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Original Article

Predation shapes behavioral lateralization: insights from an adaptive radiation of livebearing fish

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Hemispheric brain lateralization can drive the expression of behavioral asymmetry, or laterality, which varies notably both within and among species. To explain these left–right behavioral asymmetries in animals, predator-mediated selection is often invoked. Recent studies have revealed that a relatively high degree of lateralization correlates positively with traits known to confer survival benefits against predators, including escape performance, multitasking abilities, and group coordination. Yet, we still know comparatively little about 1) how consistently predators shape behavioral lateralization, 2) the importance of sex-specific variation, and 3) the degree to which behavioral lateralization is heritable. Here, we take advantage of the model system of the radiation of Bahamas mosquitofish (*Gambusia hubbsi)* and measure behavioral lateralization in hundreds of wild fish originating from multiple blue holes that differ in natural predation pressure. Moreover, we estimated the heritability of this trait using laboratory-born fish from one focal population. We found that the degree of lateralization but not the particular direction of lateralization (left or right) differed significantly across high and low predation risk environments. Fish originating from high-predation environments were more strongly lateralized, especially females. We further confirmed a genetic basis to behavioral lateralization in this species, with significant additive genetic variation in the population examined. Our results reveal that predation risk represents one key ecological factor that has likely shaped the origin and maintenance of this widespread behavioral phenomenon, even potentially explaining some of the sex-specific patterns of laterality recently described in some animals.

Key words: **asymmetry, behavioral lateralization, heritability, predation, sex-dependent behavioral responses.**

INTRODUCTION

Partitioning of specific cognitive processes into the separate hemispheres of the brain is widespread in animals and frequently manifests as a behavioral side bias, a phenomenon intimately familiar to most humans due to their handedness and footedness (Walker 1980). Such behavioral lateralization varies notably both within and among species (Bisazza et al. 1998a, 2000a; Csermely and Regolin 2012; Giljov et al. 2015; Stancher et al. 2018; Fuss et al. 2019). Contrasting ecological selective pressures, particularly variation in predation risk, has long been thought to partly underlie this variation. This largely stems from the idea that increased neural capacity, hemisphere dominance, and simultaneous processing of cognitive functions associated with enhanced laterality may allow prey to better evade their natural enemies, thus increasing fitness in high-risk environments. Accordingly, a number of correlational studies have shown that stronger lateralization is associated with increased performance in behaviors that may reduce the risk of predation, including enhanced escape performance (Dadda et al. 2010), multitasking (Rogers et al. 2004; Dadda and Bisazza 2006a), and predator recognition learning ability (Ferrari et al. 2017; Lucon-Xiccato et al. 2017). On the other hand, there are also disadvantages to lateralization (Vallortigara and Rogers 2005; Vallortigara 2006), suggesting cost-benefit trade-offs may underlie the evolution and expression of behavioral lateralization in nature. For example, although lateralized individuals may display stronger anti-predator behaviors, less lateralized individuals show enhanced competitive performance (Chivers et al. 2017b), a particularly important behavior in high-density or low-resource environments characteristic of the situation that often prevails in environments with low levels of predation risk.

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Previous studies have documented shifts in lateralization after experimental manipulations of perceived predation risk (Broder and Angeloni 2014; Chivers et al. 2017a; Ferrari et al. 2017), and more rarely found differentiation in behavioral lateralization between wild populations experiencing natural variation in predation risk (Brown et al. 2004, 2007). Although informative, such associations are frequently difficult to interpret and may only hint at the direct role of predator-mediated selection in driving shifts in lateralization. This is because, in many systems, predation risk covaries with other potential selective pressures, as predators often inhabit environments with higher species richness, greater habitat heterogeneity/complexity, larger habitat size, and greater ecosystem productivity and food availability (Grether et al. 2001; Reznick et al. 2001; Rudman et al. 2016). To better understand the general importance of predator-mediated selection in explaining the broad distribution of lateralization phenotypes in nature, we need more replicated studies (Brown et al. 2004), preferably in natural systems that can appropriately investigate predation risk without confounding it with other covarying selective agents (Hulthén et al. 2021b).

