

# **BEHAVIORAL, PHYSIOLOGICAL AND ECOLOGICAL EFFECTS OF ORGANISMS IN SYMBIOTIC ASSOCIATIONS**

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## **ABSTRACT**

The significance of coevolutionary adaptations by associated organisms at the cellular and molecular level has been the primary focus of much research in symbiology (e.g., endosymbiotic hypothesis for development of eukaryotes). Studies on the behavioral and physiological ecology of organisms involved in symbiotic associations have also demonstrated extraordinary examples of adaptation. These associations represent tremendous potential in demonstrating alternatives to competition as major evolutionary selective forces. Interactions vary tremendously within the commensalism, mutualism and parasitism subdivisions of symbiosis, and divergent examples will be discussed. For example, many organisms are limited by their anatomy to remove parasites and necrotic tissues, etc., and must rely on allogrooming by others. While terrestrial animals are usually better equipped for autogrooming, the “self-cleaning” problem is especially significant in marine environments where cohorts of animals switch from potential predators to symbiotic cleaning “clients.” Organisms that possess significant, innate adaptations for protection are potentially attractive commensalistic or mutualistic hosts if a potential symbiont can inhibit or withstand the defensive mechanisms. Parasitism has also demonstrated bizarre behavioral outcomes, including examples where a larval form can “force” an intermediate host to alter its behavior to facilitate completion of the parasite’s life history. Finally, the characteristics or phenotypes of many organisms are actually based on composite genotypes of the host and any significant symbionts.

The question of why organisms associate with each other symbiotically can best be addressed by looking at the evolutionary and biological need for all organisms to exploit necessary resources. Ecologists typically partition the ecosystem resources into biotic and abiotic components, for which organisms typically compete either directly (interference) or indirectly (exploitative). Non-human species, however, probably have less need to make such formal distinctions between living and nonliving resources; unless the resource is recognized as a direct safety threat. Thus, from the tiniest microbes to the largest organisms, symbioses are a natural and expected outcome of this competition! As such, initially, a “pioneer” organism gets on or in a host. The symbiont, being typically much smaller than the host (which can technically be called a symbiont or symbiote, too), may go relatively unnoticed if it can gain resources (e.g., shelter, consumes castaway cells or tissues) without any significant effect or damage to the host. This would constitute commensalism. However, not all associations start off this innocuously; or if they do, may eventually or episodically move to a situation in which significant negative impacts to the host may occur. In such situations, we have a parasitic association.

At this point it is certainly in the host’s best interest to minimize such deleterious effects by either ridding itself of the parasite, or neutralizing the effects. The former action is clearly not possible in many symbioses; therefore, the next best outcome is to alter the encounter to minimize harm. With many symbioses, the host – if given enough time, on an evolutionary scale – can successfully prevent significant damage. In cases where complete removal of the parasite, or prevention of infection, are impossible, an even more optimal outcome by the host would be to accrue some benefit concomitant to the neutralization of harmful effects. This, ultimately, could lead to a mutualistic encounter. Symbioses that result in benefits to both associates represent tremendous potential in demonstrating alternatives to competition as major evolutionary selective forces. For clarification, ecology also recognizes mutualisms, but does not have the requisite symbiosis. Thus, there are non-symbiotic interactions between species that are mutually beneficial, too.

In any case, long-term encounters between symbionts and hosts can certainly result in coevolutionary adaptations. Additionally, given that no organisms are devoid of symbionts (i.e., axenic or aposymbiotic)(Paracer & Ahmadijian, 2000), many evolutionarily fascinating and ecologically significant associations have been discovered. Coevolutionary adaptations of

associated organisms at the cellular and molecular level have been the primary focus of much research in symbiology (e.g., endosymbiotic hypothesis for development of eukaryotes). In this chapter, the focus will be on behavioral, physiological and ecological adaptations of organisms involved in symbiotic associations.

