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Cue-based decision rules of cleaner fish in a biological market task

Sharon Wismer [a, b], Ana I. Pinto [a], Zegni Triki [a], Alexandra S. Grutter [c], Dominique G. Roche [a], Redouan Bshary [a, *]

[a] *Institute of Biology, The University of Neuchâtel, Neuchâtel, Switzerland*
[b] *ARC Centre of Excellence for Coral Reef Studies and College of Science and Engineering, James Cook University, Townsville, QLD, Australia*
[c] *School of Biological Sciences, The University of Queensland, Brisbane, QLD, Australia*

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To develop an evolutionary theory of social decision making, we require an understanding of how individuals utilize environmental cues to form decision rules. We exposed ‘cleaner’ fish (bluestreak cleaner wrasse, *Labroides dimidiatus*) to a biological market task, where giving priority to an ephemeral (i.e. ‘visitor’ client) food plate, over a permanent (i.e. ‘resident’ client) plate, doubled the food reward. Previously published experiments revealed that adult cleaners from a complex social environment regularly solved this task and outperformed adult cleaners from a simple social environment as well as juveniles from both habitat types. In these studies, plates were differentiated by colour and/or colour pattern. However, client size is another potentially useful cue that may be used by cleaners to solve the biological market task in nature, as visitor clients are typically larger than resident clients. Here, we tested cleaners in a setting where plates differed only in size and not colour/pattern: the majority of cleaners exhibited a spontaneous preference for inspecting larger plates or were more likely to reach the task-solving criterion if the visitor plate was larger. All cleaners were able to solve the task when we incorporated both size and colour/pattern cues; however, only cleaners from the complex social environment settled on the more precise colour/pattern cue. In contrast, cleaners from the simple social environment relied on size as the primary, yet less precise, cue to solve the task. In conclusion, our results strongly suggest that intraspecific variation in the performance of cleaners in the biological market task is based on variation in the relative salience of available cues and correlates with variation in a cleaner's natural social environment. Variation in the relative salience of available cues may therefore explain a portion of the intra- and interspecific variance in cognitive performance and social behaviour documented in other animal species.

Evolutionary game theory has provided many solutions for why one individual may help another and, thereby, increase the recipient's direct fitness (Lehmann & Keller, 2006; Leimar & Hammerstein, 2010). Importantly, it assumes that social behaviour is based on underlying genetic strategies (Maynard Smith, 1982). While genes code for the development of a sensory and a central nervous system, allowing the individual to store and retrieve information for decision making (Shettleworth, 2010), reinforcement learning, that is, the adjustment of the expression of the behavioural repertoire to positive and negative feedback from the environment, provides a universal proximate mechanism for the development of learned decision rules (Kacelnik, 2012). Therefore, the decision rules used by humans and other animals often do not fit the simple genetic strategies commonly investigated in game theoretic models (e.g. Fehr & Fischbacher, 2003; Haley & Fessler, 2005; Kümmerli, Burton-Chellew, Ross-Gillespie, & West, 2010; Wismer, Pinto, Vail, Grutter, & Bshary, 2014). For example, humans partly cooperate in anonymous single interaction games, even though defection would yield the highest payoff (Fehr & Fischbacher, 2003), and partly defect when cooperating yields higher payoffs (Kümmerli, Burton-Chellew, Ross-Gillespie, West, 2010).

The importance of integrating learning theory into decision-making theory, including evolutionary theory, has emerged repeatedly over the years (e.g. Fawcett, Hamblin, & Giraldeaub, 2013; McNamara, 2013). In humans, reinforcement learning may be superior to assumed rational decision making at explaining

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* Correspondence: R. Bshary, Institute of Biology, The University of Neuchâtel, 2000 Neuchâtel, Switzerland.
E-mail address: Redouan.Bshary@unine.ch (R. Bshary).

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various deviations from, or conformity with, payoff-maximizing behaviour (Erev & Roth, 2014). Recent theoretical studies have begun to model reinforcement learning over the lifetime of individuals and selection for specific reinforcement learning parameters (i.e. the change in the probability of repeating a behaviour after receiving a reward), to investigate the consequences of these processes for social behaviour (Dridi & Akçay, 2018; Dridi & Lehmann, 2015). Such models will help further our understanding of inter- and intraspecific variation in decision rules that results from environmental variation in, for example, resource availability, group size and structure and individuals' responses to helping behaviour.

Evolved reinforcement learning parameters and individual experience are not the only factors likely to cause intra- and interspecific variation in learned decision rules and, thus, variation in social behaviour and performance in cognitive experiments. An additional component of learned decision rules is perception and the related ability to identify relevant cues from the environment (Lotem & Halpern, 2012). Early on, behavioural scientists understood that learning is affected by a species' evolutionary history (Seligman, 1970). This is because evolution may shape how a species perceives cues in its environment, where certain stimuli are more readily associated with actions and corresponding reward or punishment compared to other stimuli. For example, young rhesus monkeys, *Macaca mulatta*, readily learn to fear snakes by watching videos of conspecifics expressing fear towards a snake yet fail to learn to fear flowers by watching corresponding videos (Cook & Mineka, 1990). Similarly, rats, *Rattus norvegicus*, associate a stomach ache with previously consumed food, but not with light flashes and/or sounds (Garcia & Koelling, 1966). Early experience may also modify an individual's brain structure and performance in cognitive experiments later in life (Kempermann, Kuhn, & Gage, 1997; Kotrschal & Taborsky, 2010), although the specific underlying mechanisms are unclear. Even humans are constrained by available knowledge and time, in addition to cognitive and computational abilities, when making decisions (termed ‘bounded rationality’, Gigerenzer & Selten, 2002). Humans thus often use shortcuts for decision making, that is, they filter available information and focus on one or a few cues that have reliably helped them make appropriate decisions in the past (i.e. ‘heuristics’; Barnard, 2004). However, a cue that yields positive outcomes for a corresponding decision in one context may also be present in a different context, and may hence trigger the same decision, leading to nonfunctional behaviour (Gigerenzer, Todd, & ABC Res. Group, 1999).

Here, we explicitly tested to what extent providing different cues to solve the same problem affects performance in a learning task, and whether differences in a subject's social environment triggers the use of alternative cues, thereby affecting their performance. We selected bluestreak cleaner fish, *Labroides dimidiatus* (hereafter simply ‘cleaner’) as our study species. Cleaners have been extensively used to study cooperative strategies and their underlying proximate mechanisms (e.g. Bshary, 2010, 2011), providing an excellent system for this study. The biological market theory task mimicked a key challenge in the daily interactions of cleaners and their so-called reef fish ‘clients’ from which they remove ectoparasites: cleaners must give priority of service to ephemeral (‘visitor’) clients over permanent (‘resident’) clients, to avoid lost opportunities for food access. Although cleaner fish prefer feeding directly on nitrogen-rich client mucus (Grutter & Bshary, 2003), which constitutes so-called ‘cheating’, an individual cleaner may still remove up to 1200 ectoparasites per day (Grutter, 1996) and engage in approximately 800–3000 daily client cleaning interactions (Grutter, 1995; Triki, Wismer, Levorato, & Bshary, 2018; Wismer et al., 2014). Hence, two or more clients often seek a cleaner's service simultaneously within the cleaner's territory (i.e. ‘cleaning station’). Clients can be categorized according to their home range size, which influences their partner choice options (i.e. how many cleaning stations they have access to). Resident clients have small home ranges and typically have access to a single cleaning station, whereas visitor clients have larger home ranges that encompass several cleaning stations (Bshary, 2001). Therefore, only visitor clients have the option to choose their cleaning partner in a so-called ‘biological market’ (Noë & Hammerstein, 1995), where cleaners compete with one another over access to visitor clients by outbidding each other (i.e. by providing a higher quality cleaning service to clients; Bshary & Noë, 2003). In accordance with the biological market concept and its focus on the importance of partner choice options (Noë & Hammerstein, 1995), visitor clients typically leave the cleaning station if not serviced immediately, whereas resident clients are willing to ‘queue’ for service (Bshary, 2001). Cleaners therefore give priority of access to visitor clients to increase their food intake by reducing the number of lost foraging opportunities.

