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The Personality Behind Cheating: Behavioural Types and the Feeding Ecology of Cleaner Fish

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Abstract

The complex mutualistic relationship between the cleaner fish (*Labroides dimidiatus*) and their 'clients' in many reef systems throughout the world has been the subject of debate and research interest for decades. Game-theory models have long struggled with explaining how the mixed strategies of cheating and honesty might have evolved in such a system and while significant efforts have been made theoretically, demonstrating the nature of this relationship empirically remains an important research challenge. Using the experimental framework of behavioural syndromes, we sought to quantitatively assess the relationship between personality and the feeding ecology of cleaner fish to provide novel insights into the underlying mechanistic basis of cheating in cleaner-client interactions. First, we observed and filmed cleaner fish interactions with heterospecifics, movement patterns and general feeding ecology in the wild. We then captured and measured all focal individuals and tested them for individual consistency in measures of activity, exploration and risk taking (boldness) in the laboratory. Our results suggest a syndrome incorporating aspects of personality and foraging effort are central components of the behavioural ecology of *L. dimidiatus* on the Great Barrier Reef. We found that individuals that exhibited greater feeding effort tended to cheat proportionately less and move over smaller distances relative to bolder more active, exploratory individuals. Our study demonstrates for the first time that individual differences in personality might be mechanistically involved in explaining how the mixed strategies of cheating and honesty persist in cleaner fish mutualisms.

Introduction

Numerous reviews and empirical studies have demonstrated that the phenomenon of animal personality, or consistent between-individual variation in behaviour across contexts, is a fundamental component of contemporary behavioural biology with important consequences for ecology and evolution (Sih et al. 2004; Réale et al. 2010; Wolf & Weissing 2012). This significance is apparent both from the near taxonomic ubiquity of animal personality (fish (Wilson et al. 2010a), birds (Naguib et al. 2010), mammals (Réale et al. 2009), amphibians (Wilson & Krause 2012b), reptiles (Carter et al. 2012) and numerous invertebrates (Sinn et al. 2006; Reaney & Backwell 2007; Wilson et al. 2010b)) wherein personality plays a central role in structuring ecological processes as well as the relationship between personality and other biological phenomena [metamorphosis (Wilson & Krause 2012a,b), migration (Chapman et al. 2011), predation (Ioannou et al. 2008), group living and social networks (Krause et al. 2010; Webster & Ward 2011)].

Indeed, inter-individual variation in behavioural types has been found to be an important factor in many areas of animal ecology including host-parasite interactions, epidemiology, dispersal and invasion biology among others (Wolf & Weissing 2012).

What is currently unknown, however, is whether and how personality might influence complex interspecific interactions such as those found in mutualism. Mutualism represents a unique research challenge as while interactions are typically characterized by net benefits to both participants, the potential for conflict is high due to the interests of involved parties not being exactly aligned (Mills & Côté 2010). For example, the potential costs and benefits to both participants can change with environmental conditions or individual state-dependent considerations such as hunger level and body condition. As such, interactions can occasionally be neutral or even antagonistic (Cheney & Côté 2005), either temporarily or over parts of the species ranges (Thompson & Cunningham 2002). In terms of personality, mutualism is potentially interesting as this phenomenon can represent a system where the distribution of behavioural types in one species constitutes a portion of the ecological and selective environment of another species, therein affecting the ecological interaction dynamics as well as the coevolution of both species involved (Wolf & Weissing 2012).

Fish cleaning behaviour represents a unique opportunity to investigate the importance of personality in seemingly mutualistic interactions between species. In cleaner fish mutualisms, cleaners remove and feed on ectoparasites from other reef fishes or 'clients' that enter their territory, resulting in a net benefit to both parties (Côté 2000). However, cleaners can also cheat by removing more nutritious mucous, tissues, or scales instead of parasites, to the detriment of their client (Johnstone & Bshary 2002). While cheating does offer short term benefits to the cleaner, it is not without risk and potential long-term consequences. For example, cleaners risk being aggressively punished by cheated clients (Bshary & Grutter 2002) as well as risk losing future potential feeding opportunities by potential clients witnessing their act of cheating (audience effects; Pinto et al. 2011). Additionally, previous studies have shown that there is strong variation in propensity to cheat between-individual cleaners (Bshary 2002), an important pre-requisite of personality.

