1 **Public information use by foraging ninespine sticklebacks: social learning or**

2 **an unlearned social influence on travel direction?**

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4 Short title: Public information and learning in sticklebacks

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24 **Summary**

25 If we are to understand the cognitive basis and evolutionary origins of a particular behaviour, it

26 is necessary to identify its underlying mechanism. Ninespine sticklebacks (*Pungitius pungitius*)

27 can identify the richer of two prey patches by observing other foragers' success. This may be due

28 to social learning, or an unlearned social effect on travel direction, brought about by the fish

29 being more likely to face and subsequently travel towards areas where they have observed more

30 feeding activity. Here we show that observer orientation does not predict patch choice, and that

31 fish are still more likely to spend more time in richer patches even if they have to take an indirect

32 route to reach them. This suggests that sticklebacks can learn the location of the richer patch

33 through observation, and viewed in conjunction with other published findings, suggests that

34 learned local enhancement lies behind public information use in this species.

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36 **Key Words:** Diffusion; Local enhancement; Producer-scrounger; Social learning strategies;

37 Social transmission

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Introduction

Animals can acquire information about the quality of a resource by monitoring the behaviour of others as they sample or exploit it. Such information, usually produced passively and inadvertently, is known as public information (Valone & Templeton, 2002; Chittka & Leadbeater 2005; Danchin et al. 2005). Public information may be used in a variety of contexts. Social foragers may monitor the behaviour of group mates so as to identify those that have located food that can be scrounged (Giraldeau & Caraco 2000), using cues such as their posture or activity to indirectly locate the food upon which they are feeding (Coolen et al. 2001). The hermit crab Coenobita compressus uses public information arising from competitive interactions, and is attracted to areas of greater commotion, which can be indicative of higher quality patches of food or high quality shells, a resource necessary for shelter (Laidre 2013). Some bird species use public information about conspecific breeding success when selecting areas of habitat in which to locate their own nests. In collared flycatchers (Ficedula albicollis), breeding pairs are less likely to settle in areas where other pairs are raising fewer young, and residents leave areas at higher rates if the number and quality of other pairs' nestlings there are low (Doligez et al. 2002). Lesser kestrels (Falco naumanni) use the reproductive success of other breeders to select breeding sites over successive breeding seasons, with the number of new immigrants to a particular site depending upon the number of successful breeding pairs in the previous year (Aparici et al. 2007).

Comparative studies focussing on how animals acquire, process and learn from public information, and the conditions under which they are most likely to respond to it, inform

70   research in a diverse range of fields, from behavioural ecology and psychology to anthropology,

71   economics and artificial intelligence (Heyes & Galef, 1996; Laland 2004; Nehaniv &

72   Dautenhahn, 2007; Galef 2009; Rendell et al. 2010; 2011; Webster & Ward 2011; Hoppitt &

73   Laland, 2013; Zentall & Galef, 2013). Understanding the mechanisms that bring about

74   behavioural responses to public information is vital if we wish to infer the cognitive processes

75   that drive them and the evolutionary and developmental forces that have shaped them. This

76   entails, among other things, identifying the stimuli to which the animals are responding,

77   determining how these affect changes in the behaviour of the animal, confirming whether

78   exposure to public information results in learning, and if it does, determining what is learned. In

79   many cases, social influences upon behaviour and learning might plausibly arise via several

80   different mechanisms. It is therefore essential for researchers to discriminate between these,

81   allowing them to rule out those that cannot adequately account for the observed behaviours, and

82   thereby allowing the most likely candidate mechanisms to be identified (Byrne, 2002; Hoppitt &

83   Laland, 2013).

84

85   The social foraging behaviour of stickleback fish (Gasterosteidae) has proved to be one of a

86   range of useful model systems for studying how and when animals rely upon public information

87   (reviewed by Laland et al., 2011). A number of studies using this system have deployed a binary

88   choice assay, in which a subject, 'the observer', is given the opportunity to watch two groups of

89   demonstrator fish feeding from artificial patches that yield prey at different rates. Following an

90   observation period, the demonstrators are removed and the observer is released from its holding

