REGULAR ARTICLE

JOURNAL OF **FISH** BIOLOGY

Does visual or mechanosensory disruption influence risk assessment in coral reef fishes: a preliminary study

Riley Bowers | Nicholas Burgos | Ryan Meshanko | Sapna Thaker | Allison Yan | Sean O'Fallon | Daniel T. Blumstein

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California, USA

Correspondence
Daniel T. Blumstein, Department of Ecology and Evolutionary Biology, 621 Young Drive South, University of California, Los Angeles, CA 90095-1606, USA.
Email: marmots@ucla.edu

Abstract

Interpreting and responding to environmental cues from different modalities has survival value. In fish, the role of multimodal perception has been studied in regard to both foraging and risk assessment, with modalities including vision, olfaction, and mechanoreception via lateral lines. We studied reef fish boldness by placing novel objects that obstructed vision, lateral line use, or both into a coral reef environment with native algal samples inside, and then quantifying exploration as a function of obstruction type and as a function of functional diet groups (herbivores, omnivores, carnivores). Fish were more neophobic with more sensory obstructions, displaying longer latencies to visitation across all novel objects. Fish were also less likely to pass by objects that blocked multiple perceptual modalities. Across diets, there is early evidence that different functional groups respond differently to novelty. However, this conclusion requires further study. Overall, our findings provide key insights into perceptual ecology. In turn, this knowledge can be applied to understanding the effects of novel anthropogenic modifications in the marine environment. Such modifications may include positive activities like the construction of substrates to restore coral reefs, coral transplantation to restore reefs, as well as the negative consequences of construction and pollution.

KEYWORDS
behavior, boldness, fish, multimodal perception, novelty

1 | INTRODUCTION

Animals perceive the world through a variety of sensory systems. Multimodal perception provides an animal with more information about its environment, influencing necessary behaviors such as predation risk assessment (Lombardo et al., 2008), foraging (Kulahci et al., 2008), and social behavior (Butler & Maruska, 2016; Narins

et al., 2005). When multimodal perception occurs, there can be equivalent, enhanced, or antagonistic responses to being exposed to different modalities (Munoz & Blumstein, 2012). For instance, in Western mosquitofish (*Gambusia affinis*), chemical signaling associated with predators increases inspection distances, but the addition of a visual cue indicating predator movement increases inspection distances even further (Smith & Belk, 2001).

Fish use visual, olfactory, and lateral line systems to assess risk and identify food (Bleckmann, 1986; Guthrie, 1986; Kelley, 2008). Some species of teleost, such as zebrafish (*Danio rerio*), rely primarily

---

on vision when engaging in foraging behavior (Howe et al., 2018), but there is high variation in the morphology and sensitivity of coral reef visual systems based on ecological niche (Collin & Pettigrew, 1988a, 1988b; Cortesi et al., 2020). Despite this, studies have confirmed the ability to discriminate between colors in multiple reef species, and both herbivores and carnivores use their vision to forage and find palatable foods (Cheney et al., 2013; Miller & Pawlik, 2013; Siebeck et al., 2008). Many marine species also use visual cues in predator risk assessment, and they are often paired with olfactory or acoustic cues (Davidson et al., 2024; McCormick & Manassa, 2008).

While vision is a key sensory input for many behaviors, lateral line mechanoreception is also essential for foraging, especially when other sensory cues are absent (Hanke & Bleckmann, 2004; Schwalbe et al., 2016). Research on the omnivorous red drum (*Sciaenops ocellatus*) showed that while juveniles could hunt in complete darkness or with their olfactory systems inhibited, interfering with their lateral line system completely stopped prey-seeking behavior suggesting that foraging was most strongly influenced by lateral line mechanoreception (Liao & Chang, 2003). The lateral line also plays a major role in predator avoidance. Zebrafish larvae primarily used lateral lines to escape predators, while adult fish relied more on vision (McHenry et al., 2009). Given the importance of vision and lateral line perception for fish behavior, we conducted a multimodal study of these perceptual modalities to understand their combined effects.

Studies have been conducted on multimodal perception in fish, revealing how fish with different diets use multiple senses in combination. Multiple species of freshwater predatory fish rely primarily on vision to find prey, with lateral line mechanoreception aiding visual cues to inform striking distance or orientation (Abboud & Coombs, 2000; New, 2002). Studies on zooplanktivorous fish, including the marine piper (*Hyporhamphus ihi*), have shown that lateral line information complements visual information when detecting prey, especially in low light conditions (Montgomery, 1989; Saunders & Montgomery, 1985). Regarding risk assessment, the omnivorous orange clownfish (*Amphiprion percula*) uses mechanosensory cues in addition to visual and chemical cues to socially learn predator recognition from conspecifics, and this learning still occurs when visual and chemical cues are absent (Manassa et al., 2013). There is evidence supporting that multimodality is equally as important for herbivores, such as the Ambon damselfish (*Pomacentrus amboinensis*), which uses multimodal signaling to communicate with conspecific competitors and reduces these cues when predators are present (Davidson et al., 2024). Integrating sources of multimodal information has significant effects on fishes' boldness around new habitats or objects, especially when various sensory cues are available.

Boldness has been defined as the willingness to explore a novel environment or object (Wilson et al., 1994; Wright et al., 2006). This in turn impacts the survival of animals and their ability to carry out essential functions such as feeding (Dingemanse et al., 2004). Prior research on the response to novel stimuli and risk assessment in fish has examined several modalities such as visual (Hamilton, 2018; Wallace & Hofmann, 2021), olfactory (Valentinčič, 2004), and acoustic (Huijbers et al., 2012; Leis et al., 2002). While some novelty studies

test mechanosensory stimuli (Dunlop & Laming, 2005), we are not aware of prior multimodal novelty experiments building this into their design.

The structure of novel objects can inherently obstruct both visual and mechanosensory input in fish, influencing their willingness to explore a novel object. We therefore conducted a novelty experiment examining how interference with multimodal perception affects reef fish boldness in Mo'orea, French Polynesia. We used a community level approach, looking at the main effects of our treatments on different fish functional groups defined by diet. Based on the importance of visual and lateral line modalities for both foraging (Coombs & Patton, 2009; Montgomery, 1989; New, 2002; Newport et al., 2021) and predator avoidance (Manassa et al., 2013; Stewart et al., 2014), we predicted that fish across functional groups would be most neophobic around objects that obstructed both modalities, followed by objects that obstructed one modality. Multimodal cues provide information to make more accurate decisions and enhanced responses that aid survival, which is relevant to fish behaviors among all trophic levels.

