

Fish avoid visually noisy environments that reduce their perceptual abilities

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1

Abstract

2 The environment contains different forms of ecological noise that can reduce the ability of
3 animals to detect information. Here we ask whether animals can adapt their behaviour to either
4 exploit or avoid areas of their environment with increased dynamic visual noise. By immersing
5 three-spined sticklebacks (*Gasterosteus aculeatus*) into environments with a simulated form of
6 naturally occurring visual noise – light bands created by the refraction of light from surface
7 waves termed caustic networks – we tested how such visual noise affected the movements,
8 habitat use, and perceptual abilities of these fish. Fish avoided areas of higher visual noise, and
9 achieved this by increasing their activity as a function of the locally perceived noise level,
10 resulting in individuals moving away from noisier areas. By projecting virtual prey into the
11 environment with different levels of visual noise, we found that the fish's ability to visually
12 detect prey decreased as visual noise increased. We found no evidence that fish increased their
13 exploration (and decreased their refuge use) in environments with increased visual noise, which
14 would have been predicted if they were exploiting increased visual noise to reduce their own
15 likelihood of being detected. Our results indicate that animals can use simple behavioural
16 strategies to mitigate the impacts of dynamic visual noise on their perceptual abilities, thereby

17 improving their likelihood of gathering information in dynamically changing and noisy
18 environments.

19 **Introduction**

20 Animals live in inherently noisy environments, where noise can be defined as any environmental
21 stimulus that interferes with the ability of animals to detect or respond to biologically meaningful
22 cues (Brumm, 2013; Corcoran and Moss, 2017; Cuthill et al., 2017). Noise can take acoustic,
23 chemical or visual forms, and can also vary dynamically in the environment. For example, wind-
24 blown vegetation, turbidity (Chamberlain and Ioannou, 2019), and the refraction and scattering
25 of light through water (Matchette et al. 2018; Matchette et al. 2020) can create backgrounds with
26 dynamically changing illumination, while weather, traffic or other human activities can generate
27 varying intensities of background acoustic noise (Lampe et al., 2012; Morris-Drake et al., 2016;
28 Slabbekoorn and Ripmeester., 2008; Tasker et al., 2010; Vasconcelos et al., 2007). These forms
29 of noise can reduce the likelihood of animals detecting information in their environment through
30 two processes. First, by adding statistical error to the sensory modality being utilised, noise can
31 make detection of a stimulus within that sensory channel more difficult due to masking effects.
32 Alternatively, by distracting an animal, noise may limit its ability to detect or respond to
33 information across sensory modalities (Morris-Drake et al., 2016). Through these processes,
34 noise can reduce the ability of animals to communicate with conspecifics, (Fleishman, 1986;
35 Herbert-Read et al., 2017; Lampe et al., 2012; Ord et al., 2007; Peters et al., 2007; Slabbekoorn
36 and Ripmeester, 2008; Vasconcelos et al., 2007), detect moving targets (Matchette et al., 2018),
37 forage efficiently (Azeem et al., 2015; Evans et al., 2018; Matchette et al., 2019; Party et al.,
38 2013; Purser and Radford, 2011; Wale et al., 2013), and respond to predatory attacks (Morris-
39 Drake et al., 2016; Wale et al., 2013), all of which have significant survival and fitness
40 consequences for individuals.

41 Because noise can reduce the ability of animals to detect or respond to information in their
42 environment, prey and predators may use behavioural strategies to either exploit or avoid noisy
43 environments, thereby increasing their likelihood of detecting information, or avoid being

44 detected themselves. For example, if attempting to remain undetected, some species may
45 preferentially select noisier environments, or increase their exploration of the environment during
46 times of increased environmental noise. Indeed, fathead minnows (*Pimephales promelas*), three-
47 spined stickleback (*Gasterosteus aculeatus*), and larval pike (*Esox lucius*), show decreased anti-
48 predator behaviour in more turbid water (Abrahams and Kattenfeld, 1997; Lehtiniemi et al.,
49 2005; Sohel and Lindstrom, 2015), suggesting they may exploit times of high turbidity to avoid
50 being detected by visual predators (although see (Chamberlain and Ioannou, 2019)). On the other
51 hand, some species may attempt to avoid noisier environments as gathering information in those
52 environments becomes more difficult. Indeed, some species of bats avoid areas of their
53 environment with higher levels of acoustic noise (Bennett and Zurcher, 2013) and others spend
54 more time foraging in areas with lower levels of acoustic noise (Schaub et al., 2008) (but see
55 (Bonsen et al., 2015)). When avoidance of noisy areas is impossible, however, some species may
56 adapt their behaviour to compensate for reduced information detection. Zebra finches
57 (*Taeniopygia guttata*), for example, spend more time being vigilant in noisier acoustic
58 environments, but this comes at the cost of decreased foraging rates (Evans et al., 2018). While
59 animals' behavioural changes to noise, and in particular acoustic noise, have been relatively well
60 documented (Kunc et al., 2016; Shannon et al., 2016), whether animals adapt their behaviour in
61 response to noise in other sensory channels, and in particular dynamic visual noise, has received
62 far less attention. Moreover, whether these changes to behaviour represent adaptive behavioural
63 decisions to exploit or avoid noisy environments remains unclear.