In the laboratory, Plexiglas plates containing food items, which mimic fish clients with ectoparasites and/or client mucus, have been repeatedly and successfully used to test predictions derived from natural cleaner–client interactions (e.g. reputation management: Bshary & Grutter, 2006 based on Bshary, 2002; client punishment causing feeding against preference: Bshary & Grutter, 2005 based on Bshary & Grutter, 2002a). For the current study, the task of prioritizing an ephemeral (visitor client) food source, over a permanent (resident client) food source, was simulated by an experimenter simultaneously presenting a subject with two plates containing equal amounts of food. The ephemeral plate was removed if the test individual fed on the permanent plate first; it thus lost an additional foraging opportunity (Bshary & Grutter, 2002b). Initial comparative studies used colour/pattern as cues to discriminate between the two plates, while keeping plate size constant (e.g. Salwiczek et al., 2012, cleaner fish only). This decision was based on the ecology of cleaners: client species can be categorized as either resident or visitor (Bshary, 2001), and the defining feature of each species is its colour/pattern, rather than its size (which may vary greatly between individuals) or its shape (which is typically very similar within genera and even families that include both resident and visitor species; examples in Randall, Allen, & Steene, 1997). With colour/pattern cues, adult cleaner fish and African grey parrots, *Psittacus erithacus*, quickly learned to develop a preference for the ephemeral plate, outperforming chimpanzees, *Pan troglodytes*, orang-utans, *Pongo abelii*, and capuchin monkeys, *Sapajus apella*, in this cognitive task, despite the fact that primates were given size and shape cues in addition to colour/pattern cues (Pepperberg & Hartsfield, 2014; Salwiczek et al., 2012). Pigeons, *Columba livia*, and rats also failed in slight variations of the task, with identical levers to be pressed while lights of different colours indicated the location of the ephemeral and permanent options (Zentall, Case, & Luong, 2016, 2017, 2018; T. R. Zentall, personal communication, 2019). Several follow-up studies revealed that the presentation of the task was of importance. First, capuchin monkeys performed well if the task was instead presented on a touch screen (Prétôt, Bshary, & Brosnan, 2016a). Furthermore, both capuchins and cleaners also performed well if the food was hidden, either under a cup for capuchins or on the back of the plate for cleaners, or if the relevant cue was the colour of the food itself, while the experimental plates remained uniform in colour (Prétôt, Bshary, & Brosnan, 2016b). These results suggest that performance differences between species may sometimes be linked to their ability to identify relevant cues as salient (i.e. cues that are conspicuous and, hence, attract attention: Itti & Koch, 2001), rather than to the intrinsic problem of the task. Second, there is predictable variation in performance between cleaners: juveniles generally do not perform well in this learning task (Salwiczek et al., 2012), while most of the variation in adult performance can be attributed to the site from which an individual was caught (Wismer et al., 2014) and to various major environmental perturbations, as well as to the year in which the experiment was performed (Triki et al., 2018). For these studies, batches of poorly performing adults were caught from sites that, at that time, were characterized by low cleaner and client densities (Wismer et al., 2014; Triki et al., 2018; Triki et al., 2019). Following Wismer et al. (2014), we classified these sites as being characterized by a 'simple social environment', as opposed to a 'complex social environment,' which is characterized by high cleaner and client densities. Importantly, while our comparison between individuals caught at different sites was analogous to studies that compared different populations, our main sites were approximately 3 km apart, with other reef sites in between (Appendix Fig. A1). Given this connectivity and the fact that cleaners experience a pelagic egg and larvae phase prior to settling on a coral reef (Victor, 1986), all tested cleaners can be best described as belonging to different 'demes' of the same population. In combination with the general low performance of juveniles, this means that a purely genetic basis for the observed variation is unlikely. Instead, adults may largely learn how to behave in response to local conditions, that is, from interactions with the local client species. In this scenario, resulting differences in learned decision rules then cause variation in performance in laboratory experiments.

Importantly, the low performance of cleaners from the simple social environment in the original biological market task does not necessarily mean that they cannot prioritize visitors over residents in nature. Indeed, in nature, visitor client species are often larger than resident clients (Bshary, 2001) and cleaners preferentially clean larger fish (Grutter, Glover, & Bshary, 2005). This simple rule makes intuitive sense as parasite load and, hence, a client's quality as a food patch, correlates with body size (Grutter & Poulin, 1998). Thus, prioritizing larger clients would frequently produce optimal results in nature, whereby cleaners obtain food from the visitor and resident clients rather than just the resident. However, a size-based priority rule would not help to solve the laboratory task in which both plates are of equal size (Salwiczek et al., 2012, cleaner fish only; Wismer et al., 2014). In this study, we therefore tested the hypothesis that cleaners from sites characterized by simple social reef environments may perform well if plate size is given as the cue. In our first experiment, the resident and visitor plates differed only in size and not in colour/pattern. This experiment allowed us to answer two questions: (1) whether cleaners, including cleaners with poor performance in the original task (juveniles and cleaners from a site characterized by a simple social environment) use size as a cue for decision making and (2) whether adult cleaners from sites characterized by a complex social environment nevertheless perform better because of a more general ability to solve the problem. A general solving ability would allow cleaners not only to solve the task 'spontaneously' when the visitor plate is larger (because of a learned preference for large clients), but also to learn to give priority to a smaller plate if it plays the role of a visitor. We predicted that all cleaners would readily perform above chance (note that this performance could be independent of any learning during the task and based on innate/acquired preference for larger clients) if the visitor plate was larger, while we expected that, at best, adult cleaners from complex social environments might also readily learn to prioritize a smaller visitor plate. In the second experiment, we combined size and colour/pattern cues. This set-up approximated information conveyed to cleaners by different cues in the wild, whereby colour/pattern allowed the precise identification of a plate as a visitor or a resident, and size only correlated with plate behaviour, providing imprecise but nevertheless valuable information. We predicted that cleaners from the complex social environment would have learned, in nature, to predominately use colour/pattern as a cue, while cleaners from the simple social environment, would have learned, in nature (or potentially kept an innate preference), to predominantly use size as a cue. These differences in learned decision rules would then manifest in the experiment. We complemented the second experiment with an analysis of observations of natural cleaning interactions. We hypothesized that higher frequencies of visitors that leave cleaner territories, after being made to wait, provide the necessary learning opportunities for cleaners to switch from a size-based priority rule to a species identity-based priority rule (i.e. colour/pattern based). We therefore predicted that learning opportunities would be more frequent at the site characterized by a complex social environment.

METHODS

Field Site and Study Species

This study was conducted over 3 years (January–February 2012; March–April 2013; July–September 2014), at the Lizard Island Research Station, Queensland, Australia (14°40′S, 145°28′E). In total, 52 cleaners were caught from reefs surrounding Lizard Island: 16 juveniles in 2012, 20 adult females in 2013 and 16 adult females in 2014. Juvenile cleaners were collected from all four sites (Appendix Fig. A1), while adults were collected at two sites. Half of the fish were collected from a site characterized by a complex social environment, with high cleaner and client densities, yielding high-performing cleaners in the original biological market task involving only colour/pattern cues, while the other half were collected from a site characterized by a simple social environment, with low cleaner and client densities, and yielding poor-performing cleaners in the original biological market task (Wismer et al., 2014). A detailed description of the differences in fish abundances and cleaning interaction patterns between sites is provided in Wismer et al. (2014).

Cleaners were caught using barrier nets (2 m x 1 m, 5 mm stretched mesh) and were individually housed in glass aquaria (adults: 62 x 26 cm and 37 cm high) or plastic aquaria (juveniles: 43 x 32 cm and 30 cm high) with a continuous flow of fresh sea water. Fish were supplied with two polyvinylchloride tubes (ca. 2 cm diameter x 15 cm) for shelter. From day 1 in captivity, all fish were fed mashed prawn once daily on Plexiglas plates (10 x 5 cm) and were habituated to captivity for 1 week prior to the commencement of experiments. For experimental purposes, each individual was tested in a single experiment (e.g. experiment 1 or 2) and was subsequently released at the site of capture.

Experiment 1: Size Variation

Our experimental design is a modification of the biological market theory experiment published originally by Bshary and Grutter (2002b) and subsequently by, for example, Salwiczek et al. (2012) and Wismer et al. (2014). We summarize these original methods here. Cleaners were tested in their individual holding aquarium, which was divided into two main compartments using an opaque partition placed 22 cm from the end wall of the aquarium (Appendix Fig. A2). The smaller compartment was the cleaner fish 'holding' area, while the larger compartment was the experimental area containing the experimental Plexiglas plates. During experimental trials, the partition was lifted, and a cleaner was simultaneously presented with two Plexiglas plates, each containing one item of mashed prawn (ca. 0.001 g). One plate always represented a visitor client: this plate was removed from the aquarium if the cleaner did not feed on it first (i.e. gave priority to the other plate instead). The other plate represented a resident client, which remained in the aquarium regardless of a cleaner's foraging choice, until the end of the experimental trial. Plates were always equal in size but differed in colour/pattern (e.g. Appendix Fig. A3; Wismer et al., 2014).