91   unit and allowed to visit the locations of the two prey patches. Statistical models can then be

92   used to infer whether a majority of observers visit the richer patch first, and/or spend more time

93 within it relative to the poorer patch, and whether therefore they are selecting patches under the

94 influence of public information. Ninespine sticklebacks (*Pungitius pungitius*) have been found to

95 be particularly adept at this task (Coolen et al. 2003; Laland et al., 2011; Webster & Laland

96 2015). Research into the mechanism underlying public information use in the ninespine

97 stickleback has revealed that ninespines tend to visit the location where they saw demonstrators

98 feeding at the greatest rate, but that they are not able to generalise to other locations with similar

99 physical characteristics or landmarks as the richer patch (Webster & Laland, 2013). In other

100 words, public information use in this species operates via a form of local enhancement, but not

101 stimulus enhancement (Hoppitt & Laland, 2008; 2013).

102

103 Building upon this work on the cognitive mechanisms of public information use, in this study,

104 we sought to determine whether the observers' patch selection was based upon social learning or

105 whether it arose from an unlearned social influence upon travel direction. It is possible that if, at

106 the end of the demonstration phase, the observer is more likely to be facing towards the rich

107 patch, to which its attention has been drawn by the more frequent or intense feeding-related

108 behaviours of the demonstrators at that location, then it may simply be more likely to travel in

109 that direction when released. This might cause it to become more likely to encounter the rich

110 patch first, and perhaps once there to spend more time within it, without having necessarily

111 learning anything about patch quality. This means of patch selection seems plausible in light of

112 recent studies of social foraging that have employed diffusion analyses to infer the spread of

113 foraging-related information through freely-moving shoals. These have shown that indirect

114 social effects on foraging patch detection are an important means by which group members

115 locate hidden prey patches (Atton et al., 2012; 2014; Webster et al., 2013). Indirect social effects

116 occur, for example, when searching individuals travel together and influence each other's

117 directions of heading, and therefore encounter and learn about resources at the same time, or

118 when naïve individuals discover resources simply because they happen to be following

119 experienced individuals that have already found them for themselves.

120

121 In order to distinguish between these mechanisms, we carried out two experiments. Our first

122 experiment tested whether the direction that the observer fish were facing at the moment that

123 they were released was related to whether the rich or poor patch was entered first. Finding that

124 fish were more likely to enter first the patch that they were facing would not necessarily rule out

125 social learning. However finding that the majority of fish first entered the richer patch, even if

126 they were not facing towards it when released, would strongly suggest that an unlearned social

127 effect on travel direct was unlikely to account for such a patch choice bias. Our second

128 experiment asked whether fish were still able to select the richer patch if they were forced to

129 swim through a chicane, causing them to change travel direction, before they were able to

130 approach the prey patches. If the fish were still more likely to enter the rich patch first, even after

131 orientating away from it, then an unlearned social effect on travel direct could be ruled out,

132 leaving social learning of rich patch location as the most plausible explanation.

133

134 **Materials and Methods**

135 *Collection and housing*

136 Sticklebacks were collected from Melton Brook, Leicestershire, UK (GRID REF: SP 602075) in

137 October 2009 with testing taking place between February and April 2010. In the laboratory they

138 were held in groups of 40 to 50 in 90L aquaria. Each aquarium contained a layer of coarse sand,

139 an external filter, and artificial vegetation for cover. The light: dark regime was held at 14: 10

140 hours and the temperature was maintained at 8◦C. They were fed daily with frozen bloodworms.

141

142 *Overview*

143 The experimental set up used in these experiments is derived from that of Coolen et al. (2003).

144 Initially restrained observers were allowed to watch two groups of demonstrators feed from

145 artificial patches that yielded prey at different rates. They were then released and allowed to

146 enter goal zones located next to the prey patches. Previously published experiments that have

147 used this set up have typically found that ninespine sticklebacks exhibit a bias towards

148 approaching the patch where they saw demonstrators feeding at the higher rate (Laland et al.,

149 2011). In experiment 1 we sought to determine whether the first patch that the observer entered

150 was affected by the direction that it was facing at the moment that it was released. In experiment

151 2 we asked whether the observer showed a bias towards the rich patch if it had to navigate a

152 chicane, briefly turning away from it, after it was released.

