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Configural learning by cleaner fish in a complex biological market task

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Individuals engaged in cooperative or mutualistic interactions can benefit from adjusting their strategic behaviour according to the bargaining positions of their partners. In interaction networks in which individuals cooperate with a variety of partners, assessing partners' options and expected interaction payoffs might be crucial for such behavioural optimization to occur. However, the cognitive challenges involved in this assessment and the constraints they may pose for strategic behaviour are currently poorly understood. Here, we investigated whether cleaner fish, *Labroides dimidiatus*, can learn to optimally prioritize partners, when faced with an ecologically relevant challenge that requires them to distinguish between interaction contexts. We expanded on a relatively well-studied problem that cleaners face in nature: choosing between client fish that simultaneously seek service. In such situations, cleaners should give priority to visitor client species as these tend to leave if not serviced immediately, while resident species will readily await inspection. In laboratory 'biological market' experiments simulating this choice using ephemeral and permanent food-offering plates, cleaners could learn to prefer visitors. However, the actual challenge cleaners face is more complex: interactions in the reef form a 'complex market' whereby clients appear in all possible configurations. In homogeneous configurations (visitor–visitor and resident–resident), the payoffs received from tending residents are higher which may slow down or even prevent learning to prioritize visitors. Adjusting the plate paradigm to this more complex scenario, we found that exposure to homogeneous configurations indeed posed a challenge to cleaners' strategic prioritization, diverting their preferences towards residents. Our results also revealed individual differences in performance, as some cleaners still learned to prefer visitors. This suggests that cleaners may not only learn about each client type separately, and that learning about cue configurations, a precursor of learning complex structures, may play a role in shaping their strategic behaviour in cooperative interactions.

Cooperative interactions in which animals engage in mutually beneficial exchanges of services or commodities involve conflicts of interest between participants whereby each party is tempted to increase its own payoffs, often at the expense of its interaction partners (Axelrod & Hamilton, 1981; Bshary & Bergmueller, 2008; Leimar & Hammerstein, 2010). Evolutionary game theory helps to explain how these conflicts are resolved such that stable cooperation can evolve and persist. The models typically assume that adaptive social behaviour is the product of natural selection operating on genetic strategies. However, environmental factors may often vary within an individual's lifetime, or on small spatial scales. Under such conditions, natural selection should favour the evolution of flexible behavioural adjustments rather than of fixed evolved strategies. Learning is a key feature of such flexibility, and recent models explore learning dynamics in game theoretical contexts based on the evolution of components like updating rules, error rates and memory loss (Dridi & Lehmann, 2015; Dridi & Akçay, 2018; Leimar & McNamara, 2019; McNamara & Leimar, 2010). While learning can guide decisions regarding the conditional strategies that should increase expected payoffs in a given social interaction, it may also have constraints that limit individuals' ability to properly modulate their behaviour. An investigation of the challenges animal face during social decision making and of the learning mechanisms that may help them to respond properly, can shed light on the constraints of strategic behaviour and the selective pressures that shape cooperation dynamics (Brosnan & Bshary, 2010; Brosnan et al., 2010; Fawcett et al., 2012; McAuliffe & Thornton, 2015; Wascher et al., 2018).

A potential challenge to learning about optimal strategic behaviours can arise when the payoff outcomes of a certain action

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vary between interaction contexts. The payoffs obtained may differ, for instance, if partners' behaviour changes with environmental or social circumstances, or if the presence of bystanders or potential future partners modifies the payoffs received (e.g. by disrupting interactions, Mielke et al., 2018; Suchak et al., 2016; by increasing future payoffs, Bshary & Grutter, 2006). In such cases, a failure to recognize the circumstances in which interactions occur as distinct from one another might inhibit individuals' ability to correctly associate the outcomes of their behaviours, and thus optimize the modulation of their strategies. Making a distinction between interaction contexts may resemble other types of contextual learning, whereby individuals need to learn (often in nonsocial circumstances) about combinations of cues or elements that signify the context and are not simply the sum of their components. This ability is often termed configural learning (Pearce, 2002; Sutherland & Rudy, 1989) or chunking (Gobet et al., 2001; Kolodny et al., 2015) and has been found in animals in different associative learning paradigms (e.g. Deisig et al., 2001; Devaud et al., 2015; Sutherland & Rudy, 1989). Learning about cue compounds is also considered essential for complex hierarchical structure learning and a prerequisite for advanced cognition and language acquisition (Conway & Christiansen, 2001; Goldstein et al., 2010; Kolodny et al., 2015). Here, we tested whether such learning may also influence cooperative strategies.

We experimentally simulated the challenges bluestreak cleaner wrasse, *Labroides dimidiatus*, regularly face in their mutualistic interactions with a diversity of 'client' fish. Cleaners feed on clients' ectoparasites (Arnal et al., 2001), and occupy 'cleaning stations' to which clients come to have their ectoparasites removed (Cote, 2000). Their interactions with clients form a biological market (Noe & Hammerstein, 1994, 1995), in which clients that compete over access to cleaners vary in their strategic options: client species can be categorized based on home range size as either residents, fish that are solely dependent on one station, or visitors, fish with access to two or more stations (Bshary, 2001). As cleaners engage in ca. 2000 interactions per day (Grutter, 1994), they frequently need to choose between two clients who simultaneously seek service (Bshary, 2001). Only visitors can exert partner choice in this scenario, and indeed often swim off if ignored (Bshary & Schaffer, 2002; Soares et al., 2013). In contrast, residents lack alternatives and hence are generally willing to wait for inspection. Cleaners can thus benefit from adjusting their service quality to partners' bargaining positions, as prioritizing visitors increases their food intake. This phenomenon has been observed both in nature (Bshary, 2001) and in laboratory 'biological market' experiments, in which cleaners readily learned to prioritize an ephemeral food-offering 'visitor' plate over a 'resident' plate that always remained available (Bshary & Grutter, 2002; Salwiczek et al., 2012; Triki et al., 2019; Wismer et al., 2014). Cleaners further outperform a range of other species in comparative studies based on this task (Salwiczek et al., 2012; Zentall et al., 2016; Zentall et al., 2017b, 2017a), although both African grey parrots, *Psittacus erithacus*, and capuchin monkeys, *Sapajus apella*, could solve some versions of it (Pepperberg & Hartsfield, 2014; Pretot et al., 2016b). It was suggested that cleaners' success in solving the market task and learning to prefer visitors may reflect the relevance of this task to their unique ecology (Salwiczek et al., 2012). Nevertheless, cleaners also exhibit substantial intraspecific variation in performance that relates to their previous experience in the natural environment. Juveniles fail to prioritize visitors, although they might eventually learn socially from adults to adjust (Truskanov et al., 2020). Adult performance is variable and depends on environmental factors that modify the likelihood that visitors would switch partners (Salwiczek et al., 2012; Triki et al., 2018, 2019, 2020; Wismer et al., 2014).