In our modified experimental design, we followed the same protocol except that the visitor and resident plates differed only in size (large plate, 10 x 5 cm; small plate, 3 x 2 cm), while the colour/pattern was identical (uniform grey plates; Appendix Fig. A4). The position of the visitor plate (left or right) in the aquarium was balanced and semi-randomized across the 10 trials: a lottery constrained the position such that the visitor plate was always presented five times on each side, with no more than three presentations in a row per side. We recorded the number of trials required for the individual cleaners to learn to preferentially feed off the visitor plate first; this 'task-solving criterion' was reached when cleaners made the correct decision (i.e. fed off the visitor plate first) in at least nine trials out of a sequence of 10 or at least eight trials out of 10 in two successive sessions. We tested 16 juvenile cleaners in 2012 and 18 adult females in 2013 (our sample size was reduced to 18 (from 20) as two adults, one from each social environment, did not participate in the experiment). The plate status was counterbalanced between treatment groups (i.e. for each environment, approximately half of the cleaners were presented with a large visitor plate and half with a small visitor plate, i.e. 4x large plate, 5x small plate). One individual from the complex social environment was mistakenly tested with the small visitor plate, leading to a slight asymmetry in sample sizes for different treatments (i.e. 3x large plate, 6x small plate). We recognize that although both large and small experimental plates were rectangular, their proportions differed slightly (i.e. 10 x 5 cm versus 3 x 2 cm; Appendix Fig. A4). These minor proportional asymmetries, however, were not considered a crucial component in our study, since the subsequent experiment incorporated size variation once again, but with proportional plates. All cleaners participated in two experimental sessions per day (morning/afternoon; 10 trials per session), with a total maximum number of 120 trials.

Experiment 2: Size and Colour Variation

Our second experiment included variation in both plate colour/pattern (i.e. differentiating 'species') and size. This allowed us to determine how cleaners from environments of different social complexity, as well as different performance in the original market task, integrated information when confronted with the market task in which individuals of each species may also vary in body size. This is a scenario that is common in nature. Cleaners were once again presented with a simultaneous choice between a visitor and a resident plate, each containing one item of mashed prawn. The same protocol was applied as in experiment 1 in that (1) the visitor plate was removed from the aquarium if the cleaner fed on the resident plate first and (2) the same task-solving criterion was used. In this experiment, however, the cleaner was presented with a series of Plexiglas plate combinations of varying sizes, consisting always of one green-patterned and one pink-patterned plate (Appendix Fig. A5). For each plate colour/pattern, we used seven sizes, ranging from 2.25 cm^2 to 144 cm^2 (Appendix Fig. A5). For ecological relevance, since visitor clients are typically larger than resident clients (Bshary, 2001), we chose the five smallest for the resident role and the five largest for the visitor role. Thus, visitor plates were larger, on average, but the size of plates in the two categories overlapped. Plate pairings were counterbalanced for all possible different size combinations, thereby yielding the following relative size frequencies: visitor plate larger than the resident plate in 76% of the experimental trials, visitor plate equal in size to the resident plate in 12% of the trials and visitor plate smaller than the resident plate in 12% of the trials (Appendix Fig. A6). These values represent approximate size ratios between resident and visitor client pairs that simultaneously seek cleaner service in nature (based on observations in Bshary, 2001). Values were such that using colour/pattern as a cue would yield 100% correct choices. Using a pure size-based decision rule, however, would yield approximately 82% correct choices, consisting of 76% correct choices in situations where visitor plates were larger than resident plates, and an additional 6% correct choices (out of 12%) in scenarios where plates were equal in size (i.e. assuming an additional 50% of correct choices, based on random choice).

Each cleaner received 200 trials over 10 days. In contrast to experiment 1, we did not stop when a cleaner reached the task-solving criterion. Instead, we analysed their choices after reaching the criterion to test how far the probability of choosing the visitor plate differed as a function of visitor plate size relative to resident plate size. Visitor plate colour/pattern was counterbalanced between treatment groups. For each trial, we recorded the plate that the cleaner fed from first. This experiment was conducted on 16 adult female cleaners (eight from each site, representing a complex and simple social environment, respectively) in 2014.

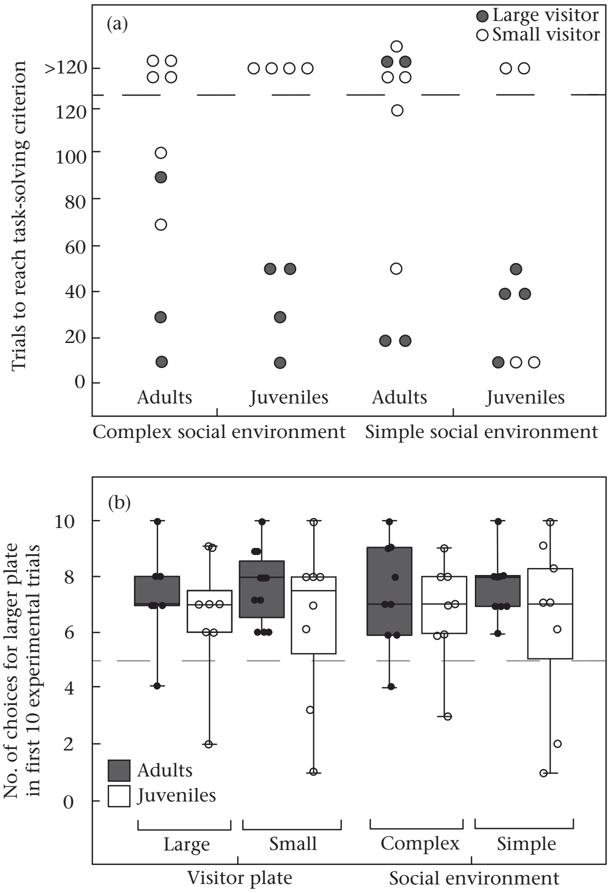

Figure 1. Performance of cleaners in experiment 1. (a) The number of trials required for cleaners to develop a significant preference for the visitor plate. Circles: one individual, exposed first to either a large or small visitor plate. Individuals above dashed line did not complete the task in the maximum 120 trials. (b) Box plots showing the number of choices for the larger plate in the first 10 experimental trials. Dashed line indicates random choice, i.e. a 50% chance of choosing the correct plate. Box plots show the median (horizontal line within the limits of the box), interquartile range (box limits), maximum–minimum values (whiskers) and data points (circles).

Field Observations: Video Analysis

Lastly, to corroborate our laboratory results and provide potential explanations, we reanalysed field-based behavioural videos recorded in 2011 (Wismer et al., 2014) and documented natural interactions between cleaners and clients from the two contrasting social environments. At each site (Appendix Fig. A1), eight cleaners were filmed for approximately 30 min each (range 24.75–31.13 min with cleaner in field of view). For each cleaner, we quantified how often it had the opportunity to choose between (1) a resident and visitor client, and (2) two visitor clients, either because (1) both visitor clients arrived at the cleaning station simultaneously or (2) a visitor client arrived while the cleaner was involved in an interaction with another visitor client. Additionally, we quantified how often a visitor client would leave a cleaner territory without being cleaned. Observations were standardized as a frequency per min.

Data Analysis

We used survival analysis (Cox proportional hazards regression model; ‘coxph’ function in the R package ‘survival’) to evaluate differences in the success rate and the number of trials required by cleaners to reach the task-solving criterion in both experiments (Figs. 1a and 2). We tested for the effects of site (simple versus complex; both experiments), life stage (juveniles versus adults; experiment 2) and visitor plate size (large versus small; experiment 1) on learning. Model assumptions (i.e. proportional hazards) were checked with the function cox.zph and model simplifications (i.e. interactions removed) performed using two likelihood ratio tests. We tested the effect of life stage, environment and visitor plate size on the number of choices for the larger plate in the first 10 trials of experiment 1 using a general linear model (GLM), to investigate spontaneous behaviour/choices (Fig. 1b). The proportion of choices for the larger plate was logit transformed (Warton & Hui, 2011). Model assumptions for this and subsequent linear models were checked with plots of residuals versus fitted values and qqplots of residuals.

We used two general linear mixed-effects models (GLMMs) to test the effect of site (simple versus complex) and plate combinations (visitor plate larger, of the same size or smaller than resident plate) on the (logit-transformed) proportion of correct choices by cleaners after each one reached the task-solving criterion (Fig. 3a) and in the last 50 trials of experiment 2 (Fig. 3b). Owing to issues of heteroscedasticity (unequal variances) in the model on correct choices by cleaners in the last 50 trials, we used the gls function in the package nlme to run a marginal generalized least square (GLS) model, specifying unequal variances among levels of the factor ‘relative plate size’ [‘weights=varIdent(form=~1|relativeplatesize)’] and repeated measurements on individual cleaners [‘corr=corCompSymm(form=~1|cleanerID)’] (see Pekár & Brabec, 2016). We calculated the marginal R^2 (variance explained by the fixed factors; $R^2_{GLMM(m)}$) and conditional R^2 (variance explained by the fixed and random factors; $R^2_{GLMM(c)}$) for these models following Nakagawa and Schielzeth (2013). Post hoc comparisons of predicted marginal means were done with the functions contrast and lsmeans (package lsmeans), which implement a Tukey adjustment of P values for multiple comparisons (Russel 2016).

