# *Marine cleaning mutualisms provide new insights in biological market dynamics*

**Redouan Bshary† and Ronald Noë***

†University of Neuchâtel, Institute of Biology, Emile-Argand 11, 2000 Neuchâtel, Switzerland. Corresponding author; redouan.bshary@unine.ch

* Tuk, The Netherlands and Arizona State University, Department of Psychology, Tempe, AZ 85287-1104, USA; ronald.noe@gmail.com

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## Abstract

Most mutually beneficial social interactions (cooperation within species, mutualism between species) involve some degree of partner choice. In an analogy to economic theory as applied to human trading practices, biological market theory (BMT) focusses on how partner choice affects payoff distributions among non-human traders. BMT has inspired a great diversity of research, including research on the mutualism between cleaner fish *Labroides dimidiatus* and other marine fish, their ‘clients’. In this mutualism, clients have ectoparasites removed and cleaners obtain food in return. We use the available data on *L. dimidiatus* cleaner – client interactions to identify avenues for future expansion of BMT. We focus on three main topics, namely how partner quality interacts with supply-to-demand ratios to affect service quality, the role of threats and forms of forceful intervention, and the potential role of cognition. We consider it essential to identify the specifics of each biological market as a basis for the development of more sophisticated BMT models.

Keywords: Game theory, market selection, punishment, coercion, negotiation

## Introduction

Research on mutual helping for direct fitness benefits, which following [1] we term cooperation within species and mutualism between species, has put strong emphasis on one problem that potentially thwarts the selection for cooperative behaviour: the loss of fitness due to a helping act if the partner does not return the favour in such a way that the helper ends up with a net fitness gain. This particular problem can be illustrated with the well-known prisoner's dilemma game [2], in which two players can choose between cooperating and defecting, and where payoffs are such that both cooperating yields higher payoffs than both defecting, but defecting always yields a higher payoff than cooperating irrespective of the partner's choice. A major part of early theory has focussed on the conditions under which conditionally cooperative strategies may evolve and be evolutionarily stable in iterated prisoner's dilemmas (summarised in [3]). Such strategies can be labelled 'partner control' [4], or 'partner fidelity feedback' [5]. Partner control models lack a number of important elements, or – put differently – fail to answer some obvious questions: Why do certain partnerships form but not others? How do partnerships form? What determines the values of investments and returns of each partner and the exchange rates of good and/or services that are exchanged during interactions? The question of the formation of partnerships logically suggests partner choice. And once partner choice is included, one almost automatically needs to consider processes such as comparing partners, preferences for partners that yield the highest net benefit, and playing off potential partners against each other [6]. This, in turn, suggests that a biological version of human market economics may help to analyse the consequences of partner choice in the context of cooperation and mutualism [7-10].

## Biological market theory

Biological market theory (BMT) uses the language of game theory to analyse situations in which individuals have multiple options to cooperate with a single or with multiple partners [9-11]. Core assumptions of BMT are that i) individuals exchange goods or services to their mutual benefit; ii) members of the same trader class compete over access to members of the other trader class; iii) the exchange value of goods or services is a source of conflict; and iv) individuals prefer partners that offer the best exchange rate. Comparing cooperating organisms to traders on human markets, BMT borrowed terminology and game-theoretical insights from economics. Another important source of inspiration was sexual selection theory (SST). SST describes and analyses the dynamics of mating markets, even though the latter term was introduced only recently in biology [see 12, for history and references].

BMT was in the first place an attempt to explain the evolution of cooperation and mutualism, which requires the identification of plausible mechanisms that make day-to-day instances of cooperation and mutualism possible and stable. Partner selection is indeed one powerful partner control mechanism in repeated games, as individuals that help less than average or even not at all will be left behind and mutually cooperative pairs remain together [13, 14]. But BMT-inspired analyses of empirical cases also showed that partner control is not necessary when the options to cheat are limited or absent. We give two examples of such mechanical constraints: In some bird species, older territorial males may benefit from letting a yearling male join to attract an extra female. Yearlings show delayed plumage maturation, which helps them in gaining access to territorial males' resources such as nest-cavities and territories but this immature plumage makes them unattractive to females. As yearlings cannot moult mid-season and then outcompete the resource owner with a shiny adult plumage, they lack the option to cheat territory owners [9, 15]. Second, many plants provide rewards, such as nectar, food bodies or nesting cavities, to insects in return for services, such as pollination or protection against herbivores. Most such rewards cannot be retracted once they have been put on offer.

