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2 **Abstract concept learning in fish**

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6 **Abstract**

7 Abstract concept formation allows animals to group stimuli based on relationships (e.g.
8 sameness/difference) rather than stimulus-specific qualities. Studies in this field have focused
9 on primates and birds, but there is growing interest in the capabilities of a wider range of
10 species to gain an understanding of differences in cognitive abilities across taxa and ecological
11 requirements. This review concentrates on abstract concept learning in fish. There have been
12 only a few studies testing this group and these have resulted in no direct evidence of abstract
13 concept learning. Further experiments following rigorous methodologies are required to
14 determine whether all fish species are truly incapable, or whether the right learning conditions
15 have not yet been met for the appropriate species.

16 **Keywords** animal behavior, vertebrate, relational concepts, abstract reasoning,
17 same/different, oddity, matching

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19 Introduction

20 Animals must constantly classify incoming sensory information and use it to decide what
21 actions to take. Abstract concepts allow animals to identify relationships between novel and
22 previously learned situations or objects, and respond based on past experience [1]. Examples
23 of abstract relationships are same/different, oddity, and less/greater than [1, 2]. Historically,
24 abstract concept learning has been associated with animals with more neural complexity [3],
25 such as primates, and has been considered a sign of intelligence. However, over the last
26 several decades, this assumption has been challenged by mounting evidence that non-
27 primate animals are capable of conceptual learning [1, 3, 4]. After all, many of the problems
28 that primates must solve, and which abstract concept learning might facilitate, are not unique
29 to this group.

30 Excluding one older study, testing the ability of fishes to learn abstract relationships has only
31 begun in the last seven years. To the uninitiated, fishes might seem like an unlikely candidate
32 for concept learning; they are often thought to have short memories and be guided primarily
33 by instinct. However, these assumptions are both untrue and unfair to this large group which
34 displays an impressive range of ecological and biological diversity. Some species of fish not
35 only demonstrate long term memory [5, 6], but there is increasing evidence of advanced
36 behaviors including cooperation [e.g. 7, 8], numeracy [e.g. 9, 10-14], and tool use [e.g. 15, 16-
37 18]. Determining whether fishes are capable of abstract concept learning is of value for several
38 reasons. 1. It will improve our understanding of the decision rules that guide their natural
39 behaviors. 2. Fishes have very different brain anatomy to mammals and comparisons between
40 their behavioral repertoires can inform how brain anatomy influences behavioral complexity.
41 3. The ecological diversity of fishes presents an opportunity to form hypotheses about how
42 ecology and environment can lead to the development of complex behavior, particularly if it is
43 found that some species of fish are capable of a task while others are not. 4. Finally, evidence
44 or lack thereof, of abstract concept learning in fish will improve our understanding of how and
45 when this behaviour evolved in animals. This review will provide a brief explanation of the

psychophysical tests used to test abstract concept learning in fishes (**Fig. 1**), summarise what is currently known about fish capabilities, and discuss some considerations when developing future tests.

Testing for abstract concept learning

Although there are a range of experimental protocols that have been used, concept learning tests generally begin with a conditioning phase, in which subjects are presented with exemplars of the task. The number of unique stimuli chosen for the experiment dictates the number of possible exemplar combinations and there has been considerable discussion about the role this number plays in learning [2]. Training with exemplars is continued until subjects reach a training criterion, typically a minimum level of accuracy. Crucially, to demonstrate true abstract learning, the learned rule must be applicable to novel stimuli. A transfer test is used to measure whether the level of performance remains consistent despite new stimuli being used. For every trial run, an entirely new stimulus should be used. In some cases, experiments are designed in which the same group of stimuli are repeatedly presented during testing. In this case, it is important to note that there is the possibility that fish can learn the task throughout testing if they are rewarded, particularly if only a small number of stimuli are used. Omitting reinforcement during testing trials ~~and trials should not have reinforcement in order~~ will ~~to~~ preclude learning. Many early studies that ostensibly demonstrated abstract concept learning in non-primates, were later deemed inconclusive because their testing procedures did not follow these guidelines and allowed for alternative explanations of the observed behaviour [1, 3].

