



Factors influencing the different performance of fish and primates on a dichotomous choice task



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Species vary in the ease with which they can solve apparently similar problems. This can be due to a variety of features. For instance, the ecological context of a problem will be interpreted differently by different species. This could relate to how they interpret the problem, but also, more basically, to which cue they see as key. Differences in the latter may influence the ability to solve the task not because of variations in cognitive ability per se, but because one species has to first learn which cue is relevant before it is able to solve the task. In our previous work, cleaner fish learned faster than three species of primates to give an 'ephemeral' food source priority over a 'resident' food source, where the relevant cue was the colour, pattern and shape of the plates on which the food sources were placed (but the foods were identical). To determine the degree to which this cue influenced the primates' ability to learn the task, relative to cleaner fish, we here repeated the task with capuchin monkeys and cleaners, using two variations designed to be more salient to capuchins (the cleaners were also tested to see whether these changes negatively affected their performance). In the first, we changed the cue from the colour of the plate presenting the food (original plate task) to the colour of the food itself (now the plates were identical). In the second, we hid the food rewards, as primates are known to have difficulties inhibiting responses to visible rewards. Primates improved their performance on both adapted tasks. Interestingly, and contrary to our predictions, fish performed at the same level across all versions of the task.

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Animals' decisions are constrained by their ecology, their cognitive ability, and the ways in which they can interact with the world, among other factors. The ecological approach to cognition posits that ecology influences decision making such that each species performs better on tasks that are naturally relevant to them (Balda & Kamil, 1989; Kamil, 1988; Kamil & Mauldin, 1987; Shettleworth, 2009). There are many possible mechanisms by which this could occur, but one likely possibility is that species have been selected to focus on cues that are relevant to them (Lotem & Halpern, 2012; for a review, see Rowe & Healy, 2014). Thus, species may be good at identifying problems that are relevant to their ecology and predisposed to look for some cues over others. For instance, research on food-caching birds has shown that nutcrackers, *Nucifraga columbiana*, which are highly dependent on stored food for surviving winters, outperform less cache-

dependent species specifically in a spatial memory task, but not in a nonspatial, colour memory task (Olson, Kamil, Balda, & Nims, 1995). Similar results were obtained for two populations of black-capped chickadees, *Poecile atricapillus* (Pravosudov & Clayton, 2002): Alaskan chickadees, which live in harsh environments and are highly dependent on food caching, performed better in spatial memory tests than Colorado chickadees, although the populations did not differ in a nonspatial version of the task. Somewhat surprisingly, such comparisons of performance between ecologically relevant and nonrelevant tasks have remained rare (Shettleworth, 2009). Here, we extend work comparing two phylogenetically distant species, cleaner wrasses, *Labroides dimidiatus*, and brown capuchin monkeys, *Cebus [Sapajus] apella*, that converge on their tendency to cooperate with conspecifics but perform differently in a dichotomous choice task derived from a cleaner-specific cooperative situation (Salwiczek et al., 2012).

In the wild, cleaner fish remove parasites and other material from client reef fish, which visit them at their so-called cleaning stations. Clients have been categorized as either residents with

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small territories (or small home ranges) that allow them to access only one cleaning station, or as choosy clients, which have larger home ranges that cover several cleaning stations. Cleaners typically compete with each other over access to choosy clients, while they each have exclusive access to their resident clients; consequently, choosy clients are expected to use their choice options by visiting stations where the service is better. Field observations found that choosy clients have priority for cleaning access over the residents (Bshary, 2001); they also typically switch to another cleaner if ignored, but are more likely to return to the same cleaning station if they are inspected (Bshary & Schäffer, 2002), thus making the clients' choosiness the likely cause of this priority of access.

To test this in the laboratory, Bshary and Grutter (2002) replaced client fish with plates; one plate simulated the choosy client, while the other represented the resident. Fish could feed on the choosy plate only if they started to feed on it before they went foraging on the resident plate, otherwise the choosy plate was withdrawn while the fish was eating from the resident plate, just as choosy clients leave if they are not inspected rapidly; the resident plate, however, always stayed in the testing area until the fish had stopped feeding on it, just as resident clients often queue for service if the cleaner fish inspects another client. Crucially, both plates offered the same foods, in equal amount, and hence were equally attractive as food patches. Within just a few trials, cleaner fish inspected the choosy plate first, supporting previous field observations of this behaviour.

In a subsequent study, Salwiczek et al. (2012) tested cleaner fish, capuchin monkeys, chimpanzees, *Pan troglodytes*, and orang-utans, *Pongo* spp., on this plate task. The goal of this study was to compare the performance of fish and primate species that converged on their tendency to cooperate with one another (e.g. capuchins: Brosnan, 2010; chimpanzees: Boesch & Boesch, 1989) and their propensity to eat both mobile and immobile food sources, which may roughly correlate with the stable resident and mobile choosy clients (e.g. plant materials versus hunting for insects and smaller vertebrates; Frigaszy, Visalberghi, & Fedigan, 2004; Goodall, 1986), and to contrast this with orang-utans, which primarily eat fruits (Galdikas, 1988) and less frequently insects or other mobile animal protein sources (Rijksen, 1978), but which do not cooperate to the same degree in natural situations (but do in captivity: Chalmeau, Lardeux, Brandibas, & Gallo, 1997; Dufour, Pelé, Neumann, Thierry, & Call, 2009). In the task, fish outperformed all of the primate species. Although most of the monkeys (but not the apes) eventually learned how to solve the task, they did not do so as quickly as the fish.

Salwiczek et al.'s (2012) results may initially seem counterintuitive given the primates' large brains and known problem-solving skills, but from the cue perspective they make sense. The fish were presented with a task that was derived from their own ecology, including the cues that were needed to solve it, whereas the primates needed to first learn which cues were relevant, and only then could they learn to solve the task. Of course, ecologically relevant cues are not the only possible causes for the differences; differences in cognition may generally be due to how individuals perceive, process and/or act upon the available information, or to their motivation for the task itself (Shettleworth, 2009). Therefore, to understand this more fully, we must test the primates on alternative versions of the task that are designed to account for some of these other potentially mediating factors. Additionally, to truly test the hypothesis, it is essential to test the fish on the modified tasks as well, to see whether and how their performance changes across the tasks. In the current paper, we independently tested two nonexclusive reasons that could explain the poor performance of primates in the original plate task, namely whether the primates understood which cue held the relevant information for the

decision, and the tendency of primates to be distracted by seeing food during the choice presentation.