153

154 *Experiment 1*

155 We established a binary choice test tank consisting of a glass aquarium measuring 90 x 30 x 30

156 cm (Figure 1). Abutting this we placed two 30 x 15 x 15 cm glass demonstrator tanks. The three

157 tanks were separated by 5 mm. The sides of the tanks that faced each other were left uncovered,

158 while the other sides were covered in black plastic sheeting. Each tank contained a 1 cm layer of

159 sand. The water depth in all tanks was 12 cm. The central aquarium housed the observer, initially

160 within a 10x10 cm base, 15 cm tall holding unit constructed from clear Perspex. This was

161 attached via a monofilament line to an arm at the top of the tank, allowing it to be raised via a

162   pulley. The holding unit was placed in the centre of the larger aquarium. The rich and poor patch

163   goal zones were located within the 15 cm wide section at each end of the observer tank, next to

164   the demonstrator tanks. They were indicated using a yellow plastic bar across placed across the

165   width of the tank and set within the sand substrate, so that the surface of the bar was level with

166   the surface of the sand. The goal zones were used to determine prey patch preferences, as

167   described below. During the test phase, described below, the movement of the observer was

168   recorded via a high-definition webcam fixed above the tank and connected to a laptop.

169

170   (Fig. 1 here)

171

172   Each of the smaller aquaria held a group of three conspecific demonstrators, and a feeder which

173   was used to deliver prey to the demonstrators during the experiment. The feeders consisted of a 4

174   by 4 cm base, 30 cm tall tower. The front wall, facing the demonstrators, and angled 90° away

175   from the observer holding unit, was transparent so that the demonstrators could see the prey as it

176   was delivered. The rear wall was white to contrast with the prey. The side walls were opaque, so

177   that the observer in the central aquarium could not see the prey. Demonstrators were unable to

178   reach the prey until it sank to the bottom of the feeder, but nonetheless attempted to do so by

179   striking at the transparent wall as the prey item fell. The front wall of the feeder stopped 1 cm

180   short of the floor of the tank, allowing the demonstrators to eat the prey once it had reached the

181   bottom of the feeder. Prey consisted of 3 mm long pieces of thawed frozen bloodworm, small

182   enough to be consumed with minimal handling by the demonstrators, ensuring that the observer

183   could see the feeding behaviour of the demonstrators, but not the prey itself. Using separate

184   tanks to hold the demonstrators prevented the observer from using prey chemical cues to acquire

185   private information about prey distribution (Webster et al., 2007).

186

187   We used 38 fish as observers, with an additional pool of approximately 200 fish as

188   demonstrators. Observers, the test subjects, were only used once. Some demonstrators were used

189   more than once, but not within the same 72h period. Fish showing signs of having entered

190   reproductive state were excluded, since this has been shown to influence public information use

191   in the species (Webster & Laland, 2011). The demonstrators and observers were deprived of

192   food for 24 h before testing. Before the start of each trial one of the two feeders was randomly

193   selected to be the rich feeder, yielding three times more prey than the poor feeder. Three

194   demonstrators were added to each demonstrator chamber and allowed to settle for 10 minutes

195   before the observer was added to the holding unit and allowed to settle for a further 10 minutes.

196

197   The demonstration phase lasted for 6 minutes and ran as follows. At the beginning of the first,

198   third and fifth minute, 2 pieces of prey suspended in 1 cm^3 of tank water were added to the rich

199   feeder, using a pipette. The poor feeders received no prey during the first and third minute, but

200   were given 'blank' consisting of 1 cm^3 of tank water at the same time that the rich feeder

201   received prey. During the fifth minute of the two-feeder treatments the poor feeder also received

202   prey. This ensured that while prey were delivered at a 3:1 ratio, the observer was unable to select

203   a prey patch simply on the basis of it being the last place it saw fish feeding. After six minutes

204   opaque black plastic walls were inserted into the 5 mm gaps between the central tank and the two

205   demonstrator aquaria. The observer was allowed to settle for sixty seconds, then the holding unit

206   was raised 5 cm using the pulley. In raising the holding unit we were careful not to disturb the

207   surface of the water, as this can startle the fish. It took less than 1 second to raise the holding

208   unit, and none of the fish displayed any fright response, such as darting away immediately,

209   erecting the pelvic spines or attempting to hide on the bottom of the tank. Raising the holding

210   unit commenced the test phase of the trial.

