



RESEARCH PAPER

Cleaner Wrasses Keep Track of the 'When' and 'What' in a Foraging Task¹

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Abstract

In recent years evidence has accumulated that at least some animals can remember the 'what', 'where' and 'when' of personal experiences. Currently, evidence for such ability is taxonomically restricted to birds and mammals. Here, we demonstrate for the first time that cleaner wrasses *Labroides dimidiatus* are able to remember *when* they interacted with *what* after a single event. In nature, cleaners remove ectoparasites from other reef fishes, so-called clients. Clients are depleted, non-stationary food patches at the end of an interaction and replenished only after a delay. In our experiments, we presented twelve cleaners every 2.5 min, a choice between two of a total of four plates with different colours and patterns. One plate was always accessible but contained a non-preferred food item while the other three contained a preferred food item, but allowed a next feeding event only after 5, 10 or 15 min. Thus, to maximise food intake, cleaners had to remember for each choice *when* they had last interacted with *which plate*. When confronted with two plates offering preferred food, cleaners showed an overall significant preference for the plate that allowed access during the trial. For six cleaners, the preference was significant. Also, on trials involving the always accessible plate, cleaners discriminated between trials in which they had to eat the non-preferred food and trials on which they could eat the preferred food. In conclusion, cleaners are able to track the 'when' and 'what' (or possibly 'who') within a biologically meaningful time period.

Introduction

For many animals, the ability to adapt their behaviour to temporal aspects of re-occurring situations is essential, thus temporal control is ubiquitous (e.g., Matell & Meck 2004). Best studied are biological rhythms, for example, in daily foraging activities (circadian) or migration (circannual) and the like, which are genetically coded and do not necessarily involve any cognitive abilities. The situation, however, changes when animals have to measure time intervals to respond to a specific situation appropriately depending on the time elapsed. For example,

the ability of interval timing evolved in nectar-feeding species like bumblebees and hummingbirds increasing their foraging efficiency: freely moving individuals adapt time of return (*when*) to the replenish rate of stationary, spatially dispersed (*where*), rapidly depleted food sources, which will replenish after predictable time intervals (e.g., Boisvert & Sherry 2006; Henderson et al. 2006; Boisvert et al. 2007).

Recently cognitive, developmental and especially comparative psychologists have become interested in an animal's capacity to make choices based on temporally dated event memories defined as long-term

memories of past events that cannot be retrieved via familiarity (Tulving 1972; Clayton & Dickinson 1998). These approaches differ from previously described designs of depleting nectar sources in that the animal is 'stationary', and cannot decide when to return to a food source, but is forced to make decisions after an unpredictable time interval has elapsed. A first breakthrough was achieved with the demonstration that Western Scrub-jays (*Aphelocoma californica*) can recall *which item* ('what') they have hidden *where* and *when* (4, 24 and 124 h ago) (e.g., Clayton & Dickinson 1998, 1999; Clayton et al. 2001, 2003; de Kort et al. 2005). The birds coherently memorised all features after only a single caching event. Episodic memories might involve more detailed information than what-where-when memories, that is *who*. Only three species have been tested on this feature yet: a chimpanzee significantly remembered *who* had hidden which type of food where (Menzel 1999); a male gorilla would remember *who* had handed him which type of food (Schwartz et al. 2002); and scrub-jays can keep track of *who* was watching *when* they cached *which item where* (Dally et al. 2005, 2006). Other mammal (e.g., rats, mice) and bird species (e.g., pigeons, chickadees, magpies) have been tested for single-trial what-where-when memories (e.g., Babb & Crystal 2005; Roberts 2006; Skov-Rackette et al. 2006; Zinkivskay et al. 2009), but with mixed results mainly due to ambiguity of the *when* component and/or lack of ecological salience (for reviews and discussions see Salwiczek et al. 2008, 2010).

