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A Mutual Affair

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I'd like to introduce you to one of my favorite animals: the shrimp goby. These pretty little fish lead lives of enviable indolence. As their name suggests, they live with shrimp (often, a pair). The shrimp build and maintain a burrow, which the goby and shrimp live in together. Each shrimp works hard, shoveling sand out of the front entrance like a miniature bulldozer. As soon as it's delivered the rubble to a suitable distance, it shoots back into the burrow.

The front entrance of the burrow is often reinforced with bits of shell and coral — all of which is done by the shrimp. The goby just sits in the entrance of the burrow, keeping guard and warning the shrimp, which is nearly blind, of danger. At any sign of danger — a diver coming too close, a passing predator — the goby darts into the burrow. If the goby zooms in, the shrimp hastily retreats deep inside. And before the shrimp emerges from the burrow, it touches the goby's tail with its long antennae. To show it's safe to come out, the goby gently wiggles its tail. When the shrimp is out of the burrow, it keeps one antenna touching the goby. If the goby suddenly retreats, so does the shrimp.

These animals are dependent on each other. Remove the fish, and the shrimp stops burrowing; the shrimp forage while burrowing, so without a fish, they grow more slowly, too. The shrimp need their guard goby. And the guard goby needs its shrimp: deny the goby shelter in a burrow, and it will promptly be killed by predators (yes, someone did the experiment). The shrimp keep the goby clean, too: they groom it.

Close, beneficial associations between creatures of different species are nothing unusual. On the contrary, they are the very fabric of nature. The lichen you see on that old gravestone is a liaison between a fungus and an alga. The fungus provides shelter and a good growing environment — a kind of greenhouse — and the alga provides the fungus with food. The corals you're snorkeling over are colonies of animal-algal partnerships; again, the animals provide the shelter, the algae provide the food, and also help the coral animal to secrete its hard outer skeleton. In some associations, the algae generate as much as 98 percent of the colony's nutrients. And look in the mirror: your digestion is aided by the bacteria you are housing in your gut.

Peer at the undersides of the leaves of the riverbank grape, *Vitis riparia*, and you'll find tufts of hair at points along the veins; the tufts are shelters for mites (*Orthotydeus lambi*). The mites feed on grape powdery mildew (*Uncinula necator*), a parasitic fungus that otherwise grows into the grape plant and steals its nutrients, at great detriment to the plant. The mites keep the leaves clear of the fungus. (Interestingly, most commercial grape varieties don't have shelters for mites on their leaves, and they are home to few mites. Unsprayed, they also have a big problem with powdery mildew.)

Or take bobtail squid. These house luminous bacteria — around a trillion — in a special chamber, the light organ. The bacteria make light, thus providing the squid with counter-illumination — a way of disguising their silhouette and blending in with moonlight filtering through the water. As a result of the counterillumination, when a predator looks up, it doesn't see a dark blotch, but a faint silvery shadow, or perhaps nothing at all. The bacteria benefit, too: they grow faster inside the squid than they do in the open sea.

Or, or, or — I could sit here describing beneficial associations for days.

Yet despite their ubiquity, much about the evolution of beneficial associations — or mutualisms, as they are usually called — remains mysterious. There are several difficulties. The first is that the term covers a huge spectrum of phenomena. For instance, some mutualisms are extremely specific, involving the same sets of species. Bobtail squid, for example, are fussy about their bacteria; they have a strong preference for a particular strain.

Other mutualisms are less tightly linked. For instance, around 120 species of goby interact with just 30 species of shrimp. Although both fish and shrimp are attracted to each other — the fish by sight and the shrimp by smell — the attraction doesn't seem to be limited to a particular species. The same goes for corals and lichens: the animal that makes the coral can host a variety of algae; ditto, the fungi that form lichens.

Different mutualisms are also perpetuated in different ways. The leaf-cutting ants of central and south America farm a fungus; the ants depend on the fungus for food. If the fungus sickens and dies, the ant colony collapses. The ant-fungus is transmitted from colony to colony by successive generations of queens. It is, in other words, transmitted from mother to daughter, like a family heirloom. (Heirloom fungus, anyone?) The clam *Calyptogena magnifica*, which lives on deep-sea vents, depends on a bacterium to supply it with nutrients; the bacterium is transmitted through the clam's eggs. The same goes for our mitochondria — the remnants of bacteria that live in our cells and provide us with energy.

In contrast, baby bobtail squid get their bacteria from the environment; the association begins anew every generation. So, too, with shrimps and gobies: both spend their larval life floating about as plankton, so you don't have successive generations of animals living in the same burrows. Indeed, shrimps don't necessarily live with the same goby throughout their lives. A small goby may be evicted from a burrow by a bigger one, and in any case, some gobies leave their burrows during the mating season, and shack up temporarily with another for spawning.

