



Does Asymmetrical Gonopodium Morphology Predict Lateralized Behavior in the Fish *Xenophallus umbratilis*?

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Why bilaterally symmetrical organisms express handedness remains an important question in evolutionary biology. In some species, anatomical asymmetries have evolved that accompany behavioral handedness, yet we know remarkably little about causal links between asymmetric morphological traits and behavior. Here, we explore if a dextral or sinistral orientation of the male intromittent organ predicts side preferences in male behaviors. Our study addresses this question in the Costa Rican livebearing fish, *Xenophallus umbratilis*. This fish has a bilaterally symmetrical body plan, with one exception—the male anal fin (gonopodium), used to inseminate females, terminates with a distinct left- or right-handed corkscrew morphology. We used a detour assay to test males for side biases in approach behavior when exposed to four different stimuli (predator, potential mate, novel object, empty tank control). We found that left morph males preferred using their right eye to view potential mates, predators, and the control, and that right morph males preferred to use their left eye to view potential mates and predators, and their right eye to view the control. Males of both morphs displayed no eye bias when approaching the novel object. Our results suggest that there is a strong link between behavior and gonopodium orientation, with right and left morph males responding with opposite directional behaviors when presented with the same stimuli. This presents the intriguing possibility that mating preferences—in this case constrained by gonopodial morphology—could be driving lateralized decision making in a variety of non-mating behaviors.

Keywords: detour test, eye-bias, laterality, livebearing fishes, mate choice, novel object, Poeciliidae, predator-mediated behavior

INTRODUCTION

Body plan can have an important effect on behavior. For example, radially symmetrical species move differently than bilaterally symmetrical species (Hollo and Novak, 2012; Wakita et al., 2020). For example, bilateral symmetry typically results in behaviors that occur in an anterior-posterior orientation, including foraging (Jumars et al., 2015; Kane et al., 2017), locomotion (Hollo and Novak, 2012), and mating (Koshio et al., 2007), whereas radial symmetry leads to no such orientation (Wakita et al., 2020). An important property of bilateral symmetry is that it also allows

an individual to express handedness, defined here as the propensity to use one side of the body preferentially over the other (Palmer, 2006; Bryden, 2016); we use the term “handed” in its broad sense as defined in previous work (Hata et al., 2011; Buchanan et al., 2015). Handedness is typically understood in a morphological context (Bock and Marsh, 1991), such as differences in the properties of structures [e.g., claw size in crabs (Spani et al., 2020)], or the orientation of structures [e.g., shell torsion in snails (Kurita and Wada, 2011)]. However, handedness can also be expressed behaviorally (Wiper, 2017). This occurs through decision-making, expressed where an individual moves to one side preferentially over the other, a phenomenon we refer to as behavioral handedness.

There is a growing body of research focused on behavioral handedness. For example, we know that such handedness can be expressed differently among closely related species (Bisazza et al., 1997b). We also know that in some cases, males and females differ from each other (Fitch et al., 1993). Further, we know that behavioral handedness can vary depending on environmental context, including factors such as individual posture or task complexity in primates, or neonatal handling in rats (Fitch et al., 1993; Fu et al., 2019). However, in each of these cases, the focal species studied exhibited morphological symmetry—that is, the morphologies on the left and right sides of the body were essentially mirror images. What happens in species that are bilaterally asymmetrical in some aspect of their morphology? We are still learning about behavioral handedness in these cases (Vallortigara and Rogers, 2005; Gunturkun et al., 2020). Clearly, such information may be critical to understanding why such behavioral biases evolved in the first place.

