

1 Title: What to copy: the key factor of observational learning in striped jack
2 (*Pseudocaranx dentex*) juveniles

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14 Abstract

15 Animals in social environments can enhance their learning efficiency by observing
16 the behaviour of others. Our previous study showed that learning efficiency of
17 schooling fish increased through observation of the behaviour of trained
18 demonstrator conspecifics. The present study aimed to verify the key factor of
19 observational learning by investigating what information is important for social
20 transmission of feeding information. A striped jack (*Pseudocaranx dentex*) observer
21 was provided with one of five observation treatments: (a) pellets observation,
22 where pellets were dropped near the aeration in an adjacent tank; (b) responding
23 conspecific observation, where a trained conspecific demonstrator responded to the
24 aeration without food in the adjacent tank; (c) foraging conspecific observation,
25 where a conspecific demonstrator foraged near the aeration in the adjacent tank;
26 (d) nearby pellets observation, where pellets were dropped in a transparent column
27 near the aeration in the observer tank, and (e) foraging heterospecific observation,
28 where a filefish (*Stephanolepis cirrhifer*) demonstrator foraged near the aeration in
29 the adjacent tank. The response to the aeration in these observers was compared
30 with that of controls who did not observe any behaviour. Only individuals which
31 observed foraging conspecifics showed a response to the aeration after observing.
32 These results suggest that observer fish acquire feeding information not through
33 recognition of prey items or through imitation of the demonstrator, but through the
34 vicarious reinforcement of a conspecific for foraging.

35

36 Keywords: behavioural transmission, conditioning, copying, fish cognition, social
37 learning

38 Introduction

39 Learning in a social environment can potentially be facilitated by social learning
40 (Kleiman and Eisenberg 1973). In social learning, an individual acquires behaviour
41 and information through observations of and interactions with other individuals.
42 This style of learning has the potential to enhance an individual's adaptation to the
43 living environment. For example, prey location can be learned through
44 observations of associating shoal mates in feeding sites, without the energetic
45 expenditure of food searching, e.g., in Atlantic salmon *Salmo salar* (Brown et al.
46 2003). The anti-predator behaviour of the Japanese flounder (*Paralichthys*
47 *olivaceus*) can also be enhanced through observation of conspecifics, without the
48 risk of predation (Arai et al. 2007).

49 About half of the teleost fishes in the world live socially in a school for at
50 least part of their lives (Shaw 1978) and thus have the opportunity to acquire
51 information through social learning. Indeed, some studies have found that fish
52 acquire survival skills by social learning in various life history contexts, such as
53 predator avoidance (Brown and Laland 2001; Kelly et al. 2003), orientation
54 behaviour (Warner, 1988; Fukumori et al. 2010), feeding (Reader et al. 2003;
55 Schuster et al. 2006; Webster and Laland 2008), and mate choice (Witte and Nobel
56 2011).

57 Social learning mechanisms have been studied in a number of species,
58 including rats (Zohar and Terkel 1991), dogs (Miller et al. 2009), primates (Hopper
59 et al. 2008; Tennie et al. 2010), and birds (Klein and Zentall 2003; McGregor et al.
60 2006). For example, McGregor et al. (2006) found in pigeons (*Columba livia*) that,
61 even when demonstrators were not rewarded while being observed, observers of
62 pecking behaviour made pecking responses more frequently than did observers of
63 stepping behaviour. This study provided evidence of imitation simply as a process

64 in which ‘B learns some aspect(s) of the intrinsic form of an act from A’ (emphasis
65 original; Hopper 2010). Hopper (2010) also defined ‘ghost display’ conditioning,
66 where an observer is able to reach a predetermined goal from seeing only the
67 pertinent parts of a given task/apparatus without an active model operating it.

