1 **Social information use and social learning in non-grouping fishes**

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3 **Lay summary**

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5 We show that some non-shoaling fish species are just as good at copying the food patch choices

6 of other fish as shoaling species. This suggests that living in groups is not a prerequisite for

7 effective social learning. We argue that many solitary species will nevertheless be regularly

8 exposed to social stimuli and can benefit, for example by obtaining information about where to

9 forage, by copying others.

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Social information use and social learning in non-grouping fishes

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SHORT TITLE: Social learning in non-grouping species

36   ABSTRACT

37

38   While it is natural to expect that group-living animals will utilise social learning, the expectation

39   for non-grouping species is less clear. Only a few studies have explored the relationship between

40   sociality and social learning. Here we presented four non-grouping fish species, fifteenspine

41   sticklebacks (*Spinachia spinachia*), bullhead sculpins (*Cottus gobio*), stone loach (*Barbatula*

42   *barbatula*) and juvenile European flounders (*Platichthys flesus*) with social information provided

43   by groups of a shoal-forming heterospecific, the threespine stickleback (*Gasterosteus aculeatus*).

44   Using a binary choice procedure we allowed individual test subjects to select between simulated

45   prey patches. While the test subjects could not sample the patches directly they were able to use

46   information generated by the heterospecific demonstrators to select the 'richer' of the two

47   patches. For comparison we also recorded social information use in two shoaling species,

48   threespine and ninespine sticklebacks (*Pungitius pungitius*). We saw evidence of social

49   information use and social learning in all six species, with no differences seen between social

50   and non-grouping species. We argue that social learning is not likely to be restricted to group-

51   living species, since many solitary species too are regularly exposed to social stimuli from both

52   con- and heterospecifics, and can benefit from using social information. We suggest that

53   researchers have much to learn about the sensory, perceptive and cognitive mechanisms

54   underlying social learning, and the extent to which these vary (if at all) between grouping and

55   non-grouping species.

56   KEY WORDS: Copying; Learning; Producer-scrounger; Social information; Social learning;

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58

Introduction

While access to social information is one of the many advantages of living in groups, there is little compelling evidence that social information use or social learning are adaptions specifically associated with sociality (Lefebvre & Giraldeau, 1996). On the one hand, Templeton et al. (1999) compared social learning between two corvid species, finding that the more social of the two was better at social than asocial or individual learning, while the other performed similarly in both types of learning. In contrast, in a meta-analysis of social learning in more than 100 primate species, no relationship was found between social learning performance and social group size after phylogeny was controlled for (Reader 1999; Reader & Lefebrve 2001). Other studies have documented social learning in non-grouping species, where such behaviour- if closely linked to group-living- might not be expected to occur. Fiorito & Scotto (1992) reported social learning in the octopus (*Octopus vulgaris*) (but see comments by Biederman & Davy 1993). Wilkinson et al. (2010) found that red-footed tortoises (*Geochelone carbonaria*) could socially learn to navigate around an obstacle, while Kis et al. (2015) demonstrated that bearded dragons (*Pogona vitticeps*) could learn to open a trapdoor after seeing a conspecific do so, with individuals being more likely to open it to the same side that their demonstrator did.

There are at least two reasons why social learning ability might not be closely tied to group living. The first is that all animals, whether solitary or gregarious, are likely to be exposed to social information some of the time, and potentially quite frequently. Cues may come from mates, offspring or broodmates, depending upon the social and mating system of the species concerned, or from conspecifics in neighbouring territories or at patchily distributed resources,

82 where non-group-living animals occasionally aggregate. Heterospecifics may also be an

83 important, and arguably overlooked, source of social information, particularly if they exploit the

84 same resources or are subject to the same threats as non-group-living observers (Sullivan 1984;

85 Coolen et al. 2003; Ward et al. 2005; Seppänen et al. 2007; Webster et al. 2008; Avarguès-

86 Weber et al. 2013; Goodale et al. 2014; Ward & Webster 2016). Second, social learning may

87 reflect learning performance more generally, with social cues being but one class of cue among

88 many that are available in the environment (Heyes 2012).