Furthermore, whilst ecology can shape population-level patterns of behavioral lateralization, intrinsic factors including sex and body size can influence individual behavioral responses within selective environments (Reddon et al. 2009; Reddon and Balshine 2010; Irving and Brown 2013). For instance, the fitness benefits of a particular behavioral trait can differ between males and females owing to differences in their ecological interactions or life history (Magurran and Seghers 1994; Magurran 2005). Accordingly, a large body of literature has documented sex-specific disparities in behavioral responses and susceptibilities of prey to predators (Magnhagen 1991; Magurran et al. 1992; Husak et al. 2006; Välimäki and Herczeg 2012). For example, female guppies are more cautious, less bold, and perform much more anti-predator responses than males, particularly in high-predation localities (Magurran and Seghers 1994; Harris et al. 2010). Sexual differences in the responsiveness and susceptibility to predation may thus favor sex-specific divergence in phenotypes known to be intimately linked to the ability to cope with predators, such as behavioral lateralization (Rogers et al. 2004; Bisazza and Dadda 2005; Dadda et al. 2010; Bibost and Brown 2014). Moreover, behavioral lateralization in particular could show sex-specific responses, given that males and females generally show differences in brain organization (Bianki and Filippova 2001). Accordingly, previous studies point towards substantial variation in laterality between the sexes (Bisazza et al. 1998a; Reddon and Hurd 2008; Ariyomo and Watt 2013; Bibost et al. 2013). Yet, sex dependence of laterality is currently understudied (Reddon and Hurd 2008; Sundin and Jutfelt 2018; McLean and Morrell 2020), particularly with respect to the role of predation-risk, since previous studies in the wild have largely been limited to a single sex, most often females (Brown et al. 2007).

Moreover, understanding the extent to which ecologically important behaviors are genetically based and show heritability within populations is important for comprehending the ability of traits to evolve in response to selection. Traits with significant additive genetic variation will generally evolve more rapidly in the face of natural selection, and can have far-reaching evolutionary consequences. To date, we have a relatively poor understanding of the heritability of cognitive traits in general (e.g., Croston et al. 2015; Boogert et al. 2018). Other than handedness in mammals (Hopkins 1999; McManus et al. 2013; Lien et al. 2015; Cuellar-Partida et al. 2020), there is a scarcity of research on the heritability of behavioral lateralization, and thus more work is needed to better understand its ecological and evolutionary importance (Bisazza et al. 2000b; Brown et al. 2007; Croston et al. 2015; Ocklenburg et al. 2016).

The post-Pleistocene radiation of Bahamas mosquitofish (*Gambusia hubbsi*) inhabiting blue holes possesses a suite of characteristics that make it an ideal empirical system for examining how natural variation in predation risk shapes behavioral laterality, the importance of sex-specific variation, and the degree to which behavioral lateralization is heritable. Bahamas mosquitofish are small, livebearing fish (family Poeciliidae) with pronounced sexual dimorphism that inhabit numerous blue holes (water-filled, vertical caves) on Andros Island, The Bahamas. Blue holes vary in predation risk due to the presence versus absence of major fish predators (mainly bigmouth sleeper, *Gobiomorus dormitor*). Hence, blue holes can be easily dichotomized into "high-predation" sites where dangerous predators impose strong mortality, thus reducing conspecific densities, and "low-predation" sites with no predatory fishes, low mortality rates, and relatively high levels of resource competition (Downhower et al. 2000; Langerhans et al. 2007; Heinen et al. 2013). As a consequence, previous research has demonstrated that Bahamas mosquitofish from high- and low-predation localities have repeatedly evolved differences in a broad suite of traits, including life history, behavior, and morphology (Riesch et al. 2013; Martin et al. 2014; Heinen-Kay et al. 2016; Langerhans 2018). Importantly, predation risk does not systematically covary with any other measured environmental variable (e.g., competitors, productivity, habitat heterogeneity, salinity, turbidity, water transparency, water color, depth, dissolved oxygen, temperature, pH), nor is genetic relatedness among Bahamas mosquitofish populations associated with predation regime (e.g., Langerhans et al. 2007; Langerhans and Gifford 2009; Heinen et al. 2013; Riesch et al. 2013; Björnerås et al. 2020). Because the fish are also amenable for laboratory study, the heritability of behavioral lateralization can be examined. This sets the scene for a study focusing more-or-less exclusively on the effects of predation risk in driving divergence in male and female lateralization phenotypes in replicated natural populations.

