



Roving and Service Quality in the Cleaner Wrasse *Labroides bicolor*

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Abstract

The cleaner wrasse *Labroides dimidiatus* occupies fixed 'cleaning stations' on coral reefs, which 'client' reef fish visit repeatedly to have parasites removed. Conflict arises because cleaners prefer to cheat by feeding on client mucus instead of parasites. Clients can prevent *L. dimidiatus* from always cheating using control mechanisms such as chasing and partner switching, which depend on repeated interactions. These control mechanisms would be undermined in the absence of frequent repeated interactions, if cleaners roved over large areas. Roving behaviour has been anecdotally described for the closely related cleaner wrasse *Labroides bicolor*. Here we report field data comparing these two species in Moorea, French Polynesia. Our results confirmed that *L. bicolor* home ranges are much larger than *L. dimidiatus* home ranges, and showed that cleaning interactions occurred all over the *L. bicolor* home range: home range of cleaning interactions increased with total home range size. Moreover, we found that cleaner initiation of interactions increased with home range size in *L. bicolor*, which would give *L. bicolor* with large home ranges additional leverage to increase cheating. In line with these results, we found that client jolt rate (used as a measure of cheating) was higher among clients of cleaners with large home ranges. Our results emphasise the importance of game structure and control over initiating interactions as parameters in determining the nature of interactions in mutualisms.

Introduction

Cooperation between individuals of different species (mutualism) is common in nature. While kin selection (Hamilton 1964) is often invoked as an explanation for helping among conspecifics, mutualism requires that individuals accrue direct fitness benefits as the partners are always unrelated. Many of the theories that have been developed to explain cooperation between unrelated individuals, such as the prisoner's dilemma game (Axelrod & Hamilton 1981), rely on repeated interactions occurring between partners (Trivers 1971). When repeated interactions do not occur, for example due to mobility of partners, cooperative systems are often

expected to break down. Computer simulations show that defectors with high mobility (rovers) can successfully invade populations of tit-for-tat strategists in an iterated prisoner's dilemma game (Dugatkin & Wilson 1991). Theoretical modelling also predicts that abundant potential victims and short search times promote 'free-riding' strategies which exploit cooperators (Enquist & Leimar 1993).

A useful model system for studying mutualism is the cleaner wrasse *Labroides dimidiatus* (Trivers 1971). This species creates fixed 'cleaning stations' on coral reefs (Randall 1958; Potts 1973), and 'client' reef fish visit the same cleaners repeatedly to have parasites and diseased tissue removed (Randall 1958). This provides nutritional benefits for cleaners

(Grutter 1996) and health benefits for clients (Grutter 1999); however cleaners also have the potential to behave non-cooperatively (cheat) by feeding on healthy client tissue and mucus (Grutter 1997) and actually prefer mucus over ectoparasites (Grutter & Bshary 2003). Clients can prevent *L. dimidiatus* from always cheating using control mechanisms, which require that individual cleaners and clients have repeated interactions with each other. Resident client species typically punish cleaners by chasing them if they cheat, which encourages cleaners to provide a better service in the next interaction to avoid being punished again (Bshary & Grutter 2002). Visitor client species typically respond to cheating by swimming off and visiting another cleaner for the next interaction (partner switching), which encourages cleaners to be more cooperative to ensure that clients come back (Bshary & Schäffer 2002).

Recent comparisons of *L. dimidiatus* with cleaning shrimps and cleaning gobies suggest that game structures and hence characteristics of interactions may vary between cleaner species (Soares et al. 2008a; Chapuis & Bshary 2009). Another useful comparison could be made with the closely related cleaner wrasse *Labroides bicolor*. Anecdotal evidence suggests that *L. bicolor* roves throughout much larger home ranges than *L. dimidiatus* (Randall 1958). If this was confirmed, it would have major implications for the nature of interactions between cleaners and clients in this system. First, if cleaners interact with clients throughout a large home range, this means that frequent repeated interactions between individual cleaners and clients are less likely to occur. In the absence of a repeated game structure, the client control mechanisms of punishment and partner switching cannot function as effective methods of reducing cheating. Second, if *L. bicolor* moves over large areas, this suggests that they will be able to seek out clients more actively than *L. dimidiatus* which typically remains in a small area waiting for clients to approach (Randall 1958; Potts 1973). Since *L. dimidiatus* individuals can be reliably found in the same area, clients would have more opportunity to initiate interactions, by seeking cleaning by *L. dimidiatus* when parasite levels are high (Grutter 2001). However in the large home ranges of *L. bicolor*, clients are unlikely to be able to reliably find individual cleaners in the same area, and in this system cleaners might have more power over controlling when interactions occur because cleaners could seek out clients while roving over large areas. Theory predicts that more power over controlling interactions could lead to more cheating (Johnstone & Bshary 2002).

