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How predation shapes the social interaction rules of shoaling fish

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How predation shapes the social interaction rules of shoaling fish

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Abstract

Predation is thought to shape the macroscopic properties of animal groups, making moving groups more cohesive and coordinated. Precisely how predation has shaped individuals' fine-scale social interactions in natural populations, however, is unknown. Using high-resolution tracking data of shoaling fish (*Poecilia reticulata*) from populations differing in natural predation pressure, we show how predation adapts individuals' social interaction rules. Fish originating from high predation environments formed larger, more cohesive, but not more polarised groups than fish from low predation environments. Using a new approach to detect the discrete points in time when individuals decide to update their movements based on the available social cues, we determine how these collective properties emerge from individuals' microscopic social interactions. We first confirm predictions that predation shapes the attraction-repulsion dynamic of these fish, reducing the critical distance at which neighbours move apart, or come back together. While we find strong evidence that fish align with their near neighbours, we do not find that predation shapes the strength or likelihood of these alignment tendencies. We also find that predation sharpens individuals' acceleration and deceleration responses, implying key perceptual and energetic differences associated with how individuals move in different predation regimes. Our results reveal how predation can shape the social interactions of individuals in groups, ultimately driving differences in groups' collective behaviour.

Introduction

Predation is often considered to be the major selective force driving the origin and maintenance of group living [1–3]. Both theoretical and empirical studies demonstrate that an individual's per capita risk is lower in larger and more cohesive groups, reducing individual risk through dilution [4–6], attack abatement [7, 8] and confusion effects [9]. Evidence that predation drives the formation of larger and more cohesive groups has come from a number of comparative studies between populations or groups exposed to varying degrees of predation pressure [10–16]. Cohesive and coordinated group behaviours emerge, however, from the decision rules that individuals use to interact in groups, and how predation has shaped these fine-scale social decisions is still unclear.

In many moving animal groups, these social decisions are characterised by simple interaction rules, such as attraction and alignment with near neighbours, that allow individuals to remain cohesive and coordinated whilst on the move together [17–19]. It has previously been demonstrated that predators can select for cohesive and coordinated moving groups, when predatory fish preferentially targeted simulated prey that had lower degrees of social attraction and alignment with near neighbours [20]. Theoretical studies also show that predation can lead to different interaction rules being selected for, subsequently creating distinct macroscopic properties

32 of groups [21]. But exactly how predation has shaped the social interaction rules within animal groups in
33 the wild is still unknown. Now using highly quantitative movement data from real animal groups [22–25], we
34 can decode how individuals are interacting within them. Further, by comparing the social interaction rules of
35 animals that have been subject to varying degrees of predation over their evolutionary and life histories, we
36 may now determine in detail how natural predation shapes individuals' social interactions.

37 The Trinidadian guppy (*Poecilia reticulata*) is a classic evolutionary study system often used to investigate
38 how predation has shaped the life-history and behavioural traits of individuals [26]. Using simple aggregation
39 measures, Seghers (1974) and subsequently others, have demonstrated that fish living in high predation
40 environments form more cohesive shoals than fish living in low predation environments [12, 13]. Using high
41 resolution trajectory data on the movements of fish originating from both high and low predation environments,
42 here we quantify how predation has shaped the social decisions that produce these differences. We first ask
43 whether the likelihood of individuals leaving or joining groups differs between fish from high and low predation
44 populations. We go on to quantify differences in the shape, structure and directional organisation of fish
45 shoals from the high or low predation populations. We then ask how these macroscopic properties emerge
46 from differences in individuals' social interaction rules. Previous methods for inferring interaction rules in animal
47 groups have applied an averaging procedure, where the movements of animals between successive recorded
48 points in an animal's trajectory have been interpreted as discrete movement decisions. While these methods
49 have been informative, they do not differentiate between the long uninformative portions of trajectories when
50 animals continue on their course without interacting with neighbours, and the few discrete times when animals
51 update their position based on the available social cues [27, 28]. To link our understanding of collective motion
52 to perceptual and cognitive processes, therefore, we require new analytical techniques to decipher exactly when
53 and how individuals in moving groups are deciding to update their position [29, 30]. In this study, we use a
54 new method to detect when individuals *decide* to update their position based on the available social cues, and
55 then ask how these decisions have been shaped by natural predation.

56 **Materials and Methods**

57 **Experimental Methods**

58 Wild adult guppies from four rivers (Aripo, Turure, Quare and Tunapuna/Tacarigua - tributaries of the same
59 river) were collected from the Northern mountain range, Trinidad in March, 2015. Within each river, we
60 collected fish from a high predation site and a low predation site. High predation sites contain either the
61 main predator of adult guppies, *Crenicichla frenata*, or other predatory fish species (*Hoplias malabaricus* or
62 *Aequidens pulcher*). Low predation sites did not contain these species, but contained *Rivulus hartii* which
63 is not considered to be a major predator of adult guppies [26]. The dispersal of predatory fishes within the
64 rivers appears to have been limited by natural barriers, such as waterfalls, occurring along the rivers [26].
65 Therefore, high predation sites and low predation sites are found respectively further downstream or upstream
66 along the rivers. As well as differing in predation regimes, these high and low predation sites can also differ in
67 environmental factors such as canopy cover, water depth and the spectral properties of the water. However,
68 there is consensus that these differences are either less important, or augment the effects of predation in
69 driving life-history and behavioural differences between fish from these populations [31–33].

70 Fish were transported back to aquaria facilities at the University of West Indies and were housed in glass
71 tanks at 24 degrees C and fed flake food *ad libitum* at the start and middle of each day to maintain satiation
72 levels. Fish were held for at least 36 hours before experimentation. Trials were run between 0800 and 1730
73 each day. Groups of either two or eight fish of the same sex, representing group sizes naturally found in the
74 wild [34], were selected and placed into a holding tube in the corner of a visually isolated rectangular arena
75 (1000 × 900 mm). The arena was filled with aged water to a depth of 45 mm and 1 litre of water from
76 the housing tanks was added to ensure that conspecific chemical cues remained relatively consistent between
77 trials. After the fish had been in the holding tube for 5 minutes, we remotely lifted the holding tube allowing

78 the fish to explore the arena. The fish were allowed to explore the arena for ~ 16 minutes. Trials were filmed
79 at 24 frames per second at a resolution of 1920×1080 pixels using a Nikon D700 camera placed directly above
80 the arena. We determined the size of each fish by taking photographs of the fish in each trial, subsequently
81 measuring them using a bespoke script in MATLAB. No fish were re-used between trials. In total we recorded
82 ~ 73 hours of footage of shoals of 2 fish ($n = 115$ male trials, $n = 109$ female trials) and ~ 35 hours of
83 footage of shoals of 8 fish ($n = 51$ male trials, $n = 78$ female trials).

84 Analysis

85 We tracked the pairs of fish using CTrax [35] semi-automated tracking software and corrected any errors the
86 software made using the Fixerrors GUI in MATLAB. We tracked the groups of 8 fish using Didson Tracking
87 Software [36] in MATLAB. From the trajectories of the groups of eight fish, we measured a number of
88 group level properties that characterised the structure and broad-scale social dynamics of the shoals. From
89 the trajectories of the pairs, we analysed how individuals were interacting with their partner whilst moving
90 together. All analyses were done using bespoke scripts in MATLAB (2016a). For full details of analyses, see
91 Supplementary Material.

92 Statistics

93 We modelled all response variables using generalised linear mixed effects models. We performed all analyses in
94 R. These were fitted with predation regime (high or low), sex, subgroup size (where applicable) and body size
95 (see Fig. S1) as fixed effects. Because males and females and fish from high or low predation environments
96 differ in body-size (see Fig. S1), we wanted to ensure that differences in body size would not drive any
97 interpretation of the differences in behaviour of fish between high and low predation environments. Therefore,
98 to control for this, we include the body-size of fish as a covariate in all statistical models. River (nested within
99 predation and crossed with sex), and trial (where applicable) were fitted as random factors to the data. Sex,
100 Predation and subgroup size (where applicable) were treated as categorical variables in all analyses, whereas
101 body size was treated as a continuous. Full details of all statistical models, analyses, and tables can be found
102 in the Supplementary Material.

103 Results

104 Group level properties

105 Before analysing the fine-scale interactions of pairs of fish, we first quantified the broad scale social dynamics
106 of groups of eight fish, and asked whether the structure of these groups differed between fish from high or low
107 predation populations. Fish from high predation populations formed more cohesive groups than fish from low
108 predation populations, especially during the early stages of the trials (Fig. 1A&B). As the trials progressed,
109 the distance to the centre of the group centroid increased in both males and females from high and low
110 predation populations (Fig. 1). The increase in distance to the group centroid over time was due to the fish
111 breaking off into smaller subgroups. These subgroups merged and split (Fig. 2A), similar to the fission-fusion
112 behaviour guppies exhibit in the wild [34]. Guppies from high predation populations were more likely to be
113 found together in a group of 8 fish than guppies from low predation populations ($p\text{MCMC} = 0.012$; Fig. 2B;
114 Table S1).