It has recently been suggested that configural learning is important for cleaners' success in prioritizing visitor clients (Quiñones et al., 2020). The reason for this is that encounters with clients in the reef form an extended or 'complex' market in which clients appear at the station at varying configurations (not only a combination of a visitor and a resident, but also homogeneous visitor–visitor and resident–resident pairs), and the payoffs obtained from choosing visitor versus resident clients differ between configuration types (Table 1). Quiñones et al. (2020) modelled this scenario using different types of learning rules. They showed that when learners do not differentiate between client combinations, encounters with homogeneous client pairs (in which tending residents is overall more profitable) are expected to divert their preferences towards residents thus hindering strategic prioritization. In contrast, learners that use configural learning and create a separate estimation for each interaction context successfully prioritize visitor clients, similarly to cleaners' observed behaviour in their natural environment (Quiñones et al., 2020). Here, we experimentally tested the predictions of this model by conducting experiments involving presentations of different combinations of equally rewarding food-offering model clients (Plexiglas plates) that adhered to the response rules of visitor and resident clients. Using this set-up, we first tested whether the complex market conditions would challenge cleaners' learning and hinder the prioritization of visitors. We then tested whether conditions that can potentially facilitate successful learning of cue configurations improved cleaners' performance in the complex market. As experiment 2 built on the results of experiment 1, we first describe general methods referring to both experiments and then present the specific methods and results of each.

GENERAL METHODS

Subjects and Housing

The experiments were conducted during autumn 2018 (experiment 1) and summer 2019 (experiment 2), at the Lizard Island Research Station, Great Barrier Reef, Australia. The fish that participated in the experiments were adult bluestreak cleaner wrasse that were caught in the reefs adjacent to the research station. The fish were captured using hand and barrier nets, transported to the laboratory, and individually housed in plastic aquaria containing a PVC pipe that served as a shelter. In these aquaria, the fish were gradually habituated to laboratory settings, and to feeding off model clients (Plexiglas plates) covered with smeared mashed prawn. This habituation phase lasted at least 2 weeks, following which the fish and their PVC shelters were transferred into experimental glass aquaria (62×27 cm and 37 cm deep). In these aquaria, the fish could acclimate for a few more days, during which they were trained to locate discrete food items on the plates and were habituated to the confining barriers that were later used in the experiments. Overall, 20 fish participated in each experiment. In both cases, there was a single fish that exhibited difficulties in habituating to the set-up and in feeding off the experimental plates, and therefore could not participate fully in the experiment. The final sample size in each experiment was therefore 19 cleaners.

Biological Market Experiments

Each experiment involved different variations of the 'biological market' task (Bshary & Grutter, 2002; Salwiczek et al., 2012; Triki et al., 2018, 2019; Wismer et al., 2014) in which cleaners are presented with a choice between two 'model client' types: Plexiglas plates that are equally rewarding (containing one visible prawn

Table 1
Payoffs associated with choosing visitor and resident clients in the simple and complex market conditions

Treatment	Plate combination	Choice	Reward sequence	Reward amount (no. of items)
Simple market	VR	V	V → R	2
		R	R	1
Complex market	VV	V	V	1
	VR	V	V → R	2
		R	R	1
	RR	R	R → R	2

When two clients simultaneously arrive at the cleaning station, visitor (V) clients are likely to leave if initially ignored, whereas residents (R) tend to await inspection. The overall payoffs cleaners obtain following their choice of whom to attend first are therefore configuration dependent: when the cleaners are faced with VR combinations, prioritizing the visitor leads to higher payoffs as it grants access to both clients, whereas choosing the resident would cause the visitor to leave. However, when the two clients belong to the same category, the payoffs obtained from tending residents are generally higher: initiating an interaction with a resident in RR combinations allows the cleaner to interact with the second resident as well. In contrast, interacting with a visitor client in VV combinations is less profitable as the nonchosen visitor will leave.

item) but differ in their willingness to await inspection. Resident plates are 'permanent' and accessible regardless of the order in which they are being approached. Visitor plates, on the other hand, are 'ephemeral', that is, unwilling to wait, and are removed from the aquarium if not approached first. In our experiments, both plate types were attached to handles, allowing the experimenter to quickly remove them when necessary. Visitor and resident plates were identical in size, but markedly differed in their colour patterns (see further details below), and their roles were counterbalanced between cleaners.