In this study, we tested two specific predictions regarding variation in behavioral lateralization and estimated the magnitude of heritability of this trait in Bahamas mosquitofish. First, based on prior research suggesting anti-predator benefits of lateralization, we hypothesized that high-predation populations would exhibit a stronger *magnitude* of lateralization (bias in side use by individuals, irrespective of direction) but not necessarily differ in the *direction* of lateralization (bias of individuals turning toward a particular direction within populations). Second, we hypothesized that sexes will likely show similar patterns of behavioral lateralization (Bisazza et al. 1998a; Bisazza and Brown 2011) with two possible exceptions: 1) females could show weaker lateralization than males as has been found before in some taxa (Bradshaw and Rogers 1993; Bianki and Filippova 2001), or 2) males could show weaker differentiation between predation regimes if lateralization in males similarly impacts mating performance across all populations (e.g., if selection always favors lateralization in males owing to its effects on mating performance) whereas lateralization offers females more advantages than males in high-predation environments (e.g., females more risk-sensitive, need to multitask in the presence of frequent male harassment [Heinen-Kay et al. 2016]). Third, we estimated how heritable behavioral lateralization is, predicting lateralization to represent a heritable trait in Bahamas mosquitofish, demonstrating moderate to high heritability (Bisazza et al. 2000b). To test these predictions, we first quantified both the strength and direction (Bisazza and Dadda 2005; Sovrano et al. 2005; Dadda and Bisazza 2006a, 2006b) of turning preferences of individuals originating from multiple populations evolving either in the presence or absence of predators. We then asked how male and female behavioral lateralization patterns have been shaped by natural variation in predation risk. We followed up our field study by executing the same test on laboratory-reared mosquitofish to test for genetic variation (i.e., heritability) in the strength and direction of behavioral lateralization.

MATERIAL AND METHODS

Subject collection and maintenance

We assessed behavioral lateralization in wild adult fish originating from six different blue holes: three high-predation blue holes (Cousteau's, Stalactite, and West Twin) and three low-predation blue holes (East Twin, Hubcap, and Rainbow). These six focal blue holes were selected a priori as a representative subsample of the larger set of blue holes on Andros Island, characterized by independent colonization events, low gene flow with outside populations, and importantly, similarity in most environmental variables other than predation regime. All fish were collected while snorkeling using hand-held dip nets and either immediately transferred to the lateralization arena and assayed on the shore of each blue hole (June 2016, $n = 183$) or transported to experimental facilities on the island (February 2016, $n = 194$) maintained in large, continuously aerated opaque coolers (45-L), fed a mixture of freeze-dried daphnia, bloodworms, and TetraMin Pro flakes under a natural light and temperature regime for at least one day prior to lateralization assays.

Lateralization assays

We used a standard detour test in a two-way T-maze arena to assess individual behavioral lateralization (Bisazza et al. 1998a; Dadda et al. 2010; Chivers et al. 2017a; Sundin and Jutfelt 2018). Briefly, the experimental arena consisted of a rectangular tank made of opaque, white acrylic [80 × 30 × 16 cm (length × width × height)], with a narrow runway in the middle [40 × 5 × 10 cm (length × width × height) filled with water to a depth of 5 cm (Fig. S1). Each trial started when a single fish was introduced into one end of the experimental arena and given 2 min to acclimatize. When this time had elapsed, the experimenter used a small aquarium net to gently maneuver the fish to the starting point of the runway. The fish would swim to the end of the runway until it faced a barrier (15 × 10 cm, length × height, made of the same opaque material as the tank), which was positioned perpendicular and 5 cm ahead of the runway, thus forcing the fish to turn either left or right around the barrier. All subjects received 10 consecutive trials, alternating the starting position between either end of the arena, requiring the fish to swim in opposite directions, to account for any possible asymmetry in the T-maze. This established protocol for assaying lateralization in fishes (e.g., Bisazza et al. 1997, but see also Roche et al. 2020) thus allows us to capture individual propensities to turn to the left or right more than expected by chance.

For trials conducted on the shore of blue holes in the field, the arena was filled with water from the focal blue hole (arena rinsed, and all water replaced between trials). For trials conducted in the laboratory, 2-L of water was replaced between trials to reduce any build-up of chemical cues and to minimize changes in dissolved oxygen. Each focal individual's 10 turning directions were recorded by direct observation with the criterion that the main axis of fish's body was parallel to the barrier. After the lateralization assay, we measured the standard length (SL) of each individual from digital photographs captured with a DSLR camera that included a ruler for scale calibration.

