

1 Population differences in how wild Trinidadian guppies

2 use social information and socially learn

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20

21 **Abstract**

22 Animals have access to information produced by the behaviour of other individuals, which they  
23 may use (“social information use”) and learn from (“social learning”). The benefits of using such  
24 information differ with socio-ecological conditions. Thus, population differences in social  
25 information use and social learning should occur. We tested this hypothesis with a comparative  
26 study across five wild populations of Trinidadian guppies (*Poecilia reticulata*) known to differ in  
27 their ecology and social behaviour. Using a field experiment, we found population differences in  
28 how guppies used and learned from social information, with only fish from one of the three  
29 rivers studied showing evidence of social information use and social learning. Within this river,  
30 populations differed in how they employed social information: fish from a high-predation regime  
31 where guppies exhibit high shoaling propensities chose the same foraging location than  
32 conspecifics, while fish from a low-predation regime with reduced shoaling propensities chose  
33 and learned the opposite foraging location than conspecifics. We speculate that these differences  
34 are due to differences in predation risk and conspecific competition, possibly mediated via  
35 changes in grouping tendencies. Our results provide evidence that social information use and  
36 social learning can differ across animal populations and are influenced by socio-ecological  
37 factors.

38

39 **Keywords:** Social learning, social information use, social transmission, information copying,  
40 comparative study

41

42 Individuals that possess reliable information about resources and threats can make strategic  
43 decisions [1]. Animals can gather information from different sources, either by interacting directly  
44 with the environment and thus acquiring ‘asocial’ information or from the behaviour or products  
45 of other individuals, a process termed social information use. Animals may retain information for  
46 later use, and thus learn from personally acquired information or socially acquired information  
47 (i.e. social learning [2]). Which type of information to use in a given context is strategic and based  
48 on trade-offs [3–5]. The respective costs and benefits depend largely on recent and current socio-  
49 ecological conditions such as predation and/or stress level [6,7] or social group composition [8].  
50 It also appears that flexibility in both social information use and social learning can be constrained  
51 by individual characteristics [9–11] and shaped by recent experience of the reliability of  
52 information [e.g. 12]. Thus, the decision to rely on social sources of information is not be solely  
53 dependent on reliability or net benefit of the information in the current situation, but also by  
54 individual tendencies. Whether these processes translate to differences in social information use  
55 between populations dwelling in different socio-ecological environments is rarely investigated,  
56 but likely.

57

58 Current local conditions shape the costs and benefits of asocial and social information. Using social  
59 cues can reduce the energy required to acquire information and is particularly beneficial if energy  
60 is limited [13]. Social information reduces risk related to personally sampling a resource [6,7],  
61 particularly in a context with predation pressure. In other cases, using social cues can be  
62 maladaptive or suboptimal if the information gathered is outdated or irrelevant to the observer  
63 [14,16], and using social information may increase competition if individuals thus converge on a  
64 limited resource [17]. Local current environmental characteristics shape which type of information

65 is most likely to be beneficial [3] and influences the decision of individuals [11,18,19]. If  
66 individuals are completely flexible in their decision, current local conditions determine which  
67 information individuals should rely on.

68

69 However, we find that individuals are constrained in their decision through early-life experience  
70 and evolutionary history with the benefits of social information. For example, bumblebees  
71 (*Bombus terrestris*) will learn to copy or avoid other individuals' foraging choices depending on  
72 whether following these social cues was previously rewarded, demonstrating the effect of recent  
73 experience [20]. Early-life experiences can also shape adult social information use, either due to  
74 direct experience with the value of following social cues [e.g. 12], or to broader differences in  
75 social experience such as maternal care [21,22]. Species differences in social information use and  
76 social learning have also been described (e.g. birds: [23]; mammals: [24]) which could be the result  
77 of evolved and/or developmental influences. For example, ninespine sticklebacks (*Pungitius*  
78 *pungitius*) who are under high predation pressure display increased propensities to socially learn  
79 than the less predated but closely related threespine sticklebacks (*Gasterosteus aculeatus*) [25,26].  
80 Furthermore, individual behavioural phenotypes that themselves could be shaped by experience  
81 and evolution, such as the speed to explore a novel environment or to solve a novel problem, can  
82 also predict social information use [10,18,27,28].