In this study, we used the experimental framework of behavioural syndromes (Sih et al. 2004) to investigate the relationship between behavioural type (personality) and the feeding ecology of the cleaner fish, *Labroides dimidiatus,* on the Great Barrier Reef. Cleaner fish are an ideal model system to investigate this paradigm as they are abundant in many reef systems throughout the world, are caught easily using simple hand nets, and acclimatize readily to laboratory conditions. Furthermore, cleaner fish are relatively easy to observe and film in the wild as they tend to occupy limited territories and spend long time periods occupying 'cleaner stations' for servicing clients.

To quantitatively assess the relationship between personality and cleaner fish feeding ecology, we first observed and filmed cleaner fish interactions with heterospecifics, movement patterns and general feeding ecology in the wild. We then captured and measured all focal individuals and tested them for individual consistency in measures of activity, exploration and risk taking (boldness) in the laboratory. Our predictions were threefold. First, we predicted that between-individual differences in personality would be consistent and repeatable in the laboratory, therein allowing the characterization of behavioural types. Second, we predicted that individual measures of foraging effort (number of clients serviced, number of pecks per client) would be inversely correlated with measures of cheating behaviour and distance travelled during the observation period. Third, we predicted that there would be a behavioural syndrome between personality and general feeding ecology in cleaner fish, with bolder more active individuals being more willing to cheat on average than other more timid individuals.

Materials and Methods

Field Observations and Collection

Between April 23 and April 30, 2012, we located and observed 22 cleaner fish (Total length: 28–50 mm, $\bar{x}$ = 38.5 mm) in a shallow (Depth: 1–2 m) lagoon near the University of Sydney research station at One Tree Island, Australia. One Tree island is a small coral cay that comprises a portion of the Capricornia Cays National Park on the Great Barrier Reef. Each focal individual was observed and filmed for 30 min using digital cameras (Panasonic Lumix DMC-TS4, GoPro HD Hero). Observations included quantifications of individual foraging effort in terms of number of clients' serviced, total number of pecks (bites) during cleaning, average number of pecks per client and total number of suspected cheating events. The term 'peck' is used to describe incidents in which an individual cleaner fish seemingly removes or attempts to remove a parasite or dead tissues from a client fish (i.e. the cleaner makes physical contact with client using their mouth), without eliciting a 'cheat' response from said client. Cheating events were identified based on patterns of client fish reaction in which affected individuals exhibit a whole-body jolt followed by either an aggressive chasing response towards the cleaner or a rapid departure from the area (Soares et al. 2008a; Mills & Côté 2010). Quantifications of general feeding ecology also involved determining the number of species serviced by each cleaner and an estimate of total distance swum during the observation period.

It is important to note that in our initial *a priori* observations, some individuals travelled considerable distances (~20 m) from their cleaning stations; as such it would not have been possible to positively identify target individuals on different occasions based solely on location in this case. Similarly, coral patches often contained multiple cleaners making this notion even more difficult. While certain marking techniques are available (VIE elastomer tags, Wilson & Godin 2009), given the highly melanistic nature of *L. dimidiatus*, particularly among juveniles, positive identification of marked individuals in the wild would have been difficult or impossible without capture. As such, we chose continuous direct observation of focal individuals over 30 min immediately prior to capture to circumvent these issues.

Following observations, focal individuals were caught using small (20 × 15 cm) hand-held dipnets and transferred to laboratory facilities (200–300 m) in small cylindrical transport containers (30 × 12 cm, opaque white PVC). Typically 3–4 individuals were collected each day over a 7-d period. Following behavioural testing, all individuals were measured for body size (total length) and returned to the vicinity of their original capture. It was not possible to positively sex individuals used in the study as this would require terminal sampling. However, *L. dimidiatus* is a protogynous hermaphrodite with small individuals being female and the largest individuals being male (Robertson 1972).