Current evidence of abstract concept learning in fishes

Goldfish

Thus far, there have only been a handful of experiments explicitly testing whether fish are capable of forming abstract concepts. The first experiments simply sought to train goldfish

(*Carassius auratus*) to perform a simultaneous matched-to-sample (MTS)/non-MTS test [19] (**Fig. 1a**). The aim was to test if fish could learn the procedure not the underlying concept, so a crucial transfer test was not done. Goldfish successfully performed the task.

Goldfish were used again in the first study to formally test abstract concept learning. An MTS/nMTS test with coloured lights as stimuli (**Fig. 2**) was employed, but only two colours were used during training (either red/green or blue/yellow) and shocks were given as ~~negative~~ positive punishmentreinforcement [20]. In transfer tests in which two novel coloured stimuli were repeatedly presented, fish continued to perform above chance, but their performance was lower than a control group that continued with training stimuli. It is important to note that ~~negative reinforcement~~positive punishment was used in transfer trials. While the authors state that the results demonstrate learning at a conceptual level, they do not discuss the possibility that subjects could have learned the task during transfer, particularly as each data point represents 90 trials, run over three days, with only two stimuli options and ~~negative positive~~ punishmentreinforcement. For many species of fish, the first 90 trials would provide ample opportunity to learn two stimulus specific associations.

Archerfish

Of all the fish species tested for abstract reasoning, archerfish (*Toxotes chatareus*) have had the largest variety of test types, training procedures, and training exemplars. Attempts to teach archerfish the concepts of matching and oddity, using the delayed (**Fig. 1b**) and simultaneous MTS/nMTS, and odd-one-out (OOO) (**Fig. 1c**) tests respectively, were unsuccessful [21]. A series of line drawings, discriminable by archerfish [21, 22], were used as stimuli (**Fig. 2**). Interestingly, when presented with the MTS/nMTS task, archerfish performance differed from that of goldfish as none of the archerfish could pass the initial training stage, and therefore no transfer tests were conducted. Instead, archerfish developed selection preferences for particular stimuli. A same/different test (**Fig. 1d**) was then tried using six different stimuli [23]. One subject learned the training procedure and proceeded to a transfer stage with six novel stimuli, but accuracy dropped to a rate consistent with chance. The fish was unable to learn a

subsequent training task with 60 images, suggesting that the individual likely solved the first task using a series of image specific rules.

Malawi cichlids and bamboo sharks

Using positive reinforcement, Malawi cichlids (*Pseudotropheus Sp.*) can discriminate drawings [e.g. 24, 25-27] and appear to form categorisation concepts [24]. An attempt was made to train cichlids to perform an MTS task using two stimuli (**Fig. 2**), but all six subjects were unable to learn the task after 40 sessions and no transfer tests were run [25].

Malawi cichlids (*Pseudotropheus zebra*) and juvenile bamboo sharks (*Chiloscyllium griseum*) were presented with a two-alternative forced-choice task (2AFC), in which stimuli were two image pairs with differing spatial arrangements (**Fig. 2**) [28]. During training, both alternatives had identical symbols that made different pairs, and the vertically stacked pair was always rewarded. A variety of transfer tests were then run in which different combinations of patterns and/or spatial arrangements were used (see **Fig. 2** for a non-exhaustive selection). When both species were presented with two alternatives with identical spatial arrangement, but where one option had identical patterns and the other did not, none of the cichlids preferentially selected the expected stimulus, but the bamboo sharks did. The authors expected subjects to select the pair with two different patterns as this is most similar to the training condition, and the fact that the cichlids did not led to the conclusion that cichlids did not spontaneously identify the similarity, but the bamboo sharks had. However, this experimental procedure is not a true same/different task and cannot be used to test for abstract concept learning. One problem is that the training stage is a 2AFC task and is unlikely to reinforce 'same' or 'different' relationships between stimuli; discriminating spatial arrangement is adequate to solve the problem. In addition, fish could have learned individual stimulus patterns, but there was no actual incentive to do so. Therefore, it is not surprising that cichlids did not preferentially select transfer stimuli with two different patterns. Alternatively, selection of non-matching stimuli by sharks could be based on feature-specific rules. One possibility is that sharks selected or avoided stimuli that had features in common with training stimuli, such as stripes and circles

which were on both training and transfer stimuli. These examples are only one possibility, but they show that other explanation for the observed behavior are possible.