Most models of biological market theory explored evolutionary time scales [10, 16-19]; for partial exceptions see [20, 21]. Some species may be adapted to market conditions that are relatively stable over evolutionary time, while others are assumed to be adapted to react optimally to fluctuations in the market values of individuals and/or good and services [12]. Such selection on ‘adaptive phenotypic plasticity’ (see [12] for references) is notably expected to result in specific cognitive mechanisms such as learning, but may also give rise to non-cognitive mechanisms with the same function. Indeed, most empirical studies inspired by BMT document the presence of market dynamics and experimentally prove the effects of partner choice on the outcome of cooperative interactions ‘in real time’ or ‘over ecological time scales’. Examples showing that individuals adapt to changes in supply and demand in real time include studies of species without brains (mycorrhiza and plants [22, 23]), invertebrates (lycaenid butterfly larvae and ants [24]; paper wasps [25]) as well as a variety of vertebrates (red bishops [26]; meerkats [27]; hyenas [28]; Mediterranean wrasse [29]; primates [30, 31]).

The traders on the cleaner market we describe here are the cleaner wrasse *Labroides dimidiatus* and its so-called ‘clients’, which are other marine fish living on coral reefs. It was one of the main examples of a biological market in the early days of BMT [4, 32-36]. While the *L. dimidiatus* mutualism, including game theoretical aspects, has been presented in various reviews (most recently as one example of fish cognition in [37], the current paper covers new perspectives. First, there are several recent key new insights [e.g. 21, 38-42] that have not been used in reviews but affect our thinking on BMT. In one paper, a reduction in cleaner densities did not lead to predicted changes in service quality [21]. Another paper documented in detail how partner choice options must be combined with other variables such parasite load, mucus quality and manoeuvrability to predict realised service quality [43]. Furthermore, while many review/perspective papers consider potential links between cooperation and cognition [44-53], the cognitive machinery necessary to exert partner prioritisation in a cleaning market has now been studied in unprecedented detail [40, 54-56]. As another motivation for the current paper, the co-authorship of RN, the main founder of BMT, offers alternative views on this cleaning mutualism. Important disagreements between the authors regarding the interpretation of available data are spelled out, most explicitly in two separate boxes. Box 1 summarises RN’s biological market view on cleaning mutualism and corresponding terminology. Box 2 summarises RB’s terminology, which is rooted in the tradition of partner control models. Such disagreements will help to put a strong emphasis on what we do not know about these cleaning markets, i.e. missing data that would have allowed us to resolve our disagreements. Furthermore, we will outline research that we consider useful to identify potentially rather idiosyncratic features of the *L. dimidiatus* market.

## Marine cleaning markets

In marine cleaning mutualisms, cleaners remove ectoparasites, scales, ectodermal mucus and tissue from clients. The vast majority of cleaners and clients are fishes, though cleaner shrimps are also quite common [57]. *L. dimidiatus* is by far the best studied cleaner fish, which is the reason why we focus on it. These cleaners typically have small territories, which are referred to as cleaning stations. Clients seeking inspection actively visit cleaners and often spread their fins as a signal to invite inspection [58]. Individual clients repeatedly visit cleaners over the course of a day, and individual cleaners have between 800 - 3000 interactions per day [59-61]. Ectoparasite removal is the core service cleaners provide to clients, and in return the ectoparasites are a food source (a good) provided by clients to cleaners. While this exchange appears to be a straightforward example of mutual by-product benefits, several complications make this kind of interactions much more interesting. First, a minority of client species are piscivorous and hence could attempt to eat a cleaner. This was one of the examples that inspired Trivers [62] for his seminal paper on reciprocity. Second, *L. dimidiatus* cleaners prefer to eat mucus, the protective layer covering client skin and scales [63], over ectoparasites [64], which may be due from *Labroides* belonging to a clade of coral mucus feeding wrasse [65]. Stomach analyses show that cleaners eat mucus [66], and body jolts of clients in response to cleaner fish mouth contact are reliable indications of mucus feeding [35]. Thus, clients provide parasites and mucus as food sources to cleaners but in order to receive a good service, cleaners must find means to make cleaners largely eat against preference. Third, *L. dimidiatus* cleaners regularly show a peculiar behaviour termed ‘tactile stimulation’: they touch the client with pectoral and particularly pelvic fins, providing a kind of massage that reduces the clients’ cortisol levels [67]. In reaction to this the clients stop making coordinated fin movements, which shows the calming effect this massage has on them. Cleaners use tactile stimulation to appease predators, to influence client decisions, and to reconcile after the client chased the cleaner in reaction to apparent mucus feeding [33]. Tactile stimulation is hence a component of cleaner fish service quality.

