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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.

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; Fragaszy, 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