Published in final edited form as:

Anim Behav. 2018 March ; 137: 161–168. doi:10.1016/j.anbehav.2018.01.003.

Intraspecific variation in cue-specific learning in sticklebacks

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Abstract

Animals must identify reliable cues amidst environmental noise during learning, and the cues that are most reliable often depend on the local ecology. Comparing the performance of populations of the same species across multiple versions of a cognitive task can reveal whether some populations learn to use certain cues faster than others. Here, using a criterion-based protocol, we assessed whether two natural populations of sticklebacks differed in how quickly they learned to associate two different discrimination cues with the location of food. One version of the discrimination task required animals to use visual (colour) cues while the other required animals to use egocentric (side) cues. There were significant behavioural differences between the two populations, but no evidence that one population was generally better at learning, or that one version of the task was generally harder than the other. However, the two populations excelled on different tasks: fish from one population performed significantly better on the side version than they did on the colour version, while the opposite was observed in the other population. These results suggest that the two populations are equally capable of discrimination learning, but are primed to form associations with different cues. Ecological differences between the populations in environmental stability might account for the observed variation in learning. These findings highlight the value of comparing cognitive performance on different variations of the same task in order to understand variation in cognitive mechanisms.

Keywords

cue-specific learning; learning; population differences; threespine stickleback

There are multiple biotic and abiotic stimuli in the environment that might be associated with factors important for fitness such as food, predators or conspecifics. When attentional capacities are limited, animals must decide which cues to prioritize, and this can lead to selective attention towards certain cues over others (Gottselig, Wasserman, & Young, 2001).

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COMPETING INTERESTS

We, the authors, declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.B. conceived of the study, designed the study, collected the fish, conducted the training of the fish, carried out the statistical analysis and drafted the manuscript. A.B. conceived of the study, designed the study and drafted the manuscript.

Animals often learn to associate salient cues with rewarding (or adverse) behavioural outcomes faster than they do with nonsalient cues (Mackintosh, 1975; Rescorla & Wagner, 1972; Treviño, 2016). Correctly identifying cues that are the most reliable and relevant to specific outcomes can improve fitness. Provided that there is genetic variation for sensitivity to environmental cues (e.g. Visser et al., 2011), the cognitive mechanisms that prime organisms to attend to the most ecologically relevant stimuli are likely to be honed by natural selection, thereby leading to adaptive differences in the rate at which animals that inhabit different environments learn to associate different types of cues with behavioural outcomes.

Indeed, animals are often primed to learn to associate certain environmental cues with specific outcomes faster than others. For example, young birds are predisposed to learn species-specific songs over heterospecific songs (reviewed in Wheatcroft & Qvarnström, 2015). Similarly, dogs prioritize attending to egocentric cues (i.e. cues relative to their body position) over allocentric cues (i.e. landmarks) to locate objects (Fiset, Gagnon, & Beaulieu, 2000). Selection should favour cue-specific learning when certain combinations of cues and outcomes are more likely to occur in nature. For example, rats quickly learned to associate an olfactory cue (but not an auditory cue) with sickness, possibly because reliable associations between olfactory cues and food-related illness are more likely to occur in nature (i.e. selective association; Garcia & Koelling, 1966). These examples suggest that differential associative learning speeds between different types of cues are likely to be adaptive and widespread. Adaptive, fine-scale variation in cue-specific learning has implications for the evolution of cognition. One promising tactic for investigating this is to compare the rates at which populations of the same species from different environments learn to associate different cues with a reward.

Threespine stickleback, *Gasterosteus aculeatus*, are good subjects for studying the adaptive significance of intraspecific variation in cognition. Sticklebacks occupy a variety of different freshwater environments that vary in water clarity, predation intensity, habitat complexity and stability. Sticklebacks exhibit tremendous intra-specific diversity in morphological, physiological, behavioural and cognitive traits (Bell & Foster, 1994). Indeed, a number of studies have reported ecologically driven variation in cue use during learning in sticklebacks (Braithwaite & Girvan, 2003; Brydges, Heathcote, & Braithwaite, 2008; Duffy, Pike, & Laland, 2009; Girvan & Braithwaite, 1998; Odling-Smee & Braithwaite, 2003; Odling-Smee, Boughman, & Braithwaite, 2008) and have suggested that populations have biases for specific spatial and/or environmental (e.g. water flow) cues. For example, sticklebacks from rivers (where visual landmarks are likely to change quickly), tend to rely more on movement-based algorithms (e.g. always turn left or use a specific turn sequence) to locate food, while sticklebacks from ponds (where visual landmarks are more likely to be stable and reliable) depend more on visual landmarks to complete a maze (Girvan & Braithwaite, 1998; Odling-Smee & Braithwaite, 2003).

