Published in Ethology, Vol. 120, Issue 6, 2014, p. 519-531
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# Variation in Cleaner Wrasse Cooperation and Cognition: Influence of the Developmental Environment?

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**Keywords:** cleaner wrasse, cognition, cooperation, environment, game theory, *Labroides dimidiatus*, ontogeny

## Abstract

Deviations from model-based predictions of strategies leading to stable cooperation between unrelated individuals have raised considerable debate in regards to decision-making processes in humans. Here, we present data on cleaner wrasse (*Labroides dimidiatus*) that emphasize the importance of generalizing this discussion to other species, with the aim to develop a coherent theoretical framework. Cleaners eat ectoparasites and mucus off client fishes and vary their service quality based on a clients' strategic behaviour. Hitherto, cognitive tasks designed to replicate such behaviour have revealed a strong link between cooperative behaviour and game theoretic predictions. However, we show that individuals from a specific location within our study site repeatedly failed to conform to the published evidence. We started exploring potential functional and mechanistic causes for this unexpected result, focusing on client composition, cleaner standard personality measures and ontogeny. We found that failing individuals lived in a socially simple environment. Decision rules of these cleaners ignored existing information in their environment ('bounded rationality'), in contrast to cleaners living in a socially complex area. With respect to potential mechanisms, we found no correlations between differences in performance and differences in aggressiveness or boldness, in contrast to results on other cooperative species. Furthermore, juveniles from the two habitat types performed similarly, and better than the adults from the socially simple environment. We propose that variation in the costs and benefits of knowledge may affect a cleaners' information acquisition and storage, which may explain our observed variation in cooperation and cognition.

## Introduction

Evolutionary game theory and empirical evidence provide a variety of mechanisms for stable cooperation between unrelated individuals (Axelrod & Hamilton 1981; Conner 1986; Clutton-Brock & Parker 1995; Milinski & Wedekind 1998; Nowak & Sigmund 1998; Wedekind & Milinski 2000; Kiers et al. 2003; Bshary & Grutter 2005). Deviations from model-based predictions of strategies leading to cooperative behaviour have, however, raised considerable debate in regards to decision-making processes in humans (Gigerenzer & Selten 2002; Boyd et al. 2003; Lehmann et al. 2007; Kümmerli et al. 2010; Baumard et al. 2013). For example, in humans, some individuals behave more cooperatively (Fehr & Fischbacher 2003; Haley & Fessler 2005) or less cooperatively (Kümmerli et al. 2010), as well as less precise (Milinski et al. 2001) or more sophisticated (Milinski & Wedekind 1998), than predicted cooperative strategies in models. This mismatch has raised questions, sparked debate, and produced new concepts such as cultural group selection (Boyd et al. 2003; Lehmann et al. 2007). Most importantly, it has spurred research and debates regarding decision-making processes (Hagen & Hammerstein 2006; Baumard et al. 2013). For example, 'bounded rationality' proposes that humans develop simple heuristics, by constantly looking for environmental cues that would trigger a response that has worked well under previous similar circumstances (Gigerenzer & Selten 2002). This allows humans to by-pass information processing of any single situation and its unique complexity, and instead, apply a general rule of thumb strategy that is likely to result in the desired outcome. These general rules of thumb work well, yet are less precise and potentially even wrong in a different context (Gigerenzer & Selten 2002). An alternative proposal is that humans generally begin at intermediate cooperative levels and initiate extreme strategies only if feedback indicates their appropriateness (Kümmerli et al. 2010).

In non-human animals, research on decision-making is on the rise (Hammerstein & Stevens 2012), but few studies have focused on the decision rules underlying cooperative behaviour. As an exception, experimental research using the iterated prisoner's dilemma framework to study reciprocity, typically describes cooperative outcomes that are based on 'Tit-for-Tat-like' decision rules (start cooperatively and then match the partner's behaviour in the previous interaction) (Milinski 1987; Krams et al. 2008; Rutte & Taborsky 2008; St-Pierre et al. 2009; Raihani & Bshary 2011). However, in primatology, it has been recognized that precise counting reciprocal strategies, like Tit-for-Tat, do not typically fit observed interaction patterns (de Waal 2000). Unfortunately, alternative propositions, such as reciprocity based on emotional book-keeping ('I help as long as I like you'; Schino & Aureli 2009) have not been experimentally tested. Here, we demonstrate important mismatches between standard theoretical predictions regarding animal decisions during cooperative interactions and experimental data. We further present evidence that variation in the social environment may be of paramount importance in explaining deviations. Collectively, our results highlight the need for an interactive approach between empiricists and theoreticians to build a cooperation theory based on the mechanistics of decision-making.

The widely published cleaning mutualism of the bluestreak cleaner wrasse, *Labroides dimidiatus,* has provided strong experimental evidence for the usefulness of evolutionary game theory for predicting cooperative behaviour (Bshary 2011). Cleaner wrasse cooperate by eating ectoparasites off visiting client reef fishes. Conflict arises, however, as cleaner wrasse essentially prefer to eat client mucus, which constitutes cheating (Bshary 2011). The resolution of the resulting conflict depends on the clients' strategic options and may involve the threat of reciprocity by predatory clients, partner switching by visitor clients with access to several cleaning stations, and punishment by resident clients that lack cleaner choice options (Bshary 2011). Cleaner wrasse have shown to fine-tune service quality and priority to the clients' strategic options (Bshary 2011). Furthermore, cleaner wrasse behave more cooperatively in the presence of bystanders to raise their image score and hence, increase the probability of subsequently accessing bystanders (Pinto et al. 2011).