115 To investigate the decisions driving the distributions of subgroup sizes, we determined the size of the
116 largest subgroup that was exploring the arena, and assessed how this subgroup changed in size over discretised
117 time points (two seconds). While the probability of individuals joining the largest subgroup was not different
118 between predation regimes ($p\text{MCMC} = 0.59$; Fig. 2C; Table S2), the probability that group members would

119 depart the largest subgroup was lower for fish from high predation populations (pMCMC = 0.026; Fig. 2D,
120 Table S2).

121 While these leaving and joining decisions describe the broad scale social dynamics of guppy shoals, they
122 do not examine how a group is structured when individuals are together. Guppies formed elliptical shoals with
123 the length of the shoal generally being larger than its width (females; Fig. 3 A&B and males; Fig. S2 A&B).
124 Both the width and length of shoals from high predation populations were smaller than the width and length
125 of shoals from low predation populations (width: $\chi^2 = 4.9$, d.f. = 1, $P = 0.03$; length: $\chi^2 = 10.5$, d.f. =
126 1, $P = 0.001$; Fig. S3). Fish from high predation populations similarly had smaller modal nearest neighbour
127 distances than fish from low predation populations (Fig. 3C and Fig. S4; $\chi^2 = 14.6$, d.f. = 1, $P < 0.001$).

128 Predation is not only expected to shape how cohesive groups are, but also coordination between group
129 members. In particular, predation is expected to make individuals in groups align with their near neighbours, as
130 these alignment responses may allow information transmission [37] or increase the confusion effect [20, 38, 39].
131 To investigate this, we measured a group's polarisation as a function of its speed. While groups travelling
132 faster were more polarised (Fig. S5), we found no difference in the polarisation of groups between high or
133 low predation populations (females: $\chi^2 = 0.34$, df = 1, $P = 0.56$; males: $\chi^2 = 1.09$, df = 1, $P = 0.30$).
134 Further, we found no evidence that fish from high predation populations spent more time in a highly polarised
135 state (polarisation scores above 0.85; pMCMC = 1.0), or moved more quickly than fish from low predation
136 populations ($\chi^2 = 0.1$, d.f. = 1, $P = 0.75$). Predation, therefore, appears to increase shoal cohesion, but not
137 directional alignment in these fish.

138 **Individuals' interactions in pairs**

139 The differences observed in group level properties between fish from high or low predation populations are a
140 consequence of the movement decisions that individuals use to interact with their neighbours. To investigate
141 in more detail how fish interact with their neighbours, we studied the movements of same sex pairs in the
142 arena used for the groups of eight fish. We can be sure that in pairs, the interactions between the two fish are
143 a result of each others' movements, and not some function of more than one neighbour. As with the groups
144 of eight fish, pairs of fish from high predation were closer together than fish from low predation populations
145 ($\chi^2 = 9.89$, d.f. = 1, $P = 0.002$; Fig. S6). In addition to a predation effect, smaller fish also had smaller
146 nearest neighbour distances than larger fish ($\chi^2 = 4.77$, d.f. = 1, $P = 0.03$).

147 To understand how fish from high predation populations reduce their separation distances, we first aimed
148 to classify how guppies typically shoal, regardless of any predation effects. Guppies swim with a saltatory
149 movement style, with intermittent bursts of speed (Fig. 4A), typical of many species of fish [40]. Many of
150 these speed bursts are accompanied by a change in angle immediately prior to the speed increase (Fig. 4A and
151 Fig. S7). The discrete nature of these bursts and turns leads us to refer to these changes in speed and angle
152 as movement *decisions*. We identified all the decisions made by each fish, and then asked how and when fish
153 were updating their positions as a function of their neighbour's position and movements. Indeed, other recent
154 methods have begun to use similar approaches to classify the collective motion of fish shoals [41–43].

155 The distance between the fish on the left-right axis was typically stable at ~ 15 -20 mm, but varied on the
156 front-back axis (Fig. S8). The decisions of each fish in the pair to move depended on their relative distance
157 apart. If the fish in front of its partner was less than ~ 43 mm ahead, then the lead fish accelerated (Fig. 4B).
158 The lead fish continued to accelerate until it reached a speed of ~ 130 mm/s, at which point it decelerated.
159 When the distance between the fish reached ~ 46 mm, the follower accelerated (Fig. 4C) with a similar
160 acceleration profile as the lead fish. This simple attraction-repulsion interaction acted to maintain cohesion
161 while pairs moved together asynchronously.

162 With an understanding of how the guppies adjusted their speed as a function of the neighbour's relative
163 position, we then asked whether these movement decisions differed between fish from high or low predation
164 populations. Sixteen percent of decisions in males and 13% of decisions in females resulted in the follower
165 'overtaking' the fish in front. While fish from high predation populations performed more overtaking events
166 than fish from low predation populations, this effect was not statistically significant (pMCMC = 0.09). The

167 mean distance between the pair when one of the fish decided to move was lower for fish from high predation
168 populations than from low predation populations ($\chi^2 = 7.13$, d.f. = 1, $P = 0.008$; inserts Fig. 4B & C). This
169 combination of more overtaking events and reduced initiation distances explains why the high predation pairs
170 were typically closer together.

171 The distance a fish moved during a decision (i.e. the distance it travelled from the start of one decision
172 to the start of the next decision) did not differ between fish from high or low predation environments (χ^2
173 = 0.13, d.f. = 1, $P = 0.72$), however, the acceleration during the decision did. Fish from high predation
174 populations had larger accelerations than fish from low predation populations ($\chi^2 = 5.21$, d.f. = 1, $P = 0.02$;
175 Fig. 4 D&E & Fig. S9 C&D). Fish from high predation population environments are also known to have larger
176 accelerations than fish from low predation environments during escape responses [44]. Therefore, differences
177 in the acceleration of fish from high or low predation environments might not be socially driven, and instead
178 may simply be a characteristic of how these fish move. To investigate this, we measured the acceleration of
179 the fish when they were at different distances from their partner. If differences in the accelerations between
180 fish from high and low predation were socially motivated, then we would not expect to see differences in the
181 acceleration of fish from high and low predation when the fish were further apart. There remained a difference
182 between the accelerations of high and low predation males when they were separated by more than 200 mm
183 ($\chi^2 = 8.0$, d.f. = 1, $P = 0.005$; Fig. S10B). While there was no difference in the accelerations of females
184 from high and low predation environments when fish were separated by more than 200 mm ($\chi^2 = 0.1$, d.f. =
185 1, $P = 0.76$; Fig. S10A), females were rarely separated by more than 200 mm. At least in males, therefore,
186 the higher accelerations of fish from high predation environments seem to be typical of how the fish swim,
187 regardless of social effects.

188 Guppies often use their pectoral fins during forward motion [45, 46], and we sometimes observed the fish
189 to use active braking; deceleration caused by flaring of the pectoral fins. This is indicative that at least some
190 of their movements also involve decisions to stop moving. In females, the average deceleration of a fish was
191 related to their body size, but not predation regime (bodysize: $\chi^2 = 10.1$, d.f. = 1, $P = 0.002$; predation:
192 $\chi^2 = 0.34$, d.f. = 1, $P = 0.56$; Fig. S9 E&F). In males, however, fish from high predation populations had
193 larger decelerations than fish from low predation populations ($\chi^2 = 9.7$, d.f. = 1, $P = 0.002$; Fig. 4 F&G).
194 To investigate whether these differences in deceleration between high and low predation males were socially
195 driven, again we investigated the decelerations of fish as function of the distance from their partner. There was
196 also a difference between the deceleration of males from high and low predation environments when fish were
197 separated by more than 200 mm ($\chi^2 = 6.61$, d.f. = 1, $P = 0.01$; Fig. S12B). Like these fish's accelerations,
198 therefore, larger decelerations in the males from high predation environments do not appear to be socially
199 driven.

200 Despite fish from high predation environments having larger accelerations and decelerations than fish from
201 low predation environments, high predation fish were not less synchronised than low predation fish in the timing
202 of their decisions. We measured the time lag between when one fish made a decision to the time when its
203 partner made a decision. There was no difference in these response times between high or low predation males
204 ($\chi^2 = 1.9$, $P = 0.17$) or females ($\chi^2 = 0.27$, $P = 0.60$). We also measured whether there was a difference in
205 the number of decisions individuals made per second between fish from high and low predation populations.
206 While it appeared that males from high predation populations made more decisions per second, this could be
207 explained on the basis that smaller males made more decision per second than larger males ($\chi^2 = 4.45$, d.f. =
208 1, $P = 0.035$). On the other hand, females from high predation populations made fewer decisions per second
209 than females from low predation populations ($\chi^2 = 7.92$, d.f. = 1, $P = 0.005$) with no effect of body size on
210 this decision rate ($\chi^2 = 0.38$, d.f. = 1, $P = 0.54$).

