

Experienced social partners hinder learning performance in naive clonal fish

Fritz A. Francisco^{1,2*}, Juliane Lukas^{2,3}, Almond Stöcker⁴, Pawel Romanczuk^{1,2,5}, David Bierbach^{1,2,3},

1 Excellence Cluster Science of Intelligence, Technical University, Berlin 10587, Germany

2 Department of Biology, Humboldt University, Berlin 10587, Germany

3 Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

**4 Department of Mathematics, École polytechnique fédérale de Lausanne (EPFL), CH-1015
Lausanne, Switzerland**

5 Bernstein Center for Computational Neuroscience, Humboldt University, Berlin 10587, Germany

*** corresponding author: fritz.francisco@hu-berlin.de**

1 **Abstract**

2 Social learning can facilitate information spread within groups and is generally assumed to increase learning
3 efficiency in animals. Here, we asked how individual learning is affected by skill level of a demonstrator
4 present during learning. We predicted that both task-naive and task-experienced individuals benefit from a
5 task-experienced, conspecific demonstrator. We used the all-female clonal Amazon molly (*Poecilia formosa*)
6 for our experiments. We further propose a model framework which lets us directly relate each research question
7 to a single model parameter. First, following a classical conditioning paradigm over five days, half the fish
8 were trained to find food inside a cylinder, while the others were provided with food randomly dispersed
9 in their tank. As a result trained individuals visited the cylinder with a higher likelihood than randomly fed
10 individuals and showed consistent individual differences in their learning performance. In a second step,
11 we allowed these fish to observe a conspecific while we continued (for those trained) or started (for naives)
12 individual training. We found that trained individuals did not benefit from a partner, regardless of the partners'
13 proficiency, but showed higher average performances compared to naives. Naive individuals showed a decrease
14 in learning performance when paired with experienced partners but not when paired with other naive ones.

15 Our results suggest that Amazon mollies learn a foraging task individually and differ consistently in their
16 individual learning ability. Further, social learning depends on own, as well as the demonstrator's skill level in
17 a way that observing informed conspecifics may hamper own learning.

18

19 **Keywords** Behaviour, Learning, Clonal, Individuality, Social Information

20 **Highlights**

- 21 • Naturally clonal fish learn operant conditioning tasks
- 22 • Individuals show consistent differences in learning abilities
- 23 • Experienced social partners are not helpful during learning

24 **Introduction**

25 In 1514 Machiavelli already stated that "Men nearly always follow the tracks made by others and proceed in
26 their affairs by imitation". This is not unique to humans alone, as many gregarious animal species often acquire
27 information about their environment from their social partners [Dall et al., 2005, Giraldeau and Caraco, 2018]
28 and is commonly referred to as observational or social learning [Bikhchandani et al., 1998, Brown and Laland,
29 2003, Webster and Laland, 2008]. It contrasts private learning, where information is gained by exploring
30 solutions alone and in absence of others [Laland et al., 2011, Kao et al., 2014]. In general, social learning
31 involves the observation of others and the copying of the observed actions [Galef and Laland, 2005]. For
32 example, task-naive Amazon Parrots (*Amazona amazonica*) have been shown to copy the behaviour of other,
33 more experienced individuals in order to access an obstructed food source [Picard et al., 2017]. Reader et al.
34 [2003] demonstrated that wild guppies (*Poecilia reticulata*) could copy the food patch preference and predator
35 avoidance behaviour from other conspecifics. However, how such social learning processes are affected by the
36 initial skill levels of both, observer and demonstrator is only poorly understood.

37 For one, observed demonstrators may differ in performance skills and thus in the quality of the information
38 they can provide. Variation in information quality can in turn lead to error propagation and accumulation,
39 giving rise to a potential trade-off between individual and social information use [Giraldeau et al., 2002,
40 Kendal et al., 2005]. Nevertheless, there is evidence that demonstrators' skill levels *per se* do not determine
41 the extent to which they are copied by less experienced observers. For example, in the guppy, familiarity

42 among observer and demonstrator seems to be much more important than demonstrator skills when it comes
43 to being copying [Kendal et al., 2005]. Similarly, Roy and Bhat [2017] found that utilizing social information
44 led to food income equality in zebrafish (*Danio rerio*), where observers relied on visual behavioural cues
45 of successful demonstrators to find food themselves. While these studies allowed for full contact among
46 individuals and targeted leader-follower interactions, it still remains unclear how an observer's performance in
47 learning a complex task by pure visual interaction with a demonstrator is, in turn, affected by the performance
48 skills of this demonstrator. Nevertheless, some pioneering work has been done decades ago, on which the here
49 presented work heavily builds on, investigating the relationships and potential costs and mismatches between
50 observer and demonstrator Kohn [1976], Biederman and Vanayan [1988], Nicol [1995].

51 Although numerous studies have highlighted the benefits of social learning to the observing or eavesdropping
52 individuals as it allows an individual to circumvent exploring all possible solutions on its own, and thus saves
53 time and energy, e.g., opportunity costs are reduced [Swaney et al., 2001, Pike et al., 2010, Webster and
54 Laland, 2012] [Brown and Laland, 2001, 2003, Reader et al., 2003, Harpaz and Schneidman, 2020], these
55 benefits might not be shared mutually with the observed and copied demonstrators [Toyokawa et al., 2019,
56 Zonca et al., 2021]. While the mere presence of more individuals is beneficial during predator encounters
57 [Krause and Ruxton, 2002], experienced demonstrators may lose task solving performance when interacting
58 with inexperienced naive individuals, either due to distraction [Roy and Bhat, 2017] or changed time budgets
59 as more time is allocated to social interactions than to the task at hand [Gartland et al., 2021]. But also direct
60 negative effects of the copying behaviour are known. For example, in many fish species males copy the mate
61 choice decisions of other males by observing these copulating with females which may help the observer
62 determine high quality females. However, this behaviour will likely increase the risk for sperm competition
63 and thus is costly for the copied male that initially mated with the female [Plath and Bierbach, 2011]. As a
64 counter strategy, males may change their mate choices to mislead others and conceal their real preferences,
65 which is referred to as audience effects [Plath et al., 2008, Zuberbühler, 2008], a form of social deception
66 [Wiley, 1994]. In the context of complex task learning by observation alone, the question remains of how a
67 demonstrator's performance is affected by being copied and whether the observer's skill levels play a role in
68 this.

69 In addition to situations where there is an information discrepancy among observers and demonstrators,
70 individuals may also face a social counterpart with the same prior experience as themselves. Here, one can
71 assume that individuals may spend more time exploring individually, thus leading to increased learning and
72 final performance. This assumption is based on the idea that no additional task-specific, social information can
73 be gained from observing such a partner, as the information would be highly correlated to the own experience

74 and therefore deemed redundant [Strandburg-Peshkin et al., 2013, Kao et al., 2014].

75 In the current study we aimed at testing how variation in skill levels between observers and demonstrators
76 affected their learning performances (for naive observers), as well as overall task performances (for experienced
77 demonstrators). We used the Amazon molly (*Poecilia formosa*), a naturally occurring clonal fish species that
78 reproduces gynogenetically and gives birth to live offspring that are genetically identical to their sisters and
79 mothers [Schartl et al., 1995, Lampert and Schartl, 2008, Stoeck et al., 2010]. Through its clonal genetic
80 background as well as its gregarious life-style, this species has been proposed to represent a useful model
81 organism for the study of individual behavioural differences and the influence of behavioural traits on the social
82 functioning of groups [Doran et al., 2019, Laskowski et al., 2019, 2021, Makowicz et al., 2022]. However, to
83 date no research has been conducted on the learning abilities of these fish. Due to this intricate natural history
84 all individuals in this study were of same genetic composition and near identical rearing background. In a first
85 step (private information acquisition), an operand conditioning procedure (5 days, 3 times training per day) was
86 used to produce two differently experienced cohorts of otherwise genetically identical individuals: One cohort
87 was trained to find food in a opaque cylinder (the task, see Figure 1) and therefore given the opportunity to learn
88 to solve the task (task-experienced/trained individuals). The second cohort was trained to find food distributed
89 randomly, with no ability to learn an association between food and cylinder location (task-inexperienced/naive
90 individuals). In a second step (social information acquisition), we paired two individuals to have visual access
91 to each other, enabling them to observe each other while we continued (for trained individuals) or started (for
92 those naive) the conditional training (5 days, 3 times training per day). Our full factorial design allowed us to
93 create pairs of fish with all possible experience combinations: naive-naive, naive-trained and trained-trained.
94 With this design, we tested first whether Amazon mollies are able to learn the task and whether there were
95 consistent individual differences in both the learning rate and overall task performance at the end of the private
96 information acquisition phase. We then explored how the skill level of the partner affected learning and
97 overall performance when social information becomes available. The prediction was that naive fish paired
98 with a trained partner will have a higher probability to reach a novel food source compared to individuals that
99 were paired with another task-naive partner. For experienced Amazon mollies, the prediction was that the
100 task performance would be worse when paired with naive individuals, compared to those interacting with a
101 similarly proficient individual. The reasoning behind this assumption being, that individuals paired with a
102 similarly skilled partner which provides redundant information may allocate more time and efforts towards
103 acquiring private information - this can outweigh the potential opportunity costs that arise through the social
104 interactions and which should be apparent when paired with both naive and experienced partners.