Genetic basis

To test for genetic variation (i.e., heritability) of behavioral lateralization we conducted lateralization assays following the protocol previously described with adult second-generation laboratory-raised fish ($n = 79$, 12 full-sibling families; Supplementary Table S1) derived from one of the focal high-predation blue holes (Cousteau's). All fish were raised under common laboratory conditions in 10-L aquaria within a recirculating system (providing biological, mechanical, and UV-filtration) at approximately 25 °C in a temperature-controlled room and fed a varied diet of live brine shrimp, freeze-dried daphnia and bloodworms, and TetraMin Pro flakes. We housed the parental generation fish for several months prior to obtaining F1 offspring, and then obtained F2 offspring after the F1 fish reached adulthood. To avoid confounding any tank effects with family effects, we split all families among multiple tanks.

Data analysis

For wild-caught fish, we first wished to test for the presence of side-independent lateralization (bias in turning preference in the detour test, irrespective of direction) and directional lateralization (bias in turning preference toward one particular direction) within each sex of each population. To do so, we followed the methods of Roche et al. (2020). Briefly, side-independent lateralization ("individual level lateralization" in Roche et al. [2020]) was tested using a chi-square test that compared the observed variance in the number of right turns per individual to the expected variance under a normal approximation to the binomial distribution (i.e., test for more observations in the tails of the distribution than expected by chance). We tested for directional lateralization ("population level lateralization" in Roche et al. [2020]) using generalized linear random-effects models in the R software program (R Development Core Team 2018), testing whether the observed number of turns to the right differed from the expected number of turns (either greater or fewer) less than a binomial error distribution of 0.5 (i.e., 50% of turns to the right). In this way, we could detect the presence of an overall side bias in turns performed during the experimental assays. These tests provide an overview of the presence of behavioral lateralization across sexes and populations.

Second, we performed generalized linear mixed models to test whether behavioral lateralization (both side-independent and directional) differed between predation regimes or sexes, or was associated with body size. For side-independent lateralization, we examined the number of turns either to the right or left that exceeded the random expectation of 5 turns in either direction for each individual. Side-independent lateralization ranged from 0 to 5. Individuals were scored 0 if they turned both directions equally, 1 if they turned to one direction one more time than expected by chance (6 turns to one side, 4 turns to the other side), 2 if they turned one direction two times more than expected by chance (7 turns to one side, 3 turns to the other side), and so on. For directional lateralization, we examined the number of right turns made by each individual during the assays, ranging from 0 to 10. Using these two indices of behavioral lateralization as dependent variables, we conducted two separate generalized linear mixed models with a Poisson distribution (log link function) using the Laplace approximation, testing for effects of $\log_{10}$-transformed SL, predation regime, sex, and the interaction between predation regime and sex. Population was included as a random effect. We found no evidence for heterogeneity of slopes (interactions with $\log_{10}$-transformed SL). We also found no evidence for differences between the two sampling occasions (all $P > 0.65$), and hence pooled the data for final analyses. Models were performed in the program R using the mixed function of the *afex* package (Singmann et al. 2015). Although females are generally larger than males in *G. hubbsi*, on average, there was extensive overlap in their body size distributions in this study, permitting us to adequately test for effects of body size and sex on behavioral lateralization (females: 18.1–45.0 mm SL, males: 19.2–34.0 mm SL). Multicollinearity was low (variance inflation factors < 1.74).

To provide intuitive metrics of behavioral lateralization, and to aid in comparison with prior studies, we also calculated two commonly used lateralization indices. We calculated a relative (directional) lateralization index (L_R) according to the formula: ([turns to the right − turns to the left]/[turns to the right + turns to the left]) × 100 (Bisazza et al. 1997). These scores range between −100 (individual always turned left) and 100 (individual always turned right). An absolute (side-independent) lateralization index (L_A) was calculated as $|L_R|$, ranging from 0 (individual turned right and left equally) to 100 (individual turned either left or right in all 10 trials). While these indices intuitively capture the degree of lateralization, we did not use these values in our statistical analyses. Metrics used in our generalized linear mixed models are equivalent to integer ranks of L_A and L_R, and have more desirable statistical properties.