To address this gap in our understanding requires a species that shows a morphological asymmetry for some functional trait, and that also has the potential to show behavioral handedness. Here we present such a system. *Xenophallus umbratilis* is a livebearing fish native to Costa Rica; it shows a morphological asymmetry in the male mating structure, the gonopodium. We posit that this forces males to approach potential mates by turning their body to the left or right, in order to evaluate a female and to successfully copulate with her. Previous work in livebearing fishes shows that in some species, males have an eye-bias wherein they use one eye to evaluate mates and the other eye to evaluate risk, such as predators (de Andrade and de Sousa, 2018). Hence, in *X. umbratilis*, it may be that such eye-biases exist, but that they are expressed differently in left morph males vs. right morph males.

In this study, we address two questions. First, does *X. umbratilis* show behavioral handedness in response to different types of stimuli? To address this question, we tested if individuals have an eye preference as they approach potential mates, predators, and a novel object. We compared eye preferences across these different stimuli between left morph males and right morph males. Second, we asked if gonopodial morph had an effect on behavioral handedness? That is, does gonopodium morphology predict the direction of detour behavior? To address our second question, we compared preferences of right and left morph males when approaching each of the different stimuli. We found that behavioral handedness does indeed occur in this

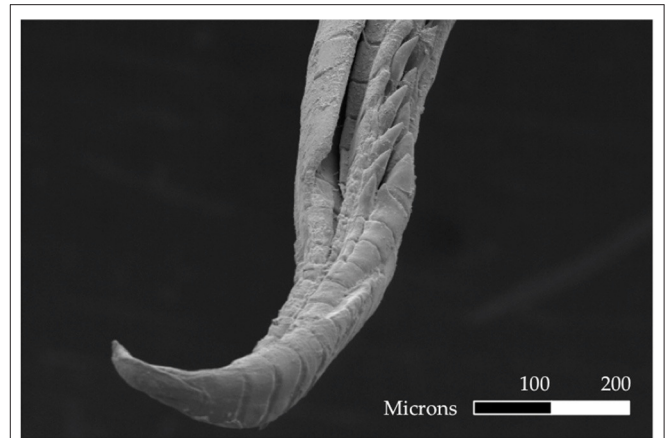


FIGURE 1 | Electron micrograph of a male gonopodium with a sinistral orientation. Scale bar is 100 microns.

species, and more importantly, that it is associated with the orientation of the gonopodium.

MATERIALS AND METHODS

Study System

We addressed our questions using the livebearing fish species, *X. umbratilis* (hereafter referred to as *Xenophallus*). *Xenophallus* is the lone species in a monotypic genus (Parenti and Rauchenberger, 1989; Jones and Johnson, 2009). Its range includes several drainages in the Arenal and Guanacaste provinces of northern Costa Rica (Bussing, 1987). This species—like all members of the family Poeciliidae—give birth to live, free-swimming young that develop from eggs fertilized inside the female. Males transfer sperm directly to females using a modified anal fin called the gonopodium, which they bring in contact with the urogenital pore of the female. This structure varies among species, ranging from relatively simple rod-like morphs to rather complex forms with barbs and hooks (Langerhans, 2011). Yet, the gonopodium of *Xenophallus* is unlike other livebearers. It shows a unique form of asymmetry. At the tip of the shaft, the gonopodium turns in either a dextral or sinistral corkscrew (**Figure 1**). In the wild, both morphs are common within populations; in fact, in all populations that have been adequately sampled ($n > 5$ males) to date, we found both male morphs (with one exception; see **Table 1**). However, the frequency of each morph appears to vary among populations at any given time; of 14 populations with both morphs that we surveyed between 1998 and 2019, we found dextral morph frequency ranged from 0.12 to 0.75 (see Results for details). Hence, gonopodium asymmetry in this species appears to be common and widespread.

To test our hypotheses, we used live fish held in captivity that we collected from two locations in Costa Rica (**Figure 2**). In June 2018, we sampled *Xenophallus* from Quebrada La Palma, a small stream in the Lake Arenal drainage of northern Costa Rica. In April 2019, we sampled *Xenophallus* from Quebrada Chorros, a similar stream, also in the Lake Arenal drainage, near the city of

TABLE 1 | Field collections of *Xenophallus umbratilis* evaluated in this study.