211

212   We recorded the direction that the focal fish was facing at the moment that the holding unit was

213   raised. Since we were only interested in the direction that the fish was facing at the moment that

214   it was allowed to exit the holding unit, we did not collect any data on the direction that it was

215   facing during the demonstration period. Facing direction was scored using six pairs of ordinal

216   category bins of 30 degrees each, such that 0 to 30 indicated a fish facing towards the rich patch

217   and 151-180 indicated a fish facing towards the poor patch (Figure 2a). We gauged facing

218   direction based upon the direction that the snout of the fish was pointing. To measure this

219   accurately we took measurements from a still image consisting of the frame of video at the

220   moment from the moment that the holding unit was raised. We used the program TPS digit

221   (Rohlf, 2010) to draw a line running from a position midway between the eyes of the fish, and

222   measured the midpoint of this line. We then drew a second line at 90 degrees to the first, running

223   from the midpoint of the first line out through the centre of the snout of the fish. A circle divided

224   into 12 sectors and aligned as in Figure 2a was superimposed over the frame and centred on the

225   holding unit. The sector through which the second line passed, corresponding to a 30 degree

226   category bin, was taken as the direction of facing (Figure 2b). After the holding unit had been

227   raised we recorded which patch the fish visited first, and how long it took to reach it.

228

229   *Experiment 2*

230   Experiment 2 used the same binary choice experimental arena as did experiment 1, with the

231   exception that half of the trials included a chicane, within which the holding unit was housed

232   (Figure 1c). The chicane measured 15 cm tall, 12 cm wide and 20 cm long. Two 8 cm barriers

233   formed the chicane itself. The inner barrier was positioned on the same side of the chicane wall

234   as the rich patch, and the outer barrier on the opposite side. This forced the fish to perform a

235   switchback, away from the rich patch goal zone, before the fish was able to exit the chicane and

236   access it. Two such chicanes were built so that each could be matched to the location of the rich

237   patch (left or right) which was randomised as in experiment 1, so that in all trials the fish was

238   forced to turn away from the rich patch before it was able to exit the chicane and enter the main

239   arena, and approach either patch.

240

241   We performed 50 trials in total, half with the chicane apparatus and half without it. Thus, half the

242   observers were able to approach the goals directly following release, while the other half were

243   forced to take an indirect route, via the chicane, to get to them. No observer was tested more than

244   once and none of the observers used in Experiment 2 had previously been used as observers or

245   demonstrators in Experiment 1. The set up and procedure during the demonstration phase were

246   otherwise the same as described for Experiment 1. During the test phase, the holding unit was

247   raised as described above, while the chicane (in those trials where it was deployed) remained on

248   the floor of the tank. In this experiment we recorded not only the first goal zone entered by the

249   observer, but also its location every six seconds for five minutes following the raising of the

250   holding unit, whether within either goal zone or the central 'neutral' zone (including within the

251   chicane), yielding a total of 50 data points.

252

253 *Ethical Note*

254 All procedures performed in this study were in accordance with the ethical standards of the

255 University of St Andrews, where the study was conducted. No fish died or suffered apparent ill

256 health after being used in this study. Following the completion of this study the fish were

257 retained in our laboratory for use in further studies.

258

259 *Statistical analysis*

260 In Experiment 1, the first goal zone that the observers entered was analysed using a binary

261 logistic regression. Direction of facing and latency to enter the goal zone were included as

262 ordinal and continuous covariates respectively, while the location of the rich patch, left or right,

263 was included as a fixed factor.