For tests of heritability of behavioral lateralization, we measured side-independent and directional lateralization in lab-raised fish using the methods described above for wild-caught fish. We conducted Model II ANCOVA with restricted maximum likelihood to estimate the variance component of full-sibling families and calculate an upper-bound estimate of narrow-sense heritability ($h^2 = V_A/V_P$) assuming no dominance or shared environmental effects on phenotypic variance (Falconer and Mackay 1996; Lynch and Walsh 1998). These models also included terms for sex, the interaction between sex and full-sib family, and $\log_{10}$-transformed SL. If the interaction term was significant, we then calculated heritability separately for each sex. Owing to our sample size, we provide heritability estimates as rough upper-bound estimates of heritability.

RESULTS

Testing for the presence of behavioral lateralization, we found that directional lateralization was relatively rare, but side-independent lateralization was observed in three populations for females and four populations for males (Table 1). Thus, most populations did not tend to show a particular directional bias in lateralization, but behavioral lateralization (as quantified irrespective of direction of the bias) was not uncommon in these fish. These patterns indicated that females only exhibited behavioral lateralization in high-predation populations, whereas males showed a more complex pattern across predation regimes (Table 1).

Testing for effects of body size, sex, and predation regime on behavioral lateralization, we found that neither body size nor sex had clear influences on lateralization, but side-independent lateralization differed between predation regimes, and this effect was sex-dependent (Table 2). Examining the interaction term, we found that high-predation populations showed a stronger magnitude of side-independent behavioral lateralization than low-predation populations, especially in females (Table 1, Figure 1). To more fully explore this pattern, we used planned contrasts within our statistical model to determine whether both females and males from high-predation populations exhibited significantly stronger lateralization than their low-predation counterparts. We found that both females ($P < 0.0001$) and males ($P = 0.0465$) indeed showed the predicted pattern; however, the evidence was much stronger for females than males, with one high-predation population in males not fitting this pattern (Figure 1).

In our laboratory experiment, we found significant genetic variation for side-independent behavioral lateralization, but only in males (Table 3; males: $h^2 = 0.72 \pm 0.27$; females: $h^2 = 0.21 \pm 0.20$). For directional behavioral lateralization, we found significant heritability irrespective of sex (Table 3; $h^2 = 0.45 \pm 0.25$). We found no effects of sex or body size on side-independent or directional behavioral lateralization (Table 3), consistent with observations in wild-caught fish.

DISCUSSION

Different ecological settings may favor different degrees of behavioral laterality, with predation risk representing one potentially important selective agent underlying the evolutionary diversity of this trait (Bisazza and Brown 2011; Wiper 2017). However, very few studies to date have tested whether lineages experiencing relatively high predation risk actually show greater behavioral laterality than those with a history of low predation risk (Brown et al. 2004, 2007). Here we provide an early and powerful comparative test of this

Table 1

Summary of sample sizes and *P* values for tests of absolute behavioral lateralization (Abs. Lat.; side-independent turning bias) and relative behavioral lateralization (Rel. Lat.; directional turning bias) in Bahamas mosquitofish (*P* values < 0.05 in bold type)

		Females			Males		
Predation regime	Blue hole	*N*	Abs. lat.	Rel. lat.	*N*	Abs. lat.	Rel. Lat.
High predation	Cousteau's	54	**<0.0001**	**0.0277**	55	**<0.0001**	0.8334
	Stalactite	17	**0.0020**	0.1851	31	**0.0044**	**0.0393**
	West Twin	12	**0.0246**	0.3598	24	0.1877	0.1943
Low predation	East Twin	16	0.3887	0.1169	35	**0.0114**	0.7986
	Hubcap	28	0.6721	0.5518	38	0.2208	0.2474
	Rainbow	28	0.2181	0.9110	39	**0.0055**	0.5619

Table 2

Results of generalized linear mixed models examining variation in absolute (side-independent) and relative (directional) behavioral lateralization across six natural populations in Bahamas mosquitofish (*P* values < 0.05 in bold type)

	Abs. lateralization		Rel. lateralization	
Source	*z*	*P*	*z*	*P*
Log$_{10}$ standard length	−0.956	0.3390	−0.549	0.5829
Predation regime (PR)	4.380	**<0.0001**	−1.321	0.1864
Sex	−0.299	0.7650	−0.180	0.8573
PR × sex	2.097	**0.0360**	−1.188	0.2347