Locality	Population name	Date	Sample	Museum #	GPS	R	L	R:L
1	Tributary to Rio Bijagua	1/05	1-A	009364b,c	N 10° 43.885' W 85° 03.321'	31	23	0.58
		5/06	1-B	009358b		3	0	1.00
		5/06	1-C	009374		4	0	1.00
		5/07	1-D	009387		4	0	1.00
2	Rio Esquivetto	5/06	2-A	009301b	N 10° 41.231' W 85° 04.002'	12	23	0.52
3	Quebrada Azul	2/06	3-A	009354	N 10° 29.955' W 84° 59.138'	6	7	0.46
4	Rio Sabalito	5/06	4-A	009381c	N 10° 32.920' W 84° 58.837'	4	9	0.31
		5/07	4-B	009395		2	2	0.50
5	Quebrada Jilguero	4/98	5-A	009308b,c	N 10° 33.647' W 84° 58.151'	22	8	0.73
6	Quebrada La Palma	5/06	6-A	009338b,c	N 10° 33.614' W 84° 56.442'	6	45	0.12
		5/07	6-B	009392a,b		9	29	0.24
		5/18	6-C	Monitored		2	22	0.08
		6/18	6-D	Monitored		0	24	0.00
		5/19	6-E	Monitored		0	29	0.00
7	Trib. to lake Arenal	4/98	7-A	009345c	N 10° 30.076' W 84° 50.436'	3	3	0.50
		2/06	7-B	009324		0	1	0.00
8	Quebrada Perez	4/98	8-A	009315b	N 10° 28.411' W 84° 49.335'	4	3	0.57
		5/06	8-B	009329b		9	3	0.75
9	Vuelta de la Borracho	5/07	9-A	Unassigned	N 10° 25.646' W 84° 45.135'	11	38	0.22
10	Rio Agua Caliente	5/07	10-A	Unassigned	N 10° 26.103' W 84° 43.402'	10	23	0.30
11	Quebrada Chorros	5/19	11-A	Monitored	N 10° 28.367' W 84° 39.450'	46	0	1.00
12	Rio Isla Grande	5/06	12-A	009300c	N 10° 23.581' W 83° 58.090'	7	10	0.41
13	Rio Corinto	5/06	13-A	009294c	N 10° 12.674' W 83° 53.114'	23	17	0.58
		5/07	13-B	009385		5	7	0.42
14	Upper Rio Tortuguero	5/07	14-A	009394	N 10° 15.565' W 83° 48.734'	2	4	0.33

