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Collective decision-making appears more egalitarian in populations where group fission costs are higher

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Abstract

Collective decision-making is predicted to be more egalitarian in conditions where the costs of group fission are higher. Here we ask whether Trinidadian guppies (*Poecilia reticulata*) living in high or low predation environments, and thereby facing differential group fission costs, make collective decisions in line with this prediction. Using a classic decision-making scenario, we found that fish from high predation environments switched their positions within groups more frequently than fish from low predation environments. Because the relative positions individuals adopt in moving groups can influence their contribution towards group decisions, increased positional switching appears to support the prediction of more evenly distributed decision-making in populations where group fission costs are higher. In an agent-based model, we further identified that more frequent, asynchronous updating of individuals' positions could explain increased positional switching, as was observed in fish from high predation environments. Our results are consistent with theoretical predictions about the structure of collective decision-making and the adaptability of social decision-rules in the face of different environmental contexts.

1. Introduction

Collective decisions involve individuals in groups combining their own imperfect estimates of the world around them to reach consensuses about travel directions, activities or choices, while at the same time remaining cohesive [1]. In many cases, if animals are to benefit from such information sharing, they should distribute decision-making evenly between group members [1]. However, because conflict exists in groups, where individuals have to balance the need for social cohesion with that of their own goal-oriented behaviour [1–4], some individuals may disproportionately influence the decision-making process, either through active or passive mechanisms.

43 Theoretical models suggest that the degree to which decision-making is shared between
44 group members is influenced by both environmental and social conditions [5,6]. In
45 environments where the benefits of remaining with other group members outweigh any
46 potential ‘consensus costs’, that is, costs of following others’ decisions, then equally
47 shared decision-making is more likely to evolve [7,8]. Unshared decision-making, on
48 the other hand, is more likely to evolve when consensus costs are relatively high
49 compared to the benefits of social cohesion [7,8]. Importantly, under both these
50 scenarios, the observed outcome of decision-making can often be the same, where
51 groups remain cohesive despite consensus being reached by relatively shared or
52 unshared decision-making processes.

53 Investigating these theoretical predictions requires an experimental system where either
54 the consensus costs or group cohesion costs differ between populations, and the degree
55 to which decisions are shared or unshared can be approximated. The Trinidadian guppy
56 (*Poecilia reticulata*) offers one such system. Populations of guppies in the Northern
57 Mountain range of Trinidad have been exposed to either relatively high or low levels
58 of predation over both their evolutionary and ontogenetic histories [9,10]. Because
59 group cohesion significantly reduces predation risk [11,12], this system offers an
60 opportunity to assess whether group decision-making appears more or less shared
61 between group members in populations where the costs of group fragmentation differ.
62 Here, we give groups of guppies a classic decision-making paradigm [13,14], where
63 groups choose to swim down one of two arms of a Y-maze. We tested multiple group
64 sizes to assess whether the patterns observed were robust to differences in group size.
65 Because positions at the front of groups are more conducive of leadership, and in many
66 animal groups information flows from the front to the back of groups, [15–17],
67 positional changes within groups appears to be informative about who is
68 disproportionately influencing the decision-making process [13,18]. We therefore
69 calculated the number of times individuals switched positions within the group before
70 they reached a decision, with increased positional switching acting as a proxy for more
71 distributed decision-making. Further, using a simple one-dimensional model, we
72 explored how differences in how individuals moved might result in different amounts
73 of positional switching within groups.

74 2. Material and methods

75 (a) Experimental Methods

76 Adult female guppies (*P. reticulata*) were caught from four locations with high
77 predation risk (Arima, Lower Guanapo, Lower Lopinot and Tacarigua rivers) and four
78 locations with low predation risk (Paria, Upper Guanapo, Upper Lopinot, Upper Turre
79 rivers) in July 2013. High predation sites contain *Crenicichla frenata*, *Hoplias*
80 *malabaricus* or *Aequidens pulcher* which prey on adult guppies, whereas these
81 predators are largely absent from low predation sites, although low predation sites do
82 contain *Rivulus hartii* which prey on juvenile guppies [9,18].