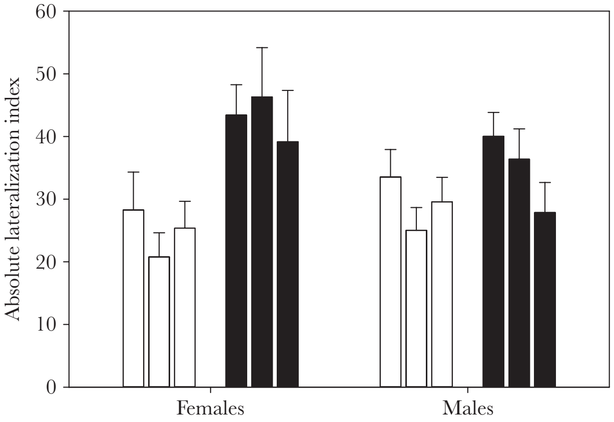

Figure 1

Variation in absolute behavioral lateralization (side-independent) of female and male Bahamas mosquitofish from multiple low-predation (white bars) and high-predation (black bars) populations. Absolute lateralization index scores are depicted for comparison with previous studies, but were derived from least-squares means (±1 SE) of turning data used in statistical analyses.

Table 3

Tests of effects of body size, sex, and full-sibling family on absolute (side-independent) and relative (directional) behavioral lateralization in laboratory-raised F2 Bahamas mosquitofish derived from one of the focal populations (Cousteau, *P* values < 0.05 in bold type)

	Abs. lateralization			Rel. lateralization		
Source	*F*	*df*	*P*	*F*	*df*	*P*
Log$_{10}$ standard length	0.07	1, 54	0.7973	0.55	1, 54	0.4627
Sex	0.13	1, 54	0.7168	0.45	1, 54	0.5048
Full-sib family	2.17	11, 54	**0.0300**	2.61	11, 54	**0.0097**
Sex × full-sib family	2.55	11, 54	**0.0112**	1.25	11, 54	0.2802

hypothesis, as we examined both sexes of six independent populations in a system where the predation regime does not covary with other potentially confounding selective agents. In Bahamas mosquitofish, we found that predation has shaped intraspecific variation of lateralization phenotypes in the wild. These fish showed a pattern of repeated adaptive shifts in behavioral lateralization across populations with different predation regimes. But effects of predation were not uniform in both sexes, as females showed greater divergence in behavioral laterality between predation regimes. For both sexes, we confirmed a genetic basis to behavioral lateralization, with evidence suggesting relatively high additive genetic variation for this trait in the focal population examined.

Matching our a priori prediction, our large-scale field experiment revealed that Bahamas mosquitofish populations coexisting with predatory fish exhibited stronger side-independent lateralization, but not a directional bias, compared with populations living without major predators. This suggests that key agents of selection, including predation risk can consistently favor a greater *degree* of lateralization in prey species, but not necessarily influence the overall *direction* of lateralization in the population (Collins 1991; Brown et al. 2007; Broder and Angeloni 2014; Ferrari et al. 2015; Chivers et al. 2017a). Indeed, we found that a directional trend of lateralization at the population level was rare in Bahamas mosquitofish even though this has been observed in a number of other fish species, including closely related poeciliid fishes (Cantalupo et al. 1995; Bisazza et al. 1997, 2000b; Facchin et al. 1999; Fuss et al. 2019). This may indicate that the fitness benefits of lateralization in this species do not often involve a particular left-right direction per se, and may even rely on a mixture of left-right behavioral asymmetries within the population (Bisazza and Dadda 2005; Bibost and Brown 2013).

