Interspecific variation in cleaning behaviour and honesty among cleaner wrasses

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Abstract

Cheating in mutualisms allows species to exploit benefits without reciprocating, blurring the line between cooperation and conflict. In cleaner fish, this occurs when individuals consume client mucus instead of ectoparasites, gaining higher nutritional reward at the client's expense. We examined cheating behaviour, measured via client jolts as a proxy, in four dedicated (relying on cleaning for sustenance) and four non-dedicated (opportunistic) cleaner fish using an interaction test with three client types (predatory, visitor and resident), and the bystander test, to evaluate potential behavioural changes in the presence of a bystander. Cheating showed a species-specific pattern, with two non-dedicated species never engaging in this behaviour. Dedicated cleaners exhibited greater variability in both the amount of time spent interacting with clients and in cheating behaviour, with some species cheating consistently regardless of client type, while others adopted more selective strategies. This was particularly evident in *Labroides dimidiatus*, which reduced cheating with socially valuable clients, suggesting behavioural flexibility shaped by local competition and interaction frequency. The presence of a bystander revealed no significant differences in behaviour. These findings suggest that cleaner fish adopt distinct behavioural tactics, potentially reflecting different selective pressures and degrees of flexibility in managing the trade-off between cooperation and exploitation in mutualistic interactions.

Keywords: Dishonesty, Cheating, Cleaning behaviour, mutualism, cleaner wrasse, mutualistic social behaviour

Introduction

While mutualism is typically characterised by a mutually beneficial exchange, some species have evolved strategies to exploit their partners, gaining the advantages of the relationship without fulfilling their roles (Bronstein, 1994). This can be referred to as cheating and determines the boundary between cooperation and conflict between species (Bronstein, 1994; Connor, 1995). Cheating can be an important adaptive mechanism for organisms, allowing them to exploit a wider range of resources and niches otherwise unavailable within a strictly cooperative framework (Wechsler & Bascompte, 2022). Moreover, it contributes to phenotypic diversity among species, providing a rich substrate for natural selection to act upon (Pellmyr & Leebens-Mack, 2000; Wechsler & Bascompte, 2022). Thus, understanding the role of cheating in mutualisms allows us to grasp how natural selection operates not only through cooperation, but also through strategic exploitation, enriching the behavioural and ecological diversity observed in nature.

Cleaning mutualisms are classic examples of interspecific cooperative interactions, where so-called client fish trade the removal of parasites and dead or infected tissue for an easy meal for cleaner fish (Grutter, 1999). The ecological relevance of these mutualisms is well documented, as the experimental removal of cleaners from small, detached patch reefs can lead to drastic abundance and diversity drops, similar to overfished areas (Grutter et al., 2003; Waldie et al., 2011). In the best-studied cleaner fish system, the Indo-Pacific cleaner wrasses *Labroides spp.*, several potential conflicts exist between cleaners and clients, namely the risk of being eaten by predatory clients (Adam, 2012; Lobel, 1976), timing and duration of interactions, partner choice (Bshary & Grutter, 2002), and the cleaners' preference for the client's protective mucus instead of parasites (Grutter & Bshary, 2003, 2004). The latter is crucial as it shows that these interactions are not simple by-product mutualisms, but clients need to control cleaners' behaviour to prevent being cheated (i.e., cleaner eating the mucus) and to make them cooperate (i.e., eating parasites) (Bshary & Bronstein, 2011). This social conflict is the likely cause for the evolution of decision rules used by cleaners during interactions, such as impulse control, image scoring, and partner value assessment, which uses tactical deception, reputation management, reconciliation, individual recognition, and social tool use (Grutter, 2004; Pinto et al., 2011; Raihani & Bshary, 2015; Soares et al., 2014).

The *Labroides* genus comprises five species, all of which are dedicated cleaners that rely on cleaning interactions as their primary trophic strategy throughout life (Vaughan et al., 2017). Despite sharing the same ecological niche, species of this genus exhibit a behavioural continuum of cooperative profiles, ranging from relatively honest cleaning to frequent cheating (Côté & Brandl, 2021; Côté & Mills, 2020; Mills & Côté, 2010). *L. rubrolabiatus* and *L. phthirophagus* tend to behave more