Experimental Holding Conditions and Experimental Arena

On arrival at the laboratory, each fish was placed singly into one of four plastic holding aquaria (23 × 15 × 13 cm). Each aquarium was provided with constant flow-through sea water from the lagoon capture site. All aquaria were exposed to diffused, natural sunlight through direct openings and windows in the research laboratory facility. Each fish was given approximately 24 h to acclimate to the laboratory prior to being transferred to the experimental arena (described below) and the onset of behavioural testing.

The experimental arena (Fig. 1) consisted of a large, opaque, plastic experimental aquarium (89 × 57 × 44 cm) containing a medium sized (11 × 12 × 6 cm) piece of dead coral to act as refuge for cleaner fish during trials. The arena was located behind an observation blind and contained fresh seawater (depth: 16 cm). As with the holding aquaria, seawater was pumped directly from the lagoon from which fish were captured, however in this case, water was replaced prior to the start of behavioural testing each day. It is important to note that the water temperature of the holding tanks did not change (i.e. <1°C) during the short testing period each day. In addition, the

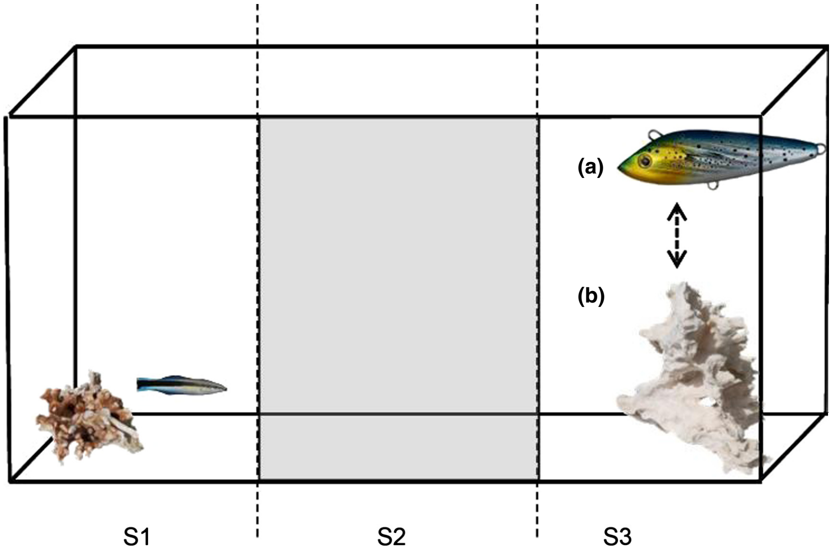

Fig. 1: Schematic representation of the experimental arena used in laboratory assessments of personality in cleaner fish. Individual fish were consecutively tested for individual willingness to explore the arena and novel objects as represented by a novel client fish decoy (a) as well as two novel structures (structure 1 shown, [b]). To quantify behavioural traits, the arena was divided into three sections (S1–S3) during analyses, however only measurements of behaviour in section 1 and 3 (with the exception of activity, which was continuously quantified) were used in our analyses. Section 2 represented a transitional space (marked in grey) between the refuge (Section 1) and the risk-assessment and structure exploration tests (Section 3) as appropriate.

arena was divided into thirds by marks on the outside of the aquarium to facilitate quantification of behavioural traits (Fig. 1).

At the onset of behavioural testing, a haphazardly selected focal fish was transferred from its individual holding aquarium to the experimental arena using a small dipnet and bucket (transit time <10 s). Fish were then placed in a cylindrical holding tube (12 cm diameter, translucent plastic) located immediately in front of the refuge located in the left section of the experimental apparatus (Section 1, Fig. 1). All fish were allowed to acclimate for 5 min prior to the onset of behavioural testing (outlined below). Following behavioural trials, test fish were transferred to other large communal holding aquaria where they were provided *ad libitum* access to standard fish flakes, flow-through seawater and ambient natural lighting until their eventual release at their location of capture (1–6 days later depending on date of capture). All behavioural trials were recorded using a remotely operated webcam (Logitech 1080HD, Carl Zeiss Tessar) connected to a laptop computer to facilitate the quantification of desired traits for each session.

