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1 **Fish pool their experience to solve problems collectively**

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25 ABSTRACT

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27 Access to information is a key advantage of grouping. While experienced animals can lead
28 others to solve problems, less is known about whether partially informed individuals can pool
29 experiences to overcome challenges collectively. Here we provide evidence of such ‘experience-
30 pooling’. We presented shoals of sticklebacks (*Gasterosteus aculeatus*) with a two-stage
31 foraging task requiring them to find and access hidden food. Individual fish were either
32 inexperienced, or had knowledge of just one of the stages. Shoals comprising individuals trained
33 in each of the stages pooled their expertise, allowing more fish to access the food, and to do so
34 more rapidly, compared to other shoal compositions. Strong social effects were identified- the
35 presence of experienced individuals increased the likelihood of untrained fish completing each
36 stage. These findings demonstrate that animal groups can integrate individual experience to solve
37 multi-stage problems, and have significant implications our understanding of social foraging,
38 migration, and social systems.

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48 Group-living provides animals with both ready access to valuable social information and the
49 potential, by processing information through social interactions, to achieve solutions to cognitive
50 problems that might lie beyond the reach of lone individuals¹⁻¹¹. Information processing by
51 groups can occur via a number of different mechanisms, and distinguishing between these is a
52 key challenge faced by researchers¹⁰. Such mechanisms include swarm intelligence, facilitation,
53 and pool-of-competence effects. Swarm intelligence refers to improved cognitive performance
54 that stems from distributed, self-organised decision making, with decisions emerging from
55 repeated local interactions between individuals^{12,13}. The many-wrongs principle of collective
56 navigation is an example of swarm intelligence. Here, individuals' motivation to follow their
57 varied and imperfect estimates of the correct travel direction interacts with their drive to remain
58 in close proximity to their neighbours, resulting in a group-level compromise on preferred
59 direction that is more accurate than the separate estimates of most individuals^{14,15}. A second
60 mechanism, facilitation, occurs when necessary costs such as vigilance for predators are shared
61 among group members, allowing individuals to allocate more effort to other problems, such as
62 searching for resources¹¹. Finally, pool-of competence describes effects arising from group size
63 and diversity, with larger groups being statistically more likely to include more experienced,
64 motivated, persistent or bold individuals that are more likely to solve problems and from which
65 others in the group can acquire information^{10,16}.

66

67 Our study is concerned with one aspect of the pool-of-competence effect, specifically variation
68 in experience amongst group members. It is likely often the case in nature that within a given
69 group, members will hold different information about the environment, with some individuals
70 possessing relevant experience in solving a particular challenge that other members lack. This

71 may be especially so in populations with fission-fusion social structure and in those where group
72 fidelity is low, resulting in high turnover of group membership and frequent disbandment and
73 formation of groups. Research has demonstrated that minorities of experienced individuals can
74 lead their uninformed groupmates¹⁷⁻²⁰. Here, leadership may emerge as an outcome of the
75 experienced individuals' attraction to the target and the mutual social attraction between these
76 and their naïve groupmates,^{3,17,21} that is without any communication or direct transmission of
77 information about the target from leader to follower occurring. Often, different group members
78 might have partial but complementary information about the component parts of a particular task
79 that can be broken down into a number of 'stages' or elements. They may be familiar with
80 different sections of a navigation route for example, or some may know where to find food while
81 others might know how to access it. Plausibly, groups of animals may be able to overcome such
82 multi-stage problems through social interactions that combines the separately-held information
83 possessed by individuals, allowing them to reach integrative solutions that lie beyond the grasp
84 of single individuals.⁵ Here we set out to test whether groups of partially informed individuals
85 could indeed pool their knowledge about the separate components of a task to solve complex
86 problems in this manner.

87
88 We presented shoals of sticklebacks (*Gasterosteus aculeatus*) with a two-stage navigation and
89 foraging task that required them first to locate a hidden patch of food within a mesh feeder box
90 by swimming through a structured environment towards a light cue (stage 1), and then to access
91 the box by swimming through a small hole in order to obtain the food (stage 2). Some subjects
92 were given prior experience of solving the navigation component of the task, and others
93 experience of accessing food from the food-box, but no single fish had prior experience of both

94 components of the task. We varied the prior experience possessed by individual fish and
95 arranged these into four different combinations, performing ten replicates per combination. One
96 combination consisted solely of individuals with no prior training (neither knowledge of stage 1,
97 nor stage 2). Two combinations consisted of a majority of untrained fish plus a minority of
98 individuals that had been trained to complete either the navigation part of the task, or to access
99 food from the feeder box (either knowledge of stage 1, or stage 2). Finally, one combination
100 consisted of shoals containing equal numbers of untrained, navigation-trained and feeder-trained
101 fish (both knowledge of stage 1, and of stage 2). We predicted that fish in this latter group would
102 access the food patch most rapidly and that more individuals overall would be successful.

103

104 RESULTS

105

106 The composition of the group (treatment) strongly influenced the number and rate of entries to
107 both the goal area and the feeder (Supplementary Fig. 1).

108

109 *Numbers of group members entering goal area and feeder*

110

111 More fish entered the green light goal area in groups that contained trained fish (light trained,
112 Wald $Z=7.37$, $p<0.01$; feeder trained, Wald $Z=3.6$, $p<0.01$; combined Wald $Z=6.36$, $p<0.01$)
113 than in shoals of untrained fish. As predicted, fish in the combined and light-trained groups
114 entered the goal area more often than those in the feeder-trained groups (light trained compared
115 to feeder trained, Wald $Z=-4.63$, $p<0.01$; combined compared to feeder trained Wald $Z=-4.9$,
116 $p<0.01$). More fish entered the feeder unit in groups with training (light trained, Wald $Z=3.17$,

117 p<0.01; feeder trained, Wald Z=3.31, p<0.01; combined Wald Z=7.2, p<0.01) than in untrained
118 groups. Again as predicted, we observed elevated rates of entry in the combined groups
119 compared to other treatments (light trained, Wald Z=-5.07, p<0.01; feeder trained, Wald Z=-
120 4.94, p<0.01 Figure 1a).

121
122 When we focused only upon the proportion of naive fish from each group that entered the goal
123 area and the feeders we see a similar pattern of results. There was an increased number of entries
124 into the goal area for shoals containing fish with any type of training (light trained, Wald Z=6.23,
125 p<0.01; feeder trained, Wald Z=3.07, p<0.01; combined, Wald Z=4.74, p<0.01) compared to
126 untrained groups. We also saw an increased rate of entry into the feeder by naive fish in
127 treatments with training (light trained, Wald Z=3.01, p<0.01; feeder trained, Wald Z=1.96,
128 p<0.05; combined, Wald Z=4.96, p<0.01).