105 **Materials and Methods**

106 **Study organism and maintenance**

107 For our experiments we used the Amazon molly (*P. formosa*), a naturally occurring clonal freshwater fish.
108 This is an all-female species that originated from a rare hybridisation event between a male Sailfin molly (*P.*
109 *latipinna*, ♂) and a female Atlantic molly (*P. mexicana*, ♀) about 100.000 years ago [Hubbs and Hubbs, 1932,
110 Schartl et al., 1995, Schultz, 1973, Lampert and Schartl, 2008, Stoeck et al., 2010, Warren et al., 2018]. This
111 species reproduces through gynogenesis which means that females require sperm from males of closely related
112 Poeciliid species to induce embryogenesis [Evans et al., 2011]. However, no paternal genetic material is
113 incorporated into the embryo, thus Amazon mollies produce broods of offspring that are genetically identical
114 to each other and their mothers [Schartl, 1995]. The herein used clonal lineage has been reared for many
115 generation in captivity and regular molecular checks confirm that individuals are clones. Fish were bred with
116 Atlantic molly males as sperm donors at the animal care facilities of XXXXXX. Fish were reared in 200-L
117 tanks filled with aged tap water at a temperature of 26 °C and fed twice daily *ad libitum* with commercially
118 available flake food as well as defrosted blood worms (*Chironomidae sp.*). All animal experiments were
119 conducted under the animal experiment number #0089/21 of the XXXXXX.

120 **Experimental design**

121 For our experiment, we first generated two different treatment groups, one that was fed three times per day for
122 one week only inside an opaque cylinder ('trained cohort', Figure 1), while the other one was fed with food
123 dispersed randomly in the experimental tank ('naive cohort'). In a second step, we visually paired fish with
124 individuals from the same or a differing training regime and either continued (for those already trained) or
125 started to feed only in the cylinder (for those habituated, but naive).
126 To start the experiment, we placed pairs of size-matched, unfamiliar fish (N=36, 23±2 mm) in each of six
127 identical test aquariums (300 × 600 × 200 mm). Fish were taken from multiple husbandry tanks ensuring
128 that familiarity was not given, and size-matched in order to reduce dominance effects and most importantly
129 to account for any age differences. All individuals were randomly distributed across all experimental tanks.
130 An opaque divider separated each tank into two same-sized compartments, each containing one fish. This
131 divider could be exchanged with a transparent one during experimentation to allow visual interactions (see
132 Figure 2). Each two-compartment tank was externally filtered (EHEIM Professional 3 250) throughout the
133 entire trial in order to maintain water quality and to provide olfactory cues to the fish. Water quality was

134 checked weekly (SERA pH, NH₃/NH₄,NO₂,NO₃) and 50 percent of the water was exchanged at the same
135 interval. The temperature was maintained within the range of 23-26 °C and adjusted through the ambient
136 room temperature. Water levels were maintained at 70 mm, resulting in a total of 18.7 l per tank and 3.5 l per
137 individual compartment. In order to enhance the learning outcome, the fish were kept on a continuous light
138 cycle, which has been shown to have no effect on the stress level of a closely related species, while improving
139 the learning abilities [Kurvers et al., 2018]. All fish were fed with frozen blood worms, which were thawed
140 approximately 30 min. before each experiment.

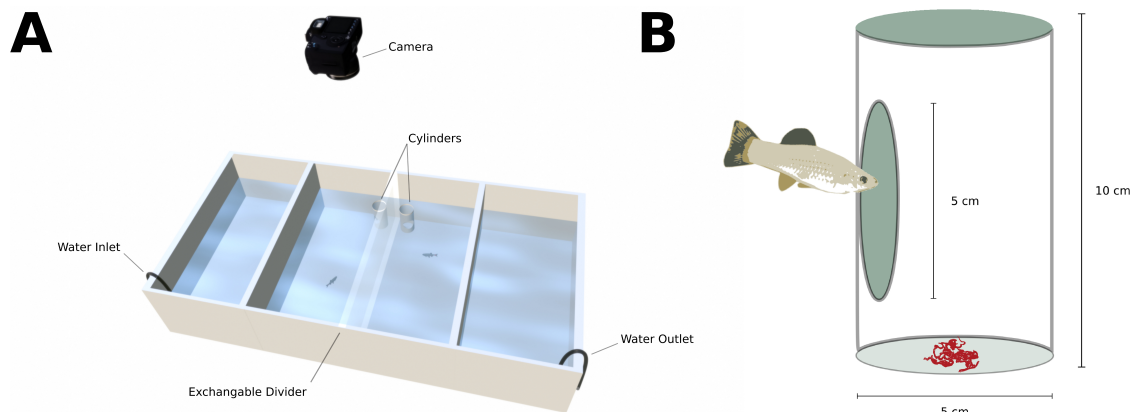


Figure 1. **A** Schematic of the general recording setup. Each inlet and outlet was attached to an individual circulating filter system. **B** Concealed food source used in the conditioning trials. Food was presented within an opaque cylinder, that could only be accessed through a horizontal opening. Entry into the cylinder was monitored through the top opening, vertically facing the camera. The cylinders were glued to ceramic plates to ensure stability. This further ensured that food particles and olfactory cues were contained within the cylinder.

141 Food conditioning experiments

142 Private Information Acquisition - Week 1

143 For the individual conditioning, we randomly selected future demonstrators and observers within each of
144 six simultaneously trained pairs. Demonstrators were then trained on six occasions per day, for at least five
145 consecutive days without visual access to the conspecific partner. Each training instance, consisting of eight
146 minutes, was recorded using consumer-grade webcams (c920 HD Pro Logitech, USB 3.0, 432 × 240 px, gray
147 scale, 30 fps) mounted above each individual tank. It was ensured that the camera was centered precisely
148 above the tank in order to keep occlusions and perspective distortion minimal and evenly distributed among
149 both individuals being recorded. During a training instance the individual was either presented with an opaque,
150 vertical PVC cylinder (height: 100 mm, \varnothing : 50 mm, see Figure 1), containing food as stimulus or with a mock

151 stimulus (50:50 - mock:real). This resulted in three mock treatments and 3 actual training instances per day,
152 for every individual. To standardize the starting distance of the fish to the food source, individuals were limited
153 to one side of the compartment at the beginning of each instance. This was done using a small separator (see
154 Figure 2). For mock treatments the fish underwent all steps, as if it was an actual training instance, being
155 constrained to one side of the compartment and having this separator subsequently removed, but without
156 the following stimulus presentation. The choice for true conditional or mock stimulus was randomized over
157 the course of the day, while ensuring that each accounted for 50% of the total daily tests (3 true, 3 mock).
158 Mock treatments were introduced to reduce any association with other neutral stimuli of the procedure and to
159 ensure that the focus was drawn to the actual task being learned Courville et al. [2006], Robinson et al. [2014],
160 Anselme and Güntürkün [2019]. For the trained cohort of fish, the cylinder was stocked with blood worms
161 ($N \approx 8$) which were visually occluded from the fish and only accessible through a round opening in the side of
162 the vertically oriented cylinder (see Figure 1). Fish of the naive cohort were treated with identical conditions
163 as their trained counterparts, with the only difference being the location at which food was presented. Here,
164 the same amount of food was distributed randomly within the tank and accessible for the duration of the test
165 instance. At the end of each test instance the cylinder as well as any remaining food particles were removed
166 from the tank using a pipette.

