



*Citation for published version:*

Darden, S, James, R, Cave, J, Bohr Brask, J & Croft, D 2020, 'Trinidadian guppies use a social heuristic that can support cooperation among non-kin', *Proceedings of the Royal Society B*, vol. 287, no. 1934, 0487.  
<https://doi.org/10.1098/rspb.2020.0487>

*DOI:*

[10.1098/rspb.2020.0487](https://doi.org/10.1098/rspb.2020.0487)

*Publication date:*

2020

*Document Version*

Peer reviewed version

[Link to publication](#)

## University of Bath

### Alternative formats

If you require this document in an alternative format, please contact:  
[openaccess@bath.ac.uk](mailto:openaccess@bath.ac.uk)

#### General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

#### Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 **Trinidadian guppies use a social heuristic that can support cooperation among non-kin**

2

3 Safi K. Darden<sup>1\*</sup>, Richard James<sup>2</sup>, James M. Cave<sup>2</sup>, Josefine Bohr Brask<sup>1</sup> and Darren P.  
4 Croft<sup>1</sup>

5

6 <sup>1</sup>Centre for Research in Animal Behaviour, Department of Psychology, College of Life and  
7 Environmental Sciences, University of Exeter, UK

8 <sup>2</sup>Department of Physics and Centre for Networks and Collective Behaviour, University of  
9 Bath, UK

10

11 Short title: Social heuristics and real-world cooperation

12

13 \*Correspondence: s.darden@exeter.ac.uk

14 **Abstract**

15 Cooperation among non-kin is well documented in humans and widespread in non-human  
16 animals, but explaining the occurrence of cooperation in the absence of inclusive fitness  
17 benefits has proven a significant challenge. Current theoretical explanations converge on a  
18 single point: co-operators can prevail when they cluster in social space. However, we know  
19 very little about the real-world mechanisms that drive such clustering, particularly in systems  
20 where cognitive limitations make it unlikely that mechanisms such as score keeping and  
21 reputation are at play. Here we show that Trinidadian guppies (*Poecilia reticulata*) use a  
22 ‘Walk Away’ strategy, a simple social heuristic by which assortment by cooperativeness can  
23 come about among mobile agents. Guppies cooperate during predator inspection and we  
24 found that when experiencing defection in this context, individuals prefer to move to a new  
25 social environment, despite having no prior information about this new social group. Our  
26 results provide evidence in non-human animals that individuals use a simple social partner  
27 updating strategy in response to defection, supporting theoretical work applying heuristics to  
28 understanding the proximate mechanisms underpinning the evolution of cooperation among  
29 non-kin.

30

31

## 32 **Introduction**

33

34 The conundrum of cooperation [1, 2], where one individual pays a cost so that another can  
35 receive a benefit, was highlighted by Darwin [3], who realised that individuals that express a  
36 trait (e.g., cooperation) must themselves benefit for the trait to be favoured by natural  
37 selection. Yet cooperation is seen at every level of biological organization (intra cellular to  
38 societal) [4] and across taxonomic groups from microbes to humans [1]. Cooperation  
39 becomes particularly difficult to explain when benefits are conferred upon unrelated  
40 individuals and the past three decades have seen substantial theoretical attention given to  
41 identifying pathways by which non-kin cooperation can evolve (e.g. direct reciprocity [5],  
42 indirect reciprocity [6], generalised reciprocity [7-9], network reciprocity [10], group  
43 selection [11] and by-product benefits [12]). The merits of each of these models have been  
44 much debated [13-17], but they all have a single unifying feature: for cooperation to persist,  
45 co-operating individuals must cluster together [reviewed in 18]. Essentially, cooperation can  
46 prevail when cooperative individuals interact at higher rates with each other than with non-  
47 cooperative individuals, because this decreases the exploitation of cooperators by defectors  
48 and increases reciprocation of cooperative benefits to cooperators. Thus clusters of co-  
49 operators can gain higher fitness payoffs than defectors in the population [19, 20]. Identifying  
50 the processes that drive the clustering of cooperation in social landscapes is thus at the heart  
51 of unravelling the conundrum of how costly behaviours that benefit non-kin have evolved  
52 [19].

53

54 Theoretical work suggests that heuristics, simple decision-making rules, can underpin social  
55 dynamics (the formation and breaking of social ties) and thereby drive assortment by  
56 cooperation [18, 21-23]. For example, decisions about joining or leaving groups in response

57 to cooperation or defection can generate social assortment by individual cooperativeness (i.e.  
58 phenotypic propensity to cooperate) [18, 22-24]. Heuristics incorporate behavioural rules for  
59 making fast and economical decisions when the information available to individuals is  
60 incomplete and the future is uncertain [25]. These conditions for decision making are likely  
61 to be prevalent in systems with noisy, rapidly varying social environments and where  
62 decision making is not supported by advanced cognitive abilities; conditions which typify  
63 many non-human social animals. Currently however, it is unclear whether heuristics have a  
64 role to play in driving the dynamical linking of social ties in non-human animals in the  
65 context of cooperation. This represents a key gap in understanding cooperation, as  
66 characterizing the behavioural rules that govern dynamical linking is fundamental to  
67 determining the mechanisms that drive the clustering of co-operators [26]. Here we probe the  
68 social heuristics that underpin the formation and breaking of social ties in the context of  
69 cooperation in Trinidadian guppies (*Poecilia reticulata*).

70

71 Trinidadian guppies live in dynamic fission-fusion societies where individuals cooperate with  
72 non-kin during predator inspection [27] and where there is evidence of social assortment by  
73 cooperative tendency [28]. During predator inspection in fish, one or more individuals will  
74 leave the shoal to approach the predator closely and gain information about the level of threat  
75 posed by the predator [29]; information that benefits all members of the group [30]. Work in  
76 guppies and other fish species has demonstrated that inspectors pay a personal cost of  
77 increased risk of predation [31, 32], which they can reduce by inspecting in cooperative  
78 partnerships [33-35]. There has been much debate on the mechanisms maintaining  
79 cooperation during predator inspection, with some evidence suggesting a ‘TIT-for-TAT’  
80 strategy is used [36]. In this strategy, individuals initially cooperate with a partner and in  
81 future, repeated iterations with this same partner, copy the partner’s last move (i.e. either

82 cooperate or defect) [36]. Given the highly dynamic nature of daily social interactions  
83 however, and the large number of individuals that make up each individual's social  
84 environment [37, 38], guppies are also likely to rely on simple behavioural mechanisms of  
85 assortment that will allow them to avoid having to process and store the high volumes and  
86 rates of social information that they are exposed to. Guppies therefore constitute a potentially  
87 powerful model system for a new avenue of empirical work to test for key assortment  
88 mechanisms proposed by theoretical models to underpin the evolution of cooperation among  
89 unrelated individuals.

