

Cleaner fish *Labroides dimidiatus* manipulate client reef fish by providing tactile stimulation

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The cleaner wrasse *Labroides dimidiatus* often touches ‘client’ reef fish dorsal fin areas with its pelvic and pectoral fins. The relative spatial positions of cleaner and client remain constant and the cleaner’s head points away from the client’s body. Therefore, this behaviour is not compatible with foraging and the removal of client ectoparasites. As clients seek such ‘tactile stimulation’, it can be classified as an inter-specific socio-positive behaviour. Our field observations on 12 cleaners (observation time of 112 h) suggest that cleaners use tactile stimulation in order to successfully (i) alter client decisions over how long to stay for an inspection, and (ii) stop clients from fleeing or aggressive chasing of the cleaner in response to a cleaner fish bite that made them jolt. Finally, predatory clients receive tactile stimulation more often than non-predatory clients, which might be interpreted as an extra service that cleaners give to specific partners as pre-conflict management, as these partners would be particularly dangerous if they started a conflict. We therefore propose that cleaner fish use interspecific social strategies, which have so far been reported only from mammals, particularly primates.

Keywords: *Labroides dimidiatus*; mutualism; cooperation; exploitation; reconciliation

1. INTRODUCTION

The ‘Machiavellian intelligence’ or ‘social brain’ hypothesis states that the evolution of a large neocortex in primates was caused by the demand for dealing with a complex social environment (Humphrey 1976; Byrne & Whiten 1988; Dunbar 1992; Barton & Dunbar 1997). A major challenge in verifying this hypothesis is to clarify which social challenges and corresponding individual strategies might be classified as complex (Cords 1997). As a first approach, primatologists noted what features of the social system and what behaviours are common in primates but rare elsewhere. Nevertheless, it is difficult to judge whether the rarity of examples outside primatology is due to the absence of these features in other taxa or whether other behavioural biologists simply ask different questions (Aureli & De Waal 2000) and whether such an approach really identifies complex cognitive behaviours (Barton & Dunbar 1997). Here we address three topics typically addressed in studies on primates in a study of the mutualism between the cleaner wrasse *Labroides dimidiatus* and its various ‘client’ reef fish species. Clients actively visit cleaners in order to have ectoparasites and dead or infected tissue removed (reviews by Feder 1966; Losey *et al.* 1999). The three topics are social manipulation, pre-conflict management and reconciliation.

Individual clients visit cleaners several times a day, sometimes more than 100 times a day (Grutter 1995). Thus, even client species with large home ranges that cover several cleaning stations (cleaners are territorial) interact repeatedly with the same cleaners, just as primates interact repeatedly with their group members (Cords 1997). There is good evidence that clients do benefit from interactions with cleaners (Grutter 1996, 1999; Losey *et al.* 1999). However, it is also evident that

there are some conflicts between cleaners and clients over what the cleaner should feed on. Stomach analyses show that cleaners not only consume parasites but also mucus and scales (Randall 1958; Gorlick 1980; Grutter 1997). Clients sometimes respond to cleaner mouth contacts with a body jolt, which is often followed by clients chasing the cleaner or swimming off (Randall 1958; Losey 1971; Bshary & Grutter 2001). Client jolts are not linked to the removal of parasites and, hence, they indicate cheating by cleaners (Bshary & Grutter 2001). More importantly in the present context, the behaviour of clients following jolts clearly indicates a momentary disturbance in their relationship with the cleaner. Other potential conflicts might arise over the timing of interactions, the duration of interactions and the possibility for some client species of choosing between several cleaners, while each cleaner would prefer to have exclusive access to them. Finally, predatory clients might sometimes be tempted to eat cleaners (Trivers 1971). There are thus several reasons why it might pay cleaners to manipulate client behaviour. In this context, we explore the function of one peculiar behaviour of cleaner fish, namely ‘tactile stimulation’.