211 Forty one percent of the decisions to speed up were accompanied by the fish turning. These changes in
212 direction occurred immediately before a fish decided to increase its speed (Fig. 4A). All fish, regardless of
213 predation regime or sex showed similar turning responses to their partner's position (Fig. 5A). Fish most often
214 turned left when their partner was on the left, most often turned right if their partner was on the right, with
215 equal turns to the left and right if their partner was behind them (Fig. 5A). The turning responses of guppies,

216 therefore, can be broken down into three 120° regions as a function of partner position, as denoted by the
217 dashed lines in Figure 5A.

218 To quantify if the turning responses differed between fish from high or low predation populations, we first
219 calculated the proportion of times a fish turned towards its partner, out of all its possible turns (in the top
220 two sections of Figure 5A). While females were more likely than males to make turns towards their partner
221 (pMCMC = 0.02), fish from high or low predation populations did not differ in the likelihood of turning
222 towards their partner (pMCMC = 0.50). There was also no difference in the mean size of a fish's turn towards
223 its partner between predation regimes ($\chi^2 = 1.18$, d.f. = 1, $P = 0.28$).

224 Turns can also be used to align with a neighbour's heading, acting to increase polarisation between the
225 pair. Alignment responses have seldom been demonstrated in shoaling fish (but see [47]), as often turning is
226 correlated with the position of a neighbour (as above) and not with the heading of that neighbour [22, 25].
227 In guppies, however, we found evidence that turns are also used to align with their neighbour's heading. We
228 partitioned occasions where a neighbour was located to the left or right of a focal individual, and facing towards
229 or away from that individual (Fig. 5B). Fish would most often turn towards a neighbour if the direction to
230 the neighbour was the same sign as the heading of the neighbour (top right and bottom left sections of
231 Fig. 5B). In these cases, the effects of position of the neighbour and heading of the neighbour cannot be
232 uncoupled. Where the signs of the direction to the neighbour and heading of the neighbour are opposite (top
233 left and bottom right sections of Fig. 5B), however, the average turning response is seen to be approximately
234 zero. This is a consequence of averaging two types of responses; 1) either the focal fish turns towards the
235 direction of the neighbour (attraction response), or 2) the focal fish turns towards the heading of the neighbour
236 (an alignment response). We identified the proportion of times a fish showed alignment responses in these
237 two regions. Females showed alignment responses with their neighbour in 46% of turns, and males showed
238 alignment responses with their partner in 43% of turns. There was no evidence, however, that predation
239 increased the number of alignment responses in females (pMCMC = 0.74, Table S8) or in males (pMCMC
240 = 0.18, Table S8). Nor was there any evidence that the size of the turn to align with a neighbour's heading
241 was different between fish from high or low predation populations ($\chi^2 = 1.29$, d.f. = 1, $P = 0.26$). This
242 result is consistent with result that groups of 8 fish from high or low predation did not differ in their average
243 polarisation (see above).

244 Discussion

245 Our results demonstrate that predation shapes the social interaction rules of individuals in moving animal
246 groups. Consistent with previous coarse-scale analyses [13,48], we found that predation increases the cohesion
247 of fish shoals and further demonstrate that this cohesion results from a reduced likelihood of group departure,
248 thereby stabilising larger group sizes. Our detailed analysis of individuals' movement decisions has revealed that
249 predation shapes fish's attraction-repulsion dynamic, decreasing the critical distance between individuals when
250 they decide to move apart or come back together. Fish from high predation environments achieve increased
251 cohesion despite having larger accelerations and decelerations than fish from low predation environments.
252 There is no evidence, however, that predation shapes individuals' alignment or turning responses, explaining
253 why shoals from high or low predation environments did not differ in group polarisation.

254 Previous studies have suggested that both alignment and attraction responses could be shaped by predation,
255 making group members more cohesive and coordinated with each other [20,21,49]. It appears in this predatory-
256 prey system, predation has shaped the cohesion but not the directional alignment of individuals. Many of the
257 predators of guppies typically attack in short bursts, striking from ambush locations without sustained chases
258 of attack [50, 51]. Belonging to a larger group and being closer together, therefore, is perhaps sufficient in
259 reducing individual risk through dilution and selfish herd effects during relatively brief predator encounters in
260 this system. In addition, larger, more cohesive, but not necessarily more aligned groups, can increase the
261 confusion effect making it more difficult for a predator to isolate prey [38, 52, 53]. An interesting area of
262 research could be to compare the behaviour of fish from high or low predation populations in the presence or

263 absence of predators, or when exposed to different types of predators (e.g. avian or fish predators). This could
264 help highlight how different rules of interaction are selected for, or indeed if the plasticity of anti-predatory
265 responses differ between populations, when prey are exposed to different levels of predation or different predator
266 tactics.

267 Fish from high predation environments increased cohesion (relative to fish from low predation environments)
268 by decreasing the critical distances at which they decided to move apart or come back together. It will now
269 be of interest to elucidate the finer neurological mechanisms that are responsible for this distance control.
270 The visual system is likely to be the primary sensory modality that is involved in detecting information about
271 the positions and movements of neighbours before a motor decision is initiated. It is interesting to note
272 that the bearing angles at which guppies attempt to position their neighbours (Fig. S8) are consistent with
273 the theoretical angles that maximise the visual sensitivity for detecting looming objects (such as a neighbour
274 getting closer) and for heading changes of those neighbours [54]. This is consistent with the positioning
275 behaviour of other fish species with stop-start movement [58]. New techniques that detect the sensitivity of
276 retinal cells to approaching and receding objects [55], as well as detailed information on how neighbours are
277 perceived in moving animal groups [29, 30] will prove useful in determining whether the sensitivity, or response,
278 to such visual stimuli differs between fish from high or low predation populations.

279 Another way for individuals in groups to decrease risk is to have effective information transfer between
280 group members [56, 57]. Swain et al. (2015) proposed that the oscillatory movements of fish in schools, like in
281 our study, enriches social information exchange between individuals by breaking the number of occlusions that
282 occur between neighbours [58]. The result that fish from high predation populations were closer together, and
283 performed more, albeit not statistically significant, switches in position than fish from low predation populations
284 is consistent with these interpretations. Predation is likely to shape multiple facets of an individuals' anti-
285 predatory behaviours including group cohesion, but also the propensity for information exchange. This in turn
286 may impact how groups make collective decisions together [59].

287 Fish from high predation environments had larger changes in speed than fish from low predation environ-
288 ments. In males, this difference persisted even when the fish were separated by more than 200 mm, suggesting
289 these responses may not be tailored around social interactions. Indeed, guppies from high predation en-
290 vironments also show stronger accelerations during escape responses compared to fish from low predation
291 environments [44]. Motion creates blur on an animal's retina [60, 61] and because of this, detecting moving
292 objects is more difficult with changing speed [62]. Because these fish move with intermittent bursts, it may
293 be more important for fish from high predation environments to minimise the time when excessive motion
294 blur occurs compared to fish from low predation environments. Strengthening both acceleration and decel-
295 eration responses could allow for this. Larger acceleration and deceleration responses, however, are likely to
296 be more energetically costly [40], and this may explain why these rapid movements are not adopted across
297 environmental contexts.

298 In our study, we used wild caught fish, and therefore cannot disentangle the effects of selection by predation
299 and environmental effects, for example, early life exposure to predators. In Seghers' previous work [13], F3-F4
300 generation fish bred from wild caught individuals and raised under identical conditions indicated that differences
301 in the schooling behaviour between populations were heritable. It seems likely, therefore, that the effects we
302 observed would also be heritable, although future studies will need to confirm this. Nevertheless, by comparing
303 the collective movement of fish from high and low predation populations, we have provided strong evidence
304 that predation shapes the interaction rules of shoaling fish. Our method to detect the discrete movement
305 decisions made by individuals in moving animal groups also provides a technique to analyse how animals with
306 intermittent forms of locomotion move together. A combination of these analytical techniques, combined with
307 comparative studies and detailed models of collective motion [63–65], will lead to an integrated understanding
308 of how the interaction rules that drive collective motion have been shaped by natural selection.

309 **Author Contributions**

310 JEH-R collected the data. JEH-R, ER, AS, CI and BR analysed the data and performed statistical analy-
311 sis. JEH-R wrote the paper with substantial input from all co-authors. All authors gave final approval for
312 publication.

