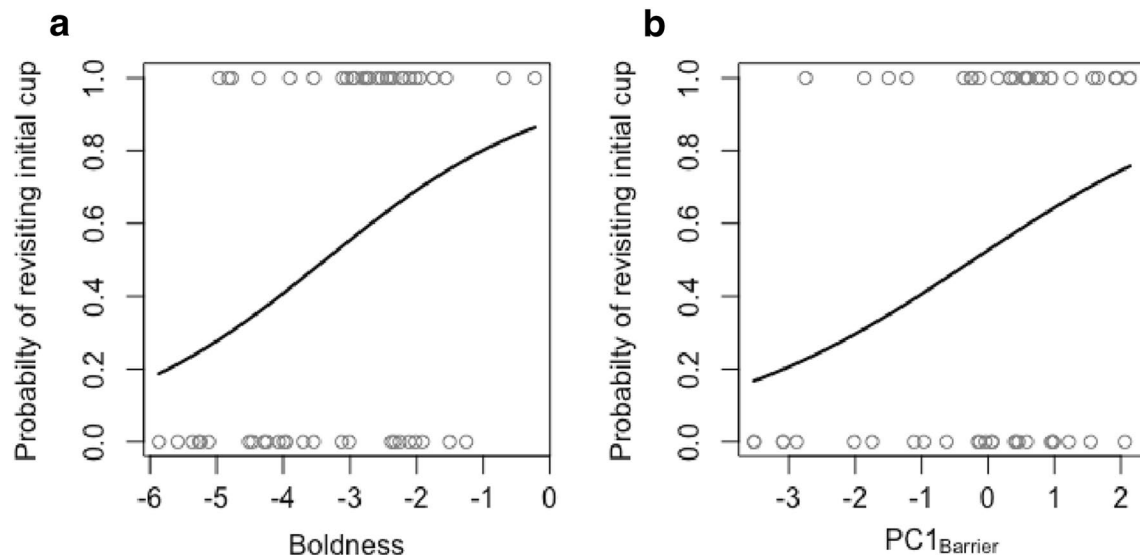
**Fig. 4** **a** Boldness and **b** behavior during the barrier detour task were associated with persistence on the initially rewarded cup during the first reversal trial. Individuals that were faster to emerge from a shelter into a novel environment (time to emerge, **a**) and that spent more time at the apex of the barrier ($PC1_{barrier}$, **b**) were more likely to revisit the cup that had been rewarded during initial learning

individuals. Proactive individuals were then predicted to be faster at learning a novel discrimination task ("initial learning"), but then show lower flexibility in the reversal learning phase of the task (i.e., take longer to switch away from the initial association and take longer to learn the reversed association).

Our results are consistent with all of these predictions, but with a twist. Specifically, we found that the flexibility results strongly depended on whether we examined an early step of reversal learning or time to criterion. While we did not observe any significant correlations with time to criterion, the results examining an early step of reversal learning were uniformly consistent with our predictions. Specifically, the individuals that performed better during an early step of the

reversal learning process, i.e. the first ten trials of reversal learning, spent more time away from the novel object and took longer to emerge from a shelter. Thus, these individuals were faster to abandon the search pattern that had been reinforced during the initial learning phase. In addition, relatively bold individuals, and those that spent more time at the barrier apex, were more likely to return to the previously rewarded location multiple times within the first reversal trial before searching for an alternative location. Finally, we found evidence for the predicted learning trade-off, but only when we focused on an early step of the reversal learning process: individuals that took longer to reach the initial criterion performed best on the first ten reversal trials. This is an important result because learning tradeoffs have been hypothesized to be an important mechanisms that can maintain variation in flexibility if they result in evolutionarily stable strategies (Wolf et al. 2008).