While these findings are consistent with the hypothesis that there is adaptive intraspecific variation in cue use during learning, the experiments did not specifically isolate the cues available during learning and, therefore, the studies were unable to decisively conclude that populations learned to follow certain cues faster than others. For example, Odling-Smee and

Braithwaite (2003) trained sticklebacks from ponds and streams in a T-maze to follow a combination of landmark and egocentric cues (e.g. food was always at the end of the left arm of the maze and a plant was always placed towards the left arm). Once a fish reached criterion, a probe trial put the two types of cues into conflict (e.g. food was moved to the right arm, but the plant landmark remained near the left arm). Consistent with the hypothesis of ecologically driven differences in cue use, the pond and river populations differed in the proportion of individuals that used landmark versus egocentric cues. However, because the two types of cues were conflated during the learning trials that preceded the probe trial, whether the populations differed in how quickly they associated one versus the other type of cue with the reward is unknown. Similarly, Girvan and Braithwaite (1998) trained sticklebacks from different populations to navigate a maze either with or without visual plant landmarks. In both treatments, the turn-sequence for solving the maze was the same across trials, which meant that the egocentric and allocentric cues were redundant in the landmark-trained group. Therefore, differences in learning speeds could not be attributed to a specific cue (for an example with isolated spatial cues that measures learning speeds in goldfish see Rodriguez, Duran, Vargas, Torres, & Salas, 1994).

Here we build upon these findings by comparing the learning performance of sticklebacks from two populations on two versions of the same task that differ in the particular discriminatory cue that is available to use during learning. In one version, sticklebacks could use visual (colour) cues to solve the task. In the other version, sticklebacks could use egocentric spatial (side) cues to solve the task. Spatial memory and colour discrimination likely involve dissociated regions of the brain (Hampton & Shettleworth, 1996), and brain regions associated with spatial memory are evolutionarily conserved in vertebrates (Rodriguez et al., 2002). Thus, comparing performance between the colour and side versions of the task may provide insights into how ecological variation can drive variation in learning that involves partially independent brain regions. We used a criterion-based protocol that allowed us to quantify how quickly individuals learned to follow a particular discriminatory cue. While previous studies suggested that populations have preferences for different cues (Girvan & Braithwaite, 1998; Odling-Smee & Braithwaite, 2003), our experiment explicitly tested whether populations differ in how quickly they associate different discriminatory cues with reward outcomes. We assume that individuals learn to form associations more readily with cues that are more reliable in their environment.

We measured fish from two populations from two different drainages in northern California, U.S.A.: Putah Creek and the Navarro River. There are phenotypic differences between fish from these populations (Bell, 2005) and the sites are different ecologically. For example, there is more vegetation and less water movement at the Putah site, while the Navarro River is much clearer, with more dramatic seasonal changes in water flow. We hypothesized that ecological differences between the two populations cause differences in the predictability and reliability of different cues, thereby causing the populations to have different learning speeds in cue-specific learning. In particular, based on the work by Girvan and Braithwaite (1998), and Odling-Smee and Braithwaite (2003), we predicted that fish from the Navarro River, where visual cues are unlikely to persist over time due to changes in water flow, would excel when given an opportunity to use egocentric spatial cues and that the fish from Putah Creek, where there is less water flow, would perform well when given an opportunity

to use visual cues. To address the possibility that population differences in cognitive performance reflect differences among individuals and/or between populations in acclimation to the laboratory and/or boldness, we also recorded acclimation time and latency to emerge from a shelter during training.

METHODS

Wild-caught, nongravid adult female threespine sticklebacks from two separate drainages (Putah Creek, CA, U.S.A. and the Navarro River, CA, U.S.A.) were randomly assigned to either a colour or side version of a discrimination learning task. On average, sticklebacks from Putah Creek are larger than sticklebacks from the Navarro River (length: Putah: 45.5 ± 0.803 mm; Navarro: 40.83 ± 0.690 mm; $t_{58} = 4.407$, $P < 0.0001$). Sticklebacks were housed individually in 26.5-litre tanks (36 × 33 cm and 24 cm high).

Pretraining

To ensure similar levels of motivation and reduce potential sampling bias, all individuals were run through a two-phase criterion-based pretraining protocol. The first pretraining phase involved training the sticklebacks to search cups for food. Two translucent cups were placed in an individual's home tank and half the daily ration of bloodworms (5 worms per cup) were placed in petri dishes at the bottom of each cup. A quarter of the cups' sides were cut out to provide access to the petri dishes. This step was repeated once a day until the individual ate from both cups within 10 min on 3 consecutive days.

