

Review article

## Cleaning Symbiosis

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### Abstract

Cleaning symbiosis is a 3-party symbiotic relationship in which cleaning organisms act as micro-carnivores and use the body surfaces of their host fishes as a feeding substratum. They graze on their hosts' ectoparasites as well as host tissues and mucus. Cleaning is not unknown in the terrestrial environment but it is a common way of life in marine and freshwater habitats with fishes as the common host.

Host fishes show much cooperative behaviour in their interactions with cleaners. However, it is unknown as to whether the actions of the cleaner are of any survival value to the hosts. Experimental demonstration of an effect is lacking and the cooperative behavior shown by hosts could be a mere response to rewarding tactile stimulation delivered by many cleaners. Indirect evidence is nonetheless convincing that, at least in some places and/or at some times, cleaning must be of advantage to the hosts.

Cleaning organisms are largely restricted to fish and shrimp. There appear to be at least two independent paths that organisms may follow as they evolve into cleaners: Substrate pickers that feed on small invertebrates appear to be the most common path. Many, if not most, of the substrate picking species on a coral reef can be seen to pick at the side of another fish. Aggressive parasites that feed on their hosts' skin and scales can provide another cleaner-precursor. Some species of what were once assumed to be parasites have ectoparasites in their gut contents and have developed means to deliver tactile stimulation to their hosts similar to specialized cleaners.

Our knowledge of how ectoparasites affect their host fishes is a major factor that now limits our understanding of cleaning symbiosis. Research is generally lacking as to how and whether they affect the survival value of their hosts and how the evolution of ectoparasites has been affected by the cleaners.

The relationship is perhaps best depicted as a form of "pseudo-reciprocity" in which the actions of the seemingly altruistic cleaner are directly instrumental in producing the partner's response. In this scheme, cheating is at least difficult. Much research is needed before we can comfortably decide as to the significance of the many separate examples of cleaning that may well represent an equally broad range of evolutionary histories and selective advantages.

Keywords: cleaning symbiosis, cleaners, ectoparasites

## 1. Introduction

Cleaning symbiosis is one of the more remarkable behavioral interactions in marine and aquatic environments. It is remarkable in its widespread occurrence and is a way of life that is largely un-matched in the terrestrial environment. It is just as remarkable that this deceptively simple relationship has defied any simple scientific proof. Researchers remain at odds to explain the evolution and adaptive nature of the relationship. This chapter outlines the very active history of research on cleaning symbiosis and proposes areas where research is most likely to produce rewarding results.

Feder (1966) defined cleaning symbiosis as "...a relationship in which certain organisms remove ectoparasites, bacteria, diseased and injured tissue, and unwanted food particles from cooperating fishes and some other organisms which visit them." It is more instructive at this point to present two typical behavioral descriptions rather than quibble about definitions.

A dark blue surgeon fish swims across the reef to a cleaning station that he visits several times per day. He stops swimming, rolls tail-down in the water and fades to a light gray coloration. A bright blue and black goby swims up from the reef and slowly moves around the surgeon fish's body in constant contact and occasionally taking an apparent feeding bite at its surfaces. The surgeon fish yawns open its mouth and gill covers as the goby pokes its head into the surgeon's gill chamber. After a minute or so the surgeon begins to twitch its body and the goby returns to its coral shelter.

A large parrot fish slowly moves about the reef biting frequently at the bottom. As it passes near a cleaning wrasse's station, the wrasse takes station above his back and slowly moves down its sides in frequent contact with its host. The parrot fish briefly stops feeding and hangs motionless above the coral but quickly resumes feeding and moves across the reef. The wrasse eventually stops its apparent grazing on the side of its departing host and returns to its cleaning station.

This is cleaning symbiosis. It may range from casual interactions to seemingly formal interchanges. The keywords are "cooperation" and "feeding." At least some of the host fish, some of the time, cooperate with or even solicit the attentions of the cleaner. Cleaners feed on the body surfaces of their hosts and ingest a range of food items that may include ectoparasites as well as the host's own mucus and tissues.

As soon as explorers and scientists began to don diving helmets, and later Scuba, the habits of the cleaners were noted. The earliest accounts ranged from insightful to highly imaginative and began to build the reputation of the cleaner fishes and shrimp. Longley (1918) did not speculate on ectoparasites or the function of the symbiosis but did note several of its details from his diving helmet in the Tortugas. He described the goby, *Elacatinus oceanops*, creeping over the body of larger fishes:

"Its jerky movement seems a source of minor irritation commonly borne with indifference or an air of hopeless resignation, even when the little fellows slip almost within their host's capacious jaws."

Beebe (1928, p. 147) was also quick to notice cleaning behavior during a diving expedition to Haiti but again failed to speculate on any ectoparasite removing function:

"During the period of verticality... a school of little wrasse darted out and thoroughly cleaned cheeks, lips, teeth and scales of all particles of organic coral debris, the parrot fish remaining quite motionless all the while."