Experimental considerations for future research

For some species such as pigeons, it has taken decades of research to find suitable protocols to test abstract concept learning, and to prove conclusively that subjects are capable of this form of learning [1]. Although not all tests can be adapted for fish, experiments from other species provide a framework of rigorous experimental methods that can be applied to future experiments with fishes. For example, Katz and Wright [29] proposed a same/different task, with a staged increase in training exemplars which has been successful with birds and primates [2, 30-32]. This could be used to determine if concept learning in fish is a function of exemplar number and would allow for comparisons with other species. However, this test potentially requires a large number of unique stimuli and extensive training. Pigeons required 128 unique images and thousands of trials [31], while two other bird species only required eight images [32-34].

Thus far, most experiments with fish have used abstract symbols as stimuli. These may still be a suitable option, but more detail-rich images (e.g. photographs) are an alternative that have been used with other species [e.g. 29, 33, 35, 36]. Photographs have a wider variety of discriminatory cues and images could be selected that are relevant to the species (e.g. prey, conspecifics), potentially increasing motivation to interact with them. However, care should be taken when choosing images as some image subjects or characteristics may cause unpredictable reaction by fish, particularly if there is a response bias to the signal [e.g. 37, 38].

Fish experiments typically involve hundreds of trials, not thousands, before subjects lose interest or get satiated, and cease participating. Newport, Wallis and Siebeck [23] observed that after relatively few trials (~200), archerfish appeared to stop trying new problem solving methods when the task was difficult and instead settled on a strategy that resulted in ~80% of possible food rewards. One solution to this problem is to select a model species whose general

ecology is likely to engender a high level of responsiveness to the task [39]. For example, ducklings were successfully trained on a same/different task using their natural imprinting behavior as motivation [40], and Clark's nutcrackers' were chosen as a model because their natural caching behavior may predispose them to relational processing [32, 33]. An equivalent species has not yet been found amongst fishes, although it was hoped that the ballistic hunting strategy of archerfish would be indicative of higher order learning [21, 23, 41]. It has been hypothesised that complex social structures can drive the development of advanced cognitive function, therefore fish species that display social behavior may be more likely to learn concepts than others [42, 43]. While there are many species that meet this condition, some candidates that have already been used in psychophysical tests are bluestreak cleaner wrasse (*Labroides dimidiatus*) which demonstrates mutualism and whose cognitive abilities have been previously investigated [e.g. 44, 45-47], and the nine-spined sticklebacks (*Pungitius pungitius*) that demonstrate social learning [48].

Finally, the choice of observing response may influence the degree of attention that fish pay to the stimuli and/or the learning of individual stimuli elements, thereby increasing their likelihood of learning the relational task [36, 49]. In both rhesus macaques and pigeons, changing how subjects interacted with stimuli affected whether relational, or some other rule type was learned. For example, when macaques were presented with a same/different task and had to first touch a sample stimulus before being presented comparison stimuli, they were more likely to learn a relational rule, and learn it faster, than those that didn't [36]. Similarly, in a MTS task, pigeons that had to peck at the sample ten or more times learned a concept based rule. However, those that had to peck once at the sample, or not at all, learned the configural pattern of stimuli instead [49]. Having subjects interact with the sample stimulus may improve relational learning by helping subjects consider stimuli as individual elements rather than as one single image [49]. Experiments with fish have yet to require this additional step. One consideration when implementing this with fish is the reward schedule used to train subjects to make multiple selection within a trial. While some species will readily make multiple

179 selections in expectation of a delayed reward, others are less willing. Decreased motivation
180 could be avoided by providing a reward for both the initial sample selection and the
181 comparison choice, but this may reduce the number of trials that can be run before subjects
182 are satiated. Another option to direct the attention of subjects is to increase the effort required
183 to make a stimulus selection. In experiments with fish, individuals have been presented with
184 two choices and have had to move into a particular response area (goldfish [20], Malawi
185 cichlids [25, 28]), press stimuli with their mouth/nose (goldfish [19], bamboo sharks [28]), or
186 shoot a jet of water at stimuli (archerfish [21, 23]) to make a selection. Observing responses
187 that require high effort are not common in fish, but there are some examples that have resulted
188 in successful stimuli discrimination. For example, damselfish have been trained to peck at
189 stimuli multiple times to indicate their selection [50], and triggerfish have had to flip over
190 weighted bottle caps [37]. There has been no research to date focused on the effect of different
191 observing responses in fish learning that I am aware of, and it is likely that effortful response
192 options will be highly species specific. Tasks in which physical contact is made with stimuli,
193 such as biting stimuli, or pushing open doors with stimuli on them, may increase attention and
194 be achievable for a range of fish species.