Here, we conducted some initial experiments to investigate cognitive time management abilities of cleaner wrasses (*Labroides dimidiatus*) in a working memory task (i.e., learning after a single trial; Shettleworth 2010) based on the ecology of this species. Cleaners are territorial and maintain a 'cleaning station' where other freely roaming reef fishes – so-called clients – will congregate at various times to get ectoparasites removed (reviews: Côté 2000; Bshary & Côté 2008). Ectoparasites constantly re-infect clients, and clients therefore visit cleaning stations up to 144 times per day (Grutter 1995). Cleaners have about 2300 interactions per day (Grutter 1995), and often two or more clients seek inspection simultaneously (Bshary 2001). Each client can be viewed as a renewable food resource: the parasites are largely depleted at the end of an interaction, but the client becomes 'replenished' (i.e., re-infected) after a delay. It is conceivable that time of replenishment varies with client species as there is a great variation in parasite loads (Grutter 1995) and home

range size. For a cleaner to optimise its foraging success, remembering time intervals between successive visits of the same individual client may help in making the correct choice. Indeed, it was observed in the field that a cleaner may ignore a returning client that had briefly swum away a few meters after the cleaner had terminated the interaction (R. Bshary, pers. obs.). To be able to avoid relatively parasite-free clients, cleaners would have to remember over a series of interactions the time elapsed since their last interaction with several clients in parallel.

We tested in the laboratory whether wild-caught adult cleaners can keep track of *with which food source (what or whom)* they interacted *when* in an optimal foraging task. We used four Plexiglas plates, distinguishable by colour patterns, as substitutes for real clients to conduct properly controlled experiments. Client plates were presented in pairs in all possible combinations, and each time the cleaners had to choose one to feed from. The problem to solve was that the client plates differed in their accessibility. One plate provided a safe option, in that it was always accessible. However, it offered only a less-preferred food item. In contrast, the other three plates offered a preferred food item but they would be removed prematurely (e.g., before the cleaner could eat off them) by the experimenter (LHS) unless a minimal time interval had elapsed since the cleaner's last feeding interaction. Minimal time intervals differed between the three plates, being 5, 10 or 15 min. The sequence of paired plates was such that whenever we presented two plates offering preferred food there was a 50% chance for each being the correct choice (see methods for details).

We asked the following questions. First, can cleaners as a whole learn to choose the accessible of two preferred food containing plates in a series of trials? If so, does their performance differ between the three possible combinations, that is 5- vs. 10-min interval, 5- vs. 15-min interval and 10- vs. 15-min interval? We also analysed data per individual to test whether there would be any evidence for individual performance above chance levels. Second, we asked how cleaners performed when given the choice between the safe low-quality plate and a high-quality plate. We assumed that cleaners could develop three different strategies: generally prefer the safe but low-quality option, generally prefer the high quality but risky option or adjust choice according to whether or not the high-quality option is accessible. The latter result as well as above chance correct choices during the presentations of two high-quality plates would provide evidence for the cleaners'

ability to remember the 'what' (i.e., which plate) and 'when'.

Methods

Animals

Twelve cleaner fish were collected around Lizard Island, Great Barrier Reef, Australia, between 4 and 9 June 2004 using a barrier net and hand-net. Fish were placed in sealed plastic bags underwater and transported to the laboratory. They were singly housed in aquaria ($90 \times 37 \times 60 \text{ cm}^3$) with continuously running sea water. Visual barriers between aquaria prevented cleaners from observing the experiments of others. Six cleaners had participated in game theory experiments (Bshary et al. 2008), while the other six individuals were naïve with respect to the general experimental procedure, namely the feeding of small food items off Plexiglas plates. All individuals started to feed from the plates by the second day.

Training

We trained the cleaners to feed off the four Plexiglas plates ($9 \times 3 \text{ cm}^2$). To be individually identifiable each plate was marked with coloured adhesive foil stripes arranged in different patterns (Fig. 1). The plate marked with red stripes was invariably used as

the safe option offering less-preferred food. For a cleaner, less-preferred food is fish flakes mixed with mashed prawn in a volume ratio of 1:3 (hereafter called 'flakes'). The other three plates offered preferred food, namely mashed prawn (Bshary & Grutter 2005); in the experiments, cleaners could only feed off them after predetermined time intervals since the last cleaning interaction (see below). On each plate, a single food item was placed in the centre of a circle (1 cm) outlined with a black permanent ink marker. Flakes had a brownish colour, which made them visibly distinguishable from the whitish prawn items in addition to the different taste (L. H. Salwiczek, pers. obs.). All food items were similar sized and $<1 \text{ mm}^3$.

