Degrees of honesty: cleaning by the redlip cleaner wrasse *Labroides rubrolabiatus*

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Abstract Cleaning symbioses among coral reef fishes are highly variable. Cleanerfishes vary in how much they cooperate with (i.e. remove only ectoparasites) or cheat (i.e. bite healthy tissue, scales or mucus) on their fish clients. As a result, clients use various strategies to enforce cooperation by cleaners (e.g. punishment or partner choice), and cleaners use tactile stimulation to manipulate cheated client behaviour. We provide the first detailed observations of cleaning behaviour of the redlip cleaner wrasse *Labroides rubrolabiatus* and ask where interactions with this cleanerfish lie on the continuum of cleanerfish honesty, client control, and cleanerfish manipulation. Ninety per cent of redlip cleaner wrasses took jolt-inducing cheating bites from their clients, but they did so at a very low rate ($\sim$ 2 jolts per 100 s inspection). Retaliatory chases by clients were uncommon. Three-quarters (30 of 40) of cleaner wrasses used tactile stimulation on their clients, but rarely did so to reconcile with cheated clients. Instead, the majority (70%) of tactile stimulation events targeted a passing client that then stopped for inspection.

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The relationship between redlip cleaner wrasses and their clients appears to be less conflictual than those documented in other *Labroides* cleanerfishes. Future studies should test whether this low level of conflict is consistent across space and time and is underpinned by a preference for ectoparasites over other client-gleaned items. As an active cleaner that appears to take few cheating bites from their clients, *L. rubrolabiatus* has the potential to be as important a driver of fish health and community structure on coral reefs as its better-known relatives.

Introduction

Cleaning symbioses among coral reef fishes are among the best documented interspecific interactions. These interactions typically involve a small cleanerfish, which removes ectoparasites and other items from the body surface, mouth, and gills of fish clients (Côté 2000). The latter often display their willingness to be cleaned through stereotypical, immobile postures, with head up or down and fins and opercula flared (Côté et al. 1998). More than 130 species of tropical reef fish are known to clean, either on an opportunistic basis or as a main mode of foraging as juveniles or throughout their life (Côté 2000; Vaughan et al. 2017). Conversely, hundreds of fish species seek the services of cleanerfishes on coral reefs (Quimbayo et al. 2018; Triki et al. 2019), and some cleanerfish have been shown to reduce the ectoparasite loads of their clients (Grutter 1999; Cheney and Côté 2001; Grutter et al. 2018), improve client health and cognitive function (Ros et al. 2011; Binning et al. 2018), as well as influence fish community structure

on coral reefs (Bshary 2003; Grutter et al. 2003; Waldie et al. 2011).

The Indo-Pacific bluestreak cleaner wrasse *Labroides dimidiatus* has emerged as a model for understanding interactions among cleanerfish and their clients. Studies of this species have dispelled the notion of cleaning as a purely mutualistic enterprise; instead, cleaning interactions are governed by conflicting interests and 'Machiavellian' behaviour and manipulation (Bshary 2001, 2011; Triki et al. 2019). While client fishes would prefer to have only their ectoparasites removed, *L. dimidiatus* often feeds on healthy tissue, scales, and mucus, which constitutes cheating (Grutter and Bshary 2003, 2004) and results in sudden jolts by the client in response to cheating bites (Bshary and Grutter 2002). In fact, when given an unconstrained choice, *L. dimidiatus* generally prefers to consume fish mucus over ectoparasites (Grutter and Bshary 2004). To enforce good cleaning service quality, clients use partner-control mechanisms that depend on their individual strategic options (Bshary and Bronstein 2011). For example, predatory clients exert the ultimate 'threat of reciprocity', whereby they could retaliate on cheating cleaners by eating them. Such a high cost of cheating largely ensures honest cleaning by *L. dimidiatus* (Bshary and Bronstein 2004). Non-predatory clients cannot eat cleaners but use two condition-dependent alternatives to punish cheaters instead. Those with access to a single cleanerfish (i.e. 'resident' clients) chase cheaters aggressively, while those with access to multiple cleanerfish (i.e. 'non-resident' clients) delay their return or simply switch cleaners after being cheated on (Bshary and Grutter 2002, 2005; Bshary and Schäffer 2002). Bluestreak cleaner wrasses, in return, manipulate client decisions by stroking their pelvic and pectoral fins on their client's dorsal area, a behaviour known as 'tactile stimulation' (Bshary and Würth 2001; Grutter 2004). This behaviour serves to reconcile cheating cleaners with their clients and prolongs interactions with jolting clients that were about to leave (Bshary and Würth 2001). Tactile stimulation appears to work because it lowers baseline and acute stress cortisol levels (e.g. Soares et al. 2011b). Bluestreak cleaner wrasses cheat less in the presence of an audience of potential clients (Pinto et al. 2011) and when there is competition from other cleaners for access to clients (Adam 2010; Triki et al. 2019). In summary, interactions between *L. dimidiatus* and their clients fit the expectations of market theory as a system characterised by supply-and-demand dynamics, partner choice, and punishment to prevent cheating (Noë and Hammerstein 1994; Bshary and Noë 2003).