Predator-mediated selection is often invoked to explain variation in side-independent behavioral lateralization (Brown et al. 2007), owing to fitness benefits of individual lateralization such as predator recognition learning (Ferrari et al. 2017; Lucon-Xiccato et al. 2017) and enhanced escape performance (Dadda et al. 2010). Predator recognition is important in Bahamas mosquitofish, and previous work has shown strong differentiation in this trait between predation regimes using the same six populations examined in this study (Fowler et al. 2018). The possible role of lateralization in explaining this pattern is currently unknown but should be investigated in the future. Further, locomotor escape abilities are critically important in Bahamas mosquitofish and show strong divergence between predation regimes (Langerhans 2009). Lateralized individuals can experience higher survival as their different directional biases make escape behaviors more unpredictable for the predator (Ghirlanda and Vallortigara 2004; Vallortigara and Rogers 2005; Garcia-Munoz et al. 2012). Previous research in another poeciliid fish (*Girardinus metallicus*) has shown that behavioral lateralization exhibited during turning in a detour test can be significantly associated with the direction of fast-start escape responses (Matsui et al. 2013). Future work could test the hypothesis that individual laterality enhances escape performance in Bahamas mosquitofish.

Previous research has suggested that directional lateralization at the population level might also increase fitness in the presence of predators, as escape performance of grouped prey (e.g., schools, flocks, herds) can be enhanced by group-level coordination of turning direction (Chivers et al. 2017a). While some animals show such directional lateralization (e.g., Denenberg 1981; Bisazza et al. 1998b; Corballis 2009), this was rarely observed in Bahamas mosquitofish, and we found no differences in directional lateralization between predation regimes. However, if fitness benefits of directional lateralization in the presence of predators mainly derive from coordinated grouping behaviors, this may explain why Bahamas mosquitofish did not show this pattern. These fish regularly encounter predators individually, not only in groups. Moreover, side-independent lateralization can provide group-related anti-predator benefits as well (Bisazza and Dadda 2005; Bibost and Brown 2013). Overall, our results match predictions that increased strength of lateralization, not the direction, confers benefits under high predation risk, but may be selected against under conditions that prevail in low-predation risk environments (e.g., higher densities of conspecific, more intense resource competition) given that more lateralized fish can suffer competitive disadvantages (Chivers et al. 2017b).

Sex-specific responses to predation risk may be an important component of inter-individual differences in behavioral lateralization. Female Bahamas mosquitofish showed greater differences between predatory environments as compared with males, where differentiation was quite weak, with one focal high-predation site (West Twin) not exhibiting evidence for increased lateralization relative to low-predation populations. Intersexual differences in lateralization are known, for example in humans, cats, and rats where males tend to show stronger lateralization than females (Bianki and Filippova 2001). In studies involving fish models, previous research has found sex-specific differences in laterality when experimental subjects were exposed to various stimuli, that in turn, can be linked to underlying differences in other behavioral traits, including aggressiveness (Reddon and Hurd 2008, 2009). Moreover, sex-specific differences in susceptibility, risk-taking behaviors, and responsiveness to predators (Magurran and Nowak 1991; Magurran and Seghers 1994; Harris et al. 2010) may act to drive disparate lateralization phenotypes among the sexes in high-risk environments. Here we found the sexes did not consistently differ in behavioral lateralization—even for side-independent lateralization, pairwise comparisons showed no evidence for sex differences within either predation regime (both $P > 0.43$). Yet, the sexes clearly showed differential responses across predation regimes in this study. Why then did females respond more strongly in their lateralization to variation in predation risk than males?

While both sexes may experience many similar antipredator benefits of lateralization, we suggest that females likely experience stronger divergent selection on lateralization between predatory environments than males owing largely to differences in their behavioral responsiveness to predators, as well as in sexual, feeding, and grouping behaviors. For instance, female Bahamas mosquitofish appear more risk averse as quantified by flight initiation distance, experience higher frequencies of male chases and copulation attempts in high-predation populations, and show higher frequencies of foraging and feeding behaviors as compared with males (Heinen et al. 2013; Pärssinen et al. 2021). This may not necessarily reflect an overall greater responsiveness of females to predation risk (e.g., see Langerhans 2018 for many cases of strong phenotypic divergence between predation regimes in males), but more specifically involve sex-dependent selection on behavioral lateralization and related behaviors. Prior research in another poeciliid fish (*Girardinus falcatus*) has found that lateralized females feed more efficiently while simultaneously avoiding unsolicited male mating attempts compared with non-lateralized females (Dadda and Bisazza 2006b). That study also found that lateralization offered no feeding advantages in the absence of a harassing male. This could contribute to a pattern of stronger selection for lateralization in females in high-predation compared with low-predation environments.

