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PARASITISM, COMMENSALISM, AND MUTUALISM: EXPLORING THE MANY SHADES OF SYMBIOSES

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ABSTRACT. – Symbiotic associations are not only ubiquitous in nature, but they also play fundamental roles in ecology and evolution. This paper discusses symbiosis with regards to the fitness costs and benefits conferred to the organisms involved in such interactions, and how the varying nature of these costs and benefits impinges on the way these associations are labelled. Focusing on recent research as examples, we discuss the influence of environmental factors, ontogenetic and evolutionary time, and the symbionts' life history traits on the interaction dynamics of symbiotic associations, and argue that symbiotic interactions are highly plastic across circumstances and timescales. We conclude that many symbioses do not fit neatly into the traditional categories of mutualism, commensalism, or parasitism, and urge caution when using such labels to describe biotic interactions.

INTRODUCTION

Symbiotic interactions are ubiquitous in nature, whether they are parasitic (Esch & Fernández 1993, Windsor 1998) or mutualistic (Douglas 1994). While the term "symbiosis" has frequently been used to describe mutually beneficial associations (referred to as "mutualism" herein), here it will be employed in its literal sense of "living together" regardless of whether the outcome is beneficial, neutral, or detrimental. For the purpose of this paper, symbiosis is defined as an intimate interaction between different organisms, where at least one of the parties is obligatorily dependent on the association as a part of its life history. This definition encompasses relationships such as cleaning symbioses, protection mutualisms and obligate pollination mutualisms, where even though the different organisms are not in constant physical contact, the parties involved rely upon the association to fulfil a major part of their life cycles. The host organism is defined as the provider of resources or the resource base, while the symbionts are the consumers of such resources, and may or may not provide services in return. This is similar to the definition of Ferrière *et al*. (2007), who considered the host as the producer of commodities and the symbiont or partner as provider of goods and services.

Given that symbiosis may be one of, if not the most widespread form of interspecies interaction in existence, the fitness outcome for the parties involved in such interactions can have major ecological and evolutionary consequences. However, the costs and benefits of symbiosis are not always clear, and fluctuate along a continuum that is influenced by environmental factors, time, and the biology of the parties involved.

In general ecological and biological textbooks (e.g: Campbell & Reece 2005, Eugene & Barret 2005, Solomon *et al*. 2005), symbiotic relationships are divided into three categories based on whether the symbiont has beneficial, harmful, or no effects on the host. In the case where both the host and symbiont reciprocally benefit from the relationship, the association represents mutualism, whereas if the symbiont utilises the host without benefiting or harming it, it is considered as a commensal. In contrast, if the symbiont is using the host as a resource and causing it harm as a result, then it qualifies as a parasite.

While useful, such a classification scheme rarely reflects the true dynamics of symbiotic relationships in nature. As pointed out by previous authors such as Starr (1975) and Lewis (1985), interactions between organisms exist along a continuous gradation, and the lines between mutualism, commensalism, and parasitism are not as neatly delineated as the textbooks might suggest. Based on such a classification, commensalism is the middle ground of a spectrum of relationships. However, in practise commensals are indistinguishable from parasites that cause their host comparatively low levels of pathology, and mutualists that exert such a heavy price for their service that it is barely compensated by the benefits of the association. While according to our labels, these organisms (parasites and mutualists) are from opposite ends of a spectrum, in reality the lines are blurred and the position they occupy along the theoretical continuum may be highly variable and circumstantial.

In this review, we explore the plasticity of symbiotic associations, and show how easily they can switch between mutualism and parasitism in response to even the slightest environmental change. Our survey of the literature is not exhaustive; instead, we focus on recent research to highlight our central argument about the ever-changing nature of symbiotic associations.

DEFINING COST AND BENEFIT

The costs and benefits of a symbiosis for a host organism are not always obvious nor easily measured because they may exist on many levels and in different currencies (Cushman & Beattie 1991). In the case of parasitism, the host-exploitation strategies of the parasite may affect a number of the host's life history traits (Poulin 2007). While for mutualism, the symbiont may be multi-functional, in that it may benefit the host in a number of different ways. The following examples illustrate how subtle additive costs or benefits are varied as well as easy to overlook.