195 **Conclusions**

196 Understanding the ability of fish to perform abstract concept learning is still in its infancy and
197 we cannot conclude whether fish learn these relationships based on current data. The results
198 of goldfish and sharks are inconclusive, and efforts to elicit this behavior with archerfish and
199 cichlids have been unsuccessful so far. It is important to note that very few subjects have even
200 been able to learn the basic testing procedure. To date, only ~0.01% of the 30,000 species of
201 fishes from across a huge range of environments and life histories [51] have undergone any
202 testing for abstract concept learning. It is clear that more species must be tested. There is also
203 a need to rigorously test a range of learning procedures to identify methods that are suitable
204 for fishes.

There are many examples of fishes performing behaviours that appear to rely on abstract relationships, making it somewhat surprising if this group is eventually found to be incapable of forming abstract concepts. For example, the targeting of rare prey in a group by predatory fish [e.g. 52, 53, 54] implies that they can identify oddity. However, many seemingly complex behaviours, including human word learning, may actually rely on 'simpler' associative learning principles [55]. Collaborative behaviour in fish is a relatively new discovery that suggests a high degree of cognitive complexity, but the decision rules that guide this behaviour in yellow saddle goatfish (*Parupeneus cyclostomus*) appear to be associative-based – choices about hunting initiation and movement trajectories were dependent on proximity to prey and collaborators [56]. A recent experiment with bees (*Apis mellifera*) retested a spatial concept learning task (i.e. above/below) that was previously used as evidence of their ability to form abstract concepts [57]. It was found that, similarly to most experiments with fish, not all individuals could pass the training stage. Those that did, solved the task by exploring the lowest presented stimuli and evaluating whether or not it was a learned reference point, and not based on a relationship between stimuli [58]. The degree of behavioural complexity that can be based on associative rules should not be underestimated, and it remains possible that some or all species of fishes will not ever learn abstract concepts even with extensive learning opportunities.

Most experiments on abstract concept learning in fishes have produced negative results. The lack of an observed behavior cannot be used as evidence that subjects are incapable of learning the task as the learning conditions may not yet have been met or experiments were not run for long enough. However, negative results are still informative and indicate which experimental methods are not practicable. In addition, accumulating negative results despite variations in procedures suggests that a particular species may be unlikely to learn at all. Therefore, if we are to build a picture of abstract concept learning for fishes, it is important to publish experiments in which fish do not learn. Determining whether some species are capable

while others are not is particularly interesting when considered in the context of the evolution of behavior, and may provide insights into why and how this behavior evolved.

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Conflict of interest statement

Nothing declared.

Figure captions

Figure 1. Illustration of stimuli presentation procedures used in experiments with fish: **(a)** odd one out (OOO), **(b)** delayed matched-to-sample (MTS), **(c)** simultaneous MTS, **(d)** Same/different. The red box indicates the correct response.

Figure 2. Summary of abstract concept learning experiments with fishes. Stimuli are adapted from Refs. [20, 21, 23, 25, 28] and not drawn to scale. In all experiments, stimuli can appear as both the rewarded target and the unrewarded distractor, except in the experiment by [28] in which only one stimulus pair is rewarded (indicated by *). For this experiment, only a selection of transfer stimuli have been illustrated.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

* of special interest

** of outstanding interest

**[2] This recent review is focused on same/different learning in animals and includes details on the theoretical background to this test, and differences in the performance of species tested thus far.

*[4] This book chapter contains a section on the topic of concept learning in animals. It includes a clear explanation of different concept types and a brief discussion of the use of other sensory modalities when designing concept learning tests for different species.

*[28] Abstract concept learning was not directly tested in this study but spontaneous application of the concept of same/different could be one explanation for the decisions of bamboo sharks in a two-alternative forced-choice task with novel stimuli.