In this study, we collected field data on sympatric *L. dimidiatus* and *L. bicolor* to accurately quantify home range sizes and compare behaviour of cleaners and clients. If species differences with respect to home range size and levels of initiation were confirmed, we predicted that *L. bicolor* would cheat more often than *L. dimidiatus*. This is because clients cannot improve service quality through chasing and partner switching in the absence of frequent repeated interactions and because clients would invoke additional costs such as loss of foraging through avoiding interactions. In the field, client jolt rate can be reliably used as a correlate of cheating by cleaner fish (Bshary & Grutter 2002; Soares et al. 2008b).

Methods

Study Species and Study Site

Data were collected on Moorea Island in French Polynesia (17°29'S, 149°49'W) from April to June 2007. The two study species *L. dimidiatus* and *L. bicolor* are obligate cleaners as adults and are found throughout the Indo-Pacific. Observations were carried out on fringing reefs in two sites: Cook's Bay (Gump reef) and Opunohu bay (White house reef), where both species are found at the same depths in similar abundance. Previous studies on *L. dimidiatus* (e.g. Bshary 2001; Bshary & Grutter 2002; Bshary & Schäffer 2002) have been carried out on patch reefs separated by sandy areas. On patch reefs, client species can be easily divided into two categories: resident (remain on one reef patch) and visitor (may travel between reef patches). On the fringing reefs where our study was carried out, it is more difficult to divide client species into equivalent categories as their movements are less constrained in the absence of sandy areas. We did not distinguish between these categories for the purposes of our analysis.

Cleaning Observations

Observations were carried out on seven adult *L. bicolor* (9.5–12.5 cm) and ten adult *L. dimidiatus* (5.5–10 cm). Four *L. bicolor* and four *L. dimidiatus* were observed at Gump reef and the rest of the focal individuals were observed at White house reef. Each focal session was approx. 30 min in duration, with a total of 240 min observation time for each cleaner split between two observers (JO and AR). Half of the observation time for each cleaner was carried out in the morning (between 07:00 and 12:00), and half was in the afternoon (between 12:00 and 17:00).

Since *L. dimidiatus* is territorial, by returning to exactly the same location we could ensure that repeat observations were carried out on the same individual fish. Where two individuals were found in a pair, the larger of the pair was observed. Since *L. dimidiatus* begins life as a female and later changes to male (Robertson 1972), it is likely that the solitary individuals which were observed were females and the larger individuals in pairs were males. Individual *L. bicolor* moved around much more and could not be reliably found in the same place, so were recognised by natural colour patterns and fin aberrations, which are highly variable between individuals. Since very little is known about reproduction in social groups of *L. bicolor*, it was not possible to determine whether the focal individuals were male or female. Data on *L. dimidiatus* suggest that the sex of a cleaner does not influence service quality (Bshary et al. 2008). Observations on *L. bicolor* whose home ranges covered a large depth range (1–15 m) were carried out using scuba equipment. Observations on *L. dimidiatus* were made at depths of between 1 and 3 m using snorkelling equipment. There are no significant differences between data collected using snorkelling equipment and diving equipment (J. Oates, unpubl. data). While following individual cleaners, the following observations were recorded on an underwater slate: species of client (as determined according to Allen et al. 2003); size of client (to nearest 5 cm); whether the cleaner alone initiated the interaction or if the client was involved in initiation (the client was involved if it invited inspection, that is adopted an immobile posture before or at the same time as the cleaner made contact, see Feder 1966); duration of interaction in seconds (measured with a stopwatch); number of jolts by client (defined as a short body shake when cleaner's mouth was in contact, following Bshary 2001). Client jolt rate per 100 s was calculated by dividing the number of client jolts by the duration of the interaction and multiplying by 100. During each observation period, the observer remained directly above, or immediately adjacent to, the focal cleaner and recorded position every 5 s using a Global Positioning System unit on the surface. Checks were made periodically by making simultaneous observations on the same individual cleaners to ensure that there were no consistent differences between observers in their recordings.