83 Fish were transported back to the University of the West Indies, St Augustine Campus
84 where they were housed in 120 cm diameter circular holding pools (~ 90 fish per pool)
85 in an outdoor enclosure that was shaded between 0800 - 1400 hrs (when trials were
86 run). Water depth in the pools was maintained between 10 - 13 cm, and the pools were
87 emptied, rinsed and refilled between stocking fish from different populations. We
88 suspended a clear polythene sheet over the housing pools and test arena throughout the
89 study to stop rain falling in the pools.

90 For each trial, groups of two, four or eight fish with approximately the same body length
91 were caught from the housing pools and placed into a 15 x 15 cm transparent plastic
92 box at the end of the stem of a Y maze (stem 15 cm wide, 71 cm long; Fig. 1A).
93 Following two minutes of acclimation, the box was remotely lifted, allowing the shoals
94 to explore the novel maze environment. Groups swam down the stem of the Y maze
95 before making a decision to swim into the left or right arm of the maze. Trials were
96 filmed with a Canon 550D DSLR camera mounted 1.25 m above the maze at 25 fps
97 and a resolution of 1920 x 1080 pixels. We tested group sizes of two ($n = 77$), four (n
98 $= 76$) or eight ($n = 77$) fish, with each group size being tested once in a block of three
99 trials, and the order of testing randomised within each block. Fish were never used in
100 more than one trial. We used automated tracking software [19] to track the positions
101 and orientations of fish as they made a decision. In particular, we measured the number
102 of times the group did not reach a consensus (defined when at least two group members
103 chose different arms of the Y-maze to swim down), the mean speed of fish, their
104 cohesion (median distance of group members to the group's centroid), the number of
105 times they switched position (see Results), and the number of movement decisions fish
106 made per second (see Results). All measures were calculated from the time a fish
107 entered the blue region in Figure 1A until a fish crossed into one of the arms of the Y-
108 maze (dashed white lines in Fig. 1A). Group cohesion was only measured during times
109 when all group members were simultaneously tracked. All measures were analysed
110 using linear or generalised linear mixed models (see Supplementary material for further
111 details). All models included predation regime (high or low), group size and the mean
112 body size of fish (standard length measured from stills in the videos) in each group as
113 fixed effects. As expected, fish from high predation populations were significantly
114 smaller (2.02 ± 0.48 , mean \pm SD) than fish from low predation populations ($2.29 \pm$
115 0.36 , mean \pm SD; Linear Mixed Model, Likelihood Ratio Test: 28.97, $P < 0.001$),
116 making body size an important covariate in our models. Population was included as a
117 random effect in all models. The significance of each term within the models was tested
118 using Likelihood Ratio Tests (LRT) to compare models with and without the term of
119 interest. All statistical analyses were carried out in R version 3.1.2, and data are
120 available as Data S1.

121 3. Results

122 The proportion of groups that split apart during the decision making process did not
123 differ between the two predation regimes (LRT = 1.61, $P = 0.20$; only 33/231 groups

124 split). Further, fish from the different predation regimes did not differ in their median
125 swim speeds as they made these decisions (LRT = 0.42, $P = 0.52$). Groups of fish from
126 high and low predation environments, therefore, made similarly fast and cohesive
127 decisions.

128 We next investigated whether individuals within groups from different predation
129 regimes contributed to the consensus decisions more or less equally. To measure this,
130 fish were ranked from 1 to n fish as they swam down the stem of the Y-maze (shaded
131 blue region in Fig. 1A), with fish at the front of the group given a ranking of one, and
132 the fish at the back of the group, n (Fig. 1A). We then calculated number of times these
133 ranks changed in the times leading up to the final decision (when the first fish crossed
134 a dashed line in Fig. 1A). Note that if a pair of fish switched their positions, this was
135 counted as two switches, and we controlled for potential differences in cohesion
136 between the populations by including cohesion as a covariate in the models. Fish from
137 high predation environments switched position more often than fish from low predation
138 environments (LRT = 5.12, $P = 0.024$; Fig. 1B), and as expected, larger groups also
139 made more switches than smaller groups (LRT = 122.8, $P < 0.001$; Fig. 1B). These
140 effects were also observed when considering only switches that occurred at the front
141 position of the group (predation: LRT = 7.07, $P < 0.01$; group size: LRT = 20.28, $P <$
142 0.001).

