



Testing the predictions of coping styles theory in threespined sticklebacks



Miles K. Bensky^{a,*}, Ryan Paitz^{a,b}, Laura Pereira^c, Alison M. Bell^{a,d}

^a Program in Ecology, Evolution, and Conservation Biology, School of Integrative Biology, University of Illinois, 505 S. Goodwin Ave., Urbana, IL 61801, United States

^b School of Biological Sciences, Illinois State University, Normal, IL, United States

^c College of Veterinary Medicine, University of Illinois, Urbana, IL, United States

^d Institute for Genomic Biology, University of Illinois, Urbana, IL, United States

ARTICLE INFO

Article history:

Received 10 August 2016

Received in revised form

14 November 2016

Accepted 19 December 2016

Available online 23 December 2016

Keywords:

Animal personality

Coping styles

Threespined stickleback

Learning

Cortisol

Individual differences

ABSTRACT

Coping styles theory provides a framework for understanding individual variation in how animals respond to environmental change, and predicts how individual differences in stress responsiveness and behavior might relate to cognitive differences. According to coping styles theory, proactive individuals are bolder, less reactive to stressors, and more routinized than their reactive counterparts. A key tenet of coping styles theory is that variation in coping styles is maintained by tradeoffs with behavioral flexibility: proactive individuals excel in stable environments while more flexible, reactive individuals perform better in variable environments. Here, we assess evidence for coping styles within a natural population of threespined sticklebacks (*Gasterosteus aculeatus*). We developed a criterion-based learning paradigm to evaluate individual variation in initial and reversal learning. We observed strong individual differences in boldness, cortisol production, and learning performance. Consistent with coping styles, fish that released more cortisol were more timid in response to a predator attack and slower to learn a color discrimination task. However, there was no evidence that reactive individuals performed better when the environment changed (when the rewarded color was reversed). The failure to detect trade-offs between behavioral routinization and flexibility prompts other explanations for the maintenance of differing coping styles.

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1. Introduction

Interest in individual variation in animal cognition is booming (e.g., Bensky et al., 2013; Chittka et al., 2009; Matzel et al., 2003; Niemela et al., 2013; Thornton and Lukas 2012). For example, a growing number of studies are showing that there is substantial intra-specific variation in performance on different cognitive tasks in a wide range of taxa (e.g., birds: Guillette et al., 2015; dogs: Nippak and Milgram 2005; primates: Herrmann et al., 2009; rodents: Galsworthy et al., 2002). Additionally, there has been increased interest in how individual variation in cognition may correspond with consistent individual differences in behavior, or animal personalities (Budaev and Brown, 2011; Carere and Locurto, 2011; Locurto, 2007; Sih and Del Giudice, 2012). As a result, studies exploring the nature of the correlations between various animal personality axes and cognitive differences are on the rise (e.g.,

Bebus et al., 2016; Ruiz-Gomez et al., 2011; Sneddon 2003; also see Guillette et al. 2017), and more attention is being called to developing best-practices for examining cognitive differences to address these types of questions (Griffen et al., 2015). However, the proximate and ultimate causes of correlations between cognition and behavior are presently unknown.

Coping styles theory offers a framework for understanding individual variation in cognition and behavior. According to this theory, variation in cognition is a part of a suite of correlated traits adapted for coping with changes in the environment, with individuals varying along the proactive–reactive axis (Koolhaas et al., 1999). At one end of a continuous distribution are proactive individuals, which are relatively exploratory, bold, and aggressive relative to their reactive counterparts at the other extreme. A key tenet of coping styles theory is that a cost of being proactive is reduced behavioral flexibility: proactive individuals establish initial learning contingencies quickly, largely due to their exploratory nature, but then become routinized and perform poorly when the reward is reversed (Koolhaas et al., 1999). Reactive individuals, on the other hand, are more stress reactive and timid, and may be slow initial

* Corresponding author.

E-mail address: bensky2@illinois.edu (M.K. Bensky).

learners but then quickly respond to environmental change. Following this reasoning, it has been suggested that variation along the proactive-reactive axis is maintained by fluctuating selection pressures (Thornton and Lukas, 2012). Specifically, proactive, inflexible individuals might have higher fitness in stable environments while reactive, flexible individuals may be better suited for environments that experience moderate change (Benus et al., 1990; Guillelte et al., 2011; Niemela et al., 2013; Ruiz-Gomez et al., 2011; Verbeek et al., 1994). Additionally, such variation may be driven by frequency-dependent benefits (Wolf et al., 2008) or differences in dispersal states (Canestrelli et al., 2016).