More detailed scientific descriptions soon followed. Eibl-Eibesfeldt (1955) described posing behavior and warning signals by hosts of cleaning fish in the tropical Atlantic. He thought that hosts actively sought the services of cleaners at their cleaning stations. Randall (1955) gave a brief description of cleaning by *Labroides dimidiatus* and verified the presence of ectoparasites in their gut contents. Randall (1958) later gave more thorough descriptions of host posing and warning behavior, the existence of cleaning stations, or "Labroides sites" that were purposefully visited by reef fish, and more detailed confirmation that *Labroides* spp. fed on fish ectoparasites. Randall also observed that host fish were not always cooperative and sometimes reacted violently to bites by the cleaner. He also drew attention to the presence of fish scales in the gut contents of *Labroides* spp. Limbaugh, et al. (1961) provided a detailed survey of cleaner shrimps and their behavior. Abel (1971) gave the first detailed field accounts of cleaning in freshwater fish. All of these early authors were convinced, or nearly convinced, that cleaning was a factor of major importance to the health of reef fishes. Cleaners were the "doctors" of

the sea and were critical for the health of fishes. In return, cleaners were not eaten or harmed by their sometimes piscivorous hosts. Feder (1966) provided a valuable review of this rapidly expanding field and captured the interest of the general scientific public.

More recent reviews have been provided by Hobson (1969), Losey (1971, 1978) and Gorlick, et al. (1978). Hobson (1969) provided a valuable criticism of several generalizations that had crept into the literature with little or no support. My efforts in this paper will focus on more recent studies.

One of the factors that has led to confusion in discussions of cleaning symbiosis is a lack of clear distinction between the ultimate and proximate causes of a behavior pattern. Animal behavior textbooks warn us of this problem in many behavioral studies. Alcock (1979) terms questions of ultimate causation to be "WHY" questions of evolution that must be answered in terms of survival value and inclusive fitness. Proximate causation is a matter for "HOW" questions that explain an individual's actions in terms of physiological mechanisms, learning, etc.

A seemingly simple statement such as... "Host fish visit a cleaner to have their ectoparasites removed" has both ultimate and proximate connotations. There is no assurance that if one interpretation is true, the other must follow. Even if ectoparasite removal is important for the survival of the hosts, this does not mean that ectoparasites must have a motivational effect on the individual.

A search for similar relationships among other animal groups is largely fruitless with a few notable exceptions. Some are of casual interest and can teach us little about the relationship in fishes: Hendler (1984) found a brittlestar that appears to clean detritus from the surfaces of sponges. On the other hand, the relationships of some birds may have more than superficial similarity to cleaning symbiosis in fishes: Some such as cattle egrets and cowbirds are frequently seen perched on the backs of large grazing mammals but they appear to use their hosts as "beaters" to flush insects from the ground and do not feed on their hosts' ectoparasites (Heatwole, 1965; Dinsmore, 1973). In contrast, Mackworth-Præd and Grant (1955) found two species of African oxpickers (*Buphagus* spp.) associated with large grazers and deriving a large portion of their diet by removing ticks from their hosts. The feeding of the Egyptian plover in the mouths of crocodiles has been likened to cleaning in fishes (Howell, 1979).

Associations between birds and deer bear the most striking similarity to cleaning in fishes. Linsdale (1946) reported blackbilled magpies to remove

ticks from elk and deer. Isenhardt and Desante (1985) provide more details for scrub jays (*Aphelocoma coerulescens*) picking ticks from black-tailed deer. The host deer freeze, similar to a posing fish, during the cleaning process while the bird hops about its back. As the bird approaches the deer's head, the deer extends its ears very similar to fin erection in fishes. They even report a sort of cleaning station where a pair of jays loud-call from a tree until deer approach and repeatedly clean from the same tree. They term the association a form of proto-cooperation.

The apparent paucity of cleaning symbiosis in the terrestrial environment may be due to at least two things. Many terrestrial animals are far more capable of auto-grooming than are fishes. Most fish can only rub against objects or depend on another individual to remove parasites. Second, many terrestrial species include allo-grooming as an important feature of their social life. Except for within cleaning species, fishes largely do not show such behavior.

## 2. The Host Fish

### *Ultimate causes*

#### *Direct evidence*

A direct test of the ultimate cause of a behavior pattern is to introduce a social or environmental perturbation that reduces a proposed survival benefit for that behavior pattern. The subjects should then change their behavior or physiology to compensate for the loss or suffer a reduction in survival value. If neither effect is seen, the proposed ultimate cause is subject to doubt.

Control of ectoparasitic infestation is the most obvious and immediately compelling candidate for an ultimate cause of host behavior. Removal of cleaning organisms from a reef is an environmental perturbation that deprives the host fish of the proposed benefit of ectoparasite removal. If ectoparasite control is an important factor, after removing cleaners the host fish should either find other means for control of their ectoparasites or suffer a survival deficit as a result of increased ectoparasitic infections. This experiment has been performed four times with mixed results. Limbaugh's (1961) results provide the only experimental support for the proposal that removal of ectoparasites (and necrotic tissue) is a critical benefit for reef fishes. After removal of all cleaners from a patch reef in the Caribbean, host fish either emigrated (a compensatory change in behavior) or became infected (an assumed survival deficit). Unfortunately, this report lacked quantitative data and controls.

Youngbluth (1968) and Losey (1972a) provided two, progressively more quantitative replicates of this experiment in Hawaii. Neither found any increase in infections and, only through the use of detailed quantitative measures was Losey able to demonstrate any behavioral changes in the host fish: When all but one cleaner fish were removed from a reef, host fish altered their distribution toward the remaining cleaner and invested more solicitation time in order to be cleaned. No behavioral compensations were observed when all cleaners were removed. The initial changes did compensate for the perturbation but were not necessarily indicative of any reduction in survival.