In the basic form of the biological market task (hereafter referred to as the 'simple market'), the cleaners are always presented with a choice between resident and visitor plates. Under these conditions, prioritizing visitors is clearly beneficial as it increases expected payoffs, enabling the cleaner to consume the food items off both plates (see payoff matrix in Table 1). The 'complex market' version used in our study is a modification of this basic task which better expresses real-life challenges: rather than only facing trials involving a choice between either a visitor or a resident plate, the cleaners were faced with a more ecologically plausible scenario involving all the possible combinations of the two client types. The different plate combinations were presented in a scrambled order, and their frequencies followed those expected under random pairing, whereby 50% of the experimental trials involved the presentation of a mixed visitor–resident plate combination (VR), and the other trials were equally divided between 25% homogeneous visitor–visitor (VV) and 25% resident–resident (RR) plate combinations. Note that in encounters with homogeneous plate combinations, the choice itself has no meaning as the two plates look identical and will respond in the same way: in a VV situation, the nonchosen visitor will leave, whereas in the RR case, the nonchosen resident will remain available. Nevertheless, due to these response rules, RR situations yield double the amount of reward compared to VV situations (see Table 1).

In both experiments, trials were carried out in two daily morning and afternoon sessions (each comprised half of the daily trial quota), divided by a ca 1 h break. Within each session, the trials were conducted in a continuous rotation between individuals. At the beginning of each trial, we confined the cleaner with a set of transparent and opaque barriers and placed the two plates at the other end of the aquarium. We first removed the opaque barrier, following which the cleaners would normally wait right behind the transparent barrier from where they could see the two plates. We would then remove the transparent barrier as well (this would normally take a few seconds), enabling the fish to swim towards the plates and choose which one to approach first. This process was generally rather quick; cleaners would 'dart' and swim towards the plate area, and we did not observe any clear differences in their approach speed between plate combinations. Once the cleaner made its choice by consuming the item on top of a plate, the other plate would 'respond' according to its role: a resident plate would stay, whereas a visitor plate would be removed.

In some cases, cleaners refrained from choosing between the two plate types. When this occurred, the experimenter would wait for up to ca. 20 s before removing the plates from the aquarium, and the missing trial would be repeated later. The instances in which cleaners exhibited reduced motivation to interact with the plates could be a result of neophobia, particularly at the beginning of the experiments/treatments when the cleaners were less familiar with the specific plates being used. Alternatively, it could also be a result of satiation due to the accumulated number of food items consumed. To reduce the chances that the fish would be satiated (which could affect the appeal of choosing the visitor and receiving more food rewards in the VR combinations), the plates were the cleaners' sole food source during the experiments, and trials were conducted in rotation with a minimum 10 min interval between consecutive trials. Note that experiencing a continuous flow of interactions further matches cleaners' ecology; in nature, clients appear at cleaning stations continuously, and cleaners have been reported to engage in ca. 2000 interactions per day. Nevertheless, even if satiation did affect the fish's behaviour to some extent, it is unlikely to create any consistent differences between treatments in our experiments.

Ethical Note

This study was performed in accordance with the guideline of the Animal ethics committee, Queensland, Australia (approval numbers: CA 2018/07/1209 and CA 2019/06/1286). Capture of wild animals is likely to induce some temporary stress. Nevertheless, cleaners habituate well to captivity; they eat well and do not hide from human experimenters, thus allowing direct observations. The experiments themselves were noninvasive and can be seen as a type of behavioural enrichment. At the end of the experiments, the cleaners were released in their habitats of origin.

EXPERIMENT 1

The goal of experiment 1 was to assess whether complex market conditions may pose a challenge for cleaners' learning, by testing the influence of encounters with homogeneous model client pairs (VV and RR) on cleaners' success in prioritizing visitors in the biological market.

Experimental Design and Procedures

Twenty cleaners participated in two consecutive experimental phases, each comprising a different treatment (a paired design, order of treatments counterbalanced). In the 'complex market' treatment, the cleaners were presented with all the possible combinations of visitor and resident plates: 140 presentations of a mixed VR combination, 70 VV and 70 RR trials. In contrast, in the 'simple market' control, the same cleaners were presented only with mixed VR pairs (140 trials) but received similar amounts of food as in the complex market treatment as generic, colourless plates containing one or two food items replaced the VV and RR trials of the complex market (70 trials with each food quantity). Overall, each cleaner participated in 280 trials per treatment, and a total of 560 trials over the experiment.

This design served a dual purpose. First, it allowed us to assess the influence of encounters with homogeneous pairs on cleaners' preferences, thus testing their ability to distinguish between different plate combinations and update their preferences based on the configuration in which the plates (or clients) appear. If, as predicted by Quiñones et al. (2020) cleaners can indeed make this distinction, we would expect that their preferences in the VR trials of the two treatments would not differ substantially as their experience with mixed-plate combinations is similar. If, however, distinguishing between client configurations is challenging, then experience with homogeneous plate combinations in which encounters with residents are more rewarding may divert the cleaners' preferences towards the resident plates. Second, the 'simple market' control provided us with a baseline measure of cleaners' performance. In previous studies, variation in performance in this task correlated with the social complexity of cleaners' habitats and further translated into the types of cues being used (Triki et al., 2018, 2019; Wismer et al., 2019). It is hence plausible that variation in habitat complexity would influence cleaners' success, and perhaps even the learning rules applied in the complex market. Inferences made based on cleaners' performance in the complex market treatment can thus be better informed by considering the level of strategic sophistication the same cleaners exhibited in the simple market control.

In each treatment, the cleaners faced a different set of visitor and resident plates (plate size: 7×9 cm) and needed to learn the regularities associated with them. Plate colours were switched between experimental phases (yellow/green in the first phase, white/pink in the second phase). Treatment order and the role assigned to each plate type were both counterbalanced between cleaners. Each experimental phase lasted 10 days, in which 28 trials were split between morning and afternoon sessions. The number of presentations of the different plate combinations was kept constant within each day: 14 mixed plate pairs (VR) and seven trials of each of the other possible plate combinations: seven VV and seven RR in the complex market treatment or seven one-item plates and seven two-item plates in the simple market treatment (supplementary food plates were not marked with colours, and their size was 5×8 cm). The order in which the different combinations were presented within the day was semirandomized: randomly determined via a computer program, but with the restriction that no more than three trials of the same type were conducted consecutively. In VR trials, plate side was counterbalanced between trials to reduce the likelihood that the fish would develop a bias towards one of the sides of the aquarium.