90

91 We aimed to test whether individuals use a simple behavioural strategy - 'leave in the face of  
92 defection' requiring only limited information on the behavioural tendencies of others. Models  
93 by Aktipis [18, 22] and Schuessler [24] show that such simple heuristics can generate  
94 assortment among cooperative mobile agents. Under a 'Walk Away' conditional movement  
95 strategy, individuals break away from defecting social partners [18, 22-24] and join a new  
96 partner or group upon encounter, without information on the behavioural tendencies of the  
97 partner or group [18, 22]. The conceptual attraction of the 'Walk Away' heuristic for  
98 generating positive assortment of cooperative phenotypes in real-world populations is that it  
99 avoids cognitively demanding bookkeeping. That is, it does not require committing to  
100 memory the identity of social partners, or indeed their behaviour over multiple iterations, to  
101 aid in making decisions to associate with a partner (or partners). This is in contrast to the  
102 TIT-for-TAT strategy, which requires remembering the last actions of specific partners (i.e.  
103 partner behaviour and identity). The strategy also differs from other exit strategies such as the  
104 well-known 'win-stay, lose-shift', where an actor continues or "stays" with an action –  
105 cooperate or defect - unless the gain no longer meets some threshold and then switches or  
106 "shifts" to the opposing action - cooperate or defect in an iterated game [39]. Like with a

107 ‘TIT-for-TAT’ strategy, an individual thus changes their own cooperativeness as a reaction to  
108 that of others [although for an approach that models ‘win-stay, lose-shift’ with ‘shift’  
109 including an option to leave the group see 23]. In contrast, in the ‘Walk Away’ strategy  
110 individuals in effect change their social environment without any prescription for who to join  
111 or how to behave (cooperate or defect) in any subsequent round or game [18, 22, 24]. That is,  
112 with a ‘Walk Away’ strategy, individuals do not need to be able to exhibit plasticity in their  
113 own cooperative behaviour, further contributing to its simplicity and, importantly, possible  
114 traits under selection [e.g., 40, 41-43].

115  
116 ‘Walk Away’ models for the evolution of cooperation were originally formulated for  
117 populations with fairly stable group structures [18, 22, 24]. However, populations of social  
118 animals typically live in societies with fission-fusion dynamics, such as those experienced by  
119 Trinidadian guppies. It is not immediately clear that under these conditions, a ‘Walk Away’  
120 strategy can allow positive assortment of cooperation to emerge against the background  
121 merging and splitting of groups, which in this and other systems is driven by myriad factors  
122 [44]. We have therefore confirmed that a ‘Walk Away’ social heuristic can generate  
123 assortment by cooperation in populations with fission-fusion dynamics similar to those in  
124 guppies using an agent-based simulation model to further support the rationale for the current  
125 study (see supplementary materials). To test the hypothesis that guppies will use a ‘Walk  
126 Away’ strategy, we exposed individuals to unfamiliar social partners, manipulated their  
127 perception of these partners’ cooperative behaviour during a predator inspection event and  
128 then monitored the propensity for individuals to change their social environment following  
129 their ostensible experience of cooperation or defection. We predicted that if a ‘Walk Away’  
130 strategy exists in this species, individuals would prefer to associate with novel social partners  
131 over social partners that they had just experienced defection from.

132 **Methods**

133

134 ***Study animals***

135 We used laboratory reared adult female Trinidadian guppies descended from wild fish  
136 collected in the lower reaches of the Aripo River (10°40' N 61° 14' W) on the island of  
137 Trinidad, a site where adult guppies experience a high risk of predation from piscivorous fish.  
138 Focal fish were housed in groups of 10 in 29 x 19 x 17 cm aquaria. Stimulus fish were housed  
139 in groups of 100 in 80 x 30 x 39 cm aquaria. Focal and stimulus fish were randomly selected  
140 from stocks of fish housed under naturalistic conditions in four physically isolated pools  
141 (approximately 2000 fish per pool). All fish were fed twice daily to satiation on their  
142 specified diet (stimulus fish diets are explained below; focal fish were fed on a diet of tropical  
143 fish flake and brine shrimp, *Artemia* sp.). The study was carried out under UK Home Office  
144 Licence PIL 30/8944, reviewed by the University of Exeter Animal Welfare and Ethical  
145 Review Body, and in strict accordance with the UK Animals (Scientific Procedures) Act  
146 1986. To minimize stress, all fish used in the study were provided with plant refugia and  
147 always had, at a minimum, visual access to social partners, with the exception of our control  
148 experiment where focal fish were without contact to social partners during testing. Power  
149 analysis after an initial data collection phase (N=6 replicates per cell) was used to ensure that  
150 we used the smallest number of animals possible while maintaining high test power (16  
151 replicates per cell, SPSS SamplePower 21 v. 3.0.1, IBM SPSS Inc.).

152

153 ***Experimental apparatus and procedure***

154

155 ***Study design***

156



157 To test for the existence of a ‘Walk Away’ strategy in Trinidadian guppies, we  
158 experimentally exposed 136 female guppies to a cooperative or non-cooperative social  
159 environment and subsequently tested their social preference for ostensibly the same social  
160 environment versus a novel one.

161

### 162 *Predator inspection*

163

164 Inspection arenas were similar to those used in other studies involving predator inspection in  
165 guppies (e.g., [28, 45, 46]). Aquaria (80 x 30 cm) were sub-divided with Perspex partitions to  
166 produce two inspection lanes and two predator enclosures (Fig. 1A). A guide system was in  
167 place between the predator enclosures and the inspection lanes where a removable opaque  
168 partition was positioned to visually isolate the predator enclosure from focal fish prior to the  
169 start of a trial. Predator enclosures were either empty or contained a single predatory fish  
170 (*Aequidens pulcher*) depending on condition (see below). A refuge was located at the end  
171 opposite to the predator enclosures with an artificial plant and a perforated transparent  
172 rectangular stimulus shoal compartment (10 x 4.5 x 18 cm). The inside of each inspection  
173 lane was lined with a reversible partition that had a mirror on one side and a uniform, light  
174 grey surface on the other side. With this design, in a mirrored lane an inspecting fish was  
175 ostensibly joined by a fish from the compartment of social partners (i.e. the stimulus shoal) in  
176 the form of its mirrored reflection, and in a non-mirrored lane also connected to a  
177 compartment of physically constrained social partners an inspecting fish ostensibly  
178 experienced defection from these partners (Fig. 1A). This experimental paradigm built on  
179 protocols used in previous studies [reviewed in 47], and recent work has illustrated that using  
180 a mirror stimulus in a predator inspection context elicits behaviour in a focal fish that aligns  
181 with its behaviour with a live partner [28]. The water depth in each subsection of an arena

182 was 11 cm. Arenas were illuminated with full spectrum 40W bulbs and filmed from above  
183 using Samsung digital colour cameras (Model: SCB-2001) fitted with a Computar 5-50mm,  
184 F1:1.3 lens.