64 Shallow aquatic environments are particularly prone to one form of naturally occurring
65 dynamic visual noise – *caustics*. Caustics are formed from the diffraction and refraction of light
66 from the disturbance of surface waves that is projected through the water column onto the
67 substrate below (Lock and Andrews, 1992). This form of dynamic illumination can reduce the
68 likelihood of humans detecting a target on a computer animated display (Matchette et al., 2018),
69 and can increase the latency of triggerfish (*Rhinecanthus aculeatus*) to attack a moving target
70 (Matchette et al., 2020). Because caustics appear to reduce the ability of animals to detect or
71 respond to information, animals could try to mitigate the impacts of, or exploit, these visually
72 noisy environments. For example, species might avoid areas with higher levels of visual noise to

73 increase the likelihood of detecting information themselves, or alternatively, could preferentially
74 associate with visually noisy environments to reduce their own likelihood of being detected. Here
75 we ask how visual noise affects the movements, refuge use and prey detection abilities of three-
76 spined sticklebacks (*Gasterosteus aculeatus*). Sticklebacks are a small (~ 2 - 6 cm) fish found in
77 both shallow marine and freshwater environments where caustics are prevalent. They feed on
78 small insects, fish fry, and crustaceans by actively searching for prey among the substrate and in
79 the water column, and are themselves predominantly preyed upon by birds and larger fishes, such as
80 pike (*Esox lucius*). To understand whether sticklebacks can exploit or avoid these visually noisy
81 areas, we performed a series of three experiments. We first asked whether stickleback preferred
82 to associate with visually noisy environments (potentially to reduce the likelihood of themselves
83 being detected by their own predators), or avoid those areas (potentially to increase the
84 likelihood of detecting their own prey). In this experiment, we also determined whether a
85 potential preference was driven by the fish actively or passively choosing to avoid or associate
86 with noisy environments by quantifying their movements in response to the locally perceived
87 level of noise, that is, the level of visual noise that surrounded the fish. Second, we tested
88 whether the fish increased or decreased refuge use in different levels of visual noise, predicting
89 that if the sticklebacks were using visually noisy environments to avoid being detected by
90 predators, they should use a refuge less frequently in higher levels of visual noise. Last, we tested
91 whether visually noisy environments affected the ability of stickleback to detect prey in their
92 environment by quantifying the likelihood that individual stickleback detected virtual prey in
93 environments with different levels of visual noise.

94

95

Methods

96 *Playbacks*

97 For each experiment, we projected video playbacks of simulated caustics into an experimental
98 arena to assess how different levels of visual noise affected the habitat choices, refuge use, and
99 prey detection abilities of sticklebacks. These refracted patterns of light naturally vary in their

100 spatial distribution, intensity, and velocity as a function of the water depth and the properties of
101 the surface waves (Lock and Andrews, 1992). To produce the playbacks, we first generated a
102 series of 600 images of caustic patterns using the software, Caustics Generator Pro (dualheights,
103 2018), cropped to an aspect ratio of 3840 by 2159 pixels (see software settings in Table S1). We
104 created animations of these images in MATLAB 2018a where the images were stitched together
105 sequentially (See Video S1). The animations were designed so that they could be looped without
106 the caustics appearing to spatially or temporally ‘jump’. To create six different levels of visual
107 noise, we wanted to ensure we manipulated only one property of the caustic patterns. For
108 example, if we had manipulated the spatial fractal nature of the caustic patterns, this would have
109 also changed the total light intensity within our animations. Therefore, we chose to manipulate
110 the speed that the caustics moved, while maintaining their spatial properties. To do this, we
111 created videos where the images looped through at different speeds, so that the slowest to fastest
112 animation took 80, 40, 20, 10, 5 and 2.5 seconds, respectively, to complete a full loop. We
113 classified faster moving playbacks as having higher levels of visual noise. We ensured that the
114 speed at which the caustics moved in the arena, and the light levels in the arena, were
115 representative of those found in nature (see Online Supplement & Figure S1). Furthermore, we
116 chose to not include a treatment of a static projected image of the caustic patterns, as we were
117 specifically interested in how different levels of visual noise affect behaviour, and note that static
118 caustics are ecologically unrealistic and never occur in aquatic environments.

119 *Study subjects and experimental arena*

120 Three-spined sticklebacks (n = 204) were caught from the river Cary in Somerton, Somerset, UK
121 (51.069990 latitude, -2.758014 longitude), and we observed that caustics were present in the
122 location that the fish were caught. Fish used in experiment one were caught in November 2017,
123 and fish used in experiment two and three were caught in March 2019. All fish were in non-
124 breeding condition when used in experiments. All fish were housed for at least two weeks before
125 experimentation. The fish were housed in glass housing tanks (40 x 70 x 35 cm, height x length x
126 width) on a flow-through re-circulating freshwater system with plastic plants and tubes for
127 environmental enrichment. The fish were held at 14°C under a 11:13 hour light:dark cycle. Each

128 tank housed approximately 40 individuals and fish were fed bloodworms once per day, six days
129 per week.

130 The experimental tank for all three experiments consisted of a test arena (1.46 x 0.84 m,
131 length x width) and a holding area (0.84 x 0.34 m, length x width) separated by white opaque
132 plastic (Figure S2). Both sections were filled to a depth of 15 cm with water from the re-
133 circulating freshwater system. Water was filtered within the tank using a Eheim classic 600
134 External Filter and chilled to between 14.2 and 15.2°C using a D-D DC-300 chiller. The holding
135 area contained plastic plants and tubes for environmental enrichment. Water was changed in the
136 experimental tank between each of the three experiments but not between individual trials. Prior
137 to each day of trials, fish that would be used in the subsequent day were placed in the holding
138 area overnight, allowing them to acclimate to the conditions of the tank. Fish were not fed for 24
139 hours prior to each experiment.