Behavioural Experiments

Quantifying activity, exploration, risk-taking and client inspection behaviour

Approximately 24 h after arrival in the laboratory, individual cleaner fish were tested in a series of consecutive behavioural tests to allow for identification of behavioural type (Wilson & Godin 2009). Behavioural tests included multiple measurements of general activity, exploration behaviour and risk taking (i.e. boldness), as well as a measurement of potential client inspection behaviour. Following the acclimation period, the holding tube in the experimental arena (see above) was raised, and individual differences in latency to become active were measured for each test fish. After an additional 5 min of exploration/acclimation, total time spent active and time spent in the section of the arena farthest from the coral refuge (Section 3, Fig. 1) were quantified for a further 10 min. These traits were chosen as they represent either measures of activity or individual willingness to spend time away from refuge (i.e. risk-taking). It is important to note that these two traits are not necessarily the same as individuals can be quite active within the refuge section (Section 1) but never venture towards Section 3. Focal fish were then given an additional 5 min without disturbance, and this 10 min observation period was repeated to allow for a measurement of consistency in behaviour for this trial.

Immediately following the second activity trial, one of two coral structures (structure 1 [29 × 16 × 28 cm] or structure 2 [17 × 16 × 13 cm]) were randomly selected to be added to Section 3 of the experimental arena (Fig. 1). In this case, both structure options were intentionally chosen to be larger and significantly more three-dimensional than the provided refuge with more area for cover as well as holes/caves in the rock to make them more attractive, yet novel options. During this set of behavioural tests, individual differences in latency to first structure inspection, number of section crosses between initial refuge and new structure, and time spent in the arena section containing the new structure were recorded over a 10-min observation period. These parameters were chosen as they represent individual differences in exploratory tendency and willingness to take risk (traverse open area between structures). As above, following the first initial round of testing in this second trial, focal fish were given an additional 5 min without disturbance, and then this 10-min observation period was repeated to allow a measurement of consistency in behaviour for this trial. However, in the second trial, the alternate structure (that was not utilized in the first test) was used to avoid habituation effects.

Lastly and following the second set of trials, a stylized fish decoy (Total length: 18 cm, Fig. 1) was added to section 3 of the experimental arena (Fig. 1). Individual differences in latency to approach/inspect the decoy, number of crosses between the refuge and the decoy, and time spent in the arena section containing the decoy were recorded over a 5-min period. These parameters were chosen as they represent individual differences in willingness to explore a potential client, or perhaps predator, and thus incorporated elements of exploration and risk.

In all trials, inspection was defined as the focal fish approaching within 10 cm of the structure/decoy. All field and laboratory footage was analysed by a single observer. It is important to note that time spent in Section 2 was not used in our analyses described below (except in the case of activity measures) as this area represented a transitional space between the refuge section and the risk-assessment/exploration section as appropriate.

Data Analyses

Comparisons of individual behavioural traits representing either feeding ecology (wild, Table 1) or personality (laboratory, Table 2) were made using non-parametric Spearman rank correlation tests (Bell 2007). In the case of repeated measures, mean values

Table 1: Spearman (r_s) correlations in field measurements of the feeding effort and general foraging ecology of cleaner fish (*Labroides dimidiatus*). The distance travelled by focal fish over the observation period is also included