As stated previously, organisms – especially relatively large ones – are under a constant barrage of attacks by opportunistic, smaller symbionts. Microscopically, these typically include prokaryotic, single-celled eukaryotic (e.g., protists) and fungal agents. Tissue defense mechanisms (e.g., immune defenses) are certainly important in regulating these types of encounters, both inside and outside the host's body. Macroscopic ectosymbionts are more likely to trigger active, behavioral engagement by the potential host organism, as direct detection visually or tactilely can occur. Completely avoiding such initial infection would be the ideal situation, and there are documented behavioral mechanisms to attempt to do so, such as evasive movements, selecting habitats that minimize exposure to parasites, etc. (Combes, 2001; Moore, 2002). However, once the symbiont has successfully “connected,” the typical reaction of most organisms would be to “clean” themselves of these potential parasites, especially if they cause physical “irritation” to the host. Some organisms are quite capable of removing ectosymbionts via autogrooming – or by themselves. Social species and interspecies groups also might supplement autogrooming with allogrooming, in which individuals groom others altruistically. In some cases, allogrooming plays a dominant role in maintaining the health of organisms and may fit the theoretical model called Biological Markets, which suggests that organisms can trade services and goods – such as cleaning or grooming – for mutual benefit. Like real markets, these interactions can be affected by current conditions of supply and demand (Noë & Hammerstein, 1995).

When different species are involved in allogrooming this is called cleaning symbioses, which Losey (1987) describes as “A three-party symbiotic relationship in which the cleaning organisms act as microcarnivores and use the body surfaces of their hosts as a feeding substratum.” “Cleaning” adaptations in terrestrial situations, including flying organisms, will be discussed first, followed by adaptations found in aquatic environments.

To accomplish self-cleaning, innate, morphological structures that can be finely manipulated are typically required. Mammals are major targets by numerous arthropods, including insects such as lice, fleas; ticks and spiders are also pests (cf., Hopla et al., 1994). Not surprisingly, all terrestrial mammals attempt to groom for removal of ectoparasites (Mooring et al., 2004); and

those with extensive hair or fur are even more prone to successful parasitic attacks (Pagel & Bodmer, 2003). Thus, extensive capabilities for cleaning have evolved in mammals. Arguably, *Homo sapiens* – the Naked Ape – is one of most adept species at both autogrooming and allogrooming. Furthermore, humans may have evolved the “relatively” hairless condition to minimize ectoparasitic loads, including wearing clothing to further reduce parasite contact (Pagel & Bodmer, 2003). Perhaps axillary and pubic hair, which develop primarily at puberty, were more important for our naked (i.e., unclothed) early human ancestors to advertise both visually and chemically (with the active scent glands associated with hair follicles) in sexual selection situations. “Clothed” humans retain these vestigial characteristics of thick body hair in these areas. Cephalic hair (including eyebrows) is likely developed primarily for both thermoregulation and visual communication purposes. Still, having these areas of relatively thick hair make us more susceptible to certain parasites (e.g., lice).

When we see or feel symbionts on us, we can use our fingers and hands to pick off these parasites, including allogrooming others (especially young children). We can also supplement our manual abilities by applying topical medical treatments to rid ourselves of external (e.g., lice) and internal (e.g., worms) symbionts. Additionally, we can attempt to avoid areas or times which would make us more vulnerable to feeding symbionts, such as mosquitoes that commonly feed at crepuscular times of day. Psychologically, when we feel more vulnerable, we are more likely to autogroom and do less allogrooming (Thompson, 2010).

Closely related primates can also engage in cleaning strategies similar to humans; and the occurrence of thicker and more body hair presumably make detection and cleaning significantly more challenging. Although non-human primates are technically not bipedal, they have excellent dexterity with their forelimbs and hands (and sometimes also with their hindlimbs and toes). As such, many primate species engage in both autogrooming and allogrooming (Dunbar, 1991). Individuals can spend considerable amounts of time meticulously picking off parasites from themselves and group members. While there are questions by some about whether allogrooming is primarily for social reasons (e.g., bonding of group members), clearly one major function and outcome is the removal of parasites (Dunbar, 1991, Mooring et al., 2004; Chancellor & Isbell, 2008).