140 A camera (Panasonic HC-VX870) located 2.15 m above the centre of the test arena filmed the
141 trials at 4K resolution (3840 x 2160 pixels) at 25 frames per second. The camera was controlled
142 remotely using the Panasonic Image App operated by an experimenter outside the room. The
143 experimenter was not present in the room while the trials were run. A BenQ W1700/HT2550
144 Digital Projector with 4K resolution operating at a 60 Hz vertical scan rate located 2.19 m above
145 the arena (Figure S2) projected the playbacks into the arena. The projections were played using a
146 Dell Inspiron 15 notebook connected to the projector via a 4K HDMI cable located outside the
147 experimental room. The arena was surrounded by black-out curtains to minimise any external
148 light source entering.

149 *Experiment 1 – Do fish prefer to associate with more or less visually noisy environments?*

150 To determine if fish tended to avoid or preferred to associate with more or less visually noisy
151 environments, individual fish were presented with a binary choice, where on one side of the
152 arena we projected one level of visual noise, and on the other side we projected a different level
153 of visual noise. As there were six different levels of noise, this gave 15 possible combinations of
154 noise pairings. We constructed six different playbacks, where each playback contained all 15

155 different noise pairings, played one after the other. Each choice (noise pairing) was presented for
156 320 seconds, with the total length of each playback equalling 80 minutes. Across the different
157 playbacks ($n = 6$), each noise level was presented evenly on each side of the test arena to control
158 for any potential side biases (Table S2). The ordering of the noise pairings within a playback
159 were also assorted (see Table S2) between the six playbacks so there was no systematic bias in
160 their ordering across the trials. For each trial, a single fish was exposed to one of these six
161 playbacks. The order of the six playbacks was randomised within each day, with each playback
162 being used a maximum of once per day.

163 For each trial ($n = 48$), an individual fish ($5.4 \text{ cm} \pm 0.7 \text{ cm}$, mean \pm SD) was moved from the
164 holding area into the test arena and left to acclimate there for 10 minutes. During this period, the
165 first frame of the playback was projected into the test arena as a static image, but the video
166 playback was not started. After ten minutes, we started the video playback remotely. After each
167 trial, the fish was removed and placed in a separate housing tank and fed. No fish were reused
168 between trials.

169
170 Fish were tracked using an adapted version of DIDSON tracking software (Handegard and
171 Williams., 2008) in MATLAB 2018a (Figure 1a). Because the fish were darker than the arena or
172 moving projections, we took a grey-scale threshold of each frame to isolate the fish within the
173 videos without requiring any background subtraction. Tracks were filtered to remove spurious
174 tracking errors and smoothed using a rolling average of 12 frames (approximately half a second).
175 In addition to plotting and manually inspecting the tracks for accuracy, we calculated that fish
176 were tracked for 88.2% of all frames (see below). The tracking accuracy was not systematically
177 affected by different levels of visual noise (see Online Supplement).

178 From the trajectory data of each fish, we calculated the amount of time the fish spent on each
179 side of the test arena in each paired choice. To do this, we used the *inpolygon* function in
180 MATLAB 2018a to determine when a fish's track was either on the left or right side of the arena.
181 We then calculated the proportion of time that the fish spent in the noisier side of the arena for
182 each noise pairing. We also calculated the amount of time the fish spent stationary, and the speed
183 they adopted when they were moving, when in different levels of noise. To do this, the

184 instantaneous speed of the fish was calculated as the displacement in their position between two
185 consecutive frames. We defined a fish as being stationary when its speed was less than 2 mm s^{-1} ,
186 informed by plotting a histogram of all the fish's speeds across all trials (see Figure S3). The
187 mean speed of a fish was calculated excluding the times when they were stationary (i.e. when
188 speeds were $> 2 \text{ mm s}^{-1}$), and was calculated when the fish was on each side of the arena
189 separately.

190 *Experiment 2 – Do fish use refuge more or less in increased levels of visual noise?*

191 To determine whether the fish were more or less likely to use a refuge in different levels of visual
192 noise, two plastic plants (each $5 \times 2 \times 15 \text{ cm}$, length x width x height at the base) were placed as
193 a refuge in the middle of the test arena (see Figure S4). For each trial ($n = 48$), an individual fish
194 ($4 \pm 0.5 \text{ cm}$; mean standard length \pm SD) was exposed to six different levels of visual noise, with
195 each level of noise being projected throughout the entire arena (unlike Experiment 1), and each
196 level of noise projected sequentially one after the other. To ensure that each noise level was
197 presented in a different order within trials, we again created six playbacks where each playback
198 contained each level of noise, but each noise level occurred in a different order within each
199 playback (referred to as order-within-trial) in a Latin-square design (see Table S3). Each trial,
200 therefore, consisted of six levels of noise, each presented for 320 seconds, with the total running
201 length of the playbacks equalling 32 minutes. Every playback was presented once per day
202 (between 9am and 5pm) and in a random order on different days. As in the choice tests,
203 individual fish were moved from the holding area and placed in the test arena for 10 minutes
204 acclimation time (while a static caustic image was projected into the arena) before the playback
205 was started remotely. Experimented fish were removed and placed in a separate housing tank and
206 later fed. Used fish were kept separately from unused fish and fish were not reused between
207 trials. Fish that were used in the refuge experiment had not been used in the choice experiment.

208

209 We scored the amount of time (in seconds) the fish spent under the refuge during each level
210 of noise. To do this, videos were imported into the software BORIS v. 7.9.15 (Friard et al.,
211 2016), where we defined the fish to be under the refuge when any part of its body was under any

212 of the fronds of the plastic plant (see Figure S4). Each fish could therefore be under the refuge
213 for a minimum of 0 to a maximum of 320 seconds in each level of visual noise.