cooperatively, with minimal partner control (Mills and Côté, 2010; Paula et al pers. communication). *L. dimidiatus* adopts an intermediate strategy, employing both cooperative behaviours and manipulative tactics such as tactile stimulation (Bshary & Grutter, 2002; Grutter, 2004). *L. bicolor*, by contrast, cheats frequently, interacts with fewer clients, and for shorter durations (Oates, Manica and Bshary, 2010). Finally, *L. pectoralis* engaged in frequent and long cleaning interactions, suggesting high investment in service provision, but its level of cooperation or cheating remains unquantified (Côté & Brandl, 2021). This interspecific variation likely reflects species-specific behavioural tendencies and ecological conditions, such as *L. bicolor*, which shows flexible cooperation levels across its home range, decreasing cheating where repeated interactions with clients are more likely (Oates, Manica and Bshary, 2010). Furthermore, although some dedicated cleaners other than *L. dimidiatus* are known to use social tools like tactile stimulation (Côté & Mills, 2020), our understanding of their social competence and behavioural sophistication remains limited. Even less is known about non-dedicated cleaners, which engage in cleaning only during certain life stages or as a supplementary feeding strategy (Vaughan et al., 2017). Since these species rely on alternative food sources, they may experience weaker selection for cleaning-related behavioural specialisation, potentially resulting in lower diversity and complexity in their cleaning behaviours.

Here, we investigate the interspecific variation in cheating, measured via client jolts as a behavioural proxy, among dedicated and non-dedicated cleaner wrasses using two behavioural tests: an interaction test, which compares interactions with three different client types (predators, residents, and non-residents), and a bystander test, which examines interactions in the presence and absence of a bystander. We hypothesise that variation in cheating will be more pronounced among dedicated cleaners, reflecting different cleaning strategies adopted by each species, while non-dedicated cleaners are expected to show less variability due to their more opportunistic use of cleaning. By focusing on these behavioural patterns, this study aims to advance our understanding of the ecological and evolutionary dynamics that shape mutualistic interactions in coral reef ecosystems and drive behavioural diversity and species adaptation.

Material and Methods

To investigate interspecific variation in cheating among cleaner wrasse species, four species of dedicated cleaners and three species of non-dedicated cleaners were tested via an interaction test with three different clients and a bystander test (Pinto et al., 2011) (Table 1, Suppl. Table 1). Dedicated cleaner species were selected from the genus *Labroides*, as it is the most studied group of dedicated cleaners (Côté & Brandl, 2021; Côté & Mills, 2020). Non-dedicated cleaner species were chosen based on their phylogenetic proximity to *Labroides* and previous knowledge on performing cleaning behaviours (Randall, 1986; Sazima, Moura and Gasparini, 1998; Baliga & Law, 2016; Baliga & Mehta, 2019). The behavioural tests were conducted at Laboratório Marítimo da Guia in Cascais (Portugal) and The Swire Institute of Marine Science (SWIMS) in Hong Kong. Within this study we used *Dascyllus trimaculatus, Zebrasoma scopas,* and *Paracirrhites forsteri* as client fish. The fishes were provided by the local suppliers Tropical Marine Centre (TMC; Portugal) and by Sealife Hong Kong limited (Hong Kong). All fish were deparasitized on arrival at the commercial suppliers.

	Species	**Cleaning Dependency**
	Labroides dimidiatus	Dedicated
	L. bicolor	Dedicated
	L. pectoralis	Dedicated
	L. rubrolabiatus	Dedicated
	Larabicus quadrilineatus	Non-Dedicated
	Halichoeres poeyi	Non-Dedicated
	Thalassoma lunare	Non-Dedicated

Table 1: *Species tested for their cheating behaviour. There are four species of dedicated cleaners from the genus Labroides, and four non-dedicated species that clean only when they are juveniles.*

Interaction Test

After three days of acclimation under laboratory conditions, an interaction test was carried out where each fish interacted with the client in the same tank. To evaluate the variation in cheating in the study species, three different types of clients were selected: a resident (*Dascyllus trimaculatus*), a non-resident (*Zebrasoma scopas*) and a predator client (*Paracirrhites forsteri*). The client species were chosen due to their widespread spatial overlap with all the cleaner species in the study. On day four, the cleaner and the client were placed on opposite sides of an experimental tank (50 x 31 x 40 cm), separated by two partitions: one opaque to avoid visual contact and prevent the cleaner from becoming stressed by seeing the client (especially the predator), and one transparent partition (Fig. 1A). After 30 minutes of acclimation to the experimental tank, the opaque partition was removed to allow five minutes of visual acclimation. Afterwards, the transparent partition was removed, and the interaction was recorded using a GoPro Hero Black 10 for 45 minutes. Then, the partitions were placed back in the experimental tank, the client was removed, and a new client was introduced into the experimental tank for another 30 minutes of acclimation. To ensure comparability across individuals and minimise uncontrolled variation due to order effects, the sequence of client presentation was kept constant: predator, non-resident, and resident. The predator was presented first to reduce the risk of heightened stress responses that might occur if it were introduced after other interactions. The resident client was always presented last, because it is a common, predictable client in the wild and helped reduce stress at the end of the trial, allowing the cleaner to finish the session in a more relaxed state.