313 **Data Accessibility**

314 All data accompanying this manuscript can be downloaded from the following link:
315 <https://figshare.com/s/acc597a873aa0567ade>

316 **Ethical Statement**

317 This research was performed in accordance with the laws, guidelines and ethical standards of Trinidad and
318 Tobago, where the research was performed. The procedures were also conducted in accordance with the
319 ASAB/ABS Guidelines for the Use of Animals in Research.

320 **Competing Interests**

321 The authors declare we have no financial or non-financial competing interests

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327 Romain Clement, Alexander Wilson, Ralf Kurvers and Stefan Krause for advice and assistance in the field. We
328 also thank two anonymous reviewers.

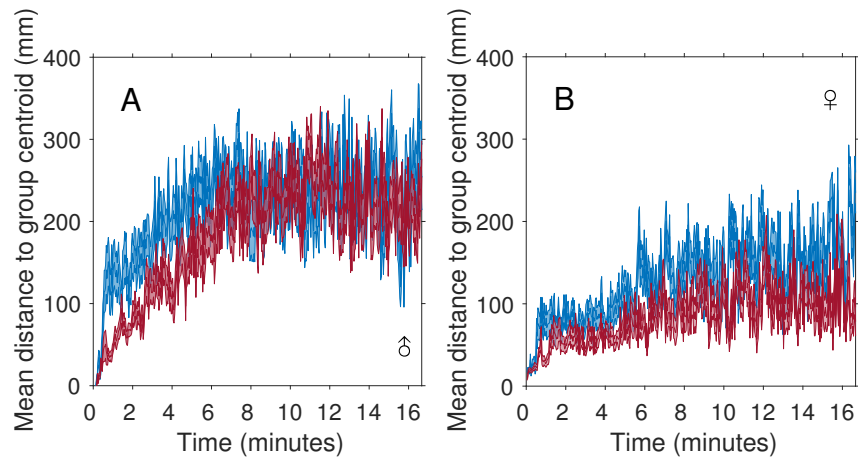


Figure 1. Mean (± 1 SE) distance individuals were from the group's centroid for shoals of eight (A) male or (B) female fish. Shoals from high predation environments are shown in red and shoals from low predation environments are shown in blue.

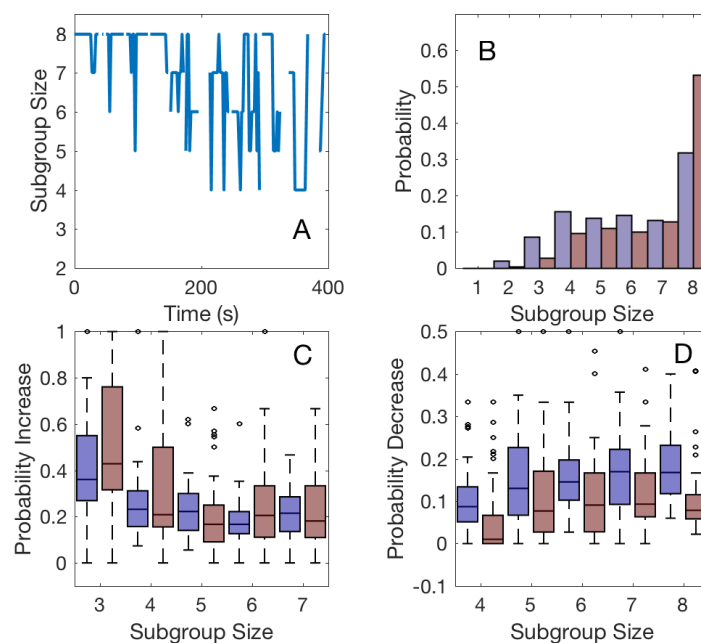


Figure 2. (A) Example of the number of fish in the main subgroup for the first 400 seconds of one of the trials with 8 female fish. Fish generally break up into smaller subgroups over the course of the trial. (B). Probability distribution of the largest subgroup size for fish from low (blue) or high (red) predation populations. (C&D) Probability that fish from low (blue) or high (red) predation populations join (C) or leave (D) the largest subgroup while exploring the arena. Fish from high predation populations are less likely to depart the group, whereas the joining probabilities between populations is the same (Table S2). The horizontal lines in the centre of each box denotes the median of each category, while the bottom and top edges of each box denote the 25th and 75th percentiles, respectively. Whiskers extends to the data points that are not considered outliers (black circles). Subgroups in this figure were classified as fish that were within 100mm of at least one neighbour (see Supp. Mat).

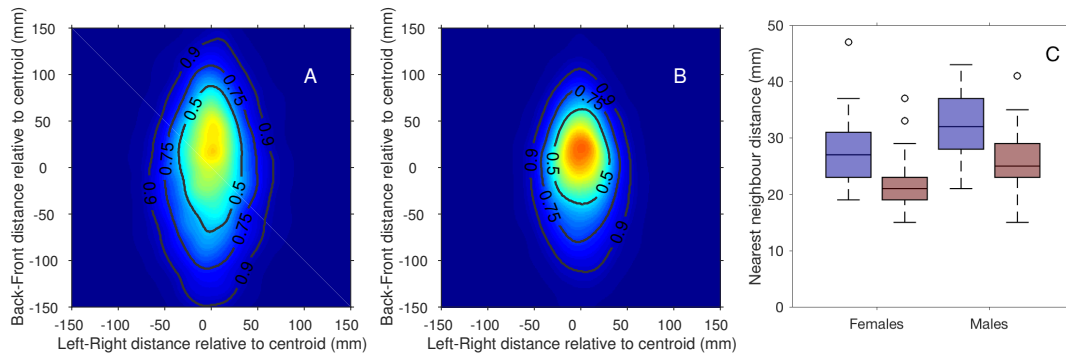


Figure 3. Shape of shoals of 8 female fish from low predation (A) or high predation (B) populations. Contour lines represent regions containing the proportion of total observations where individuals were found relative to the shoal centroid located at (0,0). Shoals from high predation populations were generally more compact than shoals from low predation populations. These patterns were consistent in shoals of 8 male fish (Fig. S2) and across different subgroup sizes (Fig. S3). (C) Modal nearest neighbour distances were also smaller for fish from high predation environments (red) compared to low predation environments (blue). This was consistent across females (left) and males (right). See Fig. S4 for a break-down of modal nearest neighbour distances by river. The horizontal lines in the centre of each box denotes the median of each category, while the bottom and top edges of each box denote the 25th and 75th percentiles, respectively. Whiskers extends to the data points that are not considered outliers (black circles).

