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Ant and human farmers face similar problems

Ants of the tribe Attini discovered agriculture 50 million years before humans (Mueller *et al* 1998). Today, nearly 200 species in 12 genera of these ants cultivate fungus gardens in the Nearctic and Neotropical regions; in the Palaeotropics, this niche is occupied by fungus-growing termites. It is believed that the act of fungus cultivation evolved just once in the attines (Wilson 1971). The primitive attines cultivate fungus on insect frass and decaying vegetation while the advanced attines are the eponymous leaf-cutting ants. These ants carefully select leaves from species that are low in fungistatic compounds, such as phenolics, carry them to underground nests where they are masticated, and plant them in soil along with fungal mycelia and glandular secretions containing proteolytic enzymes. Obligate fungal symbionts break down structural carbohydrates in the leaves and produce nutritive protruberances called gongylidia from their hyphae. The ants consume these gongylidia and also feed them to their larvae. They also prevent the fungi from forming fruiting bodies or sporophores; consequently, the fungus is clonally propagated. In the advanced attines, the queen tucks a pellet of the mutualistic fungal mycelia into her infrabuccal pouch before her nuptial flight, and then uses this fungal innoculum to seed a new fungus garden in the new colony.

Until recently, it was believed that the ants were capable of maintaining axenic gardens; that is, they were able to weed out all non-mutualistic fungi and keep the garden free of microbial pathogens and parasites. Phenylacetic acid and *b*-hydroxydecenoic acid (myrmicacin) produced by the metapleural glands of the ants have antibiotic activity which possibly aids in this process. Recently, fungus gardens were found to contain antibiotic-producing bacteria of the genus *Streptomyces*, which like the mutualistic fungus innoculum, are also transmitted vertically from colony to colony (Currie *et al* 1999b). This may lead one to suppose that the ants have the problem of pathogens and parasites well under control. However, the highly virulent microfungus *Escovopsis* (Ascomycota) can devastate fungus gardens. In a study of this phenomenon in Costa Rica, Currie *et al* (1999a) found that *Escovopsis* is more prevalent in gardens of the derived ant lineages than in those of the primitive ones. Furthermore, the fungal symbionts of the derived ant lineages, such as of the ant genus *Atta* (the classical leaf-cutter), appear to be clones of ancient asexual fungal cultivars that have co-evolved with their partners, while those of the primitive attines appear to have been domesticated relatively recently from free-living sexual stocks (Chapela *et al* 1994). Cladistic analysis based on nuclear 28S ribosomal DNA has shown that, in contrast to the monophyletic origin of the attines, their symbiotic fungi are polyphyletic (Chapela *et al* 1994). Only in *Trachymyrmex*, *Acromyrmex* and *Atta* (all three higher attines) and in *Cyphomyrmex*, which is transitional between the higher and lower attines, does the queen carry a fungal innoculum to a new nest. Amplified fragment length polymorphism (AFLP) fingerprints have shown that some cultivars grown by different ant species are genetically identical and are asexual descendants of the same clone (Mueller *et al* 1998).

Clonal propagation of asexual cultivars apparently makes the fungus gardens of the derived attines vulnerable to the pathogenic *Escovopsis* while the fungus gardens of the basal attines are more resistant to such attacks. The Red Queen at work again (Currie *et al* 1999a; Wilkinson 2000)? The Red Queen hypothesis for the evolution of sex invokes the 'arms race' between host and parasite as an explanation for the prevalence of sex despite its two-fold cost relative to asexual reproduction (Jaenike 1978; Hamilton 1980). Villesen *et al* (1999) have brought in a new angle into the ant-fungus and Red Queen story. They note that queens of the higher attines exhibit the highest levels of multiple matings among ants (up to ten mates per queen) while those of the basal attines are usually singly mated. They claim that selection for multiple matings, which would increase the genetic heterogeneity of the nest mates, is

critical in the social system of the leaf-cutters, which have large, long-lived colonies, and are under severe pressure from pathogens.

There is obviously still much to be learned about the interaction between sex, non-sex and pathogens in this mutualistic interaction between ant and fungus. Although ants were farmers much before us, their problems are the same as ours. Monocultures and a low genetic diversity of cultivars also leaves our agriculture vulnerable to attack. Even after 50 million years, ant farmers are not always ahead of the game.

References

Chapela I H, Rehner S A, Schultz T R and Mueller U G 1994 Evolutionary history of the symbiosis between fungus-growing ants and their fungi; *Science* **266** 1691–1694

Currie C R, Mueller U G and Malloch D 1999a The agricultural pathology of ant fungus gardens; *Proc. Natl. Acad. Sci. USA* **96** 7998–8002

Currie C R, Scott J A, Summerbell R C and Malloch D 1999b Fungus-growing ants use antibiotic-producing bacteria to control parasites; *Nature* (*London*) **398** 701–704

Hamilton W D 1980 Sex versus non-sex versus parasite; *Oikos* **35** 282–290

Jaenike J 1978 An hypothesis to account for the maintenance of sex within populations; *Evol. Theor.* **3** 191–194

Mueller U G, Rehner S A and Schultz T R 1998 The evolution of agriculture in ants; *Science* **281** 2034–2038

Villesen P, Gertsch P J, Frydenberg J, Mueller U G and Boomsma J J 1999 Evolutionary transition from single to multiple mating in fungus-growing ants; *Mol. Ecol*. **8** 1819–1825

Wilkinson D M 2000 Running with the Red Queen: reflections on 'Sex versus non-sex versus parasite'; *Oikos* **91** 589–596

Wilson E O 1971 *The insect societies* (Cambridge, Massachusetts: Belknap Press of Harvard University Press)

RENEE M BORGES
Centre for Ecological Sciences,
Indian Institute of Science,
Bangalore 560 012, India
(Email, renee@ces.iisc.ernet.in)