Once cleaners consistently ate off the plates, the training phase began. The goal of this phase was to give cleaners the opportunity to learn the time contingencies of each plate. To use the 5-min minimal time interval plate as an example, in a first session it was presented seven times at 5-min intervals, and hence cleaners were allowed to eat the offered 'prawn' item. After an hour, the 5-min interval plate was then presented 13 times together with the red low-quality plate every 2.5 min, where the optimal solution was to start feeding off the 5 min interval prawn plate and then alternate from trial to trial. Sides of plate presentation and consequently of rewards were counterbalanced. Once an individual succeeded on trials with the 5-min interval plate, that is chose it when it was accessible 5 min after the last interaction, and otherwise the low-quality plate, it was trained in the same fashion on the other two high-quality plates (i.e., time-colour contingencies). Sessions with a previously trained colour were interspaced to reduce forgetting. Once cleaners had learned to perform well with all three time-contingency intervals, the experiment started. The colour-time contingencies were counterbalanced between cleaners, so each plate colour was used three times as the 5-min, 10- and 15-min interval plates, respectively. Each individual received 2–3 sessions per day, separated by at least 2 h, on 3–4 successive days for each plate.

Experimental Procedure

Two cleaner fish were tested simultaneously in 30-min sessions containing a sequence of 13 trials separated by a 2.5-min inter-trial interval, with a choice between two plates per trial. The order in which such cleaner pairs were tested first or second was counterbalanced between sessions. In contrast

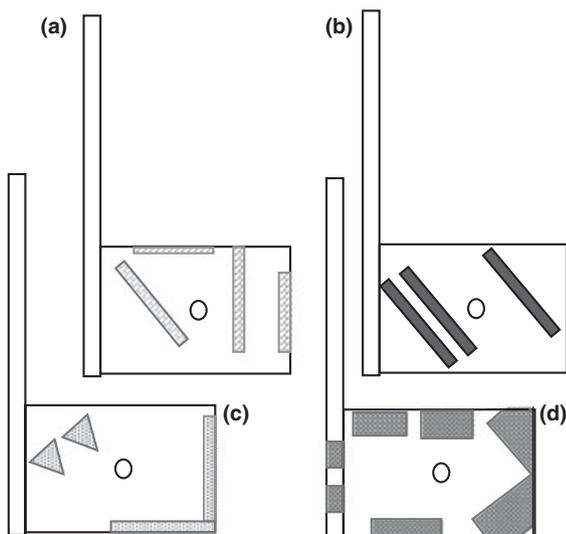


Fig. 1: Experimental Plexiglas plates replacing clients. Central circle outlined with a black permanent ink marker marked location of a single food item. Each plate was visually unique in colour stripes & stripe patterns. (a) blue plate, (b) green plate, (c) yellow plate, (d) red plate. a, b, c carried a prawn item, while d offered a flake item.

to the training, all four plates were used in each session. The aim was to present each of the three possible combinations of high-quality plates in a session, and across all sessions each high-quality plate was the correct choice on 50% of trials. The order in which the three combinations occurred in a session as well as their spatial presentation (left/right) was counterbalanced across all trials for each subject.

On the first trial of each session cleaners were free to choose from which plate to eat. Thereafter individuals could always eat freely from the low-quality plate that provided the less-preferred item 'flake', while they were only allowed to eat from high-quality plates on their first encounter and then after the appropriate minimum time had elapsed since last eating off that plate. Consequently, if, for example, the 10-min minimal time interval plate was presented 5 min after the cleaner had eaten off it and the cleaner approached it again, both the 10-min interval plate and the alternative plate were rapidly removed from the aquarium and the cleaner did not get any food reward. If the cleaner approached the 10-min interval plate after 10 or more min had elapsed, it was allowed to eat the prawn item. Session sheets containing the sequence in which pairs of plates were to be presented were prepared in advance. Nevertheless, some flexibility was necessary to accommodate possible consequences of a cleaner's current decision in one trial on future trials. To give a concrete example, if a cleaner chose the safe option in the first trial of the session where the safe option was paired with the 5-min interval plate (which offered preferred food), it would have had access to both the 5-min interval plate and the 10-min interval plate in the next trial 2.5 min later, although we generally aimed to offer such combinations only if one plate was correct and the other one false. For each kind of cleaner mistake in a sequence of trials, alternative plans for the next trials existed with the aim to keep balanced presentations of all colour/time combinations.