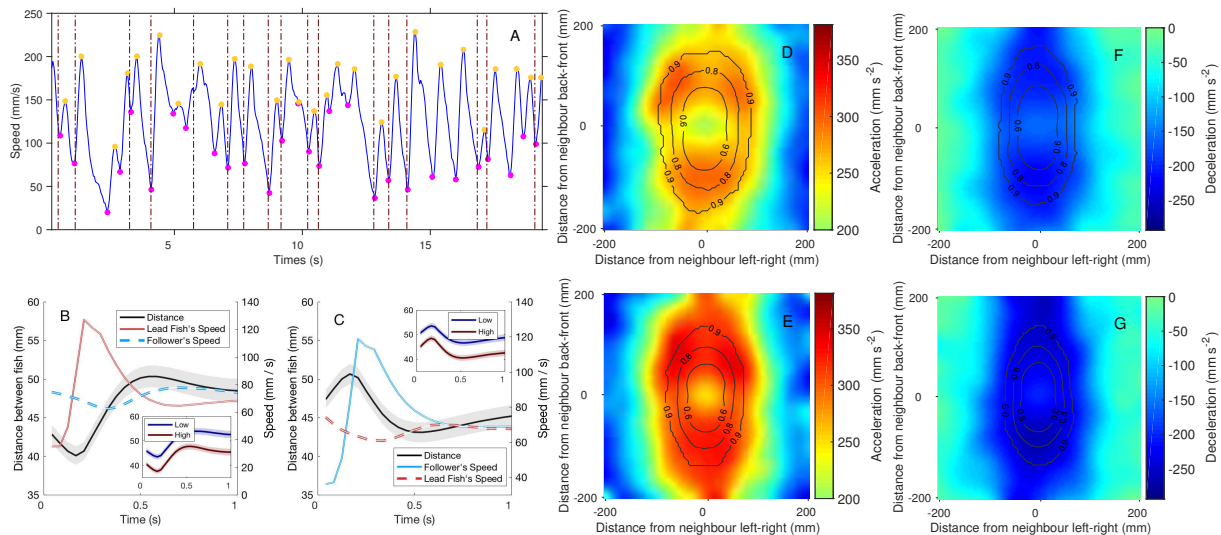


Figure 4. (A) Example of a fish's typical speed profile. For each fish's speed profile, we determined the times when it decided to 'update its position' by detecting the times when the fish's speed was in a trough (magenta points). We also detected the maximum speeds associated with these decisions (yellow points). Many of these decisions were associated with a change in angle immediately prior to the increase in speed (dashed vertical lines - see Fig. S7). (B) Speed profile of the fish at the front of the pair (red line - refer to right Y axis) when it decides to move (at 0 seconds). The lead fish decides to move when the distance between the fish reaches ~ 43 mm (averaged over both high and low predation males), but these distances are significantly lower in fish from high predation populations (red line in insert) than fish from low predation populations (blue line in insert). (C) Speed profile of the follower (light blue line - refer to right Y axis) when it decides to move. The follower speeds up when the distance between the fish reaches ~ 47 mm (averaged over both high and low predation males), but again, these distances are significantly lower in fish from high predation populations (red line in insert) than fish from low predation populations (blue line in insert). Error bars in (B) & (C) represent mean standard error per trial (only partially visible for speed due to low variation). Data are only for male fish, but females also show the same movement profile, with similar separation distances (Fig. S9) (D&E) Acceleration of male fish from low (D) or high (E) predation populations as a function of neighbour position. (F&G) Deceleration of male fish from low (F) or high (G) predation populations as a function of neighbour position. In each of these plots, the fish making the decision is located at (0,0) and facing along the positive Y axis. Males fish from high populations have higher acceleration and deceleration than their low predation counterparts. Data from lead fish and followers are combined within these plots since they show similar symmetry around $y = 0$. Contour lines represent the proportion of observations of neighbours in those respective positions.

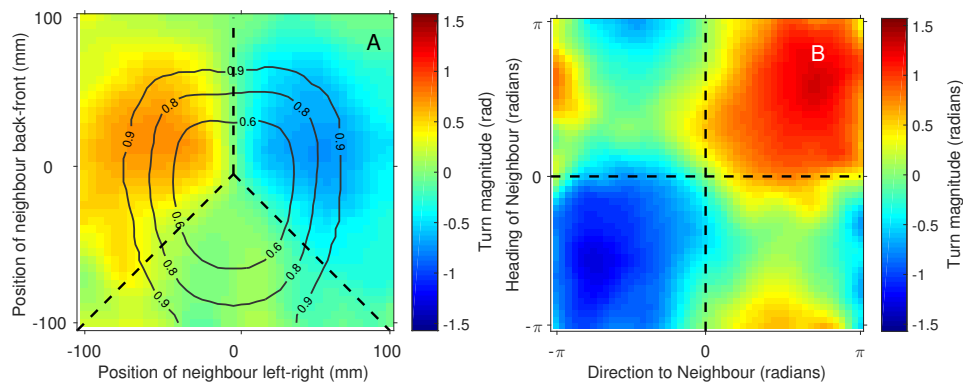


Figure 5. (A) Mean turning angle of a fish as a function of its neighbour's position, averaged across both sexes and predation regimes as all categories showed similar responses. The fish making the turning decision is located at (0,0) and facing along the positive Y axis. Fish turn left when their neighbour is ~ 45 degrees and on their left, turn right when their neighbour is ~ 45 degrees and on their right. They have approximately equal proportions of left and right turns when their neighbour is behind them. Contour lines represent the proportion of observations of neighbours in those respective positions. (B) Turning response of a focal fish as a function of its neighbour's direction (x axis) or heading (y axis). Data in this figure are averaged across males and females and across populations, as all fish showed similar turning profiles. The dashed lines in both panels separate regions of interest that were analysed in statistical models.

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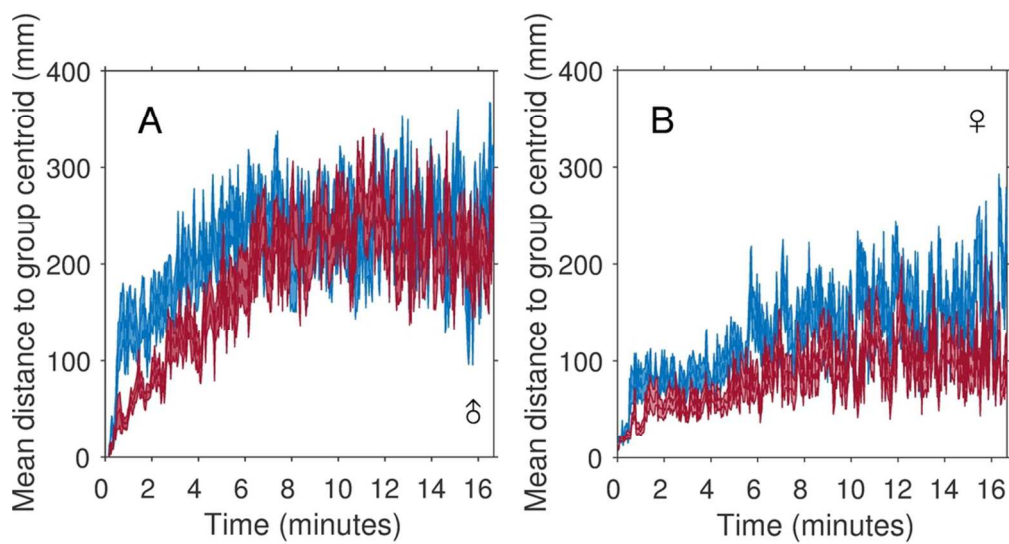


Figure 1

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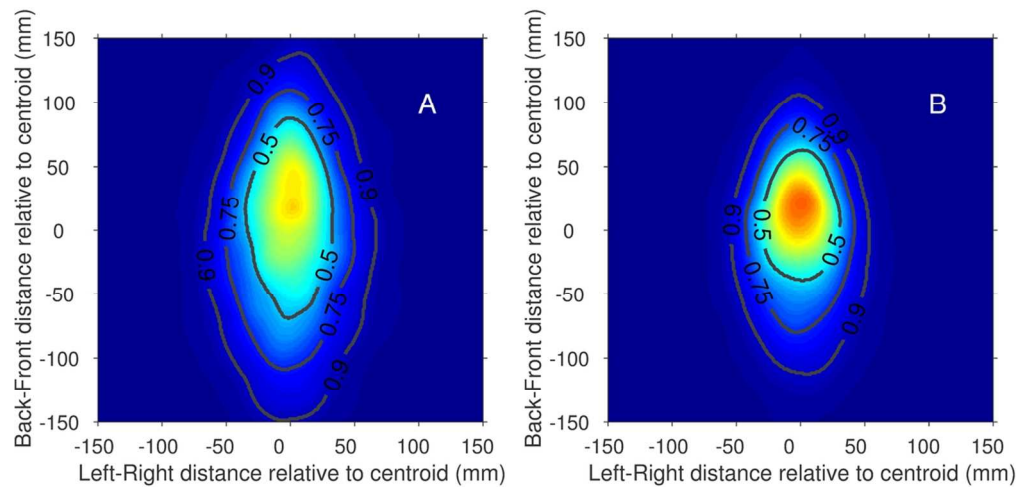


Figure 3ab

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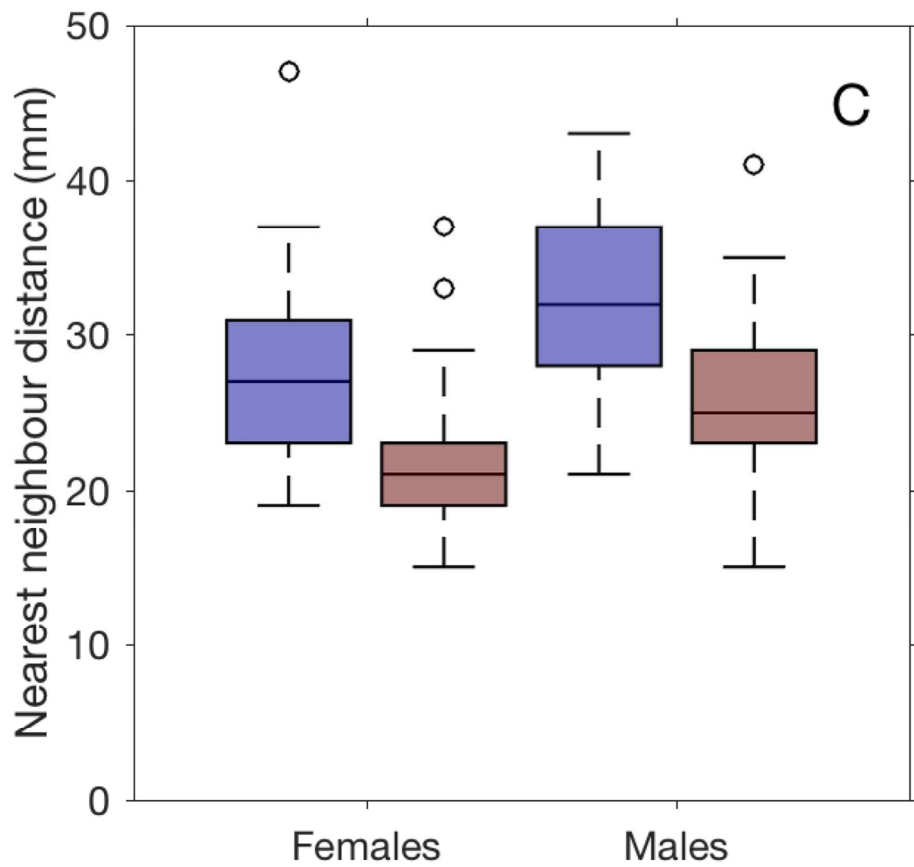