185

186 Thirty minutes before the onset of each trial, predator naïve stimulus shoals were placed in  
187 the stimulus shoal compartments of each inspection lane. Each stimulus shoal consisted of  
188 four size-matched, predator-naïve female guppies that the focal fish had not previously  
189 encountered. We manipulated identity cues of the stimulus shoals by feeding them on one of  
190 two diets (larval *Chironominae* sp. or adult *Daphnia* sp.) that were novel to the focal fish, for  
191 min. 7 days and up to 14 days prior to the trials. Guppies use odour cues for social decision  
192 making [48] and this method allowed us to generate distinct novel odour cues for groups of  
193 fish. Stimulus shoal compartment walls were perforated to allow odour cues to diffuse across  
194 the compartment barrier. During their inspection of the predator (Fig. 1A) focal fish could  
195 thus become familiar with global (shoal level) odour cues of social partners originating from  
196 their diet in tandem with experiencing either defection or cooperation, depending on  
197 treatment.

198

199 At the start of a trial, individual focal fish were released into the centre of an inspection lane  
200 and allowed 10 minutes to acclimatize. During this period the opaque partition between the  
201 predator enclosures and the inspection lanes remained in place. Focal individuals were then  
202 gently encouraged into the refuge area next to the confined stimulus shoal using a dip net.  
203 The opaque partition between the predator enclosures and inspection lanes was then lifted. In  
204 experimental test trials the lifting of the barrier revealed a live predator and in control trials,  
205 intended to account for possible effects inherent to the experimental setup, an empty  
206 enclosure. Inspection occurred when fish left the refuge area and swam towards the predator

207 enclosure. Mirrored lanes simulated cooperation by a member of the stimulus shoal, while  
208 non-mirrored lanes simulated defection by all members of the shoal. Trials ended after a 5-  
209 minute inspection period and focal fish were immediately removed from the inspection lane  
210 and transferred in a small container of water into a binary choice tank for the social partner  
211 choice test (see below). At the end of a trial all stimulus fish were removed and a complete  
212 water change of the arena was carried out.

213

#### 214 *Social partner choice test*

215

216 Immediately following the predator inspection trial, focal individuals were transferred to a  
217 binary shoal choice arena and tested for their association preferences for social partners fed  
218 either on the same diet as experienced in the predator inspection trial (i.e. *Chironominae* sp.  
219 or *Daphnia* sp. fed fish) or the unfamiliar (novel) diet. Arenas (45 x 30 cm, water depth  
220 11cm) were sub-divided into three compartments using perforated Perspex barriers similar to  
221 [49]. Two stimulus shoal compartments at opposite ends of the arena measured 7.5 x 30 cm,  
222 which left a middle compartment for the focal fish that measured 30 x 30 cm. Arenas were  
223 illuminated and filmed as above. Forty-five minutes prior to the onset of a trial a shoal of 5  
224 fish was placed in each stimulus shoal compartment of the choice arena (matched for body  
225 size across shoals). One compartment contained fish on the *Daphnia* sp. diet and the other  
226 contained fish on the bloodworm diet. Each focal fish was thus presented with one stimulus  
227 shoal composed of fish on the same diet as the fish they had experienced in the inspection  
228 trial and another composed of fish on the second novel diet, to which the focal was naive. All  
229 stimulus fish were predator naïve and had not been used in the predator exposure treatment.  
230 This design was used because the experiences of the stimulus fish during the inspection trials  
231 could potentially lead to differential behaviour between the two shoals during the choice trial

232 if they were used there as well. Using odours as identity cues allowed us to avoid this  
233 potentially confounding factor. At the start of a choice trial, focal fish that had just been  
234 removed from an inspection trial were placed in the centre of the arena and given 5 minutes  
235 to acclimatize. After acclimatization, we recorded the time that focals spent shoaling with  
236 each stimulus shoal over a 10-minute period. Focal fish were recorded as shoaling with  
237 stimulus fish if they were within 5 cm of the barrier to a shoal compartment (preference zone;  
238 based on the elective group size concept [50]). At the end of the trial all fish were removed  
239 from the arena and a complete water change was carried out.

240

#### 241 *Analysis of behavioural data*

242

243 Our analysis is based on 129 focal fish that entered the preference zone of both shoals at least  
244 once during the shoal choice trial (7 fish did not visit both sides; Supplementary material  
245 Table S1). The inspection and shoaling behaviour of each focal fish was scored manually  
246 using the Observer XT v. 10.1 by a single observer (SKD) blind to the condition and  
247 treatment that focal fish were in. For inspection trials we quantified the average distance of  
248 focal fish to the predator enclosure over the 5-minute inspection period. For shoal choice  
249 trials we calculated the proportion of shoaling time that focal fish spent with each of the two  
250 shoals which were angular transformed prior to statistical analysis as per convention for  
251 analysing proportional data in this way [51].

252

253 We used a general linear model (GLM) to test for effects of our experimental manipulations  
254 on the social partner choices made by our focal fish. In the model we used the angular  
255 transformed proportion of time spent with the novel (unfamiliar odour) shoal during the  
256 binary shoal choice trial as the dependent variable, and condition (2 levels: control and

257 experimental), social experience (2 levels: defection and cooperation) and stimulus shoal diet  
258 encountered during inspection (2 levels: *Daphnia* and bloodworm) as fixed effects..Our  
259 initial model contained the inspection behaviour of our focal fish as a covariate, however it  
260 had no effect ( $F_{1,116}=0.393$ ;  $p=0.532$ , see Supplementary materials Table S2)) and was  
261 removed from the final model. We explored a significant interaction between condition and  
262 treatment using *post hoc* one-sample t-tests with a Bonferroni corrected  $\alpha$  level of 0.0125.

263

#### 264 ***Methods of non-social control experiment***

265

266 We ran a non-social control experiment that used a modified version of the main  
267 experimental paradigm in order to investigate whether any effects found in the main  
268 experiment could alternatively be explained by the guppies connecting their experience  
269 (cooperation/defection) with the odour cues themselves, rather than with the social  
270 environments associated with those odour cues. That is, effects found in the main experiment  
271 could potentially be explained by a mechanism that caused focal individuals to, for example,  
272 avoid an odour that they associated with high predation risk in the defection condition  
273 (approaching a predator as a singleton). In this control experiment, the overall design was the  
274 same as in the main experiment (inspection then shoal choice) and odour cues derived from  
275 the same diets were used (*Chironominae* sp. and *Daphnia* sp.; see below)), but no social cues  
276 (no stimulus shoal and no mirror) were provided in the inspection trials. In the subsequent  
277 shoal choice test, focal individuals could choose between two shoals of fish, each of which  
278 was paired with one of the two odours.