The second pretraining phase involved acclimating the sticklebacks to the process of being repeatedly placed into a starting shelter from which they had to emerge to search the cups for food. Habituating them to the shelter was important because it allowed us to standardize individuals' starting location across trials. During each trial, an individual was gently transported into a shelter in a separate 26.5-litre training tank (36 × 33 cm and 24 cm high) and left to rest for 1 min. Translucent cups were placed in the tank. Olfactory cues of food were present in both cups, but food was only accessible in one cup. Specifically, there were bloodworms in a petri dish in the bottom of each cup, but one of the petri dishes had strips of electrical tape covering the entire opening, which prevented the fish from accessing the worms. Several small holes were punctured into the tape to allow chemical/odour cues to emanate from the dish. The other (rewarded) dish had the same amount of electrical tape lining the outside edge, but access to the contents was not obstructed. Each fish received two trials per day, with the location of the rewarded cup alternating between the two trials. To start each trial, a cork was removed from the shelter to allow the stickleback to exit. We measured how long it took the individual to emerge from the shelter ('time to emerge'). We interpret time to emerge as willingness to take risks ('boldness'; Wilson & Godin, 2009). The second pretraining phase continued until the individual found and ate the food in under 5 min during each trial on 3 consecutive days. We refer to the total number of days to complete both phases of pretraining as 'days to complete pretraining'. The minimum number of days to pass pretraining was 6 days. All fish passed the pretraining phase. We infer that if a fish was willing to search and consume a food reward relatively quickly during pre-training that it was well acclimated to the learning environment. We tested whether

differences in ‘boldness’ (time to emerge) and acclimation to the testing environment could explain differences in learning performance among individuals and populations.

Training

Training took place in the same 26.5-litre training tank used for the second phase of pretraining. Individuals from both populations were randomly assigned to one of two training conditions: (1) blue–yellow colour discrimination or (2) left–right side discrimination. Sticklebacks received one 10-trial learning session per day and were trained in only one of the two conditions.

Colour discrimination

In this version of the discrimination task, sticklebacks were presented with a yellow and blue cup and were trained to associate the blue cup with a food reward. Sticklebacks are known to discriminate between these two colours (Bensky, Paitz, Pereira, & Bell, 2017; Feng, McGhee, & Bell, 2015; Roche, McGhee, & Bell, 2012), and pilot experiments found no evidence of a colour bias in either of the two populations (mean $\pm$ SD proportion of preference trials in which sticklebacks chose blue: Navarro: 0.39 ± 0.303 , $t_9 = 1.1595$, $P = 0.2761$; Putah: 0.44 ± 0.227 , $t_9 = 0.8358$, $P = 0.4249$). The stickleback was placed in the shelter at the back of the tank. While in the shelter, a blue and yellow cup were placed at the front of the tank (Fig. 1a). A petri dish was then placed into the base of each cup. The blue cup was rewarded with one to two bloodworms. To control for the possible use of olfactory/chemical discriminatory cues, as described for pretraining, the dish in the unrewarded yellow cup also contained one to two bloodworms and was covered with electrical tape to prevent access to the worms, while the dish in the blue cup had tape wrapped around the outside edge. Across trials, the location of the blue cup was pseudorandomized for each individual fish according to the following two rules: (1) each side was rewarded in half of the trials and (2) a single side could not be rewarded more than two trials in a row. After the cups were in place, the cork of the shelter was removed. For each trial, we recorded four variables: (1) time to emerge from the shelter, (2) time to enter the choice region of the first cup searched (see Fig. 1a), (3) time to enter the choice region of the correct cup and (4) whether the first choice was the correct choice. Regardless of whether the first choice was correct, the fish was allowed to explore the tank until it searched the blue cup and was given a chance to eat the bloodworms. Therefore, all individuals were given an equal opportunity to associate the rewarded stimulus cue with the food reward, regardless of their first choice and how quickly they explored the cups. The colour training protocol continued until the fish met criterion (two consecutive sessions of at least 8 correct choices out of 10 trials), hereafter referred to as ‘sessions to criterion’.

Side discrimination

In this version of the discrimination task, sticklebacks were presented with two identical cups (blue) and trained to associate a particular direction (left or right) with a food reward. This task took place in a tank identical to the tank used for colour discrimination. Here, though, across trials, the shelter was moved from one side of the tank to the other with the opening facing the opposite side (see Fig. 1b). The shelter’s location for any given trial was determined by the same pseudorandomization rules used for the colour discrimination

training. The rewarded cup was based on its orientation relative to the opening of the shelter. Fish were either trained to always choose the cup that was to the left of the opening, or trained to always choose the cup on the right. To increase the difficulty of the task, individuals were always trained to the side they selected less often during pretraining. If there was no preference during pretraining, the fish were randomly assigned to a side. For both populations, eight fish were trained to the left and seven fish were trained to the right. The side discrimination training protocol continued until the fish met criterion (two consecutive sessions of at least 8 correct choices out of 10 trials).