Understanding the effects of novel objects on multimodal perception is important to assess the impact of anthropogenic changes to a marine environment, such as the construction of offshore wind turbines (Gill et al., 2020) and restorative artificial reefs (Koeck et al., 2013). The nature of these objects can obstruct different sensory modalities under water, and understanding how such obstructions impact fish behavior can help guide the construction of them to maximize recruitment and retention of all functional groups.

2 | METHODS

2.1 | Ethics statement

The care and use of experimental animals complied with French Polynesian and United States of America animal welfare laws, guidelines, and policies as approved by Convention d'accueil number 130005820 issued on November 24, 2023, as well as the UCLA IACUC protocol number 2000-147 approved on November 28, 2023.

2.2 | Study location

We conducted our study on the fringing reef of the north shore in Maharepa off Mo'orea, French Polynesia (17°29′7″S, 149°47′56″W) between January 25, 2024 and February 4, 2024 (we planned additional work, but a series of cyclone warnings and storms formally closed the waters for all activities, including research, for 2 weeks).

2.3 | Experimental methods

Inspired by Bednekoff and Blumstein (2009), we constructed 30 × 30 × 30 cm boxes made with PVC pipes. The walls consisted of

either black opaque plastic to multimodally block cues of both sight and lateral line mechanosensation, or clear acrylic to unimodally block only lateral lines (Figure 1a,b). Three of the sides in the black and clear treatments were "walled," leaving one possible entrance on the planar axis. While entry into a box from above was a possibility, this was not observed during our study. A box with only the PVC frame and no walls was also deployed to control for box effects, as well as a no-stimulus control (Figure 1c,d). Since this was originally conceived as a foraging experiment intended for herbivorous fish, each box and our no-stimulus control contained 10 g (wet weight; see Keeley et al., 2015 for methods) of *Padina boryana*, a highly favored macroalgae (Keeley et al., 2015; Mantyka & Bellwood, 2007). *P. boryana* was collected from the waters off the Gump Research Station, where it was common, about 1.5 km from our study site, where it was rare. Olfactory responses to algae were not factored into this experiment, but no treatments were watertight or prevented diffusion, so there should not be any difference between them in that regard. Boxes were weighted with dive weights to keep them submerged (all were deployed in 1–2.5 m water) and prevent their movement. The four treatments were deployed in alternating order, approximately 10 m from each other in a line across the reef flat. Exact placement sites were selected haphazardly on a day-to-day basis based on accessibility given the water conditions and distance from other sites because we believed distribution of species was relatively even across our site.

Our experiment was conducted every other day for a total of six experimental days. A "session" was defined as a series of deployments with all experimental conditions set out together within the same hour. A session contained either eight or 12 experiments depending on water conditions, with equal numbers of deployments per treatment. All but 1 day had a single session per day. The single day with two sessions had a 6-h gap between deployments. Thus, we had a total of seven sessions. All deployments occurred when Beaufort wind scale readings were ≤3. A Vemont or Crosstour CT 1080P action camera was positioned 0.7 m (Sura et al., 2021) from the front wall of each box to observe and quantify fish behavior. Between 45 min and 1.5 h of footage was recorded per deployment, during which time observers were not present around the boxes so as not to impact fish activity. Following the deployment period, observers collected the boxes and cameras.

2.4 | Video scoring

We counted the number of passes ($N = 1953$) and rare visitations inside the box. Passes were defined as a fish swimming within 25 cm on any side (front, back, left, or right) of the centrally-placed algae across all treatments. However, despite the added *P. boryana*, we observed minimal foraging. Visits were scored as repeats and not counted if a fish left the camera frame for less than 5 s before entering the field of view again. If a fish left for more than 5 s, a subsequent pass was scored again, since fish abundance at our site was high enough to infer that separate individuals were being observed. Observers ($N = 5$) were trained to accurately identify the fish to ensure consistency across observations. Treatments were done in the same general area throughout the course of the experiment. While habituation over time was a possibility, this was accounted for in our analysis by including session number as a covariate.

Each time we observed a pass, we identified the species and recorded the time of the pass. From this we calculated two variables: the latency to first pass and the pass rate (N passes/total time recorded). Passes near a frame are a measure of boldness because the boxes were a novel object within the fishes' habitat (Andersson et al., 2014; Michelena et al., 2008). While a larger sample size may allow data to be analyzed on a species-specific basis, our data were suitable only to focus functional groups.
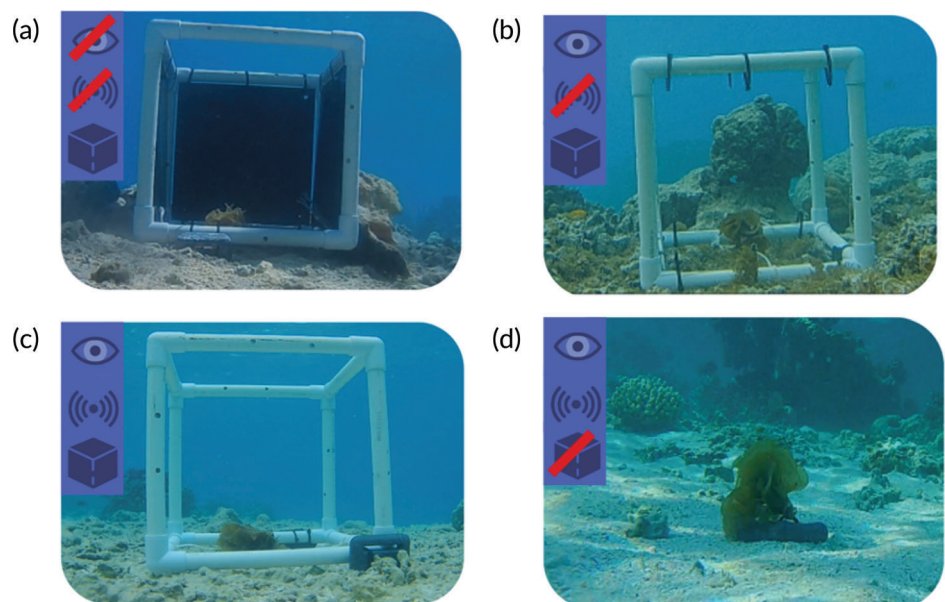

FIGURE 1 Images of treatments with decreasing levels of obstruction: (a) box with opaque walls to obstruct vision and lateral lines; (b) box with clear walls to obstruct lateral lines; (c) frame only to control for box effects; (d) algae only (control).