*[41] This is a comprehensive review of the visual and cognitive challenges associated with the unique hunting strategy of archerfish.

**[58] This study with bees aims to determine their underlying decision strategy when solving a supposed concept-based task (above/below). They found that bees were not learning a relational concept but were instead inspecting the lowest presented shape to determine whether or not it was a learned reference shape.

References

275

276 [1] Castro L, Wasserman EA, Relational concept learning in birds, in: C. ten Cate, S.D. Healy
277 (Eds.), Avian Cognition, Cambridge University Press, Cambridge, 2017.

278 [2] Wright AA, Katz JS, Kelly DM, Same/Different Learning, in: J. Vonk, T. Shackelford (Eds.),
279 Encyclopedia of Animal Cognition and Behavior, Springer International Publishing, Cham,
280 2018, pp. 1-11.

281 [3] Wasserman E, Castro L, Fagot J, Relational thinking in animals and humans: From
282 percepts to concepts, APA handbook of comparative psychology: Perception, learning, and
283 cognition, Vol. 2, American Psychological Association, Washington, DC, US, 2017, pp. 359-
284 384.

285 [4] Krichbaum S, Davila A, Lazarowski L, Katz JS, Animal Cognition, Oxford University Press,
286 Oxford, 2020, pp. 1-21.

287 [5] Brown C, **Fish intelligence, sentience and ethics**, Anim Cogn 18(1) (2015) 1-17.

288 [6] Triki Z, Bshary R, **Long-term memory retention in a wild fish species *Labroides***
289 ***dimidiatus* eleven months after an aversive event**, Ethology 126(3) (2020) 372-376.

290 [7] Vail AL, Manica A, Bshary R, **Referential gestures in fish collaborative hunting**, Nat
291 Commun 4 (2013) 1765.

292 [8] Bshary R, Hohner A, Ait-el-Djoudi K, Fricke H, **Interspecific Communicative and**
293 **Coordinated Hunting between Groupers and Giant Moray Eels in the Red Sea**, PLoS Biol
294 4(12) (2006) e431.

295 [9] Triki Z, Bshary R, **Cleaner fish *Labroides dimidiatus* discriminate numbers but fail a**
 296 **mental number line test**, Anim Cogn 21(1) (2018) 99-107.

297 [10] Agrillo C, Dadda M, Serena G, Bisazza A, **Use of Number by Fish**, PLoS ONE 4(3)
 298 (2009) e4786.

299 [11] Dadda M, Piffer L, Agrillo C, Bisazza A, **Spontaneous number representation in**
 300 **mosquitofish**, Cognition 112(2) (2009) 343-348.

301 [12] Bisazza A, Agrillo C, Lucon-Xiccato T, **Extensive training extends numerical abilities**
 302 **of guppies**, Anim Cogn (2014) 1-7.

303 [13] Agrillo C, Bisazza A, **Spontaneous versus trained numerical abilities. A comparison**
 304 **between the two main tools to study numerical competence in non-human animals**, J
 305 Neuroscie Methods 234(0) (2014) 82-91.

306 [14] Karoubi N, Leibovich T, Segev R, **Symbol-value association and discrimination in the**
 307 **archerfish**, PLoS ONE 12(4) (2017) e0174044.

308 [15] Brown C, **Tool use in fishes**, Fish Fish 13(1) (2012) 105-115.

309 [16] Millot S, Nilsson J, Fosseidengen JE, Bégout M-L, Fernö A, Braithwaite VA, Kristiansen
 310 TS, **Innovative behaviour in fish: Atlantic cod can learn to use an external tag to**
 311 **manipulate a self-feeder**, Anim Cogn 17(3) (2014) 779-785.

312 [17] Dunn RP, **Tool use by a temperate wrasse, California sheephead *Semicossyphus***
 313 **pulcher**, J Fish Biol 88(2) (2016) 805-810.

314 [18] Pryor KJ, Milton AM, **Tool use by the graphic tuskfish *Choerodon graphicus***, J Fish
 315 Biol 95(2) (2019) 663-667.