The remaining tetrapods typically lack the skills to use their forelimbs for effective grooming. They must rely on other mechanisms, such as oral grooming. Specifically, they can remove parasites with their teeth. Grazing,

wild herbivores (e.g., moose, elk, impala and deer) have to contend with ectoparasites such as ticks, and frequently employ both auto- and allogrooming by using their mouths and biting for removal (Welch et al., 1991; Mooring et al., 2004; Yamada & Urabe, 2007). Other mechanisms used by wild and domesticated grazers, such as cows, are muscle twitching (including ears), head shaking, stomping legs and tail thrashing (Hart, 1994). Additionally, cows have been observed brushing up against trees, fence posts, etc., to remove ectoparasites (Kohari et al., 2007), and they can also allogroom (Kohari et al., 2007; Val-Laillet et al., 2009). So many of these grazing mammals spend significant time budgets on grooming, although in the case of some deer species, allogrooming may play a social role primarily and cleaning role secondarily (Yamada & Urabe, 2007).

Cleaning behaviors in lower mammals, such as rodents, have also been well documented – especially for the removal of fleas. For example, squirrels employ similar auto- and allogrooming techniques mentioned above for the larger mammals. Additionally, field studies have confirmed that parasite loads can drastically decrease fecundity in some squirrel species (Hillegass et al., 2010). Again, while allogrooming plays a social role, grooming certainly has a parasite-removal function (Hawlena et al., 2007).

Birds are well known for their preening activity, as the feathers and wings must be kept in optimal condition for flight (in air or in water)(Gill, 2012). In addition to this primary function, the removal of ectoparasites is also important. Thus, birds engage in both auto- and allopreening (Lewis et al., 2007; Gill 2012). Penguins can also spend a considerable amount of time cleaning themselves of debris and parasites (Viblanco et al., 2011). Birds are also known to clean other animals. The Galapagos Islands have several examples of such ectoparasite removal by birds. The most famous involves two species of Darwin finches and the Galapagos turtle. In an amazing behavioral display, the turtle extends its legs fully to elevate the body maximally so that the finches can access soft body parts from underneath the plastron, including proximal portions of the legs inside the shell to remove ectoparasites (MacFarland & Reeder, 1974). Finches and other bird species on the island are also known to clean parasites from the surfaces of both land and marine iguanas (Christian, 1980). Finally, wild grazing animals in the savannahs of Africa are allogroomed by two species of bird known collectively as oxpeckers. They are voracious consumers of parasites, such as ticks. However, they may also trigger problems for the hosts, as their consumption can include opening wounds and drinking blood from the host.

So in some cases, the associations may transition from mutualistic to parasitic (Weeks, 2000).

Finally, the most abundant of all animals – the insects – have more than their fair share of potential parasites to remove, including closely related members within the arthropod taxon. Social insects show some of the greatest adaptations for grooming. Specifically, allogrooming is highly important to many social insect species (Fefferman, et al., 2007). Honey bees worldwide have to contend with mites, which can completely destroy bee hives when infestations become extreme (Stanimirovic et al., 2010). Thus, both auto- and allogrooming are used by honey bees for defense against mites (Danka & Villa, 2003). Ants also have to contend with a particularly vicious species of fly that lays its eggs in the head of ants and the developing larvae consume the soft tissues, including the brain. Interestingly, these tropical flies have been used in the southeastern US as biological control agents to rid areas of fire ants (which are non-native)(cf., Porter, 1998).

Leaf-cutting ants in tropical areas can potentially be devastated by toxic species of fungi. So auto- and allogrooming are important to remove fungal spores and hyphae to prevent colony damage in the nest (Walker & Hughes, 2009). Fungal infections can have bizarre behavioral effects on ants, which will be discussed later in this chapter. Ironically, leaf-cutting ants “farm” and protect less virulent fungal species in their nests for food (Little et al., 2006).