There is, however, increasing evidence that *L. dimidiatus* is not a universal model for cleaning interactions. For example, cleaning gobies *Elacatinus* spp., the main cleanerfishes in the tropical and subtropical western

Atlantic Ocean, never display tactile stimulation and their clients do not control cheating through partner switching or through aggressive chasing after a jolt (Soares et al. 2008). These differences between cleaning gobies and *L. dimidiatus* are consistent with the apparent preference of cleaning gobies for fish ectoparasites over mucus (Arnal et al. 2001; Soares et al. 2011a). Jolt-inducing bites by gobies might instead inform clients that their search for parasites has ended (Soares et al. 2008). Bicolor cleaner wrasses *L. bicolor* also deviate from the *L. dimidiatus* model. These cleaners operate not from the limited area of a cleaning station, as *L. dimidiatus* and cleaning gobies do, but from large home ranges, which reduces the likelihood of repeated interactions with individual clients (Mills and Côté 2010; Oates et al. 2010a, b). As a consequence, bicolor cleaner wrasses cheat frequently: they consume more non-parasite food items (Oates et al. 2012) and induce more jolts on their clients than bluestreak cleaner wrasses when on the same reef (Mills and Côté 2010). As with *L. dimidiatus*, *L. bicolor* cheats particularly often on resident client species (Mills and Côté 2010). Bicolor cleaner wrasses are not chased by cheated clients as much as might be expected given their level of cheating, perhaps because they offer the only cleaning option for many fishes established too far from a station-based cleaner such as *L. dimidiatus* (Mills and Côté 2010). Cleanerfish species therefore seem to present a continuum, from systems with relatively honest cleaning and little partner control to systems with frequent cheating and a range of client control strategies and cleanerfish counterstrategies (Table 1).

Here, we present the first detailed study of the cleaning behaviour of the redlip cleaner wrasse, *Labroides rubrolabiatus*, and we determine where this species lies on the spectrum of cleanerfish systems. More specifically, we examine territory size, report on clientele composition and inspection rates of redlip cleaner wrasses, and contrast their patterns of cheating, client retaliation, and tactile stimulation to those of better-known cleanerfishes. In doing so, we contribute to the growing understanding of the nuances of these charismatic interspecific interactions, which are ubiquitous on coral reefs.

Methods

Study species and location

The redlip cleaner wrasse *L. rubrolabiatus* Randall, 1958 is a small (max. 9 cm total length) reef fish found across the Eastern Central Pacific, from Samoa to the Line and Society Islands, French Polynesia, and the Pitcairn Group (Froese and Pauly 2019). It inhabits lagoon and seaward coral reefs to depths of at least 32 m (Lieske and Myers

Table 1 Summary of key characteristics of cleanerfish systems. Photographs of *Elacatinus evelynae*, *L. dimidiatus* and *L. rubrolabiatus* by Luiz A. Rocha; *L. bicolor* by Frédéric Zuberer. *Sources*: [1]Humann–Caribbean fishes; [2]Allen et al. (2003); [3]Arnal and Côté (1998); [4]Mills and Côté (2010); [5]This study; [6]Whiteman and Côté (2002); [7]Barbu et al. (2011); [8]Nedelec et al. (2017); [9]Côté, unpublished data; [10]Adam and Horii (2012); [11]Soares et al. (2008); [12]Mills and Côté, unpublished data; [13]Bshary and Grutter (2002); [14]Bshary and Schäffer (2002); [15]Bshary and Würth (2001)