On top of that, according to current evolutionary thought, mutualisms should be prone to evolutionary instability. The reason is that mutualisms depend on the continued cooperation of both parties. But cooperation is often fragile: an association that starts out being of mutual benefit can quickly evolve into one that is parasitic. This is especially true in situations where the evolutionary interests of the two parties are not tightly linked — such as when the mutualism is established anew in each generation. When the transmission of one party is dependent on the other — as in the clam — the association is expected to be more stable, because harm to one partner is harm to both.

But some of these associations may have evolved to be more stable than they appear. Consider soybeans. These — like other legumes — have bacteria living in nodules on their roots. The bacteria supply the plant with nitrogen, and receive nutrients from the plant in return. Why don't the bacteria cheat, and collect nutrients without doing any "work"? Because soybeans punish non-cooperators: apparently, they deny oxygen to nodules that fail to produce nitrogen. In a similar fashion, some species of sea anemone evict algae that divide too fast and thus threaten to overrun their anemone host.

Given the difficulties of sustaining mutualisms, why do they evolve? Why don't grapes evolve a fungicide, or bobtail squid evolve to make their own light? I think the answer is that mutualisms, for all their imperfections, are easier. Evolving an association with another organism gives access to a whole other genome, a whole new set of capacities and capabilities that have already been tested by evolution. It's faster and more powerful than going it alone.

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NOTES:

Details of the shrimp-goby mutualism differ a little bit depending on which species are involved: in the Atlantic Ocean, the relationships between shrimp and goby can be more flexible. I have based my account on Karplus, I. 1972. "Associative behavior of the fish Cryptocentrus cryptocentrus (Gobiidae) and the pistol shrimp Alpheus djiboutensis (Alpheidae) in artificial burrows." Marine Biology 15: 95-104; this paper describes the shrimp maintaining antennal contact, the fish wagging its tail to give the "all-clear," and the shrimp cleaning the fish. For shrimp growing more slowly in the absence of gobies, and for gobies evicting each other, see Thompson, A. R. 2005. "Dynamics of demographically open mutualists: immigration, intraspecific competition, and predation impact goby populations." Oecologia 143: 61-69. For the mating behavior of gobies, as well as most other details of the association, see the definitive paper by Karplus, I. 1987. "The association between gobiid fishes and burrowing alpheid shrimps." Oceanography and Marine Biology 25: 507-562.

For riverbank grapes, mites, and powdery mildews, see Norton, A. P., English-Loeb, G., Gadoury, D. and Seem, R. C. 2000. "Mycophagous mites and foliar pathogens: leaf domatia mediate tritrophic interactions in grapes." Ecology 81: 490-499.
For counter-illumination in bobtail squid, see Jones, B. W. and Nishiguchi, M. K. 2004. "Counterillumination in the Hawaiian bobtail squid, Euprymna scolopes Berry (Mollusca: Cephalopoda)." Marine Biology 144: 1151-1155. For the specificity of squid and bacteria, see Nishiguchi, M. K. 2002. "Host-symbiont recognition in the environmentally transmitted sepiolid squid-vibrio mutualism." Microbial Ecology 44: 10-18.

For the flexibility of lichen associations, see Piercey-Normore, M. D. and DePriest, P. T. 2001.

“Algal switching among lichen symbioses.” American Journal of Botany 88: 1490-1498. For corals, see Baker, A. C. 2003. “Flexibility and specificity in coral-algal symbiosis: diversity, ecology, and biogeography of Symbiodinium.” Annual Review of Ecology and Systematics 34: 661-689.

For transmission of the ant-fungus, as well as a discussion of fascinating aspects of the mutualism I didn’t have space to mention here, see Currie, C. R. 2001. “A community of ants, fungi, and bacteria: a multilateral approach to studying symbiosis.” Annual Review of Microbiology 55: 357-380. For vertical transmission of clam bacteria, see Hurtado, L. A., Mateos, M., Lutz, R. A. and Vrijenhoek, R. C. 2003. “Coupling of bacterial endosymbiont and host mitochondrial genomes in the hydrothermal vent clam Calyptogena magnifica.” Applied and Environmental Microbiology 69: 2058-2064.

Mutualisms and their stability (or lack of) have been written about extensively; see, for example, Herre, E. A., Knowlton, N., Mueller, U. G. and Rehner, S. A. 1999. “The evolution of mutualisms: exploring the paths between conflict and cooperation.” Trends in Ecology and Evolution 14: 49-53; and Sachs, J. L. and Simms, E. L. 2006. “Pathways to mutualism breakdown.” Trends in Ecology and Evolution 21: 585-592.

For punitive soybeans, see Kiers, E. T., Rousseau, R. A., West, S. A. and Denison, R. F. 2003. “Host sanctions and the legume-rhizobium mutualism.” Nature 425: 78-81. For sea anemones expelling algae, see Baghdasarian, G. and Muscatine, L. 2000. “Preferential expulsion of dividing algal cells as a mechanism for regulating algal-cnidarian symbiosis.” Biological Bulletin 199: 278-286. For a whacky discussion of the advantages of acquiring genomes, see Margulis, L. and Sagan, D. 2002. “Acquiring Genomes: A Theory of the Origins of Species.” Basic Books.

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