89

90 In this study we were particularly interested in quantifying social information use and social

91 learning by non-grouping fishes exposed to social cues from heterospecifics, predicting that they

92 would prove capable of both. To test this idea we compared social information use and social

93 learning in four non-grouping species of fish from four different families: fifteenspine

94 sticklebacks (*Spinachia spinachia*, Gasterosteidae), bullhead sculpins (*Cottus gobio*, Cottidae),

95 stone loach (*Barbatula barbatula*, Balitoridae) and juvenile European flounders (*Platichthys*

96 *flesus*, Pleuronectidae). All of the populations of these species used in this study live in locations

97 where the facultatively social threespine (*Gasterosteus aculeatus*, Gasterosteidae), the

98 heterospecific demonstrator used in this study, is common. All of these species are predators of

99 invertebrates, with bullheads, stone loaches and flounders being benthic predators and

100 fifteenspines feeding epibenthically and within the water column. Threespines are generalist

101 foragers, feeding from the substrate, vegetation and water column. They therefore represent an

102 ecologically valid source of social information about the distribution of prey resources to all of

103 these species. Moreover, threespines have previously been shown to be effective demonstrators

104 in social learning tasks using heterospecific observers (Coolen et al. 2003). In addition to testing

105 these four non-grouping species, for comparison we also tested the threespines themselves and

106 another facultatively social species, the ninespine stickleback (*Pungitius pungitius*,

107 Gasterosteidae). We performed a battery of binary choice tests in which individuals of each

108 species were presented with groups of demonstrators that were either feeding or not feeding or

109 feeding at a higher versus a lower rate. Fish were tested while these were visible (social

110 information use) or after they had been removed from sight (social learning). We also performed

111 trials in which differently sized groups of demonstrators were presented, either feeding or not

112 feeding, in order to test for shoaling behaviour. We predicted that the four non-grouping species

113 would perform equally as well as the two shoaling species in the social information use and

114 social learning treatments but that only the two social species would show a preference for

115 joining larger shoals in the shoaling conditions.

116

117 **Methods**

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119 Overview

120

121 We used a laboratory binary choice procedure to investigate how fish use socially transmitted

122 information to assess and learn about the relative quality of two simulated prey patches. A test

123 subject, hereafter the observer, was placed within a holding unit in a central test tank. At either

124 end of the test tank was a smaller tank containing a number of threespine stickleback

125 demonstrators. In some trials these were presented with a prey-like stimulus that was not visible

126 to the observer. The demonstrators attacked the stimulus, providing the observers with social

127 information and effectively simulating a social foraging scenario (see pilot experiment). The

128   observers were allowed to watch the demonstrators before being released and allowed to

129   approach them. We used the amount of time that the observer spent close to each demonstrator

130   group as a measure of its attraction, taking a bias towards one demonstrator group over the other

131   as being indicative of social information use. This approach is based upon that of Coolen et al.

132   (2003), and has been used extensively by our group in similar experiments investigating social

133   learning (Laland et al. 2011).

134

135   Study animals

136

137   We used six fish species, threespine, ninespine, and fifteenspine sticklebacks, bullhead sculpins,

138   stone loaches and juvenile European flounders. Bullheads, stone loaches and flounders are non-

139   shoaling, benthic-living species that live in and among the substrate. Flounders are diadromous

140   and enter freshwater rivers as juveniles, while the other two species live permanently in

141   freshwater. Fifteenspines are found in coastal marine and brackish environments. In both

142   bullheads and fifteenspine sticklebacks the males provide parental care. In contrast, threespines

143   and ninespines are facultatively social, occurring singly or in groups of up to several hundred.

144   Both are found in freshwater and brackish environments and threespines are also found in coastal

145   marine areas. In both of these species the males also provide parental care. Threespines co-occur

146   with all of the species used in this study, and were used as demonstrators to provide social cues

147   in all of the experiments described below.