- 316 [19] Goldman M, Shapiro S, **Matching-to-sample and oddity-from-sample in goldfish**, J
317 Exp Anal Behav 31 (1979) 259-266.
- 318 [20] Zerbolio DJ, Royalty J, **Matching and oddity conditional discrimination in the goldfish**
319 **as avoidance responses: Evidence for conceptual avoidance learning**, Anim Learn
320 Behav 11(3) (1983) 341-348.
- 321 [21] Newport C, Wallis G, Siebeck UE, **Concept learning and the use of three common**
322 **psychophysical paradigms in the archerfish (*Toxotes chatareus*)**, Front Neuro 8 (2014)
323 1-13.
- 324 [22] Newport C, Wallis G, Temple SE, Siebeck UE, **Complex, context-dependent decision**
325 **strategies of archerfish, *Toxotes chatareus***, Anim Behav 86(6) (2013) 1265-1274.
- 326 [23] Newport C, Wallis G, Siebeck UE, **Same/different abstract concept learning by**
327 **archerfish (*Toxotes chatareus*)**, PLoS ONE 10(11) (2015) e0143401.
- 328 [24] Schluessel V, Fricke G, Bleckmann H, **Visual discrimination and object categorization**
329 **in the cichlid *Pseudotropheus* sp**, Anim Cogn (2012) 1-13.
- 330 [25] Gierszewski S, Bleckmann H, Schluessel V, **Cognitive abilities in Malawi cichlids**
331 **(*Pseudotropheus* sp.): Matching-to-sample and image/mirror-image discriminations**,
332 PLoS ONE 8(2) (2013) e57363.
- 333 [26] Schluessel V, Kraniotakes H, Bleckmann H, **Visual discrimination of rotated 3D**
334 **objects in Malawi cichlids (*Pseudotropheus* sp.): a first indication for form constancy**
335 **in fishes**, Anim Cogn 17(2) (2014) 359-371.

336 [27] Schluessel V, Beil O, Weber T, Bleckmann H, **Symmetry perception in bamboo sharks**
337 **(*Chiloscyllium griseum*) and Malawi cichlids (*Pseudotropheus sp.*)**, Anim Cogn (2014)
338 1-19.

339 [28] Fuss T, John L, Schluessel V, **Same or different? Abstract relational concept use in**
340 **juvenile bamboo sharks and Malawi cichlids**, Curr Zool (2018).

341 [29] Katz JS, Wright AA, **Same/different abstract-concept learning by pigeons**, J Exp
342 Psychol Anim Behav Process 32(1) (2006) 80-86.

343 [30] Bodily KD, Katz JS, Wright AA, **Matching-to-sample abstract-concept learning by**
344 **pigeons**, J Exp Psychol Anim Behav Process 34(1) (2008) 178-184.

345 [31] Wright AA, Katz JS, **Mechanisms of same/different concept learning in primates and**
346 **avians**, Behav Process 72(3) (2006) 234-254.

347 [32] Magnotti JF, Katz JS, Wright AA, Kelly DM, **Superior abstract-concept learning by**
348 **Clark's nutcrackers (*Nucifraga columbiana*)**, Biol Lett 11(5) (2015) 20150148.

349 [33] Wright AA, Magnotti JF, Katz JS, Leonard K, Kelly DM, **Concept learning set-size**
350 **functions for Clark's nutcrackers**, J Exp Anal Behav 105(1) (2016) 76-84.

351 [34] Magnotti JF, Wright AA, Leonard K, Katz JS, Kelly DM, **Abstract-concept learning in**
352 **Black-billed magpies (*Pica hudsonia*)**, Psychon Bull Rev 24(2) (2017) 431-435.

353 [35] Cook RG, Kelly DM, Katz JS, **Successive two-item same-different discrimination and**
354 **concept learning by pigeons**, Behav Process 62(1-3) (2003) 125-144.

355 [36] Katz JS, Wright AA, Bachevalier J, **Mechanisms of same/different abstract-concept**
356 **learning by rhesus monkeys (*Macaca mulatta*)**, J Exp Psychol Anim Behav Process 28(4)
357 (2002) 358-68.

358 [37] Cheney KL, Newport C, McClure EC, Marshall NJ, **Colour vision and response bias in**
359 **a coral reef fish**, J Exp Biol 216(15) (2013) 2967-2973.

360 [38] Lucon-Xiccato T, Manabe K, Bisazza A, **Guppies learn faster to discriminate between**
361 **red and yellow than between two shapes**, Ethology 125(2) (2019) 82-91.

