Cleaning Symbiosis: The Importance of Cooperation

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0. Abstract:

Colonisation of animals by parasites and debris is common and potentially harmful. That is where cleaners come in. These small individuals form symbiotic relationships with their clients, receiving food while their clients receive increased survival. In this essay I discuss three examples of cleaning symbioses – the aquatic cleaning gobies and fish, and branchiobdellids and crayfish, as well as the terrestrial oxpecker and mammals – and how the survival of the individual is secured when individuals work together.

1. Introduction:

It is not uncommon for a relatively large species such as a fish, a crustacean, or a large mammal to host either debris or parasitic organisms such as ticks or microorganisms on their surface which may restrict their survival and reproductive abilities. Some of these species, especially terrestrial species, are capable of removing these epibiotic organisms or debris themselves through a variety of self-grooming methods. However, many species, such as fish, are either less efficient or completely incapable of removing fouling substances themselves. These species typically form mutualistic relationships, referred to as cleaning symbioses, with another species in order to remain clean and hence increase their ability to grow, survive, and reproduce. These cleaners are generally smaller than their clients, so that they can move around on top of them, and have the ability to see and remove small and difficult to uncover substances or parasites. As the cleaner receives a relatively secure food source and the client receives an effective cleaning service in return, this relationship is generally considered a mutualism[1,2]. However, as shall be discussed throughout this essay, both cleaner and client may be the recipient of disadvantages and the cost-to-benefit ratio of the relationship may fluctuate dependent on the context, possibly leading to this apparent mutualism becoming a commensal or even parasitic relationship[3]. The relationship can be controlled by either party through rewards and punishments to prevent overexploitation and ‘cheating’ and to keep the relationship mutualistic, a phenomenon that has allowed cleaning symbioses to evolve[4] and explains why it is considered an example of a mutualism enforced by partner sanctions[5].

Throughout this essay I shall introduce you to three different cleaning symbioses: the coral reef cleaning goby and its various fish clients, the freshwater branchiobdellid worm and crayfish, and the terrestrial oxpecker and its various mammal clients. Although all three case studies include different types of species, from fish to worms, birds to mammals, and take place in different habitats, saltwater, freshwater, and on land, there are many similarities which are generally common to any cleaning relationship. Whilst introducing you to the specific examples outlined above, therefore, this essay sets out the general ‘rules’ involved in cleaning symbioses, and in mutualistic relationships in general. Furthermore, this essay will touch on how relationships such as those outlined above exist on an ‘exploitation continuum’[3] from mutualism to parasitism.

2. Cleaning Gobies

Cleaning gobies (*Elacatinus spp.*) are obligate cleaners[6] meaning that they are dependent on the relationship they form with their fish clients and cannot survive without it[7]. They can be found in the coral reefs of the Caribbean where they are the main cleaner, servicing many different fish clients. This supergeneralist strategy allows the cleaning rewards for the goby to be as varied as possible[8], providing a mechanism by which their obligate nature can be maintained. As the reliance on cleaning rewards is high for obligate cleaners, cleaning gobies are typically found in specific locations throughout the reef, called cleaning stations, and do not tend to spend time away from these locations[9]. Cleaning stations allow client fish to know where to go for a cleaning and therefore the amount of cleaning conducted by the goby, and the amount of food that it can procure, is increased, as is the likelihood that the client will be cleaned.

The process of cleaning is reasonably stereotyped for cleaning gobies and begins with a client fish swimming up to the cleaning station and posing in a way that tells the cleaner that it wishes to be cleaned, typically immobile poses that show off a large amount of the fish's surface. When the cleaning goby is available, it will swim onto the client and inspects it[10]. If it deems the client worthy of a cleaning, usually if the client possesses a high enough abundance of parasites as determined by a complex association between client species abundance and body size[11], it will clean the client by feeding on its parasites, and sometimes mucus and scales[10]. If the goby does not deem it profitable enough to clean the client, however, it will return to the cleaning station and wait for another client. If a cleaning service does occur, the client can terminate the interaction through a universally recognised twitch which will cause the cleaner to return to the cleaning station and the client to retreat[10].