167 **Social Information Acquisition - Week 2**

168 In the second week of the experiment, individuals were regrouped with a new size-matched partner and
169 randomly redistributed across the six experimental tanks. This was done to ensure that each individual was
170 relocated to a new test tank. Regarding the individual's own and the partner's initial training, the following
171 social treatments were created: trained paired with trained individuals (TT), naive paired with trained (NT) or
172 trained with naive (TN) as well as naive paired with naive (NN). The previously opaque division, separating
173 the two individuals was replaced by a clear one, enabling full visual access between both individuals (see
174 Figure 2). This clear division was left in place for the entire duration of the social trial, which lasted for five
175 consecutive days. During this period all individuals were being trained and tested according to the individual
176 conditioning procedure previously described, receiving food only within the cylinder (see Figure 1).

177 **Video Analysis**

178 In order to quantify the learning outcome, fish were tracked using a custom developed tracking function (see
179 Appendix - Python Code: `track2h5`) implemented in Python and using the computer vision library OpenCV

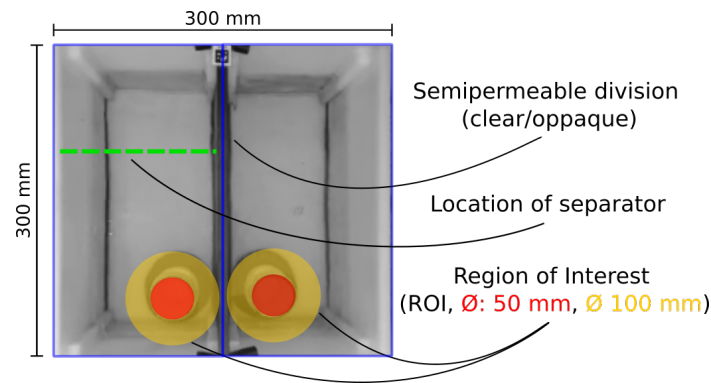


Figure 2. Top-down view of the holding tanks, showing the central most compartments, housing one individual on each side. The location at which the cylinder as food source was placed is denoted as region of interest and marked in red. The exchangeable central division, which could be either clear or opaque is shown in the middle. The position of the separator to standardize the starting distance at the beginning of each test instance is shown as green dashed line.

180 [Bradski, 2000]. The fish were detected by using frame-wise motion tracking, based on simple background
181 averaging and subsequent background subtraction. Detected objects were further filtered based on size, speed
182 and using an isolation forest algorithm to limit detections to actual fish and reduce noise due to reflections
183 and moving particles to an absolute minimum. Individual positions were given as two-dimensional Cartesian
184 coordinates, calculated as the center of mass of each filtered detection contour. Since background subtraction
185 can result in missing observations due to little movement of the animal, all coordinates were interpolated
186 linearly over time to account for this. The first 30 s of each test instance were considered the acclimation phase,
187 in which the animals were allowed to settle after having the separator removed. This period was exempted
188 from further analysis. To further standardize recordings, all recordings were restricted to a maximum duration
189 of 433 s, leading to a total duration from start to end of 403 s. Given that each individual was restricted to its
190 specific compartment, identities were maintained based on spatial discrimination. Presence and position of the
191 stimulus cylinder were automatically determined by using an implementation of the Hough transformation,
192 returning the coordinates of the center of mass and the radius of the detected cylinder. This enabled the exact
193 measurement of the Euclidean distance of each individual to the cylinder center at each given time point. In
194 addition to the automated process, all videos were manually checked for validity of cylinder detection and
195 tracking results.

196 Statistical analysis

197 All statistical analysis was run in R (R version 3.6.3 ‘Holding the Windsock’) and statistical inference based
198 on generalized mixed effects models (more specifically logit models) which were composed using the function
199 `glmer` in library `lme4`. After tailoring models to the experiment and research questions, further model
200 selection was done based on Akaike’s information criterion (AIC) or conditional AIC, where applicable, using
201 the library `cAIC4`. Validation and estimation of accuracy was done using the `check_model` function in the
202 `performance` library. Test statistics and calculations were done using `tab_model` in the library `sjPlot`. For
203 testing variance components, we use the boundary correction described by Stram and Lee [1994] for linear
204 mixed effect models. Significance is reported on a 95%-level and all confidence intervals (CIs) provided are
205 given as 95% CIs.

206 Individuals $i = 1, \dots, 36$, equipped with universal unique identifiers (UUIDs), are defined to have reached
207 the region of interest (i.e. solved the task) in test instance $j = 1, \dots, 15$ (response $y_{ij} = 1$) if their distance
208 to the cylinder center was smaller than 2.5 cm over a duration of 1 s or more, and to fail otherwise ($y_{ij} = 0$).
209 Predicting that fish should increase the likelihood to solve the task when being fed within the cylinder, we
210 associate the learning performance of individual i with its probability of reaching the region of interest and
211 employ a statistical learning model based on logit regression reflecting each of our main hypotheses in a single
212 model coefficient. Two slightly different model variants are used for experiments of Week 1 (Model 1) and
213 Week 2 (Model 2). Model 1, addressing questions of private information acquisition, is given by

$$\log \text{ODDS}_{ij} = A_i + B_i t_{ij} = \alpha_0 + \alpha_1 x_{Ti} + a_i + (\beta_0 + (\beta_1 + b_i) x_{Ti}) t_{ij} \quad (1)$$

214 where probabilities P_{ij} of success $y_{ij} = 1$ are modelled via odds $\text{ODDS}_{ij} = \frac{P_{ij}}{1-P_{ij}}$ of ‘expected # solved :
215 expected # failed’, allowing for interpretation via odds ratios (OR). The combined intercept A_i determines the
216 baseline odds of reaching the region of interest. This corresponds to the baseline likelihood of an individual
217 reaching the region of interest, before having any prior experience on entering it (Test Instances 1-2, illustrated
218 in Figure 3). The slope B_i reflects the learning rate of individual i , with ODDS_{ij} expected to increase with the
219 number of visits t_{ij} after initially solving the task (count variable, Time since solved ≤ 15 , illustrated in Figure
220 3). For the probability p_{ij} of solving the task, this results in a sigmoidal learning curve in t_{ij} (Figure 5). With
221 $x_{Ti} = 1$ if individual i is trained and 0 otherwise dummy-coding the training status, $B_i = \beta_0 + (\beta_1 + b_i) x_{Ti}$ is
222 composed of a reference slope β_0 reflecting the learning behaviour of un-trained individuals and the gain in
223 the learning rate β_1 for trained individuals as fixed effects, plus a random effect b_i reflecting subject-specific
224 deviations of trained individuals. This applies analogously for A_i as well. The random effects a_i and b_i are

225 assumed normally distributed with standard deviations τ_a and τ_b , respectively, and correlation ρ . The random
226 slope b_i is restricted to trained individuals, which are of major interest. In this model, $\beta_1 > 0$ corresponds to
227 Hypothesis I that clonal fish are capable of learning to feed inside the provided cylinder, in that it reflects
228 deviation from zero in the learning rate, and $\tau_b > 0$ corresponds to Hypothesis II that learning behaviour is
229 subject specific, as it describes the variation among individual learning abilities. Including an indicator $x_{\text{solved}ij}$
230 as additional covariate into Model 1, which is 1 if the i th individual has reached the region of interest before
231 the j th training instance and 0 otherwise, has been considered to enable less gradual learning behaviour but
232 turned out unfavorable in AIC-based model selection.