129

130 *Rate of entry*

131 The time of the first fish in each group to enter the green light goal area was lower in the
132 combined and light-trained groups than it was in the feeder-trained and untrained groups (Cox
133 regression: Wald Z= 4.05, P<0.001 and Wald Z= 4.39, P<0.001). The entry times of the first fish
134 in the combined group did not differ from that of the light-trained treatment groups (Wald Z=
135 0.93, P=0.35). Regarding entry times into the feeder, as predicted, the first fish in the combined
136 group were faster than all of the other treatment groups (untrained, light-trained and feeder-
137 trained: Wald Z= 5.42, P<0.001; Wald Z= 4.13, P<0.001; and Wald Z= 4.16, P<0.001
138 respectively, Figure 1b).

139 An identical pattern was seen when we only considered rates of entries by naïve fish from each
140 group into the goal area and the feeders. For goal area entries there was no difference between
141 the light-trained and combined groups in the rate at which untrained fish first entered the goal
142 area (Wald $Z= 0.64$, $P=0.52$). The first fish from the untrained and feeder-trained groups took
143 longer to enter the goal area compared to the combined groups (Wald $Z= 2.60$, $P=0.009$ and
144 Wald $Z= 2.21$, $P=0.027$). As predicted, the first naïve fish in the combined groups to enter the
145 feeder did so sooner than the first fish from the untrained, light-trained and feeder-trained groups
146 (Wald $Z= 3.73$, $P<0.001$; Wald $Z= 1.96$, $P=0.049$ and Wald $Z= 2.72$, $P=0.007$ respectively).

147 *Hazard models*

148

149 Following these analyses we also ran two proportional hazard models to understand the factors
150 that contributed to the fish entering each area (Figure 2).

151

152 We first ran a set of models that analyzed the rate of entry without explicit consideration of the
153 effect of social information. We found that fish who had prior light-training entered the goal area
154 faster than those without it (Wald $Z=4.62$, $p<0.01$), and that fish in the presence of conspecifics
155 with light-training entered the goal area faster than those without (Wald $Z=10.37$, $p<0.01$). A
156 similar, but weaker, effect on rate of entering the goal area was observed for feeder-trained fish
157 (Wald $Z=2.1$, $p=0.04$), and fish in a group with feeder-trained fish (Wald $Z=3.15$, $p<0.01$). We
158 also found that prior feeder-training (Wald $Z=3.09$, $p<0.01$), but not prior light-training (Wald
159 $Z=1.55$, $p=0.12$) increased the rate at which fish entered the feeder, and that the presence of
160 feeder trained fish in the group significantly increased the rate at which all fish entered the feeder

161 (Wald $Z=2.81$, $p<0.01$). Interestingly, the presence of light-trained fish significantly reduced the
162 rate at which other fish entered the feeder (Wald $Z=-2.72$, $p<0.01$).

163

164 Extended models that incorporated social information in more complex ways revealed that
165 previous training to approach the green light (Wald $Z=5.67$, $p<0.01$), the number of light-trained
166 fish (Wald $Z=5.05$, $p<0.01$), and the number of feeder-trained fish (Wald $Z=3.19$, $p<0.01$) all
167 positively increased the rate at which fish entered the goal area. We also found a strong positive
168 effect of having a shoal mate previously enter the goal area in the last 10 seconds (Wald
169 $Z=19.25$, $p<0.01$), but no effect of having had a shoal mate leave in the previous 10 seconds
170 (Wald $Z=0.48$, $p=0.63$). Overall, the number of fish in the goal area was associated with a
171 decrease in the rate of entry for other fish to enter the goal area (Wald $Z=-2.79$, $p<0.01$).

172

173 We found a similar pattern of results when analyzing entry of the feeder. Prior feeder training
174 significantly increases the rate that fish enter the feeder (Wald $Z=2.84$, $p<0.01$), and fish are
175 disproportionately more likely to enter the feeder within 10 seconds of a shoal mate doing so
176 (Wald $Z=12.83$, $p<0.01$). We did not find a significantly increased rate for fish entering the
177 feeder within 10 seconds of another fish leaving it (Wald $Z=1.53$, $p=0.13$). Overall the number of
178 fish currently in the feeder was associated with a decrease in the rate at which other fish entered
179 the feeder (Wald $Z=-5.39$, $p<0.01$). Model coefficients for the goal area and the feeder hazard
180 models can be found in Supplementary Tables 2 and 3.

181

182 DISCUSSION

183

184 This experiment provides clear evidence of experience-pooling, with groups of partially
185 informed fish integrating their experience to solve a two-stage foraging problem collectively. A
186 greater proportion of group members gained access to the food patch, and did so sooner, in the
187 mixed groups that contained some fish experienced in the navigation part and others in the
188 feeder-access aspect of the task compared to fish in other treatments which contained members
189 experienced in only one or in neither of the two components of the task. Moreover, naïve fish in
190 the mixed groups also benefitted by accessing the food sooner compared to naïve fish in the
191 other groups. Both experience and social information were significant in affecting entries into the
192 goal area, the first stage of the task. We saw that light-trained fish entered the goal area at a
193 greater rate than did untrained fish, as expected, but also that feeder-trained fish did too. This
194 latter effect possibly arose because the fish were able to see the feeder as they came close to the
195 goal area and, having learned an association between the feeder and food, were more motivated
196 to approach it and enter the goal area than were fish untrained in either task. At the group level,
197 fish in the light-, feeder- and combined groups were more likely to enter the goal area compared
198 to those in the untrained treatment group. Fish with prior feeder-training, and those that were
199 grouped with feeder-trained fish entered the feeder at a greater rate, but we also found a negative
200 effect of the presence of light-trained fish upon feeder entries. This may have resulted from the
201 fact that light-trained were given experience of feeding beneath the green lights, but not in the
202 feeder itself- they may therefore have anticipated finding food beneath the lights, causing them
203 to remain in this area, where they attracted other group members, delaying their entry into the
204 feeder. Further analyses that incorporated social transmission in more nuanced ways revealed
205 that a fish entering the feeder or goal area substantially increased the likelihood that other fish
206 did so in the next ten seconds. This is consistent with both past experimental findings analysing

207 the following behavior of fish^{22,23} and theory predicting that individuals that are both motivated
208 to move towards a particular location and socially attracted to their groupmates may be able to
209 entrain the group and move them towards the target, a principle termed ‘leading according to
210 need’.^{17,18,20,21} We found no evidence that the rate at which fish entered the goal area increased
211 immediately after a fish left either the feeder or the goal area suggesting that this effect is
212 mediated by following rather than attention to cues or locations. Such following effects were also
213 identified in a study of recruitment of naïve fish to prey patches by experienced shoal-mates by,²³
214 who termed them ‘untransmitted social effects’. Interestingly, in both hazard models we saw that
215 the number of fish in the goal and feeder areas was associated with a decrease in the rate of entry
216 for other fish into those areas. The reason for this effect is unclear. One possibility is that it was
217 due to trained individuals entering the goal or feeder areas sooner, with naïve fish either entering
218 quickly soon after (fish were more likely to enter the goal and feeder areas if a group mate had
219 entered within the last 10 seconds), or else taking much longer to find or access the patch
220 because they had been left behind. Taken together, our analyses when considered alongside the
221 findings other studies^{17,18,20,21}, suggest that leadership arising from the balance between goal
222 orientedness and social attraction may be sufficient to generate collective problem solving.