For each trial, the current location of the cleaner was determined and then the plates were inserted with the help of an attached lever at the side offering maximal distance to the cleaner, parallel to the aquarium wall and until the plates rested on the bottom. This increased the swimming distance before individuals had to make a choice. The experimenter (LHS) kept holding the levers to be able to respond quickly to cleaner choices. A choice was scored correct if the fish approached within 1 cm of the plate, which was indicated by black dots beneath the

aquarium. At that moment, if the fish had chosen the correct plate, it was allowed to eat the respective item; then both plates were removed completely and smoothly but without any chance for the fish to eat the item off the second plate too. If the subject approached the incorrect plate, that is a plate for which the minimal time interval since the last foraging episode had not yet elapsed, both plates were removed so rapidly that cleaners could not eat any item. Note that this methodology favours the null hypothesis that the fish are not able to solve the task; if a fish was close to the wrong plate, the removal meant that the trial was scored as 'wrong choice' even though it still might have turned away to swim to and eat from the correct plate instead. In contrast, choosing the correct plate was based on positive evidence, namely the fish eating the item off the plate. We assume that false scores for the 'wrong choice' were either absent or extremely rare as we never observed the opposite case of a fish approaching the correct plate within 1 cm without eating off it (and rather turning away to approach the other plate).

Data Analyses

We conducted both global analyses and analyses at the individual level. For the global analyses we simply tested a) whether a majority of cleaners chose the accessible plate more often than chance (50%) when given the choice between two plates offering preferred food and b) whether in trials that involved less-preferred and preferred food items a majority of cleaners chose the plate offering preferred food more often when it was accessible than when it was inaccessible. For the individual analyses, we first asked for each cleaner whether the probability of choosing the correct plate differed significantly from chance when given the choice between two plates offering preferred food. The criteria for individual learning were that cleaners had to choose correctly either on at least nine of ten trials, or 16 of 20, or at least 21 of 30 successive trials (with at least seven trials correct per ten trial sessions). Second, we asked whether on trials that involved less-preferred and preferred food items the choices differed significantly depending on whether or not the plate offering high-quality food was accessible. We conducted chi-square tests for each individual using Preacher (2001). Non-parametric tests were calculated with SigmaPlot 11, Systat Software, Inc., SigmaPlot for Windows, 40699 Erkrath, Germany.

Results

Interval Timing: Choosing the Correct High-Quality Plate

In a first global analysis combining all three treatments (5- vs. 10-min, 5- vs. 15-min and 10- vs. 15-min intervals), cleaners showed an overall significant preference for the plates that allowed them to forage (Wilcoxon Signed Rank test, $Z = -2.824$, $p = 0.002$, Fig. 2). On an individual level, six of twelve individuals performed correctly significantly above chance (chi-squared tests, all $df = 1$, chi-squared tests between 5.4 and 11.6, p -values between 0.02 and 0.0007). Overall, cleaners improved their performance significantly during the experiment (Fig. 3). All twelve individuals yielded positive correlations between 'block' and '% correct choices', of which eleven were significant (Spearman Rank correlations, N between seven and ten, r_s between 0.66 and 0.95, 11 significant results with p between 0.039 and 0.00006).

Because of the improvement in the performance documented above, we split the data sets for the individual plate combinations in half and analysed both initial performance (first half of the trials) and performance in the second half. The analyses revealed that the cleaners' performance did not differ significantly from chance levels in the first half (Wilcoxon signed rank tests, $N = 12$, 5 vs. 10: $Z = -1.29$, $p = 0.20$; 5 vs. 15: $Z = -1.89$, $p = 0.06$; 10 vs.