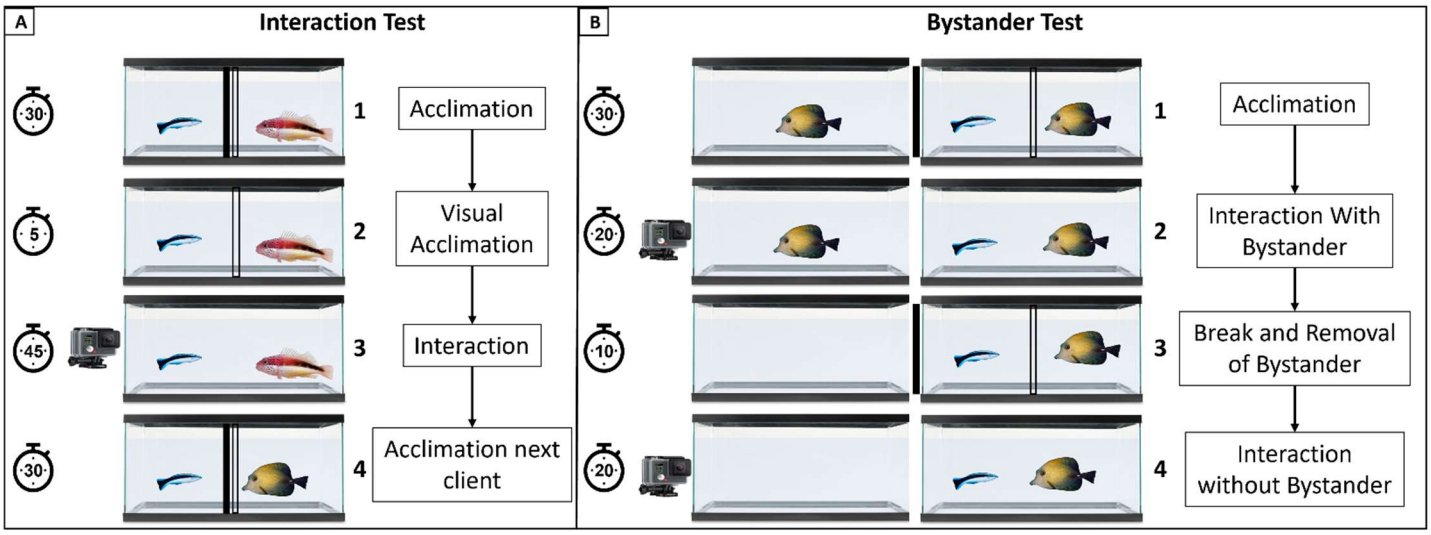

Figure 1: *Experimental design for the Interaction Test (A) and the Bystander Test (B). For the Interaction Test (A), the cleaner and client fish are placed together in the experimental tank,*

separated by an opaque and transparent barrier (1. A). After 30 minutes, the opaque barrier is removed (2. A), followed by the transparent barrier after 5 minutes (3. A), allowing interaction. Their behaviour is recorded for 45 minutes. The client is then replaced, and the process is repeated with the next client (4. A). For the Bystander Test (B), the cleaner and client are initially separated by a transparent barrier in the experimental tank, with a bystander fish in an adjacent tank separated by an opaque barrier (1. B). After 30 minutes, all barriers are removed, and interactions are recorded for 20 minutes (2. B). The barriers are then put back in place, the bystander is removed (3. B), and once the barriers are removed again, interactions are recorded for another 20 minutes (4. B).

Bystander Test

On day five, the fish were tested using the bystander test, following a protocol adapted from Pinto et al., 2011 (Pinto et al., 2011). The cleaner was placed in the experimental tank with the client *Zebrasoma scopas*, separated by a transparent partition (Fig. 1B). Another individual of *Zebrasoma scopas* was placed in an adjacent tank, separated by an opaque partition. After 30 minutes of acclimation, all partitions were removed, allowing the fish in the same tank to interact and the bystander to be visible. The interaction was recorded for 20 minutes to assess the cleaner's behaviour in the presence of the bystander. Then, the partitions were placed back for 10 minutes, and the bystander fish was removed. Finally, the partitions were removed again, and the interaction, now without the bystander, was recorded for another 20 minutes to compare the cleaner's behaviour in the absence of a bystander.