264

265 In Experiment 2, we compared first choice and time allocation to the rich and poor patches

266 within each of the two treatments (chicane or no chicane) using binomial and t-tests. Between

267 treatments, we compared first choice using a binary logistic regression. Time allocation (time in

268 rich patch minus time in poor patch) was compared between treatments using a general linear

269 model. In both models, treatment and the location of the rich patch were included as fixed factors

270 and latency to enter either goal zone was included as a continuous factor.

271

272 **Results**

273 *Experiment 1*

274 Overall, the majority of observers entered the rich patch goal zone first (27 versus 11, binomial

275 test: $N=38$, $P=0.014$). A binary logistic regression revealed that direction of facing, latency to

276   enter either patch, and the location of the rich patch did not affect the observers' first goal zone

277   choice (direction of facing: X^2=1.45, df=5, P=0.91, 95% confidence intervals (CI): -0.02, 3.62;

278   location of rich patch: X^2=1.83, df=1, P=0.17, 95% CI: -0.06, 1.66 ; latency to enter either patch:

279   X^2=0.55, df=1, P=0.46, 95% CI: -0.97, 1.01; Figure 2c).

280

281   (Fig. 2 here)

282

283   *Experiment 2*

284   We saw that observers were not more likely to enter the rich patch goal zone first more

285   frequently than would be expected by chance when each of the chicane and no-chicane

286   treatments were considered separately, but that such an effect was apparent when data from the

287   two treatments were pooled, suggesting a weak effect (binomial test, chicane: 16 versus 9, N=25,

288   P=0.23; no chicane: 17 versus 8, N=25, P=0.11; pooled, 33 versus 17, N=50, P=0.03, Figure 3a).

289   Observers did however spend more time in the rich patch goal zone than they did in the poor

290   patch goal zone in both the chicane and no-chicane treatments (paired samples *t*-test, chicane:

291   t=2.64, df=24, P=0.014; no chicane: t=3.20, df=24, P=0.004, Figure 3b).

292

293   Comparing the data for chicane and no-chicane treatments, we saw no differences between the

294   two treatments in either the number of observers first entering the rich patch goal zone (binary

295   logistic regression: treatment: X^2=0.13, df=1, P=0.71, 95% CI: -0.22, 2.70; location of rich patch:

296   X^2=1.88, df=1, P=0.11, 95% CI: 0.09, 1.11; latency to enter either patch: X^2=0.29, df=1, P=0.59,

297   95% CI: -0.98, 1.01). We also saw no difference between the two treatments in the amount of

298   time that the observers spent in the rich compared to the poor goal zone (general linear model:

299   treatment: $F_{(1, 49)}= 0.96$, $P=0.33$, 95% CI: -0.79, 5.81; location of rich patch: $F_{(1, 49)}= 0.01$,

300     $P=0.91$, 95% CI: -3.89, 1.49; latency to enter either goal zone: $F_{(1, 49)}= 2.30$, $P=0.10$, 95% CI: -

301   0.07, 3.31).

302

303   (Fig. 3 here)

304

305   **Discussion**

306   In our first experiment, the direction that the fish were facing at the moment that they were

307   released from the holding unit was not seen to have any effect upon their likelihood of entering

308   the rich or poor patch goal zone first. In experiment 2, fish spent as much time in the rich patch

309   goal zone if they first had to swim through a chicane forcing them to move in the opposite

310   direction as they did in the condition where they could swim directly towards the goal zone

311   unimpeded, with fish in both treatments spending more time in the rich than the poor goal zone.

312   Taken together, the results of these two experiments provide no support for the hypothesis that

313   patch choice results from an unlearned social influence upon travel direction. To the contrary, the

314   experiments suggest these findings are underpinned by social learning.

315

316   In a previously published study we showed that ninespine sticklebacks were attracted to the

317   location at which they saw conspecifics feeding, but that they showed no evidence of learning

318   associations between physical cues present at the demonstrated feeding site and the presence of

319   food (Webster & Laland, 2013). The combined findings of this and the present study then point

320   towards learned local enhancement as the mechanism underlying public information use in this

321   species. Useful further work could focus upon the relative importance of social learning in social

322   foraging and producer-scrounger interactions. Other recent studies have documented unlearned

323   social effects on travel direction brought about through attraction to other group members, that

324   explain the rate and order in which individual group members encounter resources as they forage

325   (Webster & Laland, 2012; Atton et al., 2012; 2014; Webster et al., 2013). It would be

326   informative to determine how this form of social learning operates in nature.