	Elacatinus cleaning gobies	*Labroides* cleaner wrasses		
		dimidiatus	*bicolor*	*rubrolabiatus*
Maximum size (total length)	4 cm[1]	11.5 cm[2]	14 cm[2]	9 cm[2]
Territory/home range size	∼ 1 m[3]	∼ up to 8 m[4]	Up to 25 m[4]	Up to 9 m[5]
Proportion of time spent inspecting	8–14%[6]	12–32%[4,7–10]	∼ 20–40%[4,9,10]	27%[5]
Cheating by cleaners	R = NR[11]	R > NR[4]	R ≫ NR[4]	R = NR[5]
	Predators ∼ 0[11]	Predators ∼ 0[7]	Predators ∼ 0[12]	Predators ∼ 0[5]
Retaliation by cheated clients	No chasing[11]	R chase[13]	R > NR chase[4]	R = NR chase[5];
		NR delay or switch[14]	Other retaliatory behaviours unknown	Other retaliatory behaviours unknown
Tactile stimulation	Absent[11]	Present[4,7,15]	Present[4]	Present[5]

R: non-predatory resident clients (i.e. species with access to no or one cleaner), NR: non-predatory non-resident clients (i.e. species with access to multiple cleaners). Territory/home range size is expressed in terms of maximum linear distance from the farthest opposite edges of the territory or home range

1994). It is characterised by black and white stripes on the head, a bright yellow to orange mid-body section, and a black tail, sometimes edged with white or blue (Table 1). *Labroides rubrolabiatus* has been described as a cleanerfish on the basis of anecdotal observations (e.g. Randall 1958; Allen et al. 2003) and included in various global lists of cleanerfish species (van Tassell et al. 1994; Côté 2000; Vaughan et al. 2017), although little appears to be formally known of its behaviour. However, the four other species (*bicolor*, *dimidiatus*, *pectoralis*, and *phthirophagus*) within the small monophyletic genus *Labroides* are all obligate cleaners throughout their ontogeny (Baliga and Law 2016). This group diverged from its immediate sister group (the monotypic, coral mucus-feeding *Larabicus*) ∼ 10–12 MYA (Cowman et al. 2009; Baliga and Law 2016), while *L. rubrolabiatus* diverged from its better-known congeners (*bicolor* and *dimidiatus*) ∼ 9 MYA (Baliga and Law 2016).

We studied redlip cleaner wrasses on the outer coral reef slope to the east and west of Tareu Pass in Opunohu Bay (17° 28′ 39 S, 149° 49′ 33 W) on the north shore of Mo'orea, French Polynesia, in February 2012. Redlip cleaner wrasses were observed at depths ranging from 7.5 to 20 m; all observation sites had low live coral cover (< 10%) but still relatively high relief owing to recent coral mortality from a crown-of-thorn seastar (*Acanthaster planci*) outbreak from 2006 to 2009 (Mills 2012; Leray

et al. 2012). Two other cleaner wrasse species, *L. dimidiatus* and *L. bicolor* (Table 1), were present at the study locations (Oates et al. 2010a, b), but we observed few interactions among the cleanerfish species.

Behavioural observations

Observations were carried out between 10.30 and 17.00 by SCUBA divers. We observed every individual *L. rubrolabiatus* encountered and mapped the location of observed fish to preclude repeat observations on subsequent days. Observations began upon sighting a new individual and were made from a distance of 2–3 m. Each individual cleaner was observed for 15 min, during which we recorded in situ on a slate the number and species of each client interacting with the focal cleaner, the duration of each interaction (to the nearest second, with a stopwatch), whether the client jolted and the client's reaction following a jolt (i.e. chase or no chase). Jolts are apparently painful reactions by clients to a cleanerfish bite, which have previously been shown to be unrelated to the removal of ectoparasites and are considered to be indicators of dishonest biting by cleaners (Bshary and Grutter 2002; Soares et al. 2008). At the end of each focal observation period, we measured the linear distance between the two most distant points reached by the cleaner during the observation, recognised by natural landmarks on the substratum

(e.g. coral colonies, sponges, crevices). We used this maximum linear distance as a rough proxy for home range size in part because of time constraints and in part because a similar proxy was available for other *Labroides* species (Mills and Côté 2010). The total length of the focal cleaner was estimated visually to the nearest 0.5 cm. Both observers were trained to estimate lengths underwater using PVC pipes of different sizes and shapes until they achieved an error of < 10%. We did not classify cleanerfish by sex or by age since there appeared to be no ontogenetic colour change in this species.