Both data and logic support the notion that most *L. dimidiatus* – client interactions are on average beneficial to both parties. Clients preferentially settle near cleaning stations [68, 69], grow larger, show better body condition, and are less anaemic when having access to cleaning [70-72]. The cleaners obviously engage in interactions voluntarily and are not constrained in their choice of clients by other clients [32]. Therefore, viewing cleaning interactions as a mutually beneficial exchange of services and goods between traders belonging to two different classes seems appropriate.

Partner choice is a key factor explaining variation in both cleaner and client behaviour, and resulting payoff distributions. Most client species can be categorized as either ‘residents’ or ‘visitors’ [32]: residents have small territories or home ranges and access to only one *L. dimidiatus* cleaning station (with one or two cleaners), while visitors roam over larger areas and have access to two or more cleaning stations. A few species can be classified occasional/conditional visitors’ (termed facultative visitors in [32]) as the sizes of their territories or home ranges are such that depending on habitat structure and local cleaner density the number of accessible stations can be either one or two, or more [32, 73]. On average, visitor species are larger than resident species but there are notable exceptions, and the indeterminate growth typical of fishes also causes a high intraspecific variation in size [32]. Visitors indeed make use of their choice options. They are likely to return if the previous service quality was good and to switch to another station for their next inspection if either the service quality was bad, or if they were made to wait for inspection in favour of another client [36, 74]. Lacking partner choice options, residents chase cleaners in response to mucus bites and wait for inspection if necessary [32, 75].

We will use the information gathered so far on the *L. dimidiatus* cleaning market to discuss four main topics: i) how partner quality and supply-to-demand ratios affect levels of cooperation / service quality; ii) the implications of threats and various other forms of forceful intervention for BMT; iii) the potential role of cognition in biological markets; and iv) the knowledge we lack for a yet better understanding of cleaning markets.

**Box 1: Disagreements between the authors I: RN's view on 'coercion' and 'negotiation'**

The cooperation and mutualism literature is riddled with terms with anthropomorphic connotations and the definitions of these terms often vary considerably (for example for cheating see [76, 77]; for punishment and coercion see [78-80]). It is therefore perhaps not surprising that the authors also stumbled over some disagreements. RN has nothing against using the term 'cheating' when it is defined as 'not paying a fair price' when one accepts that 'fair prices' vary in time and space depending on market conditions. 'Cheating' by cleaners, as defined in previous papers by RB, is something else, however: it is taking a bite of mucus by the cleaner, independent of the momentary market conditions. Thus defined RN would simply call it 'biting' or 'scraping'. No anthropomorphic label is perfect, but RN prefers terms that hint at the variable exchange rates typical of markets. Markets generally do not dictate specific exchange rates but rather a range of rates within margins that are determined by the outside options of each trader (or trader class). Traders should use all means they have available to push exchange rates towards the margin most beneficial to them. Some might take a risk of pushing too far in the process and lose a profitable trading partner. For RN 'coercion' catches this aspect better than 'cheating', but by lack of a single perfect label one can also use terms like 'short-changing', 'stealing' or 'shoplifting', whatever feels as more appropriate in a specific case. On a cleaner market, for example, 'goods' (ecto-parasites + mucus delivered by the clients) are exchanged against 'services' (ecto-parasite removal + tactile stimulation by the cleaner). A 'short-changing' client delivers food that is below average in quantity and/or quality and a cleaner 'steals' from its client by taking mucus before having finished the cleaning job. Both offer a commodity with a value below the average exchange rate dictated by the momentary market conditions, which in colloquial language is often referred to as a 'fair price'. Thus, in the eyes of RN a cleaner that is willing to clean a certain client only if allowed to take some mucus as well, rather than not clean at all, is not cheating (as defined by RB), but is trying to get the best price for its cleaning service within a market-conform price range. Short-changing during an interaction that is part of a series of interactions between two traders can be part of the negotiation processes required to reveal the limits of the range of exchange rates acceptable to both parties. Even more forceful actions, such as biting and chasing, can be seen as negotiation tactics used to this end. Further negotiation may occur when either or both parties try to reach a more advantageous deal within the bandwidth of acceptable exchange rates. They can test the waters by trying to take a little bit more or give a little bit less. Such negotiation processes are essential on markets with traders that cannot communicate otherwise over exchange rates and have no publicly known commodity prices expressed in a common currency.