In a 4 mo project conducted in 2009, however, focusing on intraspecific variation, we failed to reproduce the results of published studies. The laboratory experiments involved the use of Plexiglas plates, prawn and fish flakes as substitutes for clients, mucus and ectoparasites, respectively. These substitutions have been used repeatedly before to successfully test game theoretic predictions on cooperation (Bshary & Grutter 2002, 2005, 2006; Bshary et al. 2008; Raihani et al. 2010, 2012), and the experimental design captures the essence of cleaning interactions, as key results can be reproduced in experiments using real cleaner – client interactions (Pinto et al. 2011) and because cleaners succeed in these tasks where both closely related non-cleaning species and otherwise cooperative primate species fail (Salwiczek et al. 2012; Gingins et al. 2013). In our 4 mo project, cleaner wrasse failed to eat selectively against their preference to prolong interactions. This contrasts with results published by Bshary & Grutter (2005) and various models that predict that partner switching or punishment/sanctions should promote cooperative behaviour (Bull & Rice 1991; Clutton-Brock & Parker 1995; Ferriere et al. 2002), that is, feeding on the less preferred food in our particular case. Cleaners also failed to learn to eat more against their preference to gain access to an 'image scoring bystander' plate as shown in Bshary & Grutter (2006) and predicted by image scoring theory (i.e. Nowak & Sigmund 1998). Finally, the cleaners failed to learn to prefer a 'visitor' plate unwilling to wait for inspection over a 'resident' plate that would only be removed once depleted. Such an ability would be predicted by biological market theory, where partner choice options determine a player's leverage, and hence, the amount or quality of services that it can obtain due to the partner's adjustment in behaviour (i.e. Noë 2001). For cleaners, this ability had been shown previously in the study described by Salwiczek et al. (2012) using the same methods, and field observations suggest likewise (Adam 2010).

In contrast to all previously published studies, these cleaner wrasse were caught on small, isolated reef patches rather than from nearby continuous fringing reefs. In parallel, an experimental study on cleaner pair inspections using cleaners from a continuous fringing reef produced results as expected from previous studies (Raihani et al. 2010). We therefore repeated the study with cleaner wrasse caught simultaneously from the isolated reef patches and from a continuous fringing reef to explicitly test the possibility that individuals from one specific location fail to conform to game theoretic predictions against the alternative that some hidden variable concerning animal housing or experimental procedure had caused the failure. Given repeatability of the previous results, we asked what factors may be linked to the differences. Therefore, at both sites, we quantified cleaner wrasse density, client fish density and diversity and observed natural interspecific interactions. Taken together, these data allow an assessment of the social environmental complexity. As patch reefs were small and sparsely distributed, we predicted that we would document a lower client density and diversity there.

Differences in social environmental complexity may potentially yield a functional explanation for any observed differences between cleaners from the two habitat types, but we decided to also start investigating potential mechanisms underlying the differences. On a phenotypic level, we asked whether cleaners from the two sites differ in aggressiveness and boldness, as these personality traits may be linked to cooperation and cognition (Milinski 1987; Mathieu et al. 2012). For example, if habitats differed in predator density that may affect boldness (cleaners exposed to fewer predators being bolder; see Dingemanse et al. 2007 for a study on sticklebacks) and differences in cleaner density may affect aggressiveness (i.e. starlings: Nephew & Romero 2003; salmon: Blanchet et al. 2006). Finally, we captured juveniles from the two habitat types (two locations from each type) and repeated the same laboratory experiments to assess whether there is any evidence for the importance of ontogenetic effects on cooperation and cognition. A lack of difference in performance between juveniles from the two habitats would suggest that the observed differences between adults are due to experience.

## Study Area

Our study was conducted at Lizard Island, Great Barrier Reef, Australia. Adult cleaner wrasse were observed and collected from two habitats: the continuous fringing reef at Mermaid Cove and the small patch reefs adjacent to Corner Beach (Fig. 1). The fringing reef at Mermaid Cove measures approx. 20 000 $m^2$ (depth 1–7 m) and is located in a small bay on the northern side of the island. Corner Beach patch reefs consist of approx. 50 small and isolated reef patches (depth 5–7 m), measuring 1–15 m in diameter and separated by at least 4 m of open sand. All laboratory experiments were conducted at Lizard Island Research Station. Due to the explorative nature of the study, we progressed step-by-step, collecting data on three different field trips. The first one in 2010 focused on laboratory experiments with adult cleaners. During the second in 2011, we collected information in the field, while the decision to test juveniles during the third trip 2012 was based on the results of the first two trips.

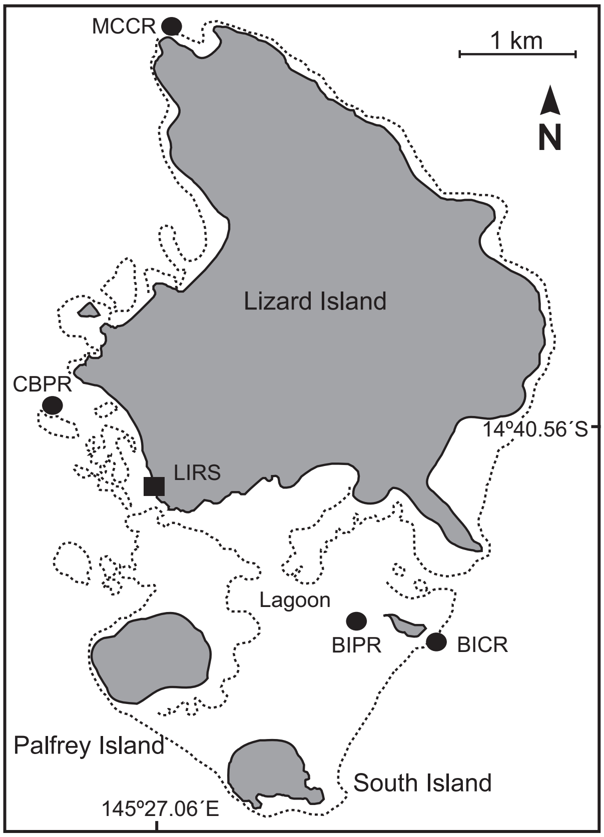

**Fig. 1:** Lizard Island Group. Study reef locations are indicated by filled circles: Mermaid Cove continuous reef (MCCR), Corner Beach patch reefs (CBPR), Bird Island continuous reef (BICR) and Bird Island patch reefs (BIPR).