83

84 Given the short-term and long-term influences on trade-offs between both types of information,  
85 differences between populations dwelling in different socio-ecological environments are likely.  
86 However, very little work has investigated such population differences, particularly with  
87 experimental tests. A notable exception is the finding that populations of Zenaida doves (*Zenaida*

88 *aurita*) differ in how they learn from a Carib grackle (*Quiscalus lugubris*), a finding that has been  
89 explained by differences in foraging ecology shaping differences in social behaviour between these  
90 populations [29,30]. Here, we investigated population differences in social information use and  
91 social learning by comparing multiple replicate populations tested in the wild, with the aim of  
92 identifying ecological factors that shape social information use.

93

94 We used wild Trinidadian guppies to investigate this question. Guppies have successfully  
95 colonizing rivers that are extremely diverse in geography and ecology [31]. Guppies readily learn  
96 from conspecifics and heterospecifics in both the field and the laboratory, which may partially  
97 explain why they thrive in diverse and new conditions [32,33]. The ecology and evolution of  
98 Trinidadian guppies is well studied, with differences in physiology, morphology, life history and  
99 behaviour found between populations that are partially separated by natural barriers, driven  
100 mostly, but not only, by the presence, density, and composition of predators [34–36]. Upper river  
101 habitats in northern Trinidad typically contain fewer predators of adult guppies, as well as a weaker  
102 current, and more access to invertebrates than lower river habitats [37]. Trinidadian guppy  
103 populations differ on numerous behavioural measures: guppies from the upper river populations  
104 display lower shoaling tendencies, higher intraspecific aggressiveness and competition, and bolder  
105 phenotypes than in the lower river [38–42]. High shoaling tendencies could increase the propensity  
106 to rely on social information since individuals are near conspecifics, while high aggression and  
107 competition may increase the net costs of social information use and social learning. Trinidadian  
108 populations provide a valuable opportunity to test natural variation in the transmission of social  
109 information between populations exposed to varying environments.

110

111 We compared propensities for social information use and social learning using a foraging task in  
112 five populations of wild Trinidadian guppies from three rivers. Our design allowed us to  
113 investigate not only if there are population differences, but also whether within-river differences  
114 were paralleled across different rivers, which would provide support for socio-ecological  
115 conditions shaping population differences in a consistent manner. We predicted guppies to prefer  
116 to forage at the same location as conspecific demonstrators, and to retain this preference when  
117 demonstrators were removed, as previously shown [33]. However, we expected these tendencies  
118 to vary across populations. In fish from the Lower Aripo, known to display high shoaling  
119 tendencies and low interspecific aggression [37], and from the Lower Marianne, we predicted  
120 subjects would copy the demonstrated location. In comparison, we expected guppies from the  
121 Upper Aripo, Upper Marianne and Paria, known to display low shoaling tendencies and expected  
122 (Marianne) or shown (Upper Aripo, Paria) to show high interspecific aggression [37], to either  
123 avoid the demonstrated location or to be unaffected by social cues. Guppies from the Paria site  
124 show particularly low shoaling tendencies and high interspecific aggression, making it an  
125 interesting comparator [42]. We expected similar population differences between the Upper and  
126 Lower sites in the Aripo and Marianne rivers, although recent literature suggests that rivers may  
127 not be perfect replicates [43]. This comparative study of social information use and social learning  
128 propensities thus allows us to determine (1) whether populations differ in these propensities, as  
129 might be predicted from hypotheses that evolutionary and developmental processes shape social  
130 information use; (2) why and when propensities change, and (3) whether these propensities change  
131 in similar manner, thus providing evidence for specific socio-ecological factors shaping social  
132 information use.

133

## 134 **Methods**

### 135 Overview

136 We used a foraging test to compare how five guppy populations used social information and  
137 learned from conspecifics. We assessed social information use and social learning by (1)  
138 comparing subjects' responses to conspecific 'demonstrators' at two feeding locations in a  
139 counterbalanced design and (2) comparing these responses to control subjects not exposed to  
140 demonstrators. Social information use was measured during a demonstration phase, when  
141 demonstrators were present (except in the control trials), while social learning was measured  
142 during a subsequent test phase, when demonstrators had been removed. Social influences on  
143 behaviour would result in subjects being more or less likely to feed at the demonstrated location  
144 than the alternative location.

