Cleaning Symbioses: Proximate and Adaptive Explanations

What evolutionary pressures led to the evolution of cleaning symbioses?

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From the standpoint of the philosophy of biology, the extent of cleaning behavior in the ocean emphasizes the role of co-operation in nature as opposed to the tooth-and-claw struggle for existence. (Limbaugh 1961, p. 49)

[C]leaner organisms and their hosts meet the preconditions for the evolution of reciprocally altruistic behavior. The host's altruism is to be explained as benefiting him because of the advantage of being able quickly and repeatedly to return to the same cleaner. (Trivers 1971, p. 43)

[C]leaners are nothing but very clever behavioral parasites...[that] have taken advantage of the rewarding aspects of tactile stimulation, found in nearly all vertebrates. They may have parasitised this reward system to train hosts to visit them for rewarding stimulation and, at the same time, provide a dining table for the cleaners. (Losey 1987, p. 249)

O n a coral reef, a fish stops swimming and is suddenly attended to by a smaller fish,

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> ## Cleaning symbioses may not be mutualistic associations but rather one-sided exploitation

which proceeds to remove ectoparasitic worms and crustaceans from the larger fish. On the African savanna, a bird lands on the back of a grazing zebra, and while the zebra stands still the bird patrols the zebra's body, searching out and eating ticks and other ectoparasites. These are two examples of cleaning symbioses—one of the most remarkable classes of ecological interactions between taxonomically unrelated organisms. Over the past few decades, as reflected in the above excerpts, the opinion of scientists regarding cleaning symbioses has changed, from selfless cooperation, to a mutually beneficial interaction, and finally to a one-sided exploitation.

This change, however, has not occurred without some debate (Gorlick et al. 1978, Hobson 1969) because researchers still know little about the evolution of these symbioses. Cleaning involves the removal by a cleaning organism of ectoparasites, diseased or injured tissue, or other particles from the external surfaces or even the buccal cavity of another cooperating organism, hereafter called the client. Although this definition of cleaning is generally accepted (Losey 1987), the extent of

the apparent cooperation is debatable and in no case have the net fitness benefits obtained by the participants been properly quantified. Such quantification also challenges students of other apparently mutualistic associations (Cushman and Beattie 1991).

Understanding the proximate and ultimate causes of cleaning symbioses is of more than mere theoretical importance. For instance, fish that can clean have recently been used successfully for the control of ectoparasites on commercially farmed fish (e.g., Bjordal 1991, Cowell et al. 1993) and are viewed as a promising alternative to the use of chemicals (Pike 1989). However, what determines the efficiency of cleaners and their compatibility with certain client species is not yet fully understood. In this article, we review the current knowledge and ideas on cleaning symbioses, focusing on their adaptive significance. Although the literature emphasizes cleaning among fish, we discuss issues relevant to all taxa involved in cleaning symbioses.

Taxonomic occurrence of cleaning

Cleaning symbioses have had multiple independent origins, as reflected by their wide taxonomic distribution (Table 1). Crustaceans, fish, and birds act as cleaners and are associated with a variety of vertebrate clients. In addition to cleaning associations observed in natural conditions, some organisms have been seen to clean members of other species when

in captivity. This is the case with many pairs of fish species placed together in aquaria (e.g., Kearn 1978, McCutcheon and McCutcheon 1964, Spall 1970, Tyler 1963). Whether these fish also engage in cleaning in nature remains to be demonstrated, but these observations reinforce the suggestion that cleaning symbioses are common.

Intraspecific cleaning is also common throughout the animal kingdom. Allopreening in birds and allogrooming in mammals occur in many species; although these interactions maintain their ectoparasite removal function in many cases (e.g., Brooke 1985, Mooring and Hart 1993), they may also serve as mechanisms of bond or alliance formation, especially among primates. Intraspecific cleaning in fish is also common (Sikkel 1986, Sulak 1975, Wyman and Ward 1973) but is more likely to operate for ectoparasite removal than intraspecific cleaning in birds and mammals.

Geographical biases in the occurrence of cleaning symbioses may be the product of ecological differences. Most confirmed instances of cleaning symbiosis have been observed in aquatic habitats. Terrestrial vertebrates are generally more capable of self-cleaning than are fish (Hart 1990, Losey 1987) and may have been under weaker selection to participate in cleaning symbioses. Limbaugh (1961) also suggested that cleaning symbioses may be more highly developed in tropical seas than in temperate ones. This observation may have been prompted by missing information; several cases of cleaning in temperate seas and in freshwater have since been reported, and cleaning symbioses may be equally likely to evolve in any aquatic habitat (Losey 1987). Losey (1987) even proposed that selection pressures for the evolution of cleaning may have been more intense in temperate zones, where fish suffer from more plentiful ectoparasites; however, the evidence for latitudinal trends in ectoparasite infections does not always support this claim (see Rohde 1993).