Given that different coping styles are expected to reflect variation in how individuals respond to challenging conditions or stressors, one of the proximate mechanisms underlying coping styles is thought to involve the hypothalamic-pituitary-adrenal (HPA) axis (Koolhaas et al., 2010). Indeed, some studies suggest that proactive individuals have relatively low stress reactivity and higher sympathetic activity (Carere et al., 2010; Sorensen et al., 2013), but some authors have suggested that stress responsiveness is an independent axis of variation (Koolhaas et al., 2010). Upon perceiving a stimulus as stressful, the hypothalamus initiates a cascade that culminates in an increase in circulating glucocorticoid levels (Sapolsky et al., 2000). Once the stimulus is removed or no longer perceived as a threat, feedback loops are triggered to shut down the production of glucocorticoids (Lupien et al., 2009). Several studies in diverse organisms have shown that individuals consistently vary in stress responsiveness (repeatability of glucocorticoid hormone levels: Boulton et al., 2015; Cockrem et al., 2009; Cook et al., 2012; Fürtbauer et al., 2015; Ouyang et al., 2011; selection on glucocorticoid responsiveness: Øverli et al., 2005; Pottinger and Carrick, 1999; Roberts et al., 2007), therefore individual variation in the transient production of glucocorticoids has been hypothesized to underlie variation in the behavioral response to stress (Carere et al., 2010; Sorensen et al., 2013). These physiological mechanisms have also tied coping styles to potential fitness differences in terms of stress-related health and disease susceptibility (Costantini et al., 2012; de Boer et al., 2016).

Individual variation in stress responsiveness has also been linked to variation in cognitive performance (Lupien and McEwen, 1997; Kosten et al., 2012). For example, lines of trout that had been selected for divergent post-stressor cortisol levels differed in cognitive performance: trout that produced high levels of cortisol in response to a stressor were quicker to alter their behavior in response to food relocation during reversal trials (Ruiz-Gomez et al., 2011). These reactive fish were also faster to stop a conditioned response during extinction trials (Moreira et al., 2004). Overall, there is a plethora of data (e.g. McEwen and Sapolsky, 1995; Øverli et al., 2005, 2007; Schoech et al., 2011) demonstrating that glucocorticoids are related to behavioral responses to stress and cognitive performance. However very few studies have characterized HPA axis function, behavior, and cognition simultaneously, and those that have tend to mostly focus on selected lines or domesticated animals (e.g. Benus et al., 1990; Bolhuis et al., 2004; Øverli et al., 2002; but see Bebus et al., 2016; Øverli et al., 2007). Attempts to simultaneously characterize several different facets of coping styles in natural populations are rare due to the time intensive nature of collecting extensive individual-based data on many subjects.

Here, we took a high-resolution approach to test the generalizability of whether individual differences in cognitive performance are part of a larger suite of behaviors, or coping styles, in a natural population. Again, much of the work on coping styles has been focused on mammalian and avian species (Carere et al., 2010), and while significant work has also been done looking at fish, particularly salmonids (Øverli et al., 2005), we were interested in further expanding the research applied to this taxa with a

focus on natural variation. Here we tested the threespined stickleback (*Gasterosteus aculeatus*), a species renowned for their natural intraspecific variation in behavior (e.g., Bell 2005; Dingemans et al., 2007; Girvan and Braithwaite, 1998; Huntingford, 1976; Mamuneas et al., 2015; Odling-Smee and Braithwaite, 2003; Stein and Bell, 2012), and a system that was recently used to investigate behavioral and endocrine associations in coping with increased predatory threat (Fürtbauer et al., 2015). Additionally, this species has been established as being conducive to fish cognition studies (Girvan and Braithwaite, 1998; Odling-Smee and Braithwaite, 2003). We repeatedly measured stress reactivity and 'boldness' towards a model predator on the same individuals and then asked whether those traits were related to variation in cognitive performance. We developed a criterion-based method to quantify the distribution of individual variation in cognitive performance in a discrimination-reversal learning paradigm. Subjects were trained to associate a food reward with one of two colors. Then, after a success criterion was reached, the stimuli and reward association were reversed. We interpret performance on the reversal task as behavioral flexibility (as in Pintor et al., 2014; see Stamps, 2015), where persistent (proactive, routinized) individuals continue to approach the previously learned cue while more flexible (reactive) individuals more quickly modify their behavior and learn the new association. According to coping styles theory, we predicted that: 1) bolder (proactive) individuals are less stress reactive; 2) bolder individuals learn faster; 3) bolder individuals are less flexible; 4) individuals that are more stress reactive are more flexible.

2. Materials & methods

2.1. Overview of the experiment

We measured stress reactivity, "boldness", learning and behavioral flexibility on the same individual sticklebacks in a fixed order. Individuals were measured for stress responsiveness on two occasions. We used a non-invasive method that samples cortisol released from the gills into the water following confinement stress for 4.5 h (Sebire et al., 2007; Sebire et al., 2009; Aubin-Horth et al., 2012). Individual differences in "boldness" were measured by testing the same individuals for their response to a model predator on four occasions. Finally, the same subjects were tested for learning performance in a color discrimination task and for behavioral flexibility in a reversal-learning task.

2.2. Subjects

Adult sticklebacks were collected from Putah Creek, CA in April 2014 prior to the onset of the breeding season. Fish were transported to the University of Illinois Urbana-Champaign where they were housed in 37 L tanks in groups of five for approximately four weeks until experiments began. Fish were housed in 20 ° Celsius water and were placed 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. The fish were fed a mixed diet consisting of frozen bloodworm, frozen brine shrimp, and frozen Mysis shrimp ad lib each day except during the learning trials (see below). Ten individuals were randomly selected for this experiment (females: n=6, average length=43.8 mm, average mass=1.02 g; males: n=4, average length=42.5 mm, average mass=0.87 g). Females were not gravid during the experiment and males showed no evidence of nuptial coloration. Each individual was marked by clipping a unique combination of their dorsal and/or pelvic spines.

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