223

224 Several factors potentially contribute to the ability of groups to process information and solve
225 problems, from facilitation, to pool-of-competence effects to swarm intelligence, with these
226 mechanisms potentially acting concert.^{10,16} For example, among flocks of songbirds, Morand-
227 Ferron & Quinn¹⁶ showed that larger groups of naïve birds were more likely to obtain food from
228 novel feeding devices, that the presence in the group of a knowledgeable bird further increased
229 the likelihood of the group accessing food and that larger groups were more likely to contain

230 such individuals than smaller ones. Moreover, birds had more success when they were in larger
231 groups and when the feeding devices were closer to cover, compared to when they further away,
232 suggesting that facilitation through reduced predation risk might also affect problem solving. In
233 our study we directly manipulated the experience of group members whilst holding group size
234 constant, allowing us to show that information held by the group could be pooled. This approach
235 also allowed us to rule out other mechanisms, although it doesn't discount the possibility that
236 multiple effects might operate together under natural conditions, as was observed by Morand-
237 Ferron & Quinn.¹⁶ Our findings suggest that for groups of ecological generalists negotiating
238 variable environments, diversity in experience and a distributed knowledge base across a group
239 may be of critical importance, potentially more-so than the presence of 'omniscient' individuals
240 will full knowledge of the challenges.²⁴ Experience pooling might be especially important within
241 populations that exhibit fission-fusion social structures, where at any point current group
242 members might be expected to possess a greater range of experience than those of more stable
243 groups that have travelled and experienced the same conditions together. We anticipate that
244 experience-pooling, underpinned by leader-follower interactions similar to those seen in our
245 study, might be found in groups of animals facing challenges ranging from learning how to
246 exploit novel foods and avoid new predators to navigating between ephemeral resources and
247 tracing long migration routes.

248

249 METHODS

250

251 Subjects

252

253 Threespine sticklebacks (N=360) were collected using hand nets from the Kinnessburn stream in
254 St Andrews, UK in July 2012, and housed in the laboratory in groups of 40 in 90l aquaria. Each
255 aquarium contained a layer of sand and artificial plants, and was connected to an external filter.
256 The temperature in the laboratory was held at 8°C, and the lights were on for 12 hours per
257 day. The fish were fed daily with frozen blood worms, unless otherwise stated below. We used
258 fish measuring 30-35mm in length that showed no signs of been in reproductive condition. Fish
259 were not sexed.

260

261 Overview

262

263 The experiment presented 40 groups of 9 fish with a two-stage navigation task. In order to access
264 a food reward, the fish first had to travel to the far end of a large structured arena, where a feeder
265 box containing the food was hidden behind an opaque screen, and to gain access to the food in
266 the feeder box by entering through one of two small holes. The end of the arena with the feeder
267 box and food reward contained two green lights. We tested groups of fish that contained different
268 combinations of individuals trained to approach green lights, trained to enter the feeder box
269 through the target holes, or not trained in either task. Fish that were not trained to the green lights
270 or to the feeder box were nevertheless exposed to these during training, so as to remove any
271 neophobic responses to the stimuli that may otherwise have confounded their behaviour in the
272 experiment proper. The training procedure and two pilot experiments designed to test the
273 efficacy of the training are described in the supplementary material. All procedures were
274 reviewed and approved by the departmental ethics committee.

275

276 Experimental Arena

277

278 The arena (Supplementary Figure 2) consisted of a black plastic box measuring 160cm long,
279 100cm wide and 40cm tall. It contained a 2cm-deep layer of fine sand, and was filled with water
280 to a depth of 25cm. The feeder box was placed 10cm from one end of the arena, 40cm from each
281 long wall. It was suspended 10cm above the sand substrate. The feeder box measured 20cm long
282 by 10cm tall and wide. It consisted of a 2mm-wide plastic frame around which were stretched a
283 fine nylon mesh. A 2cm x 2cm square hole was cut in each end of the feeder box, which enabled
284 fish to swim inside and access the food reward (20 dead bloodworms placed in the centre of the
285 feeder box). The use of a mesh feeder had the advantage that olfactory cues emanating from the
286 food would diffuse through the sides, and would not provide an odor gradient leading to the
287 entrance hole. The food was also visible through the mesh walls and floor of the feeder box,
288 leaving the fish highly motivated to solve the task. However, the fish could not find food simply
289 by swimming towards the sight or smell of it, and previous experiments have shown that this
290 arrangement leaves finding the entrance a challenging task.²⁵

291

292 A white plastic screen measuring 40cm x 40cm was placed 10cm in front of the feeder box, and
293 30cm from each of the long walls of the arena. This prevented the group of fish, which began the
294 experiment at the other end of the arena, from being able to see the feeder box. In order to reach
295 it, they had to swim either side of this barrier. Either side of the feeder box we placed a green
296 LED unit (Trimble, Milton Keynes, UK). These consisted of a circle of 24 individual LEDs set
297 within a case with a diameter of 5cm. A green filter was taped over each LED unit. Each unit
298 was suspended 10cm above the surface of the water, 20cm either side of the feeder box, and 20

299 cm from each longwall of the arena. The light produced by the LED units was visible to the fish
300 at the far end of the arena at the beginning of the experiment. A high definition webcam
301 (Logitech C920, Logitech International SA, Lausanne, Switzerland) was mounted 80cm above
302 the feeder box. This was used to film the end the arena immediately behind the barrier, which
303 was designated the 'green light goal area'.

304

305 At the other end of the arena we placed a holding unit constructed from colourless, perforated
306 plastic. This measured 20cm x 20cm, and 40cm tall. The bottom and top of the holding unit were
307 open. It was placed directly upon the sand substrate, 5cm from the back wall, and 40cm from
308 each long side wall of the arena. This was used to house the fish at the beginning of the
309 experiment.