We used FishBase to categorize the dietary habits of each fish species as herbivorous, omnivorous, carnivorous, or corallivorous (Froese & Pauly, 2023). These functional groups were selected based on the observations of fish species which visited our boxes. We excluded corallivores from subsequent analysis due to limited observations.

Finally, we noted whether each video had a full unobstructed view of the box, whether it was partially obstructed, or whether because of box movement or camera displacement it was mostly obstructed (Figure S1). We removed videos where the view of the box was mostly or fully obstructed from analysis. If a box moved during the video so that the view became mostly or fully obstructed, analysis was stopped at the point where the box was no longer in view and the video length was reduced to reflect only the scorable video time.

2.5 | Statistical analysis

To explain variation in both latency to first pass and pass rate, we fitted generalized linear models with a negative binomial distribution as a function of diet, treatment, observation session (to account for changes in tolerance over time), degree of box obstruction, video length (to account for the opportunity for longer latencies, all videos were ca. 1 h long), and interaction between diet and treatment. We checked that residuals were normally distributed with the use of the check_model function in the "performance" package in R, as well as visually analyzing Q-Q plots. For both models, observation session and the interaction between diet and treatment were not significant, so we removed them from the following analysis. For significant variables, we compared groups with Bonferroni contrasts and visualized these with box plots. All statistical analyses were conducted in R 4.3.2 (R Core Team, 2023) and R studio (RStudio Team, 2023), using the packages dplyr (Wickham et al., 2023), readr (Wickham, Hester, & Bryan, 2024), performance (Lüdecke et al., 2021), multcomp (Hothorn et al., 2023), and ggplot2 (Wickham, 2024). In all cases, we set our alpha to 0.05.

3 | RESULTS

Our final dataset consisted of 1948 passes recorded over 62 scorable deployments, which created 80 h of scorable video: 855 of these were by carnivores, 346 were by omnivores, and 736 were by herbivores. In total we observed 46 different species pass close to our novel objects (Table 1). We also calculated an accumulation curve, which allowed us to be confident that we were surveying a representative sample of the typical fish species residing in the area (Figure S2).

3.1 | Latency to pass

After controlling for significant variation explained by video length and the level of box obstruction, we found significant differences in the latency to first pass as a function of treatment, but not diet functional group (Table 2a). All of our experimental treatments (frame, clear, and black) had significantly different latencies compared to our control, but they did not differ from each other. Specifically, all of these treatments had longer latencies when compared to the control (Table 3a and Figure 2a).

3.2 | Pass rate

As with the latency to first visit, we found different responses in pass rate as a function of treatment after video length and level of box obstruction were controlled for. However, pass rate also differed as a function of diet functional group (Table 2b). Across treatments, the black treatment had a significantly lower pass rate than the control (Table 3b, Figure 2b). Also, the pass rate of omnivores was significantly different from both carnivores and herbivores. Carnivores and herbivores had higher pass rates than omnivores, but were not significantly different from each other (Table 3c and Figure 2c). Although diet and treatment had significant effects on pass rate, these main effects were independent of each other as the interaction between diet and treatment was not significant.

4 | DISCUSSION

The presence of any novel object resulted in longer latency to visit, regardless of sensory obstruction. All treatments, including the frame treatment, which we assumed obstructed no modalities and controlled for a novel structure, had significantly longer latencies, suggesting that novel objects in general are associated with greater neophobia in fish. Still, only the black treatment, which blocked both visual and mechanosensory stimuli, had a significantly different pass rate from the control. This lower pass rate for the black treatment suggests that multimodal obstructions in particular are associated with greater neophobia. This is consistent with our hypothesis and existing literature because visual and mechanosensory cues are essential to behaviors such as hunting, predator avoidance, and social interactions (Montgomery, 1989; Stewart et al., 2013). Access to multimodal cues facilitates accuracy and learning in these behaviors (Ålund et al., 2022; Manassa et al., 2013; Ward & Mehner, 2010), and we found that the obstruction of these cues in combination influenced the boldness to investigate novel objects. Although we have this evidence that multimodality is important, we are unable to conclude which modality (vision or mechanoreception) is more important in explaining variation in boldness. In regard to predator evasion, some literature supports that fish are predisposed towards using visual cues versus other stimuli (Utne-Palm, 2001). Other studies, however, have found that mechanosensory stimuli allow for faster evasion in response to close encounters with predators (Stewart et al., 2013) and are therefore just as essential. Our study had one test for the unimodal mechanosensory obstruction, but there were no treatments testing for a unimodal visual obstruction. Future studies should evaluate different modalities

TABLE 1 Fish species and families observed passing our novel objects.