Gorlick et al., (1987) performed the most detailed cleaner removal study. They included only one species of host fish infected by a single species of parasitic copepod at Enewetak Atoll in the Pacific. Finally, a quantitative effect of cleaner fish on an ectoparasite was demonstrated but the survival value of the effect remained elusive. The cleaner, *Labroides dimidiatus*, fed selectively on large copepods and altered the size frequency distribution of the copepod: On reefs without cleaners, the size-frequency distribution of the copepod population was biased toward larger individuals. This reduced the ectoparasitic biomass but not the numbers of ectoparasites: On reefs without cleaners, the presence of one larger copepod appeared to inhibit recruitment by additional parasites! The presence of several small copepods versus one larger copepod is of unknown relative survival value. The actual effects of ectoparasites on lifetime reproductive success remains to be estimated.

#### *Indirect evidence*

Indirect evidence for the ultimate causes of a behavior is far easier to obtain.

The cooperative nature of cleaning symbiosis offers a seemingly strong argument regarding survival value that is both difficult to resist and intuitively pleasing. Some host fish perform long bouts of motionless solicitation and cleaners will, on occasion, even enter the mouths and gill chambers of their hosts. Aquarists have repeatedly introduced cleaners from one ocean to tanks filled with large predators from another and witnessed a cooperative symbiosis in minutes (Coates, 1963; Herald, 1964; Keyes, 1982). Must not this cooperation mean mutual benefit? Is not ectoparasite removal an undeniable benefit? Add a few more assumptions and even mathematics can be satisfied as to the evolutionary possibility of such a "reciprocal altruism" (Trivers, 1971). However, the only conclusion that should be drawn is that either the proximate mechanisms for cooperation have been shaped by

positive survival value from cleaning *or* cooperation has arisen independent from cleaning symbiosis and has not been strongly selected against due to its appearance in a cleaning context. Logic dictates that the benefit of the doubt should go to the former, "cooperation selected for and by cleaning." The opposing viewpoint will be presented later when discussing proximate causation.

The existence of mimics of cleaner fish has been suggested for many species (e.g. Eibl-Eibesfeldt, 1955; Randall and Randall, 1960; Springer and Smith-Valiz, 1971; Kuwamura, 1981a, 1983a). Some of the suggested relationships are not convincing but the mimicry of *Labroides dimidiatus* by *Aspidontus taeniatus* is undeniable (e.g. see Wicker, 1963, 1968). This is strong evidence for *some* form of survival value link between cleaners and hosts. The most popular view is that the mimics are spared from predation by host fish due to the cooperative nature of the symbiosis, but it could easily reflect predation protection of cleaners due to their unpalatability as well as any survival value of ectoparasite removal.

Stomach contents of cleaners provides undeniable evidence that ectoparasite removal could be of survival value to hosts. Unfortunately we have little knowledge of the impact of this predation on ectoparasite populations without experimental removal of cleaners. Losey (1974a) made some tentative calculations as to the impact of cleaning fish predation on a Puerto Rican reef based on gut content analysis and census estimates. Cleaners were estimated to consume 0.5 ectoparasites per host fish per day, two orders of magnitude greater than the predation rate estimated for Hawaii. This suggests that, unlike Hawaii, removal of cleaners from this Puerto Rican reef might produce a survival value perturbation similar to that reported by Limbaugh (1961). But even this argument lacks strength since the vast majority of the ectoparasites in Puerto Rico were very small gnathiid isopods of unknown effect on the survival value of their hosts.

Another compelling form of indirect evidence results from a correlation between cleaning activity and ectoparasite density. Wyman and Ward (1972) described a cleaning relationship between two cichlid fish with *Etroplus maculatus* as the cleaner and *E. suratensis* as the host. Solicitation and cleaning were both far more common when a fungal infection infested their captive colony and decreased when the infection abated. Hobson (1971) reported on the territorial California garibaldi, *Hypsypops rubicunda*. Male garibaldi do not allow cleaning fish within their territories when guarding a nest of eggs and nest-guarding males were found to have a much higher standing

crop of one species of ectoparasite. Other species of ectoparasites were not more abundant on nest guarding males. Keyes (1982), working with captive sharks and the cleaner, *Labroides dimidiatus*, found that a bull shark began to visit the cleaning station only after it had been infested by an unidentified parasite. Solicitation of cleaning by the bull shark ceased after the number of parasites decreased. Nearly motionless posing by a bull shark is all the more remarkable since it must swim constantly in order to respire.

Foster (1985) made observations on wound healing, a more neglected suggestion for a benefit from cleaning. She found that even grievous wounds were rarely lethal for her study species, *Acanthurus coeruleus*. She observed individuals of three species who, after receiving nearly mortal wounds, altered their behavior to remain near cleaning stations and frequently solicited cleaning. Cleaner fishes paid much attention to the wounds. These fish resumed their normal habits when the healing was well advanced.

