bital behavior comes from experiments by my (R.F.D.)'s group, led by former students Toby Kiers and Ryoko Oono. Comparing soybean and alfalfa root nodules in normal air to nodules on the same plant in an atmosphere with only traces of nitrogen, we found that rhizobia reproduced less frequently when they could only fix enough nitrogen for their own needs, with no surplus for the plant. Soybean plants reduced oxygen supply to rhizobia that didn’t supply them with nitrogen. This presumably limits rhizobial metabolism so they waste fewer plant resources and may also explain their decreased reproduction. Similarly, plants supplied less energy to mycorrhizal fungi that provided them with less phosphorus. Without such sanctions by the plant host, strains that diverted resources to their own reproduction would displace more-cooperative strains over the course of evolution.

Some hosts manipulate their partners in ways that enhance current cooperation. Alfalfa and some other legume species cause rhizobia in their root nodules to swell to two or more times their usual size. Swollen rhizobia can no longer reproduce, but we (Oono and R.F.D.) found that they fix more nitrogen, relative to their cost to the plant. Similarly, researchers in Mexico and Germany found that Acacia cornigera trees protected by Pseudomonas fumigatus ants manipulate the ants to keep them loyal. The nectar they give the ants contains chemicals that prevent the ants from digesting nectar from other plants. Individual ants apparently learn to stay on their host plant. This sort of manipulation can ensure that partners continue to cooperate with their current hosts. But cooperation based on manipulation may lapse when ever manipulation does, and thus does not necessarily favor evolution of cooperation over generations. Among related individuals, kin selection favors cooperation with related individuals that are likely to also carry the same genes for cooperation. These mechanisms for enhancing cooperation are not always foolproof, however.

Obligatory cooperation

Another way to reduce cheating in interspecies relationships is to increase mutual dependence. When symbionts lose genes needed for survival outside their host, they cannot escape and may evolve to be even more beneficial, especially if their next host is their current host’s offspring.

Aphids, for example, rely on symbiotic bacteria contained in specialized cells for essential amino acids lacking in their diet of sugary plant sap. In return, bacteria gain access to their host’s offspring by entering aphid egg cells, being ingested by the offspring, or other mechanisms of transmission. Such symbiont inheritance, known as vertical transmission, means that bacterial strains benefit from helping their host lay as many eggs as possible. Thus, the most beneficial symbionts become the most frequent in the host population. Even in these systems, however, cheating can arise. When a host carries different strains or species of vertically transmitted bacteria, they may compete with each other to reach the host’s offspring. The winners in such within-host competitions will not necessarily be those that are most beneficial to

MAINTAINING COOPERATION

For cooperation between species to withstand the inherently selfish nature of evolution, individuals that fail to cooperate must have fewer descendants than cooperators, on average. This could result from fitness-reducing sanctions against cheaters or strict dependence of each partner on the other for survival. Partners may also manipulate each other in ways that enhance cooperation in the short term, without necessarily favoring evolution of cooperation over generations. Among related individuals, kin selection favors cooperation with related individuals that are likely to also carry the same genes for cooperation. These mechanisms for enhancing cooperation are not always foolproof, however.

Sanctions:
Pseudopcapa pinapes wasps that pollinate Ficus sycomorus fig trees also eat some of their seeds. Unpollinated figs make few seeds, limiting wasp reproduction and favoring the evolution of more-cooperative wasps. However, field experiments showed that nonpollinating wasp “free-loaders” can escape such sanctions if another wasp pollinates their fig.

> Maintenance of cooperation depends on the presence of sanctions that ensure the costs to the plant. The winners in such within-host competitions will not necessarily be those that are most beneficial to

> Obligatory cooperation: Another way to reduce cheating in interspecies relationships is to increase mutual dependence. When symbionts lose genes needed for survival outside their host, they cannot escape and may evolve to be even more beneficial, especially if their next host is their current host’s offspring.

> Mutual dependence: Aphids rely on the maternally transmitted bacteria Buchnera for the amino acids lacking in their diet. Over time, these Buchnera have lost the genes they need to live outside of aphids and have become dependent on their host. In the aphid genus Aphis, aphidicola has lost so many genes that it cannot produce all the nutrients its host needs, which are fulfilled by another bacteria species (Candidatus Serratia symbiotica), which is less dependent on aphid hosts and may replace B. aphidicola entirely.

> Kin selection: Aphis mellifera honeybee queens have a near-monopoly on reproduction. Fewer than 0.1 percent of workers lay unfertilized eggs, which would develop into males, and these are usually eaten by other workers, who are more related to their sisters (the queen’s daughters) than to their sisters’ sons. This policing has been undermined by a mutant strain whose workers lay policing-resistant eggs, causing problems for beekeepers in South Africa.

> Manipulation: Pseudomonas fumigatus ants manipulate Acacia cornigera trees from diverse biological threats, and the trees have a way of manipulating the ants to remain loyal. Their nectar contains chemicals that prevent the ants from digesting nectar from other plants, such that individual ants learn to stay on their host plant.