Fish species (common name)	Family	Diet functional group	Observations
Abudefduf septemfasciatus (banded sergeant)	Pomacentridae	Omnivore	1
Abudefduf sexfasciatus (scissortail sergeant)	Pomacentridae	Omnivore	5
Arothron meleagris (guineafowl puffer)	Tetraodontidae	Omnivore	2
Balistapus undulatus (orange-lined triggerfish)	Balistidae	Omnivore	95
Canthigaster bennetti (Bennett's puffer)	Tetraodontidae	Omnivore	2
Canthigaster solandri (spotted sharpnose puffer)	Tetraodontidae	Omnivore	2
Caranx melampygus (bluefin trevally)	Carangidae	Carnivore	19
Centropyge bispinosus (dusky angelfish)	Pomacanthidae	Herbivore	5
Centropyge flavissima (lemonpeel angelfish)	Pomacanthidae	Herbivore	22
Chaetodon auriga (threadfin butterflyfish)	Chaetodontidae	Omnivore	10
Chaetodon citrinellus (speckled butterflyfish)	Chaetodontidae	Omnivore	31
Chaetodon ephippium (saddle butterflyfish)	Chaetodontidae	Omnivore	1
Chaetodon lunula (raccoon butterflyfish)	Chaetodontidae	Omnivore	50
Chaetodon lunulatus (redfin butterflyfish)[a]	Chaetodontidae	Corallivore[a]	9
Chaetodon ornatissimus (ornate butterflyfish)[a]	Chaetodontidae	Corallivore[a]	1
Chaetodon reticulatus (mailed butterflyfish)[a]	Chaetodontidae	Corallivore[a]	1
Chaetodon ulietensis (Pacific double-saddle butterflyfish)	Chaetodontidae	Omnivore	1
Chaetodon vagabundus (vagabond butterflyfish)	Chaetodontidae	Omnivore	18
Chlorurus sordidus (bullethead parrotfish)	Scaridae	Herbivore	60
Coris centralis (Central Pacific coris)	Labridae	Carnivore	1
Ctenochaetus striatus (striated surgeonfish)	Acanthuridae	Omnivore	126
Epinephelus merra	Serranidae	Carnivore	1
Fistularia commersonii (bluespotted cornetfish)	Fistulariidae	Carnivore	9
Gomphosus varius (bird wrasse)	Labridae	Carnivore	5
Halichoeres hortulanus (checkerboard wrasse)	Labridae	Carnivore	11
Halichoeres trimaculatus (threespot wrasse)	Labridae	Carnivore	347
Juvenile parrotfish[b]	Scaridae	Herbivore	571
Mulloidichthys flavolineatus (yellowstripe goatfish)	Mullidae	Carnivore	83
Parapercis millepunctata (black-dotted sand perch)	Pinguipedidae	Carnivore	1
Parupeneus barberinus (dash-and-dot goatfish)	Mullidae	Carnivore	1
Parupeneus cyclostomus (gold-saddle goatfish)	Mullidae	Carnivore	6
Parupeneus multifasciatus (manybar goatfish)	Mullidae	Carnivore	118
Pygoplites diacanthus (royal angelfish)	Pomacanthidae	Carnivore	37
Scarus forsteni (whitespot parrotfish)	Scaridae	Herbivore	5
Scarus ghobban	Scaridae	Herbivore	1
Scarus oviceps (dark-capped parrotfish)	Scaridae	Herbivore	5
Scarus psittacus (common parrotfish)	Scaridae	Herbivore	3
Scarus rubroviolaceus (ember parrotfish)	Scaridae	Herbivore	1
Scorpaenopsis papuensis (Papuan scorpionfish)	Scorpaenidae	Carnivore	1
Stegastes nigricans (dusky farmerfish)	Pomacentridae	Omnivore	2
Stethojulis bandanensis (red shoulder wrasse)	Labridae	Carnivore	103
Synodus variegatus (variegated lizardfish)	Synodontidae	Carnivore	1
Thalassoma hardwicke (sixbar wrasse)	Labriade	Carnivore	16
Zanclus cornutus (Moorish idol)	Zanclidae	Carnivore	95
Zebrasoma scopas (twotone tang)	Acanthuridae	Herbivore	63

Note: We classified diet functional groups by using Fish Base (Froese & Pauly, 2023). Observations were quantified as a sum total of all passes recorded across all videos.

[a]Corallivorous fish were excluded from analysis due to limited observations.

[b]Aside from *Chlorus sordidus*, specific juvenile parrotfish species were indistinguishable and were thus considered as a single taxon when analyzing functional groups.

(a) Latency to first pass

	df	Deviance	Residual *df*	Residual deviation	*p* value
Null			130	174.47	
Diet	2	1.915	128	172.56	0.418
Treatment	3	9.728	125	162.83	0.031
Level of obstruction	1	4.196	124	158.63	0.051
Video length	1	12.104	123	146.53	<0.001
Session	6	8.061	117	138.47	0.291
Diet:treatment	6	3.413	111	135.06	0.795

(b) Pass rate

	df	Deviance	Residual *df*	Residual deviation	*p* value
Null			185	97.969	
Diet	2	3.201	183	94.768	0.002
Treatment	3	3.723	180	91.045	0.002
Level of obstruction	1	1.263	179	89.783	0.024
Video length	1	0.340	178	89.443	0.242
Session	6	2.757	172	86.686	0.085
Diet:treatment	6	1.237	166	85.449	0.546

TABLE 2 Results from the generalized linear models explaining variation in (a) latency to first pass, and (b) pass rate.

TABLE 3 Results of Bonferroni comparisons for significant predictors in fitted latency and pass rate models.

(a) Treatment contrasts for latency model

	Estimate	Standard error	z value	p value
Frame–control	0.842	0.257	3.268	0.006
Clear–control	0.795	0.267	2.975	0.018
Black–control	1.218	0.291	4.189	<0.001
Clear–frame	−0.046	0.282	−0.164	1.000
Black–frame	0.376	0.297	1.266	1.000
Black–clear	0.422	0.306	1.379	1.000

(b) Treatment contrasts for pass rate model

	Estimate	Standard error	z value	p value
Frame–control	−0.663	0.330	−2.011	0.266
Clear–control	−0.645	0.332	−1.944	0.312
Black–control	−1.365	0.403	−3.386	0.004
Clear–frame	0.019	0.372	0.051	1.000
Black–frame	−0.702	0.434	−1.618	0.634
Black–clear	−0.721	0.434	−1.659	0.582

(c) Diet contrasts for pass rate model

	Estimate	Standard error	z value	p value
Omnivores–herbivores	−0.807	0.354	−2.278	0.068
Carnivores–herbivores	0.170	0.278	0.611	1.000
Carnivores–omnivores	0.977	0.347	2.818	0.015

in comparison with each other because fish may prioritize certain novel habitats based on the cues available, for example evaluating a clear treatment obstructing only lateral line sensing compared to a treatment obstructing only vision, but that still allows water to flow through.

One caveat to our study was that we did not account for the effects of olfaction in our treatment design. It is known that fish use olfaction as a guide for many different behaviors (Kasumyan, 2004). For instance, salmon detect their specific breeding ground using olfactory cues (Døving et al., 1985; Hasler & Scholz, 1983; Wisby & Hasler, 1954). Olfaction could have played a role in the appeal of the bait because our boxes were open, therefore allowing for olfactory cues to spread. No treatments were watertight, however, so we hypothesize this did not have an effect on our analysis because each treatment equally allowed the diffusion of chemicals. Thus, our study design was limited because we did not have a way to measure the number of olfactory cues that were emitted by the depoloyed *P. boryana*. In turn, we were unable to determine if olfactory cues had any effect on the risk assessment and foraging behavior of different functional groups. While this was originally designed as a foraging experiment and one might expect olfactory cues to influence herbivore or omnivore behavior, we do not believe this biased our results because it did not result in herbivores foraging on the bait. In the future, studies may look into how olfaction is weighed in multimodal perceptual decisions for fishes in different dietary functional groups.