327

328   Further useful work might also address the relationship between social information use and

329   behavioural lateralisation. Lateralisation research has revealed evidence of left or right-eye bias

330   in some species of fish when monitoring predators or other stimuli (Bisazza et al. 1999). We saw

331   no evidence of a population level bias in direction of facing at release in the sticklebacks tested

332   here. We collected no data on eye use or direction of facing during the demonstration phase of

333   the trial, since determining whether lateralisation exists in this species and context was not an

334   objective of our study. Nonetheless, this is an interesting question that we plan to address in a

335   future study. Individual and/or population level lateralisation should be simple to detect using a

336   binary choice approach such the one used in this study, while in principle it ought to be possible

337   to identify any such biases using information diffusion analyses to in free-ranging fish, under

338   more naturally realistic conditions too (Atton et al., 2012; 2014; Webster et al., 2013).

339

340   Building further on this finding, we might ask what are animals actually learning when they

341   select resource patches under the influence of public information? One plausible explanation is

342   that public information use reflects the integration of two learned associations. Such a

343   mechanism was recently found to underlie flower colour-copying behaviour in bumblebees

344   (*Bombus terrestris*). Here, bumblebees visited artificial flowers of the same colour that they had

345 others visit only if they had previously learned to associate the presence of conspecifics with a

346 sucrose solution reward. Similarly, bumblebees that were trained to associate the present of

347 conspecifics with a bitter, unpalatable stimulus were more likely to avoid flower colours that

348 they had seen others foraging upon (Dawson et al. 2013). In the case of public information using

349 fishes (Webster & Laland 2008; Laland et al. 2011; this study), such an association might arise

350 from individuals being exposed to some aspect of the foraging behaviour of their group mates,

351 such as their posture or activity levels, while they themselves are feeding. Potentially they could

352 come to learn an association between these behaviours and the presence of food, and by

353 extension, learn that the performance of this behaviour by others at a particular location is

354 predictive of the likelihood of there being food at that location. A topic that is currently

355 interesting researchers interested in the mechanisms, function and evolution of social learning

356 relates to whether such behaviour reflects an adaptive specialisation or whether it is merely

357 asocial learning in which one or more of the learned stimuli happens to be the presence or

358 products of another animal (Lefebvre & Giraldeau, 1996; Sterelny, 2009; Heyes, 2012). This is a

359 fundamental question, and one that is likely to garner more research attention in the coming

360 years. Public information use and social learning more generally are taxonomically widespread

361 and affect behaviour in a variety of different contexts (Valone & Templeton, 2002; Chittka &

362 Leadbeater 2005; Danchin et al. 2005). Carefully designed experiments that take into account the

363 social environments that animal experience and the potential sources of information that they are

364 exposed to both before and during their participation in experiments or field studies will be

365 necessary if we are to further understand the mechanism or mechanisms that underpin these.

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Figure legends

528

529   **Figure 1.** The public information binary choice tank used in Experiments 1 and 2, consisting of a

530   larger central choice tank housing the test subject and two smaller demonstration tanks, holding

531   the demonstrators and feeder units. Solid and broken lines indicate opaque and transparent

532   barriers respectively. The grey shaded areas indicate the goal zones. Panel (a) shows the layout

533   of the tank during the demonstration phase while panel (b) shows the layout during the test

534   phase, with opaque barriers now in place between the central and demonstrator tanks, and the

535   focal fish released from the raised holding unit. Panel (c) shows the chicane used in Experiment

536   2. The fish, once released from the inner holding unit is forced to swim out through the chicane,

537   before it can enter the wider arena and enter either goal zone.