Sixty-two females started the training phase. Of those, 60 fish (30 per population) met criterion ($N = 2$ Navarro fish were removed due to reduced food motivation during training), with the resulting sample size comprising 15 fish in each of the four combinations of tasks and populations.

Statistical Analysis

Because of the size differences between populations, and the possible links between size and within-population behavioural variation (Adriaenssens & Johnsson, 2010; Gill & Hart, 1994), all analysis initially included fish length as a covariate. However, length was not significant ($P > 0.05$) and was therefore omitted from subsequent analyses.

Days to complete pretraining was non-normal, and normality was not improved by transformations; therefore, we compared population differences in days to complete pretraining using a nonparametric permutation test simulating 100,000 samples. We used a t test (R Core Team., 2016; package = 'stats'; function = 't.test') to compare the two populations' average time to emerge across the first 10 training trials. We focus on these early trials because both populations habituated to the training protocol and emerged quickly during subsequent trials. To examine whether fish from the two populations differed in their performance on the colour and side versions of the discrimination task, we took two approaches. First, to determine whether the populations differed in the rate at which individuals met the learning criterion, we conducted a survival analysis using a Cox proportional hazards regression model (Therneau, 2015; package = 'survival'; function = 'coxph'), where population, version (colour = versus side) and their interaction were included as fixed effects. Failure to reach criterion during a session was treated as 'survival'. Second, we compared how quickly individuals reached criterion on their designated training task using a two-way between-groups ANOVA, with population, version and their interaction as fixed effects (R Core Team., 2016; package = 'stats'; functions = 'lm'; 'anova'). We used t tests to examine priori contrasts between and within populations across both tasks.

To test whether individual differences in boldness (time to emerge) were related to learning performance, we used multiple regression, with population, version and average time to emerge across the first 10 trials as predictors of time to criterion (R Core Team., 2016; package = 'stats'; function = 'lm'). Time to emerge and sessions to criterion were log transformed to meet assumptions of normality. All statistical analyses were carried out using R v.3.1 (R Core Team., 2016).

Ethical Note

The experiments were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Illinois Urbana-Champaign (IACUC protocol number 15077). Fish were caught in the field using baited minnow traps under the approval of the State of California's Department of Fish and Wildlife permit to A. M. Bell (SC-3310). In the laboratory, the fish were housed in groups before and after the experiment. While the fish were undergoing training they were housed individually, but were given visual access to neighbouring fish when they were not participating in active trials in order to enhance their welfare. Fish were transferred from their home tank to the training tanks by gently scooping them in a cup to minimize stress. All experimental procedures were noninvasive.

RESULTS

Population Differences in Behaviour

On average, sticklebacks from Putah Creek acclimated faster to the laboratory and emerged faster from a shelter than sticklebacks from the Navarro River. For example, sticklebacks from Putah Creek completed pretraining faster (median = 7 days, IQR = 2, $N = 30$) than sticklebacks from the Navarro River (median = 11 days, IQR = 5.75, $N = 30$), and the difference between the medians was highly significant (permutation test: 1/100 000 samples observed difference = 4 days, $P < 0.001$; Fig. 2). Similarly, sticklebacks from Putah Creek emerged significantly faster from the starting shelter during the first 10 training trials (mean $\pm$ SD = 15.62 ± 11.27 s) compared to sticklebacks from the Navarro River (31.98 ± 27.95 s; $t_{58} = 2.98$, $P = 0.004$; Fig. 3).

Population Differences in Learning Performance

Learning performance (sessions to criterion) depended on both the population and the version of the discrimination task. Specifically, there was a statistically significant interaction between population and task version on learning performance according to both the survival analysis ($\beta = -1.6124$, $z = -2.878$, $P = 0.004$; Fig. 4a, b) and ANOVA ($F_{1,56} = 12.45$, $P < 0.001$; Fig. 4c) models. Populations performed better on one of the two versions of the task, but the populations differed in the version on which they excelled. Sticklebacks from Putah Creek performed better on the colour discrimination version than on the side discrimination version ($t_{28} = 2.62$, $P = 0.014$; mean $\pm$ SD: colour discrimination: 3.87 ± 1.30 days; side discrimination: 6.47 ± 3.76 days). Sticklebacks from the Navarro River, on the other hand, performed better on the side discrimination version than on the colour discrimination version ($t_{28} = 2.41$, $P = 0.023$; colour discrimination: 7.53 ± 3.40 days; side discrimination: 5.0 ± 3.14 days).