Considering the first potential explanation for the superior performance of the fish, the task simulated a natural situation for the fish but not for the primates, so we hypothesized that only the fish would readily identify the relevant cue to solve the task (Lotem & Halpern, 2012). In the wild, cleaner fish consume small invertebrates on the surface of client reef fish (Côté, 2000; Randall, 1958), which only become visible at short range (i.e. that need to be searched for and found). Parasite abundance varies between species, partly as a correlate of client body size (Grutter, 1995); therefore, cleaners should prefer certain clients over others because of their quality as a food patch (Grutter, Glover, & Bshary, 2005). In other words, cleaners should focus on the way the food is presented, rather than on the food itself. This was reflected in the original plate task adaptation, where the plate colour and pattern were the relevant stimuli, rather than the foods, which were identical and uninformative (Salwiczek et al., 2012).

For primates, what is important is the food itself, not the patch. Although foods may be associated with specific surroundings (e.g. a species of tree may provide hidden fruits), the general details of the source (e.g. leaf shape) do not change (e.g. the fruits will not suddenly be found in a different species of tree) and the patch may not be informative about the quality of food (e.g. the position of the leaves will not tell whether the fruits are ripe; the fruits themselves must be inspected). Therefore, for this study, we tested to see whether a cue that was potentially more ecologically relevant to primates (and presumably less ecologically relevant to fish) would increase the primates' performance. For this, we kept the plates identical, but used different coloured food items. We predicted that if the difference found in Salwiczek et al. (2012) was simply due to a difference between species in where attention was focused, the monkeys would outperform the fish in this task.

Considering a second potential explanation for the superior performance of the fish, primates are known to have difficulty making the correct choices when food is present. While primates certainly can make rational choices when food is visible, and can learn to overcome the prepotent response with modifications (e.g. using symbols to represent foods; Boysen, Mukobi, & Berntson, 1999; Murray, Kralik, & Wise, 2005), the original task by Salwiczek et al. (2012) may have been challenging for the primates because of the presence of this extraneous cue (see Pepperberg & Hartsfield, 2014). Therefore, for our second study, we adapted the task to minimize any influence of having visible foods during the subjects' choices. Note that because studies on the influence of food visibility on decision making in any context on cleaner wrasse are lacking, we had no prediction for whether visible versus nonvisible food would affect their performance; on the one hand, if the plate design was the important cue, then in principle, this task should not have been more difficult, but on the other, swimming to the opposite side to claim food was presumably atypical for them, and therefore, this may have made the task more challenging.

An important aspect of our comparative approach concerned the choice of the experimental design. Because of the scarcity of nonhuman primate subjects, the capuchin monkeys were, by necessity, tested in a within-subjects design; therefore, it was essential to collect within-subjects data for fish as well, and to give the fish equivalent experience with the paradigm. To do this, we tested cleaner fish on the original plate task prior to the two other studies. This also allowed us to compare our results for these cleaner fish (from Moorea) with those from our earlier study (from the Philippines; Salwiczek et al., 2012). To summarize, we predicted that (1) offering relevant information of the food (colour) rather than some aspect of the plate (e.g. colour, pattern) would be more ecologically relevant for primates, so they should outperform the

fish in the first experiment, and (2) primates should solve the hidden-food task more quickly than the original plate task (we had no prediction for the effect of this alteration on the fish). If primates did notably better on one task than the other, it would provide evidence as to which of these factors were most important in driving primates' outcomes in the earlier task, whereas a failure to improve performance in either task for primates would be difficult to interpret.

METHODS

Subjects and Housing

Capuchin monkeys

We tested nine captive-born brown capuchin monkeys (5 males, average age: 12 years, range 7–17 years; 4 females, average age: 15 years, range 12–18 years) from two stable social groups at the Language Research Center of Georgia State University, Atlanta, Georgia, U.S.A. All subjects participated in both studies. Subjects were always housed with their social groups except when they separated voluntarily for behavioural and cognitive testing. Subjects were fed a diet according to their species-specific needs that included primate chow and fresh fruits and vegetables. They also received enrichment foods several times per day. Animals were never deprived of food or water for testing purposes. Running water was available ad libitum, including during testing. All of the capuchin monkey experiments were approved by the Georgia State University IACUC (A12015) and met the standards of the United States. Georgia State University is fully accredited by AAALAC.

The monkeys lived in two large indoor/outdoor enclosures. Each enclosure contained ample three-dimensional climbing space as well as trapezes, perches and enrichment items. The enclosure for each social group was divided into an indoor area (approximately one-half of their total space) and an outdoor area. The subjects had previously been trained to voluntarily enter test boxes attached to their indoor area, which allowed us to separate individuals from their group for testing. Monkeys were tested in these testing enclosures. Subjects could choose not to participate at any time by walking away from the experimenter, and there were no consequences for the monkeys if they decided not to participate. No

subject was ever involved in more than one testing session for any of the studies on any given day.

Cleaner fish

Fourteen adult wild cleaner wrasses of unknown sex were tested at the University of California Berkeley Gump Field Station in Moorea, French Polynesia. Subjects were caught with hand-nets from reefs surrounding the field station, and then housed individually in glass aquaria (approximately $50 \times 40 \times 40$ cm) with a continuous flow of fresh sea water. All cleaners were supplied with an opaque Plexiglas shelter tube for hiding during the day and sleeping at night. Cleaners were first trained to feed off Plexiglas plates prior experiments. Individuals were fed mashed prawn flesh and kept for 1–5 weeks prior to commencing experiments. Once experiments started, subjects were tested every day, and were not given any food except during testing. All studies were conducted during a 4-week visit to the field station by the first author. At the end of the study, all subjects were returned to the location they were caught. This research was approved by the Regional Delegation for Research and Technology (DRRT, Délégation Régionale à la Recherche et à la Technologie, Papeete, Tahiti).

General Procedure

The experimental set-ups for both species are illustrated in Fig. 1.

Capuchin monkeys

The experimental design was based on the studies of Bshary and Grutter (2002) and Salwiczek et al. (2012). Subjects had to choose between two stimuli, each assigned to one of two specific roles, permanent or ephemeral. Choosing the permanent stimulus (which simulated a 'resident' client) always resulted in an immediate reward, and this stimulus was available throughout the trial. The ephemeral stimulus (which simulated a 'choosy' client) offered the same immediate reward, but only if it was the first one the subjects chose. If subjects chose the permanent stimulus first, the ephemeral stimulus was withdrawn out of reach and sight of the subject. Thus, the optimal outcome was to pick the ephemeral plate first for a first reward, which allowed the subject to also obtain the permanent