279

280 Odour cues in this experiment were introduced in the form of odour water. This was created  
281 by masticating frozen daphnia or bloodworm (*Daphnia* sp., and *Chironominae* sp., i.e. the

282 same diet odours as in the main experiment) in water (5 g of daphnia and 2.6 g of bloodworm  
283 per 300 ml water) and filtering the mixture through a fine sieve in order to remove  
284 macroscopic particles. The odour water was introduced into the predator inspection lane at  
285 the refuge end, where the stimulus shoal was placed in the main experiment (opposite to the  
286 predator stimulus end), via a plastic tube connected to a funnel placed over the tank. The rate  
287 at which the odour water entered the tank was controlled by a flowmeter (MMA-35, Dwyer  
288 Instruments, Michigan City, IN, USA) set to 25 ml/min. 500ml odour water was placed in the  
289 funnel prior to the trial and the flowmeter was opened at the beginning of the trial. The trial  
290 otherwise proceeded as in the main experiment (as per above in a 'no mirror' condition only).  
291 The subsequent binary shoal choice tests were also similar to the ones in the main  
292 experiment; except that the stimulus shoals each consisted of four females that had not been  
293 fed with the diets used to create odours. Instead, odour water (200 ml) with the two  
294 experimental odours was introduced into each shoal compartment prior to the test trial, one  
295 odour in each compartment. The experimental tanks were thoroughly cleaned after each trial  
296 to remove any odour remains. We used a one-sample t-test to test for a preference for shoals  
297 paired with the novel odour, taken as the angular transformation of the proportion of shoaling  
298 time spent with this shoal.

299

## 300 **Results**

301

302 We found that the presence or absence of a predator during the inspection portion of a trial  
303 (i.e. inspection condition: experimental or control) interacted with having partners that either  
304 cooperated or defected during the inspection (i.e. social experience: cooperation or defection)  
305 to influence subsequent shoal choice (Table 1). *Post hoc* analysis revealed that individuals  
306 experiencing a defecting social environment preferred partners with an unfamiliar odour over

307 partners with a familiar odour when given a subsequent choice (Fig. 1B), which was not the  
308 case for control treatments (no predator) or our experimental cooperation treatment, where  
309 we did not find any preferences (Table 2, Bonferroni corrected  $\alpha=0.0125$ ).

310

311 If the significant preference found in the main experiment was based on avoidance of the  
312 odour associated with inspecting a predator as a singleton, rather than avoidance of the social  
313 environment associated with the predator inspection experience, then a preference for a shoal  
314 bearing a novel odour (as opposed to that experienced during inspection), should also be  
315 present in the non-social control experiment. However, in this control experiment we found  
316 that focal fish did not show a preference for fish associated with the novel odour (back-  
317 transformed mean proportion of time spent with novel odour fish $\pm$ SE=0.448 $\pm$ 0.0406/  
318 0.0403;  $t_{62}=-1.275$ ,  $p=0.2070$ ).

319

## 320 **Discussion**

321

322 We found that female Trinidadian guppies experiencing a social environment where all others  
323 defected during predator inspection, preferred novel partners (that they had no prior  
324 information on) over ostensibly familiar social partners in a subsequent social choice test.  
325 This result demonstrates that individuals actively sever ties with defecting social partners and  
326 seek out links with others, even when they do not have information on the cooperative  
327 behaviour of these novel social partners; both are consistent with a ‘Walk Away’ strategy  
328 [18, 22, 24]. To our knowledge this is the first empirical evidence for the existence of this  
329 social heuristic in a non-human animal system.

330

331 In humans the option to leave a defecting partner, ‘opting out’, has been shown both  
332 theoretically and empirically to allow cooperation to prevail [52-56] and empirical work  
333 suggests that something akin to conditional movement strategies is active in humans. For  
334 example, dynamic partner updating under conditions of limited information has been  
335 demonstrated experimentally in response to low levels of cooperative behaviour in partners  
336 [40, 52, 54, 55, 57]. Indeed, one study has shown that when constrained to a set behavioural  
337 repertoire of either staying with an interaction partner or joining another, randomly assigned,  
338 partner between rounds of a cooperative game, movement (‘link-breaking’) decisions  
339 generate assortment of cooperative behaviour across a network of interaction partners [40]. It  
340 is important to note that in the majority of paradigms in these empirical studies with humans,  
341 participants operate with partner-specific information that goes beyond what is outlined for a  
342 ‘Walk Away’ strategy, so that ties are preferentially broken with defectors and new ties are  
343 preferentially made with co-operators [e.g., 52, 57] or individuals are able to log the  
344 behaviour of specific individuals and use this knowledge in subsequent encounters with those  
345 individuals [40]. Still, at the core of these paradigms, having knowledge of and control over  
346 the option to leave is critical in determining the economic decisions made by players [52, 54,  
347 55, 58, 59], even when the assignment of a new partner is made at random [54, 55, 59]. Our  
348 study provides evidence of the existence of this class of strategies outside of humans and  
349 supports its simplest use, with individuals making social association choices when they have  
350 no information on the value of future partners. The simplicity of this strategy means that it  
351 may be widespread in natural systems [60]. Furthermore, future work examining the  
352 heritability of the ‘Walk Away’ strategy and how it has been shaped by natural selection  
353 would provide valuable insights into the evolution of cooperation in natural populations.

354



355 Although our findings highlight a mechanism that may go some way to explaining the  
356 persistence of non-kin cooperation in guppy populations, they do not preclude other  
357 mechanisms that may be working simultaneously in this species; such as choosing specific  
358 partners based on immediate observation of their cooperative tendency [e.g., 61, but see  
359 below] or conditional cooperative behaviour based on the cooperative behaviour of current  
360 social partners [10, 62-64]. For example, generalized reciprocity (or ‘help anyone if helped  
361 by someone’), has been demonstrated with computer modelling to generate positive  
362 assortment of cooperative interactions via cooperative responses conditional to experience  
363 [65]. Support for cooperation via generalized reciprocity is based on experiences of  
364 cooperative behaviour that is wholly anonymous (i.e. identification of the actor is not  
365 necessary), and thus may be particularly relevant for the guppy system [23,65-66]. Future  
366 work exploring if other social heuristics are used in combination with a ‘Walk Away’  
367 strategy to support cooperation in guppies is eagerly anticipated.