148

149   These experiments were conducted in two bouts between 2008 and 2012. Bullheads (n=17, 40-

150   55 mm in length), stone loaches (n=18, 40-65 mm) and threespine and ninespine sticklebacks

151 (n= ca. 100 and 18 respectively, 35-45 mm) were collected from Melton Brook, Leicestershire

152 UK in August 2008 and transported to our laboratory at the University of St Andrews. We also

153 collected ca. 200 threespine sticklebacks at this time from the Kinnessburn stream in St

154 Andrews, UK. The threespines and ninespines were held in single species (and population in the

155 case of threespines) groups of 18-25 in 90L aquaria, while the bullheads and stone loaches were

156 held in single species groups of 5-6 in 90L aquaria. In September 2012 we collected 25 juvenile

157 flounders (35-50 mm) from the freshwater lower reaches of the Kinnessburn stream and 22

158 fifteenspine sticklebacks (45-85 mm) from rockpools on the shore of St Andrews bay, both in St

159 Andrews UK. These were held in single species groups of 8-9 and 7-8 respectively, also in 90L

160 aquaria. All aquaria were visually and chemically isolated from one another. Each aquarium

161 contained course sand, plastic plants and an internal filter. The temperature of the lab was held at

162 8°C and the light:dark regime at 12:12. The fifteenspine sticklebacks were held in seawater,

163 while the other species were held in freshwater. The fish were fed a diet of frozen bloodworms

164 and mysids once per day. They were held in the lab for 6-8 weeks before being tested. The

165 bullheads, stone loaches, threespines and ninespines were tested in September-December 2008,

166 and the flounders and fifteenspines were tested between November 2012 and February 2013,

167 using the procedures described below. After testing the threespines and ninespines were retained

168 in the laboratory for use in further experiments while the other fish were released at their point of

169 capture.

170

171 Design & Procedure

172

173 The experimental apparatus consisted of a single large glass tank (45 x 30 x 30 cm, water depth

174 12 cm) and two smaller Perspex tanks (27 x 15 x 12 cm, water depth 12 cm). The smaller aquaria

175 contained the demonstrator groups and were set 0.5 cm from either end of the larger one, which

176 held the observer. Each of the three tanks contained a 1 cm deep layer of coarse sand. The

177 observer arena contained seawater when the fifteenspines were tested and was filled with

178 freshwater for all of the other species. The threespine demonstrators were always held in

179 freshwater. Within the observer arena, yellow plastic bars, 1 cm wide and 1 cm deep, secured to

180 the base of the tank and rising to the surface of the sand divided the tank into three zones. These

181 were set 8 cm from either end of the observer arena. The two areas between the ends of the tank

182 and the bar were designated the prey patch goal zones.

183

184 Within each of the demonstrator tanks we placed a feeder unit. The feeder unit consisted of a 4 x

185 4 cm base, 30 cm tall tower. The feeder units were placed in the corner of the demonstrator

186 chamber furthest from the observer arena. The front wall of the feeder unit, facing the

187 demonstrators, was transparent so that the demonstrators could see the prey stimulus. The inside

188 rear wall was white, as was the base, to maximise the visibility of the prey stimulus. The side

189 walls were opaque blue, so that the observer in the centre of the tank could not see the prey

190 stimulus. The prey stimulus consisted of a point of red of light delivered by a laser pointer

191 mounted 45 cm above the feeder unit. This was switched on periodically as described below,

192 simulating a prey delivery. Sticklebacks readily attack red objects (Smith et al. 2004) and we

193 have previously shown that observers are attracted to others that are directing attacks towards

194 prey and prey-like stimuli, even if they are not actually able to capture these (Webster & Laland

195 2012). The demonstrators struck at and attacked the point of light, performing characteristic

196   feeding-like behaviour (see Supplementary Material). The observers were able to see this

197   behaviour but could not see the red laser point, and could therefore only base their patch choices

198   upon visual cues received during the demonstration phase. We used the red laser pointer rather

199   than actual prey because it allowed us to control the duration of the prey stimulus period

200   precisely and because it prevented the demonstrators from becoming satiated.