143 We then investigated the potential mechanism for how fish from high-predation
144 environments made more switches in position than fish from low predation
145 environments. Guppies, as in many other species of fish, move with intermittent
146 changes in speed, which can be thought of as movement decisions [20]. We identified
147 the number of movement-decisions that fish made per second by identifying the times
148 when fish's speeds were at a minimum (see grey markers in Fig. 2A). After controlling
149 for the effects of median speed (LRT = 197.6, $P < 0.001$) and body size (LRT = 22.1,
150 $P < 0.001$), fish from high predation environments still made more decisions per second
151 than fish from low predation environments (LRT = 4.31, $P = 0.038$; Fig. 2B).

152 To test whether differences in the rate at which fish updated their position could explain
153 differential switching behaviour between the populations, we built a simple one-
154 dimensional self-propelled particle model capturing the dynamics of guppies'
155 movements. On each time step, agents updated their position along a one-dimensional
156 world with a probability, p , that was determined by the mean update frequency of fish
157 in either low ($p = 0.0368$) or high ($p = 0.0463$) predation environments (Fig. 2B). If fish
158 updated their position, they moved for a uniformly randomly determined distance in
159 the range, $0 - d$ (where $d > 0$). The only social interaction we implemented was an
160 attraction rule to neighbours behind a focal individual, that is, if the focal individual
161 was in front of its closest follower by more than d , it did not update its position. One
162 hundred simulation runs were performed for the same relative number of time-steps it
163 took fish to make the decision for each experimental trial ($n = 231 \times 100$). This simple
164 model captured the switching rates observed in the experimental trials, with agents with

165 higher update probabilities switching position more often than agents with low update
166 probabilities (Fig. 2C).

167 4. Discussion

168 Groups from high predation environments switched positions more often, and made
169 more movement decisions per second, than fish from low predation environments. In a
170 simple agent based model, increased frequency of asynchronous movement decisions
171 was associated with this increased positional switching. These results are consistent
172 with theoretical predictions that collective-decision making is more equally shared
173 between group members in environments where the costs of group fission are higher
174 [7,8].

175 Oscillations in speed and switching of positions are thought to break visual occlusion
176 between group members, thereby facilitating more efficient spread of information
177 through groups [21]. Mechanisms that promote the likelihood that multiple individuals
178 contribute towards detecting and sharing information about potential sources of risk,
179 therefore, might be favoured in environments where those threats are higher. Indeed,
180 such mechanisms could allow the collective pooling of information and the emergence
181 of swarm intelligence [22], especially when information collected by group members
182 is uncorrelated [23,24]. While in our model, increased asynchronous movements could
183 explain increased positional switching, more frequent movements are also likely to be
184 coupled by increased energetic requirements. This may explain why increased
185 positional switching may not be adopted in environments where information sharing
186 might be less important, such as when predation risk is relatively lower.

187 While we interpret our results in the context of a decision-making, it is important to
188 consider other mechanisms that could contribute to increased positional switching in
189 high compared to low predation environments. Higher sensitivity to risk [25],
190 swimming performance [26], or trade-offs in occupying rewarding yet risky positions
191 in groups [12] may contribute towards increased positional switching in high compared
192 to low predation environments. While these factors are not mutually exclusive from
193 more or less distributed decision-making processes, future work should attempt to
194 control for these factors when investigating the importance of positional switching
195 during decision-making. Our work suggests, however, that populations have intrinsic
196 differences in the degree to which decision-making is shared between group members,
197 and this could be ultimately shaped by differences in the ecological conditions that
198 these populations experience.

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200 **Data accessibility.** Data accompanying the paper can be downloaded from dryad.com:
201 <https://doi.org.10.5061/dryad.nvx0k6dn6>

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208
209 **Conflict of interests.** The authors declare they have no conflicts of interest