Figure 3c

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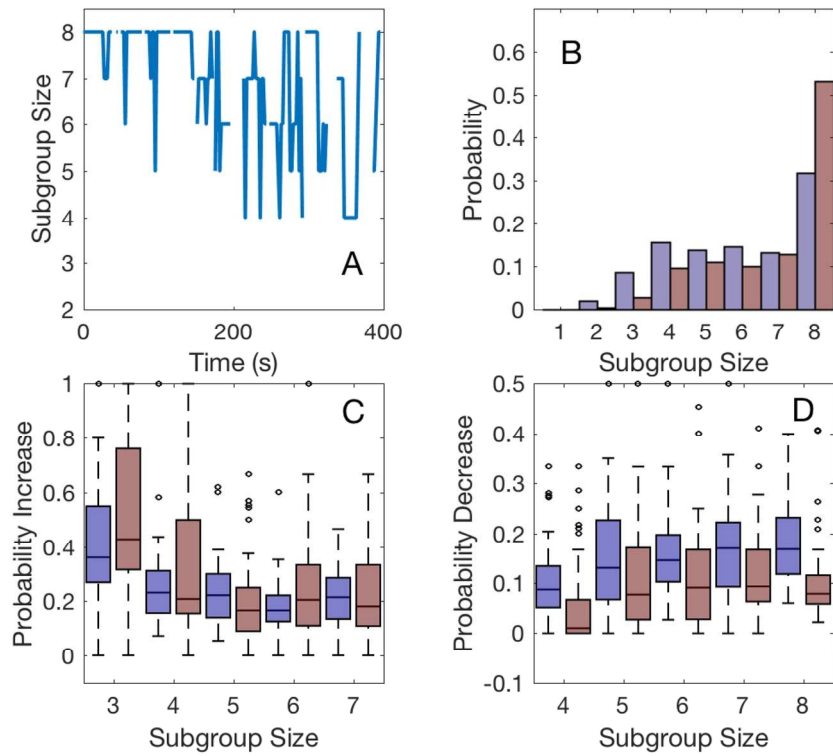


Figure 2

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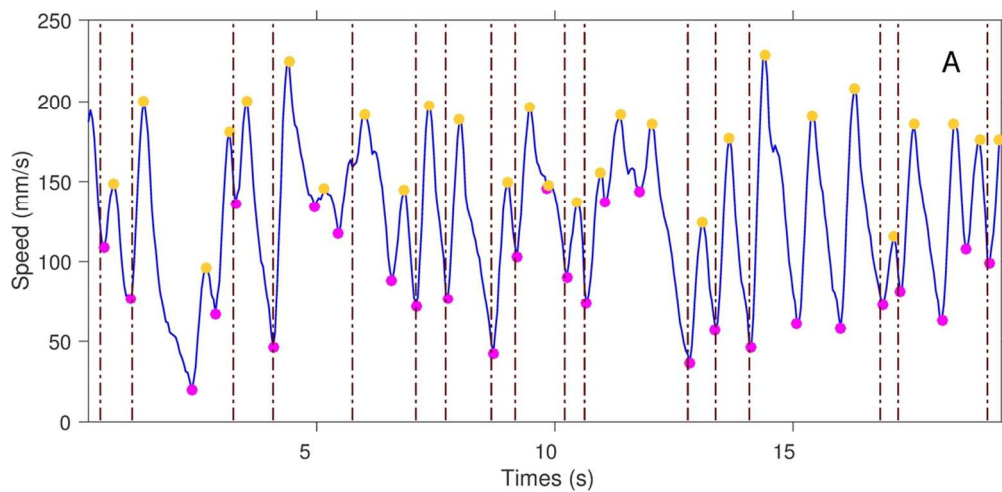


Figure 4a

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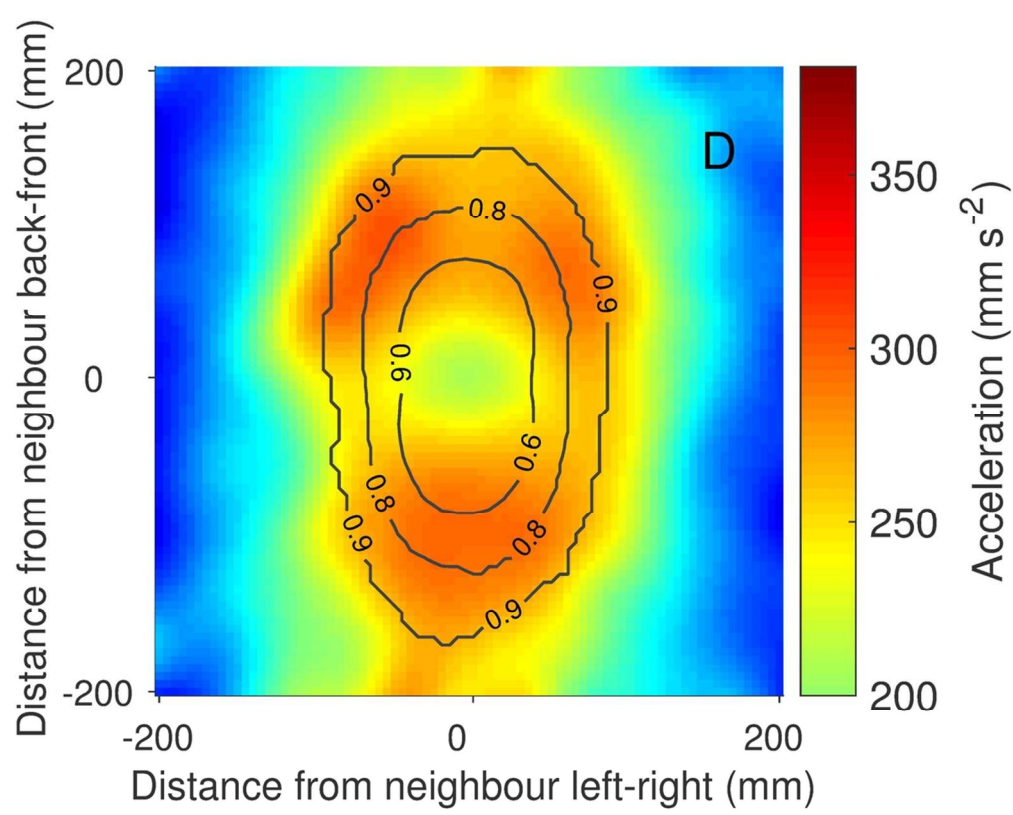


Figure 4D

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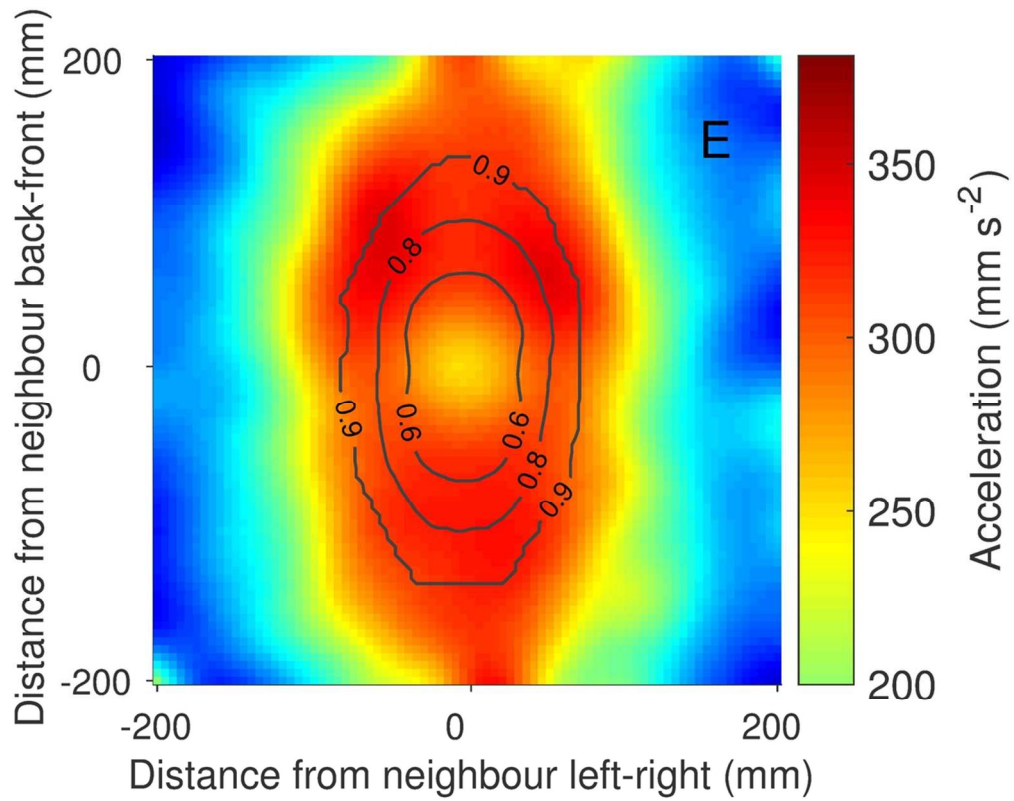