The animals discussed above illustrate that terrestrial environments have many examples of cleaning. When an animal is limited by its anatomy, the removal of external parasites and necrotic tissues, etc., becomes more challenging. Thus, many species must rely on supplemental allogrooming by others, which can also serve as an important social activity. However, terrestrial animals are usually much better equipped for autogrooming than aquatic animals (Losey, 1987). This leads to a significant “self-cleaning” problem for many aquatic organisms, especially in marine environments. From aquatic mammals, to fishes, to invertebrates... the problem of keeping the body surface clean from ectosymbionts is magnified, because in marine ecosystems the most convenient hard surfaces for larval forms to settle and grow are usually the surfaces of other organisms. For example, consolidated benthic (i.e., bottom) areas, such as rock, are usually already covered by sponges, corals, etc. This is why artificial objects, such as pilings, jetties, boat bottoms, etc., are quickly colonized by benthic organisms. These settling organisms can create a huge burden, financially, as they can “foul” these structures by decreasing the structural integrity (e.g., wooden piers) and increase drag and lower fuel economy with ships that are heavily impacted

(which can necessitate that boat bottoms be scraped clear either by divers or have the entire boat lifted out of the water periodically to be thoroughly cleaned and repainted).

Aquatic mammals also have the need to protect themselves from ectoparasites. Like humans, many aquatic mammals have reduced fur or hair levels, which can potentially minimize parasite attachments. Additionally, some aquatic mammals – such as dolphins – swim rapidly through the more dense medium of water (compared to air), which could theoretically make it more challenging for potential ectoparasites to settle. However, when comparing the morphology of primates - with their dexterous abilities - to aquatic mammals, the latter group has much fewer grooming adaptations.

Parasites of aquatic mammals are well documented, with over 300 species of macroscopic worm and arthropodan parasites known to affect marine mammals (Evans & Raga, 2001). Impacts of these parasites can be significant and dangerous for the host mammal (Geraci & Aubin, 1987). Photos of large marine mammals, like whales, typically show upon closer inspection encrusting organisms growing on the body surface. Barnacles are a particularly common ectoparasite; while they do not use the whale's skin for food, they do settle in high numbers potentially increasing fluid-dynamic drag and creating skin lesions. There is speculation that the commonly observed breaching and fin slapping at the water's surface might be related to attempts to dislodge such parasites (Felix et al., 2006). Additionally, older whales and whales that are sick, and thus slower moving, typically have greater barnacle parasite loads (Slijper, 1979; Fertl, 2002). A single humpback whale was observed with an estimated 454kg (or 1000 lbs) of barnacles on its skin (Slijper, 1979). Clearly, if whales could autogroom effectively, such instances of heavy parasite loads would be unusual. Dolphins have been observed rubbing fins with each other, which could potentially be used as a form of allogrooming. However, it is likely the primary role is social, as little evidence has been observed that these actions actually remove parasites (Dudinski et al., 2009).

Manatees can typically swim in both marine and freshwater ecosystems. One advantage in this ability is that ectoparasites picked up in saltwater may actually be killed when the manatee ventures into freshwater (cf., Olivera-Gomez & Mellink, 2005). Additionally, freshwater fishes have been observed eating parasites and vegetation growing on the surface of manatees (Nico et al., 2009).

While dolphins and whales are extremely limited in their abilities to auto- and allogroom, other aquatic mammals may be better equipped. For example,

otters have significant amounts of fur that has to be groomed and aerated for thermal insulation purposes (Osterrieder & Davis, 2011). The meticulous care of the fur involves both auto- and allogrooming, which in addition to serving a social function (as observed in many terrestrial mammals), maintains the functional aspects for swimming and presumably helps maintain a low parasite load.

Aquatic reptiles, with their exceptionally hard exoskeletons, serve as an especially attractive settlement surface. One of the most typical, aquatic reptilian representatives is the sea turtle. Like aquatic mammals, they spend most of the time in the water; although both groups are air breathers, which necessitates visits to the surface periodically. In the case of sea turtles, females typically exit the water for extended periods of time to lay their eggs in the sand. Ectosymbionts, which are aquatic, could possibly be affected during these reproductive excursions by the turtle out of water. Additionally, some sea turtles bask out of water primarily for thermoregulatory purposes, but ectoparasite removal may be a secondary function (Jantzen et al., 1992). However, barnacle symbionts would likely be unaffected as these animals can simply close the opening in the shell as those barnacles do when exposed in the intertidal zone when tidal fluctuations create extremely low tide levels. Leeches are also a problem ectoparasite for many sea turtles (George, 1997). So sea turtles have restricted abilities to autogroom, with their limited appendage length and flexibility. However, observations made by researchers with captive sea turtles that have been marked, for example with finger nail polish, show that such marks may actually be removed by the turtle either by rubbing against a hard object in the lab or attempting to rub it off with their flippers (Natasha Warraich, personal communication). The efficacy of sea turtle autogrooming for fouling organisms in the field is unclear. However, sea turtles have been observed attending cleaning stations (which will be discussed below).