## Box2: Disagreements between the authors II: RB’s view on ‘cheating’ and ‘decision-making’

RB uses terminology that is common in the ‘partner control’ literature. Most importantly, RB refers to a cleaner taking a bite of client mucus as ‘cheating’ (or ‘defecting’). As it stands, cleaners make discrete decisions during foraging, where the act of taking a mucus bite is ‘+’ for self and ‘-‘ for the client. Replacing the term ‘cheating’ by ‘stealing’, thereby introducing a new term for one particular system, could increase confusion rather than clarify the issue. Also, the use of the term ‘cheating’ helps to emphasise the fact that clients need to exert partner control mechanisms to ensure that cleaners of genus *Labroides* provide on average a net benefit rather than a net cost. Without partner control, cheating acts would become so frequent that *Labroides* would turn into cheater species. Indeed, there are indications that *L. dimidiatus* individuals may be parasites of client species that lack the manoeuvrability necessary to quickly evade a cleaner or to terminate an interaction at will. Roche and colleagues [43] observed that poorly swimming pufferfish *Arothron nigropunctatus* jolted in every interaction and in response to almost every mouth contact by adult cleaners, indicating that the latter do not remove parasites. These fish avoid interactions with any adult cleaners (they can have very long interactions with juveniles [81], but may come accidentally into their reach. Thus, adult cleaners can become net parasites if clients lack sufficient control over the duration of an interaction [82]. The need for clients to control a cleaner’s behaviour is absent when cleaners prefer to eat ectoparasites over mucus, as is the case for Caribbean cleaning gobies [83]. As an additional issue, RB considers that RN’s market terminology applied to cleaning interactions lacks a mechanistic basis of how animals may make actual decisions. For example, RB doubts that a visitor that swims off after a jolt and switches to a different cleaning station for the next inspection does so to negotiate exchange rates with its current cleaner but rather because a negative experience alters its preferences. Similarly, cleaners adjust their future behaviour because the food loss caused by the client leaving induced a negative experience. Such decision-making processes are quite different from a negotiation process in which traders exchange signals to fix an exchange rate before the interaction takes place, or negotiations during the course of an interaction.

## How partner quality and supply-to-demand ratios affect levels of cooperation / service quality

The market law of supply and demand makes some very clear predictions. Here, we focus on two of those. First, high quality partners offering high quality goods or services obtain better deals than low quality partners offering low quality goods or services. Second, if demand for a good or service goes up (or down), then the price goes up (or down). Regarding the first point, the preference for client mucus found in *Labroides* cleaners has consequences that are likely rather unique to the system. From a cleaner’s perspective, a high-quality client is large, with high parasite load and high mucus quality (a combination of quantity and nutritional value [43]). Given that large clients are normally visitors, cleaners should most strongly compete over access to these clients through outbidding, which implies offering high service quality. This leads to a conundrum: high service quality would imply that cleaners forsake the consumption of mucus, which would eliminate client mucus quality as a variable to consider. Indeed, there is a positive correlation between the mucus quality and client jolt frequency [43]. Thus, visitor clients with high mucus quality do not obtain a higher parasite-to-mucus feeding rate by cleaners. Instead, cleaners use their active role in cleaning interactions to make opportunistic foraging decisions that force such clients to accept more mucus loss, despite having partner choice options. Currently, no data exist to test whether cleaners compensate for increased mucus consumption by improving other aspects of service quality, i.e. by giving clients with high-quality mucus priority of access and/or more tactile stimulation. In contrast to mucus quality, parasite load correlates negatively with client jolt frequency [43], which is entirely in line with predictions from BMT.

The preference for client mucus may also explain why predictions on how changes in the supply-to-demand ratio will affect *L. dimidiatus* service quality are not straightforward. Triki and colleagues [21] removed almost 50% of cleaners from a reef to quantify how this reduction in cleaning supply would affect service quality. Initial predictions were that cleaners i) would respond to the increased demand by increasing the number of interactions with visitors and as a consequence largely ignore residents; ii) cause client jolts more frequently, and iii) provide less tactile stimulation as the need to manipulate client decisions for own foraging success should be greatly reduced. Client responses to the manipulation were not part of the analyses because a much larger sampling effort would have been needed to obtain enough data. As data supported only the first prediction and yielded no effects on jolts and tactile stimulation, game theoretic analyses were added [21]. These analyses revealed that the precise shape of diminishing return functions determines how service quality will change in response to changes in supply-to-demand ratios. One aspect is that clients offer food, and hence cleaner decisions should depend on their level of hunger/satiation. This aspect interacts with client responsiveness to mucus feeding. The dynamics are as follows: in principle, a market that favours cleaners leads to i) cleaners obtaining more food, and the resulting high levels of satiation should make them focus on eating what they prefer, i.e. mucus; and ii) a higher parasite load should cause clients to become more tolerant towards mucus feeding by cleaners (see also [75]). This part corresponds to the intuitive prediction that a market that favours cleaners allows them to ask for a higher price. However, two factors counteract this tendency, namely iii) a reduction in cleaners should lower the amount of time clients get cleaned, which should increase their parasite load and hence make it easier for cleaners to forage cooperatively; and iv) as long as clients still sometimes take evasive actions in response to cleaner mucus feeding, the high level of satiation should cause cleaners to become more willing to avoid inducing such actions. This is because the marginal benefits of consuming more mucus are not worth the risks of clients either fleeing and not returning anytime soon, or chasing the cleaner with some (low) probability of inflicting harm, or the resulting perturbations increasing predation risk from non-client piscivores. These arguments are in line with basic optimal foraging theory predictions that satiated individuals should be risk averse. The empirical results by Triki and colleagues [21] suggest that the opposing forces are overall in balance. Data sets were not big enough to determine whether client species differ in the way they adjust evasive action probabilities to changes in market conditions. If they did, the prediction would be that cleaners may selectively increase or decrease service quality according to client species when the market shifts in their favour [21].