214 *Experiment 3 – Does visual noise affect the ability of fish to visually detect prey in their*
215 *environment?*

216 To determine if different levels of visual noise affected the ability of fish to detect prey in their
217 environment, we created playbacks of the six different levels of visual noise (as in Experiment 2,
218 played sequentially and throughout the entire arena), that included virtual prey that appeared and
219 disappeared in random locations. In particular, the prey appeared as uniform red dots (similar to
220 the virtual-prey experiments in (Ioannou et al., 2019; Duffield and Ioannou, 2017)) on top of the
221 caustic patterns (see Video S2). When these playbacks were projected into the arena, each virtual
222 prey appeared at a random location within the arena as a looming stimulus, increasing in size
223 from 0 - 12.5 mm diameter within $\frac{3}{4}$ of a second, maintaining 12.5 mm diameter for ~ 1 second,
224 and then shrinking to 6 mm before disappearing. Each prey was visible in the arena for a total of
225 two seconds, moving on a correlated random walk at 7 cm s^{-1} . Playbacks of the caustics and prey
226 were again created in MATLAB 2018a.

227

228 Because the sticklebacks were fed on red bloodworm in their housing tanks, they were
229 highly responsive to these red dots, often attempting to peck at them if in range. Therefore, the
230 fish did not need to be trained to attack the virtual prey. However, the limited presentation time
231 of each prey (2 s) was designed to allow the fish to detect and start swimming towards the prey,
232 but reduce the likelihood of the fish sampling the prey, and hence learning that the prey was not
233 edible. Due to the short presentation times, the arena being large, and the prey appearing in
234 random locations, the prey would often appear far from the fish's position. To increase the
235 potential for the fish to detect the prey, therefore, each level of noise contained 50 individual
236 prey presentations (300 presentations within a single trial), with four seconds between the end of
237 one prey presentation and the start of another.

238 As in the refuge experiment, for each trial ($n = 108$), individual fish (3.3 ± 0.4 cm; mean
239 standard length \pm SD) were exposed to six levels of visual noise including the virtual prey. To
240 control for order effects, six different playbacks were created where each playback contained
241 each level of noise, with each noise level occurring at different times (order-within-trial) in the
242 playbacks in a Latin Square design (Table S3). Controlling for order effects was particularly
243 important here, as there was the potential for the fish to become habituated to the prey over time
244 (although this did not occur – see below). In these playbacks, we also added transitions between
245 the different levels of noise, so that the change in speed of the moving caustics between different
246 noise levels was smooth. This involved creating animations that increased or decreased in speed
247 from one noise level to another, which were subsequently placed between the respective
248 animations of visual noise with the prey. Within these transition periods, no prey were projected.
249 As in the other experiments, each level of noise lasted for 320 seconds, with each transition
250 period lasting between 70 to 90 seconds. Each playback in total, therefore, lasted for ~ 50
251 minutes and 45 seconds. Each playback was presented once per day and at different times of the
252 day (between 9am and 5pm) on different days. As in the previous two experiments, individual
253 fish were moved from the holding area to the test arena and allowed 10 minutes acclimation
254 time. During this time, the lowest level of noise was projected into the test arena for ten minutes
255 before transitioning into the start of the playback. Experimented fish were removed and placed in
256 a separate housing tank and fed. No fish that were used in the choice or refuge experiments were
257 used in this experiment and fish were not reused between trials.

258 Videos of the trials were manually inspected to determine whether the fish detected each of
259 the virtual prey. A detection was defined as when there was a noticeable change in the speed or
260 direction of the fish towards the prey (see Video S2 for examples). We quantified how many
261 prey (out of a maximum of 50) the fish detected in each level of noise within each trial.

262 *Statistics*

263 All statistics were performed in R 3.5.1 (R Core Team, Version 3.5.1). The package lme4 (Bates
264 et al., 2015) was used for all mixed models. Assumptions for all linear mixed models (LMMs)

265 were checked using standard diagnostic plots (QQ normal plots and residuals plotted against
266 fitted values). Models were also checked for collinearity. Assumptions for all generalised linear
267 mixed models (GLMMs) were checked using the DHARMA package (Hartig, 2019) including
268 checking the dispersion and the distribution of the residuals. The full models were simplified by
269 removal of non-significant terms. We used the anova function in R (R Core Team, Version 3.5.1)
270 to compare pairs of models using the chi-squared statistic. The estimates and effect sizes
271 (cohen's D) are presented in Table S4. All R graphs were created using *ggplot2* (Wickham,
272 2016). All data used here are available in the dryad digital repository
273 (doi:10.5061/dryad.rfj6q577x).

274 *Experiment 1* - To test whether fish spent more or less time in areas with more or less visual
275 noise (regardless of absolute noise level), we subtracted 0.5 from the proportion of time they
276 spent on the noisier side of the arena separately for each of the 15 noise pairings per trial. We
277 tested whether the intercept of a linear mixed model (LMM) predicting those proportions, with
278 trial included as a random effect, differed from zero (i.e. proportion of time on the noisier side -
279 $0.5 \sim 1 + (1 | \text{Trial})$ in *lme4* nomenclature). We then asked whether the absolute difference in
280 noise level within a choice affected the amount of time the fish spent on the noisier side of the
281 arena. To do this, we calculated the difference between noise levels on each side of the arena for
282 each noise pairing. For example, the difference between a choice of noise levels one and five was
283 calculated as four. We then used an LMM to ask whether this difference could predict the
284 proportion of time the fish spent on the noisier side of the arena. In this model, the difference in
285 noise was treated as a discrete numeric variable, trial (fish identity) was included as a random
286 intercept, and difference in noise level was included as a random slope.