#### *Resolution of the controversy*

The current state of our direct and indirect evidence for the survival value of host behavior in cleaning symbiosis leaves us in a quandry. The indirect evidence for the importance of ectoparasite removal is compelling but direct evidence is lacking. I have not been supportive of hypotheses that cleaning is of critical importance due to the lack of strong, directly supportive evidence and the sometimes wild speculation as to the ecological importance of cleaning symbiosis [see comments by Hobson (1969) and Gorlick et al. (1978)]. I see two possible problems that may both contribute to this situation. First, and most critical, we tend to approach cleaning symbiosis as a unitary phenomenon and assume that an indication of a phenomenon in California has direct application to Hawaii. I prefer to think of cleaning symbiosis as a feeding behavior that has a superficial similarity in different regions, with different species. There are only a limited number of ways in which a host can interact with a cleaner and have the cleaner feed on its surfaces. In some areas there may be a strong recruitment of harmful ectoparasites that is a very rare event in another. Failure to show any survival value for cleaning symbiosis in the latter location has no bearing on the former locale.

Secondly, the indirect evidence that I find most compelling, such as the outbreak of a disease, has almost always resulted while the scientists were performing some other study. Outbreaks such as this which are controlled by cleaners appear to be rare events. How many other outbreaks not controlled by cleaners have occurred? If one should set out to wait for such events, in



order to perform direct experimental tests of survival value, successes would be few and far between.

I feel that the logical solution to the problem is to perform the critical cleaner removal experiments in new ecological settings. Temperate California would be my choice as the most likely setting for a successful demonstration of positive survival value. This is the location where Hobson has found compelling indirect evidence. Ectoparasites are far more common than in Hawaii and Enewetak, the only site where detailed, controlled studies have been conducted.

### *Proximate Causes*

#### *Direct evidence*

Direct evidence for the proximate causation of behavior can be obtained by altering the physiology or experience of an individual and observing any subsequent changes in behavior. This technique is frequently used hand-in-hand with the more indirect method of correlating naturally occurring changes in behavior with suspected physiological and experiential variables.

One type of "experiment" is to deprive hosts of exposure to cleaners for a long period of time and then observe their responses to an introduced cleaner. Okuno (1969b) observed that after more than two years of isolation from cleaners, reef fishes in the Suma Aquarium showed immediate solicitation behavior to introduced cleaners. He concluded that the responses must be instinctive. However, even two years of isolation does not preclude their recall of a learned response.

Losey (1971, 1979) showed that short term (days) deprivation of exposure to cleaners led to an increase in solicitation behavior. Deprived hosts increased their response both to living cleaners and to cleaner models or other sources of tactile stimulation (Losey, 1977).

Another "experiment" is to expose naive fish to a cleaner they have never encountered. Okuno (1969a) found that rainbow trout (*Salmo gairdneri*) acclimated to sea water attacked and never solicited cleaning from *Labroides dimidiatus*, a cleaner it could never have seen. Herald (1964, 1965) exposed host fish from the Atlantic to the Pacific cleaner, *L. dimidiatus*, and found immediate recognition and solicitation behavior by the hosts. Kuwamura (1976) found that most of the species living outside of the habitat of *L. dimidiatus* in Sirahama, Japan, were in the category of "non-posing" species, individuals exposed to the cleaner did not solicit cleaning. All of these authors suggested

support for the notion that response to cleaners was innate. Alternate explanations can be argued for all of these observations. But arguments as to whether or not a behavior pattern is innate are largely without profit. Instead we should investigate how the response operates.

Fricke (1966) opened a new line of research on the proximate causes of host behavior by presenting models of cleaner fish in the field. His hosts showed a strong attraction to the models indicating the obvious importance of visual stimuli. Encouraged by these results, I began a series of studies with cleaner fish models to explore the nature of the visual stimuli involved. My intentions to perform a classic ethological study of visual releasers (Losey, 1971) met with great surprise. Any of my models or even a bare piece of stainless steel wire was almost equally effective. Tactile stimulation was the critical stimulus parameter and fish quickly learned to respond to fish models or light bulbs in order to receive a tactile reward (Losey and Margules, 1974; Losey, 1977).

I concluded that tactile stimulation, which is probably rewarding to all vertebrates, was a key to understanding cleaning symbiosis on Hawaiian reefs. Part of the "HOW" question of why reef fish come to cleaning stations is that they have learned that this is a site where tactile rewards are delivered. Pacific cleaners of the genus *Labroides* deliver their tactile reward with rapidly stroking pelvic fins as well as their lower jaw and caudal fin. Particularly during a behavior called "pelvic ride" (Youngbluth, 1968) or "host stabilization behavior" (Potts, 1973) used to stabilize uncooperative hosts the cleaners swim just behind the head of the host and stroke with their pelvic fins. Hosts will frequently stop and begin posing. Juvenile angelfish show similar contact behavior (Brockman and Hailman, 1976). Cleaning shrimp antennulate their hosts and walk gently on their sides. Sargent and Wagenbach (1975) found that this stimulation had a strong effect on the host. The Atlantic cleaning gobies, *Elacatinus* spp., deliver similar stimulation with flicks of its caudal fin. Abel (1971) recognized the possibility that appetitive behavior for stroking and rubbing might be involved with freshwater host fish. Reynolds (1977) testified on the pleasant sensations provided by a variety of facultative cleaners.