Evolution of cleaning

Many animals can serve as clients, but few animals possess the neces-

Table 1. List of documented interspecific cleaner–client associations observed under natural conditions.

| Cleaner taxa	Client taxa	Reference
Crustaceans		
Shrimp, *Periclimenes*	Various fish	Limbaugh 1961, Sargent and Wagenbach 1975
Crab, *Planes*	Turtle, *Caretta*	Davenport 1994
Fish		
Goby, *Gobiosoma*	Various fish	Darcy et al. 1974, Losey 1974
Goby, *Elecatinus*	Various fish	Limbaugh 1961
Butterfly fish, *Chaetodon*	Various fish	Limbaugh 1961
Angelfish, *Pomacanthus*	Various fish	Limbaugh 1961
Hogfish, *Bodianus*	Various fish	Limbaugh 1961
Wrasse, *Thalassoma*	Various fish	Darcy et al. 1974, Losey 1974
Wrasse, *Labroides*	Various fish	Potts 1973, Youngbluth 1968
Wrasse, *Thalassoma*	Turtle, *Chelonia*	Losey et al. 1994
Birds		
Finch, *Geospiza*	Various reptiles	Amadon 1967, MacFarland and Reeder 1974
Scrub jay, *Aphelocoma*	Deer, *Odocoileus*	Isenhart and Disante 1985
Oxpecker, *Buphagus*	Various ungulates	Hart et al. 1990
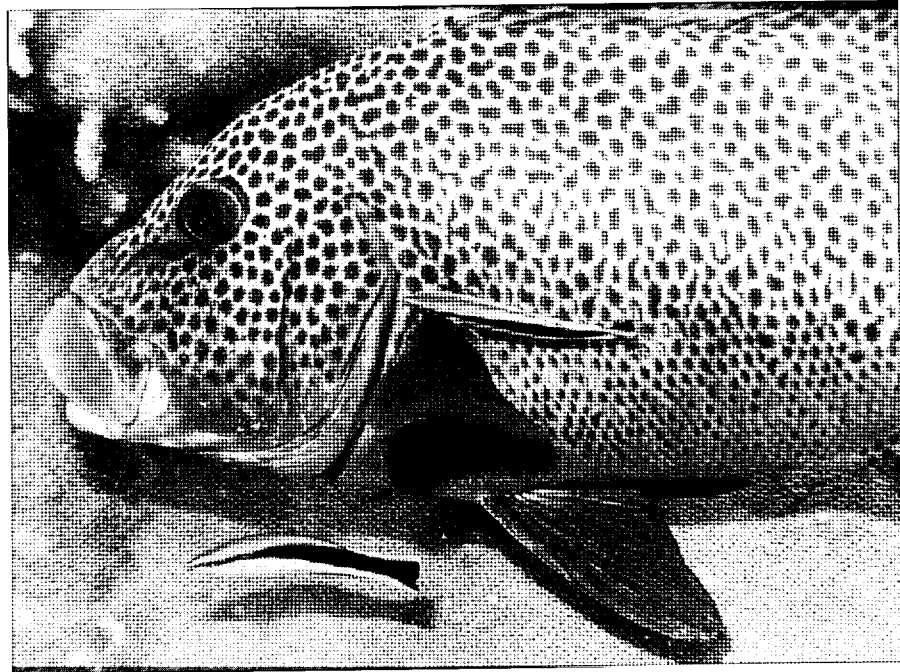
Figure 1. A cleaner wrasse (*Labroides dimidiatus*) inspects the gill opening of a client fish, the harlequin sweetlips (*Plectorhinchus chaetodontoides*), while a second cleaner hovers nearby. Photo: Mark A. Johnson.

sary characteristics to evolve into specialist cleaners. Any potential cleaner must feed on invertebrates and also be small relative to its potential clients if it is to survive on the clients' parasites. It must be mobile, have good vision, and be capable of picking with its mouth or appendages at small, concealed prey living on another animal. The need for these preadaptations limits the range of organisms that can become cleaners.