68 While many researchers have investigated the function of observational
69 learning in fish (i.e. what fishes learn through observation), there are few studies
70 regarding the mechanisms of observational learning (i.e. how fish learn their
71 behaviours through observational learning). Recent studies have shown that their
72 cognitive capacity in many domains is comparable with that of non-human
73 primates (Brown et al. 2011). For example, fishes have evolved complex cultural
74 traditions (Brown and Laland 2011; Bshary et al. 2002), that is, they not only
75 recognize one another, but they can also monitor the social prestige of and
76 dominance relations amongst others (Griffiths 2003; Grosenick et al. 2007). Thus,
77 they may be equipped with mechanisms for the observational learning that are
78 similar to those of animals of higher orders.

79 Our previous study confirmed the ability for observational learning in jack
80 mackerel (*Trachurus japonicus*) juveniles: fish that observed other individuals
81 feeding at the aeration in an adjacent tank were conditioned to aeration as a
82 stimulus to initiate feeding more quickly than fish that did not observe this
83 conspecific behaviour (Takahashi et al. 2012a). Here we tried to tease apart the
84 process of observational learning and thus elucidate the essential mechanism of
85 this social behaviour. We proposed their observational learning could be explained
86 by one of the following hypothetical processes: (i) fish are conditioned to aeration
87 with the presence of food through watching the foods and aeration stimulus, which
88 could be confirmed by a ‘ghost display condition’; (ii) observer fish copy
89 demonstrator fish in their response to aeration, suggesting that they are capable of

90 imitation; or (iii) observer fish acquire feeding information by observing
91 demonstrator fish foraging near the aeration, indicating that they need a full
92 demonstration. By testing these conditions separately, this study investigated how
93 observational learning is formed in conditioned feeding with the aeration stimulus.

94 We used striped jack (*Pseudocaranx dentex*) in this study. They consistently
95 form a school when they attain the juvenile stage at around 20 mm standard
96 length (SL; Masuda and Tsukamoto 1998) and therefore have many opportunities
97 to acquire information from conspecifics, much like *T. japonicus*. This species is
98 more resistant to stress from isolation than *T. japonicus* (Takahashi, personal
99 observation). Furthermore, in this study, we used a heterospecific demonstrator
100 observation treatment to investigate the possibility of observational learning
101 between species. Using a demonstrator fish that has a different shape from that of
102 the observer, the treatment confirmed the importance of the appearance of a model
103 for observational learning. Filefish (*Stephanolepis cirrhifer*) were used as the
104 heterospecific demonstrators. Although they live in sympatry and share feeding
105 resources with *P. dentex* (Masuda, personal observation), the body form is
106 distinctly flat compared with that of *P. dentex*, which is more spindle-shaped.

107

108 Materials and methods

109 Fish

110 Hatchery-reared *P. dentex* were purchased from Yamasaki Giken Co., Ltd. or
111 Pacific Trading Co., Ltd. and were transported to the Maizuru Fisheries Research
112 Station, Kyoto University. About a hundred juveniles were kept in each of two 500 l
113 transparent polyethylene tanks supplied with filtered seawater at a rate of 4 l per
114 min and with strong aeration (600 ml / min). Rearing tanks were indoors, and
115 water temperature was kept at about 25°C using a heater and thermostat. The fish

116 were fed with commercial pellets (Otohime C2 and Otohime S2, Marubeni Nisshin
117 Feed Co., Ltd.) to satiation once or twice a day until the fish were to be used for the
118 experiment. All the fish were kept in a tank for at least one month to be weaned on
119 pellets, as all were confirmed to forage actively on pellets near the water surface.
120 SL of all to fish used was measured after the experiments. Fish mean SL was 76.2
121 mm (standard deviation = 1.2 mm), and there was no difference between
122 treatments (according to an analysis of variance: $F_{5,44} = 1.65$, $P > 0.05$; Table. 1).
123 Juveniles used for the experiment ranged in age from 90 to 120 days old. It was not
124 possible to identify sex in these juveniles.

125

126 Apparatus and Procedure

127 Transparent glass tanks (length \times width \times height: 60 \times 30 \times 35 cm) were set up in a
128 temperature-controlled room and covered with black vinyl sheets except for one
129 side. Seawater was continuously added to the experimental tanks and drained
130 using a siphon to maintain a depth of 20 cm. Tanks were separated by a black
131 sheet to reduce disturbance from experimenters. A video camera (HDR-CX550,
132 Sony Co., Tokyo, Japan) above the experimental tank allowed recording of the fish
133 behaviour during the experiment.