Finally, we used two nonparametric Wilcoxon rank–sum tests (also called Mann–Whitney U test) to examine differences in cleaner–client interactions between the two reef sites/social environments observed on video recordings (i.e. simultaneous choices involving at least one visitor client, instances of a visitor client leaving the cleaning station without being cleaned; Appendix Fig. A7).

All analyses were done in R 3.1.2 (R Development Core Team, 2014); we specified ‘type III’ sum of squares for significance testing where necessary.

Ethical Note

Experiments were approved by DEEDI Animal Ethics Committee, Queensland Government, Australia (CA2012/05/612; CA2014/08/796).

RESULTS

Experiment 1: Size Cue

There was no effect of reef environment or life stage on the number of trials required for cleaners to solve the task (survival analysis: P for both main effects > 0.30); the two- and three-way interactions of environment, life stage and visitor plate size were also nonsignificant (survival analysis: all $Ps \geq 0.12$; Fig. 1a). However, the size of the visitor plate significantly influenced the time to reach the task-solving criterion (survival analysis: $\chi^2_1 = 11.98$, $P < 0.001$; Fig. 1a): cleaners required more trials to reach the task-solving criterion when the visitor plate was smaller than the resident plate (survival analysis: coefficient ± SEM = -1.74 ± 0.53, $z = -3.28$, $P = 0.001$). The majority (71.4%) of seven adult cleaners solved the initial phase of the task in less than 120 trials when presented with a large visitor plate, whereas seven of 11 cleaners (63.6%) failed to solve the task when the visitor plate was small (Fig. 1a). Juveniles performed similarly: 100% of individuals solved the initial phase of the task in less than 120 trials when the visitor plate was large, whereas 75% failed to solve the task when the visitor plate was small (Fig. 1a).

Cleaners of all life stages and environments exhibited a significant spontaneous preference for the larger plate, irrespective of plate status (resident/visitor), i.e. cleaners chose the larger plate during the first session of 10 trials more than expected by chance (Helmert contrasts intercept estimate ± SEM = 1.20 ± 0.45, total $N = 34$, $t = 2.66$, $P = 0.012$; Fig. 1b and see Appendix). Life stage, environment and visitor plate size had no effect on the proportion of choices for the larger plate in the first 10 trials (all $Ps > 0.24$, $R^2 = 0.05$; Fig. 1b).

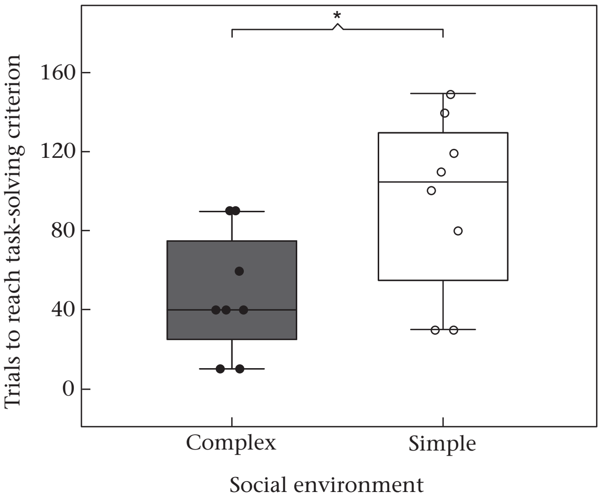

Figure 2. Performance of cleaners in experiment 2: time to reach the task-solving criterion. Box plots show the number of trials required for cleaners from the two reef environments to develop a significant preference for the visitor plate. *$P < 0.05$. Box plots show the median (horizontal line within the limits of the box), interquartile range (box limits), maximum–minimum values (whiskers) and data points (circles).

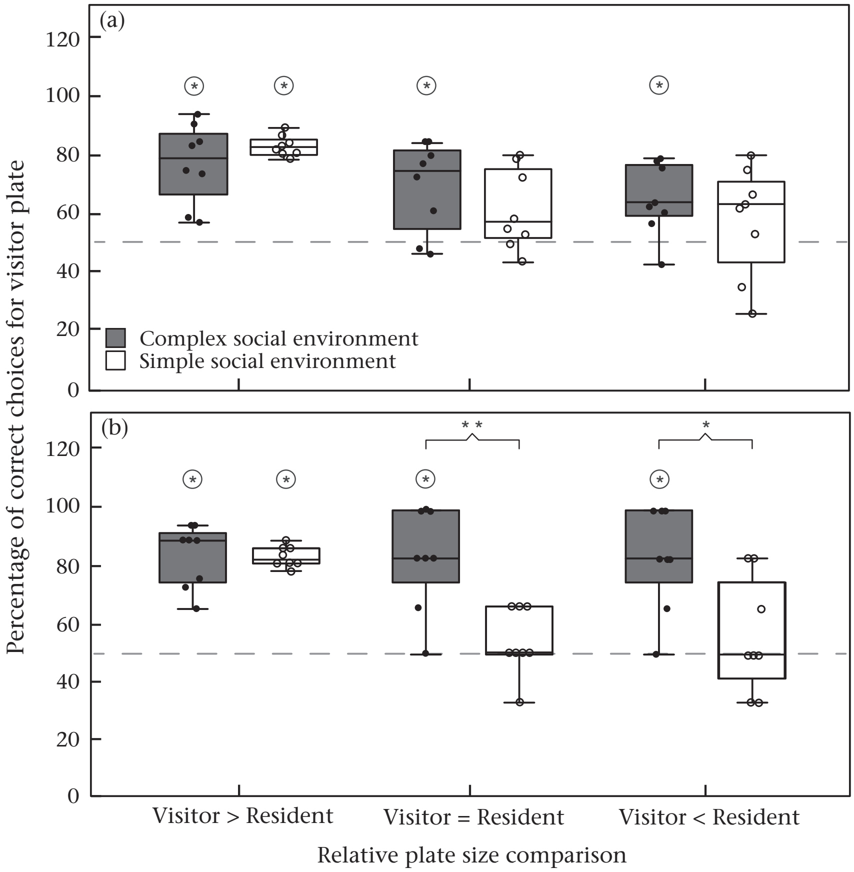

Figure 3. Performance of cleaners in experiment 2: variation across three relative plate size combinations. Box plots show the percentage of correct choices for the visitor plate when it is larger, the same size or smaller than the resident plate (a) after each cleaner has reached the task-solving criterion and (b) after all cleaners have reached the task-solving criterion, i.e. only in the last 50 experimental trials. Asterisks indicate significant differences between cleaners from the two sites: $^{**}P < 0.005$; $^{*}P < 0.05$. Asterisks inside circles indicate significant performance above chance level (50%, indicated by dashed line). Box plots show the median (horizontal line within the limits of the box), interquartile range (box limits), maximum–minimum values (whiskers) and data points (circles).

Experiment 2: Size and Colour/Pattern Cues

When both size and colour/pattern cues were incorporated into the experimental design, all adult subjects reached the task-solving criterion. However, site/social environment had a significant effect on cleaner task-solving time (survival analysis: $N = 20$, $\chi^2 = 5.56$, $P = 0.018$; Fig. 2). Cleaners from the simple social environment required more time to reach the task-solving criterion (coefficient ± SEM = -1.53 ± 0.70, $z = -2.20$, $P = 0.028$), i.e. cleaners from the complex social environment solved the task in 40 trials (median), whereas cleaners from the simple social environment required 105 trials (median; Fig. 2).

Detailed analyses of cleaner choices after reaching the task-solving criterion revealed that individuals from the complex social environment prioritized the colour/pattern cue: they preferentially chose the visitor plate whether it was larger than, the same size as or smaller than the resident plate as indicated by performance significantly above chance in all three conditions (Fig. 3a). This preference was consolidated towards the end, when all individuals had reached the task-solving criterion, i.e. during the last 50 trials (Fig. 3b). In contrast, cleaners from the simple social environment consistently preferred the visitor plate only when it was larger than the resident plate (Fig. 3a), but did not perform significantly above chance if both plates were of equal size or if the resident plate was larger, settling on random choices during the last 50 trials (Fig. 3b). As a consequence, while the full data set does not yield significant differences in performance between cleaners from the two habitats (LMM: site∗relative plate size interaction, $N = 16$, $\chi^2_2 = 2.72$, $P = 0.256$, $R^2_{LMM(m)} = 0.32$, $R^2_{LMM(c)} = 0.51$; Fig. 3a), cleaners from simple and complex environments differed in their ability to correctly choose the visitor place depending on the relative sizes of the two plates during the last 50 trials (GLS: site∗relative plate size interaction, $\chi^2_2 = 15.29$, $P = 0.0005$, pseudo-R^2 not available for GLS). Cleaners from both environments performed as well when the visitor plate was larger (lsmeans: $N = 16$, $t_{42} = 0.55$, $P = 0.589$), but cleaners from the complex social environment outperformed cleaners from the socially simple site when the plates were the same size (lsmeans: $N = 16$, $t_{42} = 3.51$, $P = 0.001$) and when the resident plate was larger (lsmeans: $N = 16$, $t_{42} = 2.71$, $P = 0.010$; Fig. 3b). Importantly, the general preference for colour/pattern of cleaners from the socially complex environment developed fairly late during experimental trials (Fig. A8), implying that learning led to a shift in cue preference, i.e. from a preference for the size cue to a preference for the colour/pattern cue.