Hidden costs of parasites

In addition to the pathology usually associated with parasitic infections, the parasite's presence may impose additional cost to the host beyond the immediate physiological effects. For example, cardinal fish *Cheilodipterus quinquelineatus* are regularly parasitised by cymothoid isopods – ectoparasites that feed on blood and other tissues of their hosts. But in addition to the injuries caused to the fish, because of the size of the isopod (which can be up to a quarter the length of the host) and the asymmetrical position that it occupies on the fish's body, its presence also imposes severe hydrodynamic drag, impairing the fish's capacity to forage or evade predators (Östlund-Nilsson *et al*. 2005).

Other additional costs imposed by parasites involve the role of parasitism in mediating sexual selection (Hamilton & Zuk 1982). For instance, male deep-snouted pipefish *Syngnathus typhle* that are infected with metacercariae of the trematode *Cryptocotyle* sp. are less able to discriminate against parasitised females (i.e. poor-quality partners), which can be detrimental to their reproductive success (Mazzi 2004). Pélabon *et al*. (2005) found that while microsporidian infection has no significant effects on the body condition of male two-spotted gobies *Gobiusculus flavescens*, parasitised males showed on average a 30 % decrease in courtship rate. Thus, the microsporidian is causing a reduction in its host's overall fitness despite the lack of negative effects on host condition. As a final example, while acanthocephalans are known to alter the phenotype of their crustacean intermediate hosts to make them more susceptible to predation by the worm's definitive host (Sparke *et al*. 2004). Sparkes *et al*. (2006) also found that male isopods harbouring infective stages of *Acanthocephalus dirus* have lower pairing success with females than males with uninfective stages of the parasite. Prior to the seminal paper of Hamilton & Zuk (1982), these kinds of subtle costs went unnoticed by biologists.

Likewise, other cost of a symbiosis may be hard to detect, possibly even completely hidden due to the host's phenotypic plasticity. Schwanz (2006) found that deer mice *Peromyscus maniculatus* infected with the trematode *Schistosomatium douthitti* were able to maintain the same basal and maximal metabolic rate as uninfected mice through physiological and morphological modifications that ameliorate the cost of infection.

In addition, according to a mathematical model by Miller *et al*. (2006), if the host has evolved tolerance instead of resistance as a way of mitigating the harm caused by a parasite, depending on the life history characteristics of the parasite, the host may eventually evolve to completely tolerate the parasitic infection, resulting in what superficially appears to be a commensal relationship. However, this "apparent commensalism" has come about at a significant fitness cost to the host, which has since been masked over evolutionary time (Miller *et al*. 2006).

Hidden benefits for mutualists

Similarly, mutualist partners may be able to convey multiple benefits to their hosts. One of the best-known and highly visible examples of mutualism is that between anemones and damselfish in the genera *Amphiprion* and *Premnas* commonly known as anemonefish or clownfish. This obligate association is based around protection mutualism, where the anemone's stinging tentacles provide predator-free territories for the anemonefish, while the anemonefish defends its host from predators that specialise in preying on anemones, such as butterfly fishes (Chaetodontidae) (Fautin 1991). However, in addition to the enhanced survivorship deriving from the protection provided by the anemonefish, the host anemone also appears to benefit from the association in another way. Holbrook & Schmitt (2005) found that anemones hosting anemonefish also experienced significantly enhanced growth rate and underwent more frequent asexual reproduction. This is most likely due to the ammonium excreted by the fish enriching the surrounding water with nitrogen, which is not only directly absorbed by the anemones, but also causes an increase in the abundance of the anemone's endosymbiotic algae which provide it with energy-rich photosynthetic products (Porat & Chadwick-Furman 2005).

Such hidden benefits have also been found in another, rather different system which is also based on protection mutualism. The marine isopod *Santia* spp. from the coral reefs of Papua New Guinea are hosts to unicellular algae that grow in a dense layer covering the surface of the isopod's exoskeleton. While the algal growth gives the isopod a conspicuous fluorescent red colouration, Lindquist *et al*. (2005) found that the algae provide protection for their host from fish predation through the production of noxious secondary metabolites. But in addition to providing protection, *Santia* have been observed to feed on the algae growing on their surface, and the isopods appear to promote the growth of the algal symbiont by inhabiting exposed sunlit surfaces. Appropriately, it is the protection conferred by the symbiont that allows these highly-visible

and slow-moving isopods to exhibit such behaviours (Lindquist *et al*. 2005). Thus, in addition to protection, the algae also provide the isopod with a reliable source of food.