310

311 In the middle section of the arena we placed four artificial plants. These measured approximately
312 10cm tall and 10cm in diameter. One pair of plants were placed 20cm apart, 30cm from each
313 longwall of the arena, and 40cm from the end of the arena where the fish holding unit was
314 placed. The second pair of plants were placed 20cm from these, and 50cm from the white plastic
315 barrier. The plants provided cover for the fish once they were released into the main arena at the
316 beginning of the trial, and facilitated movement throughout the centre of the arena.

317

318 Experimental groups

319

320 Fish were allocated using a random number algorithm to replicate groups in four treatments that
321 differed in the experience (i.e. prior training) possessed by constituent members. Each group

322 contained nine fish, and we ran 10 replicates in each of the four treatments. The first treatment
323 consisted of groups of nine naïve (i.e. non-trained) fish. In the second, each group contained
324 three fish that had been trained to approach the green light and six naïve fish. The third treatment
325 comprised shoals that contained three fish that had been trained to enter the feeder box and six
326 naïve fish, and the fourth contained shoals with three fish from each training regime plus three
327 naïve fish. Hereafter, these treatment groups respectively are referred to as *untrained*, *light-*
328 *trained*, *feeder-trained* and *combined*. For clarity, individual fish that had not been trained are
329 referred to as naïve, while the treatment consisting entirely of naïve fish is referred to as
330 untrained. Because familiarity has been shown to affect social foraging interactions in this
331 species,²⁶ within each group each fish was drawn from a separate holding tank, ensuring that all
332 were equally unfamiliar to one another. Within each group, every fish was fitted with a non-
333 invasive, colour-coded circular tag on its first dorsal spine.²⁷ These were fitted on the last day of
334 training, and the day before the experiments were performed. This allowed us to recognise each
335 individual fish in the videos. Sample sizes were informed by an earlier social foraging
336 experiment conducted in our laboratory.²⁶

337

338 Experimental procedure

339

340 For each trial, the experimental arena was established as above, and food items (20 dead
341 bloodworms) added to the feeder box. The experimental group was added to the holding unit and
342 allowed to acclimate for 15 minutes, before the holding unit was raised 15cm using a pulley,
343 releasing the fish and beginning the trial. The trial ran for a further 45 minutes. From the
344 webcam footage we recorded the identity of each fish as it entered the green light goal area. For

345 every second of the trial we recorded whether each fish was inside or outside the goal area and
346 inside or outside of the feeder box. We performed five such trials each day (see Supplementary
347 Table 1 for schedule). Following each trial we replaced the water and sand substrate and feeder
348 box prey in the arena. The experimenter was not blind with respect to treatment group.

349

350 Data availability

351

352 The datasets analysed during the current study are available from the corresponding author on
353 request.

354

355 Statistical analysis

356

357 We analyzed the total proportion of fish and the proportion of untrained fish that entered the
358 green light goal area and the feeder box during the trial using a binomial model. We examined
359 the time at which the first fish entered each area for different groups using Cox regressions,
360 focusing upon the entry times of the first fish (irrespective of training) and the first naive fish
361 from each group. We then used Cox proportional hazard models to model all entries in the group
362 and gain a finer temporal resolution of the factors that predict whether and when fish enter either
363 the goal area or the feeder, and the frequency at which they enter the areas. We examined the rate
364 at which fish entered the feeder and goal area predicted by their previous training, previous time
365 spent in the goal area during the trial, the number of light trained fish, the number of feeder
366 trained fish, and three social cues: the number of fish that had entered the goal/feeder area in the
367 last 10s, the number of fish that had exited the goal/feeder area in the last 10s, and the total

368 number of fish in the goal/feeder area. Our data met the assumption of proportional hazards
369 expected by these tests. All proportional hazard models were run in R²⁸ using the “survival”
370 package.²⁹

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373

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470 AUTHOR CONTRIBUTIONS

471

472 MMW designed and performed the experiments, MMW, AW & KNL analysed the data and co-
473 authored the paper.

474

475 COMPETING FINANCIAL INTERESTS

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477 We declare no competing financial interests.

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488 FIGURES

489 **Figure 1.** (a) The number of fish in each group to enter the green light goal area and the feeder
490 (mean +/- 95% CI). (b) Survival plots showing the time for the first fish in each group to enter
491 the goal area and feeder. 9U: 9 untrained fish; 3L,6U: 3 light-trained and 6 untrained fish;
492 3F,6U: 3 feeder-trained and 6 untrained fish; 3L,3F,3U, 3 feeder-trained, 3 light-trained and 3
493 untrained fish.

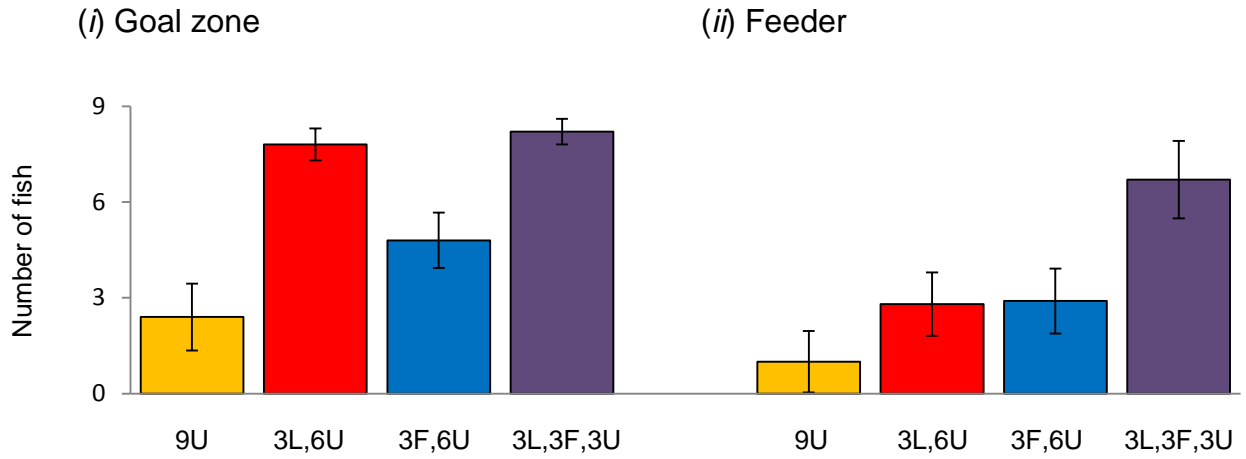
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495 **Figure 2.** (a) The proportion of fish for each level of training to enter the green light goal area
496 broken down by treatment group. (b) The proportion of fish for each level of training to enter the
497 feeder area broken down by treatment group (c) The proportion of fish for each level of training
498 who entered the goal area and then entered the feeder area broken down by treatment group. In
499 each case, mean +/- 95% CI is shown. 9U: 9 untrained fish; 3L,6U: 3 light-trained and 6
500 untrained fish; 3F,6U: 3 feeder-trained and 6 untrained fish; 3L,3F,3U, 3 feeder-trained, 3 light-
501 trained and 3 untrained fish.

