

Mutualism and cheating in a Peruvian ant-plant symbiosis

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Abstract

Mutualisms are evolutionarily unstable, and a key question is how they persist in the face of cheating by symbionts or infiltration by parasites. Using the ant-plant *Cordia nodosa* and its principal, protecting symbionts *Allomerus octoarticulatus* and *Azteca* spp., I investigate the mechanism of mutualism reassembly, the mechanisms which prevent cheating, and the mechanisms which determine whether *Allomerus* is a castration parasite or a non-castrating mutualist.

During horizontal transmission, ant-plants and their symbionts disperse separately as seeds and winged alates. Using Y-tube olfactometry, I show that both *Allomerus* and *Azteca* queens distinguish between the volatiles of their host plant saplings and other commonly occurring plants, which suggests that dispersing alates use host plant volatiles to locate saplings during mutualism reassembly.

I review the roles that sensory traps, signal mimics that elicit out-of-context behaviours, could play in the origin and maintenance of mutualisms, and suggest four roles: assembly, error reduction, enforcement, and cost reduction. I test for a possible sensory trap which might elicit protection of new leaves: new shoots emit volatile chemicals that mimic ant brood, thus attracting ant workers. Using a petri-dish bioassay protocol, I test the preferences of two putative castes, new leaf patrolling and brood-tending nursing workers, to hexane extracts of new leaves and brood. Under the sensory trap hypothesis, we would expect nurses to be 'fooled' into patrolling new leaves. However, patrollers respond more positively to new leaf than to brood extracts, whereas nurses respond more positively to brood than to new leaf extracts. I also identify size differences between the castes. Thus, the presence of behaviourally and morphologically distinct castes is not consistent with the brood-mimicking sensory trap hypothesis.

I test the host sanctions hypothesis i.e., that the host is able to impose a cost at the site of exploitation. Specifically, I experimentally simulated leaf herbivory on developing shoots (i.e., making the ant cheat) and measured the effect on domatia growth. Simulated herbivory reveals reduced survival and growth of the attached domatia, supporting the host sanctions hypothesis. Using these data, I calculate that there is a net fecundity benefit of domatia growth which suggests that the host sanction mechanism selects for ants to continue to patrol new leaves.

Allomerus is a castration parasite, destroying the floral buds and flowers of its host plant, preventing fruiting. At one site *Allomerus* reveals variation in castration, from most plants being castrated to a few plants that are not castrated. I found that this variation in castration can be partially explained by *Cordia nodosa* 'hiding' its floral buds on new shoots, which exploits the poor castration ability of patrollers. On a geographical scale, however, I did not find a similar pattern of castration; at several other sites *Allomerus* is a completely castrating parasite. I finish by suggesting that variation in castration has evolved as a vertically transmitted kin selected benefit, in response to a sapling bottleneck.

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