One of the most recognisable benefits of mutualistic symbiosis is niche expansion for the host. Moran (2007) views symbiosis as a route through which multicellular organisms can acquire capabilities that allow them to exploit novel resources and thus expand into new ecological niches – this in turn has considerable fitness benefits even if these are not immediately measurable, at least in the short term.

One such example could be found in two species of closely-related plataspid stinkbugs, *Megacopta punctatissima* and *Megacopta cribraria* in Japan. The two species are usually hosted by a species of wild leguminous vine, but while *M. punctatissima* has also successfully colonised crop legumes and has become a pest species, *M. cribraria* remains restricted to its original host plant and suffers low egg hatching rates when transferred to crop legumes (Hosokawa *et al*. 2007). Hosokawa *et al*. (2007) found that the ability of *M. punctatissima* to exploit the crop legume is entirely due to the endosymbiotic bacteria in its gut, which are vertically transmitted through a unique system involving a "symbiont capsule" attached to the egg that is then consumed by the hatchling. When the symbionts of *M. punctatissima* are swapped with those of *M. cribraria*, the situation is completely reversed. Therefore, it seems that the ability of *M. punctatissima* to exploit a novel plant host depends entirely upon the symbionts it carries (Hosokawa *et al*. 2007).

An even more extraordinary example involves siboglinid polychaetes of the genus *Osedax*. This worm lacks a functional mouth and gut, but harbours heterotrophic bacterial symbionts within highly-vascularised root-like structures that allow the worm to obtain nutrients from the bones of whale carcasses (Goffredi *et al*. 2005). The great density at which these worms occur at whale-fall sites on the sea bed (Rouse *et al*. 2004) clearly illustrates the success of that particular partnership.

For a more familiar example of the niche-expanding ability of obligate mutualism, the symbiosis between plants and mycorrhizal fungi has been suggested as *the* key innovation that has allowed vascular plants to colonise the terrestrial environment (Simon *et al*. 1993). At the same time, it has also been recognised that the interaction between plants and mycorrhizal fungi exists along a continuum, ranging from mutualistic to parasitic, that is both context-dependent and variable over time (Kiers & van der Heijden 2006). This is a general trend that applies to all symbioses and that will be discussed with greater details later in this paper.

While the examples above show why fitness outcomes of symbiosis are not always easily measurable, sometimes costs and benefits with respect to certain fitness traits can be directly measured or at least inferred.

SYMBIOSES AND CIRCUMSTANCES

By considering the various forms of symbioses as existing along a continuum of fitness outcomes, it is possible to see that the cost incurred by a mutualist for its service and the virulence of a parasite may in fact be two sides of the same coin. Virulence is often taken as synonym of fitness losses incurred by the host because of infection by a parasite (Poulin & Combes 1999), but virulence can also be thought of as how much resource a parasite takes from the host, coincidentally reducing host fitness in the process. Similarly, mutualists also demand resources from their host, however this cost is usually compensated by the benefit simultaneously conferred on the host by the symbiont. The balance between the costs and benefits for the two participants in a symbiosis depends on a range of factors, and often only a small push is needed to shift that balance.

While digenean trematodes are usually considered as parasites, there may be at least one case where a species of trematode can be regarded as a mutualist. The trematode *Podocotyloides stenometra* utilises coral polyps as its second intermediate host. The infected polyp is easily distinguished by its profoundly altered appearance – it becomes bright pink, swollen, and incapable of retracting back into its protective skeleton (Aeby 1992). These modifications make the polyp a more accessible prey to the trematode's definitive host, the butterfly fish *Chaetodon multicinctus*, which preferentially feeds upon the infected polyps (Aeby 1992). The phenotypic changes induced by the trematode infection also greatly enhance the energetic value of each coral polyp, firstly because a swollen polyp allows the fish to obtain more tissue per bite, and secondly, because parasitised polyps do not retract in an attempt to avoid predation, less energy is used by the fish to harvest the tissue (Aeby 2002). The rate of establishment of the trematode in *C. multicinctus* is low compared with the rate of parasitised polyp consumption, and due to the comparatively small mass of the trematode compared with its host, the resource drain for the fish of even a heavy infection is quite low and may even be more than compensated by the greater energetic gains (Aeby 2002). Aeby (2002) has found no detectable negative impact of *P. stenometra* infection on its fish definitive host, and given the benefits of feeding on parasitised coral polyps, the trematode may actually be considered as a mutualist of *C. multicinctus*.