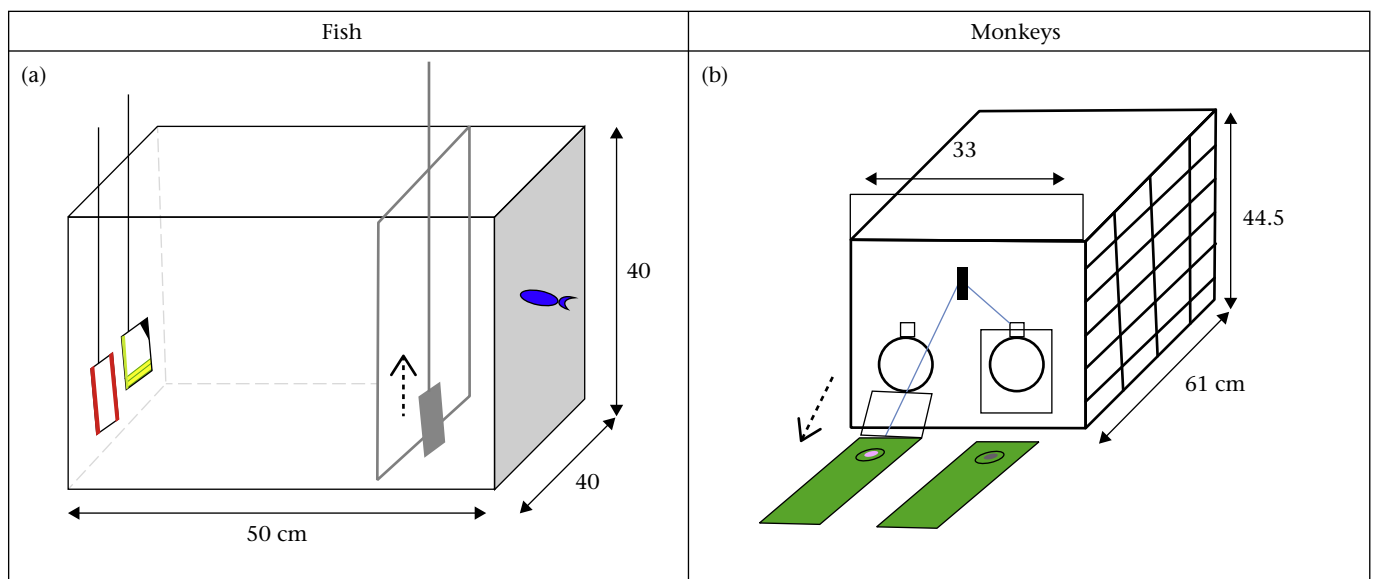


Figure 1. Experimental set-up. Subjects used a door system before they could access the plates and food: (a) fish used a sliding door; (b) monkeys used 'Velcro' doors.

stimulus for an additional reward. The side on which each stimulus was presented for each trial was randomly determined but counterbalanced within a session so that they were on each side an equal number of times, but with no more than three trials in a row on the same side (see Salwiczek et al., 2012). Each subject received 10 sessions of 10 trials each (unless otherwise noted).

Subsequent to the initial learning test, subjects were tested on a reversal test (Rumbaugh, 1971, 1997; Salwiczek et al., 2012). The procedure was identical to the initial test, but the role of each stimulus was reversed (i.e. the previous ephemeral stimulus now behaved like the permanent one, while the previous permanent stimulus now became the ephemeral one). If subjects initially preferred the ephemeral stimulus and then reversed to prefer the newly ephemeral (formerly permanent) stimulus, this would indicate that they are consistent in their preference. The outcomes are more difficult to interpret if subjects initially preferred the permanent stimulus. Reversing to maintain a preference for the newly permanent (formerly ephemeral) stimulus would indicate a consistent preference for the permanent stimulus; however, maintaining a preference for the newly ephemeral (formerly permanent) stimulus would be uninformative because we would not know whether they preferred that physical stimulus (e.g. the plate or food colour), or whether they recognized the utility of choosing the ephemeral stimulus first when 'forced' to do so after the stimuli were switched. Although we report data on reversal tasks in all cases, it is difficult to know what these latter data mean.

Choices were made using a choice apparatus designed for Salwiczek et al. (2012; see Fig. 1). This apparatus was attached to the front of the monkey's test box and was designed to limit the monkey to a single choice. It consisted of two doors fastened by Velcro, attached to each other by a string that worked in a drawbridge-like fashion; that is, pulling one door closed when the other was pushed open (for further detail, see Salwiczek et al., 2012). Foods were presented to subjects on two plates placed on a single larger Plexiglas tray (to standardize the location of the plates) carried by the experimenter, who wore an opaque face shield at all times in order to minimize experimenter cueing (one subject was afraid of the face shield and so it was not worn for this subject). The larger tray had a central opaque barrier that kept the two choice plates clearly separated. The trial started once the subjects faced the two food options. If a subject chose the permanent option first, the ephemeral option was removed from the larger Plexiglas tray and put on the top of the testing box, out of sight of the animal. Subjects were tested in four to five sessions per week, but never in more than one session per day. The intertrial interval (ITI) was 5 min, chosen because, in previous testing, it was the ITI at which the monkeys did the best (Salwiczek et al. (2012) started with a 15 min ITI, as with the fish, and tried a variety of different options until the monkeys succeeded). Rewards were 750 mg banana-flavour precision pellets (Bio-Serv, Frenchtown, NJ, U.S.A.), which could be dyed different colours, as needed, in study 2 (see below). All monkey studies were carried out prior the fish studies.

Cleaner fish

Subjects were tested in their aquarium, in which a separation with an opaque central sliding door was introduced at approximately four-fifths of the aquarium length to create a large 'experimental' compartment and a small 'resting' compartment (see Fig. 1; for previous training studies using a similar apparatus, see Bisazza, Agrillo, & Lucon-Xiccato, 2014; Gierszewski, Bleckmann, & Schluessel, 2013; Miletto Petrazzini, Agrillo, Izard, & Bisazza, 2015). The foods were placed on two plates that were attached to handles so that they could be moved towards subjects but also be retracted rapidly. A given trial started by confining the subject to the resting compartment of the aquarium (subjects quickly learned to swim

behind the door before a trial started). The stimuli were then placed at the opposite end of the experimental compartment. After a few seconds, the door opened and the cleaner could enter the experimental compartment at will. Fish received two sessions per day, consisting of 10 trials each. The ITI was set at 15 min (as in Salwiczek et al., 2012). The two plates were placed far enough apart that following a choice of the permanent option, the experimenter could remove the ephemeral option before the subject could take the food.

Prior to testing, a different set of fish from the same population were pretested for colour preferences on a variety of colours to determine which ones to use during the testing. Pretesting was done on a different set of fish to avoid the possibility of inadvertently biasing the test subjects themselves. Colours were based upon those used in Salwiczek et al. (2012). Preferred colours for all fish were red and yellow, and nonpreferred colours were green and black.