We define tactile stimulation as the cleaner hovering above the client and touching its dorsal fin area with its pectoral and, in particular, pelvic fins (‘host stabilization’) (see Potts 1973). The relative spatial positions of the cleaner and client remain constant during this behaviour, both while clients remain motionless or when they swim and the cleaner’s snout points away from the client. Alternatively, cleaners might touch the client’s belly with their dorsal fin (Bshary 2001). This behaviour is not compatible with the search for and the removal of parasites. Note also that, during foraging, cleaners are in almost constant contact with their clients through their pelvic fins (Losey 1987), but we did not score this form of contact as it does not conflict with the cleaner’s foraging behaviour. Clients

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obviously ‘like’ tactile stimulation as they often start drifting motionless in response and clients seek and behave towards an automatically turning brush very much like they do towards a cleaner (Losey 1977). Tactile stimulation can therefore be termed an interspecific socio-positive behaviour. Cleaners might thus be able to use this behaviour in order to manipulate client decisions, as proposed by Potts (1973) and Losey (1979, 1987).

For our questions outlined below, it is important to distinguish between different classes of client species (Bshary 2001; Bshary & Grutter 2001). Some species have very small home ranges or territories, which at best cover one cleaning station only. Other client species have larger home ranges or territories, which cover two or generally several cleaning stations. Only the latter class of client species can therefore choose between cleaners. In addition, one has to distinguish between the few predatory client species and the vast majority of client species that feed on algae or plankton and, therefore, pose no threat to cleaner fish survival. Predatory clients rarely jolt during interactions but other clients regularly do (Bshary 2001). Clients without choice options often react to jolts by ‘punishing’ (Clutton-Brock & Parker 1995) the cleaner through aggressive chasing (Bshary & Grutter 2001), while clients with access to several cleaning stations swim off and usually seek a different cleaning station for their next inspection (Bshary & Schäffer 2001). A list of the species that can be categorized as clients with or without choice options and as non-predatory or predatory is published in Bshary (2001).

We quantified when cleaners actually use tactile stimulation and what effects tactile stimulation had on client behaviour in order to test four possible functions of tactile stimulation.

- (i) Tactile stimulation is used to manipulate client’s decisions on whether or not to stop at a cleaning station and on how long to stay (Losey 1979, 1987). In that case, we predicted that tactile stimulation should occur while clients are moving but not when they remain still. In addition, tactile stimulation should be more efficient in making moving clients stop than other behaviours, namely inspection of the client.
- (ii) Tactile stimulation is used as pre-conflict management (Aureli & De Waal 2000) in order to reduce the probability that a conflict might occur due to the client’s decision. In that case, cleaners should provide tactile stimulation mainly to clients, who could inflict very negative fitness consequences on the cleaners during a conflict. As conflicts with predatory clients are particularly dangerous for cleaners, we therefore predicted that cleaners should provide ‘actively’ (i.e. without just reacting to clients’ behaviour) more tactile stimulation to predators than to non-predatory clients.
- (iii) Tactile stimulation is used as a special service for manipulating clients’ decisions about whether or not to come back to the same cleaner for their next inspection. According to market theory (Noë *et al.* 1991; Noë 2001), we expected that species with choice options will receive tactile stimulation more often

than clients without choice options as only the former can choose between cleaners.

- (iv) Tactile stimulation is used for reconciliation after a client’s jolt followed by a client’s negative response. Reconciliation is the occurrence of affiliative behaviour between two former opponents shortly after the conflict (De Waal & Van Roosmalen 1979). The functions of reconciliation are to re-establish characteristic levels of tolerance between the former opponents (Cords 1992), thereby reducing the probability of further aggression (Aureli & Van Schaik 1991) and to relieve stress enhanced by the conflict (Aureli & Smucny 2000). We therefore expected that tactile stimulation will occur more often than usual after a conflict. In addition, it should be more efficient than other behaviours, like inspection or fleeing from an aggressive client, in making clients stop fleeing or attacking so that the interaction can continue. In cases where client aggression terminated the interaction, tactile stimulation should be more likely to occur in the follow-up interactions between cleaners and the same clients than during average interactions.

2. METHODS

(a) *Study site*

The study site was at Mersa Bareika, Ras Mohammed National Park in Sinai, Egypt. In this area, incoming sand through wadis (riverbeds which are dry most of the time) has led to the formation of patch reefs, which are separated from each other by sand, rather than to the formation of a continuous reef. Each of the 12 cleaners studied inhabited a separate patch reef that was separated from other patch reefs by at least 5 m of sand, with the depth at the bottom varying between 2 and 6 m.