The remaining examples discussed below represent animals that typically are fully aquatic. Thus, settling ectoparasites would not typically have to deal with exposure to air as a possible means to facilitate removal. For example, fishes are one of the major groups of macroscopic organisms in any aquatic environment, and parasites are likely found in or on all species (Feist & Longshaw, 2008). Fishes are under constant attack by ectoparasites, some of which are merely present as an intermediate larval stage in a complex life history. In any case, ectoparasites – including flatworms and copepods - are a major problem for fishes (Feist & Longshaw, 2008). Fishes autogroom primarily by chafing, or rubbing up against a hard object to dislodge the

parasite (Wisendon et al., 2009). This behavior could be followed by body shakes, rapid acceleration swimming and “coughing” motions (Baker & Smith, 1997). Those who have had fishes in aquaria have likely observed these same behaviors, as ectoparasites can be a significant problem in such closed systems. Because of the limited abilities of fishes to autogroom, and the tremendous biological presence of potential parasites in the aquatic environment, allogrooming of fishes is extremely pervasive.

One of the most famous examples of an ectobiont on fishes (and almost any other large aquatic organism, including sea turtles and whales) involves another fish call the remora. Although most data suggest these fishes are commensalistic, by being phoretic or simply “hitching a ride,” some research has demonstrated a reduced load of ectoparasites with the presence of some remora/host combinations (Mucientes et al., 2008). Additionally, those fishes (and other large aquatic vertebrates) that possess numerous or relatively large remora individuals could experience additional drag while swimming or even skin irritation (cf., Brunnschweiler, 2006). Thus, one of the more ubiquitous, and seemingly innocuous, fish ectosymbionts may actually be a parasite under certain conditions with some hosts. Interspecific cleaning by fishes is also prevalent in aquatic systems, and can be extremely effective, too (see cleaning stations discussion below).

Fishes are also involved in one of the most extreme, non-lethal (typically) parasitic associations, in which an isopod attaches to and consumes the fish’s tongue and resides permanently in the oral cavity (Brusca, 1981; Bariche & Trilles, 2006; Jones et al., 2008; Bowman et al., 2010). Specifically, the isopod causes the fish’s tongue to atrophy by consuming its blood supply and then attaching to the muscles of the remaining tongue base with powerful appendages. This is likely the only parasite that can functionally replace an organ, as the parasitized fishes continue to consume food normally – albeit, sharing the meal with its “prosthetic, parasitic” isopod.

Invertebrates are also known to allogroom fishes. The best known examples involve shrimp, which are effective at removal of flatworms and other parasites (McCammon et al., 2010) - but they consume the mucus of fishes, too. Interestingly, some cleaner shrimps also reside in sea anemones (Gwaltney & Brooks, 1994) and receive protection (Mihalik & Brooks, 1997), which is interesting because cleaners typically are not consumed. The efficacy of cleaning by these shrimps may vary depending on the shrimp/host combinations (McCammon et al., 2010). Perhaps those shrimp that are less involved in cleaning fishes of ectoparasites, and more involved in consuming fish mucus are more susceptible to predation by the fish host.