368

369 In our experiment, in addition to guppies ‘walking away’ from defecting partners it could  
370 also be expected that they would prefer the social environment where they had experienced  
371 cooperation. Both of these would work toward driving the positive assortment by cooperative  
372 propensity [reviewed in 67 and see Supplementary materials Section 1] that we have seen  
373 evidence for in wild guppy populations [28]. We did not, however, find clear evidence that  
374 our focal individuals preferred partners that had cooperated during predator inspection over  
375 partners for whom they had no information on their propensity to cooperate. Previous  
376 evidence from this study system indeed suggests that individuals have a preference for a more  
377 cooperative over a less cooperative partner when given a choice between the two [61]. .  
378 However, a key paradigm difference between the experiment presented here and this previous  
379 work [61] is that individuals were able to choose from social partners for whom they had

380 complete information; that is, they had knowledge of the cooperative propensity of each  
381 potential partner in a binary choice test. This means that although fish may have been actively  
382 choosing the more cooperative partner, they may alternatively have been actively choosing to  
383 leave the defecting partner as in our study. In support of this latter explanation, we can  
384 consider evidence from work in humans suggesting a higher propensity to remember traits or  
385 experiences associated with defectors compared to cooperators [68]. In humans this effect  
386 appears to be linked to the importance of the information in predicting trait characteristics of  
387 individuals and thus the outcome of future interactions [69, 70]. In this case, a negativity bias  
388 can exist when ‘negative’ cues are more diagnostic than ‘positive’ cues [70]. With a ‘Walk  
389 Away’ heuristic, the important diagnostic information regarding the behaviour of an  
390 unfamiliar social group is whether they defect during predator inspection, as opposed to  
391 whether they cooperate, as this is what drives the decision to leave. It could be that the  
392 underlying premise for this strategy is a negativity bias, particularly when an entire group of  
393 individuals defects compared to when just one individual from a group cooperates (i.e. the  
394 diagnostic value of the ‘positive’ information is low). An increased propensity to remember  
395 social partners from a situation where they defected, but not where they cooperated, and then  
396 acting on this information for subsequent social association decisions, thus seem like  
397 plausible explanations for the updating behaviour and lack of preference for cooperative  
398 shoals that we observed.

399

400 Theoretical work over the last decade has striven to identify simple behavioural mechanisms  
401 that can maintain cooperation among non-kin [most recently reviewed in 63, 67, 71], with  
402 social heuristics likely being important drivers in systems with high levels of social mixing  
403 [e.g., 72]. In our experimental design, individuals did not have the opportunity to use  
404 individual recognition or other information when making partner choices. The work we

405 present thus truly represents evidence of a real-world heuristic for dynamical linking of social  
406 ties in non-human animals. It most closely resembles a ‘Walk Away’ heuristic, which can  
407 generate positive social assortment by cooperative behaviour in populations of mobile agents  
408 ([18] and see Supplementary materials Section 1). The simplicity of this strategy means that  
409 it may be a general mechanism contributing to the maintenance of cooperation across a broad  
410 range of taxa where individuals can detect non-cooperative behaviour, but where more  
411 complex processes involving, for example, intent and knowledge attribution or bookkeeping  
412 of behaviour [73-76], are not necessarily present. We look forward to further developments in  
413 this area.

414

#### 415 **Acknowledgements**

416

417 We thank R. Cope and M. Edenbrow for assistance with data collection and M. Cant and our  
418 reviewers for comments on earlier versions of the manuscript.

419

#### 420 **Funding**

421

422 The study was funded by a Leverhulme Trust Early Career Fellowship (ECF/2010/0672) to  
423 SKD, a Leverhulme Trust Research Grant (RPG-175) to DPC and a Framework Grant (DF  
424 – 1323-00105) to SKD and DPC from the Danish Research Council for Nature and Universe.  
425 JBB was supported by an internationalisation postdoc fellowship from the Carlsberg  
426 Foundation.

427

#### 428 **Ethics**

429

430 The study was carried out under UK Home Office Licence PIL 30/8944, reviewed by the  
431 University of Exeter Animal Welfare and Ethical Review Body, and in strict accordance with  
432 the UK Animals (Scientific Procedures) Act 1986.

433

#### 434 **Data, code and materials**

435

436 Data: <http://hdl.handle.net/10871/18463>

437

#### 438 **Competing interests**

439

440 The authors declare no competing interests.

441

#### 442 **Authors' contributions**

443

444 The main empirical study was conceived and designed by SKD and DPC and data collection  
445 overseen by SKD. The empirical validation study was designed and carried out by JBB in  
446 discussion with SKD. The simulation model was conceptualized by SKD, RJ and DPC,  
447 designed by RJ and implemented by JC. SKD wrote the first draft of the manuscript in  
448 discussion with DPC. All authors contributed to subsequent revisions. SKD and DPC  
449 designed and produced the figures in discussion with RJ.

450

#### 451 **References**

452

453 [1] Pennisi, E. 2009 On the Origin of Cooperation. *Science* **325**, 1196.

454 [2] Hamilton, W.D. 1963 Evolution of Altruistic Behavior. *American Naturalist* **97**, 354-356.

- 455 [3] Darwin, C. 1859 *The Origin of Species*. London, J. Murray.
- 456 [4] Queller, D.C. & Strassmann, J.E. 2009 Beyond Society: The Evolution of Organismality.  
457 *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **364**,  
458 3143-3155.
- 459 [5] Trivers, R.L. 1971 Evolution of Reciprocal Altruism. *Quarterly Review of Biology* **46**, 35-  
460 57.
- 461 [6] Nowak, M.A. & Sigmund, K. 1998 Evolution of Indirect Reciprocity by Image Scoring.  
462 *Nature* **393**, 573-577. (doi:10.1038/31225).
- 463 [7] Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M. & Bonhoeffer, S. 2005 Evolution of  
464 Cooperation by Generalized Reciprocity. *Proceedings of the Royal Society B: Biological*  
465 *Sciences* **272**, 1115-1120.
- 466 [8] Nowak, M.A. & Roch, S. 2007 Upstream Reciprocity and the Evolution of Gratitude.  
467 *Proceedings of the Royal Society B: Biological Sciences* **274**, 605-610.
- 468 [9] Rutte, C. & Taborsky, M. 2007 Generalized Reciprocity in Rats. *Plos Biology* **5**, 1421-  
469 1425. (doi:10.1371/journal.pbio.0050196).
- 470 [10] Ohtsuki, H. & Nowak, M.A. 2007 Direct Reciprocity on Graphs. *Journal of Theoretical*  
471 *Biology* **247**, 462-470. (<https://doi.org/10.1016/j.jtbi.2007.03.018>).
- 472 [11] Wilson, D.S. 1975 Theory of Group Selection. *Proceedings of the National Academy of*  
473 *Sciences of the United States of America* **72**, 143-146.
- 474 [12] Brown, J.L. 1983 Cooperation—a Biologist's Dilemma. In *Advances in the Study of*  
475 *Behavior* (eds. J.S. Rosenblatt, R.A. Hinde, C. Beer & M.-C. Busnel), pp. 1-37,  
476 Academic Press.
- 477 [13] Wilson, D.S. 2008 Social Semantics: Toward a Genuine Pluralism in the Study of Social  
478 Behaviour. *Journal of Evolutionary Biology* **21**, 368-373. (doi:10.1111/j.1420-  
479 9101.2007.01396.x).