So the labels we attach to various symbionts may not necessarily be accurate descriptions of the relationship they have with their host. Even among parasites that induce obvious fitness cost to their host, the degree of harm they cause are by no means fixed. This plasticity in virulence (i.e., in the rate at which host resources are exploited) has been documented in *Ascogregarina taiwanensis*, a protozoan parasite of the mosquito *Aedes albopictus*. Tseng (2006) found that while the virulence

of the parasite is generally mild, under conditions where the host received higher levels of food, the parasite exploits its host at a higher rate and the oocysts derived from well-fed hosts were more virulent than those originating from hosts that were not as well-fed.

The costs and benefits of a symbiotic relationship can therefore be highly state-dependent. Even with supposed "mutualistic" symbionts, the fitness costs of the association are not always offset by the benefits, and are highly dependent on environment and circumstances. The following example illustrates this point. Pea aphids, *Acyrthosiphon pisum*, are associated with an obligate endosymbiont, *Buchnera aphidicola*, which provides its host with the essential amino acids lacking in the aphid's diet of plant phloem sap (Douglas 1998) but necessary for successful aphid reproduction (Douglas 1996). In addition, *A. pisum* can also harbour a range of facultative secondary symbionts, one of which is *Hamiltonella defensa* which confers to its host resistance against attack by parasitoid wasps (Oliver *et al*. 2005). However, the symbiont also imposes a serious cost to *A. pisum* for this benefit. While *A. pisum* infected with *H. defensa* is resistant to parasitoids and exhibits even greater resistance to parasitism when co-infected with another secondary symbiont, *Serratia symbiotica*, aphids with the secondary symbionts experience a severe fecundity reduction in comparison with uninfected aphids (Oliver *et al*. 2006). Thus, while in the presence of parasitoids aphids with *H. defensa* and *S. symbiotica* might be able to out-survive and hence outreproduce their uninfected conspecifics, the fecundity cost imposed by these secondary symbionts means that the net benefit of infection is at best marginal and in certain circumstances (absence of parasitoids) may even result in comparative fitness loss.

The interaction between *A. pisum* and its secondary symbionts shows us how facultative associations can often hover between mutualism and parasitism. But what happens when an obligate relationship with a usually beneficial symbiont becomes too costly? Consider the following example.

A rather unique digestive mutualism has evolved between the South African carnivorous plant *Roridula dentata* and its associated hemipteran *Pameridae marlothii*. While *R. dentata* usually traps insect prey with sticky droplets on its leaves, *P. marlothii* is able to walk unhindered over the sticky traps of *R. dentata* while feeding on the trapped insects and defecating on the plant's leaves. *R. dentata* then absorbs nitrogen in the faecal matter through its thin cuticle, and in this manner, the plant can gain more than 70% of its nitrogen (Anderson & Midgley 2002). Because *R. dentata* has no digestive enzyme to digest the prey, it is reliant upon this mutualistic relationship to facilitate the digestion process. Anderson & Midgley (2007) found that plants fed with prey that had moderate numbers of hemipteran living on them experienced a positive level of growth, while both control plants (which were not fed) and plants that were fed with prey but lacked the hemipteran *P. marlothii* experienced negative growth. However, in addition to feeding on insect prey, *P. marlothii* also sucks sap from its host plant, and it was found that at high density, *P. marlothii* also causes its host plant to experience negative growth, at a similar level to plants from the control and zero hemipteran treatments (Anderson & Midgley 2007). So at high density, the benefit provided by the hemipterans is cancelled out by the cost to its host, with the net effect on the plant being the same as if the hemipterans were absent. Thus the relationship shifts from mutualism to something more akin to commensalism, despite the vital service that *P. marlothii* provides for *R. dentata*.