After the first experimental phase was over, we allowed the fish to rest for 1 day, and then started running the second phase with a pair of black and red plates. After 2 days in which it seemed that the fish, regardless of their treatment group, were strongly biased towards one of the plate colours (black), we decided to terminate this experiment, and start again with a new set of plate markings (white and light pink). Therefore, if treatment order had a significant effect on our results, we would not be able to tell if this is due to an effect of cleaners' experience in the first experimental phase on their performance in the second, an effect of this intermediate phase or both. Colour biases were further exhibited in the second experimental phase (the cleaners tended to prefer the plate marked in white). Nevertheless, as the roles of the plates were counterbalanced between treatments, this bias could not have led to a significant effect of the experimental treatment.

Statistical Analysis

Statistical analysis was conducted in R version 3.5.1 (R Core Team, 2016) statistical software. To test differences in learning dynamics between treatment groups, we conducted a generalized linear mixed model (GLMM; R package lme4, Bates et al., 2015) with a binomial distribution in which cleaners' binary choices in the mixed pair (VR) combinations served as the dependent variable (i.e. for each cleaner, the input to the model was a set of 280 binary choices between V and R, 140 for each experimental treatment). The predictors that were added to the model included the treatment group (complex or simple market), treatment order (phase 1 or 2), experimental day within each phase (standardized using the scale() function in the base R package), and all two-way interactions between these variables. Fish identity was fitted as a random intercept. Experimental day within fish identity was fitted as a random slope, quantifying variation between individuals in the change in preference over time, and was retained in the model after we verified that including it improves model fit (by comparing models with and without the random slope using the anova() function). No fixed predictors were dropped from our analysis and the reported P values of the global model were extracted using the function Anova() from the R car package. Model's diagnostics were checked using residual plots and the normality of residuals for the random effects was examined using qqplots and Shapiro–Wilk tests.

We further assessed the performance of the cleaners in each treatment by testing whether their overall preferences differed from those expected by chance. For this purpose, we a priori split the data into two: an initial sampling phase (VR trials 1–70 within each treatment) and a subsequent preference phase (VR trials 71–140) and conducted our analysis on the latter. We used the R emmeans function to extract the significance of the visitor preferences in each treatment from a GLMM based on cleaners' binary choices in the preference phase (the last 80 trials in each treatment), while adjusting the P values using the Bonferroni correction method. Finally, in addition to group level analysis, we also analysed the cleaners' individual performance: In each treatment, we tested the significance of the plate preference of every individual cleaner using two-tailed binomial tests. We then assessed whether the frequencies of cleaners with significant preferences in the two treatments (eight cases of individuals that clearly preferred the visitor plate and seven in which individuals preferred the resident) differed from those expected by chance using Fisher's exact test.

Results

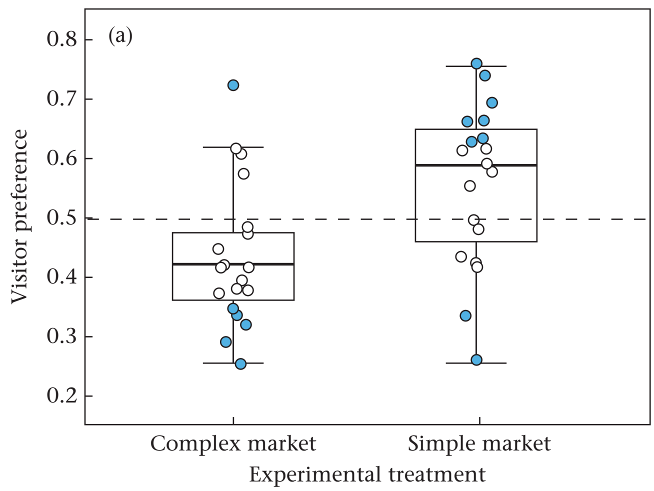
Complex market conditions challenge cleaners' learning

Our results reveal a clear negative effect of complex market conditions on cleaners' strategic prioritization (Model A, Table 2, Fig. 1a). Exposure to homogeneous model client pairs (VV and RR) influenced cleaners' choices in VR trials, hindering their success in prioritizing visitors and diverting their preferences towards the resident plates. Treatment differences were also exhibited in the

Table 2
Predictors influencing cleaners' plate preferences in the two experiments

Model	*N*	Effects	χ^2	*df*	*P*
A	19 (paired design)	Treatment	40.693	1	**<0.0001**
		Experimental day	0.99	1	0.319
		Treatment order	2.667	1	0.102
		Treatment*experimental day	4.19	1	**0.040**
		Treatment*order	0.298	1	0.585
		Experimental day*order	6.094	1	**0.013**
B	19	Treatment	1.07	1	0.301
		Test day	22.968	1	**<0.0001**
		Treatment*test day	0.258	1	0.611

Generalized linear mixed models exploring the effects of different predictors on cleaners' choices between the two plates in the mixed visitor–resident trials of experiment 1 (model A) and of the test phase of experiment 2 (Model B). In both models, the dependent variable was the cleaners' binary choices in the visitor–resident trials and 19 cleaners were tested. The models included intercepts (not shown) and, in both, fish identity was added as a random effect. In model A, the slope of day within fish identity was further added as a random predictor. Significant *P* values (<0.05) are in bold.