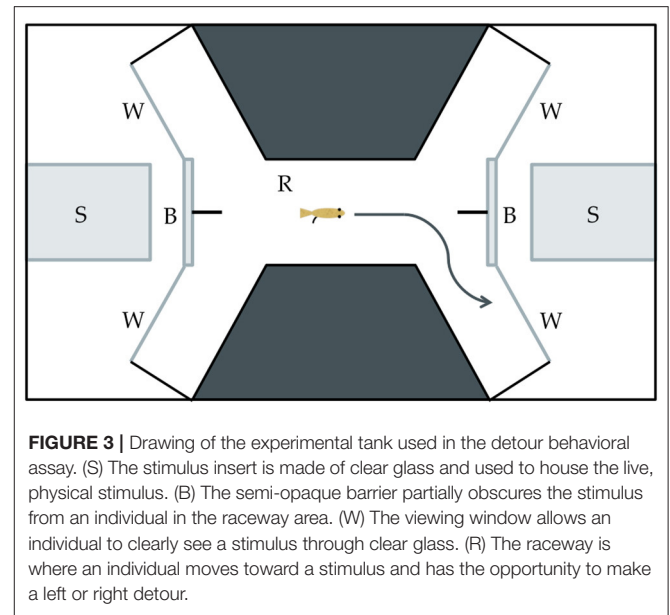
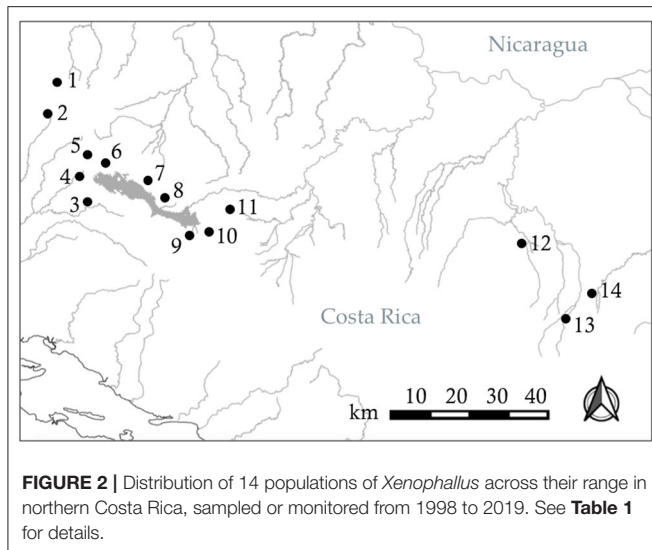
Locality numbers correspond to those found on the map in **Figure 2**. Date depicts the month/year that the collection was made; where multiple collections were made from the same locality, they are designated by a letter. The museum # indicates the population accession number in the Brigham Young University Monte L. Bean Life Science Museum (MLBM); "Monitored" indicates populations where fish were collected, scored, and returned unharmed to the stream; "Unassigned" indicates samples that have yet to be assigned a number in the MLBM. R and L show the number of individual males with a right morph and left morph gonopodium, respectively, from each sample. R:L indicates the right to left morph ratio.

Fortuna. We chose these two locations for several reasons: first, they are geographically close to each other, and therefore likely to experience similar micro-climate effects in the wild (**Figure 2**); second, the locations are ecologically similar for a variety of measures (**Supplementary Table 1**); and finally, at the time of collection, the two localities differed in the relative frequency of left- and right-morph males, allowing us to bring both morph types into the lab (**Table 1**). For both sampling events, we collected and transported 150 live fish to the fish breeding facility at Brigham Young University, where they were treated for parasites and held under common laboratory conditions (as described below). By chance, all adult males available for this study from Quebrada La Palma were left morph males and all adult males available from Quebrada Chorros were right morph males (see **Table 1** for collection details). We recognize the potential confounding influence of locality with male morph type; however, our sampling was designed to minimize ecological differences between sites (see above). Hence, if locality effects exist, they are less likely to be ecological than genetic, a topic we will address in future work focused on the inheritance of male gonopodial morphs. Fish held in the lab, both males and females, were fed *ad libitum* twice daily and kept in 10-gallon tanks at

23°C on a 12L:12D light cycle. For both collections, individuals were kept in this common laboratory environment for 4 months prior to testing; in this way, we attempted to minimize any affect that condition might have on behavior during the trials.

Experimental Design

Our study was designed to determine if *Xenophallus* males show a bias with respect to the side that they use to approach different stimuli, and if this bias differs between left morph males and right morph individuals. We isolated 15 males of each morph (30 total fish) by placing them in individual tanks so each fish could be exposed to each stimulus (details explained below). We used a detour test approach similar to the one used by Bisazza et al. (1997a,b) to test for behavior handedness, a technique widely adopted in behavioral research (Kabadayi et al., 2018). This involved placing a single male in an arena built within a tank (**Figure 3**) and allowing him to swim back and forth from one end to the other. At each end of the raceway in the arena the male came to a fork where he was given a choice to proceed to the right or left. In a screened area behind the detour, we placed a visual stimulus. This enabled the individual in the trial to see the stimulus as it approached the detour fork, but in order to clearly