Thresher (1977) described "Pseudo-cleaning" behavior in which parrot fish "solicited" cleaning from waving gorgonians. They posed, as for cleaning, near a gorgonian such that its branches rubbed over the fish. Beebe (1928, p. 142) noted similar behavior but did not suggest a similarity to cleaning symbiosis: "The fretwork gorgonia fans were frequently abraded, or showed

great holes torn or worn in their substance. To my delight I found that these were used as scratching places by passing fish; the parrots especially enjoyed oozing slowly through these tears and rubbing back and forth against the broken ivory strands"

As I pointed out (Losey, 1977) regarding my own studies with tactile stimulation, causal similarity between cleaning and pseudocleaning must be confirmed. Even though the poses and posture are similar for both, these may be a passive result of a fish hovering with minimum fin movements. Different causal systems might be producing an outwardly similar behavior pattern. One must show, as I did for response to models of cleaner fish (Losey, 1977), that variability in the response to the model or gorgonian correlates positively with variability in response to cleaners. While Thresher (1977) cautions that it might be coincidental, there are very few cleaners found in the area where pseudocleaning was most common and deprivation of cleaning is known to increase solicitation for cleaning by host fish (Losey, 1971, 1979).

One might well be able to establish a difference in the initial responses to models of different color patterns but I suspect that such a line of research might be disappointing for several reasons: First is the frustration of variable responses and sample size. Since the fish is learning as well as "responding" to the models, only the first few initial responses of an individual can be used. Second, unless naive fish are reared from the egg, wild-caught host fish will have been exposed to much learning in their field experience and they doubtless must differ in their learning experience. Even if there is an innate disposition in reef fishes to respond to certain color patterns it would likely be masked by the very strong effects of learning through tactile reward.

Isenhart and Desante's (1985) observation of scrub jays cleaning deer hints at a similar relationship. They observed the jays to use two different types of pecks while feeding on the deer: "Forceful" pecks were thought to be removal of ticks and "soft" pecks related to feeding on other parasites. I suggest that, regardless of the food ingested, the soft pecks probably serve as a tactile reward for the deer and are critical for the learning of this proto-cooperation.

Regardless of the degree to which learning and tactile stimulation are involved in the host's behavior, one can study other influences on the tendency or motivation to respond to cleaner fish. Infection by ectoparasites is an obvious candidate. If removal of ectoparasites is an important ultimate cause of behavior, one can expect (but not demand) that ectoparasitic infections have a proximate effect on individuals. Several lines of indirect evidence for

such an effect were given in the previous section on ultimate causation. All suggest that ectoparasitic infections exert a proximate influence.

Losey (1979) provided the only experimental study of the influence of ectoparasites on host behavior but included only two species of Hawaiian reef fishes. Both species showed a strong response to a model of a cleaner fish, regardless of the presence of ectoparasites. In one species, infected hosts showed somewhat lower rates of fin erection, an element of posing behavior, and various twitch-like behaviors that purportedly serve to terminate a cleaning boat. In the other species infected individuals increased the duration of response to a cleaner model and fin erection, but also increased the rate of twitch-like behaviors that terminate cleaning interactions and decreased pose tilting of the body. At best, the proximate influence of ectoparasites in these species was poorly adapted to the ultimate demands of ectoparasite control.

#### *Indirect evidence*

Cleaner fish have rarely been seen to be eaten by their predatory hosts. The ability to enter the mouths of large predators without being consumed is an undeniable indication of cooperation. While spearing *Labroides* spp. of cleaners I have found severely wounded individuals hours later on reefs where any other wounded species would have been eaten by the numerous predators. However, we have no knowledge as to whether the proximate causes are a behavioral inhibition of the host relating to the cooperative mutualism, distastefulness of the cleaners, or some other causes. In addition, cleaners are occasionally eaten. Kuwamura (1976) mentions several species who showed "predatory behavior" toward *Labroides dimidiatus*. Philip Lobel (pers. comm.) observed a hawkfish in Hawaii predate on a *L. phthirophagus* cleaner. At best there is doubt as to the proximate causes of immunity from predation. There has been little progress since Hobson (1971) stated: "Any so-called "immunity" from predation that a cleaner may enjoy probably relates (1) to an ability to recognize predators that are not intent on feeding and to limit cleaning to such individuals, and (2) to the fact that behavior exhibited by a cleaner servicing a predator is so unlike that of prey that the predator does not regard the cleaner as food. However, their role as cleaners probably does not afford these fish any security from being eaten during noncleaning situations." Potts (1973) added support to Hobson's views when he found that *L. dimidiatus* appears to learn how to inspect and clean various species of hosts. They may avoid presenting an opportunity for predation.

*Ultimate — proximate synergy*

Just as it is important to not confuse arguments regarding ultimate and proximate causation, one must not ignore one when considering the other. Knowledge of proximate causal systems provides a snapshot of how a species has responded to evolutionary forces. Since experimental work has included only two of the thousands of host species, conclusions lack generality. However, I feel that the circumstantial evidence is compelling and suggests a not so intuitively obvious conclusion.

My two species of tropical host fishes do not appear to be efficiently adapted for cleaning symbiosis. Unparasitized hosts will solicit cleaning for hours when none should be needed. More casual observations suggest that this is true for many species (Losey, 1971). Behavior patterns that initiate and end cleaning sessions do not show expected patterns of correlation and may both be positively correlated to the same causal factors. These supposedly specialized signals can hardly have evolved in the context of and for the purpose of cleaning symbiosis.

