

MAINTAINING COOPERATION

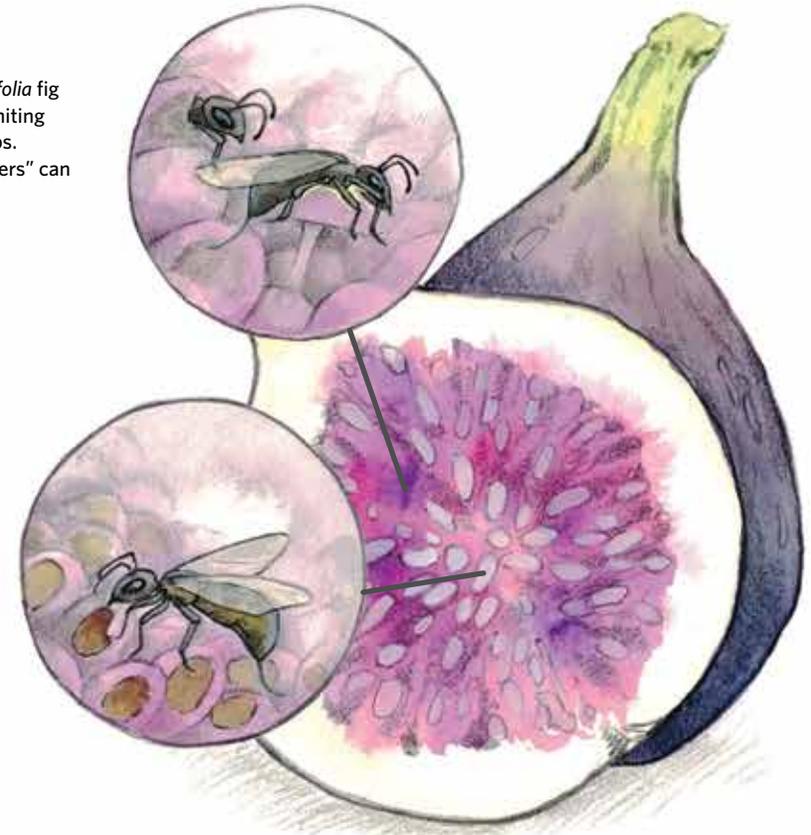
For cooperation between species to withstand the inherently selfish nature of evolution, individuals that fail to cooperate must have fewer descendants than cooperators, on average. This could result from fitness-reducing sanctions against cheaters or strict dependence of each partner on the other for 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.



⚡ **MANIPULATION:** *Pseudomyrmex ferrugineus* ants protect *Acacia cornigera* trees from diverse biological threats, and the trees have ways 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.¹

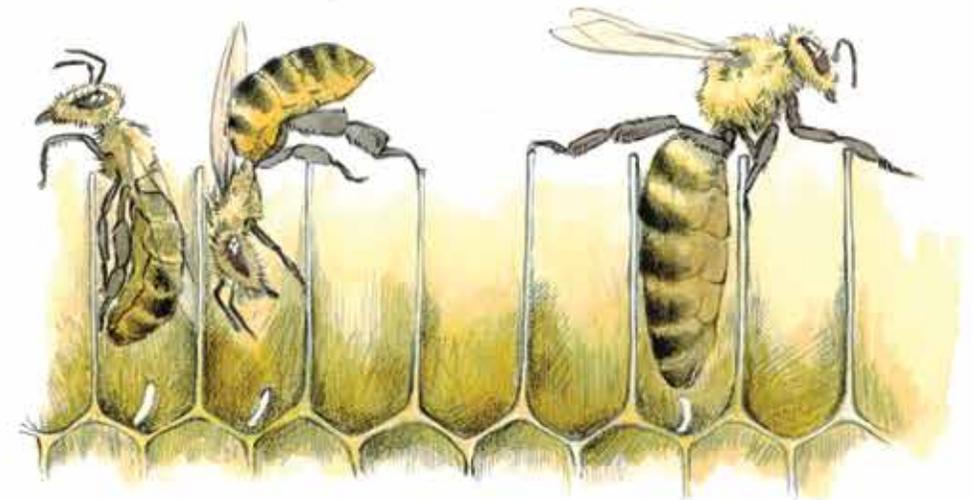


» **SANCTIONS:** *Pegoscapus piceipes* wasps that pollinate *Ficus nymphaeifolia* fig trees also eat some of their seeds. Unpollinated figs make few seeds, limiting wasp reproduction and favoring the evolution of more-cooperative wasps. However, field experiments showed that nonpollinating wasp “free-loaders” can escape such sanctions if another wasp pollinates their fig.²



« **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 *Cinara cedri*, *B. 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.³

» **KIN SELECTION:** *Apis 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.⁴



1. M. Heil et al., “Partner manipulation stabilises a horizontally transmitted mutualism,” *Ecol Lett*, 17:185-92, 2014.
2. K.C. Jandér et al., “Precision of host sanctions in the fig tree/fig wasp mutualism: consequences for uncooperative symbionts,” *Ecol Lett*, 15:1362-69, 2012.
3. V. Pérez-Brocal et al., “A small microbial genome: the end of a long symbiotic relationship?” *Science*, 314:312-13, 2006.
4. K.J. Loope, “Queen killing is linked to high worker-worker relatedness in a social wasp,” *Curr Biol*, 25:2976-79, 2015.