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Erik S. Johnson  
*Brigham Young University*

Jerald Johnson  
*Brigham Young University*

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# Why does handedness exist in bilaterally symmetrical organisms?

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## Erik S. Johnson, Jerald Johnson, Department of Biology

Over the past year I accomplished almost everything I outlined in my ORCA proposal. My project focused on why organisms display handedness and how this is maintained in wild populations over time.

I address this question in a tropical livebearing fish species that shows a unique form of morphological asymmetry and an unusual form of behavioral laterality. The livebearing fish *Xenophallus umbratilis* exhibits a mating morphology where the male gonopodium—a structure used to inseminate females—terminates with either a dextral or sinistral corkscrew. That is, males are either 'left handed' or 'right handed' with respect to their gonopodium. We think that this might be related to a phenomenon in which individuals show a lateral bias in eye use to approach different stimuli, a form of behavioral laterality, that in other vertebrates is linked to cerebral lateralization of the brain. In other words, it is possible that brain lateralization exists in fishes and is related to morphological handedness. But why does such handedness exist in the first place?

I first examined fish collections from the Monte L. Bean Life Science Museum. I found that populations of *Xenophallus* sampled over 20+ years vary in the ratio of right- to left-handed males. Moreover, this ratio appears to be dynamic as evidenced by our sampling of a single population over time wherein my adviser and I found an extreme shift in the ratio of left- to right-handed males over a relatively short period of time, from March to June in 2018. We also scored several of our museum populations and found that there is incredible variation in left to right ratios between wild populations. We test the hypothesis that the evolution and maintenance of handedness is controlled by negative frequency dependent selection. The idea is simple: traits are evolutionarily favored when they are rare, but disfavored when they become common. In *Xenophallus* the male gonopodium could be favored when rare if females actively try to avoid male harassment due to unwanted forced copulation attempts.

With these results in mind, I focused on three objectives:

1. Describe and evaluate variation in male gonopodium morph ratios among populations in the wild.
2. Test for behavioral lateralization based on eye preference and male-female interactions.
3. Test for a link between behavioral lateralization in females and female avoidance behavior.

### Detour Test

An individual was placed in a special arena and allowed to swim toward a partially obscured stimulus at the end of the tank. As the fish approaches it detours left or right of an obstacle to clearly see the stimulus. Individuals were allowed to move in the tank in both directions, making a lateral choice each time they move from one end to the other. Each fish was given 20 minutes in the tank and we recorded the number of right and left detours. We ran 20 female trials and 15 male trials.

### Female Avoidance Assay

If males are only able to successfully mate with females from one side, then females should position their bodies to the opposite side to avoid male mating attempts. In this assay, we test if females show such a bias when placed with sinistral males. A single female was placed in a round tank for 10 minutes with 5 randomly chosen sinistral males and the position of males relative to her body was recorded. We ran 18 trials. We analyzed these data using a paired ttest and a more conservative Wilcoxon signed-rank test. Both analyses yielded the same conclusion.

Our findings were all consistent with our hypotheses. We found the following:

- Xenophallus populations vary in the frequency of gonopodial morphs. Frequency of left handed morphs ranged from 0.11 to 0.79.
- Detour test. We found that males most frequently detoured to allow them to see the stimulus with their right eye. In contrast, females most often detoured to allow them to see the stimulus with their left eye.
- Female Avoidance Assay. Females consistently kept left-handed males in a position where they were forced to approach from the left side of the female (two-tailed t test:  $p < 0.001$ ,  $df = 17$ ; Wilcoxon signed-rank test significant at  $p < 0.05$ ).
- Females who avoided males by keeping them to the left of their body also tended to detour in a way that allowed them to see the stimulus with their left eye.

Although the data we collected is consistent with morphological asymmetry being driven by negative frequency depend selection, we will continue to test this hypotheses. In the future we will: (1) Repeat assays using right-handed males; (2) track frequency of gonopodial morphs over time at multiple locations; (3) run detour tests for multiple stimuli to determine if behavioral lateralization changes as a function of stimulus (potential mates, predators, food, novel); (4) using genomic approaches, determine the genetic basis for gonopodial morphs and behavioral phenotypes; and (5) determine if cerebral lateralization exists in these fishes, and evaluate if/how costs and benefits of morphological handedness affects brain lateralization.

I presented my results at the 50th Annual Desert Fishes Society Meeting in November 2018. My poster was awarded the Best Student Poster Award.

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