134 An air stone was positioned set at the centre of each tank, and aeration was
135 remotely controlled and was turned off except in the conditioning trial, when
136 aeration was set to be gently turned on to provide approximately 12 ml of air per
137 minute. The tanks of the observer fish and the demonstrator fish were arranged so
138 that the uncovered sides of its tanks faced each other, and a removable black board
139 (length \times height: 60 \times 35 cm) was placed between tanks except during an
140 observation trial.

141 A single fish was introduced into the demonstrator tank, and that fish was

142 used as a demonstrator. All demonstrator fish were conditioned to respond to
143 aeration as a conditioned stimulus and feeding pellets as an unconditioned
144 stimulus, as in Takahashi et al. (2012b); that is, 30 s after the onset of aeration,
145 pellets were dropped near the aeration. The demonstrators were trained until they
146 showed a prominent response to aeration without pellets. Different demonstrator
147 fish were used for each observer fish, except for the foraging heterospecific
148 observer. Some of the observer fish that had been trained to respond to aeration
149 were used as demonstrators after the test trial, but no demonstrator fish were used
150 as observers.

151 Single fish were randomly selected from each rearing tank, introduced into
152 one of four replicate observer tanks on the previous day, and allowed to acclimate
153 overnight. A few pellets were provided before initiating the experiment, which
154 began once the observer fish ate these initial pellets. When the fish was foraging
155 for the pellets, the black board between the tanks was removed at 30 min before
156 the start of observation trials so that demonstrator fish were visible to observer
157 fish in the adjacent tank. Observer and demonstrator fish used for an experiment
158 trial were drawn from the same stock tank. Therefore, they were likely to be
159 familiar with each other during the observation trial.

160

161 Observation trial

162 Observer fish were provided with one of the following treatments, performed by
163 demonstrator fish in the adjacent tanks: pellets, responding conspecific, foraging
164 conspecific, nearby pellets, and foraging heterospecific observation (Fig. 1a-e). Five
165 observation trials were provided for each observer, and the observation trial was
166 video recorded to evaluate fish behaviour. The response to aeration of these
167 treatment groups was compared with that of the control group, where no

168 demonstrator fish was provided (Fig. 1f). Eight fish were used in the control group
169 and in each observational treatment except for the nearby pellets treatment, in
170 which five fish were used.

171 In the pellets treatment, pellets were dropped near the aeration in a
172 demonstrator tank that contained no demonstrator fish. The observation trial
173 lasted for 60 s; after aerating for 30 s, three to five pellets were dropped near the
174 aeration source three times at 15 s intervals. In the responding conspecific
175 treatment, an observer fish was allowed to observe a *P. dentex* demonstrator that
176 was responding to aeration without pellets. The observational trials ran for 30 s,
177 which was the same as the duration of aeration in the demonstrator tank. In the
178 foraging conspecific observation treatment, the observer fish observed the
179 behaviour of a conspecific demonstrator that was responding to aeration and
180 foraging pellets near it. The observation trials ran for 60 s; after the aeration was
181 turned on for 30 s, three to five pellets were dropped near the aeration three times
182 at 15 s intervals.

183 The nearby pellets treatment investigated the possibility of observational
184 learning in a situation where the observer can recognize the food at close range
185 within the observer tank, because there was a possibility that during the pellets
186 treatment, observer fish would not be able to recognize the pellets in the adjacent
187 demonstrator tank. In this treatment, the pellets were so that the observer could
188 see them but the fish was not allowed to forage the pellets. A transparent oval
189 column (10cm × 7.5cm × 30 cm height) was positioned at the centre of the
190 conditioning tank, and the air stone was put outside of the column. An observer
191 was provided with the observation trial for 60 s, during which the aeration was
192 turned on for 30 s, and after that the pellets were dropped into the oval column
193 near the aeration three times at 15 s intervals. The pellets were removed using a

194 pipette after turning off the aeration.