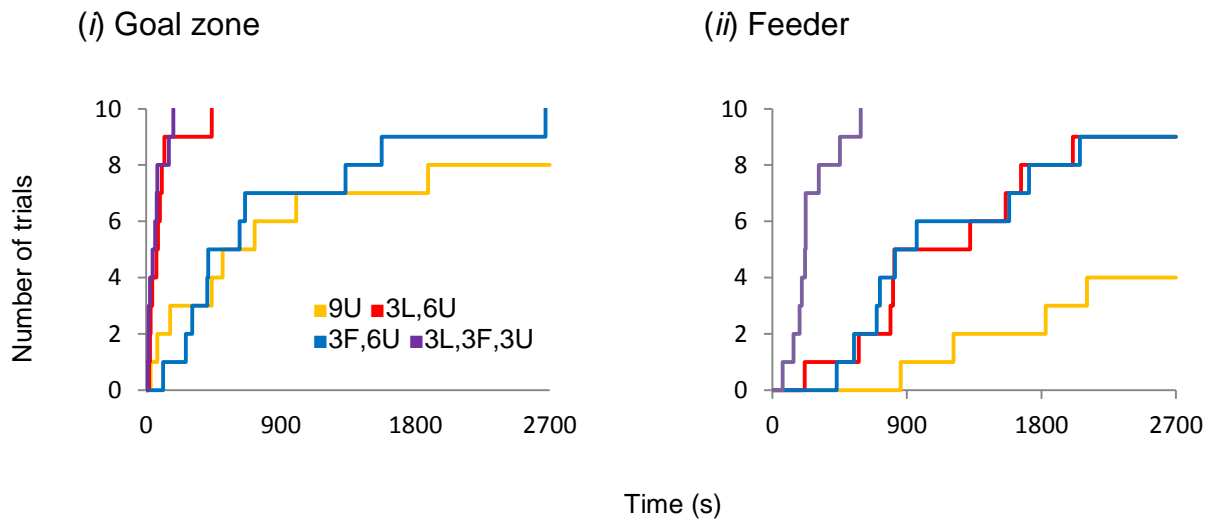
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520 **Figure 1. Number and rate of goal zone and feeder entries**
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(a) Proportion of fish entering zone



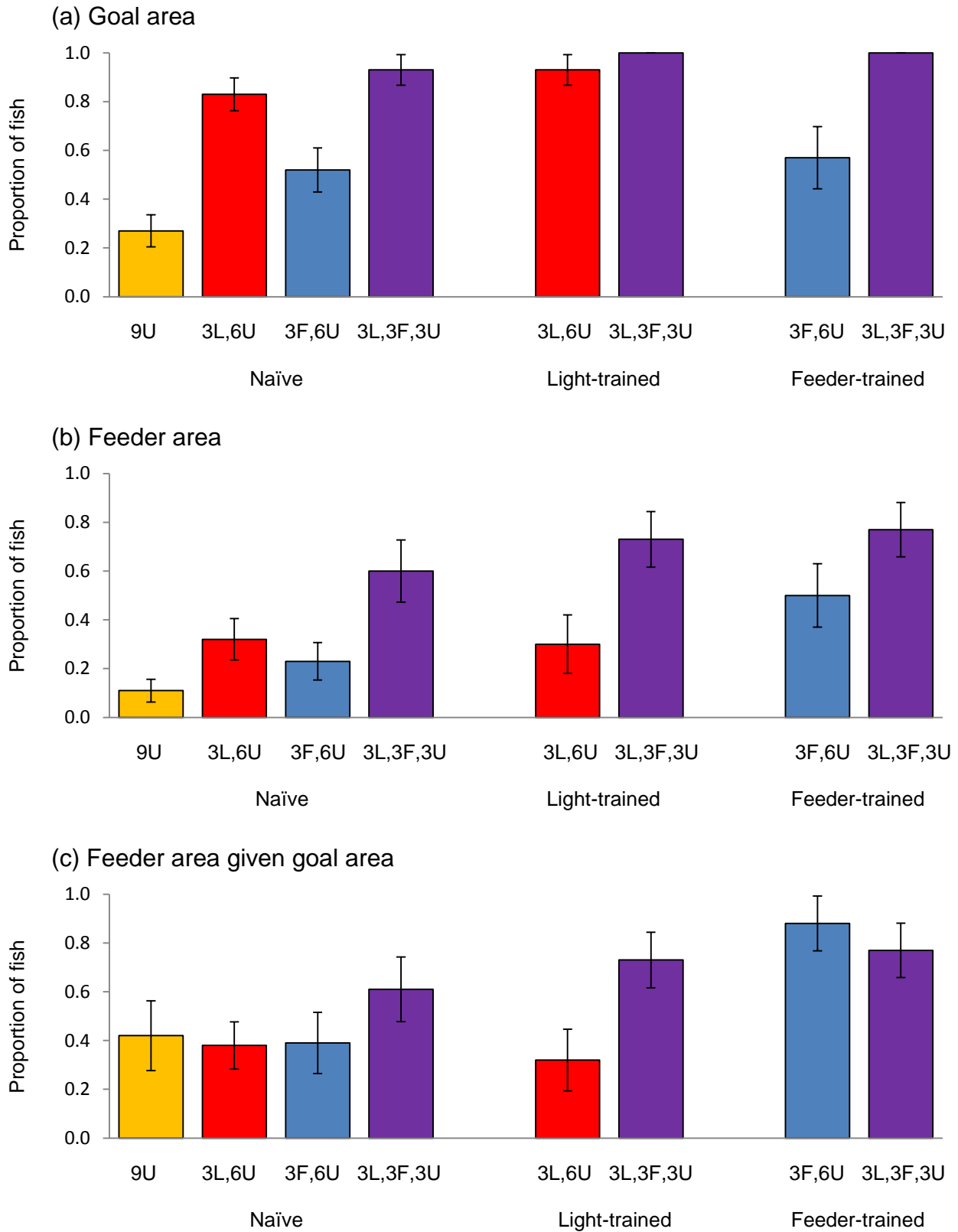
(b) Time for first fish to enter zone



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Figure 2. Proportion of naïve fish entering the goal and feeder areas



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533 Supplementary information for:

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535 **Fish pool their experience to solve problems collectively**

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537 Mike M. Webster, Andrew Whalen & Kevin N. Laland

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570 **Supplementary Methods**

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572 **Training fish to approach the green lights and to access the feeder box**

573

574 Prior to beginning the experiments it was necessary to first train the fish. Some fish were trained
575 to approach the green light, some were trained how to enter the feeder box and other fish were
576 not trained to either task. The fish were trained in six batches (Supplementary Table 1). The fish
577 from batches one and two were used in pilot experiments designed to assess the efficacy of the
578 training, with the fish from the third to sixth batches being used in the experiment proper.