The cleaning symbiosis between obligate cleaner fishes and their clients is a well-known and well-studied system that also provides revealing insights into the state-dependent nature of costs and benefits in symbiotic relationships. Client fishes seek out cleaners to have their ectoparasites removed and this behaviour has fitness benefit for both clients and cleaners (Grutter 2001). The client fish is cleared of its parasitic burden while cleaner wrasses receive a reliable source of food. However, there is an element of conflict in this seemingly reciprocally beneficial relationship.

While cleaner wrasses readily eat ectoparasites such as gnathiid isopods and monogeneans found on the skin of the fish they are servicing, their preferred food is actually mucus and tissue from their clients (Grutter & Bshary 2003). However, mucus and other tissue are costly for the client to produce, thus if the cleaner fish were to feed according to their preference, they would be "cheaters" since they would impose a cost on their clients without providing a service (removal of ectoparasites), resulting in a conflict of interest (Grutter & Bshary 2003). The incentive to cheat threatens the stability of this mutualistic relationship, and the cost to the client can potentially shift the relationship along the spectrum toward parasitism. For the cleaners, the impetus to cheat or not is mediated by the ectoparasite load of the client fish. Cheney & Côté (2005) found that at locations where the client had more ectoparasites, the cleaners removed less client-produced material, whereas the reverse was true where the client fish had few ectoparasites. Cheney & Côté (2005) suggested that the outcome of interactions between cleaner fishes and their clients may be dependent upon variation in ectoparasite abundance (see also Bansemer *et al*. 2002). The availability of ectoparasites for cleaners to feed on seems to be a key external factor determining whether this association leans toward mutualism or parasitism. The persistence of such cleaning symbioses means that there must be control mechanisms in place to prevent over-exploitation.

A simple game-theoretical model by Johnstone and Bshary (2002) showed that the clients have control over the cleaners by having the ability to terminate an encoun-

ter, thus denying the cleaner of its resource base (the cleaner's food source regardless of whether it is ectoparasite or mucus), enforcing cooperation and reducing exploitation. The predictions of the model match reported observations of cleaner and client fish interactions (Johnstone & Bshary 2002) and results of experiments that show clients can enforce cooperative behaviour by either punishing or fleeing from cheaters (Bshary & Schäffer 2002, Bshary & Grutter 2005).

EXPLOITERS AND CONTROL MECHANISMS

The studies discussed above seem to indicate that cleaner fishes are situational exploiters and indeed most mutualisms appear to be vulnerable to exploiters or "cheaters" that obtain the benefits offered by the host while returning none of the services an "honest" partner provides (Bronstein 2001). While some exploiters are obligate, others are mutualists that switch to being opportunistic exploiters due to changes in circumstances, as illustrated by the cleaner fish example. So how has mutualism persisted in the presence of exploiters?

The issue of cheaters in mutualism and the control of such exploiters has been investigated and discussed by previous authors in far greater details than possible here (Ferrière *et al*. 2002, Bronstein *et al*. 2003, Stanton 2003, Foster & Wenseleers 2006, Ferrière *et al*. 2007). However, we shall address the issue briefly in the context of its implications for the spectrum of symbiosis. The example set by the clients of cleaner fishes provides hints to the general mechanism for controlling exploiters of mutualism. A common theme that has arisen from studies investigating the stability of mutualism involves the host organism ultimately having control over the resources that the symbiont seeks. The implementing of "sanctions" or otherwise denial of resources to uncooperative symbionts or exploiters appears to be a strategy shared by hosts of a range of well-known mutualisms such as that between cleaner and client fish (Bshary & Schäffer 2002, Bshary & Grutter 2005), yucca and yucca-moth (Shapiro & Addicott 2003, Holland & DeAngelis 2006), fig and fig-wasp (Yu *et al*. 2004), and legume and rhizobial bacteria (West *et al*. 2002, Kiers *et al*. 2003).

While not entirely applicable to the traditionally viewed host-parasite interactions, as parasites are exploiters by definition, might host resistance and immunological responses be viewed as analogous to the "policing" of beneficial symbionts? Ultimately, the need for such mechanisms has resulted from the conflict of interests that exists within any obligate biological association, and both symbiont policing and immunological responses perform the role of limiting harm or preventing overexploitation of the host by the symbionts in question. The only difference is that in the case of host-parasite interaction, the relationship is more antagonistic – the host is attempting to completely deny any resources to the symbiont, whereas the latter is attempting to exploit the host while returning nothing of benefit.