Behavioural trait 1	Behavioural trait 2	r_s	p-value
Total number of pecks	Number of clients	0.6951	0.001*
Total number of pecks	Mean pecks per client	0.7878	<0.001*
Total number of pecks	Distance travelled	−0.4659	0.05
Total number of pecks	Number of species	0.5884	0.01*
Total number of pecks	Proportion of cheats	−0.5854	0.01*
Proportion of cheats	Distance travelled	0.4864	0.04
Proportion of cheats	Number of clients	−0.4814	0.04
Proportion of cheats	Mean pecks per client	−0.6533	0.003*
Number of species	Number of clients	0.6634	0.004*
Distance travelled	Mean pecks per client	−0.6993	0.001*

*All Spearman correlations at $p \leq 0.05$ are shown; correlations that are significant at the appropriate false discovery rate B–Y adjusted alpha level ($\alpha = 0.014$).

were taken to create a single parameter and simplify comparisons with other individual traits such as body size. To avoid an inflated chance of type 1 statistical error, the alpha levels used in these tests were adjusted to be more conservative using the false discovery rate B–Y adjustment (Laboratory: $\alpha = 0.011$, Wild: $\alpha = 0.014$) (Nakagawa 2004). However, repeated measures were also compared within themselves in a separate analysis to assess individual consistency in behavioural expression (Table 3).

Lastly, to test for the presence of a behavioural syndrome between personality and feeding ecology in cleaner fish, individual representative traits for each context were collapsed into first principal component scores using principal components analysis (PCA) (Table 4) (Huntingford 1976; Wilson et al. 2010b; Wilson & Krause 2012b). Across-context correlations between these scores were then calculated using Spearman rank correlation tests as above. Personality was divided into two axes based on the direction of the relationship between personality traits, as such latency to become active or inspect a structure (where bolder individuals have the lowest values) were held separate from all other personality traits (where bold individuals have the highest values) as appropriate. Our alpha level for this analysis was also adjusted to be more conservative using the false discovery rate B–Y adjustment ($\alpha = 0.027$) (Nakagawa 2004).

Results

All correlations that were significant or suggested strong trends ($p < 0.05$) are shown in Tables 1–4. In the case of repeated measures (Table 3), all correlations are shown as they are important for subsequent analyses. Only those correlations that are important for understanding our research objectives are discussed in further detail below.

Behavioural Correlations in the Feeding Ecology of Cleaner Fish in the Wild

Individuals that invested greater effort in terms of foraging/cleaning (i.e. greater number of total pecks) also tended to service more clients, spent more effort

Table 2: Spearman (r_s) correlations in laboratory measures of activity, exploration, risk taking, and client inspection in the cleaner fish (*Labroides dimidiatus*)

Behavioural trait 1	Behavioural trait 2	r_s	p-value
Mean time spent active (T1)	Latency to first movement (T1)	−0.43	0.04
Mean time spent active (T1)	Mean time spent in open area (Section 3, T1)	0.81	<0.001*
Mean number of crossings between structures (T2)	Mean latency to first structure inspection (T2)	−0.89	<0.001*
Mean time spent in novel structures (Section 3,T2)	Mean latency to first structure inspection (T2)	−0.83	<0.001*
Mean time spent in novel structures (Section 3,T2)	Mean number of crossings between structures (T2)	0.85	<0.001*
Latency to first decoy inspection (T3)	Mean latency to first structure inspection (T2)	0.55	0.008*
Latency to first decoy inspection (T3)	Mean time spent in novel structures (Section 3, T2)	−0.45	0.04
Latency to first decoy inspection (T3)	Time spent with client decoy (Section 3, T3)	−0.99	<0.001*
Time spent with client decoy (Section 3, T3)	Mean latency to first structure inspection (T2)	−0.57	0.006*
Time spent with client decoy (Section 3, T3)	Mean time spent in novel structures (Section 3,T2)	0.44	0.04
Number of crossings between refuge and client decoy (T3)	Mean latency to first structure inspection (T2)	−0.59	0.004*
Number of crossings between refuge and client decoy (T3)	Mean time spent in novel structures (Section 3, T2)	0.46	0.03
Number of crossings between refuge and client decoy (T3)	Latency to first decoy inspection (T3)	−0.99	<0.001*
Number of crossings between refuge and client decoy (T3)	Time spent with client decoy (Section 3, T3)	0.98	<0.001*

Trials 1–3 are marked T1, T2 and T3 respectively.