In addition to evidence that fish respond to differences in the modality of obstruction, our study also provides early evidence that different functional diet groups respond differently to the presence of novel objects. Specifically, carnivores had significantly higher pass rates when compared to omnivores, suggesting carnivores were more
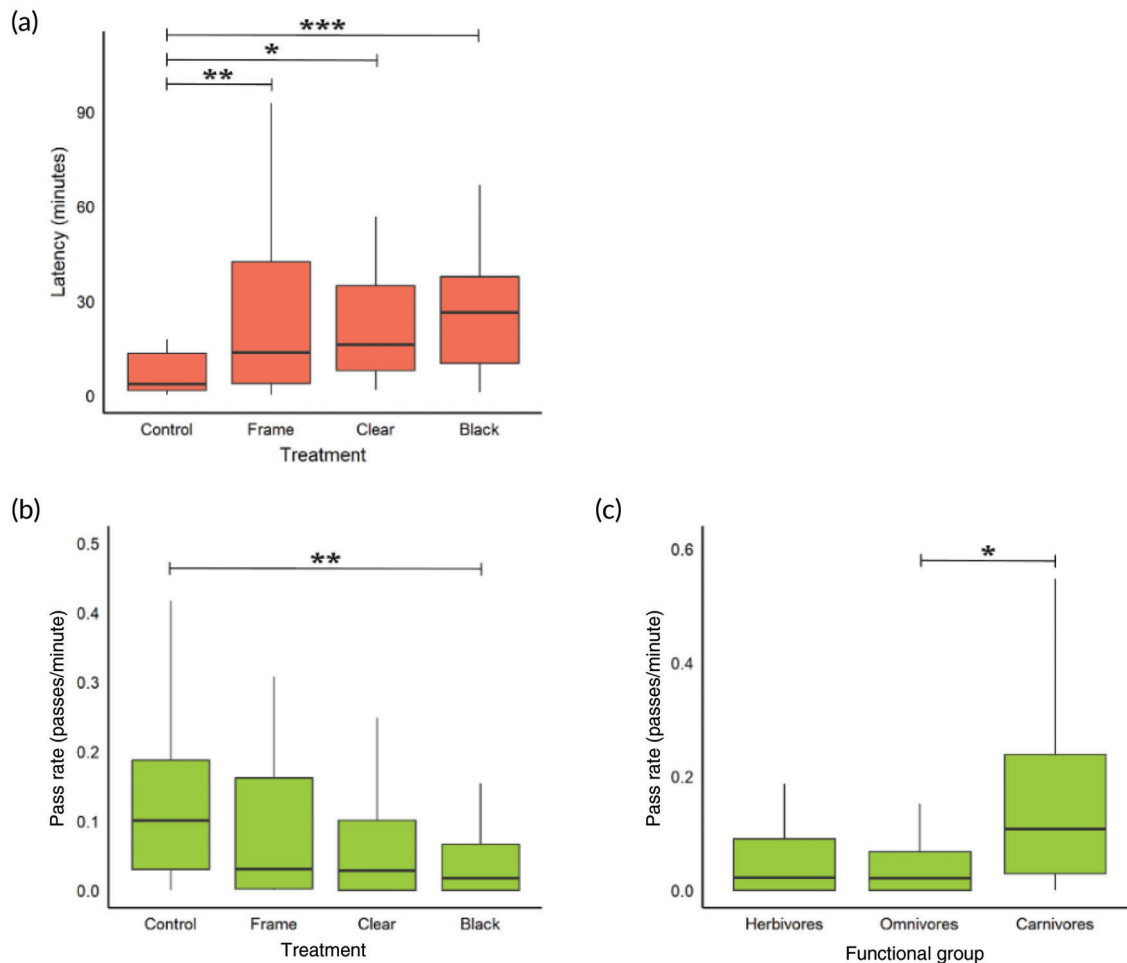
FIGURE 2 Boxplots for (a) latency by treatment, (b) pass rate by treatment, and (c) pass rate by diet. The black treatment had opaque walls, obstructing both sight and lateral line mechanosensation, the clear treatment had clear walls, obstructing only lateral line mechanosensation, the frame treatment had no walls and only PVC frames, and the control consisted of only algae. Bars indicate groups that are significantly different from each other. Levels of significant differences (p <0.05, <0.01, and <0.001) are denoted by *, **, and *** respectively.

likely to visit and less neophobic around novel objects compared to omnivores. Many species of fish and aquatic prey are documented to use underwater structure as a means of refuge to hide from predators (Caley & St John, 1996; Lehtiniemi, 2005; Persson, 1993). Thus, after a period of initial neophobia (latency to visit), carnivorous fish may be attracted to these possible refugia as a means of hunting prey as well as hiding from even larger predators. There were no other differences observed between functional groups so more research is needed to further evaluate the differences in neophobic behavior among diet functional groups. Importantly, the reef fish across functional groups of our study site were similar in size and habitat so these fish at similar trophic levels may be facing similar pressures regarding predation and competition, regardless of diet (Crane & Ferrari, 2017).

Considering the limited differences between functional groups, analysis on a finer scale may be required to further understand differences in neophobia. While similar studies have measured boldness on a functional group scale (Rhoades et al., 2019), others have looked at species level differences in boldness and how they influence different species' abilities to disperse and colonize new habitat

(Rehage & Sih, 2004). Furthermore, many studies have found individual variation of boldness within taxa (Ward et al., 2004; Wilson & Stevens, 2005). One study examining boldness and risk-taking behavior of juvenile bluegill sunfish (*Lepomis macrochirus*) found that individual-level differences could impact decisions to explore novel objects or take risks (Wilson & Godin, 2009). Thus, even species-level analysis itself may be inadequate to fully explain fish responses to multimodal cues from novel objects. Since our average sample size per fish species was too small to permit detailed study, we opted to focus on the functional group level instead. This was a relatively short study, limited both by the duration of our stay in the South Pacific and by inclement tropical weather during much of the expedition. Longer studies would help increase sample size and allow for analysis on smaller scales.

Our study provides new insights about the effects of novel objects on multimodal perception and provides a groundwork for future research that can integrate sensory perception to understand how novel structures influence marine environments. This knowledge will help us understand the impact of novel anthropogenic

infrastructure that includes physical objects such as breakwaters, pilings, and aquaculture poles/cages that are now changing many shallow water marine systems (Bulleri & Chapman, 2010). As noted by Gill et al. (2020), contemporary novel structures, such as offshore wind farms, change the sensory environment by producing alternative water currents, wind wake, and also emitting electromagnetic fields. Using a multimodal sensory approach to analyze response to anthropogenic structures can be important to understand the differential effects of these novel structures, and understanding the impacts at the level of functional groups can be important for understanding how physically modified environments may change fish diet and community structure.