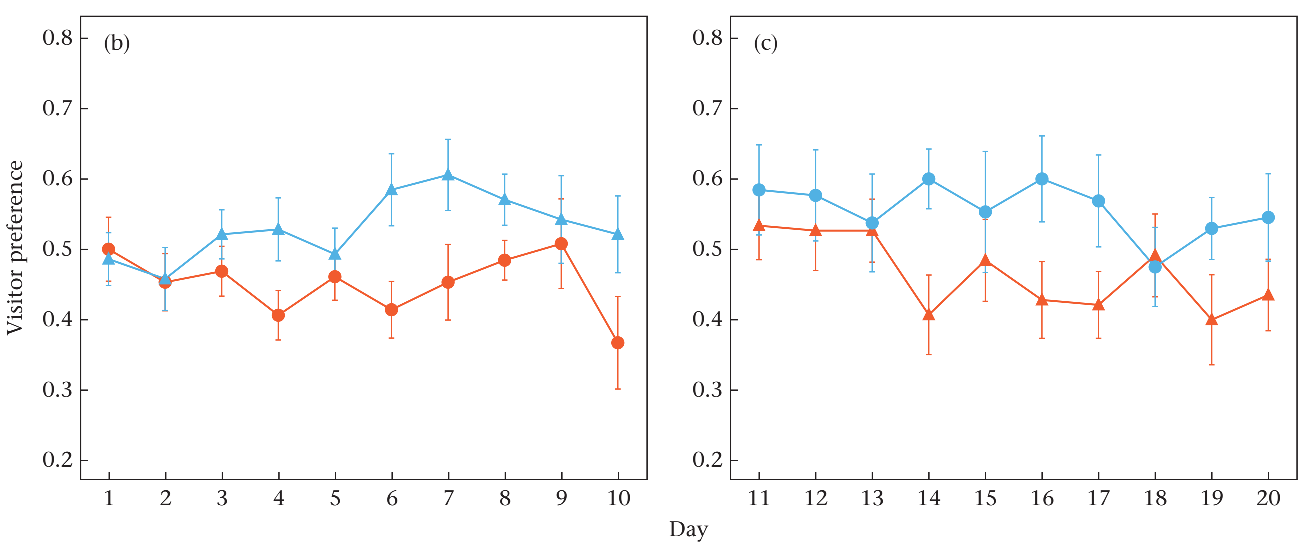


Figure 1. Cleaners' preference for the visitor plate in visitor–resident (VR) trials of experiment 1. (a) Cleaners' overall preferences in the second half of the complex and simple market treatments. Box plots show the median and interquartile range, whiskers denote 1.5×interquartile range and dots mark individual data points. Blue dots mark individuals that exhibited significant preferences for one of the two plate types. The dashed line marks the preference score expected by chance (0.5). $N = 19$ fish in both treatments. (b, c) The cleaners' daily average preferences (mean ± SE) in (b) the first and (c) second experimental phases. The complex market treatments appear in red and the simple market controls in blue. Dots mark the cleaners that started with the complex market treatment and then transitioned to the simple market ($N = 9$). Triangles mark the group of cleaners for which the order of treatments was reversed ($N = 10$).

cleaners' learning trajectories: the preferences in the two treatments gradually diverged during the experiment, as indicated by the significant interaction between the treatment group and experimental day (Model A, Table 2, Fig. 1b and c). The interaction between treatment order and day was also significant, suggesting that there were some differences in the learning process between the first and second experimental phases (Model A, Table 2). Taken together, these results suggest that differentiating between cue configurations is not trivial for cleaners and that exposure to the ecologically relevant contextual challenge ingrained in the complex market task can indeed hinder their strategic prioritization of clients.

An analysis of the cleaners' choices in the second half of each experimental phase revealed that in the simple market control, overall group performance was higher than expected by chance ($Z = 2.49$, $P = 0.026$) while in the complex market treatment, the cleaners preferred the resident plate (($Z = -2.66$, $P = 0.016$; Fig. 1). On an individual level, binomial tests performed on the choices of each cleaner reveal that the number of fish that significantly preferred the visitor plate was seven versus one in the simple and complex market treatments, respectively, while the number of fish that preferred the resident plate was two versus five. The single solver in the complex market group manifested its preference from very early stages. Therefore, we cannot rule out the possibility that this preference was a by-product of an initial bias towards this plate rather than due to learning the food-optimizing choice. The distribution of solvers and nonsolvers in the two groups differs from that expected by chance (Fisher's exact test: $P = 0.040$).

EXPERIMENT 2

After establishing in experiment 1 that complex market conditions where resident and visitor clients appear in all possible combinations can be challenging to cleaners, we were interested in whether modification of the sequence in which cleaners are exposed to the client combinations may affect their success in solving this task. Theoretical work on chunking processes predicts that repeated exposure to relevant configurations in a small time window, can help learners to make a better distinction between meaningful combinations of elements (Goldstein et al., 2010). We therefore hypothesized that initial exposure only to VR combinations might allow the cleaners to better distinguish between VR and the other client combinations of the complex market. According to this possibility, such initial exposure would make the cleaners more resilient to the difficulty posed by the complex market and prevent their visitor preferences from declining in the same way as these preferences decline when cleaners face only complex market conditions.

Experimental Design and Procedures

In experiment 2 we exposed a new batch of 20 cleaners to different initial training regimes, and then tested them under complex market conditions. In the ‘complex market prior’ group, the initial training involved presentations of all the potential combinations of visitor and resident plates: 80 VR trials, 40 VV and 40 RR trials. In the ‘simple market prior’ treatment, the cleaners were exposed only to VR trials, 160 in total. Thus, while the cleaners in both treatments were exposed to the same number of visitor and resident plates, in the simple market treatment this experience was channelled into VR trials only, allowing us to test how this boosted experience may influence success in the complex market test phase. This differs from the design of experiment 1 where the amount of exposure to the VR combination was kept constant. While it could have provided the cleaners of the simple market prior treatment with an additional initial advantage in learning to prefer visitors, we should nevertheless expect that unless they manage to distinguish between configurations, this advantage would gradually disappear as their preference declines following exposure to VV and RR combinations in the complex market test phase. Therefore, while we did compare the performance of the fish in both treatments, the focus of our analysis was on the change in preference over time during testing, in both groups.