2.1. Cleaner benefits and disadvantages:

As indicated previously, the main benefit for cleaning gobies to participate in a cleaning relationship is the presence of an abundant food source. Gnathiid isopods are highly common tropical ectoparasites that can be transiently found on the surface of fish[6]. Cleaning gobies have a strong preference for these and other ectoparasites found on tropical fish and therefore their apparent ubiquity presents gobies with a seemingly never-ending food source, which they are able to tap during cleaning.

There is a theoretical disadvantage to cleaning for the goby, however. The relatively small size of the goby compared to the client and the proximity of the goby to the mouth of the client during cleaning could present a risk of predation. It has been shown that cleaning gobies do clean predators but generally at a faster rate than other clients. The rapid service could signal that the goby is a cleaner instead of prey and reduce the amount of time that the predator is in the vicinity of the cleaning station[12, 13]. As a consequence of this, there has been no reported predation of cleaning gobies by predatory clients at cleaning stations[12]. An additional potential disadvantage of cleaning is the possibility of infection[14]. The prolonged intimate contact between the cleaner and client required for effective cleaning may lead to the cleaner becoming infected with the very parasites that they are attempting to remove from the client[6]. Although theoretically a possibility, this is rarely a reality[14], so it is generally agreed that the benefit of a constant food source without the risk of hunting is much greater than the potential disadvantages of predation and infection.

2.2. Client benefits and disadvantages:

The main benefit for clients involved in a cleaning relationship is, predictable, the removal of ectoparasites[15]. As ectoparasites such as gnathiid isopods can cause skin irritation and blood disease[10], it is unsurprising that the removal of these parasites by cleaning gobies confers a lower risk of disease on the clients and allows for the clients to grow larger and live longer than they would otherwise[6].

There are, however, several disadvantages associated with cleaning relationships. If a client must travel a long distance to find a cleaning station, and especially if the cleaning station is outside of their territory, the client may receive injuries, lose energy, and may even be predated upon by other fish. Additionally, if the client is away from their territory for an extended period of time, as would be the case if the cleaning station was a long distance away, they may lose resources or even the entire territory to another fish[14]. Finally, it is not uncommon for cleaner fish to feed on scales and mucus of their clients as well as their parasites, which can be highly disadvantageous for the client[15]. However, as cleaning gobies tend to prefer ectoparasites to other food[13] this disadvantage may be limited in this particular relationship. On the whole, the disadvantages for the client fish in a cleaning relationship can be quite high. It is therefore necessary for the client to balance the potential benefits of parasite removal with the disadvantages of being cleaned. This usually means that clients with a high abundance of parasites, typically but not exclusively large, schooling, and abundant fish[11], and those that live reasonably close to a cleaning station seek out cleaning more often than others as the benefits of cleaning outweigh the costs[14].

2.3. Maintenance of mutualism:

The previous section highlighted that there are both benefits and costs for both the cleaner and the client in a cleaning relationship. In any relationship, especially ones between different species, it could be assumed that natural selection would favour the individual that maximises their own benefits and minimises their own costs, potentially at the expense of their symbiotic partner. Mutualisms (relationships in which both parties benefit) therefore seem destined to descend to commensalisms (relationships in which one party benefits and the other does not) or parasitisms (relationships in which one party benefits and the other loses). How do cleaning relationships maintain their mutualistic status?

As they are less likely to receive negative effects for a cleaning encounter, it is typically the cleaning goby which is most likely to attempt to exploit their clients. They do this by feeding on the scales and mucus of the client, as well as the parasites. Depending on the effect of this on the client, this indicates that the relationship has become commensal or parasitic as the client does not benefit from the removal of their scales or mucus while the cleaner does benefit from an additional food source[14]. It should be noted that, as previously discussed, cleaning gobies have a strong preference for parasites over client scales and mucus, so unlike with other cleaning fish such as cleaner wrasses which happily feed on their clients, cleaning gobies do not tend to cheat very often[10]. However, this does not mean that they do not cheat at all and the fact that the Caribbean, and especially Barbados, has a low abundance of ectoparasites means that cleaning gobies may feed on the more abundant mucus and scales when necessary[9]. As the cleaner is able to exploit the client, the client must have a way to maximise their own benefits from the encounter or prevent the exploitation, in order to maintain the mutualistic relationship.