Data Analysis

We calculated two home range estimates for each individual cleaner: total home range (using all posi-

tion coordinates) and home range of cleaning interactions (using position coordinates for all cleaning interactions). Home range analysis was carried out using the Local Convex Hull (LoCoH) 2.1 extension (University of California, Berkeley, CA, USA) in ARCVIEW GIS 3.2 (Environmental Systems Research Institute, Redlands, CA, USA). We used the non-parametric LoCoH method for home range estimation rather than traditional parametric kernel methods (Jennrich & Turner 1969; Worton 1989), because LoCoH is suited to datasets such as ours with lots of observational data collected in an environment with 'sharp' features (Getz & Wilmers 2004). LoCoH is a k -nearest neighbour convex hull method. It produces home ranges by first considering each observed location and identifying its k nearest neighbouring locations (where k is defined by the user). It then produces minimum convex polygons (local hulls) of each point and its selected nearest neighbours. After arranging the hulls in increasing order of size, they are merged until the required proportion of points is included, so, for a 10th percentile isopleth, hulls are merged until 10% of points are included. As hulls are merged in increasing order of size, the lower isopleths represent the most used part of the home range (i.e. the densest area in terms of points). The number of neighbours k was selected following the 'minimum spurious hole covering' rule (MSHC; according to Getz & Wilmers 2004). We found that the most appropriate value of k for total *L. bicolor* data was 55, and for cleaning data was 5; these values of the parameter were used for all *L. bicolor* individuals. Due to the different distribution of the data for *L. dimidiatus*, the higher values $k = 200$ (total data) and $k = 10$ (cleaning data) were required to satisfy the MSHC rule, and these values of the parameter were used for all *L. dimidiatus* individuals. To confirm the robustness of our analysis, we repeated the home range estimation using parametric kernels (Jennrich & Turner 1969; Worton 1989), but as this does not qualitatively change the results, only the LoCoH analysis is presented in this paper. The 90% isopleths were used as measures of home range size as this is considered to be the most valid measure of home range size (Börger et al. 2006).

Statistical analyses of the behavioural data were carried out in GENSTAT 8.1 (Rothamsted Experimental Station, Harpenden, UK) and MINITAB 15 (Minitab Inc, State College, PA, USA). To compare home range sizes between the two species of cleaner (units of analysis were individual cleaners), we used a Mann–Whitney U-test (two-sided). The relationship between total home range size and home range of

cleaning interactions was analysed using a General Linear Model of area of cleaning home range 90% isopleth (response variate) with cleaner species as a factor and area of total home range 90% isopleth as covariate (units of analysis were individual cleaners). After finding that there was a significant positive relationship between these two home range estimates (see Results), we used total home range 90% isopleth as the representative measure in the other analyses, because the regular sampling method (5 s intervals between position coordinates) made these estimates more accurate.

The initiation of cleaning interactions was analysed by modelling the likelihood of a cleaner initiating an interaction, using a Generalised Linear Mixed Model with cleaner initiation (coded as 0 or 1) as the response variate with a binomial error structure. Units of analysis were individual cleaning interactions; cleaner identity and client species were included as random factors to account for repeated measures. To account for site differences, we included site (Gump reef and White house reef) as a fixed factor. The other predictors considered were cleaner species, client size, client type (predatory and non-predatory; classified according to Randall et al. 1997 and Froese & Pauly 2009) and \ln (area of total home range 90% isopleth), which produced a model with a better fit than untransformed area of total home range 90% isopleth.

To investigate the factors that affect client jolt rate, we built a General Linear Mixed Model of the number of jolts per 100 s (response variate). Units of analysis were individual cleaning interactions; cleaner identity and client species were again included as random factors to account for repeated measures. We used area of total home range 90% isopleth as a predictor, which produced a model with a better fit than \ln (area of total home range 90% isopleth). The other predictors considered were the same as above.