145

### 146 Study sites and sampling

147 We tested in three rivers located in different watersheds of the Northern Range Mountains in  
148 Trinidad: the South slope Aripo river (June 2013), the North slope Paria river (June 2013), and the  
149 North slope Marianne river (July 2014). We tested at previously studied sites (Ar2 Ar4, Ma14,  
150 Ma8, Pa14) detailed in [44] and [45]. Guppy lineages from these rivers are genetically  
151 differentiated [46]. 'Upper' and 'Lower' river locations from the Aripo and Marianne rivers are  
152 separated by waterfalls, with large teleost fish predators absent from upper but not lower locations,  
153 and numerous other ecological differences between the locations [37]. There is no similar 'Lower'  
154 location in Paria, so we thus sampled only one site that has no large teleost fish predators (similar  
155 to other 'Upper' locations), but where large predatory prawns *Macrobrachium crenulatum* are  
156 present [47,48]. We chose sites where the ectoparasite *Gyrodactylus* has been recorded [44,45].

157 To ensure independent fish were sampled, we typically selected subsequent sampling pools by  
158 going upstream, or by selecting physically separated pools. We used butterfly nets to gently collect  
159 female guppies, and ran our tests in enclosures within rivers. Fish were held in a water-filled  
160 enclosure placed in the river for a maximum of 5 hours. During this time, we presented them with  
161 the social information use and learning tests, then moved them to an enclosure for tested fish, with  
162 fish released at their capture site at the end of a testing day.

163

#### 164 Testing apparatus

165 The testing apparatus consisted of a small floating box made of mosquito net (23 cm high, 38 cm  
166 wide and long), which allowed stream water to flow freely through the apparatus, with the front  
167 and back of the apparatus made of transparent plastic. Since fish were tested in an enclosure, they  
168 were physically separated from any local predators and the experiment was not a field test of social  
169 learning on free-living animals [49]. However, they were in field conditions until the experiment  
170 began, were tested in their local environment, and were exposed to olfactory and visual cues from  
171 outside the enclosure. We mounted a waterproof camera (1080p at 30fps, GoPro3 Black Edition,  
172 San Mateo, California) on one wall to record behaviour at the removable feeder (36 cm width)  
173 positioned on the opposite side. This feeder consisted of two feeding locations separated by 10 cm,  
174 with each location made up of two vertical 5 cm wide feeding columns placed 3 cm apart, creating  
175 patches of food that were accessible to multiple individuals simultaneously. The feeding columns  
176 were made of food sprinkled on gelatin (KNOX, Treehouse Foods, New York State, USA) mixed  
177 with food colouring (Club House, McCormik Canada, London Ontario, Canada) poured on a  
178 patterned background. We created two types of feeding column on the feeding wall. One was made  
179 of freeze-dried bloodworms (*Chironomus* spp., Omega One, Omegasea Ltd, Sitka, Alaska)



180 sprinkled on green-coloured gelatin, placed on a black-striped background. The other was made  
181 of flake food (TetraMin, Tetra, Germany) sprinkled on yellow-coloured gelatin placed on a black-  
182 dotted background. We used a variety of food, pattern, location and colour cues to provide multiple  
183 discriminatory cues for the subjects and to increase differences between the feeding columns. For  
184 demonstrations by conspecifics, we put “demonstrator” fish in a small “demonstration box” (10  
185 cm height, 5 cm width and depth) made of perforated transparent plastic so that demonstrators  
186 reliably fed on one column without requiring extensive training. We placed the box directly in  
187 front of one column, with a similar but smaller feeding column inside the box.

188

### 189 Experimental methods

190 Each trial consisted of a 1) habituation, 2) demonstration, and 3) test phase. In the 1) habituation  
191 phase, we placed a group of four fish in the testing apparatus without the feeding wall for 10  
192 minutes. We tested fish in groups as guppies are typically highly social and may show population  
193 dependant stress responses when placed in isolation [41,50], potentially impacting the social  
194 information use we examine here. Simultaneously, two fish from the previously tested subject  
195 group, selected at random to act as demonstrators, were habituated to the demonstration box  
196 outside of the apparatus. All demonstrators fed during this phase. Between the habituation phase  
197 and the demonstration phase, we inserted an opaque partition between the fish and the foraging  
198 area. With the partition in place, we inserted the feeder wall and demonstration box out of view of  
199 the subjects. The demonstration box was placed in front of one of the four columns, and thus at  
200 one of the two locations and at one of the two column types, except for the control groups which  
201 viewed no demonstrators. The control groups were run twice per testing day, as the first test each  
202 day (thus providing demonstrators for the first demonstration of the day) and a second test chosen