Training lasted 6 days and the number of trials per day differed between days, as the fish took time to adjust to the set-up and some of them initially refused to approach the plates and participate in the trials. This caused substantial delays and therefore we conducted fewer trials on the first few days than initially planned (on the first day, we conducted 20 trials, while on day 6 there were 32) and the training phase also lasted longer than planned. The distribution of trials was kept similar across days (i.e. in the complex market prior group, the different plate combinations were constantly mixed and to a similar extent). A single pair of plates marked with either green or pink stripes (size: 7×10) was used in this experiment. Plate roles were counterbalanced between individuals and were kept constant throughout the experimental phases.

At the end of the initial training phase, the cleaners in both treatments participated in a complex market test phase. Testing lasted 5 days with 32 trials on each day: 16 VR, eight VV and eight RR, presented in a scrambled order. Altogether, during the test phase the cleaners experienced 80 VR, 40 VV and 40 RR trials. During the experiment itself, we noticed that some cleaners, in both treatments, did manage to develop/maintain a significant preference for the visitor plate, even under complex market conditions. As we were interested in the extent to which these preferences remained stable, we decided to test these individuals in an additional test phase, similar in length and format to the original test (i.e. 80 VR, 40 VV and 40 RR trials presented to the fish over a 5-day period). The cleaners were selected to participate in this additional test phase based on their earlier performance, using criteria for assessing success in solving the market task that were implemented in previous studies: we divided the VR trials into blocks of 10 trials each, and defined cleaners with a ‘solving potential’ as cleaners that chose the visitor plate nine or 10 times in a single block, at least eight times in two consecutive blocks or at least seven times in three consecutive blocks of choices. Any cleaner that reached these criteria during the test phase, the last four blocks of initial training, or both, was chosen to participate in the additional test phase (this involved three individuals from the complex prior group and four from the simple prior one).

Statistical Analysis

Our main analysis of the results of this experiment involved a GLMM (R package lme4, Bates et al., 2015) with a binomial distribution in which cleaners' binary choices in the mixed pair (VR) combinations of the complex market test phase served as the dependent variable (80 binary choices for each cleaner). The experimental treatment (prior training of complex or simple market), testing day (standardized using the scale() function in the base R package) and the interaction between the two were added to the model as fixed predictors. Fish identity was added as a random factor. The slope of day within fish identity was initially added to the model as a random effect but was removed as adding it did not improve model fit. Similarly to experiment 1, no fixed predictors were removed and the P values reported were extracted using the Anova() function. The model's diagnostics were checked using residual plots and the normality of residuals for the random effects was examined using a qqplot and a Shapiro–Wilk test. The emmeans function again enabled us to extract the significance of the preferences in each treatment during this test phase.

To assess the integrity of the initial training regimes, we tested whether the preferences of the cleaners in the two treatments diverged at the end of the initial training phase, as anticipated by our experimental design. To that aim, we conducted a generalized linear model with a quasibinomial distribution (to account for overdispersion in a binomial version of the model) in which we tested whether the training regime affected the cleaners' choices of the visitor versus the resident plates at the last 40 VR trials of the initial training.

Finally, we also analysed the cleaners' individual performance in both the complex market test phase and the additional test phase and assessed the significance of their preferences using two-tailed binomial tests. To verify that cleaners that preferred the visitor plate in the test phase were not simply biased towards this plate from the start (which would hence suggest that their preference was not learned), we used a paired *t* test to compare their preferences at the beginning and end of the initial training (the first and last 40 VR trials) and assess whether they were indeed modified along the trials. The normality of the difference between these two measures was verified using a Shapiro–Wilk test.