538

539   **Figure 2.** Experiment 1: effect of facing direction at release upon patch choice. (a) Direction of

540   facing at moment of release was placed within six ordinal category bins of 60 degrees each, with

541   fish facing directly towards the rich patch, 0-30 degrees, up to fish facing directly towards the

542   poor patch, 151-180 degrees. (b) The (categorical) angle of orientation was determined using a

543   digital imaging program. Using a still image taken from the video, a straight line was placed

544   between the fish's eyes, and a second line, 90 degrees to the first, was drawn between the point

545   midway between the eyes and the centre of the tip of the snout. A 12-sector circle was

546   superimposed over the frame and centred on the holding unit. The sector that this line passed

547   through was taken as the fish's direction of facing. (c) Count data indicating the first goal zone

548   entered by the fish, grouped by the direction that they were facing at the moment they were

549   released. The colours of the bars correspond to the sectors in (a), and indicate direction of facing.

550   The solid and hatched portions of the bars indicate the number of fish that entered the rich and

551   poor patch goal zone first respectively. The numbers on each bar indicate the number of trials in

552   which the fish was facing in that direction. Direction of facing was not seen to influence first

553   goal zone entered.

554

555   **Figure 3.** Experiment 2: (a) Comparing the first goal zone entered by fish that were either

556   allowed to swim unimpeded following release, or which had to first navigate a simple chicane.

557   The solid and hatched portions of the bars indicate the number of fish that entered the rich and

558   poor patch goal zone first respectively. There was no difference in first goal zone entered

559   between the two treatments. (b) Comparing the time spent in the rich (solid bars) and poor

560   (hatched bars) goal zones for fish tested in the chicane and no chicane conditions. In both

561   treatments, fish spent more time in the rich than the poor goal zones. There was no difference in

562   net time allocation (time in rich patch – time in poor patch) between the two treatments.