Trading nutrients for other types of nutrients or services like protection, pollination or transport is widespread in mutualisms [84]. The benefits of nutrients will invariably yield diminishing return functions due to satiation. Therefore, studying the effects of satiation on exchange rates in these mutualisms would be an interesting exercise. In addition to exchange rates, estimates or correlates of fitness consequences of changes in market conditions need to be studied. In the cleaning mutualism, a lack of change in standard measures of cleaner service quality (interaction duration, client jolt rate and cleaners providing tactile stimulation) does not mean that clients do not suffer from a change in market conditions. Instead, clients should be worse off when the market favours cleaners because the latter do not increase the time spent cleaning. Therefore, clients will be inspected less frequently and as consequence harbour more ectoparasites, which causes more anaemia [72].

To summarise this section, the relationship between market conditions and exchange rates needs to be studied in detail. A trader class that is overly favoured by market conditions may forsake to ask for very high prices due to diminishing return functions. As a result, members of the partner trading class may still obtain a ‘reasonable’ exchange rate, though they may suffer through reduced amounts of trading. Possibly, the *L. dimidiatus* (*Labroides sp.*) cleaning mutualism may yield rather unique dynamics because as far as we can see, only cleaners have to constantly choose between three discrete actions, i.e. searching and removing ectoparasites, taking bites of mucus, and providing tactile stimulation.

## The role of threats and forms of forceful intervention

Exchange rates are best predicted by the market law of supply and demand only if the outbidding competition provoked by partner choice is the single most important factor determining exchange rates. The cleaner fish market provides ample opportunities to assess how additional factors affect service quality. Clients may bias exchange rates in their own favour by causing harm or threats to do so [32]. The latter notably applies to piscivorous clients as they could try to eat a cleaner. Apparently to keep the probability of such predation attempts low, cleaners provide an excellent service to piscivorous clients, characterised by the virtual absence of client jolts and high frequency of tactile stimulation [32, 33]. This service quality is better than for harmless clients, and it is independent of whether a piscivore is resident or visitor, i.e. whether or not it has partner choice options. Thus, a mere threat causes cleaners to provide a better service than expected by the piscivorous clients’ market values. A second example of clients increasing service quality above market value involves harmless (non-piscivorous) residents. Lacking partner choice options, residents should jolt more frequently than visitors, and receive less tactile stimulation. However, this is not supported by the data when body size is controlled for [32, 33]. The explanation is that residents are much more likely than visitors to respond to mucus bites by chasing the cleaner [75]. Chasing leads to the termination of an interaction, and cleaners must use acceleration and fast manoeuvres to avoid being hit by the client. Subsequently, cleaners provide a high service quality in the next interaction with the same client, abstaining from causing jolts and providing tactile stimulation [33].

Not only clients but also cleaners try to improve the exchange rate dictated by the local market, at least in interactions with harmless clients. The key variable is the degree to which clients or cleaners control the duration of interactions. If cleaners have high control, they can prolong interactions against the client’s will. This sets the stage for cleaners being able to eat more mucus without immediately losing a client. Field observations combined with experiments that measure acceleration and manoeuvrability of individuals in response to a startling stimulus revealed that clients with slow acceleration and low manoeuvrability (and hence reduced control over the duration of interactions) jolt most frequently [43]. These observations are supported by game theoretic models [17, 82] and lab experiments testing for cleaners' willingness to feed against preference [85]. The roving cleaner wrasse *L. bicolor* provides complementary data: their mobility allows these cleaners to initiate more interactions than *L. dimidiatus*, and as predicted from such increased control over the occurrence of interactions they cause more jolts and have more scales in their stomachs [86-88]. Thus, if given the opportunity, cleaners combine mucus feeding with following a fleeing client to increase food intake beyond market value. Note that in addition to the ability to initiate interactions, *L. bicolor* also adjust service quality to the likelihood of a follow-up interaction with the same client in the near future: service quality is higher in the core area of their home range where the local clients can seek or avoid them compared to more peripheral areas [89].