201

202   Within the observer arena, the observer was held within a holding unit for the duration of the

203   settling period and demonstration phase. The holding unit consisted of a tower of clear,

204   colourless perforated Perspex measuring 10 x 10 cm x 15 cm tall. It was attached via a

205   monofilament line to a 15 cm long arm clamped to the top of the observer arena, allowing the

206   holding unit to be raised by the experimenter. The holding unit was placed 5 cm from the side

207   wall of the observer arena and half way between the end walls that abutted the demonstrator

208   chambers. We used two opaque black plastic screens measuring 30 x 30 cm square by 2 mm

209   thick to separate the observer arena from the demonstrator chambers during the choice phase of

210   the trial. These were designed so that they could be slid into place between the tanks without

211   causing any significant vibration that might alarm the observer. The exterior walls of both the

212   observer arena and demonstrator chambers were screened in black plastic. Observations were

213   made via a webcam fixed 90 cm above the tank and connected to a laptop computer.

214

215   Subjects

216

217   In total we tested six species of fish for social information use, using threespine sticklebacks as

218   demonstrators in all of these experiments. Neither demonstrators nor observers were sexed.

219   Within trials the demonstrators were matched to each other by body length to within 3mm. Since

220   the demonstrators were drawn from a limited pool of available fish some demonstrators were

221   used in multiple trials. No individual was used more than once in any three-day period. In

222   between testing days, each observer was held within a 30x30x30 cm aquarium containing a 2cm

223   deep sand substrate, an artificial plant and an air stone. These were visually and chemically

224   isolated from each other.

225

226   Procedure

227

228   The demonstrators and observers were deprived of food for 24 h before testing in order to ensure

229   that they were motivated to forage. The demonstrators were added to the demonstrator chambers

230   and allowed to settle for 30 minutes before the observer was added to the holding unit in the

231   central test and allowed to settle for a further 10 minutes. During this period opaque black

232   screens were placed between the observer arena and the two demonstrator chambers, and the

233   observers could not see the demonstrators.

234

235   The demonstration phase lasted for 6 minutes and ran as follows. The prey stimulus consisted of

236   a ten second presentation of the laser pointer. This was performed at the beginning of the first,

237   third and fifth minute of the demonstration period of both the demonstration and the choice

238   phase for the 'rich' patch demonstrator groups (treatments Feeding A-D), both demonstrator

239   groups in Group size A and in the rich patch of the Prey stimulus only treatment. The prey

240   stimulus was also presented during the first 10 seconds of the fifth minute of each phase in the

241   'poor' patch for treatments Feeding C and D. This ensured that while prey stimuli were

242   presented at a 3:1 ratio in these treatments, the focal fish was unable to select a patch simply on

243   the basis of it being the last place it saw others feeding. The location of the rich patch, either to

244   the left or to the right of the observer arena, was randomly selected for each trial.

245

246   After the six minute demonstration phase, the opaque black screens were slid into place between

247   the observer arena and the two demonstrator chambers. This took approximately 10 seconds and

248   did not appear to stress the observer or demonstrators. These were retained for the remainder of

249   the trial in treatments Feeding B and D. In all other treatments they were held in place for 10

250   seconds and then removed again. The observer was allowed to settle for a further 1 minute

251   before being released from the holding unit. The observer was released by raising the holding

252   unit 5 cm from the base of the arena, using the pulley mechanism. The base of the holding unit

253   was left suspended beneath the water surface, so as not to disturb the surface of the water and

254   startle the observer. This commenced the choice phase of the trial, which lasted for five minutes.

255   Using the videos of the choice phase of the trial we recorded the location of the observer every

256   six seconds, whether within either goal zone or the central neutral zone, yielding a total of 50

257   data points.

258

259   Treatments

260

261   Each fish was tested seven times, once in each of the treatments described below. We adopted a

262   repeated measures design, with the order of testing in each treatment randomised for each

263   subject. Fish were tested every three days and were fed daily, but never less than 24h before

264   being tested.