233 Model 2, designed for comparing learning behaviour of individuals in pairs with different training history, is
234 given by

$$\begin{aligned} \log \text{ODDS}_{ij} = A_i + B_i t_{ij} = & \alpha_0 + \alpha_1 x_{\text{NT}i} + \alpha_2 1_{\text{TN}}(i) + \alpha_3 x_{\text{TT}i} + a_i \\ & + (\beta_0 + \beta_1 x_{\text{NT}i} + \beta_2 x_{\text{TN}i} + \beta_3 x_{\text{TT}i} + b_i) t_{ij} \end{aligned} \quad (2)$$

235 where $x_{\text{NT}i} = 1$ if individual i is in group NT, i.e. was not trained in Week 1 but has an experienced partner,
236 and 0 otherwise. Analogously for TN and TT. Accordingly, β_0 describes the baseline learning rate in reference
237 group NN and $\beta_1, \beta_2, \beta_3$ reflect the deviation from that in the other treatment groups. In particular, $\beta_1 \neq 0$
238 indicates differences in learning behaviour of naive fish with trained partners (Hypothesis III). Random effects
239 a_i and b_i are specified analogously to Model 1 to account for subject-specific variations.

240 Results

241 I. Amazon mollies are able to quickly learn foraging task

242 Our first question was whether clonal fish were capable of learning to feed inside the provided cylinder. We
243 verify this based on Model 1, which captured the variance within the data well, while random effects accounted
244 for a large proportion of the variance (marginal R^2 : 0.083, conditional R^2 : 0.839, following Nakagawa et al.
245 [2017]). At baseline, we obtain odds of about 1 : 9 (probability $P_{ij} = 0.10$) for an untrained fish to reach the
246 region of interest within a test instance (given by intercept $\alpha_0 = -2.18$, $\text{CI} = [-2.80, -1.57]$, for $b_i = 0$). This
247 corresponds to the probability of an individual to enter the region of interest without having ever entered it
248 before (see Figure 3: Test Instance 0-2). For individuals being trained, and thus not being fed outside the
249 region of interest, we obtain a slightly higher baseline probability, with the odds increased by a factor of

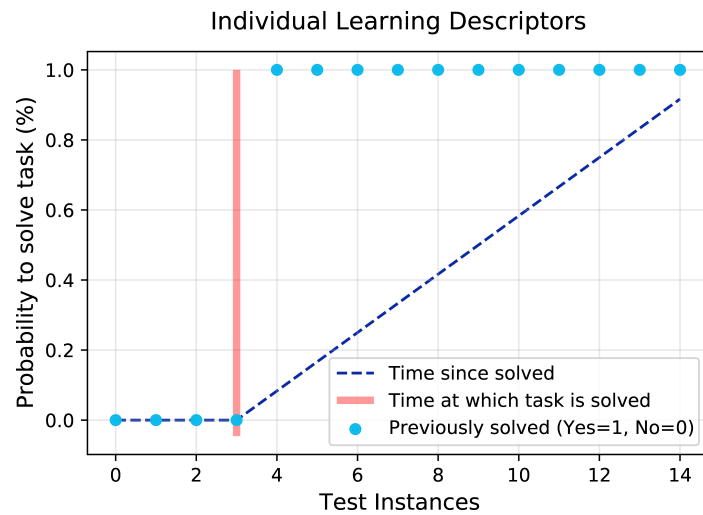


Figure 3. Definition of the ‘time since solved’ t_{ij} used as variable for individually describing the learning process. Until the food inside of the cylinder was first found by individual i at test instance $J_i = \min\{j : y_{ij} = 1\}$, no training effect can occur and $t_{ij} = 0$ for $j < J_i$. After that, individual training commences and training time monotonically increases as $t_{ij} = j - J_i$.

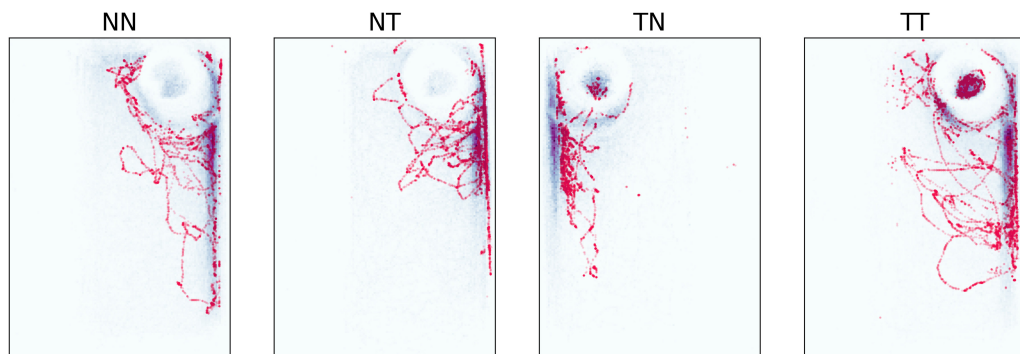


Figure 4. Overview of space use across treatment groups in the second week of training (order from left to right: NN, NT, TN, TT). Only instances where the cylinder was present are shown. Darker coloration represents higher number of occurrences, lighter lower. Sample trajectories are shown for random individuals of each treatment group. All trajectories were centered on the cylinder, for better visualization.

250 $\exp(\alpha_1) = 1.55$ (CI = [0.67, 3.56], $p = 0.302$), which is, however, not significantly different to those not being
251 trained. While we even observe a slightly negative ‘learning effect’ of entering the cylinder ($\beta_0 = -0.14$,
252 CI = [-0.35, 0.065], not significant) for individuals not being trained, a significant positive learning effect
253 is obtained for trained individuals ($\beta_1 = 1.37$, CI = [0.60, 2.14], $p < 0.001^{***}$). The likelihood of trained
254 individuals to reach the food source significantly increased, once they had solved the task for the first time (see

255 Figure 3: Test Instances > 3), with an odds ratio of $OR = \exp(\beta_0 + \beta_1) = 3.42$, $CI = [1.60, 7.30]$ more than
256 tripling the odds for the next visit (in a conditional ceteris paribus interpretation used also in the following).
257 Figure 5 depicts estimated mean learning curves with and without training, showing probabilities P_{ij} of solving
258 the task in dependence on t_{ij} , and illustrates how the time spent by fish in the region of interest increases with
259 t_{ij} .