Supervised machine learning video analysis

All the videos produced were processed to have the same resolution and length (1920 x 1080; 30 fps, 40 minutes duration, with the last 5 minutes removed) to eliminate minor variations in video length and ensure all data were standardised. SimBA (v.2.3.5) (Goodwin et al., 2024), an open-source package that uses pose-estimation to create supervised machine learning classifiers of social behaviour, was used to analyse variations in cheating and time spent interacting by the fish in the two behavioural tests. Pose-estimation data were generated using DeepLabCut (v.2.3.9) (Nath et al., 2019), creating 21 models (one for each species tested per client). Approximately 400 frames were labelled for each model to ensure a good representation of behavioural variation across videos. A ResNet-50-based neural network was trained with default parameters for 500k iterations (batch size 1), chosen for its optimal balance of high accuracy in distinguishing complex poses and computational efficiency, making it particularly effective for multi-animal tracking in scenarios with overlapping or interacting subjects. The models were validated with two shuffles, achieving a test error of 5.03 pixels and a training error of 3.77 pixels. We applied a p-cutoff of 0.6 to filter X, Y

coordinates for downstream analysis, ensuring sufficient data quality while excluding unreliable predictions, aligned with standard practices in pose-estimation tasks. The behavioural annotation required for training the machine learning model in SimBA was produced using the software BORIS (v.7.13.8) (Friard & Gamba, 2016), focusing on two key behaviours: client's jolts (rapid movements of the client away from the species after receiving a bite) and interaction time (defined as the duration in which the cleaner fish was actively inspecting or cleaning the client). Client jolts were used as a behavioural proxy for cheating, following established conventions in cleaner fish research (e.g., Bshary and Grutter, 2002; Pinto et al., 2011). The pose-estimation data from DeepLabCut and the behavioural annotations from BORIS were then used together to train the supervised machine learning model in SimBA, using the Random Forest algorithm with 400 estimators and 'entropy' as the metric to measure the quality of splits. Following model training (F1-scores calculated by SimBA: 0.72 for interaction time and 0.75 for client's jolts), we generated a validation video and used it to set discrimination thresholds of 0.7 for interaction time and 0.5 for client's jolts.

Statistical Analysis

For the interaction test, the data obtained from supervised machine learning analysis were analysed using R (4.3.1) (R Core Team, 2020). Generalised linear mixed models (GLMM) were created using the "glmmTMB" package (Brooks et al., 2017). Models were selected based on their performance, including the lowest mean squared error (MSE), the best residual distribution and the highest R^2 (Suppl. Table 2; Supplementary Figure 1). Specifically, the variable client's jolts was modelled using a Poisson GLMM, while interaction time was analysed with a Gamma GLMM. Additionally, a new variable was created to standardise the number of jolts relative to interaction time, representing the number of jolts per 100 seconds of interaction. This variable was modelled using a Negative Binomial GLMM. These models were chosen as they provided the best fit for the data and the highest predictive accuracy. For the bystander test, a two-tailed Wilcoxon test was performed to compare behavioural differences between the behaviour in the presence and absence of the bystander to assess within-species differences for the same variables analysed in the interaction test.

Results

Interaction test

The interaction test revealed significant interspecific differences in both cleaning and cheating behaviours, with dedicated cleaners exhibiting greater behavioural variability (from 0 to 5.33 jolts; interaction times ranging from 8.7 to 359 seconds) compared to non-dedicated cleaners (from 0 to 1 jolt; interaction times from 1 to 68 seconds) (Supplementary fig. 2). When comparing across client types, dedicated cleaners interacted more with non-residents (mean = 230.62 s, range = 0-831.27 s) than with predators (84.37 s, 0-677.77 s) or residents (40.27 s, 0-254.47 s), while non-dedicated cleaners showed more uniform interaction times across clients (24.43 s, 0-158.60 s, with non-residents; 17.52 s, 0-134.30 s; with predators, and 28.10 s, 0-99.00 s, with residents). Dedicated cleaners differed markedly in their interaction patterns with non-resident clients (Fig. 2C), with *L. bicolor* spending significantly more time interacting (mean = 411.87 ± 97.42 s) than *L. dimidiatus* (79.49 ± 24.07 s), *L. pectoralis* (209.61 ± 64.00 s), and *L. rubrolabiatus* (216.60 ± 66.08 s) (all $p < 0.005$, Gamma GLMM, Suppl. Table 3, Fig. 2C). Additional variation within the group emerged, with *L. dimidiatus* interacting significantly more than *L. pectoralis* ($p = 0.027$, Gamma GLMM, Fig. 2C). When interacting with the predator client, *L. bicolor* (mean = 189.71 ± 70.99 s) also spent significantly more time than *L. dimidiatus* (45.63 ± 17.02 s) and *L. rubrolabiatus* (13.57 ± 10.17 s) (both $p < 0.05$, Gamma GLMM, Fig. 2A). Among non-dedicated cleaners, *L. quadrilineatus* (mean = 44.16 ± 18.38 s) interacted significantly longer with non-resident clients than *T. lunare* (18.96 ± 4.09 s) (both $p < 0.05$, Gamma GLMM, Supp. Table 3, Fig. 2C). Client's jolts followed a similar pattern reflecting the behavioural variation among dedicated cleaners. *L. bicolor* and *L. dimidiatus* elicited client jolts across all client types, while *L. pectoralis* and *L. rubrolabiatus* elicited client jolts only when interacting with non-resident clients (Fig. 2B, D and F). When interacting with predator clients, *L. bicolor* elicited significantly more client jolts per 100 seconds of interaction than *L. dimidiatus* ($p = 0.0006$, Poisson GLMM), with means of 6.79 ± 2.30 and 2.65 ± 1.92, respectively (Fig. 2B). Considering the non-resident client (Fig. 2D), *L. bicolor* showed the highest rate of client jolts per 100 seconds of interaction (mean = 5.46 ± 1.41), followed by *L. pectoralis* (2.87 ± 1.14), *L. rubrolabiatus* (2.26 ± 1.59), and *L. dimidiatus* (0.62 ± 0.51). However, none of these differences reached statistical significance (Poisson GLMM, $p > 0.05$ for all comparisons). In contrast, when interacting with resident clients (Fig. 2E), *L. dimidiatus* exhibited a significantly higher rate of client jolts per 100 seconds than *L. bicolor* (mean = 8.14 ± 4.80 vs 0.45 ± 0.37; $p = 6.78\times10^{-9}$, Negative Binomial GLMM, Suppl. Table 3). Among non-dedicated cleaners, client jolts were occasionally observed in *T. lunare*, across different client types. In contrast, *L. quadrilineatus* and *H. poeyi* did not elicit any client jolts under any condition.