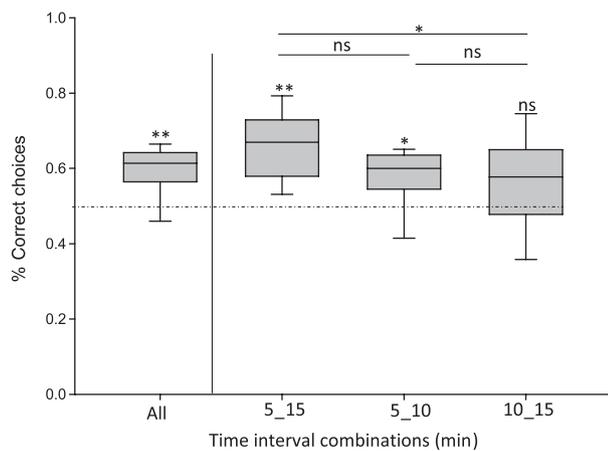


Fig. 2: Choice between two high-quality plates. All: analysis combining all three treatments (i.e., time interval combinations); 5_15/5_10/10_15: Choice between two high-quality plates, separate analyses of different recovery intervals [minutes]. N (individuals) = 12. Box: upper quartile, median and lower quartile. * $p < 0.05$, ** $p < 0.01$; ns: not significant. Dashed line: values expected if cleaners chose randomly (50%).

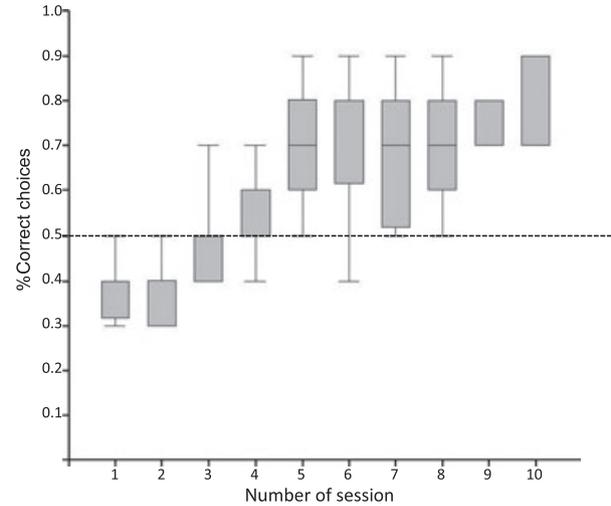


Fig. 3: Improving performance of cleaner wrasses ($n = 12$) based on % correct choices per session. Box: maximum, upper quartile, median, lower quartile and minimum. Dashed line: Percentage of correct choices predicted by chance (50%).

15: $Z = -1.63$, $p = 0.10$, Fig. 4). In contrast, the performance was significantly better than chance during the second half of the trials (Wilcoxon signed rank tests, $N = 12$, 5 vs. 10: $Z = -2.67$, $p = 0.008$, 5 vs. 15: $Z = -3.06$, $p < 0.001$; 10 vs. 15: $Z = -2.39$, $p = 0.017$, Fig. 4). The colours of the plates did not

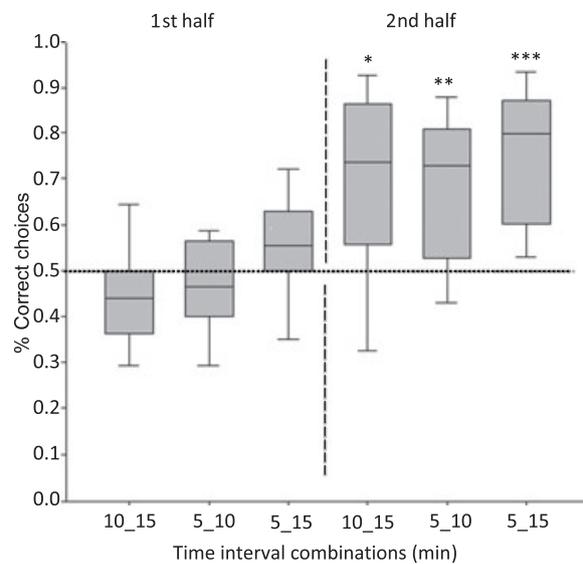


Fig. 4: Performance of cleaner wrasses ($n = 12$) based on % correct choices between two high-quality plates. Separate analyses for performance in the first half and second half of treatments (i.e., time interval combinations: 5_15/5_10/10_15), respectively. Box: maximum, upper quartile, median, lower quartile and minimum. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Dashed line: Percentage of correct choices predicted by chance (50%).

significantly influence the cleaners' choices (Friedman Repeated Measures Analysis of Variance on Ranks, $n = 12$, $\chi^2 = 2.667$, $df = 2$, $p = 0.264$), indicating that cleaners did not have any colour preferences or that any colour combination was more difficult than others.