To summarise this section, recent results on the *L. dimidiatus* mutualism emphasise the need to complement research on the effects of partner choice with research on the effects of other strategic components. In particular, the role of coercion has been under-investigated. This observation equally applies to cooperation concept focussing on partner control.

## The role of cognition in partner choice

In principle, partner choice can be based on simple feedback loops between individual actions and the environment [44, 90, 91]. Little is known about the use of more complex cognitive processes to adjust behaviour to current market conditions. As an exception, cognitive mechanisms have been studied and modelled in some detail in *L. dimidiatus* to understand how cleaners can prioritise visitors over residents [32]. Bshary and Grutter [35] developed a laboratory test that mimics simultaneously visiting clients and that has since been replicated in various forms and with members of various species in the role of 'cleaner'. The 'biological market task', also called 'ephemeral reward task', consists of the simultaneous presentation of two food items of equal value. One of the two plates always remains accessible to subjects until they have eaten the food item (a 'resident' or 'permanent' plate), while the other plate is removed if the subject does not eat its food item first (a 'visitor' or 'ephemeral' plate). Therefore, visiting the latter plate first yields two food items, while visiting the permanent plate first only yields one. In the original version, the two items were identical and the plates could differ in size, shape, colour and patterns to allow discrimination.

In a comparative study in which a preference for the visitor plate above chance levels was used as the criterion for successful learning, all six adult cleaner fish learned to solve the task, outperforming chimpanzees, orangutans and capuchin monkeys [92]. Most primates failed to solve the task within 100 trials, as did juvenile cleaners. Rats and pigeons also failed in skinner box versions of the task [93]. Only African grey parrots matched the performance of adult cleaners [94]. Various follow-up experiments on cleaner fish revealed a major role of experience on performance. Individuals from sites with a high density of fish (both cleaners and visitors) outperformed individuals from low density sites [59, 60]. At high density sites, it is easier for visitors to exert partner choice, and hence cleaners experience higher competition over access to these visitors. Indeed, the combination of high fish densities and visitors switching-if-made-to-wait predicts high performance in the lab experiment [40]. Thus, cleaners bring learned decision rules to the laboratory that explain variation in performance. In summary, the task turned out to be surprisingly difficult, given that primates typically easily learn to prefer an option that yields the double amount of food relative to an alternative option [95].

Additional experiments with the biological market task yielded two important insights regarding the cognitive processes that underly the ability to solve the task but also the intra-specific variation in performance. First, the cues provided can affect performance as some appear to be more salient than others [96-98]. Second, learning models show that basic reinforcement learning mechanisms do not suffice to explain successful performance in the market task or in the more complex natural conditions, where resident-visitor visits are interspersed between visits by singletons, resident pairs and visitor pairs [56, 99, 100]. Instead, cleaners must apply two cognitive processes, namely configurational learning and chaining. Configurational learning allows cleaners to identify that visitor-resident should be treated as a special situation with its own rules (creating a 'chunk' in a sequence of events [101]). Chaining enables cleaners to assess that choosing the 'visitor' subsequently yields access to the 'resident' while choosing a 'resident' yields nothing more afterwards [55, 56].

BMT is needed to explain why cleaners must understand the chain of events and show low discounting of the near future (i.e. the next few seconds) that allows to couple current payoff with its future payoff consequences (the other client stays or leaves). In principle, a supposedly simpler alternative mechanism would have been that cleaners experience the leaving of the visitor (plate) as a negative reinforcer, which would reduce the probability that they chose the resident in the future. However, negative reinforcement would cause cleaners to prioritise visitors the most when it is not needed, i.e. when the market is biased in the cleaner's favour: under such conditions, many clients are visiting a cleaning station, and as a consequence it happens more frequently that a client swims off (even if the probability of swimming off is low in each single case). But when cleaning services are in high demand, visitors are more likely to return anyway, any empty slots are readily filled by alternative clients, and cleaners tend to have overall a surplus offer of food. Therefore, cleaners should now exert partner choice, i.e. prioritise clients according to own preferences rather than according to client choice options [38]. Combining data with a learning model [21, 40, 55] revealed that temporal discounting mechanism allows for such a decision-rule when market conditions favour cleaners, and also to prioritise visitors if market conditions are more balanced [38].