203 at random. We counterbalanced the demonstration groups between the four columns every day.  
204 The 2) demonstration phase started upon lifting of the partition and lasted 6 minutes and was used  
205 to determine the propensity of subjects to use social information. During this phase we allowed  
206 fish to freely move and access the food resources. This procedure differs from many social learning  
207 tests where subjects only observe feeding behaviour (but see [49] for similar procedures). We  
208 considered it important to maintain ecological relevance and match much guppy foraging in the  
209 wild. Moreover, blocking subject access to food could represent a situation where conspecifics  
210 prevent foraging access. Between the demonstration and test phase, the opaque partition was  
211 reinserted, the feeding sheet rinsed to remove any odour cues and placed inverted (to reverse the  
212 order of the columns and further remove odour biases), and the demonstration box was removed.  
213 The 3) test phase started upon lifting of the partition and lasted 8 minutes, and was used to evaluate  
214 if social learning had occurred. As on the demonstration phase, the subjects could feed and were  
215 rewarded at any foraging location.

216  
217 From the video recordings, one of two observers blind to the population tested counted the number  
218 of feeding pecks [51] on each food column. Since we could not discriminate individuals, we  
219 summed the feeding pecks of the four subjects tested together as a group. No feeding pecks were  
220 observed away from the food columns. Inter-observer reliability was measured for 30 videos and  
221 was high (ICC= 0.81, 95% C.I. = 0.73 < ICC < 0.86). In total, we tested 82 groups with  
222 demonstrators and 25 control groups. Of these, 17 were from the Lower Aripo, 15 from the Upper  
223 Aripo, 33 from the Lower Marianne, 30 from the Upper Marianne, and 12 from the Paria.

224

225 Statistical analyses

226 All statistical analyses were performed using R version 3.2.2 [52] and the packages ggplot2 [53]  
227 and lme4 [54]. We found no evidence that the demonstrated feeding column type affected foraging  
228 behaviour (unpublished data), and thus below we examined feeding locations and feeding rate  
229 only.

230

### 231 *Population differences*

232 We wanted to investigate if and why populations differed in social information use and social  
233 learning. We thus examined the influence of demonstrator location on subjects' foraging location  
234 choices for the fish exposed to demonstrators. We ran generalized linear mixed-effect models  
235 (GLMMs) with a binomial distribution with the distribution of pecks between the demonstrated  
236 and the undemonstrated location as the response variable for the demonstration phase, and for the  
237 test phase. This approach, compared to examining the total or percentage of pecks at the  
238 demonstrated location, accounts for differences in groups' propensities to feed.

239

240 We investigated population differences between the five sites we tested: Lower Aripo, Upper  
241 Aripo, Lower Marianne, Upper Marianne, and Paria. The model also included an observation-level  
242 random effect to correct for overdispersion [55]. In this model, an effect of site indicates that  
243 populations differed in their proportion of pecks at the demonstrated location. The reference for  
244 the site model was the Lower Aripo, so this site model already provided a population comparison  
245 within the river Aripo. We followed by specifically investigating population differences within the  
246 Marianne river, by running a GLMM that included the main effect 'population' ('Upper' or  
247 'Lower'). We only had one population in the river Paria, so we did not do any follow-up analysis.

248

249 *Social information use and social learning*

250 While the site model above examined whether populations differed in their reaction to the  
251 demonstrators, we also need to know how they reacted to the demonstrator. If demonstrator  
252 location had no influence, we would expect subjects to peck equally at both locations. We therefore  
253 tested whether the observed distribution of pecks differed from chance expectation, which we set  
254 at 50% assuming fish randomly feed at both feeders. We did this by removing the intercept of the  
255 site model, thus forcing the model to compare the population's estimates to zero on the latent scale  
256 or 50% on the original scale.

257

258 *Feeding rate*

259 To investigate whether demonstrator presence changed the total number of pecks subjects  
260 performed (i.e. feeding rate), we ran generalised linear mixed effect model (GLMM) with a  
261 Poisson distribution for each river and each phase. Rivers rather than populations were analysed  
262 so that an adequate amount of control data was available. The models had the response variable  
263 'total pecks', and the main effect 'demonstration' ("control" or "with demonstration") to compare  
264 the absolute number of pecks of fish from the control group to the fish with a demonstration. We  
265 included as random effects population and group as well as an observation-level random effect to  
266 correct for overdispersion. A significant main effect of demonstration with a positive estimate  
267 would indicate that exposure to demonstrators increased feeding rate.