Moreover, this form of analysis is important for predicting potential changes in community structure following the introduction of novel objects during restoration efforts. For instance, the transplant of nursery-hatched coral onto a man-made frame to create artificial reefs has been used to rebuild and revitalize habitats that have been destroyed or degraded by human activity (Ammar, 2009; Epstein et al., 2003). Prior work has shown different responses to restored reefs. Koeck et al. (2013) found that white seabream (*Diplodus sargus*) fed mainly during the day on natural reefs and mainly at night on artificial reefs. Another study conducted by Døving et al. (2006) found that five-lined cardinalfish (*Cheilodipterus quinquelineatus*) preferred the scent of artificial reef sites that had been previously occupied by conspecifics to the scent of similar reefs not occupied by conspecifics. Thus, it is important to understand how perceptual details of artificial reef construction may affect the behavior of colonizing fish, and studying the response of fishes to novel objects is a first step towards this understanding.

AUTHOR CONTRIBUTIONS

CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code to reproduce these analyses are available at OSF: osf.io/b2mha.

ORCID

Daniel T. Blumstein https://orcid.org/0000-0001-5793-9244

REFERENCES

Abboud, J. A., & Coombs, S. (2000). Mechanosensory-based orientation to elevated prey by a benthic fish. *Marine & Freshwater Behaviour & Physiology*, 33(4), 261–279. https://doi.org/10.1080/10236240009387097

Ålund, M., Harper, B., Kjærnested, S., Ohl, J. E., Phillips, J. G., Sattler, J., ... Keagy, J. (2022). Sensory environment affects Icelandic threespine stickleback's anti-predator escape behaviour. *Proceedings of the Royal Society B*, 289(1972), 20220044. https://doi.org/10.1098/rspb.2022.0044

Ammar, M. S. A. (2009). Coral reef restoration and artificial reef management, future and economic. *The Open Environmental Engineering Journal*, 2, 37–49. https://doi.org/10.2174/1874829500902010037

Andersson, A., Laikre, L., & Bergvall, U. A. (2014). Two shades of boldness: Novel object and anti-predator behavior reflect different personality dimensions in domestic rabbits. *Journal of Ethology*, 32, 123–136. https://doi.org/10.1007/s10164-014-0401-9

Bednekoff, P. A., & Blumstein, D. T. (2009). Peripheral obstructions influence marmot vigilance: Integrating observational and experimental results. *Behavioral Ecology*, 20(5), 1111–1117. https://doi.org/10.1093/beheco/arp104

Bleckmann, H. (1986). Role of the lateral line in fish behaviour. In T. J. Pitcher (Ed.), *The behaviour of teleost fishes* (pp. 177–202). Springer. https://doi.org/10.1007/978-1-4684-8261-4_7

Bulleri, F., & Chapman, M. G. (2010). The introduction of coastal infrastructure as a driver of change in marine environments. *Journal of Applied Ecology*, 47(1), 26–35. https://doi.org/10.1111/j.1365-2664.2009.01751.x

Butler, J. M., & Maruska, K. P. (2016). Mechanosensory signaling as a potential mode of communication during social interactions in fishes. *Journal of Experimental Biology*, 219(18), 2781–2789. https://doi.org/10.1242/jeb.133801

Caley, M. J., & St John, J. (1996). Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology*, 65(4), 414–428. https://doi.org/10.2307/5777

Cheney, K. L., Newport, C., McClure, E. C., & Marshall, N. J. (2013). Colour vision and response bias in a coral reef fish. *Journal of Experimental Biology*, 216(15), 2967–2973. https://doi.org/10.1242/jeb.087932

Collin, S. P., & Pettigrew, J. D. (1988a). Retinal topography in reef teleosts: I. Some species with well-developed areae but poorly-developed streaks. *Brain, Behavior and Evolution*, 31(5), 269–282.

Collin, S. P., & Pettigrew, J. D. (1988b). Retinal topography in reef teleosts: II. Some species with prominent horizontal streaks and high-density areae. *Brain, Behavior and Evolution*, 31(5), 283–295.

Coombs, S., & Patton, P. (2009). Lateral line stimulation patterns and prey orienting behavior in the Lake Michigan mottled sculpin (*Cottus bairdi*). *Journal of Comparative Physiology A*, 195, 279–297. https://doi.org/10.1007/s00359-008-0405-4

Cortesi, F., Mitchell, L. J., Tettamanti, V., Fogg, L. G., de Busserolles, F., Cheney, K. L., & Marshall, N. J. (2020). Visual system diversity in coral reef fishes. In *Seminars in Cell & Developmental Biology* (Vol. 106, pp. 31–42). Academic Press.

Crane, A. L., & Ferrari, M. C. (2017). Patterns of predator neophobia: A meta-analytic review. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1861), 20170583. https://doi.org/10.1098/rspb.2017.0583

Davidson, I. K., Williams, B., Stratford, J. E., Chapuis, L., Simpson, S. D., & Radford, A. N. (2024). Context-dependent multimodal behaviour in a coral reef fish. *Royal Society Open Science*, *11*(5), 240151. https://doi.org/10.1098/rsos.240151

Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *271*(1541), 847–852. https://doi.org/10.1098/rspb.2004.2680

Døving, K. B., Stabell, O. B., Östlund-Nilsson, S., & Fisher, R. (2006). Site fidelity and homing in tropical coral reef cardinalfish: Are they using olfactory cues? *Chemical Senses*, *31*(3), 265–272. https://doi.org/10.1093/chemse/bjj028

Døving, K. B., Westerberg, H., & Johnsen, P. B. (1985). Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*(10), 1658–1667. https://doi.org/10.1139/f85-207

Dunlop, R., & Laming, P. (2005). Mechanoreceptive and nociceptive responses in the central nervous system of goldfish (*Carassius auratus*) and trout (*Oncorhynchus mykiss*). *The Journal of Pain*, *6*(9), 561–568. https://doi.org/10.1016/j.jpain.2005.02.010

Epstein, N., Bak, R. P. M., & Rinkevich, B. (2003). Applying forest restoration principles to coral reef rehabilitation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *13*(5), 387–395. https://doi.org/10.1002/aqc.558

Froese, R., & Pauly, D. (Eds.). (2023). FishBase. World Wide Web electronic publication. Available at: http://www.fishbase.org/Search.php.