view the stimulus, the focal male had to detour either to the right or the left. Individuals were allowed to move in the tank in both directions, making a choice each time they move from one end to the other. They were allowed to move freely without prodding so we could attribute their detour behavior directly to the stimulus. Each fish was given 20 min in the arena and we recorded the number of right and left detours. The male was then removed from the arena and the water was filtered for 10 min prior to the next trial. This was repeated for up to 30 individual males (15 dextral and 15 sinistral) for each visual stimulus, although for some treatments we tested slightly fewer males ($n = 13\text{--}15$ per male morph per treatment). Individuals were randomly assigned to each stimulus treatment (see below). We deemed this sample size sufficiently large based on similar studies in other species (Bisazza et al., 1997a; Torres-Dowdall et al., 2019), but not so large as to unnecessarily use live animals as per our approved IACUC protocol (see Acknowledgments). The entire arena was housed in a walk-in, sound-proof room, allowing all observations to be made remotely via a camera mounted over the tank.

We predicted that *Xenophallus* males might respond differently to different stimuli. Hence, we ran our detour assay with three different live stimuli as well as a control. The stimuli we tested were: (1) *Xenophallus* adult females (potential mates); (2), the fish *Parachromis dovii* (a known predator of *Xenophallus*); (3) a novel object (Lego, see explanation below) that *Xenophallus* would have never previously encountered; and (4) a negative control which consisted of an empty stimulus tank. These stimuli were chosen with the idea that males might specialize in the eye that they use to secure this visual information, perhaps as a function of their gonopodial anatomy. The stimuli were physically placed at either end of the tank. When viewed from straight on, the stimulus was partially obscured (see **Figure 3**), requiring the fish to make a lateral choice to view it clearly. Because teleost fish are unable to use both eyes to focus on the same object (Land, 2015), this test reveals which eye a fish actually uses to view the stimulus. We

isolated six size-matched females to be used as potential mate stimuli, randomly selecting two of them to use in each trial. Predators were similarly selected for use from four different *P. dovii* individuals held in the lab. Finally, we chose a Lego stack, consisting of orange, yellow, blue, white, and red blocks in the shape of a “Y” as a novel object. This was an item that we thought would attract the interest of *Xenophallus* males, but that was completely foreign to this species. Overall, this design allowed us to determine if there is a behavioral bias in the way that male *Xenophallus* approach different stimuli, and also if this bias is at all affected by male gonopodial morph type.

Statistical Analyses

To determine if these fish show a bias in behavioral handedness, we followed the statistical approach of Torres-Dowdall et al. (2019). This required us to first calculate a laterality index (LI), which we used as a measure of the degree to which an individual shows a bias in right- or left-handed detours. We calculated this metric as follows:

$$LI = \frac{\text{Detour Right} - \text{Detour Left}}{\text{Detour Right} + \text{Detour Left}} * (100)$$

Positive LI values indicate a right-handed detour bias, consistent with a preferred use of the left eye to view the stimulus. Negative LI values indicate a left-handed detour bias, consistent with a preferred use of the right eye to see the stimulus. A laterality score statistically indistinguishable from “0” indicates no bias in lateralized behavior. We calculated a mean laterality score for each treatment for both left morph and right morph males, resulting in eight tests. We analyzed these results using a two-tailed, one-sample *t*-test to determine if the observed LI in each treatment showed a significant departure from zero. All statistical tests were run in program R (R Core Team, 2020; version 3.6.3).