*All Spearman correlations at $p \leq 0.05$ are shown; correlations that are significant at the appropriate false discovery rate B–Y adjusted alpha level ($\alpha = 0.011$).

Table 3: Spearman (r_s) correlations in repeated laboratory measures of activity, exploration, and risk-taking behaviour in the cleaner fish (*Labroides dimidiatus*)

Behavioural trait 1	Behavioural trait 2	r_s	p-value
Time spent active (M1)	Time spent active (M2)	0.75	<0.001*
Time spent in open area (Section 3, M1)	Time spent in open area (Section 3, M2)	0.65	0.001*
Latency to first inspection structure 1 (M3)	Latency to first inspection structure 2 (M4)	0.48	0.02*
Number of crosses between familiar refuge and novel structure 1 (M3)	Number of crosses between familiar refuge and novel structure 2 (M4)	0.40	0.06
Time spent in novel structure 1 (M3)	Time spent in novel structure 2 (M4)	0.41	0.06

M, Measure.
*All correlations between repeated traits are shown; correlations that are significant ($p \leq 0.05$).

Table 4: PCA loadings of within-context behavioural variables used to generate first principal component scores (PC1) to assess across-context correlations in the personality and feeding ecology in Cleaner fish (*Labroides dimidiatus*)

Behavioural context	Behaviours within each context	Loadings for PC1	% variation explained
Personality 1 (activity, exploration, risk taking)	Mean time spent in open area (Section 3, T1)	−0.15	42.26
	Mean time spent active (T1)	0.09	
	Mean number of crossings between structures (T2)	0.44	
	Mean time spent in novel structures (Section 3, T2)	0.51	
	Number of crossings between refuge and client decoy (T3)	0.53	
	Time spent with client decoy (Section 3, T3)	0.46	
	Distance travelled in field	0.16	
Personality 2 (latencies)	Latency to become active (T1)	−0.45	53.63
	Mean latency to structure (T2)	0.60	
	Latency to client decoy (T3)	0.67	
Feeding effort	Number of clients	0.53	52.96
	Number of total pecks (feeding and cheating)	0.66	
	Mean pecks per client fish	0.48	
	Proportion of cheating relative to total pecks	−0.21	

T, Test.

on each client (i.e. more pecks per fish) and serviced a greater diversity of species than individuals that exhibited a lower foraging effort. Interestingly, individuals that exhibited a greater foraging effort (in terms of number of pecks and average pecks per client) also moved over smaller distances and tended to cheat less. Cheaters also tended to service fewer clients and performed fewer pecks per client on average (Table 1). Body size was not significantly correlated with any behavioural traits in the wild ($p > 0.05$).

Behavioural Correlations Among Personality Traits in the Laboratory

Individuals that were more active in general also demonstrated shorter latencies to become active and more willing to spend time away from the refuge (Section 1) in an open environment than less active individuals. Upon introduction of novel structures, individuals that had shorter latencies to first structure inspection also spent more time in the vicinity of the novel structure and were willing to cross the open area more frequently than individuals that took longer to first inspection events. These individuals also exhibited shorter latencies to inspect the decoy client upon presentation and were also more willing to cross the open area between refuge and decoy (Table 2). Body size was not significantly correlated with any behavioural traits in the laboratory ($p > 0.05$).

Most repeated measures of individual traits were highly correlated between trials. However, traits involving the inspection and general exploration of different novel structures were not correlated significantly, although these traits did show the same strong positive trends (Table 3).