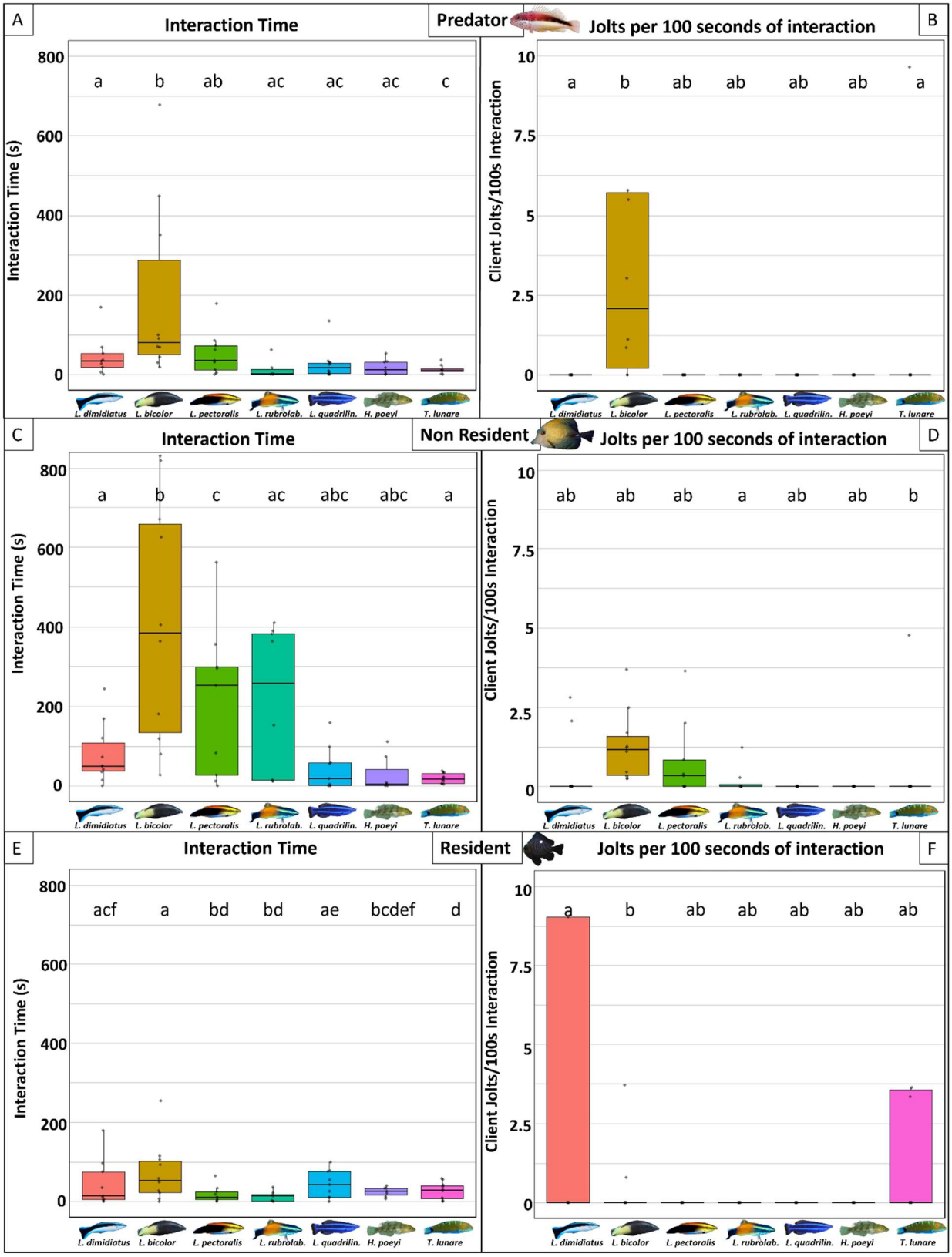

Figure 2. *Variation in interaction time and client jolts per 100 seconds of interaction across cleaner fish species and client types. Boxplots show (A, C, E) interaction time (in seconds) and (B, D, F) rate of client jolts per 100 seconds of interaction across the seven cleaner fish species interacting with three client types: predators (A–B), non-residents (C–D), and residents (E–F). Different lowercase*