195 To conduct heterospecific observation trials, two *S. cirrhifer* (93 mm and 95
196 mm SL) were captured using a cage trap in Maizuru Bay (35° 49' N; 135° 36' E) and
197 transported in a bucket of seawater. They were kept in a 500 l transparent
198 polyethylene tank, like that was to the *P. dentex*. Rearing tanks were indoors, and
199 water temperature was kept at about 25°C using a heater and thermostat. After
200 confirming active foraging on pellets (Otohime S2) in the water column, they were
201 transferred to two separate tanks. They were trained until both showed prominent
202 responses to aeration, and could thus be used as demonstrators. Five observation
203 trials were conducted in the same manner as the foraging conspecific observer
204 treatment, i.e., after the onset of aeration for 30 s, pellets were dropped near
205 aeration for 30 s. After the experiment, *S. cirrhifer* were measured in their SL and
206 subsequently released at the capture site.

207 Five observation trials were conducted with about 30 min intervals for each
208 of the observation treatments. After the fifth trial, the black separation board was
209 placed between observer and demonstrator tanks to avoid further interaction
210 between them; in the nearby pellets treatment, the column was removed from the
211 observer tank. Each observer fish was given a test trial at 30 min after the fifth
212 observation trial.

213

214 Test trial

215 A test trial was conducted to confirm the observer fish's response to aeration in
216 observation tank without feeding pellets; aeration was turned on for 1 min. The
217 response was then compared with that of the control group. In the test trial,
218 behaviour of each observer and control was video recorded for 2 min, 1 min pre-
219 aeration and 1 min post-aeration.

220

221 Behavioural analyses

222 Attraction to the demonstrator tank was used as an index of the observation
223 behaviour in the first observation trials except for the nearby pellets treatment.

224 The attraction was measured by the staying duration of fish within 7.5 cm (approx.
225 one fish SL, and 25% of experimental tank) from the side of the demonstrator tank.

226 Attraction behaviour was measured for 30 s in each observation trial: while pellets
227 were dropped near the aeration three times in the pellets treatment, while the

228 aeration of the demonstrator tank was turned on (i.e. demonstrator fish responded
229 to aeration without pellets) in the responding conspecific treatment, and while

230 pellets were dropped near the aeration three times (demonstrator fish foraged near
231 aeration) in the foraging conspecific or heterospecific treatment. The attraction

232 duration to a demonstrator tank was compared among observation treatments
233 using a Kruskal-Wallis test followed by a Steel-Dwass multiple comparison as a

234 post hoc test. The attraction duration to a demonstrator tank in the first
235 observation trial was also compared with 7.5 s as the significance level (chance

236 level: 25% of 30 s), in each observation treatment using a one-sample Wilcoxon test
237 ($n = 8$), because the data were not normally distributed.

238 In the nearby pellets observation treatment, attraction behaviour to pellets

239 was measured using the duration of fish staying near the aeration (within 7.5 cm
240 around the oval column). The duration was measured to 30 s in each of the pre-

241 aeration and post-aeration periods, and then the average durations of the five
242 observation trials ($n = 5$) were compared between pre- and post-aeration periods

243 using a paired t -test to confirm observers' recognition of the pellets. The data
244 showed normal distribution and homogeneity of variance between pre- and post-

245 aeration.

246 In the test trials, observers' frequency of staying near the aeration in the test
247 fish tank was used as an index of their response to aeration. The staying frequency
248 in the aeration area (which was defined as 20 × 20 cm surrounding the aeration
249 stone) was counted during 2 s every 1 min of the pre-aeration and post-aeration
250 periods. Attraction to the aeration was evaluated by the staying index, calculated
251 by subtracting the frequency during pre-aeration from that during post-aeration.
252 To investigate how well the observation trials promoted transmission of response to
253 aeration, the staying index of each observation treatment was compared using a
254 Kruskal-Wallis test, and each observation treatment was compared with the
255 control treatment using Steel's multiple comparison. Some of the data lacked
256 homogeneity of variance between treatments; this is why the analyses were
257 conducted using non-parametric methods.