362 [39] Wright AA, Kelly DM, **Comparative approaches to same/different abstract-concept**
363 **learning**, Learn Behav 45(4) (2017) 323-324.

364 [40] Martinho A, Kacelnik A, **Ducklings imprint on the relational concept of “same or**
365 **different”**, Science 353(6296) (2016) 286-288.

366 [41] Newport C, Schuster S, **Archerfish vision: visual challenges faced by a predator with**
367 **a unique hunting technique**, Semin Cell Dev Biol In Press (2020).

368 [42] Bshary R, Brown C, **Fish cognition**, Curr Biol 24(19) (2014) R947-R950.

369 [43] Dunbar RIM, **The social brain hypothesis**, Evol Anthropol: Issues, News and Reviews
370 6(5) (1998) 178-190.

371 [44] Bshary R, Wickler W, Fricke H, **Fish cognition: a primate's eye view**, Anim Cogn 5(1)
372 (2002) 1-13.

373 [45] Bshary R, Grutter AS, **Punishment and partner switching cause cooperative**
374 **behaviour in a cleaning mutualism**, Biol Lett 1(4) (2005) 396-399.

- 375 [46] Salwiczek LH, Prétôt L, Demarta L, Proctor D, Essler J, Pinto AI, Wismer S, Stoinski T,
376 Brosnan SF, Bshary R, **Adult cleaner wrasse outperform capuchin monkeys,**
377 **chimpanzees and orang-utans in a complex foraging task derived from cleaner–client**
378 **reef fish cooperation**, PLoS ONE 7(11) (2012) e49068.
- 379 [47] Gingins S, Werminghausen J, Johnstone RA, Grutter AS, Bshary R, **Power and**
380 **temptation cause shifts between exploitation and cooperation in a cleaner wrasse**
381 **mutualism**, Proc R Soc B Biol Sci 280(1761) (2013) 20130553.
- 382 [48] Kendal JR, Rendell L, Pike TW, Laland KN, **Nine-spined sticklebacks deploy a hill-**
383 **climbing social learning strategy**, Behav Ecol 20(2) (2009) 238-244.
- 384 [49] Wright AA, **Concept learning and learning strategies**, Psychol Sci 8(2) (1997) 119-123.
- 385 [50] Parker AN, Fritsches KA, Newport C, Wallis G, Siebeck UE, **Comparison of functional**
386 **and anatomical estimations of visual acuity in two species of coral reef fish**, The Journal
387 of Experimental Biology 220(13) (2017) 2387.
- 388 [51] Nelson JS, Fishes of the world, J. Wiley, Hoboken, N.J, 2006.
- 389 [52] Landeau L, Terborgh J, **Oddity and the ‘confusion effect’ in predation**, Anim Behav
390 34(5) (1986) 1372-1380.
- 391 [53] Almany G, Peacock L, Syms C, McCormick M, Jones G, **Predators target rare prey in**
392 **coral reef fish assemblages**, Oecologia 152(4) (2007) 751-761.
- 393 [54] Theodorakis CW, **Size segregation and the effects of oddity on predation risk in**
394 **minnow schools**, Anim Behav 38(3) (1989) 496-502.

395 [55] Wasserman EA, Brooks DI, McMurray B, **Pigeons acquire multiple categories in**
396 **parallel via associative learning: A parallel to human word learning?**, Cognition 136(0)
397 (2015) 99-122.

398 [56] Steinegger M, Roche DG, Bshary R, **Simple decision rules underlie collaborative**
399 **hunting in yellow saddle goatfish**, Proc R Soc B Biol Sci 285(1871) (2018) 20172488.

400 [57] Avarguès-Weber A, Dyer AG, Giurfa M, **Conceptualization of above and below**
401 **relationships by an insect**, Proc R Soc B Biol Sci 278(1707) (2011) 898-905.

402 [58] Guiraud M, Roper M, Chittka L, **High-Speed Videography Reveals How Honeybees**
403 **Can Turn a Spatial Concept Learning Task Into a Simple Discrimination Task by**
404 **Stereotyped Flight Movements and Sequential Inspection of Pattern Elements**, Front
405 Psych 9(1347) (2018).

406