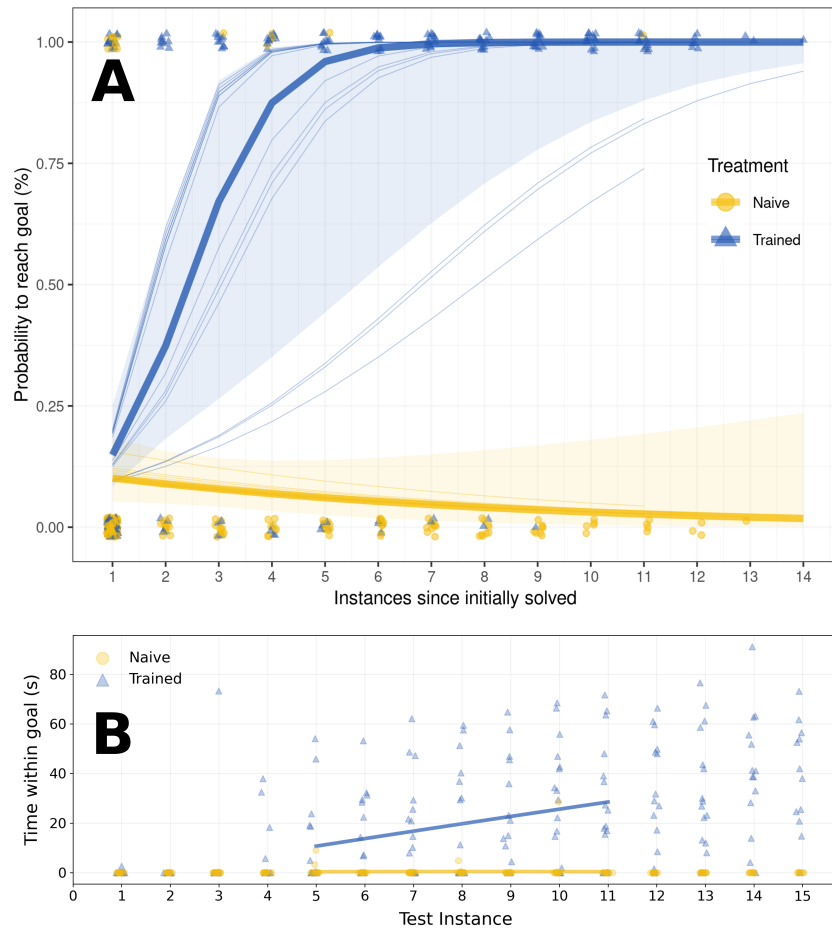


Figure 5. Learning outcome of the two treatment groups (trained/naive) in the first week. Both graphs show results from 36 individuals: Naive: N=18, Trained: N=18. **A:** Model output the first week of training in form of estimated marginal means (lines, thin: individual; bold: group mean) and raw data (points). Instances along the x-axis are in respect to the first time the goal was reached. Confidence intervals are based on the Upper Control Limit (UCL) and the Lower Control Limit (LCL) at a 95% confidence level. **B:** Visualization of time spend within goal area across both treatment groups (trained/naive) and over all test instances in the first week. A truncated linear fit is shown as trend line (between instance 5-11), estimated over all data points and for each treatment group. A slight jitter was applied along x in order to reduce overlap.

260 **II. Clonal Amazon mollies individually differ in learning ability**

261 We approached the question, whether individual variability was observable among the learning abilities,
262 and more specifically the probability to reach the goal area, using the same model as in I (Equation (1)) by
263 investigating the the random effect b_i on the learning rate of trained individuals. A standard deviation of
264 $\tau_b = 0.74$ is estimated for b_i which bespeaks considerable variation across individuals accounting for about
265 $\tau_b / (\beta_0 + \beta_1) = 60\%$ of their mean learning rate, and testing for $\tau_b > 0$ confirms significant inter-individual
266 differences in the learning behaviour ($p < 0.001^{***}$). Aside of differences in the learning rate, the standard
267 deviation $\tau_a = 0.43$ of the random intercepts a_i could be interpreted to reflect differences in the exploration
268 behaviour of individual fish. It is, however, not significantly > 0 ($p = 0.386$). Inter-individual differences
269 are also supported in terms of model selection, preferring Model 1 with random effects (marginal AIC = 314,
270 conditional cAIC = 259) over an analogous model without random effects (AIC = 342).

271 **III. Evident social effects of informed partner can hinder own learning**

272 The pairwise interactions in the second week, allowed to assess whether task performance was worse in
273 observers paired with naive demonstrators, compared to those interacting with task-proficient ones. For this
274 purpose we refer to results of Model 2, which are also illustrated in Fig. 6 A. Overall the model (see Model
275 2) to determine these effects captured the variance within the data well (marginal R^2 : 0.716, conditional R^2 :
276 0.903). In Week 2, naive individuals showed similar baseline probabilities for initially entering the region of
277 interest when paired with naive partners as they did in Week 1 (reference group NN: odds $\exp(\alpha_0) = 0.07$,
278 $CI = [0.02, 0.25]$). The baseline probabilities are substantially increased for experienced individuals (TN
279 vs. NN: $OR = \exp(\alpha_1) = 24.74$, $CI = [2.82, 216.76]$, $p = 0.004^{**}$) in accordance with the training effect
280 affirmed above. However, there was no evidence for a positive effect of the partner's experience on own
281 probability of initially entering the cylinder. By contrast, our data indicates a negative effect of having an
282 experienced partner on both naive and trained individuals (NT vs. NN: $OR = \exp(\alpha_1) = 0.39$, $CI = [0.04, 4.04]$,
283 $p = 0.432$; TT vs. TN: $OR = \exp(\alpha_3 - \alpha_2) = 0.92$, $CI = [0.10, 7.79]$, $p = 0.938$) which is smaller for the
284 trained: the odds to initially reach the goal area were decreased by $\sim 61\%$ in naive individuals, when paired
285 with an informed individual. For already trained individuals paired with another trained partner this effect
286 was smaller, amounting for a 8% decrease. Although these effects on the initial detection probability are
287 subject to considerable estimation uncertainty and not significant, a significant negative effect of the partner's
288 experience on the learning rate (reference NN: $\beta_0 = 2.03$, $CI = [1.14, 2.92]$) is found for naive individuals
289 ($\beta_1 = -1.77$, $CI = [-2.99, -0.56]$, $p = 0.004^{**}$). For NT vs. NN, the probability for reentering the region of

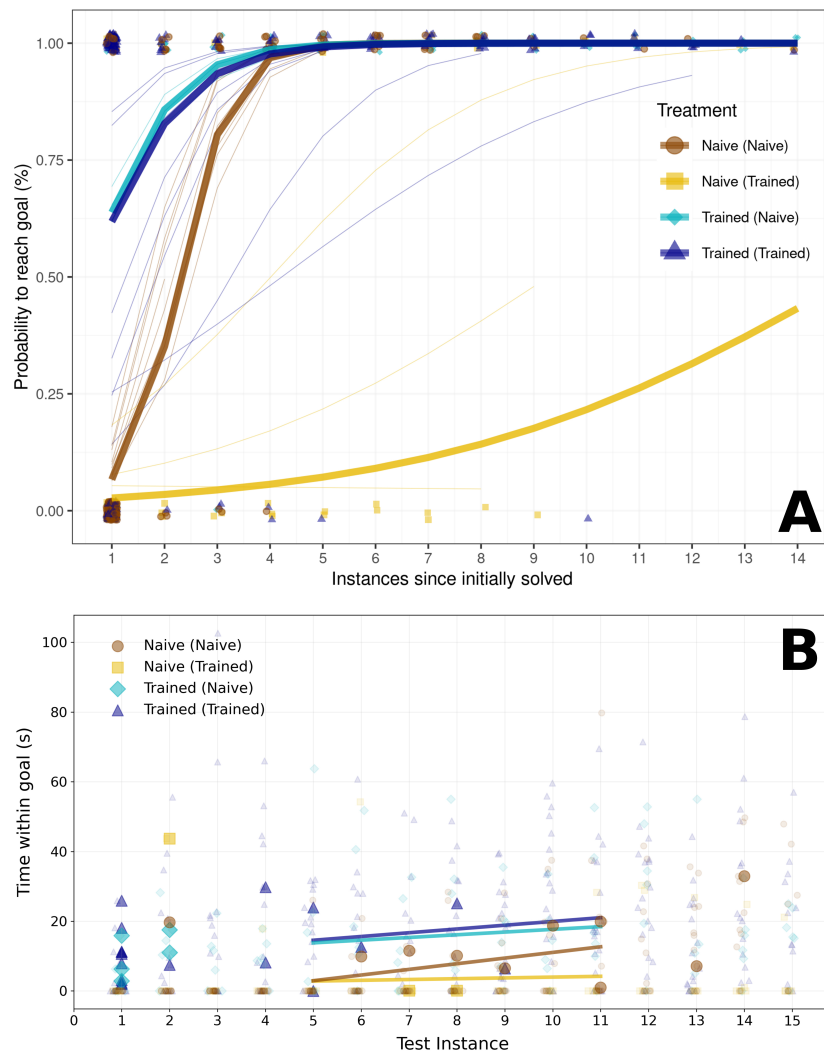


Figure 6. Learning outcomes of four treatment groups, depending on the focal individual and partner denoted in brackets: Naive (Naive): $N = 12$, Naive (Trained): $N = 6$, Trained (Naive): $N = 6$, Trained (Trained): $N = 12$. **A:** Model output the second week of training in a social context. Results are shown in form of estimated marginal means (lines, thin: individual; bold: group mean) and raw data (points). Instances along the x-axis are in respect to the time the goal was reached. **B:** Visualization of time spent within goal area across all treatment groups and over all test instances in the second week. For better visibility, first solved instances are shown with large icons and higher contrast. All remaining data is shown with less contrast. A truncated linear fit is shown as trend line (between instance 5-11), estimated over all data points, for each treatment group independently. In order to reduce overlap in the plot a slight jitter was applied to the data.