258

259 Results

260 There was a significant difference in the attraction to the demonstrator tank
261 among treatments in the observation trials (Kruskal-Wallis test: $n = 8$, $\chi^2_{3, 32} = 11.2$,
262 $P < 0.05$); the attraction duration in the responding and foraging conspecific
263 treatments was significantly longer than that in the pellets observer treatment
264 (Steel-Dwass multiple comparison test: pellets vs. responding conspecific: $n = 8$, $t =$
265 -2.76 , $P < 0.05$, pellets vs. foraging conspecific: $n = 8$, $t = 2.97$, $P < 0.05$; Fig. 2).
266 Furthermore, the attraction behaviour to the demonstrator tank in the responding
267 and foraging conspecific observer treatments significantly differed from the chance
268 level, but that was not the case in pellets observers or in foraging heterospecific
269 observers (one-sample Wilcoxon test; pellets: $n = 8$, $t = 6$, $P > 0.05$, responding
270 conspecific: $n = 8$, $t = 2$, $P < 0.05$, foraging conspecific: $n = 8$, $t = 1$, $P < 0.05$,
271 foraging heterospecific: $n = 8$, $t = 17$, $P > 0.05$; Fig. 2). In the nearby pellets

272 observation treatment, the attraction duration near aeration increased from pre- to
273 post-feeding (paired t-test; $df = 4$, $t = -2.64$, $P < 0.05$), suggesting that the observer
274 fish were attracted by pellets in the oval column during the observation trial.

275 In the test trials, there was a significant difference in staying index between
276 treatments (Kruskal-Wallis test; $\chi^2_{4, 37} = 11.5$, $P < 0.05$); the staying index in the
277 test trial in the foraging conspecific treatment was significantly different from the
278 control treatment (Steel-Dwass multiple comparison test; foraging conspecific: $n =$
279 8 , $t = -2.46$, $P < 0.05$; Fig. 3). However, there was no such difference in staying
280 index between other treatments and the control (pellets: $n = 8$, $t = -0.11$, responding
281 conspecific: $n = 8$, $t = -0.00$, nearby pellets: $n = 5$, $t = -0.54$, foraging heterospecific
282 observer: $n = 8$, $t = -0.50$; $P > 0.05$).

283

284 Discussion

285 Naïve observer fish that were given the opportunity to see a conspecific model were
286 more likely to attend to the adjacent ‘demonstration’ tank, regardless of whether
287 model fish was eating food pellets (foraging conspecific treatment) or not
288 (responding conspecific treatment). However, only after seeing a conspecific eating
289 food pellets near the aeration bubbles (foraging conspecific treatment) did the
290 observing fish spend more time foraging by the aeration bubbles, a reaction
291 indicative of observational learning. Merely seeing either food pellets (pellets
292 treatment) or a responding conspecific (responding conspecific treatment) near the
293 bubbles was not sufficient to encourage directed foraging by the observing fish.
294 Furthermore, seeing the ‘complete’ demonstration of a fish eating food pellets only
295 induced social learning when the demonstrating fish was a conspecific (*P. dentex*),
296 not when the model was heterospecific (*S. cirrhifer*).

297 Whereas the *P. dentex* juveniles can learn feeding information through the

298 observation of foraging conspecifics, observational learning did not occur in
299 responding conspecific observers even though observer fish watched the
300 demonstrator responding to aeration. These results imply that the observational
301 learning in this species was not imitation—that is, copying the responses of other
302 individuals. Fiorito and Scotto (1992) found that octopuses (*Octopus vulgaris*) chose
303 the ‘right’ ball through the observation of demonstrators, despite the fact that the
304 demonstrator received neither reward nor punishment in the observation trial. In
305 Laland and Williams (1997), when untrained guppies (*Poecilia reticulata*) were
306 given the experience of swimming with conspecific demonstrators trained to take
307 one of two equivalent routes to food, subjects preferred to use the route of their
308 demonstrator when tested alone. These behavioural transmissions were considered
309 imitations, a reflex response that was programmed to copy the demonstrator’s
310 behaviour. On the other hand, the formation of observational learning in this study
311 suggested that *P. dentex* juveniles learned through recognizing a feeding
312 conspecific near the aeration.