Field Observations: Video Analysis

Cleaners from the complex social environment experienced simultaneous choices involving at least one visitor client significantly more frequently than cleaners from the simple social environment (Wilcoxon: $W = 60$, $P = 0.004$; Appendix Fig. A7). Most importantly, they also experienced visitors leaving after being made to wait more frequently (Wilcoxon: $W = 59.5$, $P = 0.002$; Appendix Fig. A7). Assuming 11 h of cleaning activity per day

(Bshary, 2001), cleaners from the complex social environment would experience 51.8 ± 40.7 (mean ± SD) instances of visitors leaving prior to being cleaned per day, i.e. on average 20 times more frequently than cleaners from the simple social environment (2.6 ± 7.4 times per day).

DISCUSSION

Learned decision rules are likely to interact with genetic programs to produce a repertoire of sophisticated social behaviours. Therefore, identifying the processes underlying interindividual variation in decision rules is key in understanding how natural selection may adjust social behaviour to ecological demands. Our aim was to determine whether previously observed variation in cleaner fish performance, in a biological market task, is driven by variation in either (1) task-solving abilities per se, that is, by variation in decision rules or (2) an individual's ability to identify relevant cues as salient. Our results provide evidence for the paramount importance of cue identification. Importantly, variation in cue identification appears to be based on previous experience and resulting learning in nature.

Previous experiments on capuchin monkey performance in variants of the biological market task demonstrated that cue type is important in determining whether individuals can solve the biological market theory task at the species level: using plate colour/pattern, in combination with plate size and shape, as a cue impeded learning, whereas using food colour as a cue facilitated learning (Prétôt et al., 2016a; Salwiczek et al., 2012). Our current results show that cue type may also lead to intraspecific variation in learning how to solve a biological market task. First, when the relevant information was entirely encoded in the size of the plate (experiment 1), juvenile and adult cleaners from complex and simple social environments performed equally well or poorly: all fish spontaneously preferred the larger plate and readily solved the task only if the larger plate was the visitor. Therefore, all cleaners identified size as an informative cue (based on learning or on innate preferences) and cleaners from the complex social environment did not appear to be systematically better at solving the biological market task than conspecifics from the simple social environment. More specifically, they did not seem to have more efficient learning mechanisms, such as the ability to generalize that one of two plates needs to be given priority in order to maximize food intake. Second, in experiment 2, cleaners from a complex social environment were eventually capable of identifying plate colour/pattern as a more informative cue than plate size. In contrast, cleaners from the simple social environment relied primarily on size and not colour/pattern.

We suggest the following scenario to explain the results from both experiments, as well as the field observations on client fishes leaving cleaner territories. First, all juvenile cleaners learned that ‘larger is better’. Indeed, on average, larger fish have more ectoparasites than smaller fish (Grutter, 1995; Grutter & Poulin, 1998). For juvenile cleaners, this simple decision rule appears to be optimal since they rarely interact with visitor clients (Potts, 1973; R. Bshary & S. Wismer, personal observations) and, hence, have little to gain from incorporating colour/pattern cues to identify species and learn which ones are willing to wait for service. As cleaners grow and their territory increases, size remains a good indicator of client category (Bshary, 2001), meaning that a size-based priority rule typically allows cleaners to give priority to visitors. As a consequence, the size-based rule appears to be maintained in the simple social environment: few events of ignored visitors leaving imply that the cleaners are exposed to few learning opportunities and also face little pressure to depart from this decision rule. Only in areas with high social complexity, do cleaners eventually learn to identify colour/pattern as the more relevant cue and switch from using a size-based rule to using a colour/pattern-based rule when leaving visitors exert enough pressure. Nevertheless, both experiments show that size cues were not abandoned: they were used in the first experiment in the absence of colour/pattern cues, and initially dominated decisions in the second experiment, with colour/pattern cues only becoming prevalent in the second half of trials. Also, the second experiment shows that cleaners from the simple social environment did not completely ignore colour/pattern because, if they had, their performance during the small visitor–large resident trials would have been below chance. Indeed, recognizing client species can be useful outside the biological market context, owing to a key conflict of interest between cleaners and clients: cleaners prefer to eat client mucus over ectoparasites, which constitutes cheating (Grutter & Bshary, 2003). Species recognition helps cleaners to predict whether a cheated client would swim off or turn around and chase the cleaner, and to avoid cheating predators that could try to eat the cleaner in response to cheating (Bshary, 2001). Furthermore, parasite load differs between client species, as well as between fish of different size (Grutter, 1994), as does the mucus quality (Arnal, Côté, & Morand, 2001), and cleaners can distinguish between the mucus of different species (Grutter & Bshary, 2004). It therefore appears that all cleaners benefit from recognizing both size and colour/pattern as potentially relevant cues, but that the relative salience varies according to local social complexity. It would be interesting to use learning paradigms that are less ecologically relevant (such as choosing one cue to avoid an electroshock) to test the extent to which cleaners from different social environments consistently differ with respect to what cues facilitate high performance.

Given that juvenile cleaners start with learning the size-based rule, how do they start to incorporate species identity (colour/pattern) in their decision making as adults? Cleaners in complex social environments generally have 2000 interactions per day (Grutter, 1995; Wismer et al., 2014) and, according to our videos, only 132 (6.6%) of them involve a visitor seeking cleaning service simultaneously with a resident. With a size-based rule, the cleaners would make the correct choice in approximately 116 (88%) of 132 interactions, based on a large data set estimating body length of simultaneously cleaner-seeking residents and visitors from the Red Sea (Bshary, 2001). Thus, this rule yields a very high performance. Although recognition of client species may already be present in all cleaners for reasons unrelated to the biological market task, cleaners still have to filter sequences of interactions in order to assess the limitations of the size-based cue and learn that the colour/pattern cue provides superior information. Integrating sequences of interactions is a valid hypothesis to explain how individual cleaners may overcome that problem. Kolodny, Edelman, and Lotem (2014, 2015) showed mathematically that sequence analysis may greatly enhance performance in optimal foraging tasks compared to basic reinforcement learning: identification of meaningful sequences found in a chain of interactions (called ‘chunking’ by the authors) leads to the formation of units that lead to better decisions, where performance can be further enhanced through generalization across units based on their contextual similarity. Crucially, a learning model predicts that the market task cannot be solved without the ability to chunk (Quiñones, Lotem, Leimar, & Bshary, 2019). Furthermore, cleaners have indeed been shown to have the ability to generalize between combinations of predatory and nonpredatory clients when predators provide safe havens against aggressively chasing nonpredatory clients (Wismer, Grutter, & Bshary, 2016).

In conclusion, the results highlight a well-established insight from animal cognition literature, namely, that the ability to identify relevant cues from the environment is the first aspect of cognitive processing of information (Shettleworth, 2010). Indeed, it has been proposed that differences in individual and/or species performance in cognitive tasks may often be based on their ability to identify such cues, even if the underlying cognitive processes are the same (Lotem & Halpern, 2012). The current study extends these insights to the context of social behaviour and biological market theory (Noë 2001), in the *L. dimidiatus* mutualism, as only cleaners that frequently experience visitors leaving in nature regularly used colour/pattern as a cue to solve the biological market task. The high performance of cleaners from the simple social environment, in situations where visitor plates were large, shows the primordial importance of cue salience for performance. Future progress in modelling the evolution of cooperation will hence require a shift in paradigm, investigating the evolution of cue salience and reinforcement learning parameters underlying decision making rather than the evolution of genetically coded strategies like the famous 'tit-for-tat' (Kacelnik, 2012; Lotem & Halpern, 2012). Several initial models of this kind exist, for example either modelling phenotypic plasticity (Fischer, Van Doorn, Dieckmann, & Taborsky, 2014; Frankenhuis & Panchanathan, 2011) or explicitly modelling reinforcement learning (Dridi & Lehmann, 2015; Dridi & Akçay, 2018). Our study highlights the importance of adding cue salience within an ecological framework to understand variation within and between species with respect to evolved and/or acquired social decision rules.

Conflicts of Interest

None.

Data Availability

The data and analysis script for this study are archived in the repository figshare (Wismer et al., 2019; https://doi.org/10.6084/m9.figshare.5463787) following best practices (Roche, Kruuk, Lanfear, & Binning, 2015) and were made available to the editors upon initial submission.