290 interest after the first visit is, hence, significantly reduced with an odds ratio of $OR = 0.17$ ($CI = [0.05, 0.57]$),
291 when paired with a experienced social partner. For experienced individuals, the negative effect of having
292 an experienced partner is less distinctly expressed, yielding $OR = 0.87$ ($CI = [0.20, 3.64]$), $p = 0.847$, not

293 significant) for TT vs. TN. In our experimental setup, we thus consistently find performance decreased for
294 individuals with experienced partners when comparing them to individuals with naive partners – an effect that
295 is significant, however, only for the learning rate of naive individuals with experience partners, where it is also
296 most pronounced.

297 **Discussion**

298 In the present study, we found that clonal Amazon mollies can be trained according to a classical operant
299 conditioning task, that they exhibited among-inter-individual differences in their learning performance, and
300 that the presence of a task-experienced social partner reduces own learning and task-solving performance,
301 especially for task-naive individuals.

302 Clonal Amazon mollies can learn in an operant conditioning paradigm within a few days and a low number
303 of repeated training sessions to associate food with a location in their laboratory environments. This is in
304 line with current research on fish cognition, which shows that fish are avid learners and have sophisticated
305 cognitive abilities [Brown et al., 2008, Kohda et al., 2019, Bshary and Triki, 2022, Bierbach et al., 2022].
306 Further, Fuss and Witte [2019] and Fuss et al. [2021] found similar learning capabilities in both parental
307 species of the Amazon molly, *P. latipinna* and *P. mexicana*, and also in the closely related guppy (*P. reticulata*).
308 It was shown that both mollies and guppies are capable of operant conditioning as well as reversal learning,
309 thus it is not surprising that we found similar cognitive capabilities in the clonal Amazon molly. Our results
310 suggest consistent individual variation in the learning curves during the solitary phase of the experiment.
311 There is substantial knowledge about consistent individual differences in behavioural traits [Réale et al.,
312 2007], including clonal animals like Amazon mollies [Schuett et al., 2011, Freund et al., 2013, Bierbach et al.,
313 2017]. However, learning as an individual trait has only recently been shown in great detail in the fruit fly *D.*
314 *melanogaster* [Smith et al., 2022]. Here, we show that this individuality in learning can also be found in a
315 naturally-occurring clonal vertebrate. Eager learning can be seen as an adaptation, allowing individuals to
316 respond to environmental changes and unforeseen circumstances. Why even genetically-identical individuals
317 differ in their learning performance may have multiple reasons, including pre-birth processes like epigenetics
318 differences, maternal effects [Kasper et al., 2017] and developmental stochasticity [Honegger and de Bivort,
319 2018], and may be due to post-birth processes like differences in previous experience [Kieffer and Colgan,
320 1992] and encountered, environment conditions [Freund et al., 2013, Akhund-Zade et al., 2019]. In the here
321 presented study all individuals were genetically identical and reared under near identical conditions. However,
322 we used individuals from different mothers and individual variability among our test subjects can thus be due

323 to a variety of these variance-inducing processes [Bierbach et al., 2017]. Further experimentation is needed in
324 order to point out which factors are the most prominent drivers of among-individual variation in the learning
325 performance of this clonal vertebrate species.

326 As shown here, the skill level and performance of a social partner indeed has a strong influence on own
327 performance but in an unexpected way. We found that naive individuals paired with trained ones exhibited
328 slowest learning, when compared to naive individuals paired with other naive ones. Trained individuals that
329 were associated with naive partners did not significantly differ from trained individuals that were paired with
330 other trained ones, although our results tend towards hindering, rather than supportive effects of observing
331 trained partners. Therefore, it seems as though being accompanied by highly skilled conspecifics did not
332 improve own learning performance, and that having a naive social partner was more beneficial during learning,
333 when being naive to the task as well. So, how can such counter-intuitive effects be explained? First, the
334 goal areas of both social partners were in mirrored locations (see Figure 2), such that the behaviour of the
335 other would not necessarily lead to the same information, visual cues and ultimate learning outcome. Trained
336 individuals have acquired experience and established a procedure of solving the task. This can manifest in
337 behaviours such as accessing the goal from a certain direction, location or at a specific time, which in turn do
338 not necessarily match those of the social partner leading to a dissonance between observed and performed
339 behaviour. For two naive individuals performing the task together this could not have such an impact, since both
340 individuals are acquiring the knowledge about the novel task at the same time, leading to more synchronous
341 experience between both individuals. Following the logic that naive social partners simultaneously learning
342 the task from initial non-proficiency show more undirected and variable behaviour, Kohn [1976] argued that
343 a continued perception of change, as would be the case when watching another naive individual trying to
344 perform a novel task, can maintain attention and act reinforcing to the observer. The experienced partner
345 would merely repeat its already learnt behaviour and result in less variation and subsequent reinforcement for
346 the naive observer. Second, our task was designed in a way that the observer did not see the demonstrator
347 actually feed. In studies that found local or stimulus enhancement effects [Brown and Laland, 2003], observers
348 could actually see demonstrators getting the benefit and we argue that a lack of seeing the direct benefit in our
349 study hampered the social learning especially from experienced demonstrators that virtually disappeared when
350 performing the task. This is underpinned by the fact that trained partners have little effect on initially reaching
351 the cylinder and food source in their naive social partners, where we only observe a smaller, non-significant
352 effect. However, the detrimental effect of having an experienced partner is clearly pronounced in the chance to
353 subsequently re-visit the region of interest in the naive individuals, where we observe a strong and significant
354 decrease in their learning rate. This indicates a more complex effect than pure spatial misguidance, due to mere

355 copying and also rules out positive effects such as stimulus enhancement [Spence, 1937] or local enhancement
356 [Thorpe, 1956] due to the trained demonstrator.

357 **Conclusion**

358 In congruence with our results, weak or absent positive effects of highly skilled partners have been found in
359 studies using full-contact designs during demonstrator-observer interaction and path learning tasks. In the
360 guppy, naive individuals were following familiar, but less skilled partners more readily through unknown
361 maze setups [Swaney et al., 2001]. Similarly, in zebrafish food income equality was enforced via social
362 information, where observers relied on visual, behavioural cues of successful demonstrators to find food
363 themselves [Roy and Bhat, 2017]. In pigeons, Biederman and Vanayan [1988] showed that naive individuals
364 observing demonstrators performing a task at chance and gradually improving, outcompeted those observing
365 well proficient demonstrators in speed of learning and overall task accuracy. Further, although near identical
366 and clonal, our tested individuals show consistent differences in their learning behaviour which is in line
367 with previous studies proposing consistent among-individual differences being common also in clonal animals
368 [Schuett et al., 2011, Bierbach et al., 2017, Freund et al., 2013] In sum, this study builds upon the well
369 established field of operant learning and conditioning, utilizing a naturally clonal fish species as model
370 organism, in which learning has not yet been studied. The here presented work adds a sleek and interpretable
371 approach to analysing both the learning efficiency, as well as the inter-individual differences in the learning
372 performance. This is done by carefully constructing a statistical model, along side the experimental design, in
373 which all components represent key aspects of interest, and biologically relevant terms such as learning rate
374 and overall exploration.

375 The here highlighted insight, that prior knowledge, or information contained within one's social partners has
376 an effect on the own performance in certain contexts has broad implications for collective behaviour and group
377 performance. It has already been shown that information differences can explain dynamics within animal
378 collectives [Ioannou et al., 2011, MacGregor et al., 2020]. Information quality [Kao et al., 2014], such as
379 uncertainty and redundancy, as well as the processes by which novel information is generated or affected
380 by the social environment most likely play a key role in the learning behaviour of gregarious individuals
381 [Hofmann et al., 2013, Rodriguez-Santiago et al., 2020]. In light of learning - a process of information uptake
382 and integration over time - the here presented results give a concise approach to shed light on the timing of
383 such events. The process of learning and timing of informational cues gives rise to a multitude of interesting
384 questions, such as how information is being distributed in a multi agent system, or fish school, in order to

385 achieve optimal exposure and learning for each of its individual members.
386 In more biological terms, what drives an individual to take on a certain role in the group, move to a specific
387 location or perform a given behaviour is still very much an open question, which yearns to be answered. As
388 shown here, the experience and prior knowledge of social partners has an effect on the learning performance
389 of individuals. Therefore, the social environment during certain experiences likely effects the ability of
390 individuals to learn and adapt to novel situations. These insights, as well as the unique modelling approach
391 shown here to address such learning processes and their timing, should pave the way for more experiments in
392 this exciting direction.