RESULTS

Detour Tests

Xenophallus shows clear behavioral handedness in detour decisions when approaching various stimuli (Figure 4). Of the eight tests that we ran, six showed average LI scores that differed significantly from 0. Only the novel object treatment failed to elicit a significant response, which was true for both left morph (LI = -4.96, $t_{13} = 0.72$, $p = 0.49$) and right morph (LI = 3.92, $t_{12} = 0.62$, $p = 0.54$) males. Left morph males responded to the potential mate stimulus and the predator stimulus completely opposite of the right morph males. Left morph males detoured left in response to potential mates (LI = -34.22, $t_{13} = 4.41$, $p < 0.001$) and in response to predators (LI = -33.11, $t_{13} = 7.39$, $p < 0.001$). In contrast, right morph males detoured right in response to potential mates (LI = 20.16, $t_{13} = 2.07$, $p = 0.05$) and predators (LI = 21.65, $t_{12} = 2.37$, $p = 0.03$). Finally, in response to a no-stimulus control, we found the interesting pattern that both left morph males (LI = -23.71, $t_{14} = 2.49$, $p = 0.03$) and right morph males (-24.73, $t_{14} = 2.35$, $p = 0.03$) preferentially detoured to the left, rather than approaching the control at random.

Male Morph Frequencies in the Wild

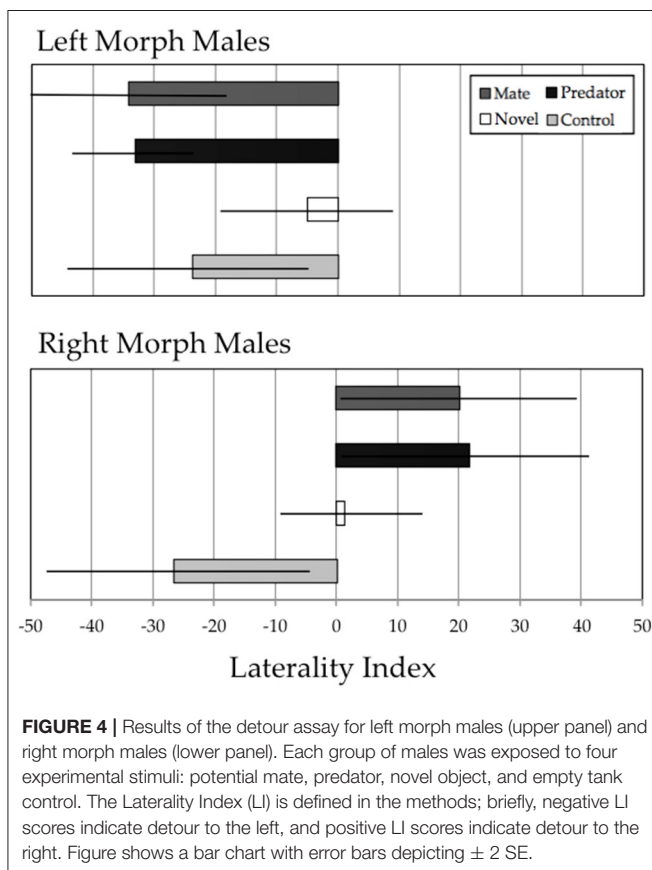
Of 14 populations of *Xenophallus* sampled between 1998 and 2019, almost all contained both left morph and right morph males (Figure 5; Table 1). In fact, we found no evidence that