579

580 In batch one and two we set up nine aquaria. Batches three to six contained 18 aquaria. These
581 were sub-divided into two sets of nine aquaria each (referred to as a and b in Supplementary
582 Table 1), with the training and testing regimes in the first set running one day ahead of those in
583 the second. This allowed us to split the experimental trials over two days. Each aquarium
584 contained 10 fish. Only five fish from each aquarium were randomly selected for use in the
585 experiments. We trained additional fish because we anticipated that we would lose some to
586 mortality over the course of training. In fact, none of the trained fish died, but we did not have
587 time to test them all. Untested fish were retained in the laboratory for use in a separate
588 experiment.

589

590 Each aquarium had a volume of 45l and contained a 2 cm deep layer of fine sand, and was
591 equipped with an external filter. The aquaria were visually and chemically isolated from one
592 another. The training procedure lasted for four weeks. During the first week the fish were

593 allowed to acclimate. They were fed daily with frozen bloodworms and were not exposed to the
594 green lights or to the feeder box during this time. At the beginning of the second week training
595 began.

596

597 In batches one and two, three aquaria were randomly selected and assigned to green light
598 training, three to feeder box training, and three were not trained in either task. In batches three to
599 six, which contain 18 aquaria overall, each subset of nine aquaria was randomly assigned to one
600 of the four experimental treatments (described in main text), such that all nine aquaria received
601 no training, three were trained to the green light while six received no training, three were trained
602 to the feeder while six received no training or three were trained to the feeder, three to the light
603 and three received no training. See Supplementary Table 1 for an overview of the training order
604 and schedule. Fish that were not trained to the green lights or to the feeder box were nevertheless
605 exposed to these, so as to remove any neophobic responses to the stimuli that may otherwise
606 have confounded their behaviour in the experiment proper.

607

608 A pair of green lights identical to those used in the experimental arena described above were
609 fitted to the end of each aquarium. These were switched on for 15 minutes twice per day at 10am
610 and 4pm. In the aquaria where fish were trained to approach the green lights, food was provided
611 directly beneath the lights at the same time they were switched on. The food was always
612 consumed within the 15 minute period during which the lights were on. In the aquaria where the
613 fish were not trained to associate the lights with food, the lights were kept off during the two
614 daily feeding periods, and were only switched on for 15 minutes one hour after the fish had been
615 fed, and after they had consumed all of the food. Training was repeated daily for three weeks.

616

617 In each aquarium we also placed a feeder box, as described above. This was suspended 10cm
618 above the bottom of the tank. In the aquaria where fish were trained to access the feeder box,
619 training was structured as follows. During the first week they were presented with a feeder box
620 in which both ends had been removed. Food was placed within the feeder box twice per day at
621 10am and 4pm. The fish were easily able to access the food by swimming into the feeder box
622 through the open ends. During the second week, the feeder box was replaced with one with 5cm
623 square holes in either end, with food placed inside as before. During the third week the feeder
624 box was replaced with one with 2cm square holes, identical to the one used in the experiment
625 itself. In both the second and third weeks fish were seen to readily enter the feeder box and eat
626 the food. In the aquaria where the fish were not trained to this task, we used feeder boxes with
627 completely closed ends. For these groups food was provided directly on the sand substrate
628 beneath the feeder box. The fish in these groups had no experience of entering the feeder boxes
629 and no experience of detecting food within them.

630

631 **Training: pilot experiments**

632

633 Fish were tested individually in an experimental arena measuring 45cm long by 30cm tall and
634 wide. The arena was screened in black plastic and contained a 2cm deep layer of fine sand, and
635 was filled with water to a depth of 25 cm. At one end of the arena we placed a holding unit
636 measuring 5x5cm wide, and 35cm tall. This was constructed from colourless perforated plastic.
637 It was open at the top and bottom, and was placed directly upon the sand substrate. A high-

638 definition WebCam was fixed directly above the experimental arena. This was used to record the
639 trials. Five such arenas were established, allowing five trials to be run simultaneously.

640

641 We performed two pilot experiments, one in which fish were given the opportunity to approach
642 two green lights located at one end of the tank, and one in which they were presented with a
643 feeder box containing 20 dead blood worms. The lights and the feeder box were as described for
644 the experiment proper, above. We tested the fish from batch one in the green light pilot
645 experiment and those from batch two in the feeder box pilot experiment. Of the 10 fish in each
646 training aquarium, we randomly selected five to be tested. For each pilot experiment we tested
647 three treatment groups (the fish trained to the green light, fish trained to the feeder box and fish
648 that were trained to neither), with 15 replicates in each treatment group. They were tested on the
649 day immediately following the end of the training period.

650

651 In the green light pilot experiment, two green lights were suspended 10cm above the surface of
652 the water at the end of a tank directly opposite the holding unit (Supplementary Figure 3a). No
653 prey were present in the tank in this experiment. The holding unit was used to contain the test
654 subject at the start of the trial. A fish was randomly selected, and carefully transferred from its
655 training aquarium to the holding unit in the experimental arena. It was allowed to acclimate for
656 10 minutes. During this period the green lights were switched off. The lights were then switched
657 on and the fish was allowed to settle for another 10 minutes. Following this, the holding unit was
658 carefully raised and removed, releasing the fish and beginning the trial. The trial lasted for a
659 further 10 minutes. From the videos of the trials, we recorded the latency of each fish to enter a
660 10cm wide goal zone beneath the lights.

661

662 In the feeder box pilot experiment, we suspended a feeder box 10cm above the substrate and
663 10cm from the back wall of the arena (Supplementary Figure 3b). The feeder box was accessible
664 via two 2x2cm holes, identical to the one described above, and as used in the experiment proper.
665 The feeder box contained 20 dead bloodworms. These were added to the feeder box immediately
666 before the fish was added to the holding unit. The fish was allowed to acclimate for 20 minutes
667 before the holding unit was carefully raised and removed, beginning the trial. The trial lasted for
668 10 minutes. We recorded the latency of the fish to enter the feeder box.

669

670 Statistical analyses

671

672 In the green light and feeder box pilot experiments respectively we compared the latency of the
673 fish to enter goal zone beneath the lights or to enter the feeder box. We used Cox regressions to
674 compare the performance of the fish trained to the green light, to the feeder box and fish that
675 were trained to neither, using the untrained fish as a reference category for an indicator contrast.