Choosing Between a Safe but Unattractive Plate and an Attractive Plate

Overall, all twelve cleaners approached the attractive plate more often when it was accessible than when it was inaccessible, yielding an overall significant result (Wilcoxon Test, $n = 12$, $Z = -3.059$, $p < 0.001$, Fig. 5). On an individual level, eleven of twelve cleaners distinguished significantly between trials in which the high-quality plate was accessible and trials in which only the low-quality plate was accessible: they approached the high-quality plate significantly more often in trials in which it was accessible (Yates chi-square tests, all $df = 1$, chi-square between 4.85 and 44.4, individual p -values: $p_1 = 0.028$, $p_2 = 0.018$, $p_3 = 0.005$, all other individuals $p < 0.0001$). Only one individual failed to discriminate significantly (Yates chi-square test, $\chi^2 = 1.34$, $p = 0.24$).

Discussion

We asked whether cleaner wrasses were able to remember jointly the 'what' (*which client plate*) and

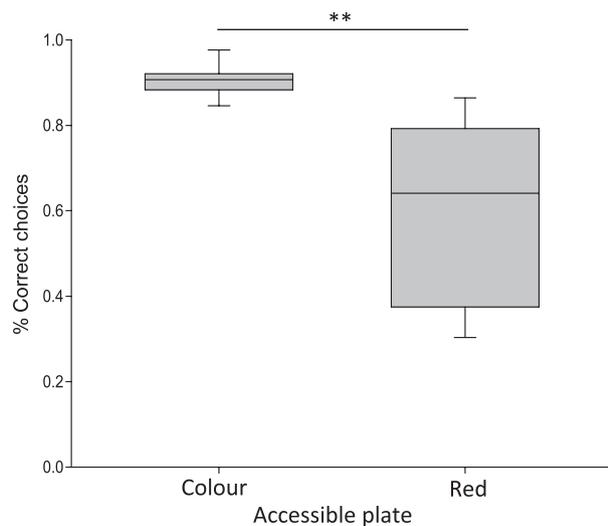


Fig. 5: Choosing between a safe but unattractive plate offering a flake item and a preferred high value plate offering a prawn item ($n = 12$). Prawn: choices if the high value plate was accessible; flake: choices if only the low value plate were accessible but not the preferred high value plate. Box: maximum, upper quartile, median, lower quartile and minimum. $**p < 0.01$.

'when' of past cleaning interactions based on a single prior interaction. To test for such a cognitive ability, a subject had to make a choice between two simultaneously presented 'client plates' that differed with respect to food items offered and/or with respect to minimal time interval from a foraging event to future accessibility. Overall, cleaners demonstrated control above chance in their approach behaviour to client plates with differing 'recovery' (i.e., accessibility) intervals. In principle, solving tasks involving the 5-min interval plate could have been achieved without measuring time: a decision rule that specified 'avoid the plate if it was accessed in the previous trial and access it otherwise' would have worked as well as using a mechanism that measures time intervals. Therefore, the most critical test was the combination of the 10-min and 15-min interval plates, because no such simple contingencies existed in this combination. The cleaner fish adapted their approach behaviour to the temporal characteristics specific for each client plate also in the 10- vs. 15-min plate trials; we therefore conclude that they can remember the *when* and *which plate* in a single-trial working memory task with time intervals ranging from 5 to 15 min.