To summarise this section, the ability to prioritise visitor (ephemeral) clients over resident (permanent) clients when market conditions allow, requires a set of supposedly more 'complex' cognitive tools [56]. Species lacking these cognitive abilities would not be able to be competent cleaners if they faced the conditions of the *L. dimidiatus* cleaning market. Thus, BMT can be linked to cognitive evolution once other biological markets have been analysed in similar detail in order to identify market-specific cognitive demands (if any).

## The full cleaning market

The *L. dimidiatus* cleaning mutualism has been extensively studied. However, more than 200 other species (fish and shrimps) have been observed cleaning as well, including many species in the Indo-Pacific [57]. As a consequence, *L. dimidiatus* is never the only cleaner species present within its range. Therefore, individuals do not only compete with conspecifics but also interspecifically with other cleaners. The cleaning behaviour of several sympatric species has been studied, sometimes including direct comparisons of client composition and jolt rates to *L. dimidiatus* [81, 86, 88, 102, 103]. However, it has never been studied how the presence of different cleaning species affects the overall market, and as a result the interactions between *L.*

*dimidiatus* and its clients. We currently do not know whether residents with access to one *L. dimidiatus* cleaning station alter their behaviour if alternative cleaners of other species are also present. A comprehensive understanding of the cleaning market involving multiple cleaning species would require answers to many open questions, including the following ones. a) Would 'residents' with access to *L. dimidiatus* and another cleaner species behave like visitors and use partner switching between cleaner species as a means to obtain a good service? b) If so, how does variation in cleaning abilities – the frequency with which ectoparasites can be removed by different cleaner species – affect resident partner choice behaviour? c) Is the observed variation in client composition within and between cleaner species driven by client preferences or by cleaner preferences? Linked to this question, would all clients in principle prefer obligate cleaners over facultative cleaners? d) Why do facultatively cleaning species show strong intraspecific variation in cleaning (in these species typically only juveniles clean but many juveniles do not clean at all) and why do even the most active individuals clean much less than *Labroides* cleaners [81]? e) How does variation in ectoparasite abundance affect the relative value of different cleaning organisms? The limited available evidence suggests that only *Labroides* cleaners prefer client mucus over ectoparasites [64, 81, 83]. In *L. dimidiatus*, high parasite load appears to reduce their mucus feeding [43, 75], meaning that service quality is best when a client benefits most from it. Such a relationship should not exist in non *Labroides* cleaners, as these always focus on eating parasites.

Addressing most of the open questions above in a large comparative approach will be very challenging. The research group of RB has tried three times without success to establish whether facultative cleaners choose which client species to inspect, or whether client species deciding to pose in front of a facultative cleaner trigger cleaning. The general problem was that too few individuals cleaned at all. Failure on this level means that we do not know whether swapped facultative cleaners would have stayed where we put them (the manipulation necessary to establish whether translocated cleaners keep their previous client species composition or adopt the previously established local client composition). Quantification of ectoparasite abundance in the environment and on clients is challenging and yields high variance in data, leading to small effect sizes [104, 105]. Finally, measuring correlates of fitness consequences of choosing different cleaners would require long-term field manipulations, as it is impossible to add up the different components of service quality, i.e. parasite removal, mucus consumption, search efficiency, tactile stimulation, and waiting time for popular cleaners.

## Conclusions/outlook

By now, biological market theory is well established within behavioural ecology. The future focus should be on investigating how it can be adapted to the particularities of specific biological interactions. Here we focussed on the *L. dimidiatus* mutualism to provide avenues for such extensions: the cognitive tool box of partner species, the importance of means to force the partner to accept exchange rates below market value, and optimality considerations with a focus on diminishing return functions. Recent studies have shown that cleaners need a specific cognitive tool set to be able to adjust decisions to market conditions but also that partner choice needs to be combined with other variables to explain variation in service quality. Roche and colleagues [43] identified five variables that were equally important in explaining variation in client jolts: partner choice options, client manoeuvrability as a measure for its ability to control the occurrence and duration of an interaction, and three measures of client quality as a food patch, namely body size, parasite load and mucus characteristics. The fact that mucus consumption conflicts with clients' interests can explain why changes in cleaner-to-client ratios and hence supply and demand do not necessarily lead to changes in service quality [21].