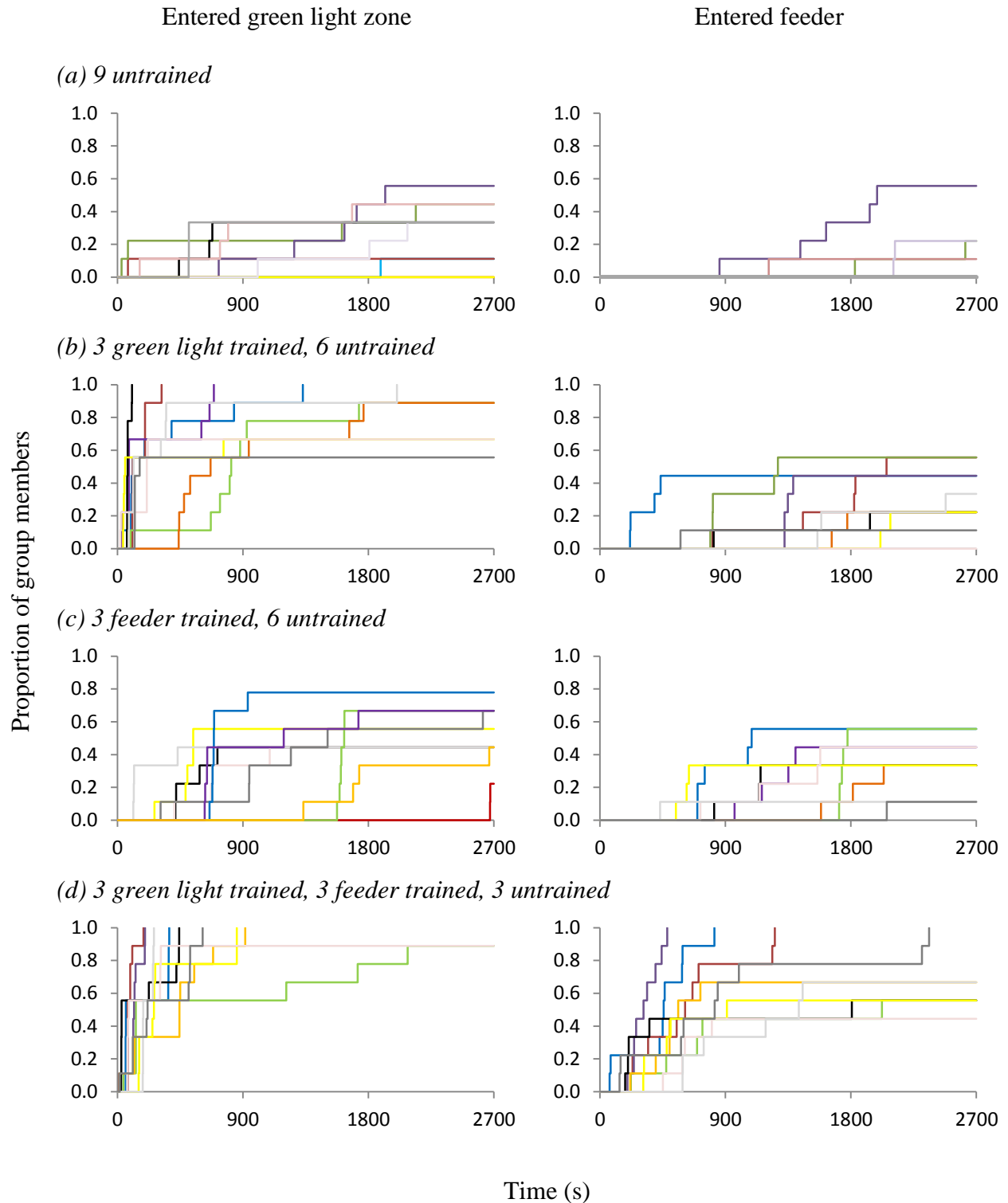
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677 Pilot experiment results

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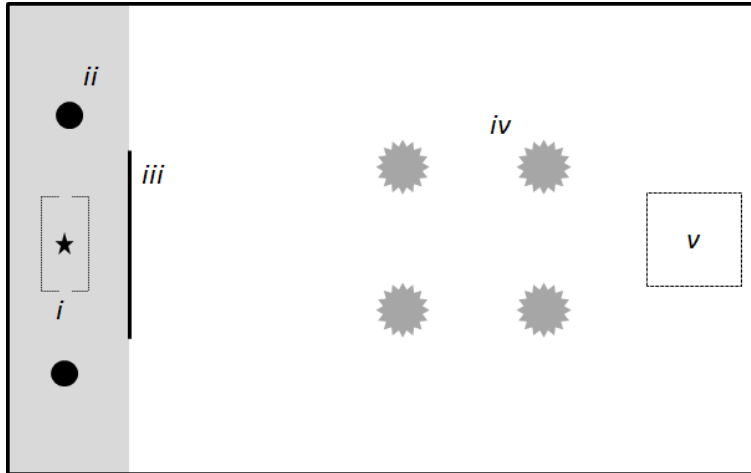
679 In the green light pilot experiment fish that had been trained to associate the green light with
680 food approached it sooner than did the untrained fish (Wald $X^2= 21.24$, $df=1$, $P<0.001$), while the
681 feeder-trained fish were no faster than the untrained fish ($X^2= 0.91$, $df=1$, $P=0.34$ Supplementary
682 Figure 4a). In the feeder box pilot experiment it was the feeder box-trained that entered it sooner
683 than the untrained fish (Wald $X^2= 18.06$, $df=2$, $P<0.001$), while the light-trained fish and the

684 untrained fish did not differ ($X^2 = 0.81$, $df=1$, $P=0.37$ Supplementary Figure 4b). In this
685 experiment, while all of the feeder box-trained fish entered the feeder during the trial, only four
686 of the green light-trained and two of the untrained fish (out of fifteen) entered feeder box. Based
687 on these findings we determined that the two training protocols had been effective.
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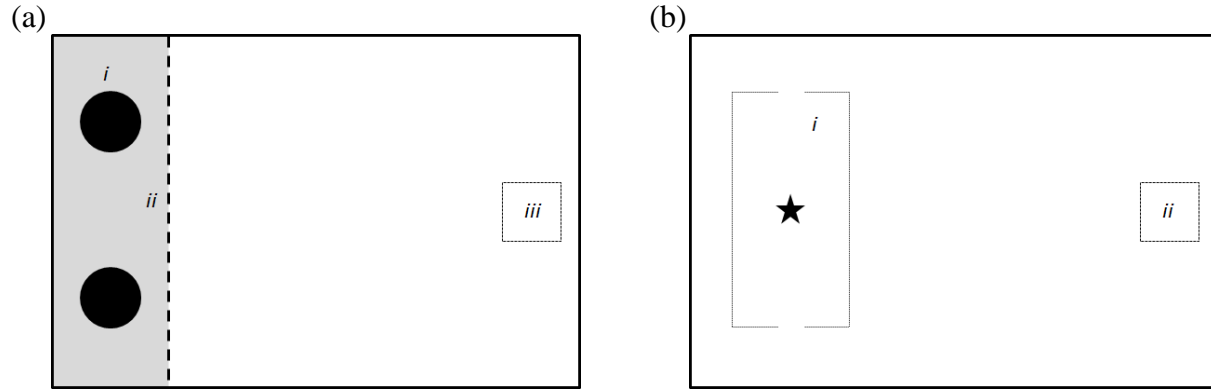
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690 **Supplementary Figure 1.** Survival plots showing the time (s) that each fish first entered the
 691 green light goal zone (left panels) and the feeder (right panels). Each line represents a single
 692 replicate, with the same coloured line referring to the same replicate between the left and right
 693 panels. (a) - (d) present results for the four different treatments.