In both models, we started with a full model including all possible explanatory variables and second order interactions. Subsequently, terms were sequentially dropped until a minimal model was derived containing only terms which, when excluded, led to a significant decrease in the explanatory power of the model. Significance for terms in the minimal model was obtained by dropping each term from the model; significance for terms not included in the minimal model was obtained by adding the term to the minimal model. Random terms were excluded from the minimal model if found to be non-significant (however, we checked that

including all random terms did not affect qualitatively the result).

Results

Home Range Size

The home ranges of *L. bicolor* were significantly larger than those of *L. dimidiatus* ($U = 6.0$, $n = 7, 10$, $p = 0.003$; Fig. 1). Interactions between clients and cleaners of both species were distributed across the whole area of the home range: area of cleaning home range 90% isopleth increased as area of total home range 90% isopleth increased, which was a significant effect ($R^2 = 0.83$, $F_{1,15} = 72.59$, $p < 0.001$, Fig. 2). In this model the factor cleaner species was not significant ($F_{1,14} = 1.75$, $p = 0.206$), and neither was the

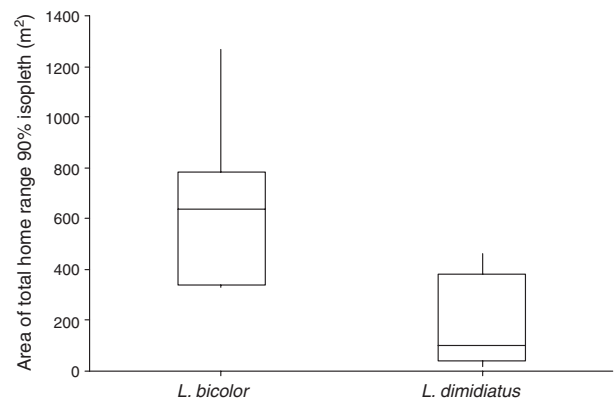


Fig. 1: Median and interquartile range of the area of total home range 90% isopleth (m^2) for *L. bicolor* ($n = 7$) and *L. dimidiatus* ($n = 10$). The 90% isopleth is the smallest shape to contain 90% of the position coordinates for an individual cleaner.

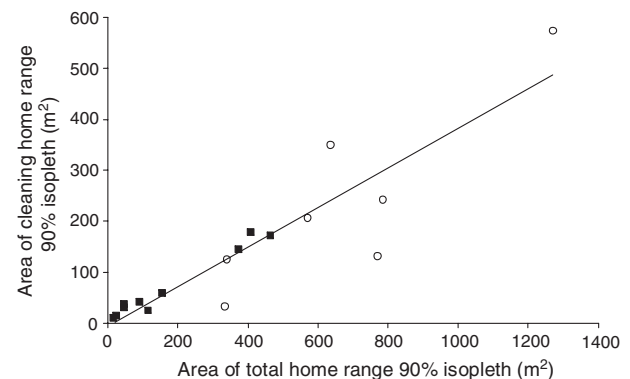


Fig. 2: Area of 90% isopleths (m^2) for total home range and home range of cleaning interactions for individual *L. bicolor* (white circles) and *L. dimidiatus* (black squares), with regression line. The 90% isopleth is the smallest shape to contain 90% of the position or cleaning coordinates for an individual cleaner.

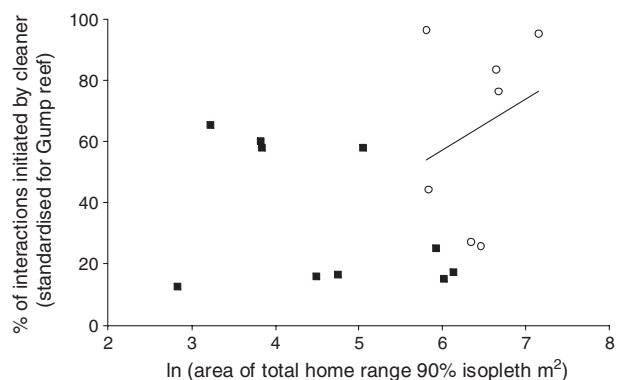


Fig. 3: Mean proportion of cleaning interactions which the cleaner initiated for individual *L. bicolor* (white circles, with regression line) and *L. dimidiatus* (black squares) against \ln (area of total home range 90% isopleth) in m^2 . Means are standardised for the study site Gump reef, which was a significant predictor in the model on cleaner initiation. The 90% isopleth is the smallest shape to contain 90% of the position coordinates for an individual cleaner.