letters indicate significant differences between species within each panel (interaction time was modelled with a Gamma GLMM, and the number of jolts per 100 seconds of interaction was analysed with a Negative Binomial GLMM). The boxes are coloured differently to visually distinguish species. Boxes show the median and interquartile range; whiskers indicate the full data range excluding outliers, which are plotted as individual points.

Bystander test

No significant bystander effects were detected for any of the cleaner fish species across the behavioural variables (all p-values > 0.05, Wilcoxon test, Suppl. Table 4) (Fig. 3). For example, in *L. bicolor*, client jolts per 100 seconds of interaction were slightly lower in the presence of a bystander (mean ± SD: 0.51 ± 0.56) than in its absence (0.74 ± 1.11), though this difference was not statistically significant. However, interaction time remained similar between conditions (418.6 ± 268.8 s with bystander vs. 404.4 ± 266.9 s without) (Fig. 3B).

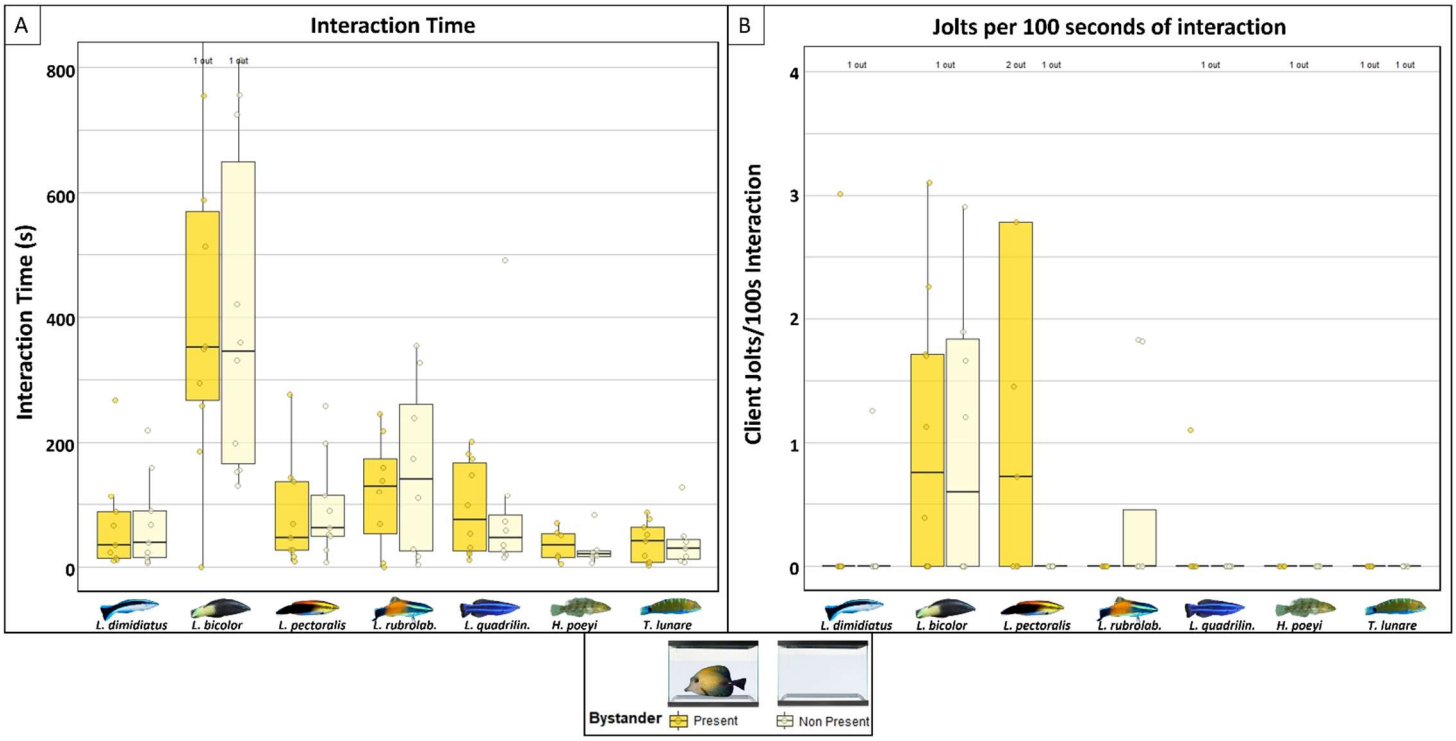

Figure 3: *Effect of bystander presence (Present vs. Non-Present) on interaction time and client's jolts for 100 seconds of interaction for each cleaner fish species. Panels represent (A) interaction time (in seconds) and (B) client jolts per 100 seconds of interaction. Each dot corresponds to the average value for a single individual. Boxes show the median and interquartile range; whiskers indicate the full data range excluding outliers, which are plotted as individual points. Labels above the boxes indicate the number of outliers exceeding the y-axis limit. Box colour denotes bystander condition (yellow = Present, light yellow = Non-Present).*

Discussion

We investigated interspecific variation in cheating behaviour, measured via client jolts as a behavioural proxy, among four dedicated and three non-dedicated cleaner species, using two behavioural assays that measured responses to different client types and the presence of a bystander. Our results reveal distinct interspecific strategies in cleaning behaviour among wrasses. Dedicated cleaners spent more time interacting with clients but exhibited higher variability across species in cheating compared to non-dedicated species, where cheating was almost non-existent, confirming that cheating is positively correlated with cleaning dependency (Barbu et al., 2011). Dedicated cleaners also displayed preferences for specific client types and adopted species-specific cheating strategies that varied according to client identity. While no significant audience effects were detected, observed behavioural patterns in some species raise the possibility that ecological or social context may influence audience sensitivity.