There was no indication that sticklebacks from one population had overall better learning performance than sticklebacks from the other population, or that one version of the task was more difficult than the other: when the population*version interaction term was removed from the model, there was not a main effect of either population ($F_{1,57} = 1.29$, $P = 0.26$) or version ($F_{1,57} = 0.039$, $P = 0.85$) on learning performance.

DISCUSSION

If animals prioritize attention to the most ecologically relevant cues, then animals inhabiting different environments might rely on different cues during learning. Here, we measured the learning performance of sticklebacks from two populations on different versions of a discrimination task. One version required the fish to discriminate between colour cues, while the other version required the fish to find a reward based on its position relative to the fish's starting point. By isolating the two different discriminatory cues between the two versions of the task, we were able to compare how these two types of cues influence learning speeds in two populations. On average, across both versions, the two populations performed equally well. In other words, both populations were equally 'smart'. Moreover, there was no evidence that one version of the task was generally more difficult than the other. However, both populations showed cue-specific learning speeds (i.e. they performed better on one version over the other), but they excelled on different cues. Fish from one population (Navarro) performed better on the side discrimination version than on the colour discrimination version, while the opposite was observed in the other population (Putah). These findings suggest that animals from different environments are primed to use different cues during learning and, therefore, learn to make associations with certain cue types faster than others.

Fish from Putah Creek emerged significantly faster from a shelter (a behaviour often interpreted as 'boldness'; Brown & Braithwaite, 2004; Burns, 2008; Toms, Echevarria, & Jouandot, 2010) than fish from the Navarro River. Previous studies have suggested that differences in boldness can contribute to differences in learning performance (e.g. DePasquale, Wagner, Archard, Ferguson, & Braithwaite, 2014; Dugatkin & Alfieri, 2003) because bolder, exploratory individuals are more likely to encounter relevant information needed to learn new contingencies (Carere & Locurto, 2011; Sih & Del Giudice, 2012). Despite these population-level differences in 'boldness', the average performance of the two populations across the two versions of the discrimination task was the same. One possible explanation for this finding is that fish were always given an opportunity to find the reward regardless of how long it took them to approach the cups or if they initially went to the incorrect cup. This meant that an association between the discriminatory cue and the reward could be made on every trial. Therefore, all individuals, independent of their boldness, had the same opportunity to learn during training. A previous study that compared stickleback populations similarly found that behaviours such as activity level and exploration were independent of learning rates when all individuals were allowed to receive the food reward after each trial (Park, 2013).

The populations also differed in how quickly they acclimated to the experimental environment: on average, fish from Putah Creek completed pretraining in fewer days than fish from the Navarro River. Previous studies have suggested that individuals that have acclimated to the laboratory are better able to learn in a laboratory environment (Carere & Locurto, 2011; Guillette, Naguib, & Griffin, 2016). Even though they acclimated faster, fish from Putah Creek were not at an advantage in this experiment because we used a criterion-based pretraining protocol in which fish were only allowed to move forward with the next step of training if they completed the previous step at their own pace. This meant that the

fish were equally prepared to start training despite initial behavioural differences that might have otherwise influenced training (e.g. reluctance to explore, motivation or acclimation to the testing environment). Our approach, while time consuming, was effective and minimized biased sampling because over 96% (60/62) of the fish completed the training.

Despite similar average performance on the discrimination task, fish from Putah Creek did better on the colour version of the task, while fish from the Navarro River did better on the side version, which suggests that the populations are primed to associate certain cues with a food reward faster than others. While there is widespread evidence that animals rely on some cues over others during learning (Fiset et al., 2000; Garcia & Koelling, 1966; Wheatcroft & Qvarnström, 2015), and growing evidence that stickleback populations differ in the environmental cues they encode when foraging (Braithwaite & Girvan, 2003; Girvan & Braithwaite, 1998; Odling-Smee & Braithwaite, 2003; Odling-Smee et al., 2008), our results build on these studies by showing that populations vary in how quickly they are able to associate different discriminatory cues with reward outcomes. Differences in learning speed can influence foraging efficiency and therefore fitness (Schoener, 1971). Thus, this suggests differences in learning speeds may be a key source of cognitive variation between populations. This insight was only possible because cognitive performance was compared between two versions of a task that isolated the specific cues that were available to use during learning.