At the end of each observation, we also performed a 5-min point count within a 3 m × 3 m plot centred on the middle of the focal cleaner's home range (see Bohnsack and Bannerot 1986; Colvocoresses and Acosta 2007 for point count method). We noted natural landmarks at the corners of each plot to delineate the survey area. The recording diver hovered approximately 3 m from the bottom and 5 m away from the edge of the plot to minimise disturbance. We recorded on a slate the species and numbers of all fish within or crossing the plot and used these data to reflect the potential clientele available to each cleanerfish.

Data analyses

We examined the trajectory of client species accumulation with increasing number of redlip cleaner wrasses observed by plotting a rarefaction curve, with the SPECACCUM function in the library 'vegan' in R (v. 3.3.2). We used the rarefaction method, which is appropriate when samples are individuals rather than sites.

To examine potential preferences by redlip cleaner wrasses for specific clients (i.e. species and body size), we calculated the proportions of the cleaner wrasse clientele and of the general reef fish assemblage (obtained from cleaner-matched point counts) accounted for by each fish species. We examined the relationship between both proportions to identify fish species that were inspected more or less than expected on the basis of their abundance on the reef. We then correlated the residuals of this relationship to species-specific maximum total length, derived from Allen et al. (2003). For sex-changing species with obvious sex-associated colour patterns (e.g. parrotfishes, wrasses), we used the maximum length of the initial colour phase because terminal-phase individuals were rare at the study location.

From the focal observations, we obtained the proportion of time cleaners spent inspecting clients. We also extracted measures of cleaner cheating (i.e. jolting), client punishment (i.e. chasing), and cleaner appeasement behaviour (i.e. tactile stimulation), first across all clients combined, and then for three specific classes of clients that might be

expected to vary in their interactions with cleanerfishes: predators, non-predatory residents (i.e. species with access to only one cleanerfish), and non-predatory non-residents (i.e. species with access to multiple cleanerfish) as per Bshary (2001; electronic supplementary material, Table S1). The extents of jolting, chasing, and tactile stimulation were measured as rates per 100 s of inspection overall (or 100 s of inspection of predators, residents, or of non-residents, as appropriate) and as proportions of either cleaners or clients performing the behaviour. Because few predatory clients were inspected, we report their statistics first. We then compared rates and proportions between non-predatory resident and non-predatory non-resident clients (referred to as 'residents' and 'non-residents') with paired *t* tests (i.e. data paired within cleanerfish). Because not all cleanerfish inspected clients of both types, the sample sizes in paired tests are variable.

Results

Clientele

We observed 40 individual *L. rubrolabiatus*, which ranged in total length from 5 to 9 cm. They travelled over a linear distance of 9.0 m (95% CI 6.2–11.8 m), on average, in 15 min.

These cleaners collectively inspected 1354 individuals of 62 client species across 16 families (Table S1). The client species rarefaction curve approached an asymptotic number of clients with the observation of 40 individual cleaners (Fig. S1). Four species accounted for nearly half (49.8%) of all clients inspected: three surgeonfishes (family Acanthuridae) (lined bristletooth *Ctenochaetus striatus*, 28.9%; whitecheek surgeonfish *Acanthurus nigricans*, 6.6%; brushtail tang *Zebrasoma scopas*, 5.8%) and one damselfish (Pomacentridae) (Pacific half-and-half chromis *Chromis iomelas*, 8.5%). We observed 89 reef fish species in 24 families in point counts.