Learning Criterion and Statistics

We based success on the behaviour of cleaner fish in previous experiments, which was a preference for the outcome that maximized their food intake (Bshary & Grutter, 2002; Salwiczek et al., 2012). Therefore, subjects were considered to have solved the test when they met the preference criterion for choosing the payoff-maximizing ephemeral option. They failed if they either developed a preference for the permanent option (using the same criterion as for the ephemeral preference) or did not develop any preference within 100 trials. Subjects who developed a preference for either option were then tested on a reversal test so that all subjects had similar experience prior to subsequent studies. Subjects met the preference criterion when they showed a statistically significant preference for one of the options, which could be achieved by choosing the stimulus (1) 10/10 trials on one session, (2) 9/10 or 8/10 trials on two consecutive sessions or (3) 7/10 trials on three consecutive sessions. These criteria were more conservative than those used by Salwiczek et al. (2012) in two ways. First, we still used the 10/10 criterion on one unique session, but only if the subject selected each of the two stimuli in at least one trial of a previous session (to ensure that they had experience with both outcomes). This did not apply to the reversal test, because a subject was considered to have already experienced both options in the initial phase. Second, the 9/10 criterion on one unique session was dropped because it came to our attention that, while used frequently as a criterion in cognitive and behavioural testing, Monte Carlo simulation showed that this criterion allowed for performance that exceeded chance levels (so we required two consecutive sessions of 9/10). Although we planned to limit subjects to 10 sessions, if a subject chose either option 9/10, 8/10 or 7/10 in the last session (i.e. session 10), it was given another set (or two, in the case of sessions with 7/10, followed by a second session with 7 or more out of 10) of 10 trials to maximize its chances of reaching criterion (Prétôt, Bshary, & Brosnan, 2016). Subjects then received reversal trials.

To compare subjects' performance across species and conditions, we used two statistical tests. First, a two-tailed Fisher's exact test allowed us to compare the number of individuals who met criterion for preferring the ephemeral option to those who did not; in this way, we could include data from all subjects, even those who developed a preference for the permanent option. We used a within-subjects design for the comparisons between tasks, and a between-subjects design to compare performance between species.

Our primary goal was to compare the capuchin monkeys' responses to those of the Moorean fish across all three tasks (the

original plate task and the two new studies reported here). However, to do this, we also needed to test the Moorean fish on the original task (Salwiczek et al., 2012) in order to give them equivalent experience to the monkeys for our within-subjects analysis. Repeating this test also allowed us to compare the outcomes of this Moorean population of cleaner fish to the previous Philippine population. Second, a two-tailed Mann–Whitney *U* exact test allowed us to analyse species' differences in speed of learning. For this, we compared the results only from the learning phase for the Moorean fish and the capuchin monkeys because they were the only populations for which we had results from all three tests.

Study Counterbalancing

We tested two groups of fish and two groups of monkeys. The two groups of fish were both first tested on the original plate task (study 1) before being tested in either the colour task (study 2) or the cup task (study 3). We were able to test some subjects that completed one task on the other task (i.e. some subjects participated in all three studies; the length of the field site visit constrained how many subjects could be tested in both study 2 and study 3). All monkeys had previous experience with the task from Salwiczek et al. (2012) and/or in an analogous computerized format (Prétôt et al., 2016); two monkeys had experience only with the computerized format. Therefore, in monkeys, we did not replicate the first study. The first group was tested in study 2 and then study 3, while the second group was tested in study 3 before study 2.

STUDY 1: PLATE TASK IN FISH

Procedure

We replicated the study of Salwiczek et al. (2012; original work: Bshary & Grutter, 2002), to allow for (1) the fish to have the same previous experience as most of the monkeys (all but two subjects had previously experienced this study) and (2) a within-subjects design in comparing how subjects did on the adapted tasks (studies 2 and 3), as we did for the monkeys. This secondarily allowed us to compare results from the two different populations of cleaner fish.

The 14 fish tested had a choice between two pieces of mashed prawn (0.001–0.005 g) placed on two different Plexiglas plates.

Each plate was marked with a central black dot to help both experimenters and fish to locate the food on the plate. Both plates had the same surface, but differed in shape, colour and pattern. Plate 1 was rectangular, with two yellow/green-striped edges and a black triangle, while plate 2 was square, with two edges in red and one in black (Fig. 2). The colours were the same as the colours used in previous testing on the Philippine fish (see Salwiczek et al., 2012; we switched black for white because unlike in Salwiczek et al.'s (2012) task, the plates in the current study were white), and each contained one of the favoured and one of the less favoured colours based on our pretesting of the Moorean fishes' colour preferences (see General Procedure). Each plate was fixed to a wooden stick, which ended with a parafilm hook that allowed the experimenter to attach it to the inner glass surface of the aquarium. Both plates and food were presented at equal distance from the central sliding door. Half of the individuals were tested with plate 1 as the ephemeral choice, while the other half was tested with plate 2 as the ephemeral choice. As described above, if a subject picked the ephemeral plate first, it was allowed to take the food from the permanent plate as well. In contrast, if it picked the food from the permanent plate first, the ephemeral plate was withdrawn from the aquarium and placed out of sight of the subject. All subjects were then tested on the reversal learning task.

Results

Individual data for all subjects are in Table 1.

Initial learning phase

Nine out of the 14 subjects tested on the initial learning phase solved the task within 110 trials (range 20–110 trials, mean \pm SD = 54.44 \pm 34.68 trials). More subjects met the criterion when plate 2 was the ephemeral plate (seven of seven subjects) than when plate 1 was the ephemeral plate (two of seven subjects), possibly indicating a preference for that plate (Fisher's exact test: $P = 0.02$).

Reversal learning phase

Two of the nine subjects that solved the initial learning task solved the reversal task within 80 trials (range 40–80 trials, mean \pm SD = 60 \pm 28.28 trials). Six of the seven subjects that did not reverse their preference showed a side bias (binomial/sign test:

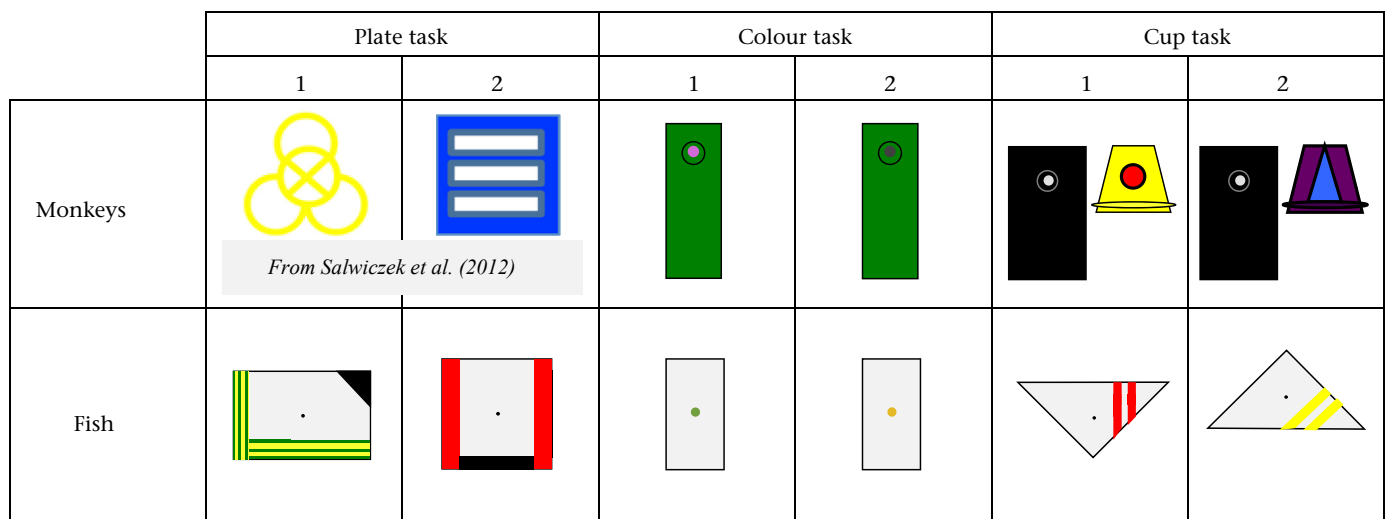


Figure 2. Sets of stimuli. Pairs of stimuli (labelled 1 and 2) used in the plate, colour and cup tasks.

Table 1
Two-choice Moorean fish plate task (ephemeral vs permanent reward): number of trials needed for each subject to solve the plate task for the initial learning phase and the reversal phase in study 1

Subject	Initial	Reversal	Ephemeral option
D1	60	40	Plate 1
D2	70	80	Plate 2
D3	20	>100	Plate 2
D4	20	>100	Plate 2
D5	20	>100	Plate 2
D6	30	>100	Plate 2
D7	60	>100	Plate 2
D8	100	>100	Plate 2
D9	110	>100	Plate 1
D10	>100	–	Plate 1
D11	>100	–	Plate 1
D12	>100	–	Plate 1
D13	>100	–	Plate 1
D14	>100	–	Plate 1

Stimulus options (plate 1 vs plate 2) are shown in Fig. 2. Subjects that did not reach preference criterion in the initial learning phase were not further tested on the reversal phase.

all P s < 0.01), and the seventh one did so from trial 50 to trial 100 (binomial/sign test: P < 0.01).

Moorean versus Philippine fish (between-subjects)

We compared the fishes' performance on the initial and reversal phases of the plate task to the performance of the Philippine fish population. There was no significant difference in the initial learning phase between Moorean fish (nine of 14 subjects succeeded in the task) and Philippine fish (all six subjects succeeded; Fisher's exact test: $P = 0.26$). However, more Philippine fish succeeded in the reversal phase (six of six subjects) than Moorean fish (two of nine subjects; Fisher's exact test: $P < 0.01$).

Fish versus monkeys (between-subjects)

We compared the Moorean fishes' performance on the initial and reversal phases of the plate task to the performance of the capuchin monkeys in the previous study (Salwiczek et al., 2012). More fish succeeded on the initial phase (nine of 14 subjects) than did monkeys (all eight subjects failed in the task; Fisher's exact test: $P < 0.01$), while more monkeys succeeded on the reversal phase (seven of eight subjects) than fish (two of nine subjects; Fisher's exact test: $P = 0.02$).

Discussion

As with previous work in cleaner fish, Moorean fish learned the plate task more rapidly than capuchin monkeys in Salwiczek et al. (2012). This allowed us to continue with our central comparison, between the Moorean cleaner fish tested in the current study, which were able to solve the initial learning task, and capuchin monkeys, which were not. Unless otherwise specified below, all comparisons between monkeys and fish were with the Moorean fish in the current study.

Interestingly, however, although the two populations did not differ in performance on the initial learning task, the Moorean fish were less likely to solve the reversal task than were the Philippine fish. Although our task cannot determine why this difference exists, there are several possible (nonmutually exclusive) reasons. First, recent evidence from Australia suggests that client species' density and diversity as well as cleaners' density may have important effects on cleaner performance in cognitive tasks (Wismer, Pinto, Vail, Grutter, & Bshary, 2014; also see Salwiczek et al., 2012). While we do not have measures for these two parameters, they

do appear to differ on basic measures of client diversity and density; reports indicate that there are at least twice as many species of reef fish in the Philippines as in French Polynesia (Fish-Base: <http://www.fishbase.org>), making the Philippines the richest concentration of marine life on the planet (Carpenter & Springer, 2005). It is possible that these (or other smaller-scale) parameters influence the two populations differently.

Second, the aquaria used in the current experiments were shorter than those used in the previous work with Philippine fish, which reduced the distance to make a choice. In primates, differences in the size of the enclosure (Bräuer, Call, & Tomasello, 2007), the orientation of the experimenter to the stimuli (Mulcahy & Call, 2009), and seemingly minor changes in procedure (e.g. providing one tool rather than two; Girndt, Meier, & Call, 2008) influence responses in cognitive tasks, and it is possible that the same was true here. Supporting this, all of the Moorean fish that failed to reverse their preferences showed robust side biases, something not seen in previous work (R. Bshary, personal observation).

Finally, despite our use of the same colours as in our previous work (Salwiczek et al., 2012) and our efforts to make both plates equally attractive, the Moorean fish showed a preference for one of the plates (the one with red stripes) in the initial task. This was somehow surprising, because none of the adult fish showed such biases in our previous study, although one juvenile did so (Salwiczek et al., 2012). Unfortunately, the apparent colour preference makes it somewhat more difficult to interpret our fish data, and it may have influenced the fishes' ability to solve the reversal task. We find it very interesting that one population should show a much stronger colour preference than the other, and we hope to explore this topic further in the future.

Because of the inconsistency between the two populations on the reversal task, we do not compare these two populations of fish further on the reversal phase, although we note that these population differences are a very fruitful avenue for future research.

STUDY 2: COLOUR TASK

Procedure

The procedure was identical to the plate task described in study 1, except that in this case, the plates had the same colour, pattern and shape, and the foods on the plates differed in colour.

Capuchin monkeys

The two plates were green and rectangular, and rewards were 750 mg banana-flavoured precision pellets (Bio-Serv) that were coloured pink or black with spray food colouring (Fig. 2). Of the nine subjects, six (in one social group) were tested first in this study and subsequently on study 3, while the other three (in a separate social group) were tested first in study 3 and subsequently on this study.

Cleaner fish

The two plates were white and rectangular (presented vertically, as opposed to horizontally as in study 1) and the foods were coloured yellow-orange and purple-pink with liquid food colouring (Fig. 2; these colours were chosen because both were favoured by cleaners in pilot testing). Only nine of the 14 fish were tested in this task (two of these nine subjects were previously tested in study 3; all subjects were previously tested in study 1). For the initial learning phase, four subjects were tested using yellow-orange as the ephemeral choice, while five subjects started with purple-pink as the ephemeral choice. One of these five subjects (D12) chose purple-pink in 10/10 trials in each of the first four sessions and so was dropped from the study, leaving a sample size of eight fish. Because of time constraints on how long the experimenter could

stay at the field site, one subject (D1) received three sessions on one day, and another subject (D5) received three sessions on two different days.

