

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

2

3 **Lay summary**

4

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

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35 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, fiftenspine
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

59 **Introduction**

60

61 While access to social information is one of the many advantages of living in groups, there is
62 little compelling evidence that social information use or social learning are adaptations specifically
63 associated with sociality (Lefebvre & Giraldeau, 1996). On the one hand, Templeton et al.
64 (1999) compared social learning between two corvid species, finding that the more social of the
65 two was better at social than asocial or individual learning, while the other performed similarly
66 in both types of learning. In contrast, in a meta-analysis of social learning in more than 100
67 primate species, no relationship was found between social learning performance and social group
68 size after phylogeny was controlled for (Reader 1999; Reader & Lefebvre 2001). Other studies
69 have documented social learning in non-grouping species, where such behaviour- if closely
70 linked to group-living- might not be expected to occur. Fiorito & Scotto (1992) reported social
71 learning in the octopus (*Octopus vulgaris*) (but see comments by Biederman & Davy 1993).
72 Wilkinson et al. (2010) found that red-footed tortoises (*Geochelone carbonaria*) could socially
73 learn to navigate around an obstacle, while Kis et al. (2015) demonstrated that bearded dragons
74 (*Pogona vitticeps*) could learn to open a trapdoor after seeing a conspecific do so, with
75 individuals being more likely to open it to the same side that their demonstrator did.

76

77 There are at least two reasons why social learning ability might not be closely tied to group
78 living. The first is that all animals, whether solitary or gregarious, are likely to be exposed to
79 social information some of the time, and potentially quite frequently. Cues may come from
80 mates, offspring or broodmates, depending upon the social and mating system of the species
81 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: fiftenspine
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 fiftenspines 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**

118

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 fiftenspines 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 coarse 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 fiftenspines 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 fiftenspines 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 fifteen spines 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

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

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

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

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

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

271

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

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

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

275 seeing the demonstrators during this period.

276

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

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

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

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

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

282

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

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

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

286 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

310

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

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 ($F_{(5, 119)} = 3.91, P=0.003$) fiftenspines 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 fiftenspines. 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 fiftenspines ($P=0.002$ 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 threespine 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 (Avergues-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 & Lefebvre'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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429

430 DATA ACCESSABILITY

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