(b) *Data collection*

Data were collected in May to July 1999. Single cleaners were present in six cleaning stations, while pairs lived in the other six cleaning stations. When a pair was present, we always observed the smaller individual. Note that cleaners could not be recognized individually, but they are very stationary and territorial (Losey 1971). During our observations, we witnessed only two excursions to adjacent reef patches, each lasting for 15 min. We are therefore confident that we repeatedly observed the same individuals.

Observations were made by scuba diving. We sat 2–3 m in front of a cleaning station on the surrounding sand. The schedule for both authors was to make 60-min observations on cleaner–client interactions starting at 07.00 h, 10.00 h, 13.00 h and 16.00 h, respectively. Each author visited each station at all four different times of day. Thus, a total of 8 h of observations are available for each cleaning station. The total observation time for cleaner–client interactions was 96 h. No cleaner was observed more than once on the same day. Each recorded interaction between the cleaner and a client was first observed over the entire duration and, immediately afterwards, the following information was noted on a Plexiglas plate.

- (i) Client species, which was determined according to Randall (1983).
- (ii) Client length, including the caudal fin, was compared to a reference measuring stick and estimated to the nearest centimetre.

- (iii) Duration in seconds was measured with a stopwatch.
- (iv) Client jolts, client reaction and cleaner counteraction. We noted all short client body jolts and the clients' reaction, which could be 'no further reaction', 'swimming off' or 'aggressive chasing of the cleaner'. Cleaners could respond to the client's behaviour by providing tactile stimulation, inspection of the client's body or fleeing. We also noted whether or not clients would react to cleaners' behaviour by stopping to move and let the interaction continue.
- (v) Client swims off. This behaviour could occur at the beginning of an interaction, indicating that the client did not want to interact at all or during an interaction, indicating that the client had had enough, without the occurrence of a jolt. Cleaners could respond to the clients' behaviour by either providing tactile stimulation, inspecting the client or by no reaction. Again we noted whether or not clients would react to the cleaners' behaviour by stopping to move.
- (vi) Whenever a client terminated an interaction through aggressive chasing of the cleaner we tried to observe the client rather than the cleaner until it came back for its next interaction with the cleaner in order to obtain data on follow-up interactions after a conflict. An exception was individuals of a few large species, which occurred in pairs at our patch reefs and which could be reliably identified by either size, specific colour patterns or wounds.

Each hour of observation was interrupted after 30 min for a scan lasting 10 min. We thus had eight of these scans for each cleaning station. During the scans, we looked at the cleaner every 5 s and, whenever we saw the cleaner interacting with a client, we noted client species, client behaviour (swimming or staying still) and cleaner behaviour (inspecting or tactile stimulation).

(c) Data analysis

We distinguished between non-predatory species without choice options, non-predatory species with choice options and predatory species. We followed the classification given by Bshary (2001) for this purpose. Each cleaning station had a unique set of client species of these three categories. Due to this variation, data obtained at different cleaning stations were not directly comparable. We therefore did not treat each cleaner fish as the independent unit but used client species instead. We first calculated the mean value for client length, cleaning duration and client jolt rate, and the percentage of interactions with tactile stimulation for each client species and cleaning station. In addition, we calculated the success rates of cleaners in stopping clients unwilling to interact, willing to terminate an interaction, swimming off after a jolt or chasing the cleaner after a jolt, by either using tactile stimulation or continuing to inspect. The values obtained from each cleaning station for each species and variable were added and divided by the number of stations where individuals of the species were observed to interact with cleaners. Thus, for each species and variable, a single (mean) value was used for the calculations. As a previous study found no effects of phylogenetic relatedness between species on the course of interactions between cleaners and clients (Bshary 2001), we did not correct for potential phylogenetic dependencies in the present study.

(d) Statistics

All data were analysed using non-parametric tests with either the statistical program SPSS-X or with the program SsS. All p -values are two-tailed.