393 **Supporting Material**

394 All supplemental files, such as code for tracking and statistical analysis, as well as the data used in this study
395 can be found here: <https://github.com/XXXXXX>

- 396 1. [dataset] Author: F.Francisco, 2022, Learning Data, Data_AmazonMollyLearning.csv
- 397 2. Statistical Code, Rstats_AmazonMollyLearning.Rmd, 2022, Authors: F.Francisco, J. Lukas, A. Stöcker
- 398 3. Tracking Code, TrackingCode_AmazonMollyLearning.py, 2022, Author: F.Francisco

399 **Author Contributions**

400 FF, DB and PR derived the research question and experimental design. FF conducted the experiments. FF, JL
401 and AS conducted the statistical analysis and designed the analytical structure. FF wrote the initial draft of the
402 manuscript with input from all coauthors. All authors acknowledge no conflict of interests and have proofread
403 the final version of the manuscript and agreed on submission.

404 **Ethical Note**

405 Animal experiments were conducted under the animal experiment number #0089/21 of the German State
406 Office for Health and Social Affairs (LAGeSo). A total of N=36 fish were used over the course of this
407 experiment. All animals used for this research were kept under best possible holding conditions, in order to
408 assure healthy, natural behaviour. After the experiment, animals were released to designated holding tanks.
409 All animal facilities and maintenance protocols were kept in accordance to the LAGeSo.

⁴¹⁰ **Funding**

⁴¹¹ This work was supported by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation)

⁴¹² under Germany's Excellence Strategy – EXC 2002/1 “Science of Intelligence” (Project number 390523135).

References

- Jamilla Akhund-Zade, Sandra Ho, Chelsea O’Leary, and Benjamin de Bivort. The effect of environmental enrichment on behavioral variability depends on genotype, behavior, and type of enrichment. *Journal of Experimental Biology*, 222(19), 2019.
- Patrick Anselme and Onur Güntürkün. How foraging works: uncertainty magnifies food-seeking motivation. *Behavioral and Brain Sciences*, 42, 2019.
- GB Biederman and Marina Vanayan. Observational learning in pigeons: The function of quality of observed performance in simultaneous discrimination. *Learning and Motivation*, 19(1):31–43, 1988.
- David Bierbach, Kate L Laskowski, and Max Wolf. Behavioural individuality in clonal fish arises despite near-identical rearing conditions. *Nature communications*, 8(1):1–7, 2017.
- David Bierbach, Luis Gómez-Nava, Fritz A Francisco, Juliane Lukas, Lea Musiolek, Verena V Hafner, Tim Landgraf, Pawel Romanczuk, and Jens Krause. Live fish learn to anticipate the movement of a fish-like robot. *Bioinspiration & Biomimetics*, 2022.
- Sushil Bikhchandani, David Hirshleifer, and Ivo Welch. Learning from the behavior of others: Conformity, fads, and informational cascades. *Journal of economic perspectives*, 12(3):151–170, 1998.
- Gary Bradski. The opencv library. *Dr. Dobb’s Journal: Software Tools for the Professional Programmer*, 25(11):120–123, 2000.
- Culum Brown and Kevin N Laland. Social learning in fishes: a review. *Fish and fisheries*, 4(3):280–288, 2003.
- Culum Brown, Kevin Laland, and Jens Krause. *Fish cognition and behavior*. John Wiley & Sons, 2008.
- Culum Brown and Kevin Laland. Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, 59(3):471–493, 2001.
- Redouan Bshary and Zegni Triki. Fish ecology and cognition: insights from studies on wild and wild-caught teleost fishes. *Current Opinion in Behavioral Sciences*, 46:101174, 2022.
- Aaron C Courville, Nathaniel D Daw, and David S Touretzky. Bayesian theories of conditioning in a changing world. *Trends in cognitive sciences*, 10(7):294–300, 2006.

- Sasha RX Dall, Luc-Alain Giraldeau, Ola Olsson, John M McNamara, and David W Stephens. Information and its use by animals in evolutionary ecology. *Trends in ecology & evolution*, 20(4):187–193, 2005.
- Carolina Doran, David Bierbach, and Kate L Laskowski. Familiarity increases aggressiveness among clonal fish. *Animal Behaviour*, 148:153–159, 2019.
- Jonathan P Evans, Andrea Pilastro, and Ingo Schlupp. *Ecology and evolution of poeciliid fishes*. University of Chicago Press, 2011.
- Julia Freund, Andreas M Brandmaier, Lars Lewejohann, Imke Kirste, Mareike Kritzler, Antonio Krüger, Norbert Sachser, Ulman Lindenberger, and Gerd Kempermann. Emergence of individuality in genetically identical mice. *Science*, 340(6133):756–759, 2013.
- Theodora Fuss and Klaudia Witte. Sex differences in color discrimination and serial reversal learning in mollies and guppies. *Current zoology*, 65(3):323–332, 2019.
- Theodora Fuss, Simone Flöck, and Klaudia Witte. Sex-specific cognitive flexibility in atlantic mollies when learning from male demonstrators exploring a new food source. *Animal Behaviour*, 173:9–19, 2021.
- Bennett G Galef and Kevin N Laland. Social learning in animals: empirical studies and theoretical models. *Bioscience*, 55(6):489–499, 2005.
- Lizzy A Gartland, Josh A Firth, Kate L Laskowski, Raphael Jeanson, and Christos C Ioannou. Sociability as a personality trait in animals: methods, causes and consequences. *Biological Reviews*, 2021.
- Luc-Alain Giraldeau and Thomas Caraco. *Social foraging theory*, volume 73. Princeton University Press, 2018.
- Luc-Alain Giraldeau, Thomas J Valone, and Jennifer J Templeton. Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 357(1427):1559–1566, 2002.
- Roy Harpaz and Elad Schneidman. Social interactions drive efficient foraging and income equality in groups of fish. *Elife*, 9:e56196, 2020.
- Volker Hofmann, Juan I Sanguinetti-Scheck, Silke Künzel, Bart Geurten, Leonel Gómez-Sena, and Jacob Engelmann. Sensory flow shaped by active sensing: sensorimotor strategies in electric fish. *Journal of Experimental Biology*, 216(13):2487–2500, 2013.

- Kyle Honegger and Benjamin de Bivort. Stochasticity, individuality and behavior. *Current Biology*, 28(1): R8–R12, 2018.
- Carl L Hubbs and Laura C Hubbs. Apparent parthenogenesis in nature, in a form of fish of hybrid origin. *Science*, 76(1983):628–630, 1932.
- Christos C Ioannou, Iain D Couzin, Richard James, Darren P Croft, and Jens Krause. Social organisation and information transfer in schooling fish. *Fish cognition and behavior*, 2:217–239, 2011.
- Albert B Kao, Noam Miller, Colin Torney, Andrew Hartnett, and Iain D Couzin. Collective learning and optimal consensus decisions in social animal groups. *PLoS Comput Biol*, 10(8):e1003762, 2014.
- Claudia Kasper, Mathias Kölliker, Erik Postma, and Barbara Taborsky. Consistent cooperation in a cichlid fish is caused by maternal and developmental effects rather than heritable genetic variation. *Proceedings of the Royal Society B: Biological Sciences*, 284(1858):20170369, 2017.
- Rachel L Kendal, Isabelle Coolen, Yfke van Bergen, and Kevin N Laland. Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, 35:333–379, 2005.
- James D Kieffer and Patrick W Colgan. The role of learning in fish behaviour. *Reviews in Fish Biology and Fisheries*, 2(2):125–143, 1992.
- Masanori Kohda, Takashi Hotta, Tomohiro Takeyama, Satoshi Awata, Hirokazu Tanaka, Jun-ya Asai, and Alex L Jordan. If a fish can pass the mark test, what are the implications for consciousness and self-awareness testing in animals? *PLoS biology*, 17(2):e3000021, 2019.
- Bruno Kohn. Observation and discrimination learning in the rat: Effects of stimulus substitution. *Learning and Motivation*, 7(2):303–312, 1976.
- Jens Krause and Graeme D Ruxton. *Living in groups*. Oxford University Press, 2002.
- Ralf HJM Kurvers, J Drägestein, F Hölker, A Jechow, J Krause, and D Bierbach. Artificial light at night affects emergence from a refuge and space use in guppies. *Scientific reports*, 8(1):1–10, 2018.
- Kevin N Laland, Nicola Atton, and Michael M Webster. From fish to fashion: experimental and theoretical insights into the evolution of culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567):958–968, 2011.
- KP Lampert and M Scharfl. The origin and evolution of a unisexual hybrid: *Poecilia formosa*. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1505):2901–2909, 2008.