Losey (1979) discussed the probable origin of these behaviors both as social conflict behavior and, for the head or tail down postures, the natural result of a fish "freezing" in midwater. I suspect that cleaners have "parasitized" an existing tactile reward system in their hosts. This step initiated or made possible a cooperative relationship as host individuals learned how and where to receive this reward. Hosts that hover nearly motionless to solicit the attentions of the cleaner end up in the "pose" posture. Any selection pressure exerted by ectoparasite removal began after the cooperative relationship had formed. In Hawaii and, I suspect, throughout the tropical Pacific, fish ectoparasites are not a strong selective factor and hosts have shown little evolution of proximate systems for cleaning symbiosis.

The origin and the evolutionary significance of the tactile reward system are unknown to me. However, I know of no vertebrate species that is *not* rewarded by gentle tactile stimuli. I cannot disagree with arguments that it must be adaptive to be so widespread. At the same time I can find no universal answer to the question.

I must hasten to add that studies of new species and particularly new areas could easily falsify this conclusion for those species and areas. While I do expect some degree of similarity, I would be amazed if there was not an even greater diversity of evolutionary paths and current states of proximate causal systems.

### *Major gaps in our knowledge of hosts*

Experimental analysis of freshwater and temperate marine host fishes is the largest gap in our knowledge. I suspect that study of the proximate causes of cleaning in temperate marine hosts may yield very different results from my studies. Ectoparasites are far more common and may be a more important factor for reproductive success. I find it somewhat ironic that research on cleaner hosts has centered on the tropics where even Hobson (1969) admits that the most highly specialized brightly colored cleaners are found. This fauna of specialized cleaners may include relatively unspecialized (for cleaning) hosts due to a paucity of ectoparasites and resultingly low selection pressures on hosts. Selection pressure from more plentiful ectoparasites may have favored specialized hosts in temperate zones that have attracted less research.

I agree with Kuwamura (1976) that study of hosts that are only rarely or never cleaned is another deserving but neglected area. If tactile reward is an important causal factor are these species somehow not susceptible? Have they gained immunity? Or do other factors such as fear or aggression prevent their response? However, we must also be certain that these species are not cleaned at night or under the cover of the reef.

Experimental analysis of additional tropical species, particularly from outside of Hawaii would also be worthwhile. For a group as diverse as tropical reef fishes, knowledge of two species does little more than point out the need for more study.

### **3. The Cleaners**

#### *Cleaning organisms*

An endless variety of fish and crustaceans can be found to clean. Hardly any diverse assemblage of species has been studied without finding at least facultative "cleaning." Reynolds (1977) provides a prime example: He found some organism that would at least pick at his fingernail cuticles in a wide variety of habitats. I group these organisms into three general types with full realization that actual species will usually fall somewhere in the triangular state-space defined by these three types.

"Specialized cleaners" are the species usually discussed. *Labroides* spp. are perhaps the best example amongst the fishes. All members of the genus are cleaners and, although some species also exploit other food supplies (Losey, 1972a), at least one species, *L. phthirophagus* is an obligate cleaner (Randall, 1958; Youngbluth, 1968; Losey, 1971, 1972a). Tedman (1980a,b) has pointed

out several aspects of the anatomy of *Labroides* spp. that adapt it to cleaning symbiosis. Wickler (1963) has discussed the probable evolution of some aspects of its signaling behavior. Gorlick (1978, 1980, 1984) showed how the food preference of *L. phthiophagus* is closely tied to cleaning.

Many other fish and shrimp species can qualify as specialized cleaners, particularly as juveniles, but no other genera contain only specialized cleaning species. Hobson (1969) has pointed out the fallacy of several generalizations comparing tropical and temperate cleaners. In particular, the less striking coloration of most temperate cleaners must not be taken as evidence of lesser specialization as compared to the tropics. Several drab temperate species qualify as highly specialized cleaners.

"Substrate pickers" include the vast number of species that pick items from the substrate and, on occasion, pick items from another fish. Especially in captive fish, at least some cleaning behavior can be found in nearly any group of substrate picking fishes. Many, such as scarids, are very poorly adapted for such behavior but do clean on rare occasions (personal observation). Such fishes have probably provided the evolutionary precursors for most of our specialized cleaners.

"Aggressive parasites" at first appear to have little in common with cleaners but, after close examination, the distinction becomes less clear. Many species are specialized as scale feeders and attack larger fish to eat their scales (e.g., Hoese, 1966; Major, 1973; Losey, 1972c; Marlier and Lelup, 1954; Mok, 1978; Sazima, 1977; Roberts, 1970). Other species include both scales and ectoparasites in their gut contents (e.g. DeMartini and Coyer, 1971; Lucas and Benkert, 1983; Ribbink, 1984). These latter species are a diverse group of, at best, facultative cleaners. Most do not elicit a pose or cleaning solicitation posture from their hosts but others do evidence cooperation from at least some host species (DeMartini and Coyer, 1981).

#### *Ultimate causes*

The ultimate cause for the cleaners' behavior is simple: exploitation of a new food supply. Regardless of the evolutionary path that has been followed, from substrate picking or from aggressive scale eating, cleaning is merely another kind of micro-carnivorousness. Many aspects of the behavior and morphology of cleaners maximize their ability to access this feeding niche and avoid being preyed on in the process. Tedman (1980a,b) discusses the cranial morphology of *Labroides dimidiatus* and several specializations for cleaning. Gorlick (1978, 1980, 1984) related the preference of *L. phthi-*

*rophagus* for various host species to the food value offered by their mucus and ectoparasites. Potts (1973) indicated that *L. dimidiatus* treats each host species in a different manner probably to maximize food intake and avoid predatory dangers.