## Materials and Methods

### Cognitive cooperation experiments (July–September 2010)

Twenty adult female cleaner wrasse, 10 from each habitat (Mermaid Cove and Corner Beach), were caught using hand and barrier nets (2 m × 1 m, 5 mm mesh) and individually housed in aquaria (62 cm × 27 cm × 37 cm) for 7 d prior to the commencement of experiments. All experiments on game theory followed established protocols involving Plexiglas plates as surrogates for clients (Bshary & Grutter 2005), using mashed prawn and fish flakes as food items to mimic preferred mucus (i.e. cheating) and less-preferred ectoparasites (i.e. cooperating), respectively. We first confirmed that cleaner wrasse preferred to feed on mashed prawn significantly over fish flakes mixed with equal volume of prawn, termed 'flake' (Bshary & Grutter 2005), and subsequently, exposed them to the opportunity to learn that eating a prawn item would lead to the removal of the plate. Each cleaner was exposed six times to a plate containing 12 flake items and 2 prawn items, where eating prawn led to the immediate removal of the plate. Due to the skewed ratio, cleaners were more likely to consume a flake item, prior to consuming a prawn item, and hence, experienced that eating flake is accepted while eating prawn is not.

### 'Feeding against a preference' experiment

We measured the willingness of cleaner wrasse to feed against their preference to prolong an interaction (Bshary & Grutter 2005). The willingness to feed against their food preference was tested by offering each cleaner a novel Plexiglas plate containing three prawn and three flake items. Cleaner wrasse were allowed to forage until a prawn item was consumed; thereafter, the plate was removed until the next test trial, 60 min later. Thirty rounds were conducted over 3 d.

### 'Bystander effect' experiment

In a simplified version of Bshary & Grutter (2006), we tested whether cleaner wrasse are able to eat more against their preference in the presence of an 'image scoring bystander' plate that only became accessible if the cleaner avoided prawn on the first plate. Cleaner wrasse had to avoid eating any prawn item on a current plate in the presence of a 'bystander' plate, to subsequently gain access to the 'bystander' plate. If prawn was consumed on the first plate, both plates were removed. If only flake items were consumed on the first plate, the second plate remained in the aquarium. If a prawn item was consumed on the bystander plate, both plates were removed. Cleaner wrasse were alternatively offered a single Plexiglas plate containing two flake and two prawn items (control: as in the 'feeding against a preference' experiment) or two differently coloured Plexiglas plates, each containing two flake and two prawn items (treatment). The ratio of flake to prawn items eaten and the total number of times a cleaner succeeded to the bystander plate were recorded. A total of 30 control and 30 treatment trials were conducted over 6 d, the order of presentation being counterbalanced over each four consecutive trials. No pre-training was offered, apart from the knowledge cleaners had obtained in experiment 1. To test for a change in the response of cleaners over feeding trial session depending on which habitat they came from, we carried out a general linear mixed-effects model (glmmPQL function in R3.02 on response data [binomial family] with factors habitat, treatment and trial and fish identity as a random factor in the error term. Fixed effects: FlResponse ~ Group + Trial + Habitat + Group * Habitat + Trial * Habitat + Group * Trial + Group * Trial * Habitat).

Bshary & Grutter (2006) had tested cleaners also in a third situation, namely offering two plates that were retrieved independently of each other, that is, each one only once the cleaner had eaten a prawn item off it. This control was important to demonstrate that the increased feeding against preference on the first plate was due to the 'image scoring' of the second plate. As cleaners from the continuous reef did not adjust their likelihood to feed against their preference when offered one or two independent plates, we saw no need to replicate these results in the current study.

### 'Biological market' experiment

We tested the cleaner wrasse' ability to learn to prefer an ephemeral plate over a plate which offered an equal value of food and was always accessible (initial learning and learning after role reversal) (Salwiczek et al. 2012). Cleaner wrasse were presented simultaneously with two different Plexiglas plates, each containing one prawn item. One represented a resident client, which was willing to wait to be inspected, while the other plate represented a visitor client, which was removed from the aquarium if the cleaner fed on the 'resident' plate first. The optimal solution was to always feed from the 'visitor' plate first. The status of each plate was predetermined and plate positions were counterbalanced. The number of trials that a cleaner required to develop a significant preference (9/10 trials or two consecutive 8/10) for the ‘visitor’ plate was recorded. To control for plate preferences, the status and behaviour simulated by each plate was subsequently reversed, and the experiment was repeated. The task was reversed after the initial treatment was learned. A maximum of two-hundred trials were conducted over 10 d per cleaner.

### Personality Experiments (July–September 2010)

Cleaner wrasse aggression was measured by placing a mirror inside the aquarium against a wall and recording the number of mirror ‘mouth fights’ within the subsequent 2 min. Boldness was measured by offering the cleaner wrasse food on a Plexiglas plate with novel colour patterns, and recording the time required to touch it. Two sessions were performed, one prior to and one after cognitive cooperation experiments, 25 d apart.

### Fish Censuses and Field Observations (July-August 2011)

The abundance and diversity of client reef fishes and cleaner wrasse was estimated using ten replicate 30 m transects within each reef environment, which were haphazardly placed either parallel to the reef crest (Mermaid Cove) or parallel to the shoreline across a patch reef (Corner Beach patches). SCUBA divers recorded all visible fish clients and cleaner wrasse in either a 5 m (client individuals > 10 cm total length (TL)) or 1 m (client individuals < 10 cm TL) wide area along the 30 m transect. All fishes were identified to species level when possible and census methods followed Wismer et al. (2009).

Natural cleaning interactions were recorded for 16 randomly selected adult female cleaner wrasse (8 from each reef environment), which were filmed (Cannon G9, Lumix TZ3) on SCUBA for 30 min, between 09:00 and 10:30 h, at a distance of 2 m. For each cleaner-client interaction, we recorded client species (including ‘visitors’ with access to several cleaning stations) and the duration of cleaning interaction.

### Juvenile Cleaner Wrasse (January 2012)

All aforementioned plate experiments were repeated on juvenile cleaner wrasse (measuring < 2.5 cm TL). In total, sixteen juvenile cleaner wrasse were caught from both habitat types (i.e. continuous reef and patch reefs). Due to the low availability of juveniles at Corner Beach patch reefs, we captured juvenile cleaner wrasse at two locations for each habitat type, including the patch reefs and the fringing continuous reef adjacent to Bird Island on the exposed side of Lizard Island (i.e. four individuals were collected per site) (Fig. 1). Collection and experimental protocols followed that of adults.