A particularly fascinating behavioral event occurs in some aquatic environments in which cohorts of animal hosts switch from potential predators to symbiotic cleaning “clients.” Such events are best known in marine coral reef environments where fishes, sea turtles and other large species aggregate and wait their turn to be cleaned. Smaller cleaner fishes (e.g., wrasses, gobies, damsels) and cleaner shrimps occupy a particular area on a reef and through behavioral posturing (e.g., angle of the fish in water or waving brightly colored antennae of shrimp) signal to the larger client fish that their cleaning services are currently available. Additionally, and most importantly, the behaviors signal to the clients that the cleaner should not be consumed. Thus, some amazing events have been documented wherein the cleaner can even be allowed to enter the wide-open mouth of the client to remove parasites. Even sharks attend cleaning stations (Sazima et al., 2000). The evolution of cleaning stations demonstrates the clear need by many fishes to be cleaned and even possibly receive physical tactile stimulation (Poulin & Grutter, 1996). However, assessments of such associations to determine ultimate, long-term benefits are difficult to do in the field (Cote, 2000). Thus, we cannot categorically call all such associations mutualistic, as in some cases there may be no clear benefit – especially in the case of cleaner mimics like the saber-toothed blenny that eats host fish flesh while visually similar to the cleaner wrasse which focuses on parasites (cf., Sazima, 2002). But there are clear cases where shrimp have been examined and found fish parasites in their guts (Becker & Grutter, 2004).

There are some invertebrates with high potential to remove parasites. For example, echinoderms have numerous tube feet which they typically use for locomotion and feeding. These same structures could potentially be efficient for autogrooming. The reality, however, is that echinoderms still have numerous ectoparasites that clearly are not effectively removed (Jangoux, 1984). Other invertebrates with significant potential to autogroom are cephalopods, which typically have multiple, highly dexterous arms and tentacles with strong suckers. They, too, are victims to external parasites, such as copepods, flatworms and protists, (Hochberg, 1983; Gonzalez et al., 2003).

In summary, organisms in both terrestrial and aquatic environments are potential targets to parasites attempting to attach and gain resources from these potential hosts. Therefore, the need for cleaning is high, as potential parasites are diverse and abundant in both terrestrial and aquatic ecosystems.

In spite of all the host defenses discussed previously, parasitism is one of the most successful evolutionary strategies. Essentially every organism on Earth is a potential host! Thus, what happens once a parasite inevitably

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establishes and maintains a presence on or in the host? From the host's perspective, it should attempt to minimize the damage the parasite causes (which in most cases would involve an immune response of some kind). From the parasite's perspective, damage to the host should be minimized; otherwise, the parasite risks a decrease in its own fitness and survival. That is why with the exception of parasitoids – which are typically wasp larvae that purposely consume the host for food (Vinson & Iwantsch, 1980) – a good parasite does not kill its host. Or can it? What if the behavior of the host reduces reproductive success of the parasite? Can the parasite do anything about host behaviors? If the host is expendable at some point in the life history of the parasite, then the paradigm of non-lethal damage by a parasite is irrelevant. This can occur when a host serves as a vector or intermediate host for a parasite that must somehow get a larval stage (sometimes there are multiple, morphologically distinct larvae) into another habitat or organism. Research has uncovered some fascinating examples of behavioral and physiological changes in hosts that are induced by the parasite, typically to facilitate completion of a complex life cycle. While there may be skepticism about the behavioral effects of parasites on hosts (cf., Poulin, 2000), more studies are illustrating the potential for such interactions with compelling observations and data.

A recent landmark study has shown that bacteria in the guts of mice can not only influence digestion, but also influence brain hormonal activity and subsequent adult behaviors (Heijtz et al, 2011). The specific interactions discovered were that microbes were critical in development of neural pathways for motor activities and anxiety behaviors. These results suggest that symbiotic microbes – some of which are helpful and others harmful - may be critical components of development, both physiologically and behaviorally, in mammals.

While examples of parasite-induced behavioral changes in mammals are rare, lucid examples are present in some remaining vertebrates and invertebrates. Fishes are commonly intermediate hosts for numerous aquatic parasites. Killifishes can be infected by a trematode that directly affects the brains (specifically, neurotransmitter activity) of these fishes by inducing behavioral changes that make the fishes up to 30 times more susceptible to bird predators, which serve as the primary or definitive host to these parasites. Specifically, those killifishes infected with trematodes engaged in conspicuous swimming patterns making them more visible and susceptible to bird predators. Typical swimming by uninfected fish were more cryptic; thereby, minimizing predation (Lafferty & Morris, 1996; Lafferty, 2008).