Figure 4E

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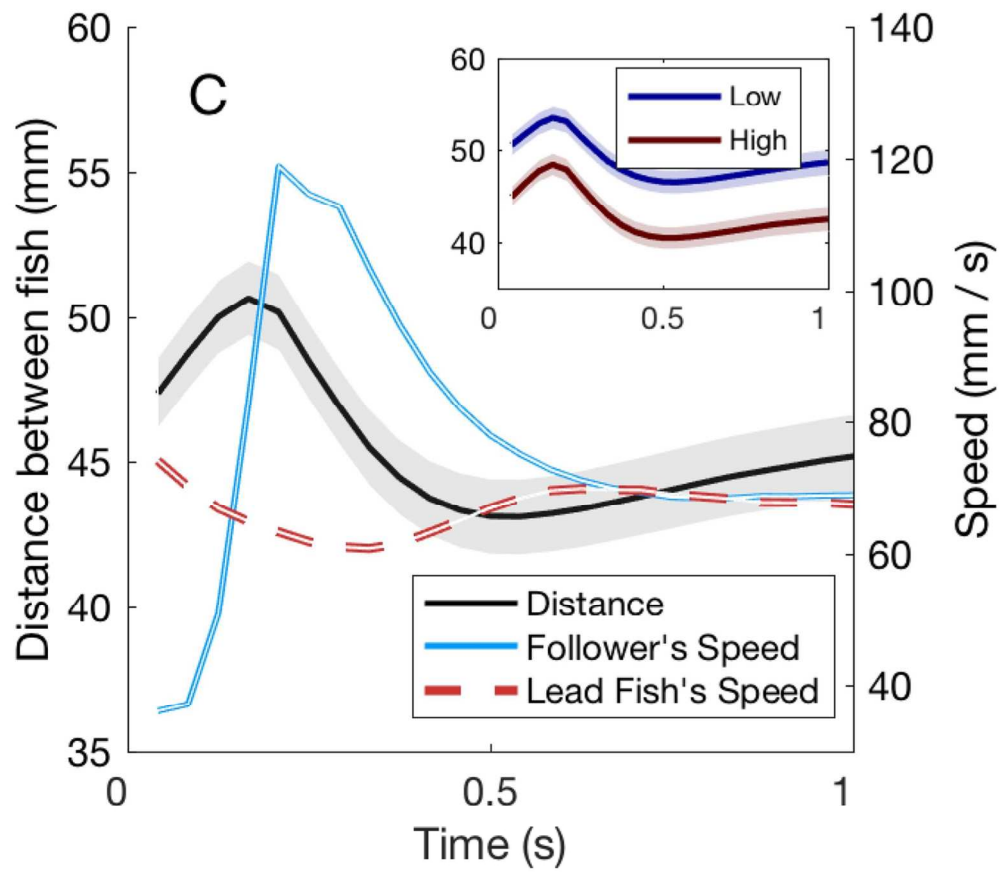


Figure 4C

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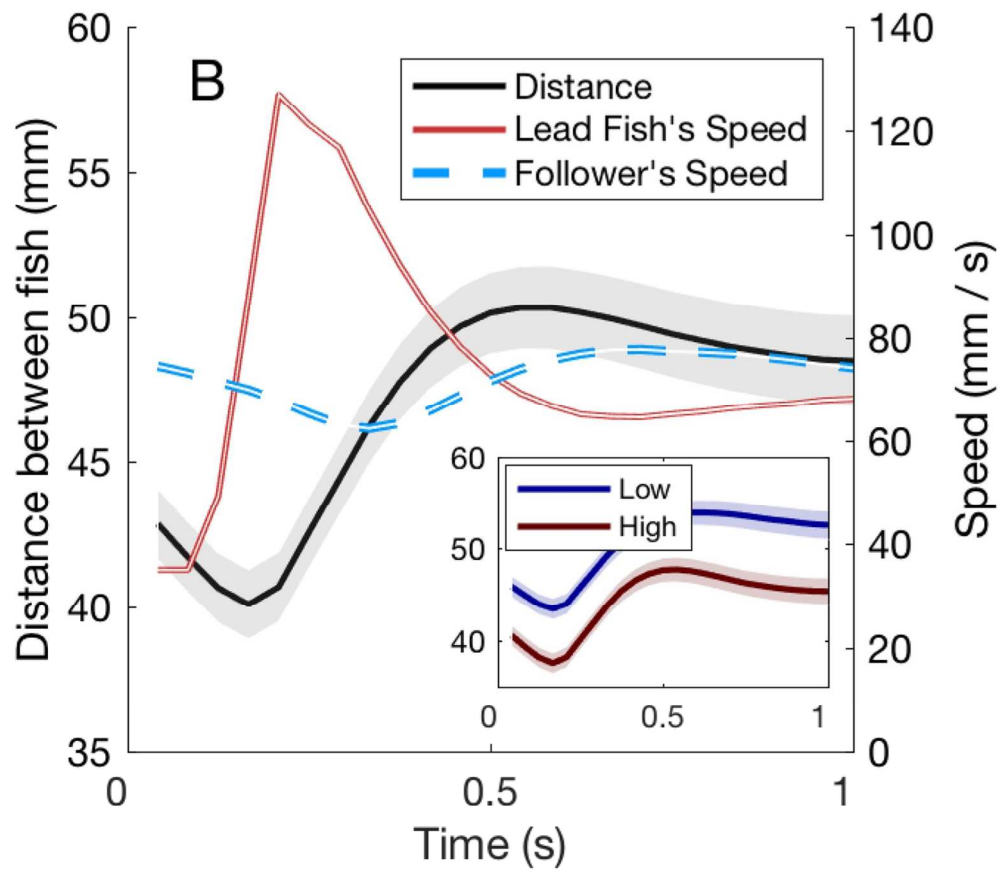


Figure 4B

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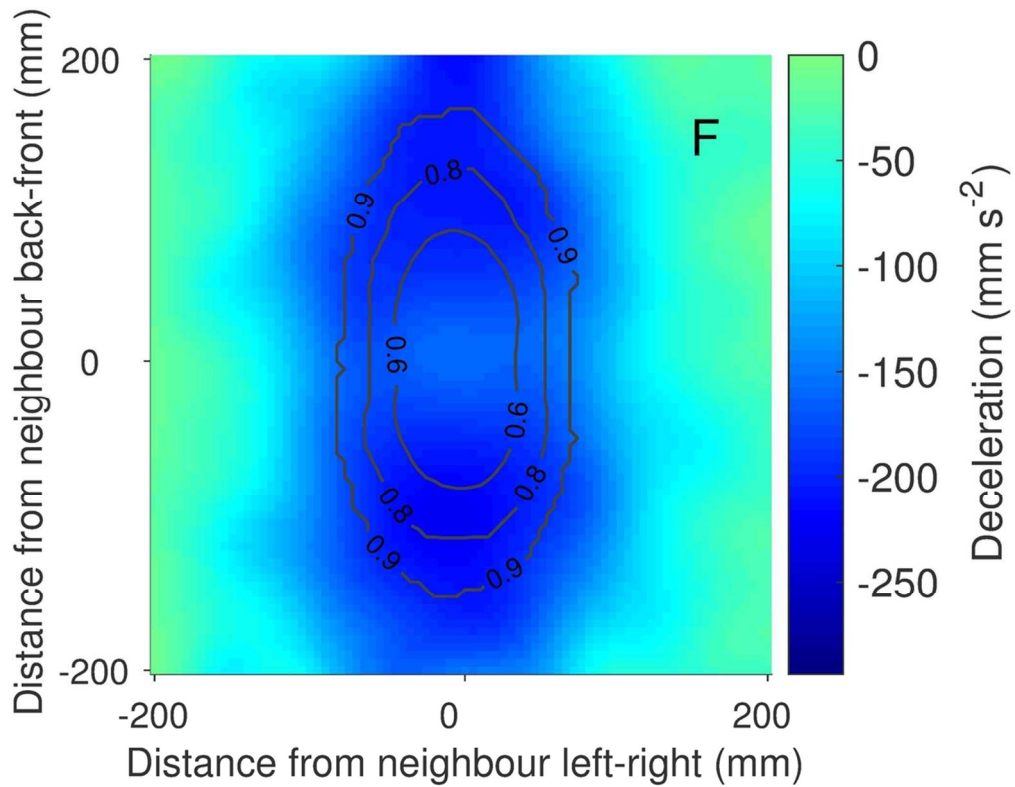