Principal Components Analysis (Consistency in Behaviour Between Personality and Feeding Ecology)

Spearman rank correlation tests between the personality axes and the feeding ecology of cleaner fish in the wild suggest a strong relationship between traits. Personality (axis 1; activity, time spent near novel structures/object) in the laboratory was strongly negatively correlated with feeding effort measurements in the wild and individual differences in latency to become active or inspect objects (Personality axis 2) (Fig. 2). In other words, bolder individuals (as measured by high levels of activity and willingness to take risks and explore novel objects and environments in the laboratory), were also more willing to cheat clients while cleaning and exhibited a lower overall feeding effort compared to more timid individuals (who serviced more clients, more often and cheated less). For this portion of analyses, total estimated distance travelled in the wild was more appropriately combined with personality axis 1 due to its relationship with exploration, risk taking and activity (Table 4).

Discussion

Our study demonstrates for the first time that individual differences in behavioural type are important for understanding the mutualistic interactions of cleaner fish. As predicted, a syndrome incorporating aspects of personality (represented by activity, exploration and risk taking) and foraging effort are central components of the ecology of *L. dimidiatus*. Our results also indicate that individuals that exhibited greater feeding effort also tended to cheat less and move over smaller distances. In contrast, bolder more active, exploratory individuals were more willing to cheat on average and travelled greater distances from their station. Similarly, cheaters tended to service fewer clients and perform fewer pecks per client than non-cheaters.

A central tenet to understanding mutualistic interaction dynamics of the cleaner and client reef fish model system is to determine the importance of cheating in governing such traits. Both cleaners and clients are under strong selection to derive the maximum benefit from each interaction (Côté 2000). However, as client fish are small and/or herbivorous in most instances, opportunities for cheating are largely asymmetrical (except in the case of comparatively rare large predatory clients) (Bshary & Grutter 2002). Numerous studies have shown that cleaners will feed on client mucus in preference to ectoparasites, due presumably to higher nutrition content (Bshary & Grutter 2002). As such, one would expect such one-sided cheating events to lead to general instability and the demise of mutualistic interactions. However, this breakdown often does not happen and as Mills & Côté (2010) suggest, this is likely due to symbiotic organisms evolving coping mechanisms to deal with such cheating including active punishment or alternatively, rewarding cooperators. In the case of cleaner fish, it appears active punishment (chasing) and sanction type punishments (future avoidance of cheaters by client fish or those witnessing cheating via audience effects) largely keep the system in balance (Bshary & Grutter 2002). However, the role that consistent between-individual differences in behaviour, or personality, might play in influencing these interaction dynamics is unknown.

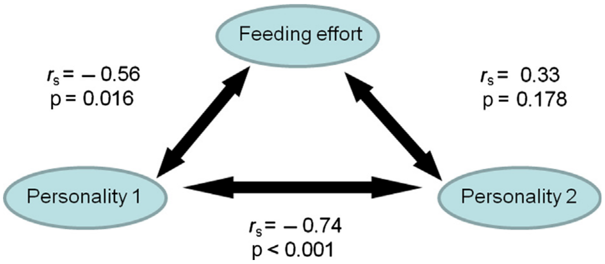

Fig. 2: Behavioural syndrome showing the relationship between personality (axes 1 and 2) and feeding effort in cleaner fish. Numbers shown represent results from Spearman rank correlation tests (r_s). Our alpha level for this analysis was adjusted to be more conservative using the false discovery rate B–Y adjustment ($\alpha = 0.027$).

Personality could be important for understanding mutualistic interactions as individuals tend to behave consistently across a range of contexts in the form of syndromes and these traits often include social, foraging and risk-taking traits (Sih et al. 2004). So how do individuals of different behaviour types (risk-prone, risk-averse) persist in mutualistic systems that also involve cheating and what mechanisms (e.g. frequency-dependent selection) are involved in maintaining them? Our results provide some novel insights into this ecological paradigm. We demonstrated that individuals that were least likely to cheat tended to interact with/service more clients, for longer durations, and with more effort per unit time than cheaters. These individuals also tended to travel over the smallest distances during our observation periods. In contrast, cheaters tended to range over greater distances, serviced fewer clients and generally exhibited lower feeding effort (in terms of number of pecks while cleaning). Mechanistically, these data might suggest that bold and timid individuals possess alternative foraging/cleaning tactics with timid individuals being more client faithful and bold individuals being more opportunistic. If cheating individuals are in fact cheating (Soares et al. 2008a), this likely explains their reduced cleaning efforts. As typical target items of cheating events are thought to be higher in nutritional value, bolder fish obtaining such higher quality foodstuffs could potentially afford to interact with fewer clients and for shorter durations. As such, understanding potential trade-offs associated with foodstuff quality (mucus of different species, parasite load) and cheating, as well as how this might translate to increased fitness or growth in terms of cheaters would be a fruitful area of future research interest.