268

269 *Feeding location consistency*

270 To analyse whether control fish acquired a preference about feeding locations regardless of social  
271 cues, we analysed whether the group random effect significantly helped explain a significant part

272 of the variation. We did this by creating an overall river model for the control trials. In the model,  
273 we included the main effect ‘river’ and ‘phase’ to create a repeated measure model. Using a  
274 likelihood ratio test (LRT), we compared the overall river model with the same model from which  
275 we removed the group random effect, to evaluate if a significant amount of variation is explained  
276 by groups.

277

## 278 **Results**

### 279 *Site differences*

280 Demonstration phase: During the demonstration phase, which examined differences in social  
281 information use, sites varied in the proportion of pecks at the demonstrated location: fish from the  
282 Upper Aripo, Lower Marianne and Paria pecked significantly less ( $P = 0.0046$ ;  $P = 0.028$ ;  $P =$   
283  $0.018$ , respectively; table 2; figure 1) at the demonstrated location than our reference site Lower  
284 Aripo. Examining the two Marianne populations alone, there were no significant differences in the  
285 proportion of pecks at the demonstrated location during the demonstration phase (table 2).

286

287 Test phase: During the test phase, which examined differences in social learning, Upper Aripo fish  
288 pecked significantly less at the demonstrated location compared to Lower Aripo fish ( $P = 0.0093$ ;  
289 table 2, figure 1). Other sites did not differ in the proportion of pecks at the demonstrated feeder  
290 during the test phase ( $P_s > 0.2$ ; table 2). Examining the two Marianne populations alone, there  
291 were no significant differences in the proportion of pecks at the demonstrated location during the  
292 test phase (table 2).

293

### 294 *Social information use and social learning*

295 Demonstration phase: During the demonstration phase, when demonstrators were present, fish  
296 from the Lower Aripo pecked significantly more than expected by chance at the demonstrated  
297 location, with 97% of pecks ( $P = 0.033$ ; figure 1.2, table S1). In contrast, fish from the Upper Aripo  
298 pecked significantly less than expected by chance at the demonstrated location, with only 8% of  
299 pecks ( $P = 0.05$ ; table S1). Fish from the Lower Marianne, Upper Marianne, and Paria did not peck  
300 at the demonstrated location significantly more or less than the chance expectation of 50%.

301  
302 Test phase: During the test phase, when demonstrators had been removed, fish from the Lower  
303 Aripo made 86% of pecks at the previously demonstrated location, but this was not significantly  
304 different from chance ( $P = 0.14$ ; figure 1; table S1). Upper Aripo fish made only 9% of pecks at  
305 the previously demonstrated location, significantly different from chance ( $P = 0.020$ ; table S1).  
306 Fish from the Lower Marianne, Upper Marianne, and Paria did not peck at the previously  
307 demonstrated location significantly more or less than the chance expectation.

308  
309 *Feeding rate*

310 Demonstration phase: In the Aripo river, exposure to demonstrators increased slightly the total  
311 number of feeding pecks compared to the control condition, but this was not significant ( $P = 0.055$ ;  
312 Figure 1). Exposure to demonstrators did not significantly increase the total number of feeding  
313 pecks in the other rivers ( $P_s > 0.3$ ; Figure 1).

314  
315 Test phase: Exposure to demonstrators did not significantly increase the total number of feeding  
316 pecks in any river ( $P_s > 0.1$ ; Figure 1).

317

318 *Feeding location consistency*

319 There was no evidence that fish from the control groups, without a demonstration, had a consistent  
320 preference for a feeding location over the two experimental phases. That is, the model with a group  
321 random effect that accounted for repeated measures was not a significantly better fit than the model  
322 without for control groups (LRT  $X^2 = 1.17$ ,  $df=1$ ,  $P = 0.28$ ). We did find evidence that groups with  
323 demonstration had a consistent preference for a feeding location. The model with the group random  
324 effect was significantly better at explaining variation than the model without for groups with a  
325 demonstration (LRT  $X^2 = 7.45$ ,  $df = 1$ ,  $P = 0.006$ ). In other words, only fish with a demonstration  
326 showed a consistent preference for a certain feeder.