287

288 In some choices (53 out of 720 choices) a fish did not visit both sides of the arena. These
289 instances might not reflect, therefore, a true choice of the fish, as a fish could have been
290 unaware of the noise level on the other side of the arena. Therefore, to test whether our results
291 were robust to the removal of these instances, we performed the same analyses as described
292 above, but only included data from when a fish had visited both sides of the arena during a

293 choice. Our results did not qualitatively change when these cases were removed (see Online
294 Supplement), and therefore we present results below including these cases.

295 The proportion of time that the fish spent in different levels of noise could result from fish
296 adopting different movements as a function of the noise level they were in, and potentially the
297 noise level on the other side of the arena. For example, if the fish adopted different speeds, or
298 spent less time moving, this could result in the fish spending unequal amounts of time in each
299 level of noise. To investigate this, we used LMMs to predict whether a fish's speed, and in a
300 separate model the time spent stationary, on the side of the arena the fish was in could be
301 predicted based on the level of noise on each side of the arena (modelled as separate fixed
302 effects: noise level on the side occupied by the fish and noise level on the unoccupied side).
303 Mean speed and the proportion of time stationary were square root transformed due to a slight
304 positive skew of these data. Order-within-trial (1-6) was also added as a fixed effect and trial
305 was included as a random intercept along with noise level on the side occupied by the fish as a
306 random slope.

307 Because a fish's speed, and time spent stationary, were dependent on the noise level they
308 were in (but not dependent on the noise level on the other side of the arena – see below), we
309 asked whether the differences observed in speed and time spent stationary could solely explain
310 the amount of time fish spent in the corresponding levels of visual noise. To do this, the mean
311 speed that the fish adopted in different levels of noise, along with the proportion of time spent
312 stationary, were added as covariates to the model investigating proportion of time spent on the
313 side of the arena with more visual noise.

314 *Experiment 2* - We tested if the level of visual noise had a significant influence on the time the
315 fish spent under refuge. We initially attempted to model the time spent in the refuge as a
316 binomial response (time in versus time out of shelter), however, these models were over-
317 dispersed. Therefore, due to the relatively bimodal distribution of the response variable (Figure
318 S5a) we transformed the time spent in refuge into a binary response variable, where fish that

319 spent over 50% of their time in the refuge were given a value of 1, and less than or equal to 50%
320 a value of 0. This binary response variable was modelled using a GLMM with a binomial error
321 structure. Noise level was included as a fixed effect (discrete numeric as before) along with
322 order-within-trial, and trial (fish identity) added as a random effect. We did not include noise as a
323 random slope in the refuge experiment because there was no effect of noise on the response
324 variable.

325 *Experiment 3* – To test if the level of visual noise affected the likelihood that fish detected the
326 prey, we used a GLMM with a Poisson family error structure. The response variable was the
327 number of prey detections at each level of noise, and fixed effects were the level of visual noise
328 and order-within-trial. Trial was added as a random intercept to account for the nonindependence
329 of each noise level within a trial. Noise was not added as a random slope in this case due to the
330 model not converging.

331 **Results**

332 *Experiment 1 – Do fish prefer to associate with more or less visually noisy environments?*

333 Fish spent more time on the side of the arena with less visual noise (Figure 1b) (LMM; $t_{47} =$
334 $-7.8, p < 0.001$). Furthermore, the relative difference between the noise levels on each side of
335 the arena affected the time the fish spent in the noisier side of the arena. As the relative
336 difference in noise between the two sides of the arena increased, fish spent less time on the side
337 of arena with more visual noise (Figure 1 c; LMM; $\chi^2 = 9.77, df = 7, p = 0.002$).

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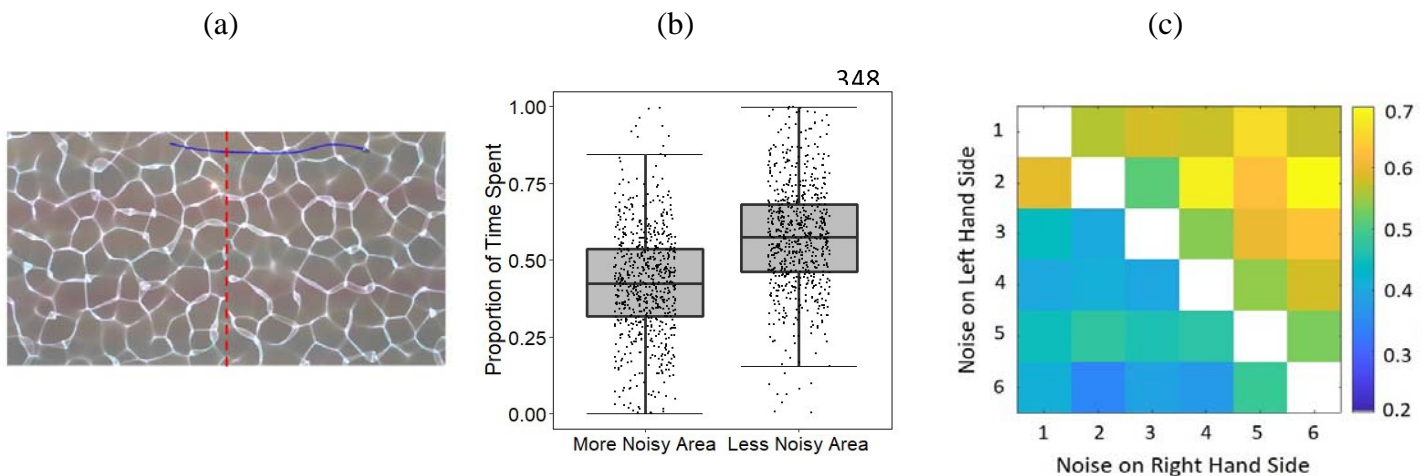
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353 Figure 1: Experimental arena and choice test. a) Still image from a video of a choice trial
354 depicting a section of the trajectory of a fish superimposed in blue. The red dotted line shows the
355 virtual boundary between the two choice areas. b) Proportion of time the fish spent on the side of
356 the arena with more or less visual noise (ignoring absolute differences in noise level). Fish spend
357 more time on the side of the arena with less visual noise. The central line of each box shows the
358 median value while the upper and lower lines of the box show the upper and lower quartiles of
359 the data, with the whiskers extending to the most extreme data point within $1.5 \times$ the interquartile
360 range. Jittered dots represent raw data points. c) Matrix showing the mean proportion of time