Hobson (1971) indicated that cleaners may run the risk of themselves being infected by parasites from their hosts. This is particularly true for many crustacean parasites that show little host specificity. Hobson showed that the types of parasites found on seniorita cleaner fish was related to the host species they had been cleaning.

#### *Proximate causes*

Little work has been done on the proximate causes of cleaner behavior. Potts (1973) indicated that many aspects of the behavior of *L. dimidiatus* developed through interactions with their hosts and were likely learned. Gorlick (1978, 1980, 1984) showed that presence of ectoparasites was important in determining host species preference but, in the absence of ectoparasites, the degree of mucus production appeared to be important.

Posing or solicitation behavior by hosts is an obvious cue to cleaners (Losey, 1971) but is not necessary for cleaning to occur. It is tempting to speculate that various details of the pose are signals that the cleaner responds to — that an erected gill cover indicates irritants on the gills or an erect fin attracts attention to parasites in the region. Unfortunately, I do not know of any experimental evidence that this is true. However I would expect cleaners to quickly learn any set of stimuli associated with finding food.

Nearly every popular treatment of cleaning speaks of cleaners responding to warning signals from the host or "parting gestures" (Potts, 1973). Again, I am not aware of any quantitative treatment of this proposed signal but I would be surprised if cleaners did not respond to any expression of conflict or tension in their hosts.

Lenke (1982) investigated the hormonal basis of cleaning behavior in *L. dimidiatus*. He claims to have identified a motivational system for cleaning that is partly separate from hunger. The hypothesis is strongly appealing since, if tactile reward is important to ensure that host fishes continue to visit this cleaner, it should not depend on hunger in the cleaners. Cleaners should deliver the reward according to some variable schedule but not only when hungry. Losey (1974a) indicated that cleaners did tend to spread their attention across a broad spectrum of hosts. However, Lenke used a series of gradually increasing doses in the same individual with no controls. His



interpretation of a correlation between behavior and hormone dosage could easily be caused by some other time-dependent factor.

*Major gaps in our knowledge of cleaners*

We have little knowledge of the degree of dependence on cleaning. Some appear to be obligate cleaners in that they are rarely seen to exploit other food sources and are difficult to maintain in captivity without host fishes. Much of our research with *L. phthirophagus* has been frustrated by an inability to hold captive individuals without cleaning. Other species of cleaners do exploit alternate food sources. Some *L. dimidiatus* spend the majority of their time feeding on zooplankton during periods of abnormal plankton abundance. However, we have no knowledge of how effectively these cleaners might compete with other micro-carnivores on the reef if they lacked hosts as a food supply. We also have no idea as to how the population size of cleaners is limited.

Geographical comparison of the strategies of cleaners, particularly between areas with strong differences in ectoparasite density, is bound to be rewarding. Losey (1974a) found many interesting comparisons between Puerto Rico and Hawaii but the questions raised during my short saturation dive in Puerto Rico were far more numerous than the answers. As with hosts, we need to have more detailed study of cleaners from areas where ectoparasites pose a more substantial hazard for hosts.

*Labroides* spp. offers a wealth of research topics in sociobiology and evolution. *L. dimidiatus* is a protogynous hermaphrodite with a single male defending a harem of females (Robertson, 1972, 1973; Kuwamura, 1984). Females fall into one, or sometimes two, dominance hierarchies within the harem and sex change is prevented by aggression from the male and/or dominant female(s). The members of the harem are frequently distributed over several cleaning stations. Males and dominant females may be faced with conflicting pressures to allow all subordinate fish to clean and thus reward hosts to ensure a successful cleaning station, as apposed to aggressive competition with these fish for food. Males and dominant females must spread their time amongst the stations included in the harem to suppress sex change.

#### 4. The Ectoparasites

Fish ectoparasites, the third member of the symbiotic triad, are the least well known. Cleaning organisms are known to ingest literally all types of small fish ectoparasites but we have little knowledge of the effects of this predation on the parasites or of their effect on cleaner and host.

The relative degree of camouflage of ectoparasites can serve as indirect evidence of the importance of predation by visually hunting cleaners. Many ectoparasites are strongly camouflaged either through having a mostly transparent body (e.g. many caligoid copepods) or through matching the pigments of their host, presumably by ingesting host tissues (e.g. monogeneid trematodes). Subjecting a seemingly parasite-free butterflyfish to a fresh water bath frequently results in a catch of trematodes of a variety of colors, one color for each of the colors of their host. This does not demonstrate the importance of cleaning symbiosis on ectoparasite evolution but it is consistent with such a hypothesis.

Other ectoparasites make little or no attempt at camouflage, at least to my sensory systems. Many lernaeid copepod gill parasites are tiny transparent critters that are very difficult to find unless they have egg masses. The eggs are highly contrasting and easy to detect. Are these inviting predation to aid in dispersal or infection of an intermediate host? Large cymothoid isopods make little attempt to camouflage but their size and armor may protect them from predation. Some ectoparasitic copepods trail parts of their body from the host's skin and are highly visible and should be vulnerable to predation.

I suspect that a study of the relative palatability, accessibility and degree of camouflage of ectoparasites would give valuable clues as to the functions of cleaning symbiosis. It is difficult for me to imagine cleaning as an important form of micro-carnivorism without significant effects on their prey.