The best way that the client can prevent exploitation by the cleaner is through partner sanctions. For obligate cleaners like the cleaning goby, it is essential that fish continue to come to the cleaning station so that they can feed on their parasites. Therefore, if a goby were to cheat and feed on a client's scales and mucus, that client and others watching may be more resistant to approach this cleaner in the future and so the goby will lose food sources[5]. This is not very common in cleaning gobies due to their lower likelihood of cheating but is a possible sanction[10]. A more common partner sanction for cleaning gobies is restriction of cleaning time. If a client feels a cleaner feeding on their scales or mucus, they may jolt, signalling the end of the transaction, and move away from the cleaning station. This means that cleaners that commonly cheat will have shorter cleaning interactions and therefore less food[4]. Partner sanctions are not the only way in which clients can prevent exploitation, however. It is known that cleaners are less likely to cheat on clients with high parasite loads as the costs of partner sanctions outweighs the benefits of feeding on mucus and scales when there are abundant parasites. Therefore, clients may wait until they have a high enough parasite load before initiating a cleaning interaction in order to gain maximum benefit while incurring minimal cost from the interaction[17].

In conclusion, it is not uncommon for cleaner fish to attempt to exploit their clients and move the cleaning relationship from mutualism to parasitism, but clients tend to have methods to prevent this. This shows how an unusual relationship that should not exist according to natural selection has evolved and is maintained.

3. Branchiobdellids:

Cleaning relationships are not exclusive to marine environments, however, as exemplified by the relationship between the North Carolina freshwater Branchiobdellidan *Cambarincola ingens* and New River crayfish *Cambarus charmodactylus*[17]. Like the cleaning goby, branchiobdellid worms are typically obligate cleaners that feed on the various debris that can accumulate on their crayfish clients including fungi, bacteria, and algae[4]. However, branchiobdellids do differ from cleaning fish by being ectosymbionts instead of endosymbionts[3]. This means that they live on their host and so their own survival and reproductive success is tied to the survival of the crayfish on which they live. This leads to a lower likelihood of parasitism and more consistent outcomes from the cleaning relationships for both participants[2]. As the relationship between branchiobdellids and crayfish is different to the one between cleaning gobies and their client fish, the benefits and disadvantages each participant may receive are also different.

3.1. Cleaner benefits and disadvantages:

The most obvious benefit for the cleaner in this relationship is, like for cleaning gobies, an abundant food source. Indeed, this benefit is even more pronounced for *C. ingens* as they do not need to wait for the client to approach them due to their presence on the crayfish client. The ectosymbiont nature of branchiobdellids means that an additional benefit of the relationship is the production of habitat that is relatively safe from predators. However, as the crayfish host may remove worms through grooming, as will be discussed later, the habitat may not be as safe as it appears.

The main disadvantage of the relationship for the branchiobdellid is that, due to the strong symbiotic nature of the relationship, they can only reproduce when they are on a live crayfish host. This tightly ties the success of the worm to that of the crayfish so that if crayfish populations decline, so will worm populations[3].

3.2. Client benefits and disadvantages:

Like the tropical fish in the previous example, *C. charmodactylus* may benefit greatly from being cleaned as, when fouling is high, such as in areas with low water flow, growth rates are decreased and mortality is increased due to sensory, respiratory and locomotor activities being compromised[2]. Removal of this debris by *C. ingens,* especially from around the gills, has been shown to promote greater growth and longer life in crayfish[3] indicating a direct benefit of the cleaning relationship.

Interestingly, crayfish have natural anti-fouling mechanisms such as moulting so the precise benefit that they may receive from the cleaning relationship with branchiobdellids is context dependent[4].

Similar to the previous example, low fouling and high *C. ingens* abundance has the potential to cause problems for the crayfish host as the worms may begin to feed on the crayfish itself due to scarce food availability[3] and may even begin to prevent effective movement or vision due to high worm abundance[2].