There was a strong relationship between the proportional representation of individual species in the clientele of redlip cleaner wrasses and in the general reef fish assemblage ($r^2 = 0.88$, $F_{1,90} = 713.4$, $P < 0.001$; Fig. 1). The commonest species on the reef were either slightly over-represented (e.g. lined bristletooth, by 6%) or slightly under-represented (e.g. half-and-half chromis, bullethead parrotfish, whitecheek surgeonfish, by 4%) among the clients of redlip cleaner wrasses (Fig. 1). There was no relationship between the extent of over- or under-representation in clientele and client maximum length ($r^2 = 0.003$, $F_{1,85} = 0.31$, $P = 0.58$).

Seven per cent of clients were predators. Thirty-six per cent of clients were non-predatory residents with small
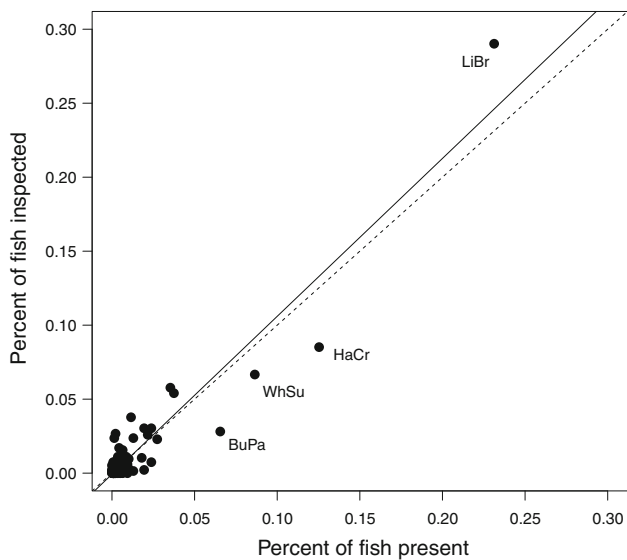
Fig. 1 Relationship between the proportional representation of individual reef fish species in the clientele of redlip cleaner wrasses and of species present on the same reef in Mo'orea, French Polynesia. Each point represents a reef fish species. The solid line is the line of best fit ($y = 1.067 * x - 0.0007$); the dashed line is the 1:1 relationship. *LiBr* lined bristletooth, *HaCr* half-and-half chromis, *WhSu* whitecheek surgeonfish, *BuPa* bullethead parrot. Scientific names are given in Table S1

territories that were likely to have access to only one cleanerfish; 57% were non-predatory, non-resident fish that ranged more broadly.

Cleaner and client behaviour

Redlip cleaner wrasses spent, on average, just over one-quarter of their time inspecting clients (26.7%, 95% CI 18–34.9%), during which they inspected, on average, 32 clients per 15 min (95% CI 22–42 clients per 15 min).

Most redlip cleaner wrasses (90%) inflicted jolt-inducing bites on their clients, but they did so at a low overall rate (mean = 2.12 jolts per 100 s inspection, 95% CI 1.45–2.78 jolts per 100 s inspection). Only 5% of predatory clients inspected jolted, at an overall rate of 0.9 jolt per 100 s of inspection of predatory clients (95% CI = 0.7–1.3). The jolting rate of resident clients (3.8 jolts per 100 s inspection of resident clients [95% CI 2.6–5.0]) was similar to that of non-resident clients (2.6 jolts per 100 s inspection of non-residents [95% CI 1.8–3.4]; paired t test, $t_{36} = 1.25$, $P = 0.22$; Fig. 2a). On average, 17% of resident clients jolted (95% CI 12–22%) compared to 11% of non-resident clients (95% CI 8–14%; paired t test, $t_{36} = 1.75$, $P = 0.09$).