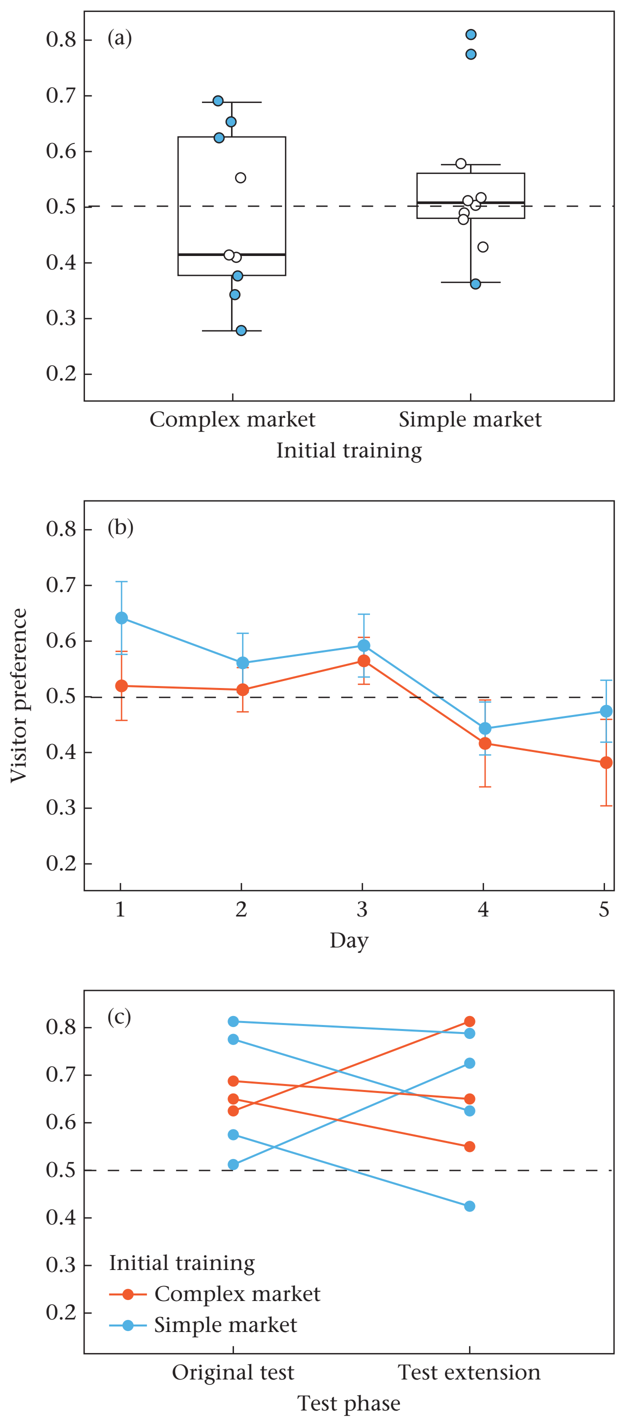


Figure 2. The effect of initial training regime on cleaners' preference for the visitor in the test phase of experiment 2. (a) Cleaners' overall preferences during the test. Box plots show the median and interquartile range, whiskers denote 1.5×interquartile range, dots mark individual data points. Blue dots denote individuals that exhibited significant preferences for one of the two plate types. (b) Cleaners' daily average preferences (mean ± SE) in each treatment during the test phase. (c) The performance of 'solvers' in the original and additional test phases. In (b, c) the complex prior group ($N = 9$) appears in red and the simple prior group ($N = 10$) in blue. The dashed line marks the preference score expected by chance (0.5).

Results

Effect of initial exposure to mixed client pairs

Contrary to our expectations, we found no effect of initial experience on cleaners' preferences. The group level performance in both treatments did not differ substantially, and neither of them exhibited a clear preference for one of the two plate types in the test phase (Model B, Table 2, Fig. 2a). Furthermore, the preference for the visitor plate in both treatments declined during testing and hence the interaction between treatment group and experimental day was not significant (Model B, Table 2, Fig. 2b). This suggests that initial exposure to the VR combination did not make the cleaners in the simple prior treatment more resilient when faced with complex market conditions. An analysis of cleaners' choices in the last 40 VR trials of pretraining revealed that in contrast to experiment 1, this training did not generate clear differences between the two groups (GLM: χ^2=0.476, $P = 0.49$; Fig. A1). Thus, the lack of a treatment effect in the subsequent complex market test could also stem from the fact that our initial training did not seem to influence cleaners' behaviour.

Learning to prefer visitors in the complex market

A closer look at individual performance in the test phase revealed that some of the fish in both treatments did develop and maintain a preference for the visitor plate despite the potential confusion of the complex market. Seven individuals exhibited a preference for the visitor plate and for five of them this preference was statistically significant according to a binomial sign test: three individuals in the complex prior treatment and two in the simple prior group whose performance was particularly strong compared to the rest of the individuals in this treatment (see coloured dots in Fig. 2a). These preferences were maintained overall and remained above chance level in the additional test phase (Fig. 2c). Furthermore, these preferences did not seem to result from initial biases and hence were learned during the course of the experiment: a comparison of the preferences of these cleaners at the beginning and end of the initial training (the first and last 40 VR trials of pretraining) reveals that their preferences were significantly increased as they gained experience with the task (paired *t* test: $t = -4.835$, $P = 0.003$).

DISCUSSION

In this study, we asked whether cleaners can use configural learning to solve the contextual challenge that they face in their natural environment when having to choose between clients that seek service simultaneously. In contrast to previous experiments conducted on cleaners and a variety of other species (Bshary &

Grutter, 2002; Pepperberg & Hartsfield, 2014; Pretot et al., 2016a, 2016b; Salwiczek et al., 2012; Triki et al., 2018; Triki et al., 2019; Wismer et al., 2014; Wismer et al., 2019; Zentall et al., 2016; Zentall et al., 2017a, 2017b), we exposed cleaners not only to the visitor–resident configuration (in which one model client is ephemeral and the other is permanent) but also to visitor–visitor and resident–resident configurations, referring to the paradigm as a 'complex market'. Our experimental approach precluded the use of various cues that cleaners could potentially use in nature to prioritize a visitor over a resident, including systematic differences in client body size, familiarity or approach distances, and focused only on the difference in response between the two client types. Our results suggest that 'complex market' conditions can hinder cleaners' success in strategically prioritizing partners based on their expected responses: in both of our experiments, exposure to all the possible combinations of visitor and resident model clients gradually diverted the cleaners' average preferences towards residents. Such a result can be expected in the absence of configural learning, as the resident–resident combinations increase the mean value of the resident option, while the visitor–visitor combinations decrease the mean value of the visitor option, countering the effects of exposure to visitor–resident combinations. Nevertheless, our results further reveal individual differences in performance, and show that some cleaners did manage to cope with this challenge, learned to prefer the visitor plate and maintained this preference over time. In fact, some successful learners were never exposed to the simple market condition, which shows that chance fluctuations leading to longer visitor–resident sequences are not needed to solve the complex market, contrary to our hypothesis tested in the second experiment. Thus, despite the apparent difficulty, learning about cue configurations may indeed play a role in shaping cleaners' strategic decision making.

The results of our two experiments reveal three levels of success in solving the biological market task. The first level involves failure to solve the simple/basic market, which applies to most species tested so far. The second level involves the ability to solve the simple market but not the complex market. Interestingly, and in contrast to the results of the model of Quiñones et al. (2020), this suggests that learning about cue configurations is not essential for solving the basic form of the biological market task. When presentations of visitor and resident clients always invoke the same context (of VR combinations), taking chains of actions and rewards into account suffices, as in the case of 'chaining' models (Enquist et al., 2016; Kolodny et al., 2014; Quiñones et al., 2020). This level has been shown for African grey parrots as well as for capuchins in modified versions of the standard market task (Pepperberg & Hartsfield, 2014; Pretot et al, 2016a, 2016b). The third category of task solvers that appeared in our study involves the five fish in experiment 2 that solved the complex market task, apparently using cue configurations to develop/maintain a preference for the visitor plate. Thus, these results suggest that cleaners differ not only in their success in learning to prioritize visitors, but also in the extent to which they manage to take configural information into account. It would be interesting to test African grey parrots and capuchins on this more complex version.