327

328

329 **Discussion**

330

331 Using a comparative experiment in wild habitats, we compared the effect of a social demonstration  
332 on foraging rate and foraging location across guppy populations. We found that the response to  
333 social information varied between populations. We only found evidence for social information use  
334 and social learning in fish in the Aripo river. Moreover, within the Aripo river, populations differed  
335 in how they reacted to social information: fish from the Upper Aripo avoided the location where  
336 conspecifics were seen feeding and retained this bias after the removal of the demonstrators, while  
337 fish from the Lower Aripo foraged at the demonstrated location, but this bias was not statistically  
338 significant (although still substantial) when demonstrators were removed. Our results show  
339 population variation in social information use and social learning, suggesting that evolutionary  
340 and/or developmental experiences shape social information use and social learning propensities.

341

342 Perhaps our most interesting finding is that Aripo populations reacted differently to social  
343 information. Their habitats differ on multiple characteristics, such as food productivity, light  
344 levels, and predation pressure, providing multiple possible explanations for the differences we  
345 observed. However, predation pressure and competition provide the most likely explanations. The  
346 Lower Aripo population is characterised by very cohesive and large shoals, a result of the local  
347 predation regime, with little intraspecific aggression [37,42]. In contrast, in the Upper Aripo,  
348 predators of adult guppies are mostly absent, and food is more scarce than in the lower reaches  
349 [43], with fish displaying lower shoaling tendencies and higher aggression [41]. Thus fish in the  
350 Upper Aripo will suffer intraspecific competition if foraging in a group, will gain little in terms of  
351 anti-predator benefits, and resource patches may be more rapidly depleted, potentially explaining  
352 their tendencies to avoid locations where conspecifics are or were foraging [56]. While most work  
353 on social information use has focused on animals matching demonstrator behaviour, animals can  
354 employ social information in a variety of ways, including avoiding the choices of others  
355 [20,57,58]. Fish in the Lower Aripo suffer increased risks of individual exploration and leaving  
356 the group, suffer little intraspecific competition when foraging where others forage, and have easy  
357 access to social information, potentially explaining their copying behaviour. Previous work has  
358 linked between-individual variation in shoaling tendency with social information use in fish [8,28],  
359 and with sociality more broadly in corvids [23]. Competition and limited resources availability has  
360 been proposed as an important influence on social information use in species as varied as Japanese  
361 quail (*Coturnix japonica*) [57] and fruitfly *Drosophila melanogaster* larvae [59].

362



363 Fish from the Aripo, but not the Marianne or Paria rivers, showed evidence for social information  
364 use and social learning. Thus, we did not find evidence of parallelism between rivers in this  
365 foraging test. A parallel response would have been indicative of a strong effect of specific socio-  
366 ecological factors like the presence of predators. Recently, work has highlighted important  
367 differences between rivers and drainages in the flow, productivity, and canopy cover [60]. So while  
368 certain traits, like coloration, may be selected independently of the composition of the predator  
369 community [47,48], some are particular responses to the type, composition, and density of  
370 predators [36,43,60,61]. Additionally, other habitat characteristics and how they interplay with  
371 predation may be important. For example, guppy density strongly impacts competition and mate  
372 choice [62], and light spectrum affects mating tactics [63]. Environmental characteristics that  
373 shape competition are particularly likely to shape social information use [56].

374  
375 Much research on social learning investigates cases of observational learning, in which subjects  
376 are unable to access the food resource during the demonstration phase. Somewhat atypically, our  
377 fish could access the food resources during the demonstration phase of the test, mimicking usual  
378 foraging conditions in the wild. Thus, shoaling or avoidance could have mediated the discovery of  
379 a food location, and a learned association between the food reward and its location would lead to  
380 fish subsequently favouring this location [64–66]. The mechanisms underlying different social  
381 learning processes are an open question [67,68]. However, from a functional viewpoint, the social  
382 learning we describe here and observational learning have the same outcome: both result in  
383 individuals' foraging choices being biased depending on the choices of other individuals. We note  
384 that fish without a demonstration, our “control” group, did not form a strong preference for one

385 feeder over the other through repeated feeding, suggesting that demonstrators may have not only  
386 biased learning to a particular location but also facilitated learning of that location.