One possible explanation for the failure to detect correlations with reversal time to criterion is that the causes of variation in reversal time to criterion are heterogenous and reflect both the ability of an animal to switch away from a previously learned behavior and the ability of an animal to establish a new rewarded pattern (Boulougouris et al. 2008). Interestingly, previous studies have shown that different steps of reversal learning are chemically dissociable in the brain. For example, the dopaminergic system is involved in perseveration on previously reinforced patterns, perhaps via reward-based effects (Cools et al. 2009), while serotonin influences the rate at which individuals shift away from stimuli associated with punishment or negative outcomes (Chamberlain et al. 2006; den Ouden et al. 2013).
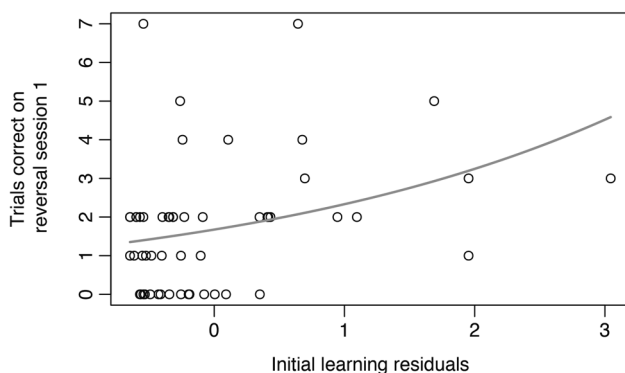


**Fig. 5** Trade-off between initial and reversal learning. Individuals that took longer to reach criterion during the initial learning phase performed better on the first ten reversal trials. Initial learning residuals are controlled for body length

The heterogeneity of mechanisms involved in reversal learning, along with the range of criterion used across studies, is probably an important factor contributing to mixed results in the literature (e.g., Bebus et al. 2016; Guillette et al. 2015; Head et al. 1998; Sorato et al. 2018; see Dougherty and Guillette 2018 for review). Regardless, the results of this study suggest it may be profitable for future studies seeking to use reversal learning performance as a proxy for behavioral flexibility to focus as much on measures of early reversal learning performance because it reflects the ability of an animal to switch away from a previously learned behavior, and is therefore more indicative of behavioral flexibility per se (see Stamps 2016) than time to criterion (but see Chudasama et al. 2001). Also, in accordance with recent studies, these results suggest that documenting "microbehaviors" within paradigm performance can be fruitful for identifying behavioral correlates of variation in cognitive processes (Chow et al. 2017; Mazza et al. 2018). Overall, as the cognitive ecology field continues to grow, there is an increasing need to examine the accuracy and validity of different measurements used to purportedly capture cognitive processes of interest (Boogert et al. 2018). Such research will help us better understand which aspects of cognitive performance generalize across behavioral contexts (Cauchoix et al. 2018; Völter et al. 2018) in order to help interpret cognitive variation.

Another promising direction for future studies of is to consider the role of memory in driving variation in behavioral flexibility (Tello-Ramos et al. 2019). While we distinguished between an early step of reversal learning and time to criterion, it is likely that the process can be further broken down to include an intermediate step in which the individual has to inhibit and forget the previously established behavior pattern (Tello-Ramos et al. 2019). There are often individual differences in memory, such that some individuals form stronger memories than others and their strong memories might interfere with their ability to make new associations (i.e., proactive interference; Anderson and Neely 1996), which could contribute to variation in overall reversal learning performance. Interestingly, other studies have found evidence for trade-offs between memory and behavioral flexibility at both the inter- and intraspecific level (Croston et al. 2017; Hampton and Shettleworth 1998; Lewis and Kamil 2006).

In summary, we found support for the hypothesis that individuals have different styles for coping with environmental challenges, and that the behavioral traits of these different styles relate to individual differences in learning and flexibility. Importantly, we could explain variation in aspects of *early* reversal learning performance, when individuals were just starting to switch away from a previously rewarded behavioral pattern, but not time to criterion, a metric commonly used in reversal learning paradigms. The fact that behavioral correlates were only found with an early step of reversal learning, and that we only observed a trade-off with initial learning and an early step of reversal learning, draw attention to the utility of dissecting the steps of reversal learning when searching for cognitive tradeoffs. This study contributes to the growing body of evidence that individuals differ in the ways in which they respond to changes in the environment, that some individuals are more behaviorally constrained than others, and that there may be costs of being flexible. Understanding the causes of variation in behavioral flexibility could help us explain how variation in behavioral flexibility is maintained within natural populations, and to predict its evolutionary trajectory.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethics approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in this study involving animals were in accordance with the ethical standards of the University of Illinois, Urbana Champaign (IACUC protocol #15077). This article does not contain any studies with human participants performed by any of the authors.

**Availability of data and material** Data available as electronic supplemental materials.

**Code availability** Analysis code available upon request.

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