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References

Arnal, C., Côté, I., & Morand, S. (2001). Why clean and be cleaned? The importance of client ectoparasites and mucus in a marine cleaning symbiosis. *Behavioral Ecology and Sociobiology, 51*, 1–7.

Barnard, C. J. (2004). *Animal behavior: mechanism, development, function and evolution*. Harlow, U.K.: Pearson Education.

Bshary, R. (2001). The cleaner fish market. In R. Noë, J. van Hooff, & P. Hammerstein (Eds.), *Economics in nature: social dilemmas, mate choice and biological markets* (pp. 146–172). Cambridge, U.K.: Cambridge University Press.

Bshary, R. (2002). Biting cleaner fish use altruism to deceive image-scoring client reef fish. *Proceedings of the Royal Society B, 269*, 2087–2093.

Bshary, R. (2010). Cooperation between unrelated individuals—a game theoretic approach. In P. Kappeler (Ed.), *Animal behaviour: evolution and mechanisms* (pp. 213–240). Berlin, Germany: Springer.

Bshary, R. (2011). Machiavellian intelligence in fishes. In C. Brown, K. Laland, & J. Krause (Eds.), *Fish cognition and behaviour* (pp. 277–297). Oxford, U.K.: Wiley-Blackwell.

Bshary, R., & Grutter, A. S. (2002a). Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Animal Behaviour, 63*, 547–555.

Bshary, R., & Grutter, A. S. (2002b). Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: The cleaner fish case. *Ecology Letters, 5*, 130–136.

Bshary, R., & Grutter, A. S. (2005). Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biology Letters, 1*, 396–399.

Bshary, R., & Grutter, A. S. (2006). Image-scoring causes cooperation in a cleaning mutualism. *Nature, 441*, 975–978.

Bshary, R., & Noë, R. (2003). Biological markets: The ubiquitous influence of partner choice on the dynamics of cleaner fish—client reef fish interactions. In P. Hammerstein (Ed.), *Genetic and cultural evolution of cooperation* (pp. 167–184). Cambridge, MA: The MIT Press.

Cook, M., & Mineka, S. (1990). Selective associations in the observational conditioning of fear in rhesus monkeys. *Journal of Experimental Psychology: Animal Behavior Processes, 16*, 372.

Dridi, S., & Akçay, E. (2018). Learning to cooperate: The evolution of social rewards in repeated interactions. *American Natuarlist, 191*, 58–73.

Dridi, S., & Lehmann, L. (2015). A model for the evolution of reinforcement learning in fluctuating games. *Animal Behaviour, 104*, 87–114.

Erev, I., & Roth, A. E. (2014). Maximization, learning, and economic behavior. *Proceedings of the National Academy of Sciences USA, 111*, 10818–10825.

Fawcett, T. W., Hamblin, S., & Giraldeaub, L. A. (2013). Exposing the behavioral gambit: The evolution of learning and decision rules. *Behavioural Ecolology, 24*, 2–11.

Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature, 425*, 785–791.

Fischer, B., Van Doorn, G. S., Dieckmann, U., & Taborsky, B. (2014). The evolution of age-dependent plasticity. *American Naturalist, 183*, 108–125.

Frankenhuis, W. E., & Panchanathan, K. (2011). Balancing sampling and specialization: An adaptationist model of incremental development. *Proceedings of the Royal Society B*, rspb20110055.

Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science, 4*, 123–124.

Gigerenzer, G., & Selten, R. (2002). *Bounded rationality: the adaptive toolbox*. Cambrdige, MA: The MIT Press.

Gigerenzer, G., Todd, P. M., & ABC Res. Group. (1999). *Simple heuristics that make us smart*. New York, NY: Oxford University Press.

Grutter, A. S. (1994). Spatial and temporal variations of the ectoparasites of seven reef fish species from Lizard Island and Heron Island, Australia. *Marine Ecology Progress Series, 11*, 521–530.

Grutter, A. S. (1995). The relationship between cleaning rates and ectoparasites loads in coral reef fishes. *Marine Ecology Progress Series, 118*, 51–58.

Grutter, A. S. (1996). Parasite removal rates by the cleaner wrasse *Labroides dimidiatus*. *Marine Ecology Progress Series, 130*, 61–70.

Grutter, A. S., & Bshary, R. (2003). Cleaner wrasse prefer client mucus: Support for partner control mechanisms in cleaning interactions. *Proceedings of the Royal Society B, 270*, S242–S244.

Grutter, A. S., & Bshary, R. (2004). Cleaner fish, *Labroides dimidiatus*, diet preferences for different types of mucus and parasitic gnathiid isopods. *Animal Behaviour, 68*(3), 583–588.

Grutter, A. S., Glover, S., & Bshary, R. (2005). Does client size affect cleaner fish choice of client? An empirical test using client fish models. *Journal of Fish Biology, 66*, 1748–1752.

Grutter, A. S., & Poulin, R. (1998). Intraspecific and interspecific relationships between host size and the abundance of parasitic larval gnathiid isopods on coral reef fish. *Marine Ecology Progress Series, 164*, 263–271.

Haley, K. J., & Fessler, D. M. T. (2005). Nobody's watching? Subtle cues affect generosity in an economic game. *Evolution and Human Behavior, 26*, 245–256.

Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience, 2*, 194.

Kacelnik, A. (2012). Putting mechanisms into behavioural ecology. In P. Hammerstein, & S. J. Stevens (Eds.), *Evolution and the mechanisms of decision making* (pp. 21–38). Cambridge, MA: The MIT Press.

Kempermann, G., Kuhn, H. G., & Gage, F. H. (1997). More hippocampal neurons in adult mice living in an enriched environment. *Nature, 386*, 493–495.

Kolodny, O., Edelman, S., & Lotem, A. (2014). The evolution of continuous learning of the structure of the environment. *Journal of the Royal Society Interface, 11*, 20131091.

Kolodny, O., Edelman, S., & Lotem, A. (2015). Evolution of protolinguistic abilities as a by-product of learning to forage in structured environments. *Proceedings of the Royal Society B, 282*, 20150353.

Kotrschal, A., & Taborsky, B. (2010). Environmental change enhances cognitive abilities in fish. *PLoS Biology, 8*, e1000351.

Kümmerli, R., Burton-Chellew, M. N., Ross-Gillespie, A., & West, S. A. (2010). Resistance to extreme strategies rather than prosocial preferences, can explain human cooperation in public good games. *Proceedings of the National Academy of Sciences USA, 107*, 10125–10130.

Lehmann, L., & Keller, L. (2006). The evolution of cooperation and altruism—a general framework and a classification of models. *Journal of Evolutionary Biology, 19*, 1365–1376.

Leimar, O., & Hammerstein, P. (2010). Cooperation for direct fitness benefits. *Philosophical Transactions of the Royal Society B, 365*, 2619–2626.

Lotem, A., & Halpern, J. Y. (2012). Coevolution of learning and data-acquisition mechanisms: A model for cognitive evolution. *Philosophical Transactions of the Royal Society B, 367*, 2686–2694.

Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge, U.K.: Cambridge University Press.

McNamara, J. M. (2013). Towards a richer evolutionary game theory. *Journal of the Royal Society Interface, 10*, 20130544.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution, 4*, 133–142.

Noë, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology and Evolution, 10*, 336–339.

Noë, R. (2001). Biological markets: Partner choice as the driving force behind the evolution of cooperation. In R. Noë, J. van Hooff, & P. Hammerstein (Eds.), *Economics in nature, social dilemmas, mate choice and biological markets* (pp. 93–118). Cambridge, U.K.: Cambridge University Press.

Pekár, S., & Brabec, M. (2016). Marginal models via GLS: A convenient yet neglected tool for the analysis of correlated data in the behavioural sciences. *Ethology, 122*, 621–631.

Pepperberg, I. M., & Hartsfield, L. A. (2014). Can grey parrots (*Psittacus erithacus*) succeed on a "complex" foraging task failed by nonhuman primates (*Pan troglodytes, Pongo abelii, Sapajus apella*) but solved by wrasse fish (*Labroides dimidiatus*)? *Journal of Comparative Psychology, 128*, 298–306.

Potts, G. F. (1973). The ethology of *Labroides dimidiatus* (cuv. & val.) (Labridae, Pisces) on Aldabra. *Animal Behaviour, 21*, 250–291.

Prétôt, L., Bshary, R., & Brosnan, S. F. (2016a). Comparing species decisions in a dichotomous choice task: Adjusting task parameters improves performance in monkeys. *Animal Cognition, 19*, 1–16.

Prétôt, L., Bshary, R., & Brosnan, S. F. (2016b). Factors influencing the different performance of fish and primates on a dichotomous choice task. *Animal Behaviour, 119*, 189–199.