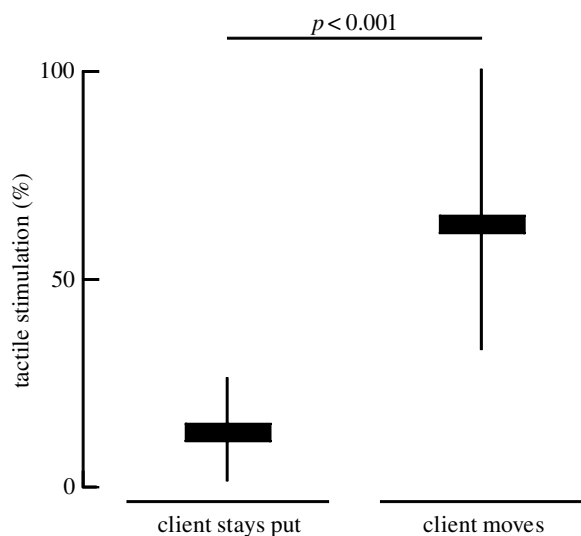


Figure 1. Median and interquartiles of clients ($n = 43$ species) receiving tactile stimulation (percentage of scan observations in which tactile stimulation occurred) when they stayed still and when they moved.

3. RESULTS

(a) Do cleaners use tactile stimulation in order to manipulate clients' decisions over timing and the duration of interactions?

Cleaners were more likely to provide tactile stimulation rather than to inspect if clients were swimming than if they were staying still (scan data, sign test, one tie, remaining $n = 42$ species, $x = 8$ and $p < 0.001$) (figure 1). Tactile stimulation was more successful than inspection in stopping clients for an inspection (interaction data, sign test, four ties, remaining $n = 13$ species, $x = 1$ and $p < 0.01$) (figure 2a) and prolonging an inspection that a client wanted to terminate (interaction data, sign test, four ties, remaining $n = 27$ species, $x = 1$ and $p < 0.001$) (figure 2b).

(b) Do cleaners provide tactile stimulation as an extra service to predatory clients and/or clients with choice options?

When clients were standing still, cleaners provided tactile stimulation to non-predatory clients without choice options, non-predatory clients with choice options and predatory clients at different rates (scan data, Kruskal–Wallis test, $\chi^2_2 = 6.4$, $n = 55$ species and $p < 0.05$) (figure 3). Multiple comparisons revealed that predators received more tactile stimulation than non-predatory clients without choice options ($p < 0.05$) or non-predatory clients with choice options ($p < 0.01$). There was no significant difference between the two non-predatory client categories.

(c) Do cleaners use tactile stimulation in order to reconcile after a conflict?

Tactile stimulation occurred significantly more often in interactions between cleaners and clients which had terminated their last interaction with aggression following a jolt than during interactions which were not preceded by a conflict between cleaners and clients of the same species (interaction data, sign test, three ties, remaining $n = 33$ species, $x = 5$ and $p < 0.001$) (figure 4). Often, such