Figure 4F

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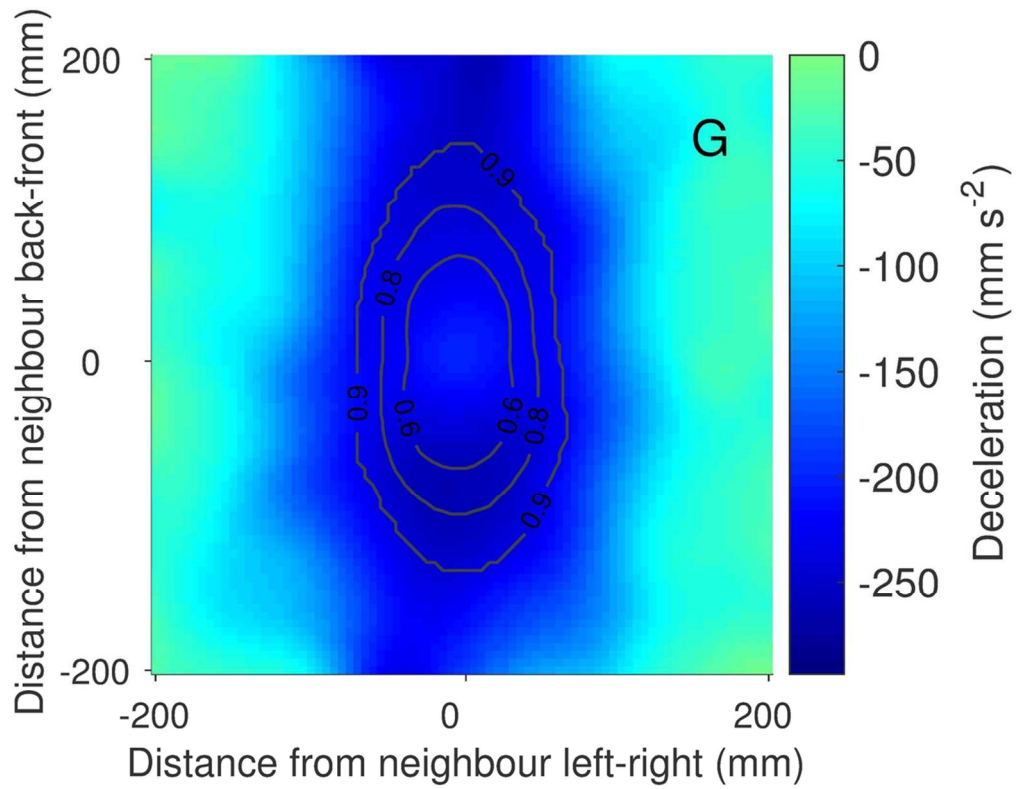


Figure 4G

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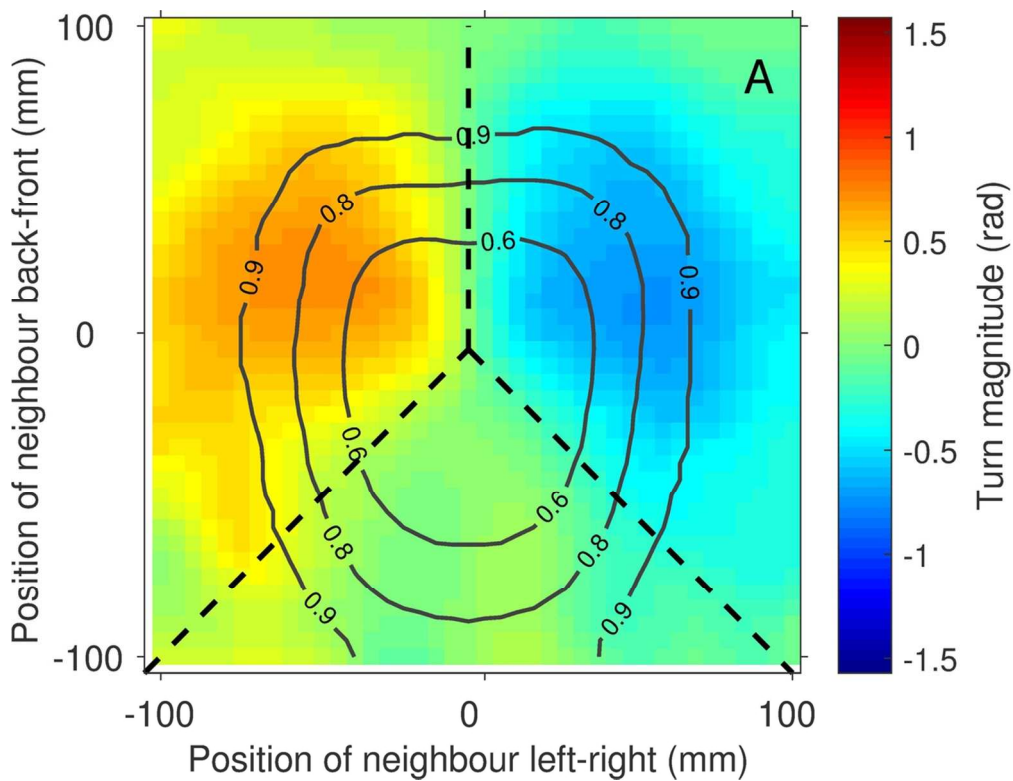


Figure 5A

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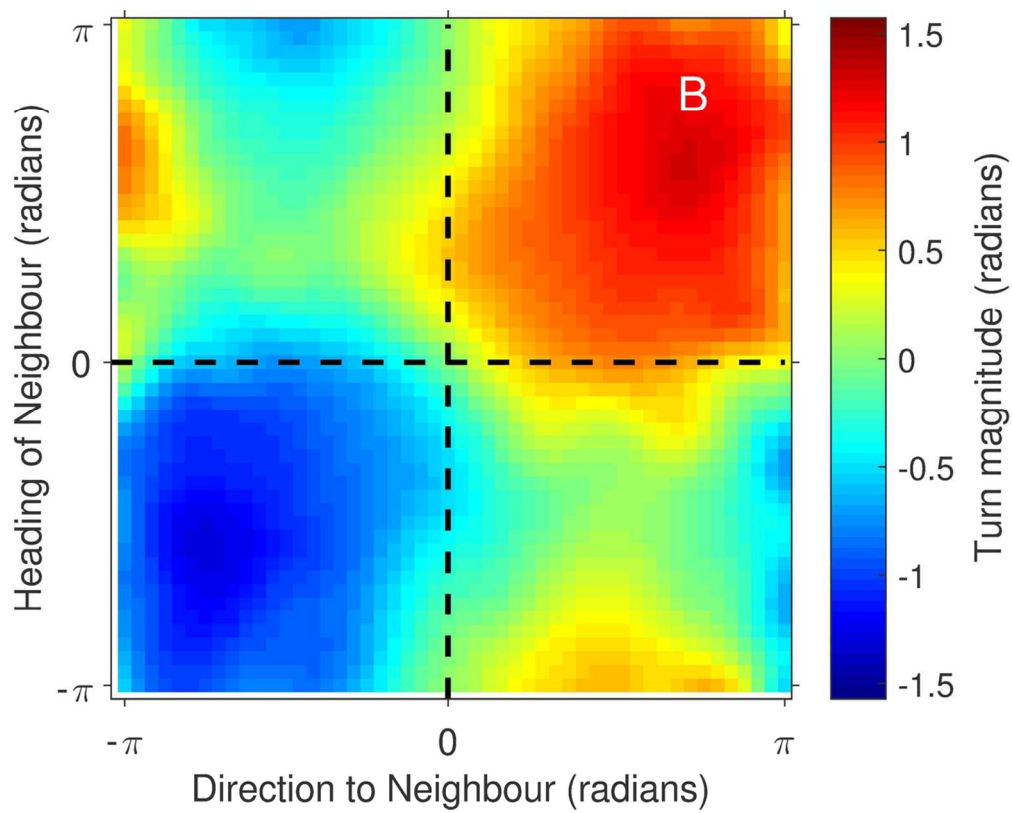


Figure 5B

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