3.3. Maintenance of mutualism:

As would be expected, the relationship between the cleaner branchiobdellids and their client crayfish is finely balanced and has the potential to move from positive to negative for the client, with the cleaner having the opportunity to exploit its host. This relationship is slightly more complex than the one described for tropical fish, however, as crayfish can actively clean themselves. When the crayfish is small, young, and in areas of low fouling, the grooming and moulting performed by the crayfish is usually efficient enough to remove debris from their surface and gills[4]. This means that there will typically be little to no benefit in allowing branchiobdellids to live upon them, and the relationship will be either commensal, due to no negative consequences for the client if low numbers of branchiobdellids that can be hosted on the small crayfish[2], or non-existent, due to the crayfish removing the ectosymbionts before they can cause any problems[4].

As the crayfish grows older and larger, however, they moult less frequently and become less able to remove debris themselves so begin to experience greater benefits from hosting ectosymbionts like branchiobdellids[4]. Under high fouling pressures, this benefit is at its highest and therefore the relationship would typically be considered mutualistic. However, a consequence of growing size, increased debris abundance, and higher tolerance for branchiobdellid, is an increase in the abundance of branchiobdellids on the crayfish host[17]. As the number of ectosymbionts increases, so does the likelihood that their food source of debris will become limiting which will subsequently lead to an increase in feeding upon the tissue and blood-like fluid of the crayfish itself. Therefore, just like the previous marine example, this symbiotic relationship may become parasitic under specific conditions[3]. To prevent this slide to parasitism, the crayfish will remove branchiobdellids through grooming. A counter-characteristic has evolved in the branchiobdellid cleaners who may choose to attach to less accessible sites of the crayfish, typically away from the gills. Although these positions are not optimal for food acquisition, the branchiobdellids will at least avoid complete removal by the crayfish host which is beneficial, especially as branchiobdellids are completely dependent on crayfish for their survival and reproduction[4]. This is an example of not just how mutualism is maintained in a relationship but also how evolution can cause the production of strategies and counter-strategies to increase the benefits of a given relationship for an individual.

4. Oxpeckers:

Cleaning symbioses are not exclusive to aquatic habitats as displayed by the relationship between terrestrial oxpeckers and their various ungulate clients. Oxpeckers are African birds that depend on whatever they can scavage from their clients, i.e. they are obligate cleaners[18]. Red-billed oxpeckers (*Buphagus erythorynchus*) can clean a large variety of mammals including impala, giraffe, cattle, zebra, rhino, and buffalo[19], while the larger yellow-billed oxpecker (*Buphagus africanus*) is restricted to the larger ungulates such as buffalo, giraffe, and rhino[20]. Oxpeckers have several mechanisms to remove the ticks, insects, and loose skin from their clients including scissoring, favoured by red-billed oxpeckers[21], which involves rapid opening and closing of the bill over the hosts surface[22], and pecking, favoured by yellow-billed oxpeckers[21], which involves a closed or slightly opened bill being used in a ‘pickaxe’ motion[22]. Just as with the aquatic examples above, both cleaner and client may benefit or suffer from partaking in a cleaning relationship.

4.1. Cleaner benefits and disadvantages:

As for most cleaners, a major benefit of the cleaning relationship for oxpeckers is the abundant food source provided by their clients. Ticks, especially the blood-engorged ticks found on other animals, are an important food source for oxpeckers[18], especially for nestlings[22]. Oxpecker breeding has been shown to occur at times when ticks are most abundant indicating that breeding is reliant on the cleaning relationship, especially as breeding occurs on the host[22]. This reliance may be a disadvantage of the relationship if client or tick abundance declines.

As red-billed oxpeckers spend all day and yellow-billed oxpeckers spend all day and night on their mammalian clients[20], an additional benefit of the relationship is the increased safety experienced by the cleaner[23]. Incidentally, yellow-billed oxpeckers must nest on their clients as a way to maintain their food supply due to their smaller range of clients which may move away from the cleaner during the night[20], which indicates that yellow-billed oxpeckers are even more reliant on their clients than their red-billed cousins. This is disadvantageous if client populations decline.

Finally, red-billed oxpeckers commonly use hair[22] and faeces[24] from their clients to build and maintain their nests, indicating an additional benefit to participating in a cleaning relationship.