SYMBIOSES OVER TIME

The changes in circumstance that bring about shifts in the nature of a symbiosis can also have a temporal element. Over different timescales, a lineage of symbiont may make the transition from parasitism to mutualism, and then back again to parasitism. This may occur over evolutionary timescales, or within the lifetime of the symbiont itself. Below we review some examples of the changing nature of symbioses over short and long timescales.

While the associations of brachyuran crabs with pelagic cnidarian hosts have been documented from various parts of the world (reviewed in Towanda & Thuesen 2006), the exact nature of these associations has remained largely unknown. Along with the hyperiid amphipod *Hyperia medusarum*, larvae and juveniles of the crab *Cancer gracilis* are often found to be riding the bell of the pelagic scyphozoan jellyfish *Phacellophora camtschatica*. While the younger crab instars actively feed upon host tissue and can be considered as parasitic, Towanda & Thuesen (2006) found that as the crab develops, the breadth of its diet also changes. As it grows, the crab feeds less frequently on host tissue and instead a major part of its diet eventually consists of the amphipod *H. medusarum*, which the crab gathers from the oral arm of the host jellyfish (Towanda & Thuesen 2006). Since hyperiid amphipods such as *H. medusarum* are considered as harmful parasitoids of their gelatinous host (Harbison *et al*. 1977, Laval 1980), by consuming the parasitoids, *C. gracilis* forms a valuable and unusual facultative cleaning symbiosis with its scyphozoan host. Over ontogenetic time, the status of *C. gracilis* shifts being from a parasite to a beneficial mutualist.

Figs (*Ficus* spp.) and their pollinating wasps (Agaonidae) are one of the classic examples of co-evolving mutualists due to their dependency on each other for their reproductive success and the seemingly high fidelity of their relationships (Anstett *et al*. 1997). However, recent studies have shown that the fig and fig-wasp relationship is in constant turmoil with frequent host-switching and conflicts of interests (Machado *et al*. 2001, Cook & Rasplus 2003, Marussich & Machado 2007). In the light of these recent findings, perhaps it should not be surprising that members of fig-wasp mutualistic lineages have been found to have made the transition to parasitism. While the non-pollinating fig wasp *Ceratosolen galili* retains features such as pollen pockets which suggest that it has evolved from pollinator fig-wasps, it does not pollinate its host fig, *Ficus sycomorus*, which is actually serviced by an active pollinator species, *Ceratosolen arabicus* (Mach-

ado *et al*. 2001). While superficially, this may appear to be a case of a "mutualist turned bad" – a symbiont that has evolved to exploit instead of servicing its original host – Kerdelhue *et al*. (1999) instead showed that *C. galili* and *C. arabicus* are not closely related, and that the former is a "cuckoo" species that has probably colonised *F. sycomorus* through a series of host changes.

In addition to former pollinators evolving into parasites, figs are also frequently exploited by parasitic Non-Pollinating Fig Wasps (NPFW) belonging to the Chalcidoidea superfamily (which also includes the pollinating agaonids) that have evolved various ways of exploiting the fig syconium without providing the reproductive service of pollinating the fig inflorescence (Cook & Rasplus 2003). However, in another twist of the fig and fig-wasp story, Jousselin *et al*. (2001) found that two genera of internally ovipositing NPFW, *Diaziella* and *Lipothymus*, both from subfamilies that are usually considered as parasites of their respective *Ficus* hosts, appear to be responsible for pollinating their host and do so as efficiently as *Waterstoniella*, the fig's "legitimate" pollinator. Therefore it would appear that *Diaziella* and *Lipothymus* have made the evolutionary transition from parasites to mutualists. Thus, the co-evolutionary story of figs and fig-wasps shows us the constant shift in the position of this association along spectrum from mutualist to parasite and vice versa over evolutionary time.