361 across trials (the heat) the fish spent on the left side of the arena where each cell represents the
362 choice a fish was given between two levels of visual noise. Six represents the highest level of
363 noise, and one the lowest. When the noise level was *lower* on the left side of the arena (upper-
364 right corner of the plot), the fish spent *more* time on that side. When the noise level was *higher*
365 on the left side of the arena (lower-left corner of the plot), the fish spent *less* time on that side.
366 Note that 1 minus this matrix would give the proportion of time spent on the right-hand side of
367 the arena.

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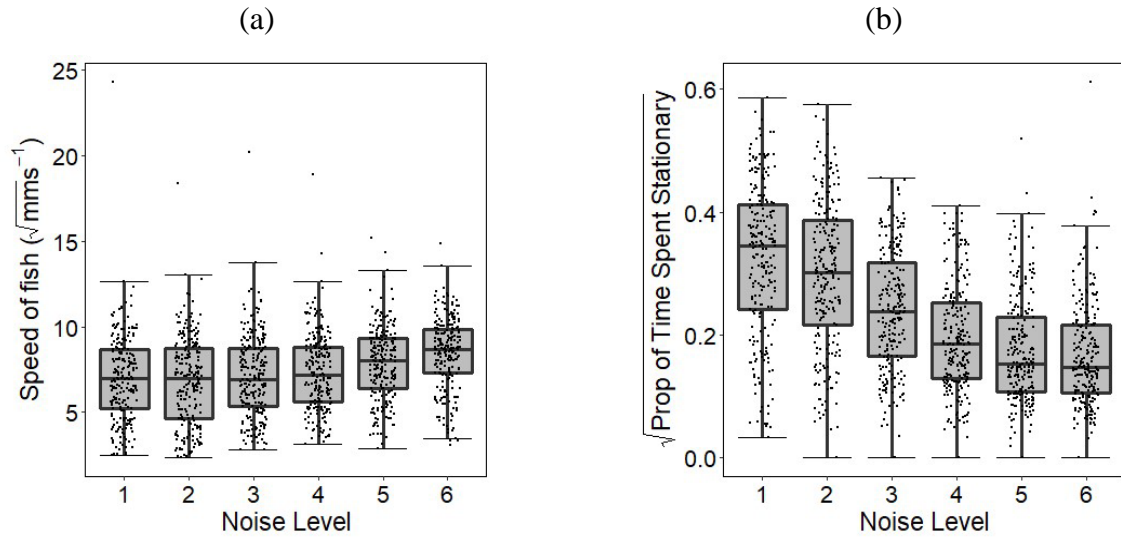
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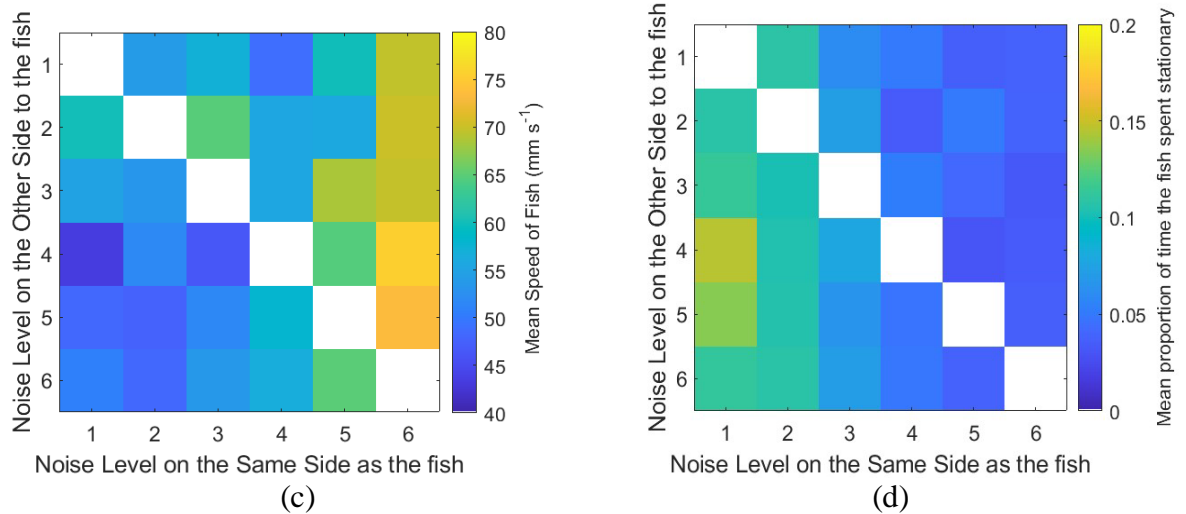
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373 The fish's movements were only affected by the level of visual noise on the side of the arena
374 they were in. Fish moved faster (Figure 2a; LMM; $\chi^2 = 52.3$, $df = 8$, $p < 0.001$), and spent less
375 time stationary, when on the side of the arena with more visual noise (Figure 2b; LMM; $\chi^2 =$
376 90.8 ; $df = 8$, $p < 0.001$). The noise level on the other side of the arena (to that which the fish was
377 on) did not affect the fish's speed (Figure 2c; LMM; $\chi^2 = 0.35$, $df = 8$, $p = 0.55$), nor the
378 proportion of time it spent stationary (Figure 2d; LMM; $\chi^2 = 0.34$, $df = 8$, $p = 0.56$). When these
379 movement variables were added as covariates to the model, the difference in noise level between
380 the two sides of the arena was no longer a significant predictor of the time the fish spent on the
381 noisier side (LMM; $\chi^2 = 1.61$, $df = 11$, $p = 0.20$). The fish's speed and its time spent stationary on
382 the noisier side of the arena, therefore, could explain the proportion of the time spent on that side
383 of the arena. In other words, how a fish adapted its movements to the locally perceived level of
384 noise determined the amount of time it spent in that region.