One antipredator behavioral strategy employed by many animals is the avoidance of areas or times when light is abundant. This avoidance could be called photophobia. There are examples where a parasite clearly converts such light avoidance behavior to photophilia, which enhances the prospects of detection of the host by a predator. For example, there is a snail species that is parasitized by a trematode that first positions itself in one or both antennae of the snail. The snail host normally moves on the inferior surfaces of leaves and other vegetation during the day. However, infected snails are induced to move on top of the leaves where the pulsating, brightly striped larvae are easily seen through the transparent tissue of the antennae by bird predators. Consumption of the antenna/larva complex completes the parasite's life history (Wesenberg-Lund, 1931; Dobson 1988). Examples also exist wherein crustaceans are converted from photophobia to photophilia by parasitic flatworms, which subsequently doubled the rate of consumption by predators of the host (Moore, 1995, 2002).

There are also examples where parasites alter behavior in other dramatic ways. For example, grasshoppers and crickets infected with a nematomorph hair worm jump from land into an aquatic system. The hosts typically drown, but the parasitic worms swim away in search of a potential reproductive partner (cf., Libersat et al., 2009). Even fungi can affect host behavior, as seen in parasitized ants that are forced to position themselves in such a way to maximize dispersal of spores, which have developed inside the body of the soon-to-be dead ant (cf., Libersat et al., 2009).

Parasites can also take advantage of relatively programmed behaviors of hosts. So instead of altering the behavior of the host, the stereotyped behavior of the host enables the parasite to redirect the behavior in a beneficial way. Clear examples of such strategies exist in social groups where brood parasitism occurs. Some female cuckoo birds are known to lay their eggs in the nests of other bird species. The host species apparently does not recognize the "foreign" egg (as shell mimicry may occur) or even the cuckoo hatchling. The cuckoo hatchling will typically kill all of the resident hatchlings thereby ensuring the "host" mother feeds it as if it were one of its own hatchlings (Payne, 1998; Kruger & Davies, 2002).

Another example of brood parasitism involving cowbirds may in some ways have a more positive outcome in that most cowbirds do not kill host hatchlings, and some species may actually remove ectoparasites from the nest and host hatchlings. In one study, nests without a cowbird hatchling were likely to have much higher infestation rates of parasitic flies (Rothstein & Robinson, 1994). Thus, while brood parasitic birds can have devastating

effects on host bird populations, in the latter case of cowbirds where parasite removal is an added factor, the association may trend toward mutualism (i.e., less parasitic with mutual benefits) in some specific instances (Winfree, 1999; Paracer & Ahmadjian, 2000).

## CONCLUSION

One significant outcome of looking at the thousands of studies on symbioses is that rarely is there adequate data to accurately assess the cost-benefits in such associations. Such analysis would require detailed knowledge about nearly every aspect of each symbiont's life history, including their ecological niches. Additionally, many symbioses will likely vary temporally. That is, depending on the specific conditions the characterization of the association might vary. For example, commensalistic bacteria present on and in all animals can turn problematic when disturbance affects either the abundance and/or composition of the biota (Tiwari et al., 2011), or viral conversions turn normally safe bacteria into virulent forms (Blaser, 1998; Brüßow et al., 2004), which can also lead to activation of oncogenes and cancer in digestive tracts of humans (Blaser & Parsonnet, 1994). Essentially, characterization of an association as commensalistic, mutualistic or parasitic depends on the conditions at a particular time.