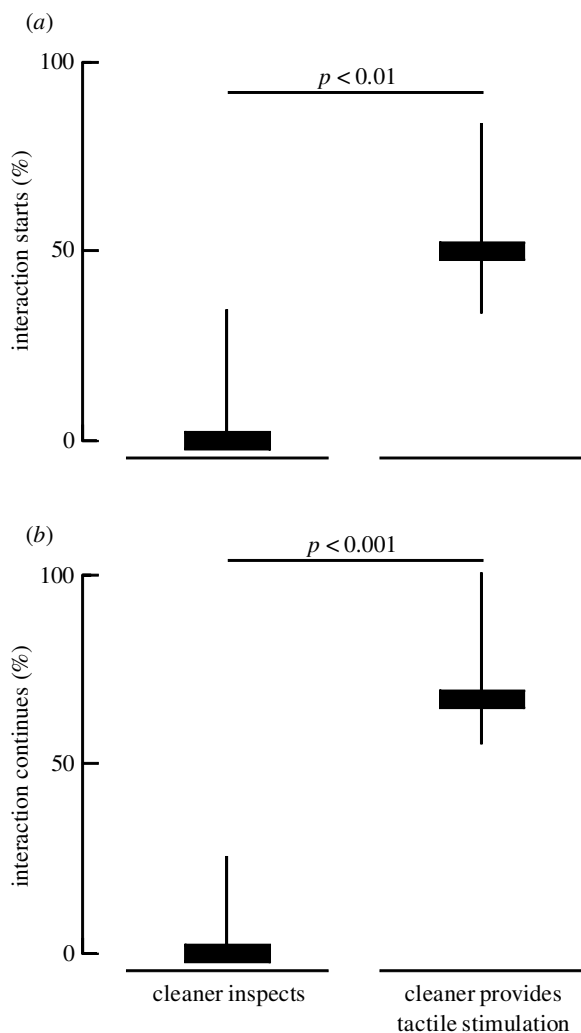


Figure 2. Median and interquartiles of interactions (%) in which swimming clients stopped while cleaners provided either tactile stimulation or inspected. We distinguished between (a) the beginning ($n = 31$ species) and (b) the continuation ($n = 17$ species) of interactions.

follow-up interactions occurred immediately after the conflict. Still, when we analysed only follow-up interactions, which were delayed by at least 1 min, we found the same significant effect (sign test, one tie, remaining $n = 13$ species, $x = 0$ and $p < 0.001$). The probability that tactile stimulation occurred during follow-up interactions depended on the size of the client. The larger the client, the more likely tactile stimulation was to occur (Spearman rank correlation, $r_s = 0.48$, $n = 33$ and $p < 0.01$).

In addition, tactile stimulation was more successful than inspection in stopping clients that swam off after a jolt (interaction data, sign test, $n = 14$, $x = 2$ and $p < 0.01$) (figure 5a) and more successful than fleeing in stopping clients behaving aggressively after a jolt (interaction data, sign test, $n = 11$, $x = 0$ and $p < 0.001$) (figure 5b). Note that, when clients responded aggressively, we could not compare the success rates of tactile stimulation and inspection as we never observed inspection in response to client aggression.

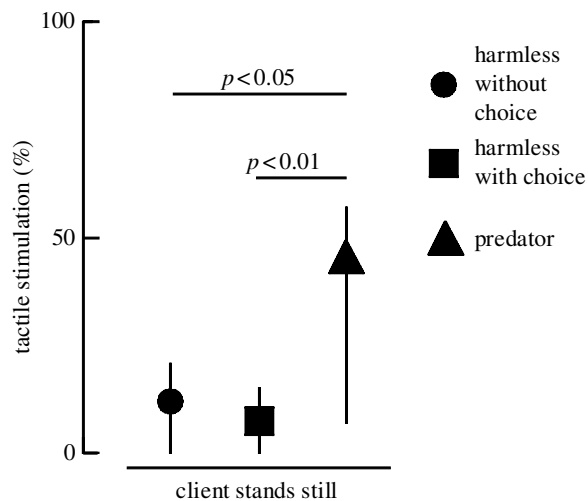


Figure 3. Median and interquartiles of non-predatory clients without choice options ($n = 22$ species), non-predatory clients with choice options ($n = 25$ species) and predatory clients ($n = 8$ species) receiving tactile stimulation (percentage of scan observations in which tactile stimulation occurred) while standing still.

4. DISCUSSION

(a) *The function of tactile stimulation*

Our results support the view that tactile stimulation serves multiple functions.

- (i) Our data support Losey's hypothesis (1979, 1987) that cleaners exploit the sensory system of clients by providing tactile stimulation. The client receives treatment and stops moving and the cleaner can afterwards continue to search for food on a client that did not want to stay originally. Losey (1979, 1987) even suggested that clients visit cleaners in order to receive tactile rewards rather than to have parasites removed, but our data are not designed for testing that idea. It is also important to know whether clients seek tactile stimulation for 'hedonistic pleasures' or whether such treatment has any positive effect on client fitness, for example via a reduction in stress hormone levels in the clients.
- (ii) The data also fit the hypothesis that cleaners employ tactile stimulation as a pre-conflict management strategy (Aureli & De Waal 2000). It was directed mainly towards those partners (predatory clients) with whom good relations are of particular value, as predators that initiate a conflict pose a most serious threat to a cleaner's survival. It remains to be tested whether tactile stimulation in fact reduces the risk of subsequent conflict. We found no evidence that cleaners use tactile stimulation as an extra service for clients with access to several cleaning stations with the possible function of increasing the probability that these clients will return for their next inspection. Thus, it appears that market theory (Noë *et al.* 1991, Noë 2001), while being helpful in understanding various other phenomena in this mutualism, does