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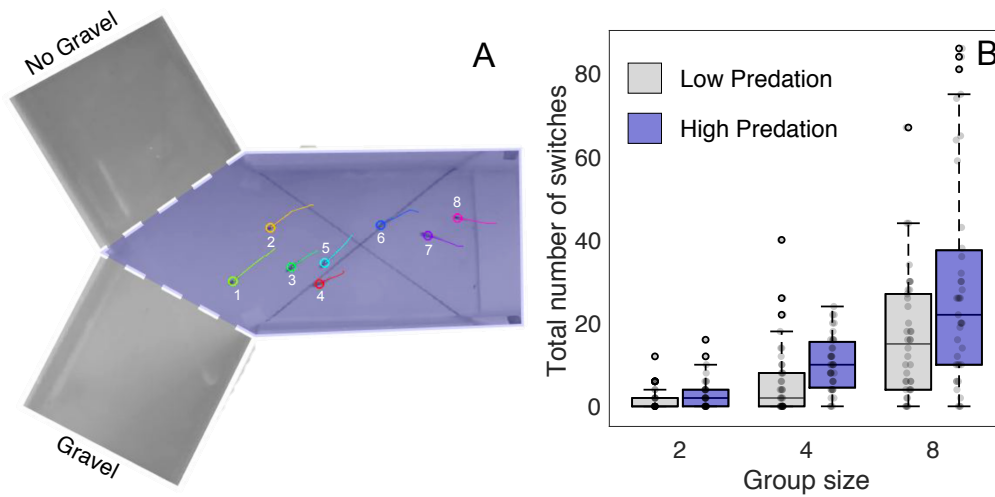
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296 Figure 1: (A) The experimental Y maze. Tracking is superimposed on a frame for one
297 of the trials of eight fish. The numbers next to each fish represent their positional ranks
298 within the group on that frame. The left arm of the Y maze contained a gravel patch
299 (off-screen), while the right arm contained no patch. This was designed to create an
300 asymmetric choice. (B) Boxplots of the total number of times individuals switched
301 position in the group. Raw data points are shown as grey circles. The central line on
302 each box depicts the median, and the top and bottom edges of each box represent the
303 25th and 75th percentile. Whiskers extend to data points not considered outliers.

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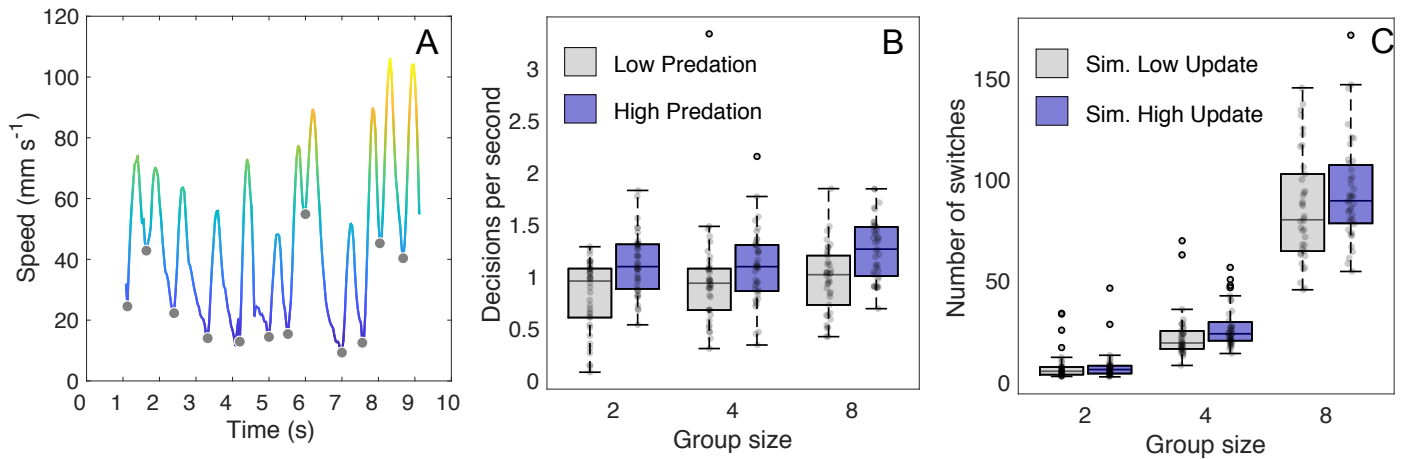
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316 Figure 2: (A) Example speed profile of a fish as it moved through the Y-maze. Grey
 317 markers represent times when the speed profile has local minima, indicating times
 318 immediately before the fish made a decision to move. (B) Boxplot of the number of
 319 decisions fish made per second as a function of group size and low (grey) or high (blue)
 320 predation environments. (C) Results of the simulation where each point represents the
 321 average switches a group made out of 100 simulation runs. Simulations were given two
 322 update frequencies; low (grey), or high (blue), respectively matching the update
 323 frequency of fish from low or high predation environments. The central line on each
 324 box depicts the median, and the top and bottom edges of each box represent the 25th
 325 and 75th percentile. Whiskers extend to data points not considered outliers.

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