Thus, the current study further contributes to the growing number of studies comparing cognitive performance among populations inhabiting different environments to understand the evolution of cognitive mechanisms (e.g. Audet, Ducatez, & Lefebvre, 2015; Bond, Kamil, & Balda, 2007; Pravosudov & Clayton, 2002; Tebbich & Teschke, 2014). Our results are consistent with the hypothesis that ecology can drive adaptive cognitive processes, such that the local environment leads populations to more quickly associate specific cues with certain behavioural outcomes. Although only measuring two populations limited our ability to identify specific ecological factors, our results are consistent with previous studies suggesting that habitat stability can drive differences in cognitive performance among stickleback populations (Girvan & Braithwaite, 1998; Odling-Smee & Braithwaite, 2003). For example, Girvan and Braithwaite (1998) suggested that sticklebacks from riverine environments are likely to experience high environmental variation due to water flow and, therefore, might rely more on egocentric cues than on visual cues, while sticklebacks from stable pond environments rely more on visual landmarks. Consistent with this hypothesis, fish from the Navarro River learned faster when the reward was associated with a specific turn sequence rather than with a visual cue. In contrast, fish from Putah Creek (subject to less dramatic changes) were faster to learn to follow a visual cue (colour). Further studies on replicate creek and river populations are needed in order to determine whether differences in habitat stability are responsible for driving the observed patterns, and it would be useful to know whether the population-level variation has a genetic basis (as in Pravosudov et al., 2012; Roth, LaDage, Freas, & Pravosudov, 2011). Additionally, the current study demonstrates that population variation in visual cue use extends to nonspatial variables such as colour.

Elucidating the aspects (e.g. perception, learning and memory) of cognition that contribute to variation in cognitive performance will allow us to better understand the ecological factors that drive cognitive evolution. Here, we show that animals not only learn faster with certain types of cues over others, but that animals from different environments differ in the type of cues with which they more readily form associations. Future studies that use a battery of tests to isolate different cognitive mechanisms are likely to further uncover the nuances of cognitive variation between populations and taxa. This is key to identify the ecological and evolutionary pressures that lead to fascinating variation in how animals process, learn and adapt to their environment.

Acknowledgments

We thank Emilee Johnson, Tyler Seal, Erika Carlson and Amy Schneider for their help with data collection. We also thank the Bell lab, as well as the editor and anonymous referees, for their comments to improve the manuscript. M.B. was supported by the National Science Foundation's (NSF) Integrative Graduate Education and Research Traineeship programme and funds from the University of Illinois Urbana-Champaign's School of Integrative Biology and Program in Ecology, Evolution, and Conversation Biology. This work was supported by grants from the National Institutes of Health (NIH R01 GM082937) and NSF (1121980) to A.M.B.

References

- Adriaenssens B, Johnsson JI. Shy trout grow faster: Exploring links between personality and fitness-related traits in the wild. *Behavioral Ecology*. 2010; 22(1):135–143.<https://doi.org/10.1093/beheco/arq185>
- Audet JN, Ducatez S, Lefebvre L. The town bird and the country bird: Problem solving and immunocompetence vary with urbanization. *Behavioral Ecology*. 2015; 27:637–644.<https://doi.org/10.1093/beheco/ary201>
- Bell AM. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*. 2005; 18(2):464–473.<https://doi.org/10.1111/j.1420-9101.2004.00817.x> [PubMed: 15715852]
- Bell MA, Foster SA. The evolutionary biology of the threespine stickleback. Oxford, U.K: Oxford University Press; 1994.
- Bensky MK, Paitz R, Pereira L, Bell AM. Testing the predictions of coping styles theory in threespined sticklebacks. *Behavioural Processes*. 2017; 136:1–10.<https://doi.org/10.1016/j.beproc.2016.12.011> [PubMed: 28017848]
- Bond AB, Kamil AC, Balda RP. Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*. 2007; 121(4):372–379.<https://doi.org/10.1037/0735-7036.121.4.372> [PubMed: 18085920]
- Braithwaite VA, Girvan JR. Use of water flow direction to provide spatial information in a small-scale orientation task. *Journal of Fish Biology*. 2003; 63(s1):74–83.
- Brown C, Braithwaite VA. Size matters: A test of boldness in eight populations of the poeciliid *Brachyrhaphis episcopi*. *Animal Behaviour*. 2004; 68:1325–1329.<https://doi.org/10.1016/j.anbehav.2004.04.004>
- Brydges NM, Heathcote RJ, Braithwaite VA. Habitat stability and predation pressure influence learning and memory in populations of three-spined sticklebacks. *Animal Behaviour*. 2008; 75:935–942.
- Burns JG. The validity of three tests of temperament in guppies (*Poecilia reticulata*). *Journal of Comparative Psychology*. 2008; 122(4):344–356.<https://doi.org/10.1037/0735-7036.122.4.344> [PubMed: 19014258]
- Carere C, Locurto C. Interaction between animal personality and animal cognition. *Current Zoology*. 2011; 57(4):491–498.<https://doi.org/10.1093/czoolo/57.4.491>