- 480 [14] Nowak, M.A. 2006 Five Rules for the Evolution of Cooperation. *Science* **314**, 1560-  
481 1563. (doi:10.1126/science.1133755).
- 482 [15] Wilson, E.O. 2005 Kin Selection as the Key to Altruism: Its Rise and Fall. *Social*  
483 *Research* **72**, 159-166.
- 484 [16] West, S.A., Griffin, A.S. & Gardner, A. 2007 Social Semantics: Altruism, Cooperation,  
485 Mutualism, Strong Reciprocity and Group Selection. *Journal of Evolutionary Biology*  
486 **20**, 415-432. (doi:10.1111/j.1420-9101.2006.01258.x).
- 487 [17] Foster, K.R., Wenseleers, T. & Ratnieks, F.L.W. 2006 Kin Selection Is the Key to  
488 Altruism. *Trends in Ecology & Evolution* **21**, 57-60.  
489 (<https://doi.org/10.1016/j.tree.2005.11.020>).
- 490 [18] Aktipis, C.A. 2011 Is Cooperation Viable in Mobile Organisms? Simple Walk Away  
491 Rule Favors the Evolution of Cooperation in Groups. *Evolution and Human Behavior* **32**,  
492 263-276. (<http://dx.doi.org/10.1016/j.evolhumbehav.2011.01.002>).
- 493 [19] Fletcher, J.A. & Doebeli, M. 2009 A Simple and General Explanation for the Evolution  
494 of Altruism. *Proceedings of the Royal Society B: Biological Sciences* **276**, 13-19.
- 495 [20] Nowak, M.A., Tarnita, C.E. & Antal, T. 2010 Evolutionary Dynamics in Structured  
496 Populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**,  
497 19-30.
- 498 [21] Pepper, J.W. & Smuts, B.B. 2002 A Mechanism for the Evolution of Altruism among  
499 Nonkin: Positive Assortment through Environmental Feedback. *American Naturalist*  
500 **160**, 205-213.
- 501 [22] Aktipis, C.A. 2004 Know When to Walk Away: Contingent Movement and the  
502 Evolution of Cooperation. *Journal of Theoretical Biology* **231**, 249-260.

- 503 [23] Hamilton, I.M. & Taborsky, M. 2005 Contingent Movement and Cooperation Evolve  
504 under Generalized Reciprocity. *Proceedings of the Royal Society B: Biological Sciences*  
505 **272**, 2259-2267. (doi:10.1098/rspb.2005.3248).
- 506 [24] Schuessler, R. 1989 Exit Threats and Cooperation under Anonymity. *The Journal of*  
507 *Conflict Resolution* **33**, 728-749.
- 508 [25] Gigerenzer, G. & Gaissmaier, W. 2011 Heuristic Decision Making. *Annual Review of*  
509 *Psychology* **62**, 451-482. (doi:10.1146/annurev-psych-120709-145346).
- 510 [26] Pacheco, J.M., Traulsen, A. & Nowak, M.A. 2006 Co-Evolution of Strategy and  
511 Structure in Complex Networks with Dynamical Linking. *Physical review letters* **97**,  
512 258103-258103.
- 513 [27] Croft, D., Hamilton, P.B., Darden, S.K., Jacoby, D.M.P., James, R., Bettaney, E.M. &  
514 Tyler, C.R. 2012 The Role of Relatedness in Structuring the Social Network of a Wild  
515 Guppy Population. *Oecologia* **170**, 955-963. (doi:10.1007/s00442-012-2379-8).
- 516 [28] Brask, J.B., Croft, D.P., Edenbrow, M., James, R., Bleakley, B.H., Ramnarine, I.W.,  
517 Heathcote, R.J.P., Tyler, C.R., Hamilton, P.B., Dabelsteen, T., et al. 2019 Evolution of  
518 Non-Kin Cooperation: Social Assortment by Cooperative Phenotype in Guppies. *Royal*  
519 *Society Open Science* **6**, 181493. (doi:10.1098/rsos.181493).
- 520 [29] Pitcher, T.J., Green, D.A. & Magurran, A.E. 1986 Dicing with Death - Predator  
521 Inspection Behaviour in Minnow Shoals. *Journal of Fish Biology* **28**, 439-448.
- 522 [30] Magurran, A.E. & Higham, A. 1988 Information Transfer across Fish Shoals under  
523 Predator Threat. *Ethology* **78**, 153-158.
- 524 [31] Dugatkin, L.A. 1992 Tendency to Inspect Predators Predicts Mortality Risk in the  
525 Guppy (*Poecilia Reticulata*). *Behavioral Ecology* **3**, 124-127.

- 526 [32] Milinski, M., Luthi, J.H., Eggler, R. & Parker, G.A. 1997 Cooperation under Predation  
527 Risk: Experiments on Costs and Benefits. *Proceedings of the Royal Society B: Biological*  
528 *Sciences* **264**, 831-837.
- 529 [33] Dugatkin, L.A. 1988 Do Guppies Play Tit for Tat During Predator Inspection Visits.  
530 *Behavioural Ecology and Sociobiology* **23**, 395-399.
- 531 [34] Milinski, M. 1987 Tit-for-Tat in Sticklebacks and the Evolution of Cooperation. *Nature*  
532 **325**, 433-435.
- 533 [35] Croft, D.P., James, R., Thomas, P.O.R., Hathaway, C., Mawdsley, D., Laland, K.N. &  
534 Krause, J. 2006 Social Structure and Co-Operative Interactions in a Wild Population of  
535 Guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology* **59**, 644-650.
- 536 [36] Dugatkin, L.A. & Alfieri, M. 1991 Tit-for-Tat in Guppies (*Poecilia reticulata*) - the  
537 Relative Nature of Cooperation and Defection During Predator Inspection. *Evolutionary*  
538 *Ecology* **5**, 300-309.
- 539 [37] Croft, D.P., Arrowsmith, B.J., Bielby, J., Skinner, K., White, E., Couzin, I.D., Magurran,  
540 A.E., Ramnarine, I. & Krause, J. 2003 Mechanisms Underlying Shoal Composition in  
541 the Trinidadian Guppy (*Poecilia reticulata*). *Oikos* **100**, 429-438.
- 542 [38] Croft, D.P., Krause, J. & James, R. 2004 Social Networks in the Guppy (*Poecilia*  
543 *reticulata*). *Proceedings of the Royal Society B: Biological Sciences* **271**, S516-S519.
- 544 [39] Nowak, M. & Sigmund, K. 1993 A Strategy of Win-Stay, Lose-Shift That Outperforms  
545 Tit-for-Tat in the Prisoner's Dilemma Game. *Nature* **364**, 56-58.  
546 (doi:10.1038/364056a0).
- 547 [40] FehI, K., van der Post, D.J. & Semmann, D. 2011 Co-Evolution of Behaviour and Social  
548 Network Structure Promotes Human Cooperation. *Ecology Letters* **14**, 546-551.  
549 (doi:10.1111/j.1461-0248.2011.01615.x).