## Results

### Adult Cleaner Wrasse in the Cognitive/Cooperative Laboratory Experiments

Adult female cleaner wrasse caught from the continuous reef performed better across all laboratory learning tasks compared with their patch reef counterparts. In the ‘feeding against a preference’ experiment, continuous reef cleaner wrasse ate a significantly higher ratio of flake to prawn items in comparison with patch cleaner wrasse (Mann–Whitney-*U*-test, $m = 10$, $n = 10$, $z = -2.95$, $p = 0.003$, Fig. 2a). In fact, continuous reef cleaners ate significantly against their preference, i.e. more than the 0.75 flake items per round expected if cleaners eat randomly (Gingins et al. 2013) (Wilcoxon one sample test, $n = 10$, $T = 7.5$, $p < 0.05$), while patch reef cleaners ate significantly according to their preference, that is, < 0.75 flake items per round (Wilcoxon one sample test, $n = 10$, $T = 3$, $p < 0.01$). In the ‘bystander effect’ experiment, the Repeated Measures ANOVA revealed a significant difference with respect to the interaction between feeding against preference between the ‘single’ plate and the ‘first’ plate in the image scoring situation and location ($F_{1,17} = 27.9$, $p < 0.001$). Only individuals from the continuous reef significantly increased feeding against their preference in the image scoring situation (Fig. 2b). As patch reef cleaner wrasse largely failed to adjust their behaviour to the image scoring situation, they succeeded to the second plate less often than continuous reef cleaner wrasse (Mann–Whitney *U*-test, $m = 10$, $n = 9$ $z = 2.20$, $p = 0.027$, Fig. 2c). Interestingly, continuous reef cleaner wrasse responded to ‘bystander’ plates from the onset of feeding trials. In our full model, the effects of situation (one plate or two plates) and the cleaners’ habitat (continuous reef or patch reef) were both significant ($p = 0.024$ and $p = 0.0006$, respectively), while neither treatment group improved during the experiment (General linear mixed-effects model, df = 1115, $t = 1.23$, $p = 0.22$), and none of the interactions were significant either (all df = 1115, all $t < 1.2$, all $p > 0.24$) (Fig. 2d, e). Lastly, continuous reef cleaner wrasse completed the ‘biological market’ experiment

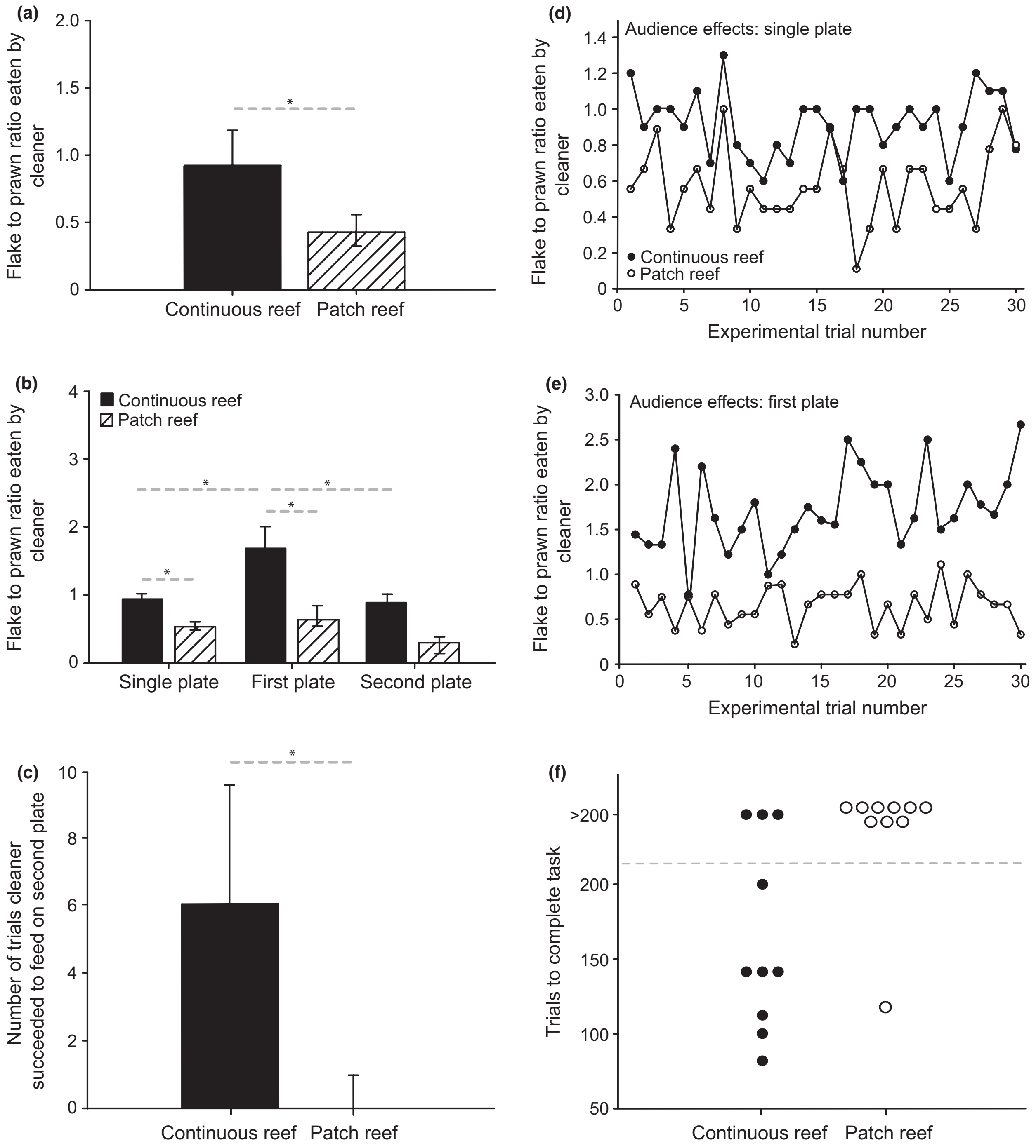

**Fig. 2:** Behaviour of adult cleaner wrasse in the laboratory. 'Feeding against a preference' experiment, a) median flake to prawn ratio consumed. 'Bystander effect' experiment, b) median flake to prawn ratio consumed per plate type, c) median number of times cleaner succeeded to feeding on second plate in the 'two-plate, image scoring' scenario, d) median flake to prawn ratio consumed over 30 trials in 'single' plate control and e) 'first' plate treatment scenario. 'Biological market' experiment, f) number of trials needed to complete both initial and reversal component (maximum 200 trials). Error bar: interquartiles. *: significant differences between cleaner wrasse of the two reef environments (all $p < 0.03$).