Gill, A. B., Degraer, S., Lipsky, A., Mavraki, N., Methratta, E., & Brabant, R. (2020). Setting the context for offshore wind development effects on fish and fisheries. *Oceanography*, *33*(4), 118–127.

Guthrie, D. M. (1986). Role of vision in fish behaviour. In T. J. Pitcher (Ed.), *The behaviour of teleost fishes* (pp. 75–113). Springer.

Hamilton, T. J. (2018). Object novelty and object location recognition memory in fish – Recent advances. In *Handbook of Object Novelty Recognition* (Vol. 27, pp. 151–161). Academic Press. https://doi.org/10.1016/b978-0-12-812012-5.00009-4

Hanke, W., & Bleckmann, H. (2004). The hydrodynamic trails of *Lepomis gibbosus* (Centrarchidae), *Colomesus psittacus* (Tetraodontidae) and *Thysochromis ansorgii* (Cichlidae) investigated with scanning particle image velocimetry. *Journal of Experimental Biology*, *207*(9), 1585–1596. https://doi.org/10.1242/jeb.00922

Hasler, A. D., & Scholz, A. T. (1983). *Olfactory imprinting and homing in salmon*. Springer-Verlag. https://doi.org/10.1007/978-3-642-82070-0

Hothorn, T., Bretz, F., & Westfall, P. (2023). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363.

Howe, H. B., McIntyre, P. B., & Wolman, M. A. (2018). Adult zebrafish primarily use vision to guide piscivorous foraging behavior. *Behavioural Processes*, *157*, 230–237. https://doi.org/10.1016/j.beproc.2018.10.005

Huijbers, C. M., Nagelkerken, I., Lössbroek, P. A. C., Schulten, I. E., Siegenthaler, A., Holderied, M. W., & Simpson, S. D. (2012). A test of the senses: Fish select novel habitats by responding to multiple cues. *Ecology*, *93*(1), 46–55. https://doi.org/10.1890/10-2236.1

Kasumyan, A. O. (2004). The olfactory system in fish: Structure, function, and role in behavior. *Journal of Ichthyology*, *44*(2), 180–223.

Keeley, K. N., Stroh, J. D., Tran, D. S. C., Fong, C. R., & Fong, P. (2015). Location, location, location: Small shifts in collection site result in large intraspecific differences in macroalgal palatability. *Coral Reefs*, *34*, 607–610. https://doi.org/10.1007/s00338-015-1274-2

Kelley, J. L. (2008). Assessment of predation risk by prey fishes. In C. Magnhagen (Ed.), *Fish behaviour* (pp. 269–302). CRC Press.

Koeck, B., Alós, J., Caro, A., Neveu, R., Crec'hriou, R., Saragoni, G., & Lenfant, P. (2013). Contrasting fish behavior in artificial seascapes with implications for resources conservation. *PLoS One*, *8*(7), e69303. https://doi.org/10.1371/journal.pone.0069303

Kulahci, I. G., Dornhaus, A., & Papaj, D. R. (2008). Multimodal signals enhance decision making in foraging bumble-bees. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1636), 797–802. https://doi.org/10.1098/rspb.2007.1176

Lehtiniemi, M. (2005). Swim or hide: Predator cues cause species specific reactions in young fish larvae. *Journal of Fish Biology*, *66*, 1285–1299. https://doi.org/10.1111/j.0022-1112.2005.00681.x

Leis, J. M., Carson-Ewart, B. M., & Cato, D. H. (2002). Sound detection in situ by the larvae of a coral-reef damselfish (Pomacentridae). *Marine Ecology Progress Series*, *232*, 259–268. https://doi.org/10.3354/meps232259

Liao, I. C., & Chang, E. Y. (2003). Role of sensory mechanisms in predatory feeding behavior of juvenile red drum *Sciaenops ocellatus*. *Fisheries Science*, *69*(2), 317–322. https://doi.org/10.1046/j.1444-2906.2003.00623.x

Lombardo, S. R., Mackey, E., Tang, L., Smith, B. R., & Blumstein, D. T. (2008). Multimodal communication and spatial binding in pied currawongs (*Strepera graculina*). *Animal Cognition*, *11*(4), 675–682. https://doi.org/10.1007/s10071-008-0158-z

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, *6*(60), 3139. https://doi.org/10.21105/joss.03139

Manassa, R. P., McCormick, M. I., Chivers, D. P., & Ferrari, M. C. O. (2013). Social learning of predators in the dark: Understanding the role of visual, chemical and mechanical information. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1765), 20130720. https://doi.org/10.1098/rspb.2013.0720

Mantyka, C. S., & Bellwood, D. R. (2007). Macroalgal grazing selectivity among herbivorous coral reef fishes. *Marine Ecology Progress Series*, *352*, 177–185. https://doi.org/10.3354/meps07055

McCormick, M. I., & Manassa, R. (2008). Predation risk assessment by olfactory and visual cues in a coral reef fish. *Coral Reefs*, *27*, 105–113. https://doi.org/10.1007/s00338-007-0296-9

McHenry, M. J., Feitl, K. E., Strother, J. A., & Trump, W. J. V. (2009). Larval zebrafish rapidly sense the water flow of a predator's strike. *Biology Letters*, *5*(4), 477–479. https://doi.org/10.1098/rsbl.2009.0048

Michelena, P., Sibbald, A. M., Erhard, H. W., & McLeod, J. E. (2008). Effects of group size and personality on social foraging: The distribution of sheep across patches. *Behavioral Ecology*, *20*(1), 145–152. https://doi.org/10.1093/beheco/arn126

Miller, A. M., & Pawlik, J. R. (2013). Do coral reef fish learn to avoid unpalatable prey using visual cues? *Animal Behaviour*, *85*(2), 339–347. https://doi.org/10.1016/j.anbehav.2012.11.002

Montgomery, J. C. (1989). Lateral line detection of planktonic prey. In *The mechanosensory lateral line: Neurobiology and evolution* (pp. 561–574). Springer New York. https://doi.org/10.1007/978-1-4612-3560-6_28

Munoz, N., & Blumstein, D. (2012). Multisensory perception in uncertain environments. *Behavioral Ecology*, *23*, 457–462. https://doi.org/10.1093/beheco/arr220