Why Cleaners May Have Solved the Task

From a human perspective, our experiment tested the 'when' and 'what' because Plexiglas plates are objects. However, cleaner wrasses do not interact with inanimate objects under natural conditions but only with living reef fish clients. Plexiglas plates have been successfully used repeatedly in the past to address questions about cooperation and partner control mechanisms (Bshary & Grutter 2002, 2005; Bshary et al. 2008; Raihani et al. 2010), and results from Plexiglas plate experiments match results using real clients (Bshary & Grutter 2006; Pinto et al. 2011). We therefore consider it likely that the cleaners in our experiment perceived the plates as a social stimulus ('who') rather than as an object ('what').

Cleaners can individually recognise their clients (Tebbich et al. 2002). While the situation in the field is very complex with cleaner sometimes interacting with more than 100 species (Grutter & Poulin 1998), they adjust current service quality specifically to what happened during their last interaction with the very same client. For example, cleaners provide tactile stimulation to a client with their pectoral and pelvic fins significantly more often if their interaction with the current client ended aggressively

(Bshary & Würth 2001). In our experiments, cleaners regularly gave tactile stimulation to the plates, again indicating that the plates were perceived as a client, that is 'who'. Using an ecological approach to cognition as promoted by Kamil (1998) and by Shettleworth (2010), we consider it most likely that the cleaners' ability to remember the 'when' evolved as an adaptation to interspecific social interactions.

Remember Jointly the 'When' and 'With Which Client Plate'?

We had two experimental conditions: (1) two high-quality plates were offered simultaneously of which only one was accessible and (2) a high- and a low-quality plate were offered simultaneously but the high-quality plate was only accessible in 50% of trials. In both experimental conditions, cleaners overall performed above chance. As the presentations were counterbalanced with respect to correct choice and spatial cues, cleaners had to rely on the following information to solve the task. First, they must have learned that the three high-quality plates offered food only after a minimal time interval had elapsed since the last cleaning interaction and that these time intervals consistently differed between client plates, while the low-quality plate was always accessible. Second, to choose correctly in each trial, they had to recall *when* the last *cleaning interaction* with each high-quality plate had taken place in order; it was not enough to simply judge how recently a client plate had been seen, which renders it unlikely that the temporal content had been encoded in terms of familiarity. This is important because recency- or relative familiarity-based memories are distinct from recollection of episodic memories (e.g., Clayton & Dickinson 1999; Clayton et al. 2003; Easton et al. 2006). Further studies need to analyse the true nature of the cleaners' 'when-memory' (e.g., Clayton et al. 2003; Basile & Hampton 2011).

Towards Testing for Episodic-Like Memory in Cleaners

Furthermore, a demonstration of episodic-like memory (Clayton & Dickinson 1998) would require that the cleaner fish not only remember *when* it cleaned *which client (what or who)* and *when* an individual client will allow the next cleaning interaction, but also *which* type of a given item a client has been carrying the last time. To do so, the item ideally is not present during the test trial to prevent olfactory or visual

cuing (e.g., Clayton & Dickinson 1998). However, while in food caching designs already the inspection of certain locations can be used as behavioural indicators what has been memorised, a cleaning interaction in our fish model probably will only occur if the cleaner actually sees an item (i.e., 'parasite') to be removed. Thus, in the next step, one will have to test whether a cleaner would swim around the one client out of two presented it remembers to be accessible if the food item has been located on the side away – that is invisible – from the approaching cleaner. Like 'cache inspection' (e.g., Clayton & Dickinson 1998), such 'circling around a specific client' could be a behavioural indicator to demonstrate cleaners' memory for the type of food and accessibility; it might even allow to intersperse test trials completely without food.

The 'When' in Other Fish Species

Biological timing and time perception system act on multiple timescales that have a range of more than ten orders of magnitudes (i.e., ranging from milliseconds to years). Our experimental design is concerned with 'interval timing', that is control of timing intervals elapsed from some prior marker timing in the seconds-to-min range (Church 1984; Gallistel 1989). Little research has examined timing in fish and nearly all studies on temporal control in fish used fixed intervals (FI) between 10 and 240 s (e.g., Behrend & Bitterman 1964; Bitterman 1964; Rozin 1965; Wallace 1986; Talton et al. 1999; Higa & Simm 2004). Only one study, on the gourami *Helostoma temminckii* administered longer intervals schedules, that is FI of 10 and 20 min, respectively (Wolf & Baer 1963); unfortunately, this study is (a) based on a single individual and (b) does not provide any details on possible underlying timing mechanisms (see Talton et al. 1999), thus we cannot compare the results in more details.