(involving the choice of an ephemeral food source over a permanent one) in a fewer number of trials than patch reef cleaner wrasse, which generally failed to complete the task within the maximum of 200 trials (Mann–Whitney *U*-test, $m = 10$, $n = 9$, $z = 2.20$, $p = 0.026$, Fig. 2f).

### Laboratory Experiments on Aggressiveness and Boldness in Adult Cleaner Wrasse

In contrast to the experimental findings on cooperation and cognition, cleaners of the two sites did not differ significantly with respect to aggressiveness or exploration, in either of two experimental sessions each (Mann–Whitney *U*-tests, $m = 10$, $n = 10$, $z = -1.36$–$1.17$, $p = 0.174$–$0.364$) (Fig. 3). Individual performance correlated significantly between experimental sessions (Spearman Rank correlations, all $n = 20$; aggressiveness: $r_s = 0.689$; exploration: $r_s = 0.759$, both $p < 0.05$).

### Fish Censuses and Field Observations

The continuous reef site, compared with patch reefs, had significantly higher client abundance and diversity estimates, as well as cleaner densities (unpaired *t*-tests, all $n = 10$, client abundance: $t = 5.25$, $p < 0.001$; diversity: $t = 4.59$, $p < 0.001$; cleaner density: $t = 3.61$, $p = 0.002$, Fig. 4). This resulted in a higher cleaner to client ratio, as an indicator of between-cleaner competition, at the continuous reef (1.14 cleaner wrasse per 100 clients) versus the patch reef location (0.64 cleaner wrasse per 100 clients) (Mann–Whitney *U*-test, $m = 10$, $n = 10$, $z = 2.57$, $p = 0.010$).

Cleaner wrasse from the continuous reef, compared with patch reefs, had significantly more interactions, a higher diversity of client species, and a larger number of clients classified as visitors (Mann–Whitney *U*-tests, all $m = 8$, $n = 8$, total interactions: $z = -3.20$, $p = 0.001$; diversity: $z = -2.73$, $p = 0.006$; visitors: $z = -2.52$, $p = 0.011$, Fig. 5). Nonetheless, the duration of individual client interactions and the proportion of time spent cleaning did not differ significantly between cleaner wrasse of the two reef environments (Mann–Whitney *U*-tests, all $m = 8$, $n = 8$, duration: $z = 1.31$, $p = 0.189$; cleaning proportion: $z = -1.36$, $p = 0.172$, Fig. 5).

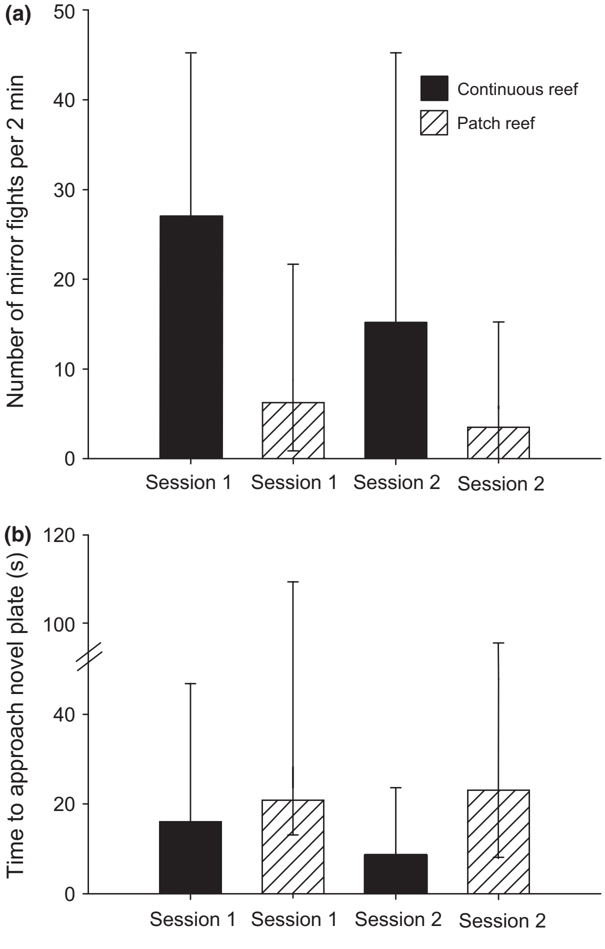

**Fig. 3:** Boldness and aggression do not differ between continuous and patch reef cleaner wrasse. a) Number of mirror fights per 2 min as a measure of aggressiveness. b) Duration (seconds) to approach a plate with novel colour patterns as a measure of boldness (or exploration). Values are median and interquartile (error bars).

### Juvenile Cleaner Wrasse

In contrast to adult cleaner wrasse, the performance of juveniles from the two contrasting habitats did not differ significantly from one another in any of the three laboratory tasks (Fig. 6). In the initial 'feeding against a preference' experiment, both continuous and patch reef juveniles fed against their preference at a relatively similar ratios (i.e. median of 1.4 and 1.33, respectively) (Mann–Whitney *U*-test, $m = 8$, $n = 8$, $z = -0.21$, $p = 0.833$) (Fig. 6a). In the 'bystander effect' experiment, both continuous and patch reef juveniles fed more against their preference on the 'first' plate in the 'two-plate image scoring' scenario than when interacting with the 'single' plate (Fig. 6b), with no significant interaction between plate identity and location (Repeated Measures ANOVA: plate identity: $F_{1,14} = 8.5$, $p = 0.011$; location: $F_{1,14} = 0.4$, $p = 0.53$; interaction: $F_{1,14} = 1.7$, $p = 0.22$). All individuals from both location managed to access the second plate in the image scoring situation and at similar rates (Mann–Whitney *U*-test, $m = 8$, $n = 8$, $z = 0.0$, $p = 1.0$) (Fig. 6c). Like adults from the continuous reef location, they fed less against their preference on the 'second' plate compared with the 'first' plate in the image scoring situation (Wilcoxon–Test, $n = 16$, $z = -2.25$, $p = 0.024$). Like the adults, juveniles responded to 'bystander' plates from the onset of feeding trials, and neither