In addition to the presence of certain morphological and behavioral traits, phylogenetic influences may also affect the appearance and subsequent evolution of cleaning behavior. Some lineages may be predisposed for cleaning, such that noncleaning species can quickly adopt a cleaning strategy under certain conditions. Among fish this is certainly the case in the family Labridae, or wrasses (Figure 1), in

Table 2. Potential benefits and costs for both cleaners and clients of engaging in cleaning symbiosis.

Participant	Benefits	Costs
Cleaner	Abundant food source	Risk of predation?
Client	Removal of parasites	Loss of skin and/or mucus?
	Faster wound healing?	Loss of foraging time?
		More visible to predators?

which most species appear capable of cleaning to some extent and in which new cleaning associations can become established rapidly (e.g., Losey et al. 1994). Most tropical labrids feed on benthic crustaceans (e.g., Hobson 1974). This preference is reflected in the diet of cleaning labrid species, which is largely composed of crustaceans (Grutter 1995a, Losey 1974) despite the abundance of noncrustacean ectoparasites (e.g., monogenetic trematodes) on fish (Grutter 1994, Rohde 1993).

The main question concerning the evolution of cleaning has not been which organisms have the potential to become cleaners or clients, but rather why they do so in the first place. Two schools of thought exist on this issue. First, the evolution of cleaning can be seen as having been driven by fitness benefits for both participants (Poulin and Vickery 1995, Trivers 1971). Ectoparasites in general can lead to significant reductions in the growth, survival, or reproductive output of their vertebrate hosts (Cressey 1983, Cusack and Cone 1986, Hart 1990, Lehmann 1993). Because most animals are incapable of removing all parasites from their bodies, the benefits of allowing another organism to do so are obvious. For that other organism—the cleaner—the benefits consist of a rich, untapped source of food. Using a game theory approach, in which costs as well as benefits are associated with cleaning or being cleaned (Table 2), and in which cleaners and clients can play different strategies, honest participation in a cleaning symbiosis is the most rewarding option for both organisms (Poulin and Vickery 1995, Trivers 1971).

Several factors can influence the adaptive value of cleaning symbioses. One factor is the likelihood that the same cleaner and client will interact repeatedly, thus forming a re-

ciprocally altruistic association (Trivers 1971). Another important factor is the frequency of "cheating" cleaners or clients in the area (cheating cleaners feed on client tissues more than on ectoparasites, whereas cheating clients attempt to eat the cleaner; Poulin and Vickery 1995). Game theory models have also produced scenarios for the origin of cleaning symbioses, in which the appearance of cooperating clients need not be simultaneous with the specialization of cleaners. Although cleaning symbiosis appears to fit general models for the evolution of cooperation (Axelrod and Hamilton 1981), the validity of cleaning as an example of reciprocal altruism has been questioned because several key assumptions lack empirical support (Gorlick et al. 1978). For example, it is not yet clear whether cleaner fish wait until a client is free of ectoparasites before feeding on its mucus.

The second explanation for the evolution of cleaning symbioses is based on the existence, in all vertebrates, of a rewarding effect of tactile stimulation. If clients respond to tactile stimuli by remaining immobile and thus allowing cleaners to pick at them, then cleaners could simply exploit this response by feeding on host tissues as well as on ectoparasites (Losey 1979, 1993). In such a scenario, cleaners are "behavioural parasites" and clients are "hedonists" willing to tolerate occasional painful bites in exchange for rewarding stimulation (Losey 1993). The weak part of this hypothesis concerns the rewarding effect of tactile stimulation: to have been exploited by early cleaners, this effect must predate the appearance of cleaning, but its evolutionary origin and phylogenetic occurrence are unknown. There is evidence supporting the tactile stimulation hypothesis, however. For instance, many client fish respond to objects rubbed against

their sides in the same way in which they respond to cleaners, whether or not they presently harbor ectoparasites (Losey 1979).

These two general hypotheses for the evolution of cleaning are not mutually exclusive. It may well be that rewarding stimulation as a proximate cause of client behavior ultimately leads to net gains in client fitness. Despite the slowly growing body of evidence from field work, appropriate experiments have yet to be performed to distinguish between the two hypotheses.

Evidence of benefits obtained from cleaning

Experimental manipulations in natural systems are often the best way to demonstrate the function and adaptive nature of behavior. For example, cleaners could be removed from an area to deprive clients of the proposed benefit of ectoparasite removal. If participation in cleaning is important for client health, clients would be expected to suffer from more severe infections, to emigrate, or to die. Five such cleaner removal experiments have been performed (Table 3), in all of which cleaners were removed from coral reefs and client fish populations were subsequently monitored for changes in abundance or parasite load. The results of these removal experiments show no solid, consistent trend, although they suggest that clients do not suffer much from the absence of cleaners. The only experiment suggesting an impact of cleaner removal on client fish (Limbaugh 1961) was not supported by hard data.