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389 Figure 2: How the fish's movements were affected by visual noise. a) Square root of fish's mean
390 speed as a function of the visual noise level they were in. Fish swam faster in more noisy areas.
391 b) Square root of the proportion of time the fish spent stationary as a function of the noise level
392 they were in. Fish spent less time stationary in more noisy areas. In a) and b) the central line of
393 each box shows the median value while the upper and lower lines of the box show the upper and

394 lower quartiles of the data. The whiskers extend to the most extreme data point within $1.5 \times$ the
395 interquartile range. Outliers are shown by the larger grey circles. Jittered points represent raw
396 data points. c) Mean speed of fish (the heat) as a function of the noise level the fish was in
397 (columns) and the noise level on the other side of the arena (rows). d) Mean proportion of time
398 the fish spent stationary as a function of the noise level the fish was in (columns) and the noise
399 level on the other side of the arena (rows). One – six corresponds to the lowest – highest levels of
400 noise respectively. The presence of a trend from left to right, but not top to bottom, in these heat
401 plots indicates that the fish moved faster, and spent less time stationary, in higher levels of visual
402 noise, but the noise level on the other side of the arena did not affect their movements.

403

404 *Experiment 2 - Do fish use refuge more or less in increased levels of visual noise?*

405 There was no evidence that the level of visual noise affected whether the fish spent the majority
406 of time under the refuge or not (Figure S5b; GLMM; $\chi^2 = 1.75$, $df = 4$, $p = 0.19$). However, fish
407 did spend less time under the refuge as the trial progressed (GLMM; $\chi^2 = 7.07$, $df = 4$, $p = 0.0079$).

408

409 *Experiment 3 - Does visual noise affect the ability of fish to visually detect prey in their*
410 *environment?*

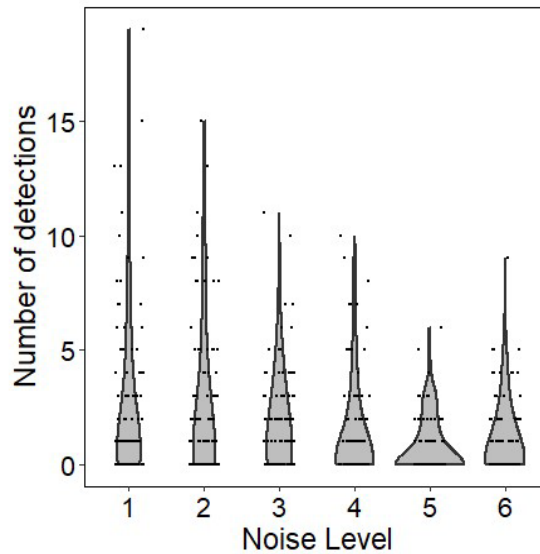
411 Fish were less likely to detect the virtual prey in higher levels of visual noise (Figure 3; GLMM;
412 $\chi^2 = 156.6$, $df = 4$, $p < 0.01$). There was no effect of the order in the trial on the number of
413 detections by the fish (GLMM; $\chi^2 = 0.003$, $df = 4$, $p = 0.99$); fish did not become less likely to
414 detect the prey over the course of the trial.

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420 Figure 3: Virtual prey experiment. Number of times the fish detected the virtual prey out of the
421 possible 50 prey presentations in each level of visual noise per fish ($n = 108$ fish in total). The
422 violin represents a mirrored probability density function, and each black marker represents an
423 individual data point jittered for clarity. Fish were less likely to detect the virtual prey in higher
424 levels of visual noise.