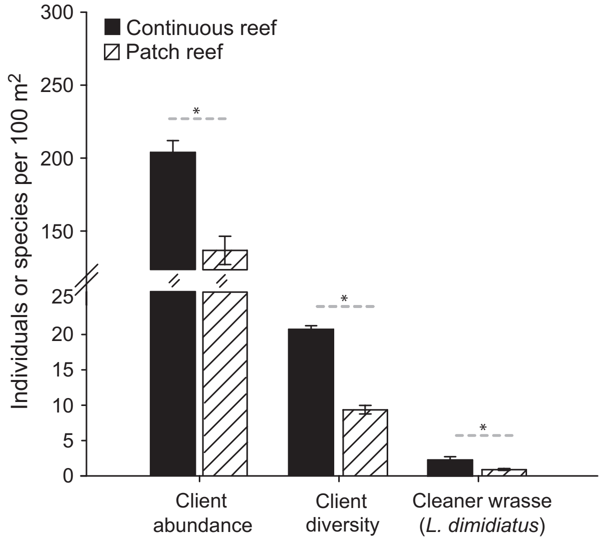

**Fig. 4:** Fish estimates on continuous and patch reefs. Abundance and diversity of reef fish clients and abundance of cleaner wrasse at the continuous fringing reef at Mermaid Cove and Corner Beach patch reefs, Lizard Island, Great Barrier Reef. Values are mean and standard error (error bar). *: significant differences between the two reef environments (all $p \leq 0.002$).

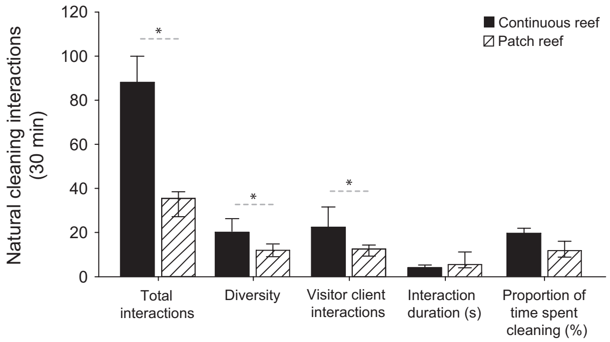

**Fig. 5:** Behaviour of cleaner wrasse on continuous and patch reefs. Characteristics of natural cleaning interactions at Corner Beach patch reefs and Mermaid Cove continuous reef. Values are median and interquartiles (error bars). *: significant differences between cleaner wrasse of the two reef environments (all $p \leq 0.011$).

treatment group improved during the experiment (General linear mixed-effects model, df = 302, $t = -0.834$, $p = 0.405$) (Fig. 6d, e). Lastly, both continuous and patch reef cleaner wrasse failed to complete the 'biological market theory' experiment in 200 trials, and hence, the performance between the two juvenile groups did not differ significantly from one another (Mann–Whitney *U*-test, $m = 8$, $n = 8$, $z = 0.420$, $p = 0.674$) (Fig. 6f).

The juveniles were collected from four locations rather than from two like the adults, and we did not quantify cleaner and client densities as well as client diversity and interaction patterns at the two added sites. As the addition might have caused uncontrolled variance, we decided to calculate explicit comparisons of performances by individuals collected only at the adult reef patch system. In experiment 1, the four juveniles ate significantly more against the preference than the ten adults from the same location (mean juveniles = 2.01 flake items per trial; mean adults = 0.51 flake items per trial; Mann–Whitney-*U*-test, $m = 10$, $n = 4$, $z = -2.70$, $p = 0.004$). In experiment 2, the four juveniles altered their foraging behaviour between single plate and first plate in the image scoring situation significantly more so than the 10 adults did (mean increase juveniles = 2.78 flake items per trial equalling 180% increase; mean adults = 0.091 flake items per trial equalling 16% increase; Mann–Whitney *U*-test, $m = 9$, $n = 4$, $z = -2.47$, $p = 0.011$). As a consequence, juveniles were significantly more likely than adults to gain access to the second plate during image scoring trials (mean 57% of trials for juveniles and 2.2% of trials for adults; Mann–Whitney *U*-test, $m = 9$, $n = 4$, $z = -2.92$, $p = 0.003$).

## Discussion

The cooperation experiments demonstrate an important mismatch between the behaviour of adult cleaner wrasse from a particular reef location, consisting of patch reefs, and published evidence linking cleaning strategies with game theoretic predictions regarding audience effects (Nowak & Sigmund 1998) and biological markets (Noë 2001; Pinto et al. 2011; Salwiczek et al. 2012). Feeding against their preference, incorporating image scoring by 'food sources', and preferring an ephemeral food source would have yielded more food and hence would have been superior decisions. Indeed, individuals from the continuous reef appeared to assimilate the necessary detailed information regarding client strategies and applied their decision rules quickly to our laboratory experiments. As such, results from the patch reefs correspond to various results on human cooperation where mismatches between predictions and observations have been documented, leading to discussions about decision rules underlying behaviour (Gigerenzer & Selten 2002; Fehr & Fischbacher 2003; Haley & Fessler 2005; Kümmerli et al. 2010).