Table 1: Generalised linear mixed model on the factors influencing initiation of cleaning interactions. Analysis conducted on cleaner initiation (0 or 1) for 1794 cleaning interactions from 7 *L. bicolor* and 10 *L. dimidiatus*. Values for Wald statistics, degrees of freedom (df) and chi probabilities (p) for all predictors and significant interactions

Term	df	Wald statistic	p
Client size	1	1.3	0.258
Client type	1	9.5	0.002
Site	1	17.6	<0.001
Cleaner species \times \ln (area of total home range 90% isopleth)	1	4.5	0.035

interaction between cleaner species and area of total home range 90% isopleth ($F_{1,13} = 0.54$, $p = 0.476$).

Initiation

The interaction term cleaner species \times \ln (area of total home range 90% isopleth) was significant (Wald statistic = 4.5, $p = 0.035$, $df = 1$; Fig. 3; Table 1); cleaner initiation increased with home range size for *L. bicolor* ($z = 2.20$, $p = 0.028$) and not for *L. dimidiatus* ($z = 1.57$, $p = 0.117$).

Across both species of cleaner, cleaners initiated interactions with only 56% of non-predatory clients compared to 88% of predatory clients, which was a significant difference (Wald statistic = 9.5, $p = 0.002$, $df = 1$; Table 1). The proportion of interactions initiated by cleaners was significantly lower at White house reef than at Gump reef (46% vs. 74%, Wald statistic = 17.6, $p < 0.001$, $df = 1$; Table 1), but the difference between the two cleaner species persisted

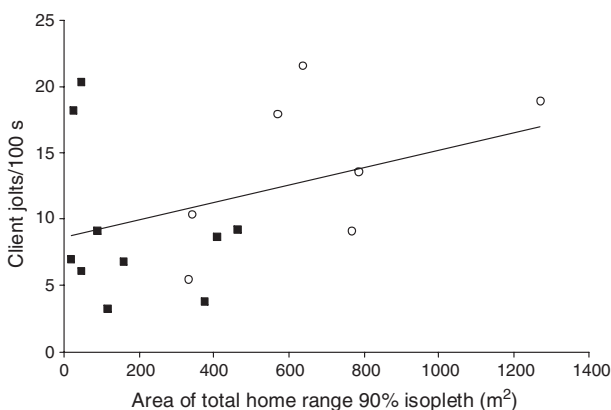


Fig. 4: Mean client jolts/100 s for individual *L. bicolor* (white circles) and *L. dimidiatus* (black squares) against total home range 90% isopleth (m^2), with regression line. The 90% isopleth is the smallest shape to contain 90% of the position coordinates for an individual cleaner.

Table 2: Linear mixed model on the factors influencing client jolt rate. Analysis conducted on client jolt rate (in jolts/100 s) for 1864 cleaning interactions from 7 *L. bicolor* and 10 *L. dimidiatus*. Values for Wald statistics, degrees of freedom (df) and chi probabilities (p) for all predictors (no significant interactions)

Term	df	Wald statistic	p
Cleaner species	1	0.2	0.630
Client type	1	0.1	0.748
Site	1	0.1	0.773
Client size	1	0.2	0.637
Area of total home range 90% isopleth	1	8.4	0.004

at both locations. The predictor client size and all other interaction terms were not significant in this model (Table 1).

Client Jolt Rate

Clients of cleaners with large home ranges jolted more frequently than clients of cleaners with small home ranges (Wald statistic = 8.4, $p = 0.004$, $df = 1$; Fig. 4; Table 2). The predictors cleaner species, site, client size, client type, and all interaction terms were not significant in this model (Table 2).

Discussion

This study shows that *L. bicolor* has much larger home ranges than *L. dimidiatus*, confirming anecdotal observations (Randall 1958). We also showed that home range of cleaning interactions increases as

total home range size increases, which means that *L. bicolor* does not interact with clients in just one area; interactions are spread across the home range. Taken together, these findings suggest that there are likely to be long and unpredictable intervals between encounters of the same individual *L. bicolor* with a given client. This implies that the system of interactions in the *L. bicolor* system may be less like the repeated game structure which exists in the *L. dimidiatus* system, and instead more similar to a one-off game structure.