Clients chased redlip cleaners at a low rate (mean = 1.25 chases per 100 s inspection, 95% CI 0.86–1.64 chases per 100 s inspection). Nearly two-thirds of these chases (mean = 61.6%, 95% CI 42–81%) occurred after a
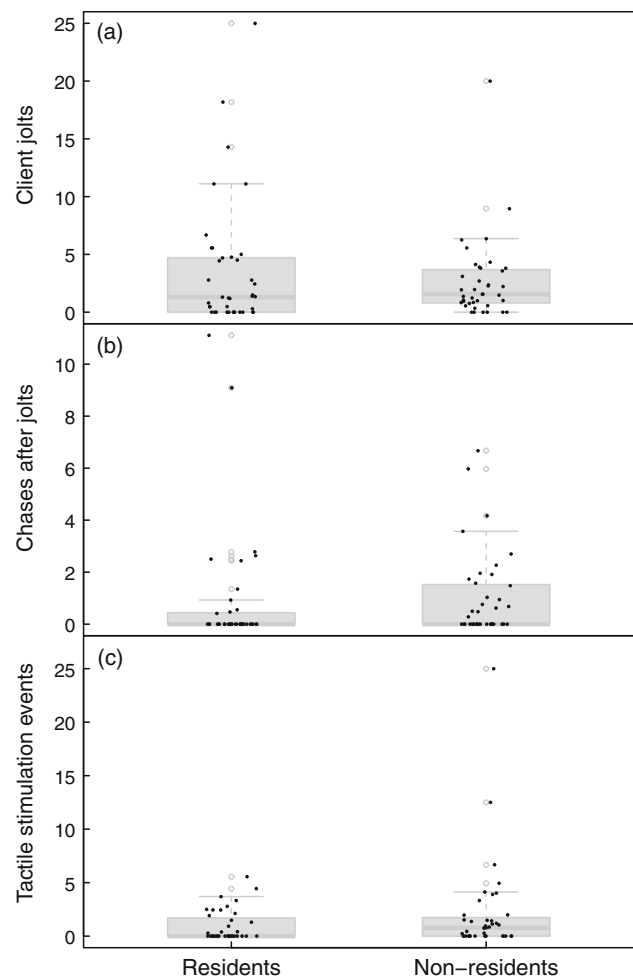

Fig. 2 Cleaner and client behaviour during cleaning interactions. **a** Rate of client jolting, **b** rate at which jolting clients chased cleaners, and **c** rate at which cleaners gave clients tactile stimulation. All rates are measured per 100 s of cleanerfish inspection of non-predatory residents or non-resident clients, as appropriate. Boxplots are shown in grey, overlaid with raw data points in black

client jolted, and 65% of jolting clients chased their cleaner. Only two predatory clients retaliated against a cheating cleanerfish by chasing it. The rate of chases after jolting by resident clients (mean = 0.9 chase per 100 s resident inspection, 95% CI 0.6–1.2) was similar to that of non-resident clients (mean = 1.0 chase per 100 s non-resident inspection, 95% CI 0.7–1.3; paired t test, $t_{36} = 0.33$, $P = 0.74$; Fig. 2b). Similar proportions of resident (mean = 63%, 95% CI 43–83%) and non-resident (mean = 69%, 95% CI 47–91%) clients chased their attending cleanerfish after a jolt (paired t test, $t_{10} = 0.24$, $P = 0.82$).

Three-quarters of redlip cleaner wrasses (75%) used tactile stimulation on their clients. However, only 10 of these tactile stimulation events (11% of all events) occurred after a client jolted. Only two tactile stimulation events (0.9% of all events) occurred after a client chased a

cleaner. There was a single occurrence of a client jolting, chasing the cleaner, and then receiving tactile stimulation. Seven cleaner wrasses (of 25 that inspected predators, 28%) delivered tactile stimulation to nine predatory clients, never following a jolt or a chase. Overall, redlip cleaner wrasses delivered tactile stimulation 1.6 times per 100 s inspection (95% CI 1.1–2.1), on average. The rate of tactile stimulation towards resident clients (mean = 1.0 events per 100 s resident inspection, 95% CI 0.7–1.3) was half that towards non-resident clients (mean = 2.1 per 100 s non-resident inspection, 95% CI 1.4–2.8; paired t test, $t_{36} = 1.24$, $P = 0.22$), but this difference was driven largely by two cleaner wrasses that each delivered one tactile stimulation event during very short inspections (Fig. 2c).