Much of this paper was dedicated to discussing how potential hosts prevent initial contact by symbionts, or once contacted, how to get them off (either through autogrooming or allogrooming). I focused primarily on macroscopic ectoparasites, as these are typically easier to see and detect (unless the endoparasite makes its presence easily detected as in the pulsating worm in the antennae of snails). The detection of ectoparasites can also be directly connected to host behaviors induced by the parasites – whether these behaviors are beneficial to the host or parasite. Clearly, in many situations, potential hosts perceive attachment attempts by other species as threats. Based on this observation, one might think that most symbioses start off as an “arms race.” Speidel (2000) discusses symbioses in the context of neodarwinism and states “...there is a tendency to see symbiotic associations as the end result of a previously parasitic relationship. In such cases, the argument could be made for the following symbiotic sequence: Parasitism → Commensalism → Mutualism. Specifically, if the host cannot remove or prevent infestation by a symbiont that immediately triggers deleterious effects, neutralization of such impacts should commence. Ultimately, the host – in some cases – can turn the

association into a mutually beneficial outcome. One of the most amazing, classical examples of this sequence comes from studies by Jeon (1972)(Jeon & Jeon, 1976) in which a pathogenic parasitic bacterium had infected an amoeba species thereby killing most individuals. However, some amoebae survived with the bacteria also still alive inside the cell. Subsequent generations (within a decade) of amoebae, with the vertically-transmitted bacteria, resulted in an obligate, mutualistic association in which both the symbiont and host would die if isolated from each other.

While many associations may start off in an antagonistic way (for at least one partner) and follow the aforementioned linear sequence, commensalism and even mutualism may also be starting points. Hosts that offer an innate defense against a variety of potential predators could serve as potential “protective” hosts to any symbionts that could neutralize the defense or feeding system against them individually. This strategy would be useful to the symbiont only if the defensive mechanism of the host remained intact; otherwise, both the symbiont and host would be vulnerable. Cnidarians, with their stinging nematocysts, represent potentially excellent hosts for the initiation of these types of associations. Sea anemones are known to host a number of symbionts, some of which just hide in the general vicinity without making contact with the virulent tentacles. Others, such as fishes (cf., Dunn, 1981; Fautin, 1991) and some crustaceans (cf., Gwaltney & Brooks, 1994; Mihalik & Brooks, 1997) have biochemically and physiologically masked themselves from stimulating nematocyst discharge thereby enabling these symbionts to move among the tentacles with impunity (Brooks & Mariscal, 1984; Elliot & Mariscal, 1996). In most cases, there is empirical evidence that such symbionts living with or near sea anemones, and other cnidarians, receive protection from predators (cf., Brooks & Mariscal, 1985; Brooks, 1989; Brooks & Gwaltney, 1993).

Although, in some cases, the symbionts may consume small amounts of anemone tissue (Brooks & Mariscal, 1984; Khan et al., 2003), the evidence is also accumulating that cnidarians can benefit from the symbiont’s presence by receiving nitrogen metabolites for symbiotic zooxanthellae living symbiotically in the host’s tissues (Spotte, 1996; Porat & Chadwick-Furman, 2005; Roopin & Chadwick, 2009), which can stimulate growth and reproductive rates (Holbrook & Schmitt, 2005). Direct observations have also confirmed that, in some cases, the symbiont can provide protection to the host (Brooks & Gwaltney, 1993; Fautin, 1991; McCammon, personal observation). So there are cases where a symbiont initiates an association with a potentially

virulent host, as a likely commensal, but eventually – and possibly initially - benefits to both partners are the outcome.

In closing, the study of symbioses can transcend determining the cost-benefit ratios that allow us to categorize these associations based on the outcomes. Speidel (2000) also states “Perhaps it would be better to see them not so much in terms of what each partner is getting out of the relationship, but in terms of how the structure as a whole is functioning.” That leads to the discussion of organismal phenotypes. Dyer (1989) points out that the phenotype is a composite of all organisms in associations, and states “Organisms as separate, completely definable entities may not exist.” For example, a termite without its microbial host can ingest but not digest wood. We could say the same for ungulates, too. Clearly, in these associations the phenotype is based on the genotypes of not only the termite (or cow) but also the microbial symbionts that provide the cellulose digestion. Arguably, all eukarotic cells are at least partially composites of bacterial genomes, given that mitochondria and chloroplasts were likely derived from bacterial endosymbiotic events (Margulis & Bermudes, 1985; de Duve, 1996). Future scientific inquiry about any biological systems should always acknowledge and account for the likelihood that symbioses have influenced behavioral, physiological and ecological aspects of the evolution of species.

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