Furthermore, many fish, including Bahamas mosquitofish, exhibit enhanced schooling or shoaling tendency as an effective antipredation strategy in the presence of predators (Krause and Ruxton 2008; Heinen-Kay et al. 2016; Herbert-Read et al. 2017). Schools composed of individuals with stronger side-independent lateralization have been shown to sometimes display enhanced coordination and cohesiveness (Bisazza and Dadda 2005). Considering that females often show greater shoaling tendencies than males in poeciliid fishes (Griffiths and Magurran 1998; Richards et al. 2010), this offers another reason why selection for lateralization in females may be stronger in high-predation compared with low-predation environments.

Meanwhile, laterality in the extremely complex and rapid mating behavior of male Bahamas mosquitofish could offer performance advantages, as laterality in male mating behaviors is known for a number of poeciliid fishes (Aronson and Clark 1952). For instance, some livebearing fish (*Jenynsia lineata*, *Xenophallus umbratilis*) show the integration between genital asymmetry and behavioral laterality in mating contexts (Johnson et al. 2020; Torres-Dowdall et al. 2020), and the Bahamas mosquitofish male genitalia has an asymmetric component (i.e., the "elbow" protrudes to either the left or right side of the gonopodium; Rauchenberger 1989; Heinen-Kay and Langerhans 2013). While this topic deserves further research, if true it would weaken divergent selection on lateralization between predation regimes in males because the effect of laterality on mating performance would likely hold similar importance in all environments. Taken together, our results highlight that predator-driven shifts in the degree of behavioral lateralization can vary among the sexes, but we are only beginning to understand exactly why that might be.

We found evidence for relatively strong genetic variation in behavioral lateralization, and hence, the potential for selection to drive evolution in this trait. We have little knowledge to date on the heritability of behavioral lateralization in wild animal populations, and thus our finding shows that genetic variation exists in some natural populations and should receive more attention. The magnitude of heritability observed in this study was similar to that observed in another poeciliid fish (Bisazza et al. 2000b), suggesting behavioral lateralization may typically have fairly high heritability in livebearing fishes. That said, our estimate included potential contributions of dominance and common environmental effects (e.g., maternal effects) which Bisazza et al. (2000b) showed could be substantial—although Bisazza et al. (2000b) still estimated heritability >0.5 in the absence of dominance and shared-environment effects. Here, we found that only males expressed significant genetic variation for side-independent lateralization, whereas both sexes exhibited heritability for directional lateralization. Supporting evidence for genetically based transmission of, and genetic variation for, behavioral lateralization in fish comes from common-garden experiments where the strength of lateralization, but not the direction, was largely conserved between generations in the poeciliid *Brachyraphis episcop*i (Brown et al. 2007). However, artificial selection experiments with the poeciliid *G. falcatus* revealed that both the strength and direction of parental lateralization were significantly correlated between parents and offspring (Bisazza et al. 2000b). In a recent study of handedness in humans, side-independent lateralization showed higher heritability than directional lateralization ($h^2 = 0.67$ vs. 0.52, respectively; Lien et al. 2015), although both values were relatively high. In this context, our results suggest that side-independent and directional behavioral lateralization may involve different (potentially overlapping) functional neuronal systems associated with cerebral lateralization, meaning the two types of behavioral lateralization have unique gene-dependent patterns. That said, we also note that a recent study of several disparate fish species failed to detect significant individual repeatability of behavioral lateralization scored in a detour test, which led the authors to question the ecological and evolutionary relevance of quantifying behavioral lateralization using detour tests (Roche et al. 2020). Future work should directly investigate the repeatability of behavioral lateralization as measured in the present study, but the presence of significant variation among full-sibling families suggests the methods can capture meaningful aspects of behavioral lateralization in this species.

In sum, this study sheds new light into 1) the role of ecological agents in driving variation in behavioral lateralization, 2) how the sexes can differentially respond to ecological variation with shifts in laterality, and 3) the existence of genetic variation for behavioral lateralization in wild populations. These results add early knowledge to these topics, informing future work, which is clearly needed on all of these fronts. Even though eye- and side-biases in non-human animal behaviors have been recognized for more than a century, and recent decades have witnessed an ever-growing appreciation for the commonality of cerebral laterality outside of humans, we are still in the early days of understanding the ecology and evolution of behavioral lateralization in nature.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Behavioral Ecology* online

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Data availability: Analyses reported in this article can be reproduced using the data provided by Hulthén et al. (2021a).

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