The behavioural profiles of dedicated cleaner species reveal how closely related species can adopt distinct strategies to navigate the trade-off between cooperation and exploitation. *Labroides bicolor*, for example, exhibited the highest cheating, suggesting a strategy aimed at maximising short-term rewards. Interestingly, unlike in the wild, where it typically engages in brief cleaning interactions (Côté & Brandl, 2021), *L. bicolor* also invested more time in interactions, possibly reflecting a shift in cost-benefit dynamics under reduced ecological constraints in captivity. In contrast, *L. dimidiatus* displayed a more balanced profile, with moderate cheating and interaction times, which may reflect its greater social plasticity and sensitivity to partner control mechanisms (Bshary & Oliveira, 2015). *L. rubrolabiatus* has been previously described as a cooperative cleaner (Côté & Brandl, 2021; Côté & Mills, 2020), and in our study, it appeared more consistently cooperative than *L. pectoralis*. *L. rubrolabiatus* spent more time interacting with clients while maintaining very low levels of cheating, suggesting a strategy based on sustained cooperative engagement, as observed in the wild (Côté & Mills, 2020). *L. pectoralis*, in contrast, showed higher cheating despite shorter interactions, which may reflect a more opportunistic approach, engaging just enough to benefit from the interaction without fully investing in client relationships. These divergent strategies highlight how, even among cooperative species, different trade-offs between investment and exploitation can shape cleaning behaviour. Regarding non-dedicated cleaners, our findings indicate that they engage in cleaning behaviours less frequently and exhibit lower instances of cheating compared to dedicated cleaners. Among them, *L. quadrilineatus* stood out by showing the longest interaction times and no cheating events, suggesting a more structured and possibly ecologically relevant cleaning strategy, whereas the other non-dedicated species (*T. lunare* and *H. poeyi*) interacted only briefly with clients and rarely cheated. This behavioural variation mirrors field observations in sympatric populations, where *L.*

quadrilineatus, despite being a non-dedicated cleaner, performs frequent cleaning, often interacting with predatory clients, and us tactile stimulation, all of which are considered markers of sophisticated social behaviour (Barbu et al., 2011). Conversely, *T. lunare* avoids predators, rarely uses tactile stimulation, and cleans infrequently, aligning with its short interaction times in our data (Barbu et al., 2011). Similarly, *H. poeyi* shows limited cleaning in the wild, typically restricted to juvenile stages or occurring opportunistically (Roede, 1972), which may reflect weaker selection for socially complex behaviours. Together, these results suggest that both the degree and duration of ecological investment in cleaning are key drivers shaping the emergence of cheating strategies and social complexity in mutualistic interactions.