313 Fish in the pellets observation treatment were not attracted to the pellets in
314 the adjacent demonstrator tank, so it is possible that the observer did not notice
315 the presence of the pellets during the observation trial in this treatment. This
316 finding also supports the idea that the presence of demonstrator fish would be
317 important for inducing the attention of an observer. However, in the nearby pellets
318 treatment, pellets were presented to make the observer aware of the presence of
319 food during the observation trial, and then the observer fish was attracted to the
320 pellets appearing near the aeration. These fish did not respond to aeration on the
321 test trial despite the fact that they had responded to the pellets dropped near the
322 aeration. This result suggests that ghost display conditioning was not formed in
323 this study—thus, the observer needed the presence of a demonstrator. In other

324 words, the visual recognition of prey did not have any value as an unconditioned
325 stimulus for *P. dentex* juveniles. These findings also suggest that the foraging of
326 demonstrator fish is a substitute reward for an observer fish, which is
327 indispensable for observational learning.

328 Observation of a heterospecific demonstrator did not induce observational
329 learning in *P. dentex* juveniles. This indicates that the presence of *S. cirrhifer* did
330 not promote the awareness of *P. dentex* in the same way as a conspecific
331 demonstrator; the distinct appearance of *S. cirrhifer* may not trigger a cognitive
332 response as a model for observational learning. On the other hand, Mathis et al.
333 (1996) reported that the brook stickleback (*Culaea inconstans*) developed an
334 avoidance response from observing the startle response of a fathead minnow
335 (*Pimephales promelas*). The authors described that these species often form a
336 mixed school in the natural environment and suggested that observational
337 learning would be established within ecologically similar species, even if they are
338 not conspecifics. Further investigations would be required to elucidate interspecies
339 observational learning; for example, a morphologically and behaviourally similar
340 heterospecific such as *T. japonicus* could be used as a demonstrator for *P. dentex*.

341 Although some past studies on social learning in fish have focused on the
342 relation between demonstrator and observer (Duffy et al. 2009; Laland et al. 2011;
343 Pike et al. 2010), few studies have investigated the mechanism of observational
344 learning in fish. We would like to propose a potential mechanism of observational
345 learning in fish in the light of the results of the present study. First, the presence of
346 a demonstrator fish is an important factor for inducing the attention of an
347 observer, and an appropriate demonstrator is required in this regard. Second, the
348 foraging behaviour of the demonstrator is a fundamental factor. Our study
349 indicated that fish cannot acquire necessary information merely with the presence

350 of food at the aeration or through imitating the responding behaviour to aeration of
351 a demonstrator; instead, they learn through vicarious reinforcement from a feeding
352 demonstrator.

353

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358 juveniles.

359

360 Ethical standards

361 All experiments were performed according to the Regulations on Animal
362 Experimentation at Kyoto University. After the experiment, the fish were kept in
363 the laboratory as brood stock.

364

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441

442 **Fig. 1** Schematic drawings of observational treatments. (a) Pellets observation:
443 pellets were dropped near the aeration in the demonstrator tank. (b) Responding
444 conspecific observation: a trained demonstrator fish responded to the aeration in
445 the demonstrator tank. (c) Foraging conspecific observation: a demonstrator fish
446 fed on pellets near the aeration in the demonstrator tank. (d) Nearby pellets
447 observation: a transparent plastic column was placed at the centre of the observer
448 tank, and aeration was put near the column. Pellets were dropped in the column,
449 on which the observer fish could not feed. (e) Foraging heterospecific observation: a
450 *Stephanolepis cirrhifer* demonstrator was fed with pellets near the aeration. (f)
451 Control: no demonstrator was provided