265

Feeding A, 5|5 Demonstrators visible, prey 3:0: Two groups of five demonstrators were used.

One group was presented with the prey stimulus 3 times during the demonstration phase while

the other group exhibited no feeding behaviour. The demonstrators were still visible while the

observers were allowed to move between patches during the choice phase, and the feeding group

of demonstrators was presented with the prey stimulus a further 3 times during this period.

271

Feeding B, 5|5 Demonstrators hidden, prey 3:0: This treatment was performed as described

above, except that the opaque barriers were placed in between the observer and demonstrator

tanks after the demonstration phase and before the choice phase, preventing the observer from

seeing the demonstrators during this period.

276

Feeding C, 5|5 Demonstrators visible, prey 3:1: Two groups of five demonstrators were used.

One group was presented with the prey stimulus 3 times during the demonstration phase while

the other group was presented with it once. The demonstrators were still visible while the

observers were allowed to move between patches during the choice phase, and the two groups of

demonstrators were presented with the prey stimulus again at the same ratio during this period.

282

Feeding D, 5|5 Demonstrators hidden, prey 3:1: This treatment was performed as described

above for Feeding C, except that the opaque barriers were placed in between the observer and

demonstrator tanks after the demonstration phase and before the choice phase, preventing the

observer from seeing the demonstrators during this period.

287

288 **Group size A, 8|2 Demonstrators visible, prey 3:3**: A group of eight and a group of 2

289 demonstrators were used. Both groups were presented with the prey stimulus 3 times during the

290 demonstration phase. The demonstrators were still visible while the observers were allowed to

291 move between patches during the choice phase, and both groups of demonstrators were presented

292 with the prey stimulus a further 3 times during this period. This condition allowed us to

293 determine whether any of the species were attracted to larger (or smaller) groups of

294 demonstrators, which many indicate a general shoaling preference.

295

296 **Group size B, 8|2 Demonstrators visible, prey 0:0**: A group of eight and a group of 2

297 demonstrators were used. Neither groups were presented with the prey stimulus during the

298 demonstration phase. The demonstrators were still visible while the observers were allowed to

299 move between patches during the choice phase. This condition allowed us to check for a general

300 shoaling preference in any of the observer species, and complements the Group size A condition

301 by removing any confounding effects of demonstrator feeding behaviour.

302

303 **No social stimulus control, 0|0 Demonstrator chambers visible, prey 3:0**: No demonstrators

304 were present in either demonstrator chamber. The prey stimulus was delivered three times to one

305 feeder only during the demonstration phase and three times during the choice phase of the trial.

306 These treatment was performed to determine whether the observers could perceive the prey

307 stimulus by any means (such as via reflected light from within the feeder unit).

308

309 Statistical analyses

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311   For each trial we subtracted the number of sampling instances (out of a total of 50 possible)

312   spent in the poor goal zone from that spent in the rich goal zone. These data were used as the

313   dependant variable in a repeated measures GLM with Poisson distribution. Treatment was used

314   as the within subject variable, with species included as a between subjects factor. We used

315   simple contrasts to compare each of the treatments and the treatment*species interaction to the

316   *no social stimulus control* treatment. In order to test for differences between species within the

317   different treatments we also performed one-way ANOVAs with Tukey post-hoc tests for each

318   treatment.

319

320   Ethical statement

321

322   These procedures were reviewed and approved by the Ethics Committee at the University of St

323   Andrews. All of the procedures described above meet the ABS/ASAB guidelines for ethical

324   treatment of animals.