On the basis of these experiments, it is impossible to conclude that ectoparasite removal is an important benefit for clients engaging in cleaning symbiosis. However, these experiments were designed to detect short-term effects of cleaner removal. A small reduction in spawning frequency caused by parasites might well be noticeable only over longer periods of time. Many coral reef fish live for several years, and the fitness benefits of being cleaned might therefore be apparent only over the lifetime of the fish. Temporal variation in parasite abundance, independent of cleaner activity, can also mask

any effect of cleaner removal over short time spans. The current use of cleaners in fish farms provides an excellent opportunity to compare the long-term growth of fish from cleaner-free pens and fish from pens stocked with cleaners.

Although experimental manipulations have not been conclusive, other lines of evidence do suggest that ectoparasite removal is of benefit to clients. Individuals of some client species are cleaned several times per day, spending a substantial amount of time being cleaned (e.g., more than 30 minutes per day for adult rabbitfish, *Siganus doliatus*; Grutter 1995b). Given that posing for cleaners may prevent some fish from engaging in important activities such as foraging or mating, it is tempting to conclude that fish obtain compensating benefits from being cleaned. Furthermore, individual cleaner wrasses, *Labroides dimidiatus*, can eat more than 1200 parasites per day (mainly gnathiid isopods; Grutter 1996). Such high predation rates can result in up to 60 ectoparasites removed per client fish per day by cleaners (Grutter 1996). Surely, where large numbers of ectoparasites are removed by cleaners the parasite load of clients must be reduced by the activity of cleaners. Because cleaner wrasses are selective feeders, however, their effects on parasites may be restricted to particular parasite species (Grutter 1995a).

The behavior of cleaners can suggest that they prefer to feed on ectoparasites rather than on client mucus or tissues. This would indicate that ectoparasite removal is important and that clients should benefit. For example, cleaner fish can discriminate between uninfected and infected client fish and prefer the latter ones (Gorlick 1984). Similarly, oxpeckers prefer foraging for ticks on larger species of ungulates, which harbor denser tick populations than do small ungulates (Hart et al. 1990).

The demonstration that heavily infected clients are more likely to seek cleaning than lightly infected ones also appears to support the adaptive nature of being cleaned. Among coral reef fish species that visit territorial cleaning wrasses, the tendency to solicit cleaning corre-

Table 3. Summary of effects on clients following the total disappearance of cleaners in cleaner removal experiments.

Cleaner	Location	Effects on clients	Reference
Fish and shrimps	Bahamas	Emigration, higher infection levels	Limbaugh 1961
Wrasse, *Labroides phthirophagus*	Hawaii	No changes in abundance or infection levels	Youngbluth 1968
Wrasse, *L. phthirophagus*	Hawaii	No changes in abundance or infection levels*	Losey 1972
Wrasse, *Labroides dimidiatus*	Enewetak Atoll (Pacific Ocean)	No changes in abundance, change in size distribution of parasites	Gorlick et al. 1987
Wrasse, *L. dimidiatus*	Great Barrier Reef (Australia)	No changes in abundance or infection levels	Grutter in press

*One cleaner fish was left on the reef.

lates positively with body size (Grutter 1995b, Poulin 1993),[1] which itself is usually correlated with ectoparasite load (Grutter 1995b). However, the apparent link between client body size and cleaning rates may be a phylogenetic artifact: the strength of the association between a client species and cleaners is determined to some extent by the evolutionary lineage to which the client belongs, independently of whether it is large bodied or small bodied.[2] Thus, these relationships with size do not prove that clients benefit from cleaning, although they mirror the selective pressures expected from the effects of parasites.

Finally, there could be other benefits derived by clients from cleaning. For instance, injured coral reef fish spend more time at cleaning stations, and it is possible that cleaning promotes wound healing (Foster 1985). This benefit may have evolved as a secondary or incidental one. More research is necessary to quantify such alternative benefits of getting cleaned.