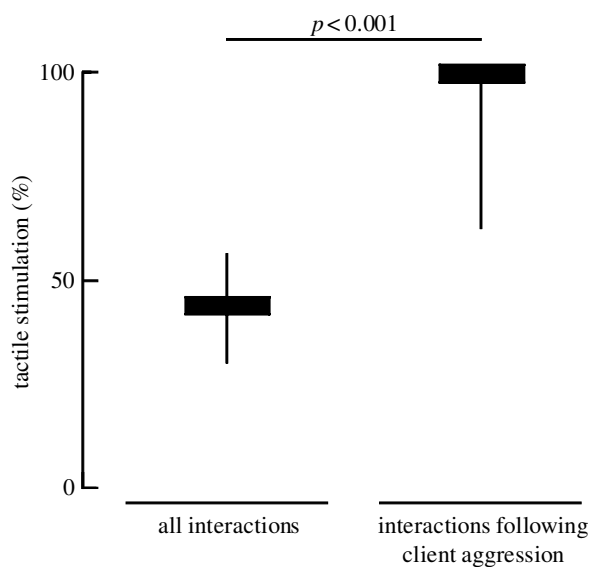


Figure 4. Median and interquartiles of clients ($n = 36$ species) receiving tactile stimulation (percentage interactions) when cleaners interacted with individuals which had terminated their last interaction with aggressive chasing of the cleaner following a jolt and when cleaners interacted with individuals of the same species without previous client aggression.

not help in explaining the function of tactile stimulation.

- (iii) Tactile stimulation fulfils both the descriptive and functional criteria for reconciliation (De Waal & Van Roosmalen 1979; Aureli & Van Schaik 1991; Cords 1992). Tactile stimulation as an interspecific socio-positive behaviour occurred more often after a conflict than on average and it functions to re-establish an intact relationship after a conflict. This is the first time that reconciliation has been observed in a non-mammalian system (see Schino 2000) and it is the first case of interspecific reconciliation, despite the fact that many primates live in mixed-species associations (Höner *et al.* 1997).

(b) Potentially confounding variables

A previous study by Bshary (2001) has dealt with the missing effect of phylogenetic dependencies on the behaviour of cleaners and clients during interactions in detail. In addition, predatory clients frequently had more interactions in which cleaners provided tactile stimulation than non-predatory clients even when body size was accounted for, despite the fact that their interactions were shorter on average. However, the methods used by Bshary (2001) failed to quantify what proportion of time cleaners spent on providing tactile stimulation. This is why we used the scan method this time. The combined data sets refute the hypothesis that predators receive more tactile stimulation than non-predatory clients because of their body size (predatory clients are not significantly larger than non-predatory client species with choice options anyway). Finally, we consider it unlikely that any significant result was due to the behaviour of one or a few individual cleaners. No single individual cleaner provided more than 12.9% or less than 4.2% of the observations for any data set.