4.2. Client benefits and disadvantages:

Ticks feed on the blood of their hosts and can cause skin infections, tick toxicosis, lack of appetite and general energy loss[18, 24], so the main advantage for ungulate clients involved in a cleaning relationship is the removal of ticks and therefore the prevention of life-limiting complications. The extent to which oxpeckers remove ticks from their clients is under debate[22, 25], however it is likely to be of some advantage, especially in regions of high parasite abundance[19]. Furthermore, oxpeckers may feed on wounds on their clients which, although open for exploitation and may therefore become disadvantageous, may aid in the cleaning and healing of wounds[19].

An interesting benefit for the client is the presence of an alarm system that enables the client to be made aware of dangers before they can see them. When an oxpecker detects danger, it makes a hissing call and flies off the client, alerting the client, which may have very poor eyesight, of the presence of a threat[22, 25]. Although not a direct benefit from the cleaning portion of the relationship, this alarm system is nevertheless reliant on the presence of a relationship between oxpeckers and ungulates.

4.3. Maintenance of mutualism:

Just as with the aquatic examples, the cleaner appears to be the participant most able to exploit the cleaning relationship due to their ability to feed on either ectoparasites or client tissue thereby rendering the relationship mutualistic or parasitic[7]. Indeed, it appears that oxpeckers feed mostly on blood[19] which may come from ticks or hosts wounds[23]. When a client hosts a large amount of ectoparasites such as ticks it is likely that the cleaner will feed mostly on these parasites, effectively cleaning the client and ensuring that the relationship is either mutualistic, if ticks are removed prior to their feeding on the client, or commensal, if blood-filled ticks are removed. When a client hosts few parasites, it is more likely that the cleaner will ‘cheat’ and either feed on existing wounds or open new ones on the client. The latter situation will typically cause the relationship to be parasitic while the former situation may be mutualistic if the wound is cleaned and not made deeper, indicating an additional context that determines the nature of the relationship, i.e. the abundance of wounds on the host[26].

Like other client species, ungulates serviced by oxpeckers do appear to have some control over the relationship as shown by the lack of oxpeckers observed on elephants. Elephants generally lack high levels of parasites so they would receive little if any benefit and perhaps incur considerable costs from permitting oxpeckers to feed on them. It is therefore unsurprising that elephants have been observed using their ears, trunks, and tails to prevent oxpeckers landing on them[24]. This is an example of rejection of the relationship to prevent parasitism, but it may also indicate that other species that have fluctuating parasite loads may have the ability to control how tolerant they are of their cleaner partners.

5. Conclusion:

Cooperation between different species is not uncommon throughout the animal kingdom and the phenomenon of cleaning symbiosis is just one example of how species co-evolve to work together in order to increase their own survival. Cleaners benefit from the relationship by receiving a constant food source and potentially a safe habitat and clients benefit by having parasites and debris removed, allowing them to grow larger and survive longer than their 'dirty' counterparts. The cleaner and client are likely to have a conflict of interest, however, as they both wish to maximise their own benefits while minimising their costs. For the relationship to remain stably mutualistic, therefore, strategies to prevent exploitation have developed. These may include punishments or may be, paradoxically, increasing the symbiotic nature of the relationship. If cleaners are highly reliant on their clients for survival, they are less likely to overexploit them and the relationship is more likely to remain stable.

Cleaning symbioses, and other similar relationships, can have implications for how we approach conservation as it is clear that declines in one species likely will lead to declines in others. For example, many rhino species, as well as other large African mammals, are highly threatened which may lead to declines in their obligate cleaner species, especially the yellow-billed oxpecker. It therefore may be appropriate to gain an holistic view of species interactions to determine how to best protect species.

Finally, cleaning symbioses and specifically what they represent has the opportunity to impact how humans relate to each other and other species. Cleaning symbioses and many other natural relationships favoured by evolution are by no means altruistic, a lot of effort is needed to prevent them collapsing altogether, but they do show that working together is often necessary for survival. The world we live in is becoming increasingly divided and individualistic, and, as a result, quality of life is decreasing. Species are becoming extinct at an alarming rate and climate change is accelerating at a speed unprecedented and frightening. The survival of humans and the entire planet Earth is at risk. Now, more than ever, it appears that we must put aside our differences, stop maximising profits and exploiting both humans and nature, and work together towards the one goal we can all agree on. Survival.

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