So why did we observe such a mismatch between theory and the data from patch reef cleaners? Our ecological data suggest that the mismatch is linked to living in a comparatively simple social environment. First, cleaners on the patch reefs have an estimated

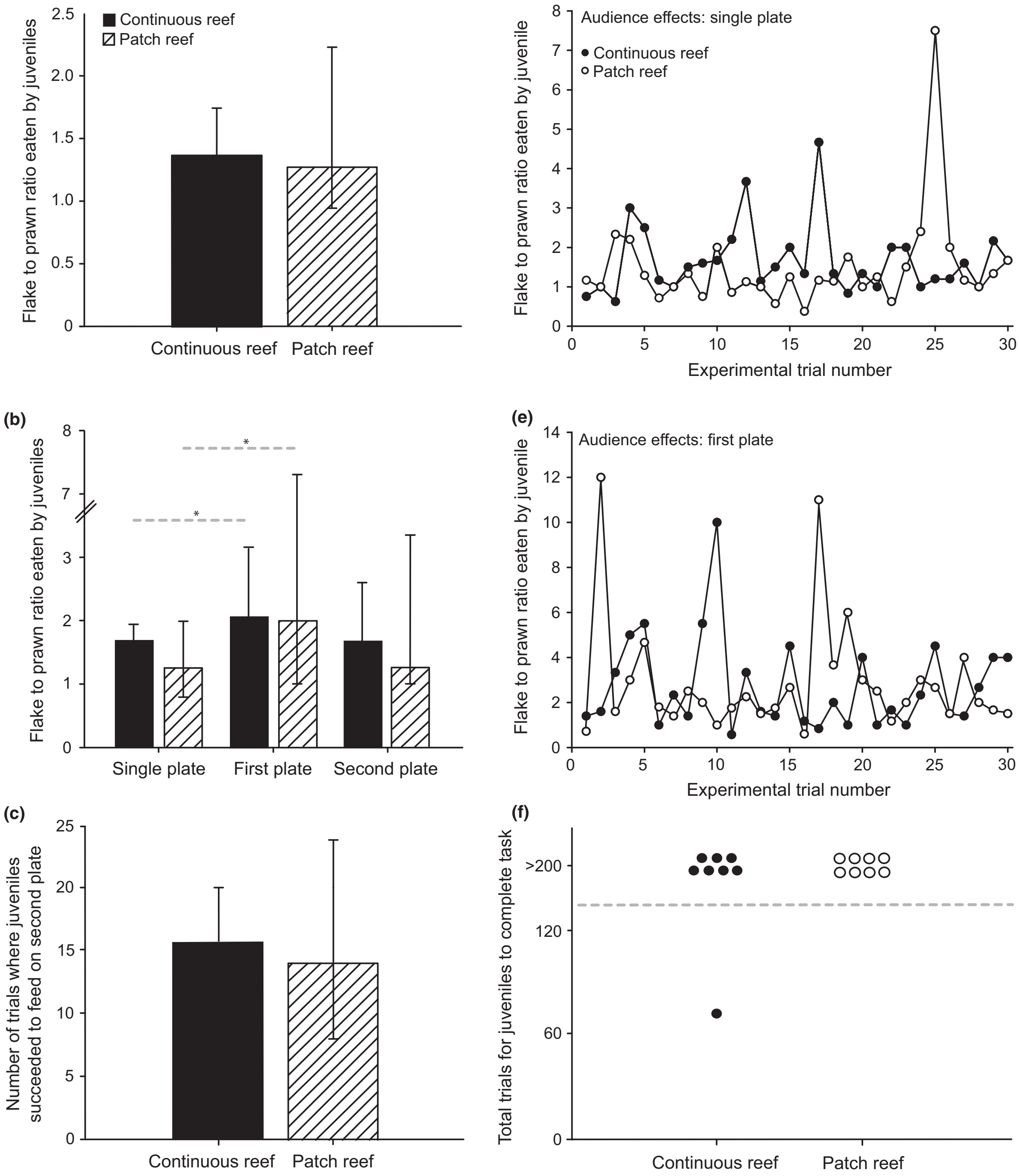

**Fig. 6:** Behaviour of juvenile cleaner wrasse in the laboratory. ‘Feeding against a preference’ experiment, a) median flake to prawn ratio consumed. ‘Bystander effect’ experiment, b) median flake to prawn ratio consumed per plate type, c) median number of times juvenile cleaner succeeded to feeding on second plate in the ‘two-plate, image scoring’ scenario, d) median flake to prawn ratio consumed over 30 trials in ‘single’ plate control and e) ‘first’ plate treatment scenario. ‘Biological market’ experiment, f) number of trials needed to complete both initial and reversal component. Error bar: interquartiles. *Significant differences of flake to prawn ratio eaten by juvenile cleaner wrasse between the single and treatment plates ($p < 0.05$).

800 cleaning interactions per day, compared to 2000 on the continuous reef site. This means that image scoring situations or resident and visiting clients seeking cleaning simultaneously will occur at lower frequencies at the patch reef site. This reduces the frequency in which benefits of detailed knowledge may

be obtained and at the same time longer time intervals and less frequent exposure probably make learning more difficult. Second, the lower cleaner density together with the lower cleaner to client ratio at the patch reefs means that it is more costly for visiting clients to exert partner choice in a biological market (Noë 2001; Johnstone & Bshary 2008), lowering the potential costs for cleaners of ignoring visitors or cheating in their presence. Taken together, these effects of a comparatively simple social environment may make it advantageous to ignore the available detailed information in nature, which leads to failure in our cognitive laboratory experiments. The experiments test for rather diverse abilities. Feeding against preference is not so much a learning experiment but a test for restraint (a psychological parameter). The image scoring experiments apparently tapped into existing decision rules: cleaners from the complex social environment spontaneously fed more against their preference in the presence of a second plate and did not improve over the course of the experiment. Finally, the market experiment tested learning abilities directly. Nevertheless, it could be that cleaners from the complex social environment had knowledge from interactions with real clients they could apply to the task, while cleaners from the simple social environment may have lacked the knowledge. In conclusion, the differences in social composition between the two locations are striking and provide a good working hypothesis for the explanation of the documented differences.