- 550 [41] dos Santos, M. & West, S.A. 2018 The Coevolution of Cooperation and Cognition in  
551 Humans. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20180723.  
552 (doi:10.1098/rspb.2018.0723).
- 553 [42] Geoffroy, F., Baumard, N. & André, J.-B. 2019 Why Cooperation Is Not Running  
554 Away. *Journal of Evolutionary Biology* **32**, 1069-1081. (doi:10.1111/jeb.13508).
- 555 [43] Smead, R. & Forber, P. 2016 The Coevolution of Recognition and Social Behavior.  
556 *Scientific Reports* **6**, 25813. (doi:10.1038/srep25813).
- 557 [44] Krause, J. & Ruxton, G.D. 2002 *Living in Groups*. Oxford, Oxford University Press.
- 558 [45] Dimitriadou, S., Croft, D.P. & Darden, S.K. 2019 Divergence in Social Traits in  
559 Trinidadian Guppies Selectively Bred for High and Low Leadership in a Cooperative  
560 Context. *Scientific Reports* **9**, 17194. (doi:10.1038/s41598-019-53748-4).
- 561 [46] Edenbrow, M., Bleakley, B.H., Darden, S.K., Tyler, C.R., Ramnarine, I.W. & Croft,  
562 D.P. 2017 The Evolution of Cooperation: Interacting Phenotypes among Social Partners.  
563 *The American Naturalist* **189**, 630-643. (doi:10.1086/691386).
- 564 [47] Soares, M.C., Cardoso, S.C., Carvalho, T.d.S. & Maximino, C. 2018 Using Model Fish  
565 to Study the Biological Mechanisms of Cooperative Behaviour: A Future for  
566 Translational Research Concerning Social Anxiety Disorders? *Progress in Neuro-*  
567 *Psychopharmacology and Biological Psychiatry* **82**, 205-215.  
568 (<https://doi.org/10.1016/j.pnpbp.2017.11.014>).
- 569 [48] Ward, A.J.W., Webster, M.M., Magurran, A.E., Currie, S. & Krause, J. 2009 Species  
570 and Population Differences in Social Recognition between Fishes: A Role for Ecology?  
571 *Behavioral Ecology* **20**, 511-516. (doi:10.1093/beheco/arp025).
- 572 [49] Darden, S.K., James, R., Ramnarine, I.W. & Croft, D.P. 2009 Social Implications of the  
573 Battle of the Sexes: Sexual Harassment Disrupts Female Sociality and Social

574 Recognition. *Proceedings of the Royal Society B: Biological Sciences* **276**, 2651-2656.  
575 (doi:10.1098/rspb.2009.0087).

576 [50] Pitcher, T.J., Magurran, A.E. & Allan, J.R. 1983 Shifts of Behaviour with Shoal Size in  
577 Cyprinids. In *Proceedings of the 3rd British Freshwater Fish Conference* (pp. 220-228).

578 [51] Sokal, R.R. & Rohlf, F.J. 1995 *Biometry: The Principles and Practice of Statistics in*  
579 *Biological Research*. New York, W.H. Freeman and Co.

580 [52] Rand, D.G., Arbesman, S. & Christakis, N.A. 2011 Dynamic Social Networks Promote  
581 Cooperation in Experiments with Humans. *Proceedings of the National Academy of*  
582 *Sciences of the United States of America* **108**, 19193-19198.  
583 (doi:10.1073/pnas.1108243108).

584 [53] Izquierdo, S.S., Izquierdo, L.R. & Vega-Redondo, F. 2010 The Option to Leave:  
585 Conditional Dissociation in the Evolution of Cooperation. *Journal of Theoretical Biology*  
586 **267**, 76-84. (doi:<https://doi.org/10.1016/j.jtbi.2010.07.039>).

587 [54] Barclay, P. & Raihani, N. 2016 Partner Choice Versus Punishment in Human Prisoner's  
588 Dilemmas. *Evolution and Human Behaviour* **37**, 263-271.  
589 (<https://doi.org/10.1016/j.evolhumbehav.2015.12.004>).

590 [55] Zhang, B.-Y., Fan, S.-J., Li, C., Zheng, X.-D., Bao, J.-Z., Cressman, R. & Tao, Y. 2016  
591 Opting out against Defection Leads to Stable Coexistence with Cooperation. *Scientific*  
592 *Reports* **6**, 35902. (doi:10.1038/srep35902  
593 <https://www.nature.com/articles/srep35902#supplementary-information>).

594 [56] Zheng, X.-D., Li, C., Yu, J.-R., Wang, S.-C., Fan, S.-J., Zhang, B.-Y. & Tao, Y. 2017 A  
595 Simple Rule of Direct Reciprocity Leads to the Stable Coexistence of Cooperation and  
596 Defection in the Prisoner's Dilemma Game. *Journal of Theoretical Biology* **420**, 12-17.  
597 (<https://doi.org/10.1016/j.jtbi.2017.02.036>).

- 598 [57] Wang, J., Suri, S. & Watts, D.J. 2012 Cooperation and Assortativity with Dynamic  
599 Partner Updating. *Proceedings of the National Academy of Sciences of the United States*  
600 *of America* **109**, 14363-14368. (doi:10.1073/pnas.1120867109).
- 601 [58] Boone, R.T. & Macy, M.W. 1999 Unlocking the Doors of the Prisoner's Dilemma:  
602 Dependence, Selectivity, and Cooperation. *Social Psychology Quarterly* **62**, 32-52.  
603 (doi:10.2307/2695824).
- 604 [59] Bednarik, P., Fehl, K. & Semmann, D. 2014 Costs for Switching Partners Reduce  
605 Network Dynamics but Not Cooperative Behaviour. *Proceedings of the Royal Society B:*  
606 *Biological Sciences* **281**, 20141661.
- 607 [60] Tomassini, M. & Antonioni, A. 2015 Lévy Flights and Cooperation among Mobile  
608 Individuals. *Journal of Theoretical Biology* **364**, 154-161.  
609 (doi:http://dx.doi.org/10.1016/j.jtbi.2014.09.013).
- 610 [61] Dugatkin, L.A. & Alfieri, M. 1991 Guppies and the Tit-for-Tat Strategy - Preference  
611 Based on Past Interaction. *Behavioral Ecology and Sociobiology* **28**, 243-246.
- 612 [62] Smith, K.M., Larroucau, T., Mabulla, I.A. & Apicella, C.L. 2018 Hunter-Gatherers  
613 Maintain Assortativity in Cooperation Despite High Levels of Residential Change and  
614 Mixing. *Current Biology* **28**, 3152-3157. (doi:https://doi.org/10.1016/j.cub.2018.07.064).
- 615 [63] Quiñones, A.E., van Doorn, G.S., Pen, I., Weissing, F.J. & Taborsky, M. 2016  
616 Negotiation and Appeasement Can Be More Effective Drivers of Sociality Than Kin  
617 Selection. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**.
- 618 [64] Bshary, R. & Grutter, A.S. 2002 Asymmetric Cheating Opportunities and Partner  
619 Control in a Cleaner Fish Mutualism. *Animal Behaviour* **63**, 547-555.  
620 (<https://doi.org/10.1006/anbe.2001.1937>).