- DePasquale C, Wagner T, Archard GA, Ferguson B, Braithwaite VA. Learning rate and temperament in a high predation risk environment. *Oecologia*. 2014; 176(3):661–667.<https://doi.org/10.1007/s00442-014-3099-z>
- Duffy GA, Pike TW, Laland KN. Size-dependent directed social learning in nine-spined sticklebacks. *Animal Behaviour*. 2009; 78:371–375.<https://doi.org/10.1016/j.anbehav.2009.05.015>
- Dugatkin LA, Alfieri MS. Boldness, behavioral inhibition and learning. *Ethology Ecology & Evolution*. 2003; 15(1):43–49.<https://doi.org/10.1080/08927014.2003.9522689>
- Feng S, McGhee KE, Bell AM. Effect of maternal predator exposure on the ability of stickleback offspring to generalize a learned colour–reward association. *Animal Behaviour*. 2015; 107:61–69.<https://doi.org/10.1016/j.anbehav.2015.05.024> [PubMed: 29046591]
- Fiset S, Gagnon S, Beaulieu C. Spatial encoding of hidden objects in dogs (*Canis familiaris*). *Journal of Comparative Psychology*. 2000; 114(4):315–324.<https://doi.org/10.1037/0735-7036.114.4.315> [PubMed: 11149535]
- Garcia J, Koelling RA. Relation of cue to consequence in avoidance learning. *Psychonomic Science*. 1966; 4(1):123–124.<https://doi.org/10.3758/BF03342209>
- Gill AB, Hart PJ. Feeding behaviour and prey choice of the threespine stickleback: The interacting effects of prey size, fish size and stomach fullness. *Animal Behaviour*. 1994; 47:921–932.<https://doi.org/10.1006/anbe.1994.1124>
- Girvan JR, Braithwaite VA. Population differences in spatial learning in three-spined sticklebacks. *Proceedings of the Royal Society B: Biological Sciences*. 1998; 265(1399):913–918.<https://doi.org/10.1098/rspb.1998.0378>
- Gottselig JM, Wasserman EA, Young ME. Attentional trade-offs in pigeons learning to discriminate newly relevant visual stimulus dimensions. *Learning and Motivation*. 2001; 32(2):240–253.<https://doi.org/10.1006/lmot.2000.1081>
- Guillette LM, Naguib M, Griffin AS. Individual differences in cognition and personality. *Behavioural Processes*. 2016; 134:1–3.<https://doi.org/10.1016/j.beproc.2016.12.001> [PubMed: 27923604]
- Hampton RR, Shettleworth SJ. Hippocampal lesions impair memory for location but not color in passerine birds. *Behavioral Neuroscience*. 1996; 110(4):831–835.<https://doi.org/10.1037/0735-7044.110.4.831> [PubMed: 8864273]
- Mackintosh NJ. A theory of attention: Variations in the associability of stimuli with reinforcement. *Psychological Review*. 1975; 82:276–298.
- Odling-Smee LC, Boughman JW, Braithwaite VA. Sympatric species of threespine stickleback differ in their performance in a spatial learning task. *Behavioral Ecology and Sociobiology*. 2008; 62(12):1935–1945.<https://doi.org/10.1007/s00265-008-0625-1>
- Odling-Smee L, Braithwaite VA. The influence of habitat stability on landmark use during spatial learning in the three-spined stickleback. *Animal Behaviour*. 2003; 65:701–707.<https://doi.org/10.1006/anbe.2003.2082>
- Park PJ. Spatial learning ability of the threespine stickleback (*Gasterosteus aculeatus*) in relation to inferred ecology and ancestry. *Evolutionary Ecology Research*. 2013; 15(2):213–239.
- Pravosudov VV, Clayton NS. A test of the adaptive specialization hypothesis: Population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). *Behavioral Neuroscience*. 2002; 116(4):515–522. [PubMed: 12148919]
- Pravosudov VV, Roth TC, Forister ML, Ladage LD, Burg TM, Braun MJ, et al. Population genetic structure and its implications for adaptive variation in memory and the hippocampus on a continental scale in food-caching black-capped chickadees. *Molecular Ecology*. 2012; 21(18):4486–4497.<https://doi.org/10.1111/j.1365-294X.2012.05721.x> [PubMed: 22882305]
- R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2016. <https://www.R-project.org/>
- Rescorla RA, Wagner AR. A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In: Black AH, Prokasy WF, editors *Classical conditioning II: Current research and theory*. New York, NY: Appleton-Century-Crofts; 1972. 64–99.
- Roche DP, McGhee KE, Bell AM. Maternal predator-exposure has lifelong consequences for offspring learning in threespined sticklebacks. *Biology Letters*. 2012; 8(6):932–935.<https://doi.org/10.1098/rsbl.2012.0685> [PubMed: 22993240]