In addition to broad interspecific patterns, species-specific strategies also emerged in response to variation in client type, especially among dedicated cleaners. *L. bicolor* generally engaged in long interactions and exhibited high levels of cheating across most client types, but both interaction time and cheating were reduced with the resident client. This pattern may reflect the resident's small body size (~4 cm), which could make it a less attractive partner, consistent with field data showing that *L. bicolor* preferentially interacts with larger client species (Côté & Brandl, 2021). In contrast, *L. dimidiatus* displayed behavioural flexibility consistent with adaptive regulation of cheating, increasing exploitation with low-risk, low-value clients (residents), while reducing it when interacting with socially valuable partners such as predators or non-residents. This aligns with prior evidence that recent predatory interactions suppress cheating (Bshary et al., 2011) and with the known capacity of *L. dimidiatus* to manage its reputation through conditional cooperation and tactical service adjustment (Bshary & Grutter, 2002; Pinto et al., 2011). These findings suggest that only *L. dimidiatus* modulates cheating according to biological market dynamics, possibly due to higher local cleaner density and competition, which may make the distinction between resident and visitor clients more salient. Other dedicated cleaners, such as *L. rubrolabiatus* and *L. pectoralis*, were observed to cheat only on non-resident clients, possibly reflecting their lower local densities compared to *L. dimidiatus*, which likely reduces the frequency of repeated interactions and weakens the selective pressure to regulate cheating based on client identity (Bshary & Oliveira, 2015; Triki et al., 2019). This pattern may reflect a lower risk of punishment when cheating on transient clients, who are less likely to return or retaliate. This interpretation supports the idea that ecological factors, such as local density and interaction frequency, may shape the extent to which cleaners adaptively regulate their behaviour. Among non-dedicated cleaners, no clear client-specific cheating pattern emerged. *T. lunare* showed a few isolated cheating events with resident and predator clients, while *H. poeyi* and *L. quadrilineatus* did not elicit any client jolts. These results suggest that non-dedicated cleaners may lack the behavioural flexibility observed in dedicated species when responding to different client

types, possibly due to reduced ecological dependence on cleaning or lower cognitive investment in client discrimination (Araujo et al., 2020; Barbu et al., 2011).

The presence of a bystander did not significantly alter the behaviours for any of the tested species. This may reflect the ecological context of the source populations, as areas with a high client-to-cleaner ratio, where many clients are available and competition among cleaners is low, may exert weaker selection to adjust behaviour in response to an audience (Triki et al., 2018; 2019; 2019). In contrast, individuals from socially complex environments, where cleaners must compete for clients and maintain long-term relationships, are more likely to evolve and express socially sophisticated behaviours, including audience sensitivity (Triki et al., 2018; 2019; 2019). We observed a pattern of reduced cheating in *L. bicolor* and *L. pectoralis* in the presence of a bystander and, although this effect was not statistically significant, it is possible that a larger sample size would increase the power to detect such subtle behavioural adjustments. Among non-dedicated cleaners, no evidence of bystander sensitivity was detected, which could be attributed to a lack of selective pressure to monitor audiences in species that clean sporadically or primarily during early life stages (Barbu et al., 2011; Roede, 1972). These results suggest that the emergence of audience effects may depend on both ecological context and species-specific social strategies.

Taken together, our findings reveal that cheating in cleaner wrasses is shaped by a complex interplay of species-specific strategies, social context, and ecological reliance on mutualism. However, an important caveat of this study is that we did not control for the presence of parasites on client fish, a variable known to influence both the expression and detectability of cheating. As such, client jolts, while commonly used as a proxy for cheating behaviour, should be interpreted with caution, as they may also result from non-parasitic interactions such as exploratory biting or unsolicited contact. Despite this limitation, we found that dedicated cleaners exhibited greater behavioural plasticity and client-specific responses, suggesting stronger selective pressures to maintain stable cooperative interactions. In contrast, non-dedicated species showed limited behavioural modulation, likely reflecting a reduced investment in cleaning and fewer incentives to develop socially sophisticated behaviours. Ultimately, cleaner wrasses adopt diverse and flexible strategies to balance cooperation and exploitation, shaped by their ecological roles and the social environments they inhabit.

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Ethics

All experimental procedures were conducted in accordance with institutional and governmental guidelines for the care and use of animals in research. Ethical approval for this study was granted by the Faculdade de Ciências da Universidade de Lisboa animal welfare committee (ORBEA – Statement 4/2023) and Direção-Geral da Alimentação e Veterinária (DGAV permit 27950/25-S) in accordance with the requirements imposed by the Directive 2010/63/EU on the protection of animals used for scientific purposes. Ethical approval was also granted by the Committee on the Use of Live Animals in Teaching and Research (CULATR) of The University of Hong Kong (Protocol number: 23-258) and by the Department of Health of the Hong Kong Government (Ref. number: 23-521).

CRediT

Conceptualization: DR, CS, JRP, Data curation DR; Formal analysis DR; Funding acquisition JRP, CS; Investigation DR, MR, MC, BP; Methodology DR, CS, JRP; Project administration CS, JRP; Resources CS, JRP; Software DR; Supervision CS, JRP; Validation DR; Visualization DR; Writing – original draft DR, CS; Writing – review & editing DR, MR, MC, BP, JRP, CS.

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