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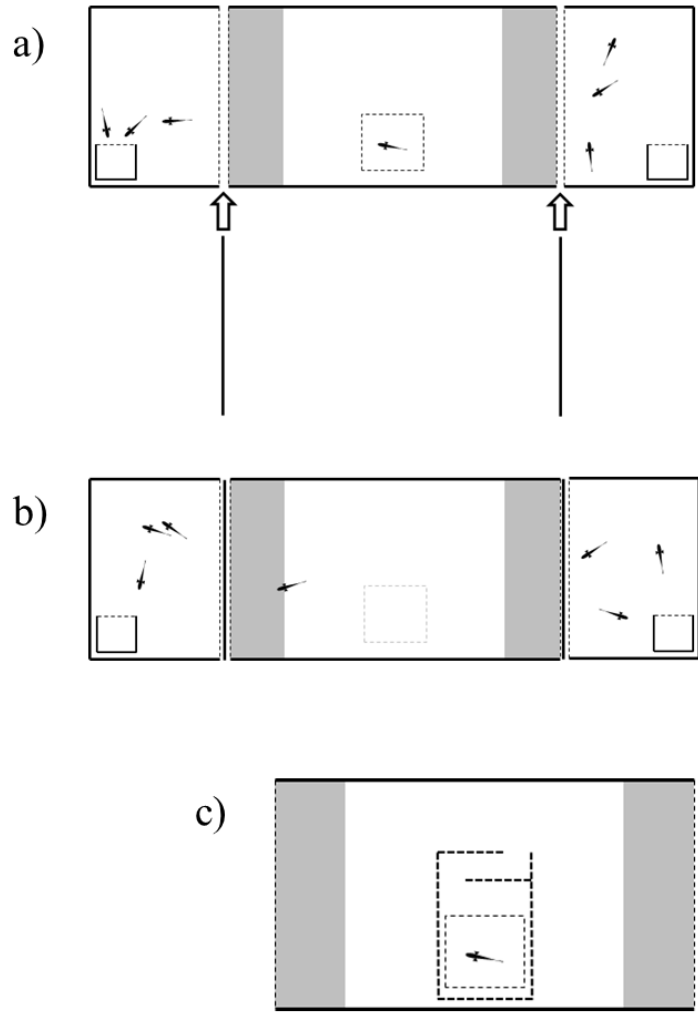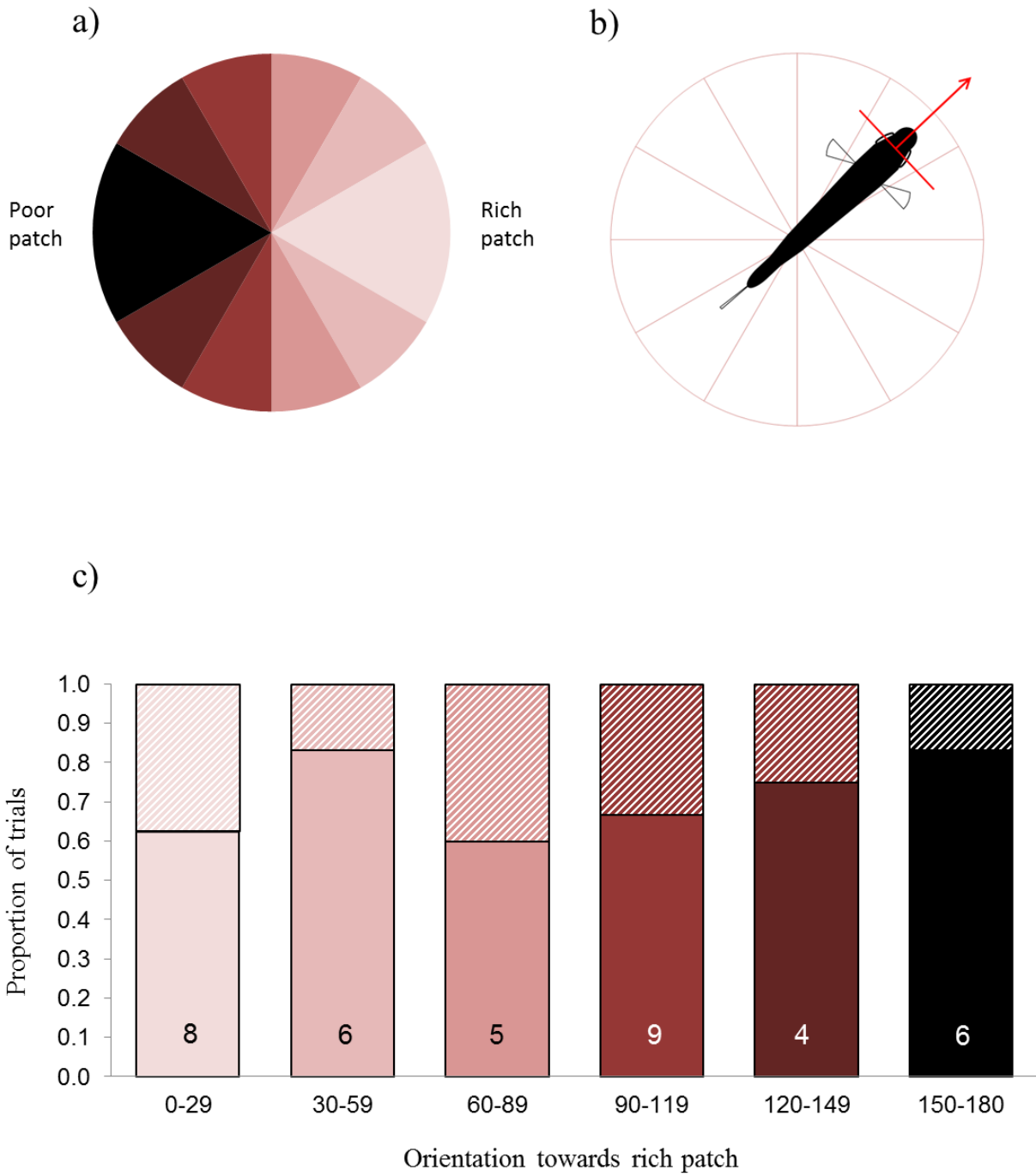**Figure 1**

Figure 2

a)

Poor patch

Rich patch

b)

c)

Proportion of trials

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0

8   6   5   9   4   6

0-29   30-59   60-89   90-119   120-149   150-180

Orientation towards rich patch

Figure 3

a)

b)

587
588