SYMBIOSES AND TRANSMISSION

After considering these extrinsic factors of circumstances and time that can influence symbiotic relationships, it is worthwhile discussing an intrinsic factor, a property of the symbionts themselves, which may influence the position that a particular symbiosis may occupy along the continuum of fitness outcomes. This factor, arguably one of the most important life-history traits of the symbiont in terms of determining its relationship with its host, is its mode of transmission.

Current theories recognise that transmission mode plays a key role in determining the virulence of a symbiont (Ewald 1995, Day 2001, Ferdy & Godelle 2005). Thus, vertical transmission means that the fitness outcomes of both the symbiont and the host are aligned, such that cooperation between the two parties (or at least lower virulence by the symbiont) would be an outcome favoured by selection (Ewald 1995). In contrast, if the fitness of the symbiont is not exclusively intertwined with that of its host, then its fitness can be improved by exploiting its host more aggressively while returning fewer benefits, which should push the association on the evolutionary path towards parasitism.

Wolbachia is a well-known maternally-inherited, vertically-transmitted intracellular reproductive parasite of arthropods, most noted for its role in distorting the sex ratio of its host's progeny. It is known to impose various fitness costs on its host, such as physiological impairment (Fleury *et al*. 2000), decreased sperm quality (Champion de Crespigny & Wedell 2006), reduced immune response (Fytrou *et al*. 2006), mortality of male embryos (Hurst *et al*. 1999, Zeh & Zeh 2006), and reproductive failure resulting from cytoplasmic incompatibility (Perrot-Minnot *et al*. 2002). However, it has been found that within a short period of less than two decades, a strain of *Wolbachia* has actually evolved to improve the fecundity of its host by an average 10 % over that of uninfected conspecifics (Weeks *et al*. 2007). Thus this particular strain of *Wolbachia* has evolved from a parasite into a mutualist. Such a result is fully compatible with the expectations of the current theories of virulence.

While the transmission mode of *Wolbachia* is predominantly vertical, with horizontal transmission occurring only on rare occasions (Huigens *et al*. 2004), changes in virulence associated with a change in the mode of transmission can be experimentally demonstrated with symbionts that have transmission routes that can alternate between the horizontal and vertical modes.

Endosymbiotic dinoflagellates provide an example of this phenomenon. Members of the genus *Symbiodinium* are known to be associated with a range of invertebrates common in the tropical and subtropical marine environments (Trench 1997). One species, *Symbiodinium microadriaticum*, is found in the upside-down jellyfish *Cassiopea xamachana* which are born free of the algae and can either acquire them from the environment or inherit them during the asexual reproduction phase (Sachs & Wilcox 2006). Sachs & Wilcox (2006) experimentally bred two lines of algae under the enforcement of either a horizontal or vertical transmission regime, and as expected, algae that were selected under the horizontal regime caused a significant reduction in host growth and budding when compared with algae selected by the vertical transmission regime. However, it was also found that the more harmful algae were impaired by their own proliferation as they debilitated the jellyfish in such a manner that hindered their own spread (Sachs & Wilcox 2006). It is conceivable that under the right circumstances, normally beneficial symbionts can evolve to become harmful, and a symbiont's status of being either a mutualist or a parasite is by no means stable.

RETHINKING OUR LABELS

While it may appear that whether or not to call a particular biological association parasitism, commensalism, or mutualism is a matter of semantics, such labels can be value-laden and lead to erroneous assumptions about the true nature of the relationship, and they may even hinder insightful research. For example, if Anderson & Midgley (2007) had simply accepted that the hemipteran symbi-

onts of *R. dentata* are mutualists on the basis of the vital service they perform for their host plant, they would not have discovered the cost the hemipterans can impose on the plant at higher densities. Likewise, if Towanda and Thuessen (2006) had observed the larvae of *C. gracilis* feeding on tissue of their scyphozoan host and concluded that the relationship is a parasitic one, they would not have found that as the crab larvae mature, they protect the host from harmful parasitoids.

While for some, the term "symbiosis" denotes mutually-beneficial relationships, we have used it here as a general term to describe any kind of intimate biological association. However, recent advances in ecological and evolutionary research have shown us that even the sub-categories under the broader umbrella of symbiosis – mutualism, commensalism, and parasitism – may not be as permanent or well defined as we would like to imagine. We therefore urge caution with the use of these labels, since the associations they characterise are highly plastic and never fixed.

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