Results

Individual data for all subjects are in [Table 2](#).

Initial learning phase

All nine monkeys reached the preference criterion within 100 trials; seven individuals solved the task and preferred the ephemeral stimulus (range 20–100 trials, mean \pm SD = 50 ± 27.08 trials), while two developed a preference for the permanent stimulus in 20 trials.

Seven of the eight fish tested reached the preference criterion within 100 trials; six individuals solved the task and preferred the ephemeral stimulus (range 50–100 trials, mean \pm SD = 63.33 ± 19.66 trials), while one developed a preference for the permanent stimulus in 20 trials.

Reversal learning phase

Six of the seven monkeys that solved the initial learning task also solved the reversal task within 100 trials (range 40–100 trials, mean \pm SD = 70 ± 21.91 trials). The two subjects who preferred the permanent stimulus in the initial task reached criterion for the ephemeral stimulus in 60 trials.

None of the fish that solved the initial task ($N = 6$) solved the reversal task, although this population of fish was also unlikely to reverse in the original plate task (see study 1). The one subject that preferred the permanent stimulus in the initial task reached criterion for the ephemeral stimulus in 20 trials.

Plate versus colour tasks (within-subjects)

For the analysis, we only included subjects that completed both the plate and colour tasks (seven monkeys and eight fish). Significantly more monkeys succeeded in the initial learning phase of the

colour task (five of seven subjects) than in the original plate task (none of seven subjects; Fisher's exact test: $P = 0.02$; [Fig. 3](#)).

The fish did not show any difference in performance between the colour task (six of eight subjects succeeded) and the plate task (five of these eight subjects succeeded in the plate task; Fisher's exact test: $P = 1.00$; [Fig. 3](#)).

Monkeys versus fish (between-subjects)

There was no significant difference in the initial learning phase between monkeys (seven of nine subjects succeeded) and Moorean fish (six of eight subjects succeeded; Fisher's exact test: $P = 1.00$). Considering only the subjects that solved the initial task, there was no difference in speed of learning between species (Mann–Whitney U exact test: $U = 11.50$, $N_{\text{monkeys}} = 7$, $N_{\text{fish}} = 6$, $P = 0.20$).

Discussion

More monkeys succeeded in the colour task than in the plate task, which supports our hypothesis that, for primates, food colour is a more salient cue than plate design. In contrast to our predictions, however, cleaner fish did as well on the colour task as on the original plate task. This could be an indication that the fish were able to generalize to a novel cue (or that the cue was more salient than predicted), but we cannot rule out the possibility that their performance was due to a colour preference.

STUDY 3: CUP TASK

Procedure

The procedure was identical to study 1, except that in this case, the foods were hidden (by cups in the case of capuchins, and placed behind the plates in the case of cleaners).

Capuchin monkeys

The food was placed under two opaque cups so that subjects could not see the food prior the choice. We used two identical black plates to hold the two different containers, one of which was yellow with one red dot on each side and the other of which was purple with a blue triangle on each side ([Fig. 2](#)). At the beginning of each trial, the subjects saw the experimenter hiding each food item under the container. Subjects were then presented the choice between the two containers. Subjects indicated their choice by touching a container, at which point, either they lifted the cup themselves, or the experimenter lifted it for them to access the food underneath. One social group completed this task prior to study 2 and the other group completed this task subsequent to study 2.

Cleaner fish

Instead of containers, which would not work under water, the food was placed on the reverse side of the plates (i.e. away from the direction from which the individual approached). Subjects made a choice by swimming behind the plate to obtain the food. All the fish learned quickly (typically on the first trial) to swim to the reverse side of the plates. The two plates were white and triangular and only differed in colour and pattern (both sides of the plates were coloured/patterned). Plate 1 had two vertical red lines, while plate 2 had two diagonal yellow lines ([Fig. 2](#)); for the initial learning phase, four subjects were tested using plate 1 as the ephemeral choice, while the other four started with plate 2 as the ephemeral choice. Eight of the 14 fish subjects were tested in this task (three of which had previous experience with study 2). Note that, because of time constraints, one subject (D12) received three sessions on two different days, while another subject (D8) was not tested on the reversal learning phase.

Table 2

Two-choice colour task (ephemeral vs permanent reward): number of trials needed for each subject to reach preference criterion for the initial learning phase and the reversal phase in study 2

Subject	Initial	Reversal	Ephemeral option	Initial preference
Monkeys				
Wren ¹	20	50	Colour 1	Ephemeral
Nala ¹	20	60	Colour 2	Permanent
Lily	20	60	Colour 2	Permanent
Logan	30	80	Colour 2	Ephemeral
Nkima ²	40	40	Colour 2	Ephemeral
Liam	40	100	Colour 1	Ephemeral
Gambit ^{2, 3}	50	>100	Colour 1	Ephemeral
Griffin ¹	70	70	Colour 1	Ephemeral
Gabe	100	80	Colour 1	Ephemeral
Fish				
D10	20	20	Colour 1	Permanent
D1 ¹	50	>100	Colour 2	Ephemeral
D11	50	>100	Colour 2	Ephemeral
D14	50	>100	Colour 2	Ephemeral
D5 ¹	60	>100	Colour 2	Ephemeral
D7	70	>100	Colour 2	Ephemeral
D3	100	>100	Colour 1	Ephemeral
D8	>100	—	Colour 1	—

Stimulus options (colour 1 vs colour 2) are shown in [Fig. 2](#). Subjects that did not reach preference criterion in the initial learning phase were not further tested on the reversal phase.

¹ Subjects previously tested in study 3.

² New subjects (not tested in [Salwiczek et al., 2012](#)).

³ Subject was tested without the opaque face shield.