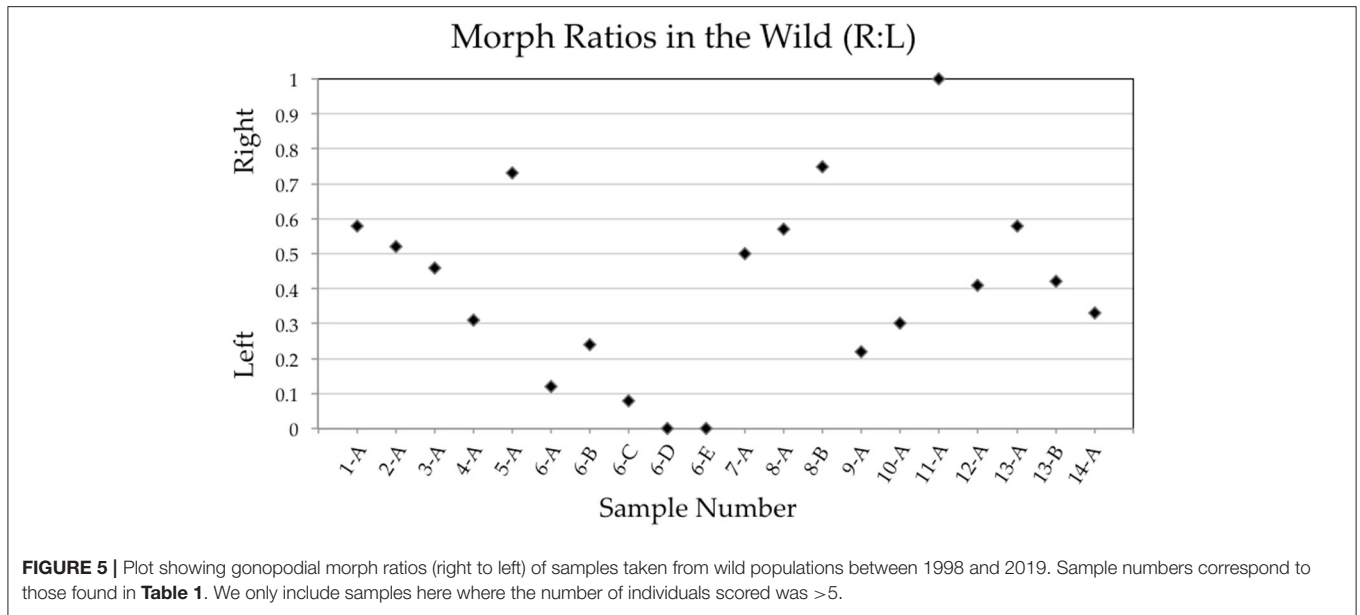
either male morph was fixed in a population where at least 5 males were sampled (see Table 1). This was true, regardless of collection locality, drainage, season of collection, or year of collection. The exception during our entire sampling were two samples taken at the La Palma site (sample 6-D, 6-E) that appeared to be fixed for the sinistral morph the last two times we sampled and one sample from Rio Chorros (sample 11-A) that appeared to be fixed for the dextral morph (Table 1). Moreover, we found considerable variation in the frequency of dextral and sinistral morphs among populations at the time they were surveyed, with some samples composed primarily of left morph males and others composed primarily of right morph males (Table 1). Interestingly, one location, Rio Corinto, was sampled at two different times with the frequency of male morphs shifting from a right bias when we first sampled in 2006 to a left bias when we later sampled in 2007.

DISCUSSION

Our study provides insight into the relationship between the anatomic asymmetry of the gonopodium and male behavior. It is perhaps not surprising to find that males approach potential mates in a non-random way—the gonopodium is used in copulation, and there is considerable evidence that the structural anatomy of the gonopodium in other poeciliids is important for successful sperm transfer (Langerhans, 2011). Specifically, in *Xenophallus* we found that males with gonopodia that terminate to the left approach females by detouring left, and the opposite was true for males with gonopodia that terminate to the right. Although we know little about how the gonopodium actually interacts with the female gonopore in *Xenophallus*, our results suggest that there may be some directionality to mating such that males with a particular morph might be more successful in mating on one side of the female than the other side. These results also set up the intriguing possibility that the success of males might depend to some extent on the frequency of each male morph in the population, with rare males having an advantage if females actively try to avoid forced copulations by more common males. Hence, this system may be well-suited for evaluating negative frequency dependent selection in the wild (Palmer, 1996), similar to the classic work on lateralized feeding on scales in cichlid fishes, where individuals with rare morphs had an advantage over their counterparts with the more common morph (Hori, 1993).