We also found that cleaner initiation increased with home range size for *L. bicolor* but not for *L. dimidiatus*. This confirmed our predictions: *L. dimidiatus* remains in a smaller area and therefore generally has to wait for clients to approach, however as home range size becomes larger for *L. bicolor*, cleaners are more likely to be able to seek out clients, which could explain the increase in cleaner initiation. Theoretical modelling predicts that increased exploitation occurs as the victim's ability to control the length of an interaction decreases; as an exploiter's 'power' to prolong interactions increases, the stable level of exploitation increases and the interaction shifts from mutualism to parasitism (Johnstone & Bshary 2002).

In accordance with theoretical predictions (Dugatkin & Wilson 1991; Johnstone & Bshary 2002) that roving and increased control over the occurrence and duration of interactions by cleaners would undermine cooperative behaviour in large home ranges, we found client jolt rate was higher for clients of cleaners with large home ranges. Roving by cleaners is likely to reduce the frequency of repeated interactions. Thus punishment (Bshary & Grutter 2002) and partner switching (Bshary & Schaffer 2002) would be less efficient in limiting cheating behaviour in large home ranges, as these control mechanisms depend on frequent repeated interactions between cleaners and clients. Since clients are likely to have less control over cheating behaviour with roving cleaners, this could explain the greater jolt rate among clients of cleaners with large home ranges.

Just like the clients of *L. bicolor* individuals with large home ranges, the cattle hosts of red-billed oxpeckers have little control over whether interactions occur (Weeks 1999). Red-billed oxpeckers prefer to feed on blood from open wounds on cattle over ticks (Weeks 1999), and thus interactions may be detrimental to hosts (Weeks 2000). In a similar way, the ability to control the initiation of interactions may allow *L. bicolor* with large home ranges to cheat more often with clients by feeding on healthy

client tissue and mucus. This hypothesis could be further tested with a laboratory experiment to examine differences in cheating behaviour between the two cleaner species in a controlled situation.

We also found a difference between sites in the proportion of interactions which were initiated by cleaners. This may be due to differences in client behaviour due to differences in reef topography at the two sites, however this is difficult to investigate with the available data. In addition, we found that across the two cleaner species, cleaners were involved with the initiation of a greater proportion of interactions with predators than non-predators. This could be explained by the fact that many of the predatory species in this study were sedentary on the reef substrate during the day and so less likely to approach cleaners, whereas most of the non-predatory species actively moved around and could initiate interactions with cleaners.

It is worth noting that the mean jolt rate for clients of *L. dimidiatus* on the fringing reefs in this study was twice as high compared to observations from previous studies conducted on patch reefs in the Red Sea (e.g. Bshary 2001). This could be explained by the fact that *L. dimidiatus* on patch reefs have much smaller home ranges than *L. dimidiatus* on fringing reefs (R. Bshary, unpubl. data). Therefore *L. dimidiatus* on patch reefs might have more frequent repeated interactions compared to *L. dimidiatus* individuals in the present study. Alternatively, since it has been shown that parasite load correlates negatively with cheating by cleaners (Grutter 1997; Bshary & Grutter 2002; Soares et al. 2008b), the difference in mean client jolt rate between the two sites could be due to lower parasite loads in Moorea compared to the Red Sea. However, we consider this explanation unlikely as available data suggest similar or higher parasite loads in the Indo-Pacific region compared to the Red Sea (Soares et al. 2008c).

In conclusion, our results show that there is a quantitative difference in home range size between *L. bicolor* and *L. dimidiatus*, and our finding that there was a greater jolt rate among clients of cleaners with large home ranges can be explained by the lower likelihood of frequent repeated interactions between cleaners and clients in large home ranges. We also found that *L. bicolor* with large home ranges were more likely to seek out clients and initiate interactions with them, which is a second factor that could allow them to exploit clients more easily than *L. dimidiatus*. The results of this study emphasise the importance of the underlying game structure in determining the dynamics of interspecific interactions.

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