Previous work suggests that cleaners' performance in the simple market task is influenced by the conditions in the reefs in which they were captured. Cleaners from rich habitats with high cleaner and client densities perform well in this task, whereas cleaners from poor or degraded habitats (in which visitor clients have fewer options and are less likely to leave if ignored) exhibit difficulties in learning to prioritize visitors in the laboratory (Wismer et al., 2014). In fact, low performance in the simple market task has recently become the norm in fish captured in our study site, where the reefs were negatively impacted by two cyclones and major coral bleaching events (Triki et al., 2018; Triki & Bshary, 2019). Apparently, the wild-caught cleaners bring their previously learned decision rules to the laboratory experiment (Wismer et al., 2019; Triki et al., 2020), and one feature of cleaners caught from low-density sites is that they tend to prioritize clients based on their size, which is a correlate of client choice options (Bshary, 2001). This could potentially explain the large number of individuals that failed to solve even the simple market task in both of our experiments (as our plates did not differ in size). It would be interesting to test a population of cleaners that perform well in the original market on the complex market paradigm to determine to what extent performance in the two is linked. Cleaners from the Maldives could perhaps be used for this purpose, as they still perform well in the original market (Paula et al., 2019).

A future experiment could also run more trials per individual. As it stands, the exposure to the different combinations in our experiments, and in particular in experiment 2, was limited compared to the learning opportunities cleaners encounter in nature. Studies in other species indicate that learning about cue configurations is challenging, may take longer than learning about simple associations, and the probability of its success differs substantially between individuals (Duncan et al., 2018). Triki et al. (2019) estimated that cleaners face choices between two clients about 120 times per day, yielding thousands of learning opportunities per month. Thus, even slow learning of configurations by cleaners would yield success in the complex market eventually and conducting longer experiments may help us to better assess the extent to which such learning is prevalent.

In nature, cleaners tend to prioritize visitors and can in principle use various shortcuts to express this preference despite the complex market conditions. Most notably, client body size is positively correlated with both its quality as a food patch (Grutter & Poulin, 1998) and home range size (visitors tend to be larger, Bshary, 2001). In previous laboratory experiments the decisions of cleaner fish were indeed affected by size (Grutter et al., 2005; Wismer et al., 2019). Additional/alternative shortcuts could be a preference for novelty (in contrast to adults, juveniles mostly clean residents, Triki et al., 2019) and/or for clients that cleaners see approaching from far away rather than simply staying in the vicinity of the station. Nevertheless, only configural learning would yield the most precise distinction between residents and visitors (although these options are not necessarily mutually exclusive, and in principle the abovementioned factors could also help cleaners in making the distinction between configurations).

In the learning models by Quiñones et al. (2020), configural learning is assumed to be either present or absent. In the former case, individual differences in performance stem from attributes of the learning process that are unrelated to the ability to take cue configurations into account (such as variation in experience with each configuration type). Nevertheless, if individuals vary in their propensity to learn about cue configurations, this can also translate into variation in their visitor preferences. For instance, it is possible that individuals 'learn to chunk' and that the identification and representation of compound units as meaningful emerges slowly through experience (Goldstein et al., 2010; Kolodny et al., 2015) and precedes learning of the statistical regularities that are associated with these units. Further theoretical investigation of the learning process that leads to configural representation can shed new light on the factors underlying the documented individual differences in cleaners' performance in the complex market and generate novel predictions for experimental work.

Finally, the ability to distinguish between configurations, or create 'chunks' in memory, has been suggested to play a key role in processes that require learning about complex structures in nonsocial contexts: from foraging in structured environments, problem solving and expert learning to human language acquisition (Gobet et al., 2001; Kolodny et al., 2015). Our results suggest that ecological needs posited by the social environment may also allow such abilities to evolve. Learning about configurations of elements and distinguishing between interaction settings can thus play a role in shaping strategic decision making in cooperative contexts.

Author Contributions

N.T. and R.B. designed the study; N.T., S.P. and Y.E. conducted the experiments; N.T. analysed the data and led the writing. All authors discussed the results and commented on the manuscript.

Data Availability

The data used for this study are available at: https://doi.org/10.6084/m9.figshare.16635346.

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Appendix

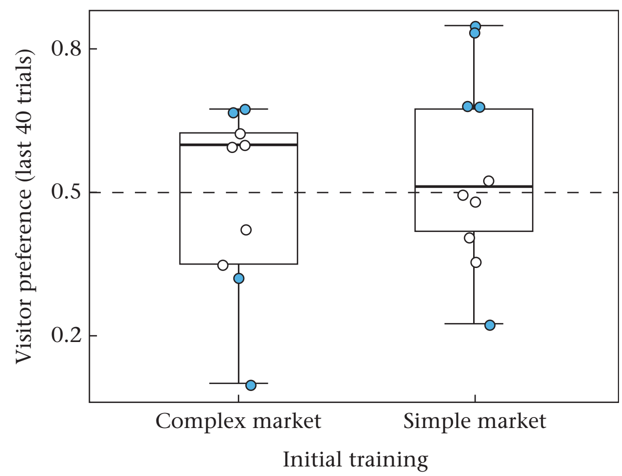

Figure A1. Preferences of cleaners in the complex and simple market prior groups at the end (the last 40 VR trials) of the initial training phase in experiment 2. Box plots show the median and interquartile range, whiskers denote 1.5×interquartile range, dots mark individual data points. Blue dots denote individuals that exhibited significant preferences for one of the two plate types. The dashed line marks the preference score expected by chance (0.5).