### Cooperation, Cognition and Personality

We found no evidence that differences in performance between the cleaners caught at the two sites can be explained with a personality syndrome that would link the two standard axes tested in animal behaviour, aggressiveness and/or boldness (i.e. Wilson et al. 1994), to cooperation and cognition. This contrasts with the limited research on the link between cooperation and personality in animals, which has hitherto provided some evidence for the importance of behavioural syndromes as explanation for individual variation (Bergmüller et al. 2010). In a classic study on predator inspection in sticklebacks, cooperative behaviour was linked to boldness (Milinski 1987). Furthermore, helpers in cooperatively breeding cichlids fall into two broad life history classes: bold individuals help in aggressive tasks (territory defense, predator harassment) and are likely to migrate, while shy individuals help in maintenance tasks (egg fanning, sand digging) and are likely to queue for breeding positions within the territory (Bergmüller 2010). Other studies also found correlations between aggressiveness and or boldness/exploration and cognitive performance (Boogert et al. 2006; Guillette et al. 2009; Sih & Del Giudice 2012). Thus, our results differ from previous studies in providing evidence for an environment-linked cooperative personality and cognitive ability in cleaner wrasse, which is independent of the two personality traits we tested.

### On the Potential Role of Ontogeny

A major challenge is to test how the differences come about. Genetic variation that is maintained by differential selection in the two habitats offers one possible explanation, while ontogenetic effects provide an alternative. Though a pelagic egg and larval stage, as found in *L. dimidiatus*, results in a lack of genetic population structure (Avise & Shapiro 1986), it could still be that an initial mixture of more/less genetically cooperative and cognitive juveniles shows different survival depending on the local conditions, or that different types of juveniles select the habitat to which their genetic levels of cooperation/cognition fits. Our results on the juveniles certainly contradict the latter hypothesis as juveniles generally performed well in the first two experiments, independently of location. The results were not due to our sampling of four sites for juveniles in contrast to only two sites for the adults as the direct comparison between adults and juveniles from our main reef patch location yielded the same significant differences. Furthermore, we find it difficult to reconcile the data with the differential survival hypothesis. As it stands, adult cleaners from the patches could not show audience effects, while juveniles from the same habitat could, and only adults from the continuous reef solved the full partner choice experiments while juveniles did not. The latter results conform to an earlier study (Salwiczek et al. 2012) and could be due to juveniles interacting relatively infrequently with visitors (Barbu et al. 2011). It thus appears that cleaners living in a socially simple environment may lose the ability to respond spontaneously to image scoring by clients, while cleaners living in a complex social environment acquire the ability to learn to prefer visiting client species. Note that these changes may well be adaptive in each environment. Possibly, clients in the marginal habitat do not image score and hence cleaners learned to stop caring, which would explain why they do not respond in the experiment either. In any case, such results seem to be more parsimoniously explained with ontogentic effects due to learning/forgetting than with differential selection on genetic strategies. In line with this view, evolutionary developmental studies have demonstrated the profound effects that rearing environments can have on an animal's learning abilities (van Praag et al. 2000; Kotrschal & Taborsky 2010; Thornton & Lukas 2012). In particular, for fishes, it has been demonstrated that their brains are highly plastic, and variation can be linked to cognitive performance (Ebbesson & Braithwaite 2012; Gonda et al. 2012). Indeed, our results indicate that natural variation in complexity may present promising experimental opportunities to investigate links between development and cognition. In our view, the 'simple' reefs still boasting an estimated 800 (vs 2000 for complex reef) social interactions per 11–12 hour day, make the cleaners' failure in our experiments even more surprising.

Nevertheless, we note that a potential causal link between low client abundance, low client diversity, low interaction frequency and the poor performance of the patch reef cleaner wrasse is amenable to further experimental examination. Translocation experiments would resolve the current shortcoming of our data. As it stands, our current evidence is correlative, and the two locations studied in detail for the comparison between adults potentially differ with respect to various factors other than client fish community. Increasing the number of locations is unlikely to provide a solution as we predict that low client density and diversity will invariably be associated with locations containing reef patches with low coral cover and poor visibility. Translocation experiments would also overcome the problems inherent in our explorative step-by-step approach, where laboratory experiments on adults, field measures and experiments on juveniles were conducted in consecutive years. While this approach was necessary due to the surprising nature of our results that are not supported by theory and previous studies, the consequence is that there is the possibility of unexplained variance due to unmeasured ecological variation between years. Another important future direction will be to test whether cleaners exposed to complex social environments are also better at solving tasks that are not specifically linked to cleaning interactions. As it stands, our results could be largely due to prior experience, leaving open the question whether complex social environments cause a general improvement in cognitive abilities.

Our results have several important implications for cooperation theory and decision-making theory in general. Most notably, our results seem to oppose the bounded rationality hypothesis (Gigerenzer & Selten 2002), which focuses on the advantage of simplification in a complex environment. According to this framework, we would have expected that cleaners from the simple social environment are more precise in their actions, instead of the opposite. We think that future empirical and theoretical research on cooperation would greatly benefit from more detailed analyses of costs and benefits underlying different decision rules. Evolutionary theory has proven useful in predicting behaviour when trade-offs are specified and mechanisms underlying behaviour are incorporated into models (Davies et al. 2012). However, this has rarely been applied to evolutionary game theory on cooperation and is currently not listed as a priority (Nowak 2012). Nevertheless, we need a theory that makes predictions about learned decision-making strategies in both animals and humans. With respect to cooperation, we need a theory that can better explain learned decision-making strategies in both animals and humans. For example, intelligence or executing precise decisions induces a cost on an individual in the form of investment of detailed learning. For patch reef cleaners, the investment and benefit of acting precise may not be worth the associated cost, and decision rules which work well in complex environments may not be applicable or even necessary in more simple environments. In contrast, cleaner wrasse from complex environments may invest in precise strategies as the net benefit may be worth the cost. Ideally, game theory should integrate assumptions about the costs and benefits of information gathering and storage, as well as, learned decision-making mechanisms (Mery & Kawecki 2003; Heyes 2010; Lotem & Halpern 2012). With such an approach we are likely to gain further insight into realistic decision rules to possibly understand when deviations from seemingly optimal strategies are adaptive and how that affects the evolution and stability of cooperation.

## Acknowledgements

We kindly thank the staff of Lizard Island Research Station for their continuous support and friendship. Likewise, D Bellwood, K Cheney, C Lefèvre, J Welsh, N Raihani, A Derendinger, P Vullioud and A Ros for field support. M Manser for external supervision and A Ros for statistical advice. Funding was provided by the Swiss National Science Foundation (grant to Redouan Bshary) and the Commission for Travel Grants, Swiss Academy of Sciences (grant to Sharon Wismer).

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