425

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Discussion

427 Fish spent less time in areas with more visual noise, and this reduction in time could be attributed
428 to how the fish adapted their movements in response to noise. In particular, fish increased their
429 speed and spent less time stationary in areas with more visual noise. There was no evidence,
430 however, that the level of visual noise on the other side of the arena affected their movements,
431 suggesting that the fish were only responding to the level of noise in their local vicinity. While
432 increases in speed and decreases in time spent stationary could be interpreted as the fish
433 exploiting these environments to increase exploration during times of increased environmental
434 noise, our second experiment provides evidence against this explanation. If fish were exploiting

435 times of higher visual noise to avoid being detected themselves, we would have expected the fish
436 to spend less time in the refuge in higher levels of visual noise (as refuge use is a key measure of
437 risk taking in sticklebacks (Bevan et al., 2018)). In fact, we found no evidence that fish altered
438 their risk-taking behaviour depending on noise level. Further, it is unlikely that fish were
439 increasing their activity in more noisy areas to match their swim speed with the movements of the
440 caustics, as the optical flow produced by the caustics did not move in a consistent direction (see
441 Figure S1a & Supplementary Video 1). Instead, we suggest that fish use a simple mechanism,
442 namely increasing their speed and activity, to avoid areas of their environment with higher levels
443 of visual noise. This mechanism will lead fish to passively move out of these areas, and towards
444 regions of the environment with lower visual noise. Indeed, similar mechanisms have been
445 proposed for how groups of animals collectively track resources in their environment (Berdahl et
446 al., 2013; Hein et al., 2015), providing a simple, yet effective mechanism to move towards or
447 away from particular regions of the environment.

448 Our final experiment provided further support that these visually noisy environments should
449 be avoided by sticklebacks, with increased visual noise reducing their ability to detect prey. Fish
450 were less likely to detect the virtual prey in these environments, consistent with other systems
451 where humans, chicks and triggerfish took longer to detect prey on backgrounds with dynamic
452 visual noise as opposed to static controls (Matchette et al., 2018, Matchette et al., 2019,
453 Matchette et al. 2020). Because animals have finite time and energy reserves, and limited
454 attention (Cuthill et al., 2019), they are expected to make optimal foraging decisions that increase
455 the rate or efficiency at which they gather resources (Schoener, 1971; Stephens and Krebs, 1986;
456 Ydenberg et al., 1994). This allows them to devote more time and energy to other fitness-related
457 activities (Pianka, 1988; Schmid-Hempel, 1991). Much like how animals choose foraging patches
458 based on their profitability (Krebs, 1979; Milinski, 1979; Milinski, 1987), we might expect
459 animals to selectively choose where to forage in their environment based not only on the resource
460 profitability of a patch, but also considering the likelihood of detecting those resources given the
461 perceptual constraints imposed by that environment. Indeed, there is large natural variation in
462 both the temporal and spatial distribution of caustics in the aquatic environment, as well other
463 forms of environmental noise. Caustics, for example, are prominent on clear, sunny days in

464 intermediate water depths (0.25 - 5 m), but are reduced in deep waters and on overcast days with
465 minimal surface waves. Such variation may lead foragers to select habitats based on the
466 environmental noise determined by the local ecological conditions (e.g. Bennett and Zurcher
467 (2013); Schaub et al. (2008)).

468 While fish avoided visually noisier environments, we may also expect individuals'
469 behavioural responses to environmental visual noise to vary as a function of other factors. For
470 example, sticklebacks have been shown to both decrease (Sohel and Lindstrom, 2015) or increase
471 (Ajemian et al., 2015; Chamberlain and Ioannou, 2019) their anti-predator behaviour and refuge
472 use in more turbid water (a form of static visual noise). This suggests their response to visual
473 noise could vary depending on context or state. Indeed, fifteen-spined stickleback (*Spinachia*
474 *spinachia*), are less risk averse when hungry, but when partially satiated, choose less productive
475 areas where they can spend more time being vigilant (Croy and Hughes, 1991). In our
476 experiments, we did not feed the fish for 24 hours prior to the experiments to induce exploratory
477 behaviour, and to promote search and targeting of the virtual prey. However, stickleback are both
478 predators and prey, hence it would be valuable to test if the fish also avoid visually noisy
479 environments when they are satiated, or when the level of risk in the environment is greater.
480 Indeed, we might expect animals to choose noisier areas of the environment when satiated or
481 when faced with greater risk. While not measured here, animals might also switch to relying on
482 other sensory modalities in visually noisy environments when their vision is compromised
483 (Partan, 2017; Suriyampola et al., 2018). For example, female three-spined sticklebacks rely
484 more on visual cues when choosing a mate in clear water, but in turbid water, where vision is
485 compromised, they rely more on olfactory cues (Heuschele et al., 2009). When habitats
486 consistently differ in their ecological noise, this could have sweeping effects on populations. For
487 example, grey squirrels from acoustically noisy urban habitats (*Sciurus carolinensis*) respond
488 more to visual alarm signals than squirrels from rural habitats, which instead rely more on
489 acoustic alarm signals (Partan et al., 2010). Hence animals from different populations may show
490 different behavioural responses, highlighting the need for cross-population comparisons. We
491 might also expect animals to rely more heavily on social information in sensory demanding
492 environments. Indeed, animals in groups often benefit from pooling imperfect estimates of the

493 world around them in order to make more accurate decisions collectively (Berdahl et al., 2018;
494 Dall et al., 2005; Ioannou, 2017; Ward et al., 2011). Using playbacks of caustic visual noise, it
495 would be possible to test how reliance on social information changes when individuals are
496 exposed to an ecologically relevant form of environmental noise that reduces their visual
497 perceptual abilities.

498

499

Conclusion

500 Our results demonstrate that natural forms of ecological noise reduce the likelihood of animals
501 detecting information in their environment. In response, animals can adapt their behaviour to
502 avoid noisy areas, ultimately increasing their likelihood of gathering information, and thereby
503 compensating for the negative impacts environmental noise has on their perceptual abilities.

504

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