Quiñones, A. R., Lotem, A., Leimar, O., & Bshary, R. (2019). *Reinforcement learning theory reveals the cognitive requirements for solving the cleaner fish market task* (Unpublished manuscript).

R Development Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org.

Randall, J. E., Allen, G. R., & Steene, R. C. (1997). *Fishes of the great barrier reef and coral sea*. Honolulu, HI: University of Hawai'i Press.

Roche, D. G., Kruuk, L. E. B., Lanfear, R., & Binning, S. A. (2015). Public data archiving in ecology and evolution: How well are we doing? *PLoS Biology, 13*, e1002295.

Russell, V. L. (2016). Least-squares means: the R package lsmeans. *Journal of Statistical Software, 69*, 1–33.

Salwiczek, L. H., Prétôt, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I., et al. (2012). Adult cleaner wrasse outperform capuchin monkeys, chimpanzees and orangutans in a complex foraging task derived from cleaner – client reef fish cooperation. *PLoS One, 7*, e49068.

Seligman, M. E. (1970). On the generality of the laws of learning. *Psychological Review, 77*, 406.

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (2nd ed.). Oxford, U.K.: Oxford University Press.

Triki, Z., Wismer, S., Levorato, E., & Bshary, R. (2018). A decrease in the abundance and strategic sophistication of cleaner fish after environmental perturbations. *Global Change Biology, 24*, 481–489.

Triki, Z., Wismer, S., Rey, O., Binning, S., Levorato, E., & Bshary, R. (2019). Biological market effects predict cleaner fish strategic sophistication. *Behavioural Ecology*. arz111. https://doi.org/10.1093/beheco/arz111.

Victor, B. C. (1986). Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Marine Biology, 90*, 317–326.

Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: The analysis of proportions in ecology. *Ecology, 92*, 3–10.

Wismer, S., Grutter, A., & Bshary, R. (2016). Generalized rule application in bluestreak cleaner wrasse (*Labroides dimidiatus*): Using predator species as social tools to reduce punishment. *Animal Cognition, 19*, 769–778.

Wismer, S., Pinto, A. I., Triki, Z., Grutter, A. S., Roche, D. G., & Bshary, R. (2019). Data for: Cue-based decision rules of cleaner fish in a biological market task. .

Wismer, S., Pinto, A. I., Vail, A. L., Grutter, A. S., & Bshary, R. (2014). Variation in cleaner wrasse cooperation and cognition: Influence of the developmental environment? *Ethology, 120*, 1–13.

Zentall, T. R., Case, J. P., & Berry, J. R. (2017). Rats' acquisition of the ephemeral reward task. *Animal Cognition, 20*, 419–425.

Zentall, T. R., Case, J. P., Berry, J. R., & Luong, J. (2018). The ephemeral reward task: Pigeons and rats fail to learn unless discouraged from impulsive choice. *Animal Behavior and Cognition, 5*, 169–180.

Zentall, T. R., Case, J. P., & Luong, J. (2016). Pigeon's (*Columba livia*) paradoxical preference for the suboptimal alternative in a complex foraging task. *Journal of Comparative Psychology, 130*, 138.

Appendix

The number of choices for the larger plate exhibited by cleaner fish in the first 10 trials of experiment 1 was significantly greater than five of 10 trials, i.e. above chance, irrespective of plate status. Back transformation (logit) verified that $P > 1/2$:

$$\text{Logit} = \log (P/1\text{-}P) > \text{or} = 0$$
$$P/1\text{-}\ P > 1$$
$$P > 1\text{-}\ P$$
$$2\ P > 1$$
$$P > \tfrac{1}{2}$$

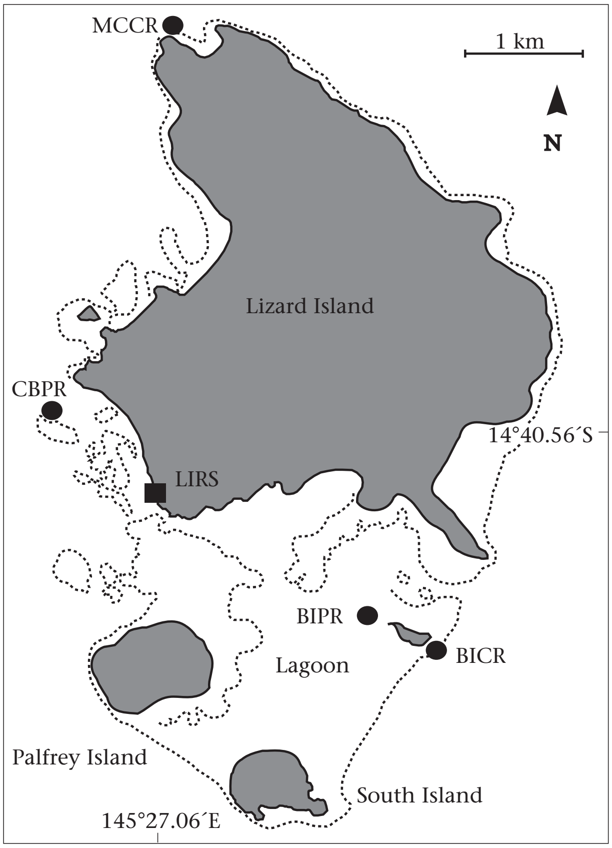


Figure A1. Lizard Island Group. Capture sites of cleaner fish are indicated by filled circles. Socially complex environments: Mermaid Cove continuous reef (MCCR) and Bird Island continuous reef (BICR). Socially simple environments: Corner Beach patch reefs (CBPR) and Bird Island patch reefs (BIPR). Juvenile cleaners were collected from all sites (2012: $N = 4$ from each site in 2012), while adults were only collected or filmed at Corner Beach patch reefs and Mermaid Cove continuous reef (2013: $N = 10$ from each site; 2014: $N = 8$ from each site). LIRS: Lizard Island Research Station .

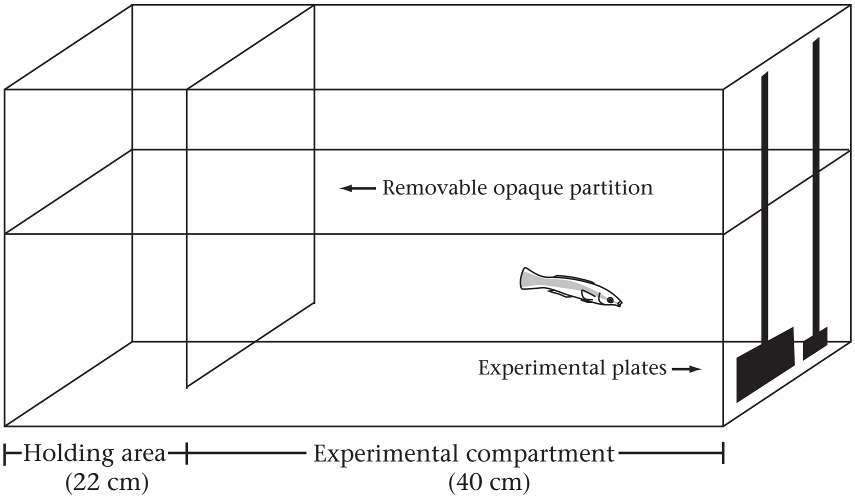


Figure A2. Experimental set-up used for adult cleaners. Both experiments used a similar aquarium arrangement: a cleaner holding compartment, an opaque removable partition and an experimental compartment containing the removable Plexiglas feeding plates. The illustration shows the size variation of Plexiglas plates in experiment 1 .

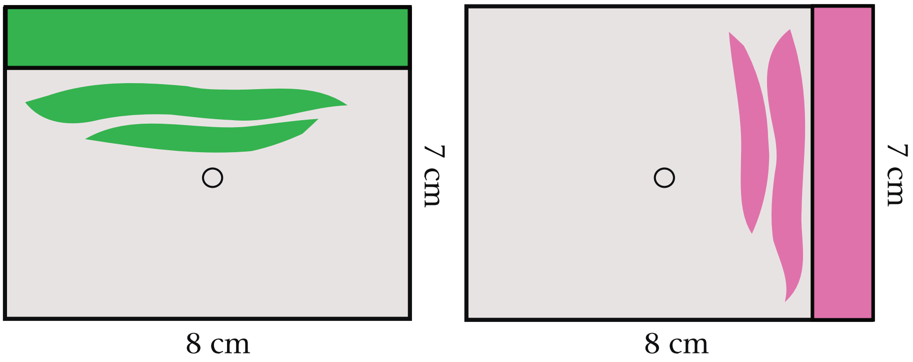


Figure A3. Experimental Plexiglas feeding plates used in a previously published biological market theory experiment (Wismer et al., 2014). Experimental plates were equal in size (approximately 7 x 8 cm), but differed in colour/pattern. A single food item (i.e. circle = mashed prawn, ca. 0.001 g) was always placed in the centre of the plate .