We also found that males detoured in a non-random way when evaluating predators. However, unlike previously published work which showed that some poeciliids evaluate predators and potential mates with opposite eyes (Torres-Dowdall et al., 2019), we found that *Xenophallus* males actually detour in the same direction in response to predators as they do to potential mates. Left morph males detour left in response to predators, and right morph males detour right in response to predators. These results are intriguing in two important ways. First, there appears to be an association between gonopodium morphology and predator inspection behavior. This is unexpected—there is





no *a priori* reason that gonopodium morphology should favor viewing predators from one direction over another. Rather, previous work has suggested that side-bias in inspection behavior in fishes may have evolved to allow prey species to preferentially use one eye, and one side of the brain, to gather and process information about predation risk. If that is true in *Xenophallus*, then our data indicate that predator inspection behavior is not fixed to one eye or the other, and it appears to be associated with gonopodium morphology. Second, our results are inconsistent with previous work that argued that fish use one eye to specialize in gathering information about potential mates and the opposite eye to gather information about predation risk (Langerhans, 2011). We found that *Xenophallus* males use the same eye for both. Hence, there appears to be no division of labor among eyes and brain processing that some authors have suggested in other species.

Two other interesting patterns emerged from our detour trails. First, we found that neither left morph nor right morph males showed a side bias when approaching a novel object. There was simply no preference. This is important because it shows that *Xenophallus* are not fixed in their detour behaviors irrespective of the stimulus present. In other words, it tells us that males are deliberate in their response to potential mates and predators. Second, we found that in our control tests, where there was no stimulus present, that both left morph and right morph males consistently detoured to the left. That is, when faced with a barrier, and nothing present to inspect, males more often went around that barrier on the left side. At face value, this is a somewhat puzzling result. Why should individuals all show a detour preference in the absence of a stimulus? Our result, however, is consistent with an intriguing hypothesis that in the absence of a target stimulus, individuals in social species might move preferentially to one side to avoid collisions with other individuals (Vallortigara and Rogers, 2005).

This so called “lateral locomotor bias” could result in social coordination resulting in the majority of individuals moving to the same side, even when that side is arbitrary. This type of lateralized social coordination has been found in a variety of other systems, including ants and bees (Frasnelli et al., 2012; Rogers et al., 2013), amphibians (Dadda et al., 2003), and fishes (Bisazza et al., 2000). In fact, a similar explanation is found for some lateralized human behaviors such as embracing, kissing, and cradling (Ocklenburg et al., 2018; Packheiser et al., 2019). Hence, our system with *Xenophallus* may also prove useful to test this more general hypothesis that social coordination can play a role in population-level lateralization.

Finally, our work might shed some light on the very fundamental question of why brain lateralization has evolved in so many vertebrate species. It is unclear why the gonopodium in *Xenophallus* is asymmetrical. It could simply have evolved as a randomly dimorphic trait. However, it appears that once this trait is present, it has potentially had an effect on lateralized behavior. We might imagine a scenario in which the evolution of anatomical asymmetries could lead to behavioral handedness, which in turn could lead to a specialization of the brain in processing information acquired from different sides of the body. Fishes have a general body form where the eyes are found on the sides of the head—not forward as in organisms with well-defined binocular vision—encouraging them to orient their body to one side or the other in order to obtain clear visual information. Hence, fishes, including systems like *Xenophallus*, are promising candidates for exploring different aspects of the origins of brain lateralization. Although future work will be necessary to evaluate these ideas, what is clear from our research is that there is a strong relationship between gonopodium morphology and lateralized behavior. Understanding the cause of this relationship may help reveal why so many forms of handedness exist in nature.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Materials**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The animal study was reviewed and approved by Brigham Young University Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

EJ and JJ conceived the idea for the study, designed the statistical analysis, and revised the manuscript in response to reviewer comments. EJ designed and built the test arena, collected the experimental data, and wrote the first draft of the manuscript. All authors reviewed and edited the manuscript, approved its final version, contributed to the preparation, research, writing of the manuscript, and were involved in the field collections.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2020.606856/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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