- Rodriguez F, Duran E, Vargas JP, Torres B, Salas C. Performance of goldfish trained in allocentric and egocentric maze procedures suggests the presence of a cognitive mapping system in fishes. *Animal Learning & Behavior*. 1994; 22(4):409–420.
- Rodriguez F, Lopez JC, Vargas JP, Gomez Y, Broglio C, Salas C. Conservation of spatial memory function in the pallial forebrain of reptiles and ray-finned fishes. *Journal of Neuroscience*. 2002; 22(7):2894–2903. [PubMed: 11923454]
- Roth TC, LaDage LD, Freas CA, Pravosudov VV. Variation in memory and the hippocampus across populations from different climates: A common garden approach. *Proceedings of the Royal Society B: Biological Sciences*. 2011; 279(1727):402–410. <https://doi.org/10.1098/rspb.2011.1020> [PubMed: 21715407]
- Schoener TW. Theory of feeding strategies. *Annual Review of Ecology and Systematics*. 1971; 2(1): 369–404. <https://doi.org/10.1146/annurev.es.02.110171.002101>
- Sih A, Del Giudice M. Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2012; 367(1603):2762–2772. <https://doi.org/10.1098/rstb.2012.0216>
- Tebich S, Teschke I. Coping with uncertainty: Woodpecker finches (*Cactospiza pallida*) from an unpredictable habitat are more flexible than birds from a stable habitat. *PLoS One*. 2014; 9(3):e91718. <https://doi.org/10.1371/journal.pone.0091718> [PubMed: 24638107]
- Therneau T. A package for survival analysis in S Version 2.38. 2015. <https://CRAN.R-project.org/package=survival>
- Toms CN, Echevarria DJ, Jouandot DJ. A methodological review of personality-related studies in fish: Focus on the shy–bold axis of behavior. *International Journal of Comparative Psychology*. 2010; 23(1):1–25.
- Treviño M. Associative learning through acquired salience. *Frontiers in Behavioral Neuroscience*. 2016; 9(353) <https://doi.org/10.3389/fnbeh.2015.00353>
- Visser ME, Schaper SV, Holleman LJ, Dawson A, Sharp P, Gienapp P, et al. Genetic variation in cue sensitivity involved in avian timing of reproduction. *Functional Ecology*. 2011; 25(4):868–877. <https://doi.org/10.1111/j.1365-2435.2011.01844.x>
- Wheatcroft D, Qvarnstrom EA. A blueprint for vocal learning: Auditory predispositions from brains to genomes. *Biology Letters*. 2015; 11(8):20150155. <https://doi.org/10.1098/rsbl.2015.0155> [PubMed: 26246333]
- Wickham H. *ggplot 2: Elegant graphics for data analysis*. New York, NY: Springer-Verlag; 2009.
- Wilson AD, Godin JGJ. Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behavioral Ecology*. 2009; 20(2):231–237. <https://doi.org/10.1093/beheco/arp018>

Figure 1.

Top-down view of the tank during training trials for (a) colour and (b) side discrimination learning. The top of each diagram represents the back of the test tank. The large black circle represents the starting shelter and the smaller circles represent search cups (light grey = yellow cup; dark grey = blue cup). The arrows point to the correct cup choice. The hatched area represents the 'correct choice' region and the area enclosed by the dotted border represents the 'incorrect choice' region.

Figure 2. Population differences in days to complete pretraining. Each data point indicates a different individual, with median and IQR shown. Graphs were made utilizing the graphics (R Core Team., 2016) and ggplot2 packages (Wickham, 2009).

Figure 3. Population differences in average time to emerge (log transformed) from starting shelter across the first training session (10 trials). Each data point indicates a different individual, with mean and SE shown. Graphs were made utilizing the graphics (R Core Team., 2016) and ggplot2 packages (Wickham, 2009).

Figure 4.

Learning performance of two populations on two versions of the discrimination task. The survival curves provide a side-by-side comparison of the rates at which fish reached criterion on each version of the task within the (a) Navarro and (b) Putah populations. Note that the *Y* axis has been flipped to help indicate that, as the curve descends, it represents more fish reaching learning criterion. (c) Comparison of the average performances on each version of the task (colour = solid circles; side = open circles) within each population. Each data point indicates a different individual's log-transformed sessions to reach criterion, with means (triangles) and SE shown. Graphs were made utilizing the graphics (R Core Team., 2016) and ggplot2 packages (Wickham, 2009).