Results from these few studies on timing in fish are mixed (for discussion see Higa & Simm 2004). The most likely explanation for such mixed results seems the lack of ecological validity of Pavlovian or operant procedures that employs highly artificial fixed-interval schedule paradigms to study properties and precision of timing. A common design is the 'peak procedure' that determines 'wait-time' of an individual until it returns to the stationary feeder; the individual has learned that the feeder will only provide food after a specific time interval has been elapsed and then only for a limited time (see Gibbon & Church 1990; Drew et al. 2005). Another reason

put forward is that 'wait-times', that is overall measures of responses during time intervals are not a sensitive measure of timing in fish because the subject's behaviour changes while 'waiting'. First, after being rewarded, response rates are very low and constant. After some time elapsed, a subject's response rate abruptly starts to increase exponentially; this 'point of rapid transition' (Schneider 1969, p. 677) has been called 'break point' and seems a more reliable measure of fish cognition (Talton et al. 1999; Higa & Simm 2004). Aside from the artificiality of the design and analyses flaws, 'waiting' means 'refraining from doing anything' and thus might rather measure impulse control but might say little about recall.

Our experimental setup was different and reflected the ecology of our study species. Cleaner wrasses in the field remain stationary waiting for their roaming clients to return to their cleaning station (Bshary & Schäffer 2002); once a reef fish arrives, cleaner wrasses can act based on their memories of the last interaction with the returning client. Similarly, our cleaner wrasses did not have to 'refrain from doing anything' while waiting until returning to a replenishing food source. Instead, and ecologically more valid, they had to make a choice when client plates were returned to their cleaning station (i.e., aquarium) based on their memory of the previous interaction and time elapsed. Thus, our subjects were not hampered by possibly low impulse control when forced to remain idle.

Feeding Against Preference and Temporal Control

To succeed on trials when faced with a choice between a low-quality and a high-quality plate, cleaners had to be able to feed half of the trials against their preference, that is to feed on the low-quality plate's flake rather than the high-quality plate's prawn. Eleven of twelve cleaners performed overall above chance, demonstrating their capability of inhibitory control to successfully overcome their own feeding preference. Bshary & Grutter (2005) found that it took cleaner overall only six learning trials to adjust their initial preference for prawn items towards feeding on flake if eating their preferred food would result in either being chased by or fleeing of the plate. This ability of inhibitory control actually formed the basis of other experiments on mechanisms that stabilise cooperation in this system (Bshary & Grutter 2006; Bshary et al. 2008; Raihani et al. 2010). Nevertheless, we note that the cleaners' performance was higher when the pre-

ferred food was the correct choice than when the non-preferred food was the correct choice (Fig. 5). For cleaners to restrain their foraging behaviour by choosing to feed against a preference appears to be easier than to solve the standard test for control of impulsiveness, the reverse-reward-contingency task, in which subjects need to choose the smaller of two food quantities to receive the larger one (Danisman et al. 2010).

Conclusions

Looking for 'what-where-when memory' (possibly including 'who memory') that cannot be explained by familiarity-based recollection (Clayton et al. 2003) is a first indicator for episodic-like memory in non-human animals. We provide first experimental evidence for cognitive interval timing in a fish species, specifically that cleaner wrasses can adjust their approach and cleaning behaviour based on remembering the *what* (or possibly *who*) and *when* within a biologically meaningful time period to improve service quality.

While it remains an open question how cleaners exactly manage to solve the task, for example how they keep track of the different time intervals, the presented results clearly support the hypothesis that cleaners remember the '*what*' and '*when*' memorised in a single, trial-unique cleaning event.

Our motivation for the current study was based on the ecology of our study species, which has many repeated interactions with a great variety of clients every single day (Grutter 1995; Bshary 2001). Therefore, our results strongly support the ecological approach to animal cognition, which states that the cognitive abilities of animals are best predicted by their environment rather than by recent shared ancestry (Clayton & Dickinson 1998; Kamil 1998; Bshary et al. 2007; Feeney et al. 2009; Shettleworth 2010).

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