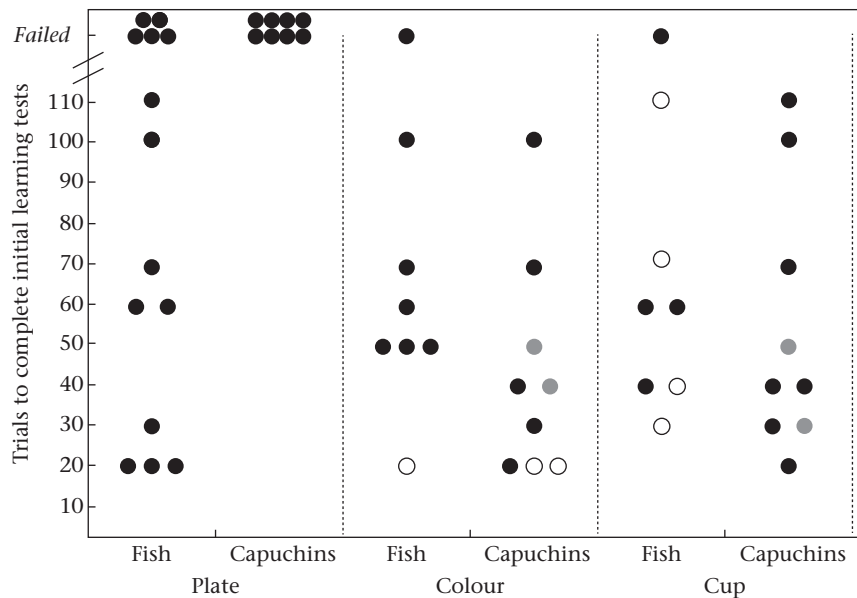


Figure 3. Initial learning phase. The number of trials required for Moorea fish and capuchin monkeys to develop a preference for the ephemeral stimulus in the plate task (capuchins' data based on Salwiczek et al., 2012; note that one subject previously tested in the plate task was no longer available for the current study) and to develop a preference for either stimulus in the colour and cup tasks. Each dot represents one individual; black dots indicate a preference for the ephemeral stimulus, while white dots indicate a preference for the permanent stimulus. For monkeys, the grey dots designate new subjects not previously tested in the plate task. Fourteen fish were tested in the plate task, eight were tested only in the colour or cup task, and four were tested in both the colour and cup tasks. As in our previous work (Prétôt et al., 2016), while criterion was set at 100 sessions, if subjects were in the process of meeting criterion on the 10th session (e.g. preferred one stimulus on at least 7 out of 10 trials), they were allowed to continue until they either met criterion or failed to do so; 'failed' indicates subjects that did not reach preference criterion.

Table 3

Two-choice cup task (ephemeral vs permanent reward): number of trials needed for each subject to reach preference criterion for the initial learning phase and the reversal phase in study 3

Subject	Initial	Reversal	Ephemeral option	Initial preference
Monkeys				
Gabe ¹	20	30	Cup 1	Ephemeral
Wren	30	70	Cup 1	Ephemeral
Gambit ^{1, 2, 3}	30	100	Cup 2	Ephemeral
Liam ¹	40	50	Cup 2	Ephemeral
Lily	40	90	Cup 2	Ephemeral
Nkima ^{1, 2}	50	80	Cup 2	Ephemeral
Griffin	70	>100	Cup 1	Ephemeral
Nala ¹	100	100	Cup 1	Ephemeral
Logan ¹	110	>100	Cup 1	Ephemeral
Fish				
D1	30	60	Plate 2	Permanent
D6	40	10	Plate 2	Permanent
D10 ¹	40	>100	Plate 1	Ephemeral
D12 ¹	60	>100	Plate 1	Ephemeral
D13	60	>100	Plate 1	Ephemeral
D4	70	>100	Plate 2	Permanent
D8 ^{1, 4}	110	–	Plate 2	Permanent
D5	>100	–	Plate 1	–

Stimulus options (cup 1 vs cup 2) are shown in Fig. 2. Subjects that did not reach preference criterion in the initial learning phase were not further tested on the reversal phase.

¹ Subjects previously tested in study 2.

² New subjects (not tested in Salwiczek et al., 2012).

³ Subject was tested without the face shield.

⁴ Subject was not tested on reversal test due to time constraints.

Results

Individual data for all subjects are in Table 3.

Initial learning phase

All nine monkeys solved the task within 110 trials (range 20–110 trials, mean \pm SD = 54.44 \pm 32.06 trials), all preferring the ephemeral plate.

Seven out of the eight fish tested reached preference criterion within 110 trials; three individuals preferred the ephemeral stimulus (range 40–60 trials, mean \pm SD = 53.33 \pm 11.55 trials), while four individuals preferred the permanent stimulus (range 30–110 trials, mean \pm SD = 62.50 \pm 35.94 trials).

Reversal learning phase

Seven of the nine monkeys that succeeded in the initial learning phase reversed their preference within 100 trials (range 30–100 trials, mean \pm SD = 74.29 \pm 26.37 trials).

None of the fish that solved the initial task ($N = 3$) solved the reversal task. Among the three subjects that preferred the permanent stimulus in the initial task and were tested in the reversal task (one was not, due to time constraints, see above), two reached criterion for the ephemeral stimulus in 10 and 60 trials, while the remaining did not reach criterion within 100 trials.

Plate versus cup tasks (within-subjects)

For the analysis, we only included subjects that completed both the plate and cup tasks (seven monkeys and eight fish). More monkeys succeeded in the initial learning phase of the cup task (seven of seven subjects) than in the original plate task (none of seven subjects; Fisher's exact test: $P < 0.01$; Fig. 3).

The fish did not differ in performance between the cup task (three of eight subjects succeeded) and the plate task (five of these eight subjects succeeded in the plate task; Fisher's exact test: $P = 0.62$; Fig. 3).

Colour versus cup tasks (within-subjects)

For the analysis, we only included subjects that completed both the cup and colour tasks (nine monkeys and four fish). Monkeys did not show any difference in the initial learning phase between the colour task (seven of nine subjects succeeded) and the cup task (nine of nine subjects succeeded; Fisher's exact test: $P = 0.47$).

The fish did not show any difference in the initial learning phase between the colour task (two of four subjects succeeded) and the cup task (one of four subjects succeeded; Fisher's exact test: $P = 1.00$).

Monkeys versus fish

Significantly more monkeys succeeded in the initial learning phase of the cup task (nine of nine subjects) than did fish (three of eight subjects; Fisher's exact test: $P < 0.01$; Fig. 3). Considering only the subjects that solved the initial task, there was no difference in speed of learning between species (Mann–Whitney U exact test: $U = 11$, $N_{\text{monkeys}} = 9$, $N_{\text{fish}} = 3$, $P = 0.71$).

Discussion

As in the colour task, monkeys improved their performance in the hidden-food task when compared to the original plate task, suggesting that the presence of food in the original task may have caused primates to act impulsively. The use of a method that obscured the food may have helped the monkeys to inhibit any possible prepotent response due to the presence of food rewards (see [Boysen & Berntson, 1995](#); [Boysen, Berntson, & Mukobi, 2001](#); [Boysen et al., 1999](#); [Murray et al., 2005](#); [Pepperberg & Hartsfield, 2014](#); [Prétôt et al., 2016](#)).