Ethology of cleaning

An understanding of the proximate causes of client and cleaner behavior can shed light on their coevolutionary history. All of the work done on this aspect of cleaning symbiosis has been performed on fish cleaning symbioses. Typically, a cleaning bout

[1] A. S. Grutter and R. Poulin, manuscript in preparation.
[2] See footnote 1.

starts either with the client posing for the cleaner, or with the cleaner first approaching the client and the client then remaining motionless, sometimes with the head pointing upward. The cleaner then begins picking at the client's body. The client may open its mouth and gill covers to give access to the cleaner. If the client wishes to depart before the cleaner is finished, it may signal its intention with twitches of its body (but see Gorlick et al. 1978). Obviously there are as many slight variations of this script as there are client species, especially with regard to the level of cooperation by clients (e.g., Potts 1973). Similar cooperative posing behavior by clients has been described in the oxpecker–mammal association, in which the behavior of client species also varies, from total indifference to active accommodation (Breitwisch 1992).

Experiments presenting cleaners or clients with various stimuli can provide important clues about the evolution of cleaning. For example, experiments in which naive fish were exposed to cleaner species they had never encountered led to the conclusion that most client species can pose for cleaners, but that responses to cleaners are either innate or learned, depending on the client species (reviewed in Losey 1987). For instance, among client species, a posing response can be elicited by the sight of anything from an actual cleaner to a simple object, as long as the client has learned that the object is accompanied by tactile stimulation (Losey 1987). In all of these experiments,

unparasitized clients responded to cleaners and/or objects by posing. This finding suggests that ectoparasite removal is not a necessary component of cleaning symbiosis and that cleaners could manipulate clients with tactile stimulation. Indeed, cleaners are often seen lightly stroking the client with their fins to "stabilize" it (Potts 1973).

Recently, however, Losey et al. (1995) found that the pomacentrid fish *Dascyllus albisella*, reared from eggs in the laboratory and with no experience with cleaners, showed a full posing response when seeing the cleaning wrasse *Labroides phthirophagus* for the first time. Small fish species other than the cleaner did not trigger a posing response. Could this innate ability to recognize cleaners be adaptive? Losey et al. (1995) suggest that it is. Cleaners approach their preferred clients whether these are posing or not. *D. albisella*, however, is not a preferred client and may need to pose to solicit cleaners and ensure ectoparasite removal. Thus selection pressures from parasites may have driven the evolution of innate cleaner recognition in some fish.

Other observations hint that cleaners may exploit a pre-existing tactile reward system. For instance, cleaners continue to attend visiting clients even when they are not hungry (Lenke 1982, Losey 1987; but see Grutter 1996 for evidence that cleaning rates drop after cleaner fish become satiated). If tactile rewards are necessary to ensure the return of clients to cleaning stations, cleaners may have to deliver stimuli even when satiated to keep their clients satisfied and obtain a meal in the future. This observation is one of many that suggest that cleaning symbioses may not be mutualistic associations after all, but rather one-sided exploitation. However, one must then ask why no counter-adaptation has evolved in clients to free them from this exploitation. If clients are the puppets of cleaners, then the fitness consequences of being exploited must be small.

Conclusions

Cleaning symbioses are perhaps the best examples of interspecific coop-

eration among vertebrates. Although biologists have been aware of their existence for many years, surprisingly little is known about their evolution and current adaptive value. Many of the major gaps in our knowledge of the cleaning phenomenon could easily be filled with adequate experiments.

Comparisons among geographical areas with different ectoparasite densities would be instructive, but even more useful would be controlled experiments. Consider what could be learned about the factors motivating clients to seek cleaning by experimental manipulations of ectoparasite load in the field. Decreased or increased parasite loads would be expected to have opposite effects on a client's responsiveness toward cleaners. These experiments, as well as further cleaner removal experiments, should be performed on a variety of cleaner–client associations and not just on coral reef fish and their cleaners. In fact, systems in which a bird is the cleaner and mammals serve as clients may be more amenable to manipulations than systems involving fish. Adding ectoparasites to an ungulate is a straightforward affair, and so should be removing parasites through the use of insecticide sprays. The tolerance of these animals to cleaning birds following manipulation of their parasite loads could indicate to what extent they accept the birds simply to receive tactile stimulation. Of course, if clients do not show any plasticity in their responses to cleaners, experimental manipulation of parasite load may prove futile.

Theory is a few steps ahead of empirical evidence in the area of animal cooperation and reciprocal altruism. Cleaning symbioses offer ideal opportunities to test some of the predictions of the theory. The use of these symbioses may also be key to the control of ectoparasite infections in fish farms, given the potential problems associated with chemical control, such as effects on nontarget species or the spread of resistance among fish parasites. We hope that the next few years will see renewed interest in the study of cleaning symbiosis and progress in the elucidation of its evolutionary history and significance.

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