Another major challenge will be to improve our understanding concerning the differences regarding how cleaner – client interactions unfold, depending on the cleaner species. BMT has been used to make predictions, including other *Labroides* species, Caribbean cleaning gobies and cleaner shrimps. While it tentatively appears that other *Labroides* species can be easily integrated into BMT framework [86-88, 106, 107], data on other cleaner species are less applicable to BMT. For example, clients in the Red Sea chase facultative cleaners after a jolt [81] though the latter seem to cause jolts rather by accident and do not seem to adjust future behaviour. This contrasts with clients of Caribbean gobies, which do not respond to jolts with partner switching and/or aggressive chasing [83], while the gobies approach predatory clients faster than harmless clients [67], in contrast to *L. dimidiatus* [32]. Cleaner shrimps advertise more when hungry[108, 109] but not specifically towards visitor clients [110], though they adjust service quality to client identity [102] but the role of partner choice remains unclear. Both shrimps and gobies are much more stationary than *Labroides* cleaners [RB personal observations], which strongly restricts their partner choice options. Instead, they have to clean the client that monopolises the space near them. Thus, their fast service to predators might be due to the cleaners' goal to make predators leave as soon as possible. Furthermore, their strategic options may well be constrained by cognitive limitations. For example, cleaner shrimp have low visual acuity [111], and cleaning gobies perform poorly compared to *L. dimidiatus* in a simultaneous two-choice task [112], which tests for a prerequisite ability to exert partner choice in the cleaning market.

The previous paragraph highlights very important gaps in our empirical knowledge on cleaning mutualisms that open the door for differences in interpretation. The terminology issues raised in the two boxes exist because of our lack of knowledge regarding the decision-making processes. These processes limit the possible strategy space, but we currently do not know to what extent. Consider for example the strategy space of piscivorous clients. Regarding payoffs of single interactions, predators could attempt to obtain short-term caloric benefits of a predation attempt, though the success probability is likely small. However, during hundreds of observations of naturally occurring cleaning interactions, RB has never observed a predator attempting to eat a cleaner during an interaction. Could this be due to an evolved mechanism that allows predators to obtain the long-term benefits of having ectoparasites removed by the same cleaner [62, 113]? Resident piscivores would suffer from eating the only accessible cleaner as it may take months before a new recruit arrives. During discussions, RN argued that visitor piscivores would still have alternatives and hence could benefit from including cleaners in their diet. While theoretically correct, this would require that a piscivore can assess the cleaner market within its home range and decide to hunt cleaners only as long as they are abundant but stop attempts when cleaners are rare. Are cleaners unconditionally cooperative towards piscivores because those would respond to own jolts with a switch to hunting behaviour? At least RB would predict that a predator would not be able to consider the rarity of the event, market values, or negotiation processes, but simply respond to the perceived pain with chasing (see also the 'limited predatory mind' described in *small gods* [117]). The cleaner fleeing would then trigger predatory instincts. The two times RB has witnessed a predator eating a *L. dimidiatus* and a cleaner shrimp *Stenopus hispidus*, both cleaners had behaved like prey (outside a cleaning interaction). As one act of cheating by the cleaner would risk to trigger an act of much more consequential cheating (a predation attempt) in return by a piscivore, Bshary and Bronstein [114] coined the term 'threat of reciprocity' as the partner control mechanism that causes cleaners to abstain from cheating in the first place. Note that this term does not fit RN's pure BMT terminology and way of thinking. Most importantly, the speculations above have been listed to show what kind of knowledge is currently missing to properly assess decision-making in cleaner – client interactions.

Adding more ecological and natural history details of a biological market, as well as the decision-making mechanisms of involved players, will unavoidably increase realism at the expense of generality. Nevertheless, we consider this the way forward. Studying traders ranging from brainless to large-brained within the larger framework of BMT will eventually provide a data base that allows an investigation about how different mechanisms underlying decision-making yield market interactions of varying complexity. Perhaps most challenging will be to incorporate the consequences of a key assumption of BMT, namely that the exchange value of goods and services is a source of conflict between traders. The conflict causes selection on traders to evolve means to shift exchange rates in their own favour. As an example, mycorrhizae store nitrogen out of reach for plants in order to change the supply for this crucial element ('hoarding' [115, 116]). The *L. dimidiatus* case study revealed aggression used by clients, and 'harassment' by cleaners, as means to increase own payoffs. Such forms of 'coercion' differ from the classic focus on 'cheating/defection' as the latter focusses on a violation of the expectation that the partner should have behaved cooperatively. In contrast, coercion should be expected if the partner has the means. As a consequence, and independently of our terminology disagreements, we expect it to be a major challenge to include various forms of force, used by traders to increase their share, in our thinking about cooperation and mutualism. In this respect biological market theory is no exception to general economic theory, which also rarely integrates theft, robbery, fraud and the like, in market models. However, such models can very well explain WHY certain items have more value under certain circumstances and are therefore more often taken by force or deceit. Empirical and game theoretical research on how interactions between market forces and coercive actions affect payoff distributions in social interactions would provide a new holistic view on the evolution of cooperation/mutualism and their potential breakdown.

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## Authors' contributions

After discussing outline and subject matter, RB wrote a first draft that was subsequently modified repeatedly by both authors.

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