While studies have previously observed cleaner fish to have pre-dominately fixed cleaning stations or territories (Bshary & Grutter 2002; Mills & Côté 2010), we noted that some individuals moved significant distances (up to 20 m) away from their cleaning sites (though generally returning to a primary area consisting of 1–2 m^2) during portions of the observation period. As our results show that bolder fish that are more prone to cheating also travel greater distances, this relationship might represent a 'loophole' that risk-prone fish are able to exploit. Indeed, Oates et al. (2010) similarly found that in the closely related cleaning goby *Labroides bicolor*, individuals that had larger home ranges also tended to cheat more, as evidenced by increased client 'jolt' rates during cleaning interactions. As most mechanisms for dealing with cheating involve individual recognition of clients or cleaners within an overlapping home range (though some clients home ranges can include multiple cleaner stations, Soares et al. 2008b), roaming cleaners might take advantage of transient visitors and non-resident clients in such a manner. Further, as some cleaners are generally more mobile, this notion might also explain why such fish spend less time cleaning on average and interact with fewer clients at fixed stations. Alternatively, this behaviour could reflect a state-dependent response in which cleaner fish that do not receive enough clients at their given station might need to supplement their diet using non-mutualistic methods such as cheating or parasitizing other fish. Indeed, on several occasions during our observations, we noted that certain cleaners (n = 4 individuals) were repeatedly willing to parasitize passing shoals of silversides (Family Atherinidae) in entirely non-cleaning interactions. These parasitic interactions were likely due to the transient presence of such species on the reef and the inherent inability of these small fish to reciprocate agonistically (Soares et al. 2008b).

There has been some disagreement about whether or not the observed client responses (as described above) truly represent cheating per se (or perhaps the clients are just responding to embedded parasite removal) (Cheney & Côté 2005). Similarly, not all studies find a relationship between client fish 'jolts' and other related correlates (parasite load) (Soares et al. 2008a), although the general trend among studies does suggest that this parameter is a reliable indicator of cheating by cleaner fish (Bshary & Grutter 2002; Pinto et al. 2011). That said, for the purposes of the current study this is not as important. As the resulting client response of either behaving aggressively or rapidly departing from the area is the same (both in level of risk to the cleaner and potential audience effects) regardless of cleaner intent, we feel confident in using this parameter as both a measure of foraging output as well as risk taking.

Mutualism and related cooperative interactions have long been the subject of scientific inquiry, both theoretically as well as empirically (Axelrod & Hamilton 1981; Bshary & Schaffer 2002; Bshary 2010). While game-theory models have indicated that the evolution of mixed strategies of cheating and honesty in many mutualisms might be unlikely and difficult to prove empirically, Freckleton & Côté (2003) show that it is at least possible in view of density-dependent payoffs (as opposed to constant pay-offs). Our application of the syndrome framework to this paradigm supports this assertion and provides the first evidence that personality could be mechanistically involved in the persistence of mixed strategies in the mutualistic interactions of cleaner fish. Additional work on understanding the role of sex over ontogeny (*L. dimidiatus* are sequential hermaphrodites with protogynous suppression) as well as the temporal longevity and extent of these differences in personality and their role in cleaner fish ecology and evolution represent potentially fruitful opportunities for future study.

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Ethical Standards

This research was performed in accordance with the laws, guidelines and ethical standards of the country in which they were performed (Australia).

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