- 621 [65] Stojkoski, V., Utkovski, Z., Basnarkov, L. & Kocarev, L. 2018 Cooperation Dynamics  
622 of Generalized Reciprocity in State-Based Social Dilemmas. *Physical Review E* **97**,  
623 052305. (doi:10.1103/PhysRevE.97.052305).
- 624 [66] Utkovski, Z., Stojkoski, V., Basnarkov, L. & Kocarev, L. 2017 Promoting Cooperation  
625 by Preventing Exploitation: The Role of Network Structure. *Physical Review E* **96**,  
626 022315. (doi:10.1103/PhysRevE.96.022315).
- 627 [67] Croft, D.P., Edenbrow, M. & Darden, S. 2014 Assortment in Social Networks and the  
628 Evolution of Cooperation. In *Animal Social Networks* (eds. J. Krause, R. James, D.W.  
629 Franks & D.P. Croft), pp. 13-23, Oxford University Press, USA.
- 630 [68] Buchner, A., Bell, R., Mehl, B. & Musch, J. 2009 No Enhanced Recognition Memory,  
631 but Better Source Memory for Faces of Cheaters. *Evolution and Human Behaviour*. **30**,  
632 212-224. (<https://doi.org/10.1016/j.evolhumbehav.2009.01.004>).
- 633 [69] Bell, R., Sasse, J., Möller, M., Czernochoowski, D., Mayr, S. & Buchner, A. 2016 Event-  
634 Related Potentials in Response to Cheating and Cooperation in a Social Dilemma Game.  
635 *Psychophysiology* **53**, 216-228. (doi:10.1111/psyp.12561).
- 636 [70] Skowronski, J.J. & Carlston, D.E. 1987 Social Judgment and Social Memory - the Role  
637 of Cue Diagnosticity in Negativity, Positivity, and Extremity Biases. *Journal of*  
638 *Personality and Social Psychology* **52**, 689-699. (doi:10.1037/0022-3514.52.4.689).
- 639 [71] van Doorn, G.S. & Taborsky, M. 2011 The Evolution of Generalized Reciprocity on  
640 Social Interaction Networks. *Evolution* **66**, 651-664. (doi:10.1111/j.1558-  
641 5646.2011.01479.x).
- 642 [72] van den Berg, P. & Wenseleers, T. 2018 Uncertainty About Social Interactions Leads to  
643 the Evolution of Social Heuristics. *Nature Communications* **9**, 2151.  
644 (doi:10.1038/s41467-018-04493-1).

- 645 [73] Cheney, D.L. 2011 Extent and Limits of Cooperation in Animals. *Proceedings of the*  
646 *National Academy of Sciences of the United States of America* **108**, 10902-10909.  
647 (doi:10.1073/pnas.1100291108).
- 648 [74] Dugatkin, L.A. 2002 Cooperation in Animals: An Evolutionary Overview. *Biology &*  
649 *Philosophy* **17**, 459-476.
- 650 [75] Milinski, M. & Wedekind, C. 1998 Working Memory Constrains Human Cooperation in  
651 the Prisoner's Dilemma. *Proceedings of the National Academy of Sciences of the United*  
652 *States of America* **95**, 13755-13758.
- 653 [76] Stevens, J.R., Cushman, F.A. & Hauser, M.D. 2005 Evolving the Psychological  
654 Mechanisms for Cooperation. *Annual Review of Ecology, Evolution, and Systematics* **36**,  
655 499-518. (doi:10.1146/annurev.ecolsys.36.113004.083814).
- 656  
657

658 **Figure legend**

659

660 **Figure 1.** (A) Predator inspection arena with illustrative examples of movement of fish in  
661 inspection lanes (red lines) (B) When focal fish had experienced defection by a shoal during  
662 predator inspection they differed from other groups in a social partner choice paradigm. They  
663 showed a preference for novel social partners over social partners that were ostensibly from  
664 the shoal they had experienced while inspecting a predator (control = condition with no  
665 predator present; \*\*=significant at  $\alpha=0.0125$ ; error bars= $\pm 1$  SEM).

666

667

668 **Table 1.** Results of the analysis of the main experiment testing for an effect of the inspection  
669 condition that fish were in (no predator present, i.e. control, versus predator present, i.e.  
670 experimental), the social environment that fish experienced during the inspection portion of a  
671 trial (cooperative vs. non-cooperative), the type of diet (daphnia or bloodworm) that novel  
672 shoaling partners had been fed on and their interactions. The significant interaction between  
673 inspection condition and social experience was further explored (Table 2). The significant  
674 effect of diet type was driven by an overall preference for fish that had been fed on a  
675 bloodworm diet.

Source	<i>F</i> (1,121)	<i>p</i>
Inspection condition	0.294	0.589
Social experience	5.491	<b>0.021</b>
Diet type	4.549	<b>0.035</b>
Inspection condition * Social experience	6.134	<b>0.015</b>
Inspection condition * Diet type	0.000	0.984
Social experience * Diet type	2.840	0.095
Inspection condition * Social experience * Diet type	0.062	0.804

676

677

678

679 **Table 2.** Results of the *post hoc* t-tests of significant interaction terms in the behavioural  
 680 dataset (see Table 1). Significance after Bonferroni-correction ( $\alpha=0.0125$ ) is shown in bold  
 681 and indicates a preference in the shoal-choice experiment for a novel social environment after  
 682 individuals have experienced defection.

Inspection condition	Social experience	t	df	p
No predator present	Cooperation	0.377	29	0.709
	Defection	0.353	32	0.726
Predator present	Cooperation	-1.675	32	0.104
	Defection	2.933	32	<b>0.006</b>

683

684