452

453 **Fig. 2** Median attraction duration with demonstrator tank on the first observation
454 trial of each observation treatment. Asterisks indicate the significant differences in
455 duration from the chance level, represented by a dotted line (7.5 s: 25% of 30 s; $P <$
456 0.05; one-sample Wilcoxon test). Bars indicate the interquartile range (n = 8 except
457 for nearby pellets [n = 5])

458

459 **Fig. 3** Median staying index in each treatment in the test trial. Asterisk indicates
460 that the duration significantly differed from controls ($P < 0.05$; Steel multiple
461 comparison test). Bars indicate the interquartile range (n = 8 except for nearby
462 pellets [n = 5])

463

464

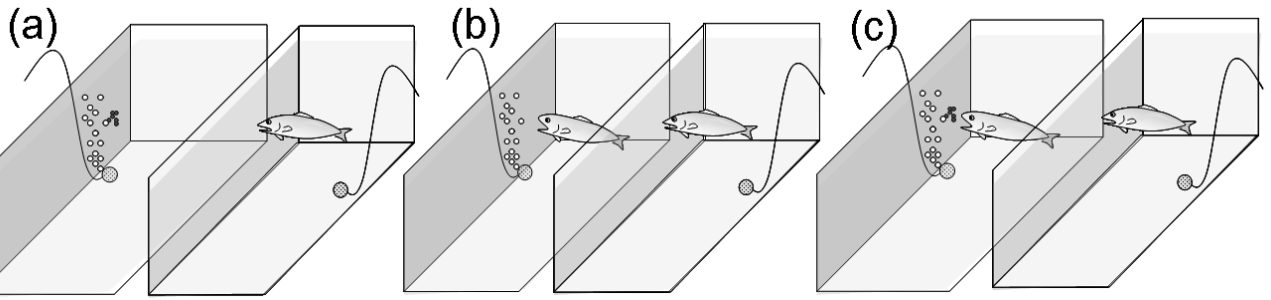
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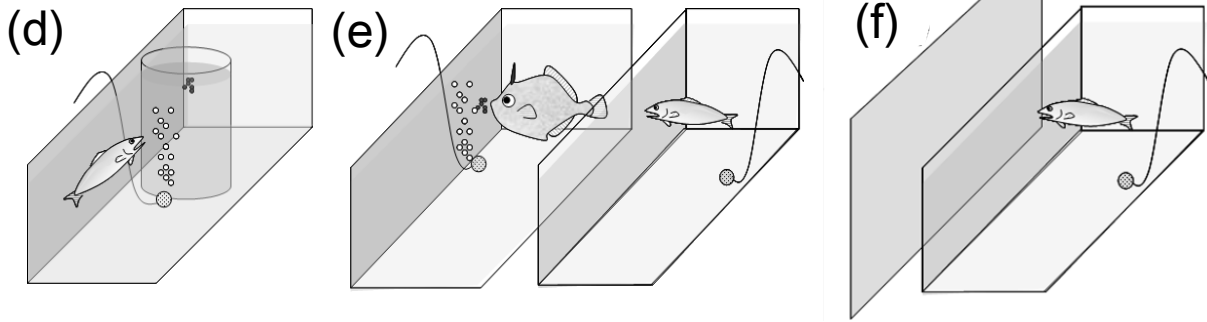
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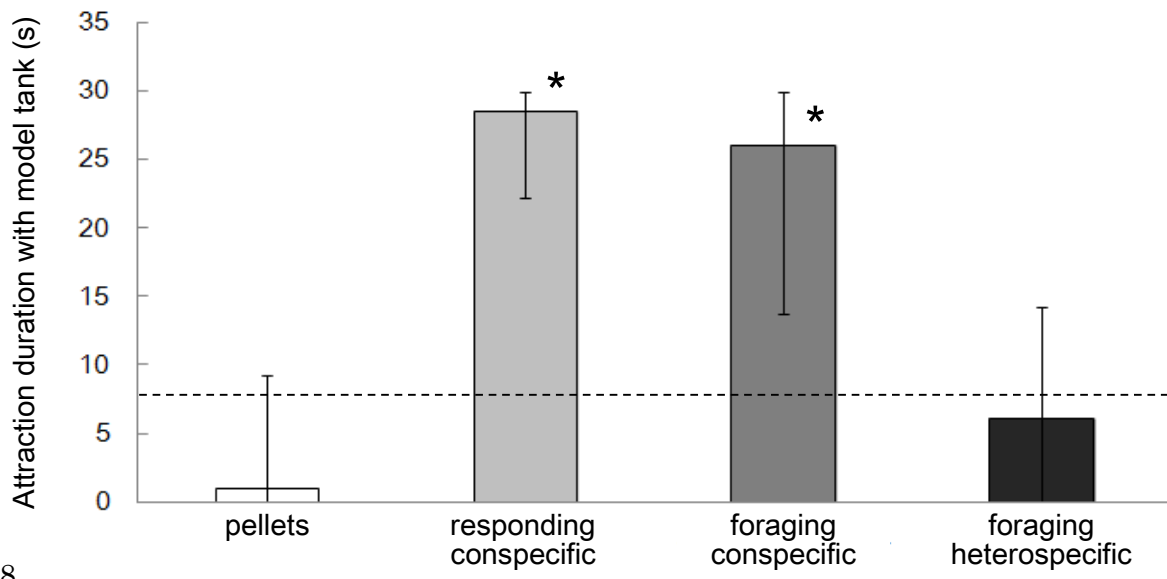
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476 Fig. 1