Although fish did not show any difference in performance between the cup task and the two other tasks, their overall performance in the cup task was poorer than that of the monkeys. If anything, this is somewhat surprising given that ectoparasites consumed by cleaners are so small that they are only visible from relatively close range, indicating that cleaners are accustomed to not seeing food on their initial approach. One possibility is that the cleaners found the procedure more difficult; unlike the other tasks, this task required them to swim behind the plate to find food (although note that all subjects swam behind the plates to obtain food on their first session of exposure to it). Alternately, cleaners' low performance might be due to a preference for one of the plates or some carryover effects resulting from the same colours (the two that they most preferred) being used on multiple tests. Based on our analyses, we propose that carryover effects, if they existed, might have been small, because most subjects took a minimum of 40 trials to develop a preference for one of the plates, which indicates that their choice was not influenced by their previous exposure in the plate task. Nevertheless, subjects apparently had a preference for the red-striped plate (seven of eight individuals preferred that plate; binomial/sign test: $P = 0.07$), which may have hindered their overall performance in the task, independently of any carryover effects.

GENERAL DISCUSSION

In the present paper, we tested two hypotheses about factors that may have caused primates to perform less well than cleaner wrasse on a previous dichotomous choice task based on the cleaners' ecology ([Salwiczek et al., 2012](#)). In particular, we altered two factors that we predicted might have made the original task more difficult for primates than for fish. First, we changed the cue from being the plate surrounding the food to being the food itself, which we predicted would be more relevant to the monkeys. The primates' performance improved, whereas the cleaners' performance was unchanged (see details in Discussion of study 2). Second, we hid the food (the cue was again the colour/pattern of the plate), because visible foods are known to inhibit decision making in primates. Again, the primates' performance improved, but the cleaners' performance was unchanged (see details in Discussion of study 3). Taken together, these results indicate that, not surprisingly, many factors play into determining what species may learn

with more or less ease, and that, as predicted, the cues themselves are an important part of decision making.

Of course, while our results demonstrate the importance of these two factors in the primates' decision making, they do not rule out the (very likely) possibility that other factors influence different species' performance in such tasks. For example, previous work showed that parrots did as well as fish on the 'fish' version of the task ([Pepperberg & Hartsfield, 2014](#)). The authors of that study proposed that this might be because fish and parrots are constrained to making a single choice at a time (e.g. with a mouth or bill), forcing them to prioritize, whereas monkeys are typically able to obtain two things at once (e.g. with both hands). As a result, the monkeys may have found the limitations of the experimental task difficult. In fact, in another study, we found that two different species of monkeys did better on a computerized version of the task, in which they chose an option with a joystick-controlled cursor, possibly because they were limited to a single choice (by necessity rather than by experimenter constraint; [Prétôt et al., 2016](#)). Continued work will help to identify all of the constraints on decision making, as well as interactions among them.

Turning now to the fish, we got two unexpected results. First, contrary to our hypothesis, neither of the cue-related changes led to decreased performance for the cleaner fish on the initial learning trials. Second, the Moorean fish were substantially worse at the reversal task than were the original Philippine fish. These are somewhat difficult to reconcile as they suggest two seemingly contradictory possibilities (on the one hand, that the fish were able to generalize across stimuli in a way that the primates were not, and on the other that the Moorean population was substantially less cognitively flexible than the Philippine fish). We discuss each of these in turn.

Considering the first outcome, cleaner fish performed similarly on the colour and cup tasks as on the original plate task in study 1, and did as well as the monkeys on study 2, although the monkeys outperformed the fish on the cup task in study 3. This is quite different than what we observed for the monkeys, which performed better on some versions of the task than others. There are a couple of possible explanations for this. First, our results could be partly due to an artefact of the fishes' apparent preference for some plates over others (which is potentially interesting in and of itself given that such a colour preference has not been reported previously for any other population). Second, the fish may have generalized from their experience in natural contexts, using cues derived from their own ecology, priming them to succeed in all versions of the task. This would be an impressive feat, particularly in light of the primates' difficulty in learning the task originally (even with what we predicted to be more ecologically relevant cues, the monkeys still did not learn the colour task in fewer trials than the fish used in this study or than the fish from the original study by [Salwiczek et al., 2012](#)). This possibility deserves further consideration because as of late, there is evidence for generalized rule learning in cleaners ([Wismer, Grutter, & Bshary, 2016](#)), and much evidence has emerged supporting greater cognitive ability in fish than was previously recognized ([Agrillo, Miletto Petrazzini, Tagliapietra, & Bisazza, 2012](#); [Brown, Laland, & Krause, 2011](#); [Bshary, Gingsins, & Vail, 2014](#); [Ferrari, Trowell, Brown, & Chivers, 2005](#); [Grosenick, Clement, & Fernald, 2007](#); [Kendal, Rendell, Pike, & Laland, 2009](#); [Piffer, Miletto Petrazzini, & Agrillo, 2013](#); [Vail, Manica, & Bshary, 2013, 2014](#); for reviews, see: [Bshary et al., 2014](#); [Bshary, Wickler, & Fricke, 2002](#); [Brown, 2015](#)). These results might thus indicate that fish have some form of general intelligence that goes beyond the ability to readily solve problems only if presented within a precise ecological context.

Considering the second finding, we were very surprised by the Moorean fishes' inability to solve the reversal task, particularly in

comparison with the performance of the original Philippine fish. Because we wished to (1) give the fish comparable experience to the primates and (2) compare the fish to themselves in a within-subjects design, as we did with the primates, we initially tested the fish on the original version of the task (study 1). This secondarily allowed us to compare two different populations of cleaners. We found that, while their outcomes were at least not significantly different for the initial learning trials (64% of the Moorean fish learned the task compared with 100% of the Philippine fish), the Moorean fish were significantly worse at the reversal task than the original Philippine population. This may indicate differences in cognitive flexibility between these two populations, possibly due to differences in their interspecific social environment (such differences due to microecology have been described for cleaners caught from different microhabitats around Lizard Island, Great Barrier Reef; Wismer et al., 2014), experimental differences (such as the aforementioned difference in the length of the aquaria in the two new studies), or the unexpected plate preferences we found in our fish population. Unfortunately, we do not have access to the original Philippine population anymore, nor do we know exactly where they came from (they were obtained from a pet store), so we cannot test the first possibility directly. However, both the ecological and procedural possibilities can be tested by exploring population-level differences in cognition and behaviour in both fish and other species. Although this was not the primary focus of our study, we find it a very intriguing avenue of research and are excited by the possibility of fully integrating ecology into studies of cognition.

Overall, we find that changing the cues given to subjects can dramatically influence their ability to learn a task. This has important ramifications for comparative work, where scientists (including us!) work very hard to equalize every possible aspect of the task across a species or population. However, these results indicate that this may backfire, with subjects not living up to their potential because they are struggling with the cues that are a part of the task, rather than the task itself. While there are undoubtedly many ways to approach this issue, we have done so by first running studies that are, to the degree possible, identical, and then iterating the design for the lesser-performing species to try to unpack what exactly caused the difficulty. This allows us to triangulate in on the fairest comparison. We are excited to see an increasing volume of research that integrates ecology, cognition and behaviour to better understand the evolution of decision making across species.

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