Discussion

Cleaning behaviour occurs widely among coral reef fishes, but there is increasing awareness that the form of these interspecific associations is highly variable. Here, we provide the first detailed documentation of cleaning by the redlip cleaner wrasse *L. rubrolabiatus*. The redlip cleaner wrasse system is characterised by low rates of cheating that target equally resident and non-resident clients, which is similar to *Elacatinus* gobies, and by retaliatory chases performed equally by all cheated clients, which is unlike other known cleanerfish. Redlip cleaner wrasses also use tactile stimulation, as do other *Labroides* cleaners, but they do so in contexts other than reconciliation with clients. Our study suggests that the relationship between redlip cleaner wrasses and their clients might be freer of the conflicts that characterise other *Labroides* cleanerfishes. If this is the case generally, it raises the question of why clients might choose to interact with dishonest cleaners such as *L. dimidiatus* and *L. bicolor* if more honest ones are present, as is the case in Mo'orea where all three species co-occur.

Redlip cleaner wrasses spent more than one-quarter of their time interacting with a broad diversity of fish clients. This makes them as active as their relatives *L. dimidiatus* (Barbu et al. 2011; Adam and Horii 2012; Nedelec et al. 2017) and *L. bicolor* (Mills and Côté 2010; Adam and Horii 2012) (Table 1). Our observations captured a large fraction of the clientele of these cleaner wrasses (Fig. S1). They did not inspect all reef fish species observed on point counts, but they did inspect clients in approximately the same proportion as their availability on the reef, with small deviations that were not related to client body size. Overall, 45% of their clients were surgeonfishes, but only 16% were squirrelfishes. The clientele of *L. rubrolabiatus* therefore appears to be more similar to that of *L. dimidiatus* than to that of *L. bicolor*, which shows a preponderance (up to 50%) of squirrelfishes in Mo'orea (Adam and Horii 2012).

A high likelihood of re-encounter plays a large role in determining the nature of interactions between individuals (Dugatkin and Wilson 1991). In cleaner wrasses, this appears to be one of the key factors that explains the presence of partner-control strategies in *L. dimidiatus* and their absence in *L. bicolor* (Mills and Côté 2010; Oates et al. 2010a, b). Redlip cleaner wrasses have home range sizes that are similar to those of *L. dimidiatus*, at least as estimated by maximum linear distance (Mills and Côté 2010; Table 1). They might therefore be expected to have a similar likelihood of re-encountering the same clients in future interactions, hence being dissimilar to *L. bicolor* in this respect (Mills and Côté 2010; Oates et al. 2010a). We should therefore see patterns of cheating and client retaliation that are similar between *L. rubrolabiatus* and *L. dimidiatus*. This is partly the case. Although most redlip cleaner wrasses inflicted jolt-inducing bites on their clients, they did so on a similar proportion of their clients as *L. dimidiatus* (13% overall, this study, vs 12% for *L. dimidiatus*, Mills and Côté 2010) but at a very low rate (1.45–5.0 jolts per 100 s inspection vs 3–21 jolts per 100 s inspection for *L. dimidiatus*, Oates et al. 2010a), which suggests more honest cleaning. Like other cleanerfish species, redlip cleaner wrasses hardly ever cheated on predatory fishes, supporting the idea that the 'threat of reciprocity' by piscivorous fishes generally enforces cleaner honesty (Bshary and Bronstein 2004). However, when inspecting non-predatory species, redlip cleaner wrasses cheated as much on non-resident as on resident clients—a pattern observed so far only in Caribbean cleaning gobies (Soares et al. 2008; Table 1). At the same time, retaliatory chases by clients were largely linked to cheating events, i.e. they immediately followed a jolt (Bshary and Grutter 2002, 2005), and they were performed by most cheated clients, but equally by resident and non-resident clients— the latter is a pattern apparently unique to redlip cleaner wrasses (Table 1). Taken together, these findings suggest that although clients do punish dishonest cleaners, client choice options might not be as strong a force driving cooperation in redlip cleaner wrasses as it is in *L. dimidiatus* (Noë and Hammerstein 1994; Bshary and Noë 2003; Bshary and Grutter 2005). We unfortunately could not examine other retaliatory behaviours by clients, such as partner switching (Bshary and Grutter 2005), but our results lead us to predict that this counter-cheating tactic usually used by non-resident clients with access to multiple *L. dimidiatus* cleaners might be uncommon in the redlip cleaner wrasse system since these clients appear to resort largely to aggressive chasing to punish cheating cleaners.