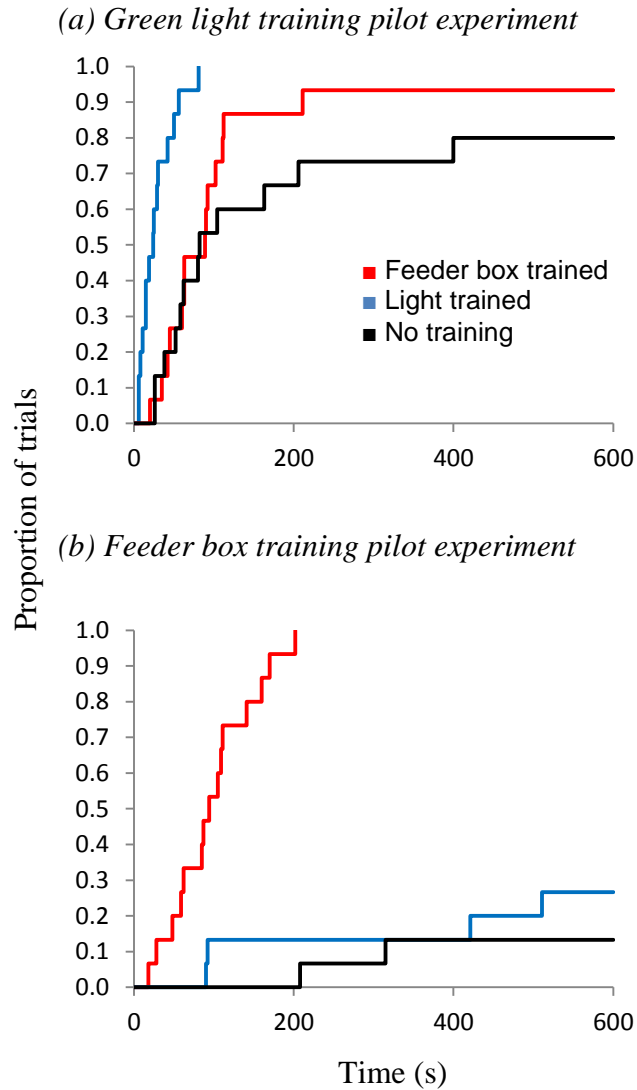
Supplementary Figure 2: The experimental arena, consisting of a feeder box (*i*) containing a prey patch, two green lights (*ii*), which fish in some trials had been trained to approach, an opaque screen (*iii*), artificial plants (*iv*) and a holding unit (*v*), within which were housed before the start of the trial. See main text for further details and experimental procedure.

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Supplementary Figure 3. The experimental areas used in the pilot experiments. (a), the light-training pilot, indicating the location of the green lights (*i*), the goal zone (*ii*) and the holding unit (*iii*) used to house the fish at the start of the trial. (b), the feeder-training pilot, with the feeder unit (*i*) and the holding unit (*ii*). See text for further details and procedure.

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Supplementary Figure 4: The latencies of fish to enter the goal zone in the green-light training pilot (a) and the feeder box in the feeder-training pilot (b). The light- and feeder-trained fish were faster in each respective experiment.

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766 **Supplementary Table 1.** Training batches and testing schedule. U refers to untrained fish, F to
 767 feeder-trained and L to light-trained, with the number of fish in each referring to the group
 768 composition of the experimental treatment. See main text for further details.
 769

Batch	Experiment	When tested	Replicates per treatment per batch			
			9U	3F, 6U	3L, 6U	3L, 3F, 3U
1	Pilot (Light)	Sept 2012	-	-	-	-
2	Pilot (Feeder)	Oct 2012	-	-	-	-
3a	Main	Nov 2012	5			
3b	Main	Nov 2012		5		
4a	Main	Jan 2013				5
4b	Main	Jan 2013			5	
5a	Main	Feb 2013				5
5b	Main	Feb 2013	5			
6a	Main	Mar 2013			5	
6b	Main	Mar 2013		5		

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800 **Supplementary Table 2.** Model coefficients for predicting the rate at which fish enter the goal
 801 zone. The social cues are linear predictors based on the number of fish that fit a criteria (e.g.
 802 number of fish in the goal area).
 803

Variable	Coefficient	SE	z	p
Experience	-0.01	0.01	-1.25	0.21
<i>Social Cues, Number of...</i>				
... fish in the goal area	-0.14	0.05	-2.79	<0.01
... entrances within 10s	2.13	0.11	19.25	<0.01
... exists within 10s	0.29	0.60	0.48	0.63
... green trained light fish	0.43	0.09	5.05	<0.01
... feeder trained fish	0.19	0.06	3.19	<0.01
<i>Training</i>				
Light	1.01	0.18	5.67	<0.01
Feeder	0.31	0.19	1.64	0.10

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834 **Supplementary Table 3.** Model coefficients for predicting the rate at which fish enter the
 835 feeder. The rates for Naïve fish are fixed to zero. The social cues are linear predictors based the
 836 number of fish that fit a criteria (e.g. number of fish in the goal area).
 837

Variable	Coefficient	SE	z	p
Experience	-0.01	0.01	-2.14	0.03
<i>Social Cues, Number of...</i>				
... fish in the goal area	-1.48	0.27	-5.39	<0.01
... entrances within 10s	6.95	0.54	12.83	<0.01
... exists within 10s	0.76	0.50	1.53	0.13
... green trained light fish	-0.23	0.14	-1.68	0.09
... feeder trained fish	0.01	0.15	0.05	0.96
<i>Training</i>				
Light	0.18	0.23	0.79	0.43
Feeder	0.63	0.22	2.84	<0.01

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