The effects of cleaning on the population structure of ectoparasites has already been mentioned in the section on host fish ultimate causation. The conclusion was that only Gorlick et al. (1987) have experimentally demonstrated an effect of predation by cleaners on ectoparasite populations. However, their results were also suggestive of density dependent population regulation by the parasites themselves. With cleaners present, hosts were likely to have several small copepod parasites. Without cleaners, most had only a single larger (ca. one mm) copepod. This suggests that a single large copepod may prevent successful recruitment of young copepods. We should not be surprised to find such density dependent population control processes in parallel with predation pressure from cleaners. Unlimited growth of parasite populations is not a necessary result of removal of cleaners from reefs. Density dependent processes may hide the effects of cleaner predation from all but the most careful study. Habitat selection (Fryer, 1966) and comparison (Yeo and Spieler, 1980) approaches could yield valuable results.

At the same time, one must be cautious about such conclusions due to the complexity of the symbiosis. Kabata (1981) points out that, even with small ectoparasites, host fishes may gain immunity after infection or with age and that even interspecific interference between ectoparasitic copepod species is not unknown. In addition, Fryer (1966) has indicated gregarious behavior of ectoparasitic copepods that could further complicate the picture.

A final area that must be studied before we thoroughly understand the symbiosis is the physiological effects of the parasites on their hosts. Large cymothoid isopods that nearly devour their hosts have an obvious effect. Nearly any parasite in large numbers can cause secondary skin infections and raw abraded areas. Kabata (1981) concluded that ectoparasites on the surfaces of fishes tended to be small and relatively harmless unless present in extremely large numbers. However, documentation of physiological effects of normal levels of infection is almost totally lacking. In most cases we are left to guess that larger, deeply attached parasites likely do, and small mobile mucus grazers probably do not have much chance of affecting the life time reproductive success of their host.

## 5. The Symbiosis

Regardless of whether one's primary interest is host, cleaner or parasite, it is critical to keep the dynamics of the overall relationship in mind. The foregoing sections set the stage for my conclusion that we can no longer simply consider cleaning as a mutualism between cleaner and host. As a worldwide form of micro-carnivorism, one in which the carnivore's hunting ground happens to be the body of a fish, a diverse set of relationships must be expected.

Two arms of the symbiotic triad (Fig. 1) probably vary only in degree. Cleaner-parasite relationships are clearly predator-prey in which their importance to each other will vary widely. Host-parasite relationships probably vary from what most would be content to call "parasitic" to a commensal or phoretic relationship. Most attention, including mine, is focused on the cleaner-host arm but the selective forces that modulate the evolution of all three arms are closely linked. We must keep all three in mind.

Theoretical treatments of the cleaner-host relationship were pioneered by Trivers (1971) as a form of reciprocal altruism. Gorlick et al. (1978) indicated the fallacy of some of his assumptions but did not negate application of the model. Conner (1986) does not mention cleaning symbiosis but presents arguments on "pseudo-reciprocity" that are directly applicable. He argues

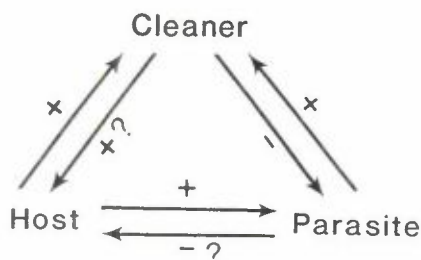


Figure 1. The survival value effects of the cleaning symbionts. A "?" indicates that a relationship is open to question.

that in truly altruistic reciprocity, the partner gives a benefit to the other that is not a direct result of the other's action. For example, a true altruist jumps into the river to save a stranger as an investment in some future, but probably unknown, reciprocity by the stranger. Cheating is very possible in this case and must be considered in any model. Pseudo-reciprocity is when the seemingly costly investment by the altruist leads directly to the return benefit from the partner — the drowning stranger was perhaps delivering the "altruist's" paycheck.

Cleaning fits most closely into pseudo-reciprocity. The cleaner's actions lead directly to the presentation of food by the host. The only true element of reciprocity, a protection from predation enjoyed by the cleaner, was outlined above as at best unproven. At the very least, application of models to cleaning must attend to pseudo-reciprocity.

Addicott (1984) produced a 3-party model that applies directly to cleaning. He introduced a mutualist into a predator-prey model and found that employing a cost of associating with a mutualist could lead to stabilization of the populations. However, he noted that both cleaning (Losey, 1972a, 1974a) and ant-aphid associations (Addicott, 1979) could vary in cost benefit ratio from mutualistic to parasitic depending on the relative density of symbionts. He predicted that this is likely to emerge as a common pattern in symbioses once the dynamics of more systems have been explored.

As is frequently the case, we lack sufficient information to make a firm statement of the survival value or the evolutionary significance of cleaning. The degree to which the cleaner-host arm of the triad represents a mutual-

istic relationship is open to question if one depends on definitions involving harm and benefit. Cheng (1967) argues that "physiological dependency" should instead be used to separate between types of symbiotic relationships. Based on this approach, the only dependencies demonstrated are for some obligate cleaners on their hosts. Cheng would then class this as a parasitic relationship with cleaners parasitic on their hosts. Losey (1979) indicated that the proximate causes of host behavior suggested that some cleaners are nothing but very clever behavioral parasites. Perhaps cleaners 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.

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