387

388 We found extensive population variation in the response to social cues. Depending on the  
389 population, social demonstration resulted in copying, avoidance, or no detectable effect on  
390 behaviour. Further work is needed to establish the relative contributions of evolution and  
391 development to the differences we observed, the underlying neurobehavioural mechanisms, and  
392 the question of whether differences in social information use are a byproduct or adaptive  
393 specialization. Furthermore, an open question is whether social information use and social learning  
394 will vary in parallel: plausibly, in rapidly-changing environments, it may be beneficial to forage  
395 with others but not to learn a foraging patch preference from this experience. The differences we  
396 observe could have sizable impacts on community dynamics, by shaping and maintaining  
397 population-specific foraging preferences or avoidances [69,70]. Our findings also suggest that  
398 social learning researchers should pay close attention to the origin and developmental history of  
399 their study subjects.

400

401 Our dataset is available in the ESM.

402

403 **Authors contribution.** LCT and SMR conceived and designed the study. LCT carried field work,  
404 collected and analysed data from videos, and wrote the first draft of the manuscript. LCT and SMR  
405 revised the manuscript. All authors approved submission of the final version.

406

407 **Ethical note.** We minimized handling time and released fish immediately after testing at their  
408 capture location. All procedures were carried out in accordance with Trinidadian and Canadian  
409 law, with Animal Behavior Society and Canadian Council for Animal Care guidelines, and were  
410 approved by the Animal Care Committee of McGill University (Protocol # 2012-7133).

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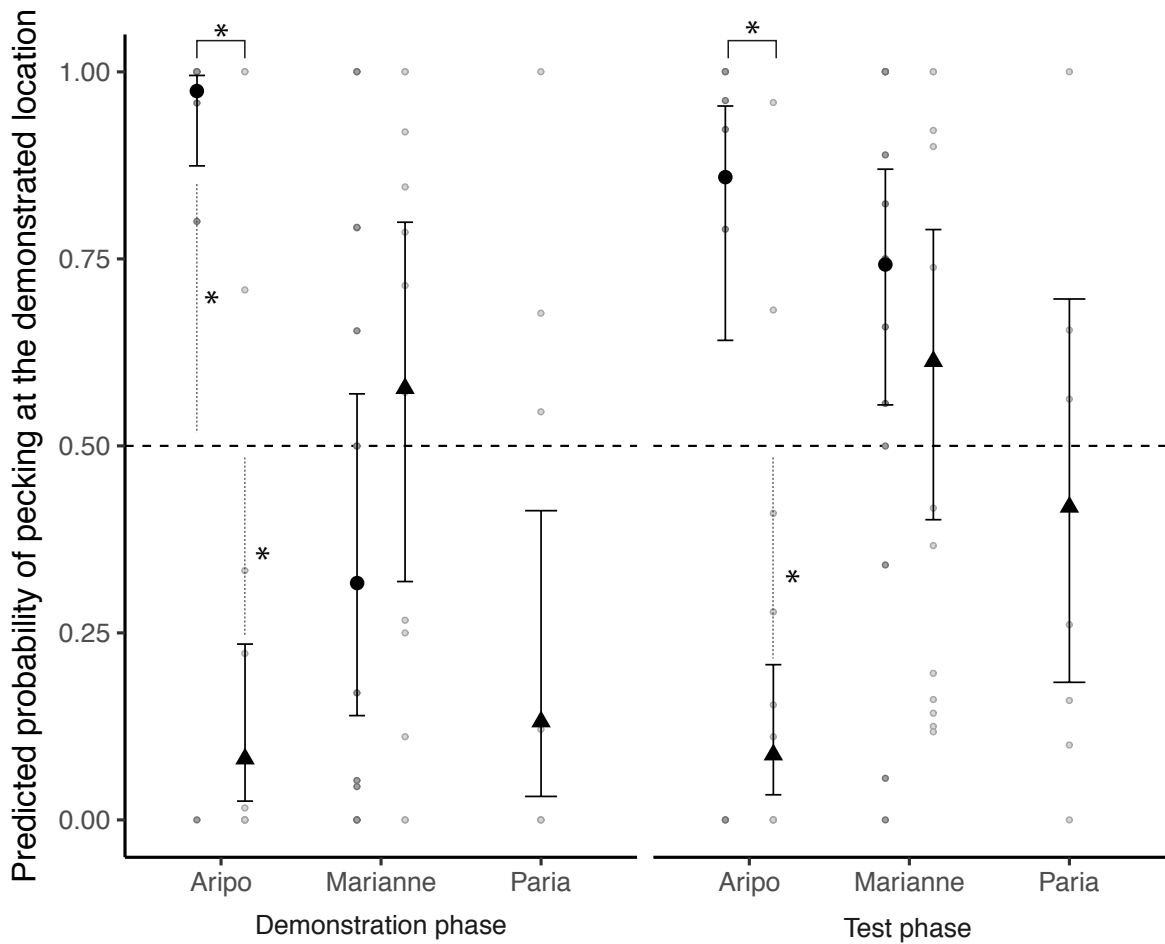
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427 **Figure 1:** Predicted probability and raw data of pecks (estimate +/- SE) performed at the  
428 demonstrated feeder by five populations of fish in the three rivers (circles: lower river; triangle:  
429 upper river) for the demonstration and test phases. The dashed line at zero represents our chance  
430 expectation of 50% on the original scale. A difference from chance (50%) is indicated by a star  
431 and a dotted line, while a difference between populations is indicated by an \* above the  
432 compared groups. Populations from the Aripo river differed from each other and from chance.