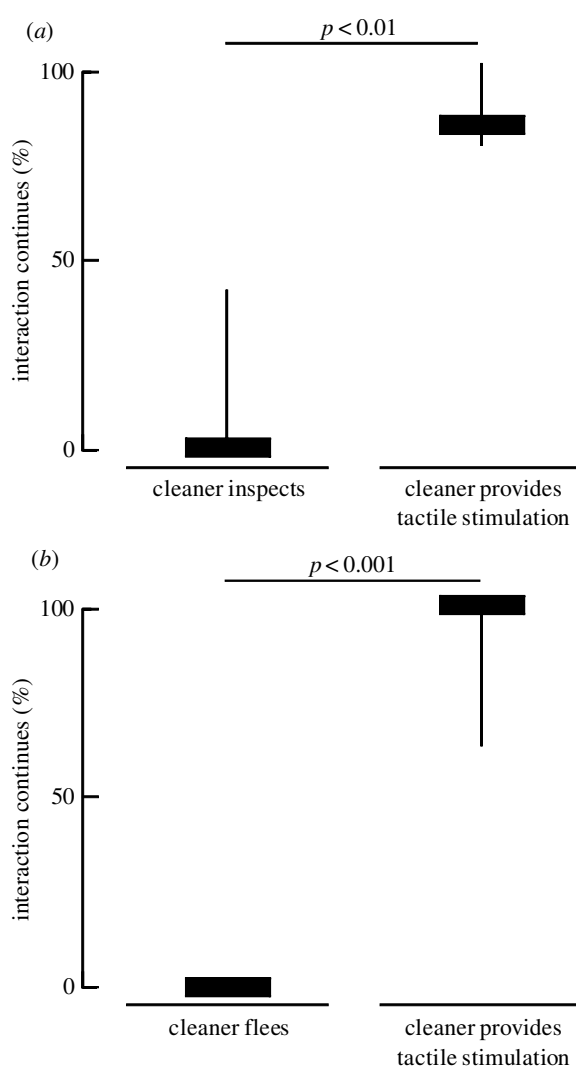


Figure 5. Median and interquartiles of interactions (percentage) in which clients stopped again for a continuation after an initially negative response to a jolt. (a) Clients ($n = 14$ species) initially swam off and cleaners provided either tactile stimulation or inspected. (b) Clients ($n = 11$ species) initially chased the cleaners and cleaners either provided tactile stimulation or fled (a).

(c) Machiavellian cleaner fish

Our results have important implications for further testing of the hypothesis that the evolution of cognitive skills and a large neocortex in primates was driven by the demands of a complex social environment (Humphrey 1976; Byrne & Whiten 1988; Dunbar 1992; Barton & Dunbar 1997). Like primates, cleaners and clients interact repeatedly over long time-periods. From the cleaner's perspective, the social network is arguably very complex. Cleaners undergo more than 2000 interactions per day (Grutter 1995) and, in our study area, each cleaner interacted in total with more than 100 individual clients belonging to 20–50 species. Similarly to primates, the reproductive success of a cleaner fish probably depends largely on the outcome of interactions with other members of the network. These similar selection pressures have led to similar outcomes in that cleaner fish are able to manipulate client decisions, use pre-conflict strategies and reconcile if a conflict occurs because of a client jolt. It

remains to be investigated on what type of knowledge cleaners base their behavioural decisions. Unpublished experimental evidence suggests that cleaners can know their clients individually (S. Tebbich, R. Bshary and A. S. Grutter, unpublished data). However, to what extent they acquire such knowledge and what role that plays in decisions concerning tactile stimulation remains to be investigated.

Our results do not contradict the Machiavellian intelligence hypothesis in general. On the contrary, it would be extremely interesting to compare the brain anatomy of cleaners with those of related fish species, which lack such a complex interspecific social environment, in order to test whether the cleaners' skills are reflected in an increase in forebrain size. If cleaners have large forebrains, this result would corroborate studies on primates, carnivores and bats, which have found a correlation between the neocortex ratio (the neocortex against the rest of the brain) and group size as a measure of social complexity (Dunbar 1992; Barton & Dunbar 1997). Still, it becomes apparent from our results that the evolution of a particularly large neocortex in primates cannot be sufficiently explained by listing phenomena such as stable group living, repeated interactions, manipulation of social partners, pre-conflict management and reconciliation.

It might be rewarding in future studies to look more closely at details of the underlying decision rules used by individuals of the species investigated. For example, the complexity of decision rules guiding reconciliation behaviour might vary greatly between species. Primates make strategic decisions about with whom they reconcile and with whom they do not (Cords & Aureli 2000). However, cleaners do this as well, as the probability of reconciliation was influenced by client body size, which correlates with parasite load (Grutter 1995) and, hence, partner quality. Cleaners thus seem to be more willing to reconcile with valuable partners than with less important partners. Still, other factors might be different. Individuals of some species might try to reconcile in public or secretly depending on the context. In addition, behaviour towards partners might depend on just the last interaction or on a long interaction history. There may be differences between taxonomic groups when it comes down to these measures.

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