Narins, P. M., Grabul, D. S., Soma, K. K., Gaucher, P., & Hödl, W. (2005). Cross-modal integration in a dart-poison frog. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(7), 2425–2429. https://doi.org/10.1073/pnas.0406407102

New, J. G. (2002). Multimodal integration in the feeding behaviors of predatory teleost fishes. *Brain, Behavior and Evolution*, *59*(4), 177–189. https://doi.org/10.1159/000064905

Newport, C., Padget, O., & de Perera, T. B. (2021). High turbidity levels alter coral reef fish movement in a foraging task. *Scientific Reports*, *11*(1), 5976. https://doi.org/10.1038/s41598-021-84814-5

Persson, L. (1993). Predator-mediated competition in prey refuges: The importance of habitat dependent prey resources. *Oikos*, *68*, 12–22. https://doi.org/10.2307/3545304

R Core Team. (2023). R: A language and environment for statistical computing (Version 4.3.2). Available at: https://www.R-project.org/

Rehage, J. S., & Sih, A. (2004). Dispersal behavior, boldness, and the link to invasiveness: A comparison of four *Gambusia* species. *Biological Invasions*, *6*(3), 379–391. https://doi.org/10.1023/B:BINV.0000034618.93140.a5

Rhoades, O. K., Lonhart, S. I., & Stachowicz, J. J. (2019). Human-induced reductions in fish predator boldness decrease their predation rates in kelp forests. *Proceedings of the Royal Society B*, *286*(1900), 20182745. https://doi.org/10.1098/rspb.2018.2745

RStudio Team. (2023). RStudio: integrated development environment for R (Version 4.3.2). Available at: https://www.rstudio.com/

Saunders, A. J., & Montgomery, J. C. (1985). Field and laboratory studies of the feeding behaviour of the piper *Hyporhamphus ihi* with reference to the role of the lateral line in feeding. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, *224*(1235), 209–221. https://doi.org/10.1098/rspb.1985.0030

Schwalbe, M. A., Sevey, B. J., & Webb, J. F. (2016). Detection of artificial water flows by the lateral line system of a benthic feeding cichlid fish. *The Journal of Experimental Biology*, *219*(7), 1050–1059. https://doi.org/10.1242/jeb.136150

Siebeck, U. E., Wallis, G. M., & Litherland, L. (2008). Colour vision in coral reef fish. *Journal of Experimental Biology*, *211*(3), 354–360.

Smith, M. E., & Belk, M. C. (2001). Risk assessment in western mosquitofish (*Gambusia affinis*): Do multiple cues have additive effects? *Behavioral Ecology and Sociobiology*, *51*, 101–107. https://doi.org/10.1007/s002650100415

Stewart, W. J., Cardenas, G. S., & McHenry, M. J. (2013). Zebrafish larvae evade predators by sensing water flow. *Journal of Experimental Biology*, *216*(3), 388–398. https://doi.org/10.1242/jeb.072751

Stewart, W. J., Nair, A., Jiang, H., & McHenry, M. J. (2014). Prey fish escape by sensing the bow wave of a predator. *Journal of Experimental Biology*, *217*(24), 4328–4336. https://doi.org/10.1242/jeb.111773

Sura, S. A., Molina, N. E., Blumstein, D. T., & Fong, P. (2021). Macroalgae and nutrients promote algal turf growth in the absence of herbivores. *Coral Reefs*, *38*, 425–429. https://doi.org/10.1007/s00338-019-01793-w

Utne-Palm, A. C. (2001). Response of naive two-spotted gobies *Gobiusculus flavescens* to visual and chemical stimuli of their natural predator, cod *Gadus morhua*. *Marine Ecology Progress Series*, *218*, 267–274. https://doi.org/10.3354/meps218267

Valentinčič, T. (2004). Taste and olfactory stimuli and behavior in fishes. In G. von der Emde, J. Mogdans, & B. G. Kapoor (Eds.), *The senses of fish*. Springer. https://doi.org/10.1007/978-94-007-1060-3_4

Wallace, K. J., & Hofmann, H. A. (2021). Equal performance but distinct behaviors: Sex differences in a novel object recognition task and spatial maze in a highly social cichlid fish. *Animal Cognition*, *24*(5), 1057–1073. https://doi.org/10.1007/s10071-021-01498-0

Ward, A. J. W., & Mehner, T. (2010). Multimodal mixed messages: The use of multiple cues allows greater accuracy in social recognition and predator detection decisions in the mosquitofish, *Gambusia holbrooki*. *Behavioral Ecology*, *21*(6), 1315–1320. https://doi.org/10.1093/beheco/arq152

Ward, A. J. W., Thomas, P., Hart, P. J. B., & Krause, J. (2004). Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, *55*, 561–568. https://doi.org/10.1007/s00265-003-0751-8

Wickham, H. (2024). *Ggplot2: Elegant graphics for data analysis*. Springer-Verlag. Available at: https://CRAN.R-project.org/package=ggplot2

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). dplyr: A grammar of data manipulation. R package version 1.1.4. Available at: https://CRAN.R-project.org/package=dplyr.

Wickham, H., Hester, J., & Bryan, J. (2024). readr: read rectangular text data. R package version 2.1.5. Available at: https://CRAN.R-project.org/package=readr.

Wilson, A. D. M., & Godin, J. G. J. (2009). Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behavioral Ecology*, *20*(2), 231–237. https://doi.org/10.1093/beheco/arp018

Wilson, A. D. M., & Stevens, E. D. (2005). Consistency in context-specific measures of shyness and boldness in rainbow trout, *Oncorhynchus mykiss*. *Ethology*, *111*(9), 849–862. https://doi.org/10.1111/j.1439-0310.2005.01110.x

Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution*, *9*(11), 442–446. https://doi.org/10.1016/0169-5347(94)90134-1

Wisby, W. J., & Hasler, A. D. (1954). Effect of olfactory occlusion on migrating silver salmon (*O. kisutch*). *Journal of the Research Fisheries Board of Canada*, *11*(4), 472–478. https://doi.org/10.1139/f54-031

Wright, D., Nakamichi, R., Krause, J., & Butlin, R. K. (2006). QTL analysis of behavioral and morphological differentiation between wild and laboratory zebrafish (*Danio rerio*). *Behavior Genetics*, *36*(2), 271–284. https://doi.org/10.1007/s10519-005-9029-4

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.