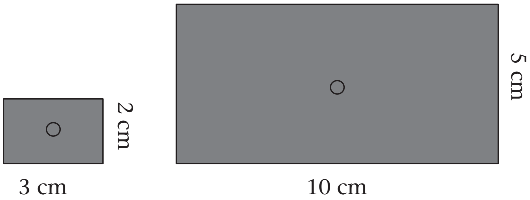


Figure A4. Experimental Plexiglas feeding plates used in experiment 1. Cleaner fish were always presented with one small and one large Plexiglas plate, which represented a visitor and resident client (visitor plate size was counterbalanced among cleaners). A single food item (i.e. circle = mashed prawn, ca. 0.001 g) was always placed in the centre of the plate .

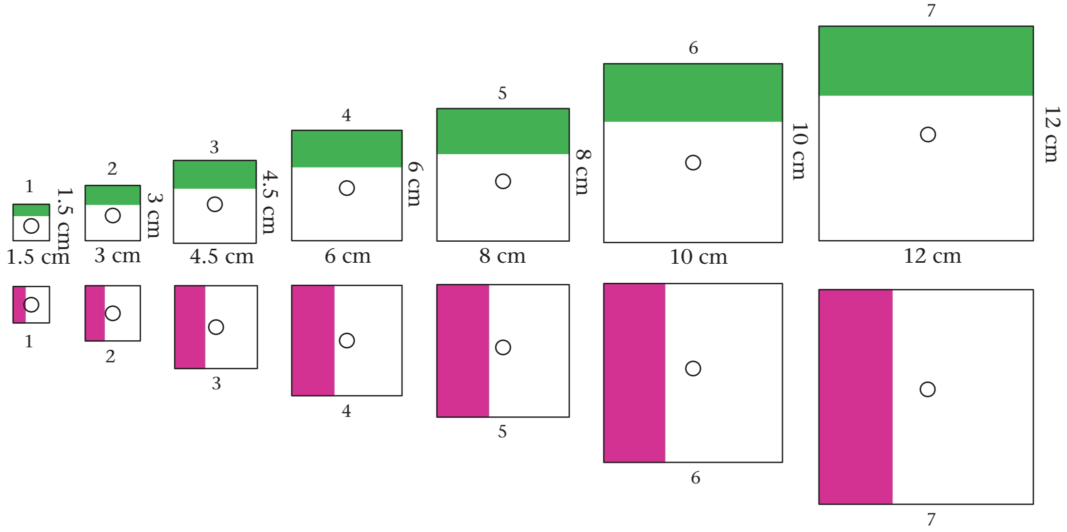
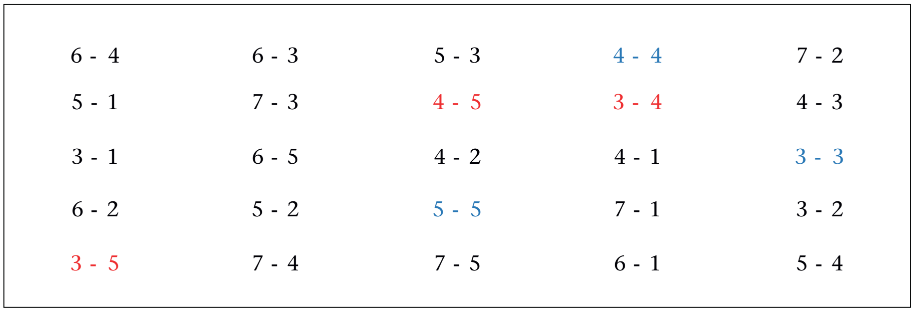


Figure A5. Experimental Plexiglas feeding plates used in experiment 2. Experimental plates were numbered 1 to 7, which corresponded to increasing plate size. Cleaner fish were always presented with one green and one pink Plexiglas plate, which represented a visitor and resident client (visitor plate colour/pattern was counterbalanced among cleaners), in various size combinations that were in proportion to the natural environment (see Figure A6). A single food item (i.e. circle = mashed prawn, ca. 0.001 g) was always placed in the centre of the plate. Numbers below (pink) and above (green) plates represent plate size IDs .



6 - 4	6 - 3	5 - 3	4 - 4	7 - 2
5 - 1	7 - 3	4 - 5	3 - 4	4 - 3
3 - 1	6 - 5	4 - 2	4 - 1	3 - 3
6 - 2	5 - 2	5 - 5	7 - 1	3 - 2
3 - 5	7 - 4	7 - 5	6 - 1	5 - 4

Figure A6. An example of one unit of 25 plate size combinations used in experiment 2. Numerical values represent plate size IDs (see Figure A5). The visitor plate size is always listed first. For the visitor plate, we used sizes 3–7, while we used sizes 1–5 for the resident plate. Red values show pairings where the visitor plate is smaller than resident plates; blue values show cases of equal sizes (i.e. 12% and 12%, respectively). All cleaners were exposed to a total of 200 trials, consisting of 8 x 25 unique plate pairing sequences .

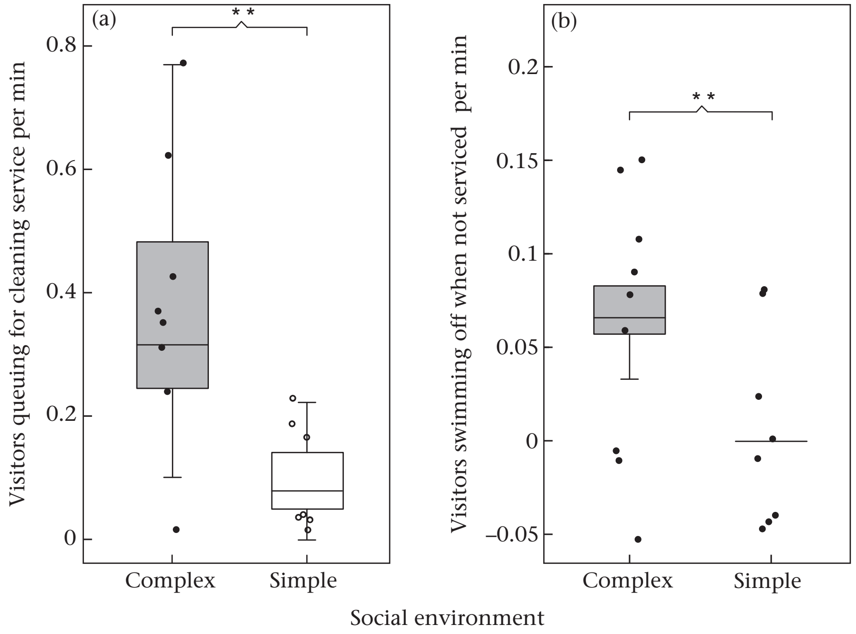


Figure A7. Learning opportunities available to cleaners under natural conditions. Box plots show the number of visitor clients per min (a) queuing for cleaner service and (b) swimming off when not serviced. $^{**}P < 0.005$. Box plots show the median (horizontal line within the limits of the box), interquartile range (box limits), maximum–minimum values (whiskers) and data points (circles) .

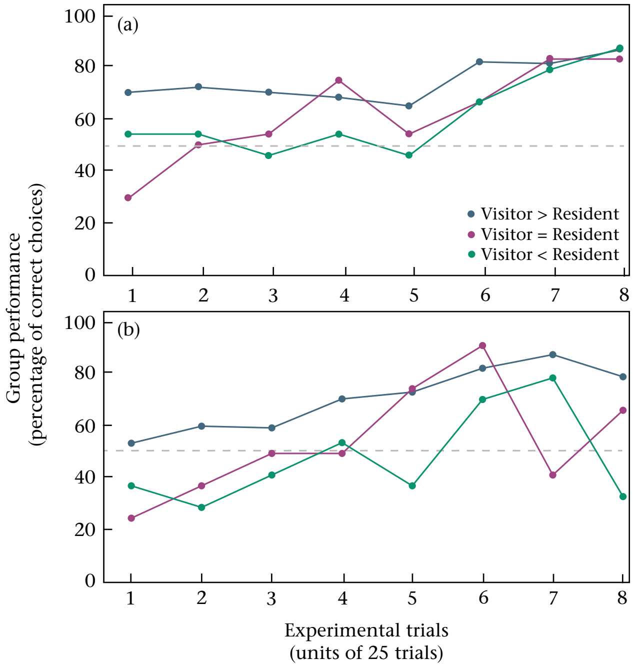


Figure A8. The performance of cleaner fish from (a) complex and (b) simple social environments in experiment 2. Values show the mean percentage of correct choices of cleaner fish ($N =$ per treatment group) per units of 25 trials (i.e. 8x units of 25 trials in total of 200 trials) in situations where the visitor plate was larger than (blue), equal in size to (pink) and smaller than (green) the resident plate. The dashed lines indicate the expectation if cleaner fish chose at random, i.e. 50% .