325

326   **Results**

327

328   A repeated measures GLM revealed effects of treatment (Wilks' $\lambda= 0.41$, $F_{(6, 113)}= 25.24$,

329    $P<0.001$), species ($F_{(5, 114)}= 7.48$, $P<0.001$) and a treatment*species interaction (Wilks' $\lambda= 0.59$,

330    $F_{(6, 113)}= 2.01$, $P= 0.001$, Figure 1). Contrasts compared the difference in the amount of time that

331   fish spent in the rich goal zone relative to the poor one in each treatment against that of the *no*

332   *social stimulus control* treatment in which no demonstrators were present (Table 1). These

333   revealed that fish tended to spend more time in the rich goal zone than they did in the control in

334   all but one treatment, Feeding D, in which the observer fish were presented with two

335   demonstrator groups attacking prey stimuli at high and low rates and then were allowed to select

336   prey patches after these had been removed from sight. There was also some variation in patch

337   selection between species with treatments, as indicated by the significant effects of species and

338   the treatment*species interaction term, above, although here contrasts revealed no differences

339   between any of the treatments and the *no social stimulus control* treatment (Table 1).

340

341   All species showed a preference for the demonstrated richer patch in the treatments where they

342   chose in real time while the demonstrators were still visible (Feeding A and C), indicated by

343   positive scores for time in rich patch-time in poor patch, with confidence intervals that did not

344   span zero, Figure 1). When choosing after the demonstrators had been removed from view, in the

345   treatment where one group of demonstrators was attacking the prey stimulus and one was not

346   (Feeding B), all species again showed a preference for the rich patch, with confidence intervals

347   not spanning zero. In the treatment where both demonstrators were attacking the prey stimulus at

348   different rates (Feeding D), only two species, ninespines and bullheads, showed a preference for

349   the richer patch. In the two treatments where the demonstrator group sizes were varied (Group

350   Size A and B), only the threespines and ninespines (the two social species) showed any

351   preference, spending more time close to the larger groups. Finally, in the *no social stimulus*

352   *control* treatment where prey stimuli were presented in the absence of any demonstrators, no

353   species showed any patch preference.

354

355   One-way ANOVAs revealed no differences between species in the treatments Feeding B, C and

356   D ($F_{(5, 119)} = 0.12$, P=0.98; $F_{(5, 119)} = 0.99$, P=0.43; $F_{(5, 119)} = 1.51$, P=0.18), and none in the No

16

357   social stimulus control (($F_{(5, 119)}$ = 0.65, P=0.66). We did see differences between species in the

358   other treatments. In Feeding A ($F_{(5, 119)}$ = 3.91, P=0.003) fifteenspines spent more time in the rich

359   patch than did stone loaches (Tukey post-hoc: P=0.002). In group size A ($F_{(5, 119)}$ = 4.56,

360   P=0.001), both threespines (P=0.039 and 0.045) and ninespines (P=0.021 and 0.025) spent more

361   time in the rich patch than did flounders or fifteeenspines. Finally, in Group size B ($F_{(5, 119)}$ =

362   11.26, P<0.001), threespines spent more time closer to the larger group of demonstrators than did

363   bullheads, stone loaches, flounders or fifteenspines (P=0.002 vs bullheads and <0.001 for the

364   other species). The same pattern was seen for ninespines compared to these species (P=0.001 vs

365   bullheads and <0.001 for the other species).

366

367   **Discussion**

368

369   Our experiment reveals clear evidence of social information use and social learning non-

370   grouping fishes. When the demonstrators were visible to the observers, all species spent more

371   time in close proximity to the group that was feeding (Feeding A) or which was feeding at the

372   greater rate (Feeding C). When the demonstrators were not visible during the period when the

373   observers were allowed to move throughout the tank, all species spent more time close to the

374   location of the demonstrator group that had been feeding than they did near the group that had

375   not fed, indicating that they had learned the location of this group (Feeding B). Moreover, one

376   species, bullheads, were seen to be capable of recalling which of two feeding groups of

377   demonstrators had fed at the greater rate when both were presented with prey-stimuli (Feeding

378   D). This form of public information use has previously been documented in the facultatively

379   social ninespine stickleback, where it has been suggested to be an adaptive specialisation for

380   gathering information under predation risk (Coolen et al. 2003).