- Kate L Laskowski, Carolina Doran, David Bierbach, Jens Krause, and Max Wolf. Naturally clonal vertebrates are an untapped resource in ecology and evolution research. *Nature ecology & evolution*, 3(2):161–169, 2019.
- Kate L Laskowski, Frank Seebacher, Marie Habedank, Johannes Meka, and David Bierbach. Two locomotor traits show different patterns of developmental plasticity between closely related clonal and sexual fish. *Frontiers in physiology*, 12, 2021.
- Hannah EA MacGregor, James E Herbert-Read, and Christos C Ioannou. Information can explain the dynamics of group order in animal collective behaviour. *Nature communications*, 11(1):1–8, 2020.
- Amber M Makowicz, David Bierbach, Christian Richardson, and Kimberly A Hughes. Cascading indirect genetic effects in a clonal vertebrate. *Proceedings of the Royal Society B*, 289(1978):20220731, 2022.
- Shinichi Nakagawa, Paul CD Johnson, and Holger Schielzeth. The coefficient of determination r^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, 14(134):20170213, 2017.
- CJ Nicol. The social transmission of information and behaviour. *Applied Animal Behaviour Science*, 44(2-4):79–98, 1995.
- Alejandra Morales Picard, Lauren Hogan, Megan L Lambert, Anna Wilkinson, Amanda M Seed, and Katie E Slocombe. Diffusion of novel foraging behaviour in amazon parrots through social learning. *Animal cognition*, 20(2):285–298, 2017.
- Thomas W Pike, Jeremy R Kendal, Luke E Rendell, and Kevin N Laland. Learning by proportional observation in a species of fish. *Behavioral Ecology*, 21(3):570–575, 2010.
- Martin Plath and David Bierbach. Sex and the public: social eavesdropping, sperm competition risk, and male mate choice. *Communicative & integrative biology*, 4(3):276–280, 2011.
- Martin Plath, Dennis Blum, Ingo Schlupp, and Ralph Tiedemann. Audience effect alters mating preferences in a livebearing fish, the atlantic molly, *poecilia mexicana*. *Animal Behaviour*, 75(1):21–29, 2008.
- Simon M Reader, Jeremy R Kendal, and Kevin N Laland. Social learning of foraging sites and escape routes in wild trinidadian guppies. *Animal Behaviour*, 66(4):729–739, 2003.
- Denis Réale, Simon M Reader, Daniel Sol, Peter T McDougall, and Niels J Dingemanse. Integrating animal temperament within ecology and evolution. *Biological reviews*, 82(2):291–318, 2007.

- Mike JF Robinson, Patrick Anselme, Adam M Fischer, and Kent C Berridge. Initial uncertainty in pavlovian reward prediction persistently elevates incentive salience and extends sign-tracking to normally unattractive cues. *Behavioural brain research*, 266:119–130, 2014.
- Mariana Rodriguez-Santiago, Paul Nührenberg, James Derry, Oliver Deussen, Fritz A Francisco, Linda K Garrison, Sylvia F Garza, Hans A Hofmann, and Alex Jordan. Behavioral traits that define social dominance are the same that reduce social influence in a consensus task. *Proceedings of the National Academy of Sciences*, 117(31):18566–18573, 2020.
- Tamal Roy and Anuradha Bhat. Social learning in a maze? contrasting individual performance among wild zebrafish when associated with trained and naïve conspecifics. *Behavioural processes*, 144:51–57, 2017.
- M Scharl. Incorporation of subgenomic amounts of host species dna in the gynogenetic amazon molly. *Nature*, 373:68–71, 1995.
- Manfred Scharl, Brigitta Wilde, Ingo Schlupp, and Jakob Parzefall. Evolutionary origin of a parthenoform, the amazon molly poecilia formosa, on the basis of a molecular genealogy. *Evolution*, 49(5):827–835, 1995.
- Wiebke Schuett, Sasha RX Dall, Jana Baeumer, Michaela H Kloesener, Shinichi Nakagawa, Felix Beinlich, and Till Eggers. Personality variation in a clonal insect: the pea aphid, acyrthosiphon pisum. *Developmental psychobiology*, 53(6):631–640, 2011.
- RJ Schultz. Origin and synthesis of a unisexual fish. In *Genetics and Mutagenesis of Fish*, pages 207–211. Springer, 1973.
- Matthew A-Y Smith, Kyle S Honegger, Glenn Turner, and Benjamin de Bivort. Idiosyncratic learning performance in flies. *Biology Letters*, 18(2):20210424, 2022.
- Kenneth W Spence. Experimental studies of learning and the higher mental processes in infra-human primates. *Psychological Bulletin*, 34(10):806, 1937.
- Matthias Stoeck, Kathrin P Lampert, Dirk Möller, Ingo Schlupp, and Manfred Scharl. Monophyletic origin of multiple clonal lineages in an asexual fish (poecilia formosa). *Molecular Ecology*, 19(23):5204–5215, 2010.
- Daniel O Stram and Jae Won Lee. Variance components testing in the longitudinal mixed effects model. *Biometrics*, pages 1171–1177, 1994.

Ariana Strandburg-Peshkin, Colin R Twomey, Nikolai WF Bode, Albert B Kao, Yael Katz, Christos C Ioannou, Sara B Rosenthal, Colin J Torney, Hai Shan Wu, Simon A Levin, et al. Visual sensory networks and effective information transfer in animal groups. *Current Biology*, 23(17):R709–R711, 2013.

Will Swaney, Jeremy Kendal, Hannah Capon, Culum Brown, and Kevin N Laland. Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, 62(3):591–598, 2001.

William Homan Thorpe. Learning and instinct in animals. 1956.

Wataru Toyokawa, Andrew Whalen, and Kevin N Laland. Social learning strategies regulate the wisdom and madness of interactive crowds. *Nature Human Behaviour*, 3(2):183–193, 2019.

Wesley C Warren, Raquel García-Pérez, Sen Xu, Kathrin P Lampert, Domitille Chalopin, Matthias Stöck, Laurence Loewe, Yuan Lu, Lukas Kuderna, Patrick Minx, et al. Clonal polymorphism and high heterozygosity in the celibate genome of the amazon molly. *Nature ecology & evolution*, 2(4):669–679, 2018.

MM Webster and KN Laland. Social learning strategies and predation risk: minnows copy only when using private information would be costly. *Proceedings of the Royal Society B: Biological Sciences*, 275(1653):2869–2876, 2008.

M.M. Webster and K.N. Laland. Social information, conformity and the opportunity costs paid by foraging fish. *Behavioral Ecology and Sociobiology*, 66(5):797–809, 2012. doi: 10.1007/s00265-012-1328-1.

R Haven Wiley. Errors, exaggeration, and deception in. *Behavioral mechanisms in evolutionary ecology*, page 157, 1994.

Joshua Zonca, Anna Folsø, and Alessandra Sciutti. Dynamic modulation of social influence by indirect reciprocity. *Scientific reports*, 11(1):1–14, 2021.

Klaus Zuberbühler. Audience effects. *Current Biology*, 18(5):R189–R190, 2008.