The observation of tactile stimulation in the redlip cleaner wrasse seems to be at odds with the idea of an honest cleanerfish. Indeed, redlip cleaner wrasses appeared to apply tactile stimulation in a different context than *L.*

dimidiatus usually does. *Labroides dimidiatus* uses tactile stimulation primarily for reconciliation by applying it to returning clients that they cheated in a previous interaction (Bshary and Würth 2001). We do not know how often redlip cleaner wrasses use tactile stimulation in this way since we could not follow cheated clients until they returned to the cheating cleanerfish to witness the start of the new interaction. However, fewer than one-quarter (24%) of tactile stimulation delivered by redlip cleaner wrasses entailed a client arriving, posing, and then receiving tactile stimulation—the usual sequence observed in cases of reconciliation (Bshary and Würth 2001). *Labroides dimidiatus* also uses tactile stimulation as a pre-conflict management strategy when interacting with predators (Grutter 2004) and to entice clients that are initially unwilling to interact to stop swimming (Bshary and Würth 2001). The latter might be the most important function of tactile stimulation in redlip cleaner wrasses since more than two-thirds (70%) of tactile stimulation events led to a passing client stopping for inspection.

The relationship between redlip cleaner wrasses and their clients, at least in Mo'orea, appears to be less conflictual than that documented in other *Labroides* cleaner-fishes. This conclusion must be tempered by the caveat that the information available for the three species of *Labroides* (and of cleaning gobies; Table 1) was collected in different places and times; hence, some differences, or lack of differences, may be due to environmental variation. Indeed, both *L. dimidiatus* and cleaning gobies, for example, can be more or less honest depending on the availability of ectoparasites on their clients (Bansemer et al. 2002; Cheney and Côté 2005). Nevertheless, major behavioural features that distinguish cleanerfish species, such as the differential treatment of resident and non-resident clients, seem to hold across locations (e.g. Bshary 2001; Mills and Côté 2010), have been replicated in aquarium studies (Bshary and Grutter 2005; Triki et al. 2019), and are expected based on fundamental theory (Noë and Hammerstein 1994).

If the comparative patterns suggested here hold generally, they lead to one prediction and one question. The conflicts that characterise the *L. dimidiatus* system, and likely that of *L. bicolor*, are underpinned by a preference for fish mucus over ectoparasites (Grutter and Bshary 2004), a manifestation in these two sister species of the ancestral coral mucus-feeding state of the labrichthyne clade (Cowman et al. 2009). A future study should therefore test the prediction that conflict in redlip cleaner wrasses is minimised because they prefer ectoparasites over other client-gleaned items. Such a preference would represent the evolutionary loss of the ancestral mucus-feeding state. Furthermore, the timing of this evolutionary novelty could be established by examining the feeding preferences of two other *Labroides* species, *L. phthirophagus* and *L. pectoralis*, which are sister species in the same lineage as redlip cleaner wrasses (Baliga and Law 2016). In addition, our results raise the question of why fish clients would interact with potentially dishonest cleaners, such as *L. dimidiatus* or *L. bicolor*, when more honest ones, such as *L. rubrolabiatus*, are present on the same reef. Indeed, we observed the same species (although not necessarily the same individuals) being inspected by *L. rubrolabiatus*, *L. dimidiatus*, and *L. bicolor* during our dives for this study. *Labroides bicolor* pursues and initiates interactions with many of its clients (Oates et al. 2010a, b; personal observations) and in doing so might effectively subvert client choice. However, we surmise that the higher abundance, and therefore greater ease of access, of *L. dimidiatus* than of *L. rubrolabiatus* (personal observations) might contribute to the use of the former as a cleaner on Mo'orea reefs. Signalling could also be a factor, since redlip cleaner wrasses lack the 'cleaner blue' stripe found on *L. dimidiatus* that provides the highest chromatic contrast across a range of coral reef microhabitats (Lettieri et al. 2009) and is most attractive to reef fish clients (Cheney et al. 2009). At any rate, as an active cleaner, *L. rubrolabiatus* has the potential to be as important a determinant of fish health and community structure on coral reefs as its better-known relatives.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights This study was carried out in strict accordance with the guidelines of the Canadian Council on Animal Care in Science. The protocol was approved by the Animal Care Committee of Simon Fraser University.

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