381

382   When considered alongside those of other researchers who have observed social learning in non-

383   group-forming animals such as octopi (Fiorito & Scotto 1992), tortoises (Wilkinson et al. 2010)

384   and lizards (Kis et al. 2015), our findings imply that living a solitary life is no barrier to being an

385   adept user of socially transmitted information. Going further, we suggest that such a link

386   between sociality and social learning performance should not necessarily be expected, since non-

387   group-living does not equate to being non-social. Even animals that actively avoid others are

388   likely to be exposed to social cues from territorial neighbours and competitors, and they may be

389   compelled to aggregate with others if they are exploiting patchily distributed resources,

390   particularly if these are scarce. Even when not directly encountering others, non-grouping

391   species may encounter the products of conspecifics, in the form of scent marks, excreted waste,

392   or food items that they have discarded, for example, and these may provide sources of

393   information and even facilitate social learning (e.g. Terkel 1996).

394

395   Our study focussed upon cues provided by heterospecifics, and for many animals the other

396   species that they encounter are a potentially major source of social information (Avarguès-Weber

397   et al. 2013). It is plausible that information generated inadvertently by heterospecifics might also

398   be widely used by other species even where these do not actively associate, as seen in the

399   laboratory in our study, and further work here, particularly in the field, would be useful.

400

401   That said, the approach to the question of whether group living is correlated with social learning

402   performance has largely been piecemeal and there is scope for systematic comparative work to

403   be done too. Reader's (1999) and Reader & Lefebrve's (2001) meta-analyses of social learning

404   performance in relation to group size in primates, which found no link between the two after

405   controlling for phylogenetic effects, is a nice example of the form that such work might take. It

406   would also be informative to consider multiple aspects of sociality, including the nature and

407   distribution of interactions between group members, rather than simply group size, alongside

408   other factors such as primary functions of grouping in those species that do so, such as to

409   mitigate predation risk or to socially forage, and the context in which social information is used.

410   Finally, Heyes (2012) has argued that proficiency in social learning may be affected by selection

411   acting upon input channels such those governing perception of and attention and motivation

412   towards social cues, even if the underlying cognitive mechanisms underpinning social learning

413   are unspecialised. A more interesting question than whether non-grouping animals can socially

414   learn then might be one that takes a phylogenetic approach to ask whether more effective social

415   learning is found in lineages with longer evolutionary histories of group living, and whether

416   adaptive specialisation, either in input channels or cognitive processing, is seen in these.

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430 DATA ACCESSABILITY

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432 Analyses reported in this article can be reproduced using the data provided by Webster & Laland

433 (2017).

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516   TABLES

517

518   **Table 1.** Simple contrasts performed as part of a repeated measures GLM used to compare prey

519   patch goal zone preferences for each of six experimental social information treatments against a

520   seventh treatment in which no social stimulus was presented. See main text for further details.

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	Treatment	df	F	P
Treatment	Feeding A	1	86.031	<0.001
	Feeding B	1	9.019	0.003
	Feeding C	1	51.696	<0.001
	Feeding D	1	0.751	0.388
	Group size A	1	9.908	0.002
	Group Size B	1	7.225	0.008
Treatment*Species	Feeding A	5	1.991	0.085
	Feeding B	5	0.237	0.945
	Feeding C	5	0.621	0.684
	Feeding D	5	0.697	0.627
	Group size A	5	0.763	0.578
	Group Size B	5	2.025	0.080

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529   FIGURE LEGEND

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531   **Figure 1.** Proportional time allocation (time in 'rich' goal zone – time in 'poor' goal zone, mean

532   +/- 95% CI). Here rich goal zone refers to the goal zone associated with the group feeding at the

533   higher rate (Feeding A-D), the larger group (Group size A & B) or the prey stimulus object (Prey

534   stimulus). A positive score indicates that the fish spent more time close to the group of

535   demonstrators feeding at the greater rate (Feeding A-D), or the largest group (Group size A &

536   B). We found effects of treatment, species and a species*treatment interaction (see Results and

537   Table 1). Asterisks indicate differences between species within treatments.

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