433

434 **Table 1:** Site differences in proportion of pecks at the demonstrated location. Estimates and  
 435 standard error of fixed parameters and their interaction for the GLMM looking at the effect of site  
 436 on the proportion of pecks at the demonstrated location, defined as a binomial variable of number  
 437 of ‘successes’ (proportion pecks at demonstrated location) and number of ‘misses’ (proportion  
 438 pecks at the undemonstrated location). Estimates are presented on the logit scale. The reference  
 439 level was Lower Aripo for “site”. The model also included an observation-level random effect to  
 440 correct for overdispersion.

	Demonstration phase				Test phase			
	Estimate	Std. Error	z value	P-value	Estimate	Std. Error	z value	P-value
Intercept	3.64	1.70	2.14	<b>0.033</b>	1.81	1.23	1.47	0.14
Upper Aripo	-6.07	2.14	2.83	<b>0.0046</b>	-4.16	1.60	2.60	<b>0.0093</b>
Paria	-5.53	2.33	2.38	<b>0.018</b>	-2.13	1.70	1.26	0.21
Lower Marianne	-4.41	2.01	2.20	<b>0.028</b>	-0.75	1.50	0.50	0.62
Upper Marianne	-3.33	2.01	1.66	0.098	-1.35	1.50	0.90	0.37

441  
 442 **Table 2:** Population differences in the Marianne river. Estimates and standard error of fixed  
 443 parameters and their interaction for the GLMM looking at the effect of population on the  
 444 proportion of pecks at the demonstrated location in the Marianne river, defined as a binomial  
 445 variable of number of ‘successes’ (proportion pecks at demonstrated location) and number of  
 446 ‘misses’ (proportion pecks at the undemonstrated location). Estimates are presented on the logit  
 447 scale. The reference level was Lower Marianne for “population”. The model also included an  
 448 observation-level random effect to correct for overdispersion.

	Demonstration phase				Test phase			
	Estimate	Std. Error	z value	P-value	Estimate	Std. Error	z value	P-value
Intercept	-0.70	0.85	0.82	0.41	0.94	0.69	1.35	0.18
Population (Upper Marianne)	1.01	1.23	0.82	0.41	-0.56	0.99	0.56	0.58

449 **Table 3:** Effect of having a demonstration on total number of pecks of fish. The estimates are  
 450 presented on the log scale for the demonstration phase (left) and the test phase (right) for the  
 451 river Aripo (top), Marianne (middle) and Paria (bottom). Our reference levels were no  
 452 demonstration for the demonstration factor. The GLMM included also a correction for  
 453 overdispersion in the random effects. Significant p-values ( $P < 0.05$ ) are presented in bold.

	<b>Demonstration phase</b>				<b>Test phase</b>			
	Estimate	Std. Error	z value	P-value	Estimate	Std. Error	z value	P-value
<b>Aripo</b>								
Intercept	-0.71	1.09	0.65	0.52	0.63	1.05	0.60	0.55
Demonstration (demonstration)	2.24	1.16	1.92	0.055	1.74	1.15	1.51	0.13
<b>Marianne</b>								
Intercept	0.28	1.03	0.27	0.79	0.057	1.03	0.056	0.96
Demonstration (demonstration)	-0.22	1.14	0.20	0.84	0.61	1.10	0.55	0.58
<b>Paria</b>								
Intercept	0.079	1.70	0.047	0.96	2.20	1.53	1.44	0.15
Demonstration (demonstration)	1.64	1.82	0.90	0.37	0.041	1.73	0.024	0.98

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