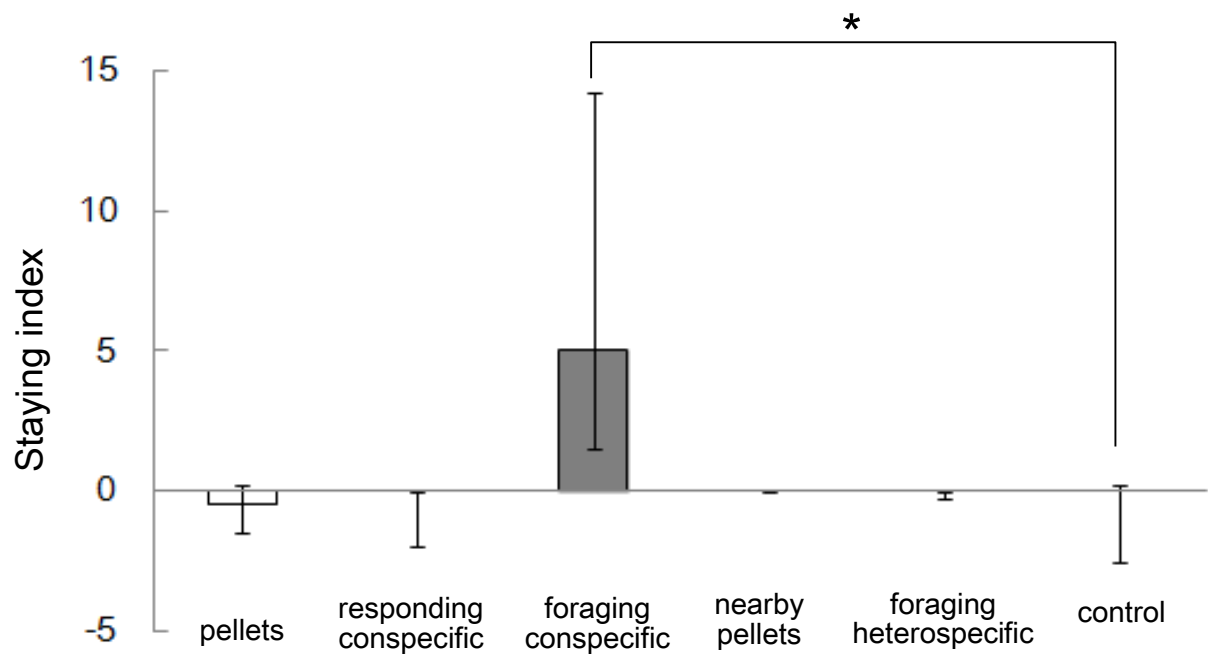
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478

479 Fig. 2

480



481

482 Fig. 3

483