SHORT COMMUNICATION

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Garden sharing and garden stealing in fungus-growing ants

Abstract Fungi cultivated by fungus-growing ants (Attini: Formicidae) are passed on between generations by transfer from maternal to offspring nest (vertical transmission within ant species). However, recent phylogenetic analyses revealed that cultivars are occasionally also transferred between attine species. The reasons for such lateral cultivar transfers are unknown. To investigate whether garden loss may induce ants to obtain a replacement cultivar from a neighboring colony (lateral cultivar transfer), pairs of queenright colonies of two *Cyphomyrmex* species were set up in two conjoined chambers; the garden of one colony was then removed to simulate the total crop loss that occurs naturally when pathogens devastate gardens. Garden-deprived colonies regained cultivars through one of three mechanisms: joining of a neighboring colony and cooperation in a common garden; stealing of a neighbor's garden; or aggressive usurpation of a neighbor's garden. Because pathogens frequently devastate attine gardens under natural conditions, garden joining, stealing and usurpation emerge as critical behavioral adaptations to survive garden catastrophes.

Introduction

All of the over 200 known species of fungus-growing ants (Attini: Formicidae: Hymenoptera) are obligately dependent on the cultivation of fungus for nourishment. The ants optimize fungal growth through complex manuring schemes and control garden pathogens through secretion of antibiotic "herbicides" (Weber 1972; Currie et al. 1999a). Paralleling the history of human agriculture (Cowan and Watson 1992; Diamond 1997), attine ants domesticated multiple fungal cultivars during their evolution and transfer these cultivars between ant species (Mueller et al. 1998; Diamond 1998). Phylogenetic analyses of both ants and associated fungi (Mueller et al. 1998) indicate that cultivar transfers among attine farmers occur relatively frequently over evolutionary time, suggesting that the history of ant fungiculture may have been characterized by the same lateral spread of cultivars that shaped the history of human agriculture (Diamond 1997).

The ecological causes and behavioral mechanisms underlying cultivar transfers among attine ants are unknown. We hypothesized previously (Mueller et al. 1998) that transfers may occur (1) accidentally (e.g., gardens from neighboring nests are simultaneously disturbed and mixed), or (2) after garden loss due to garden pathogens (Currie et al. 1999b), forcing ants to obtain a replacement cultivar from a neighboring colony. We describe behavioral experiments with two species of *Cyphomyrmex* ants that provide support for the second mechanism. Garden loss triggers one of three responses in attine farmers: joining a neighboring colony and cooperation in a common garden, stealing of a fungal starter for a replacement garden, or aggressive raiding and usurpation of a neighbor's garden.

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Materials and methods

Live colonies of the two sympatric sister species *Cyphomyrmex longiscapus* and the undescribed *Cyphomyrmex* sp.nov. (T.R. Schultz et al., in preparation) were collected in September and October 1999 at Pipeline Road (km 6) in Soberanía Park, Republic of Panama, following the methods of Mueller and Wcislo (1998), and tested in November 1999 at the University of Texas at Austin. Ant vouchers are deposited at the Museum of Natural History, Smithsonian Institution, Washington D.C., under collection numbers RMMA990914 to RMMA991002. Each of the two sympatric sibling species cultivates a distinct fungus, and these

two fungi are distantly related to each other (Mueller et al. 1998).

Pairs of queenright colonies were set up in two chambers (3.5 cm diameter; bottom filled with moistened plaster of Paris to generate an environment of high humidity) of a Nunc Multidish 6 tissue culture plate. Each nest chamber was connected via a small (3 mm i.d.) tube to a dry foraging chamber (also 3.5 cm diameter) where forage was provided ad libitum as substrate for the gardens. The two foraging chambers were connected to each other via another small tube that was kept plugged initially to prevent contact of the two colonies during habituation to the experimental chambers.

Experiments paired either two Cyphomyrmex sp.nov. colonies (nov/nov; $n=7$ trials), two C. longiscapus colonies (long/long; $n=9$), or one from each of the two ant species (nov/long; $n=8$), with respective workforces adjusted to ten versus five workers. These workforces are typical of relatively young colonies (natural colony size averages 24 workers; Mueller and Wcislo 1998), and such small colonies are most vulnerable to garden loss (Weber 1972; Currie et al. 1999b). All workers and queens were marked with a dab of acrylic paint on the mesosoma to identify colony members during observations. Colonies were allowed to habituate for 5 days, after which the plug between the two foraging chambers was opened. The garden was then removed from the larger colony (ten workers) within each pair to simulate the kind of total crop loss that occurs naturally when pathogens devastate entire gardens in the field (Currie et al. 1999b), or when Megalomyrmex parasite ants evict Cyphomyrmex colonies from their gardens (R.M.M. Adams et al., in press). In the between-species pairs, the larger colony experiencing garden loss was always Cyphomyrmex sp.nov., because pilot experiments had revealed that Cyphomyrmex sp.nov. ants would readily accept gardens of C. longiscapus, but not vice versa. Behavioral outcomes and worker mortalities (percentage of workers dead) were scored at the end of the experiment after 17 days of daily observation.

Results and discussion

In 100% (nov/nov) and 78% (long/long) of the within-species pairs, but in only 25% (nov/long) of the between-species pairs, the garden-deprived colony re-

gained a garden through either (1) joining the neighboring colony and cooperation in a common garden; (2) stealing parts of the neighbor's garden as a starter for a new garden; or (3) overpowering the neighboring colony and usurping their garden (Table 1). In the remaining cases, the ants from the different colonies were intolerant of each other, fought violently, and the garden-deprived colony did not succeed at regaining a fungal cultivar. Average worker mortality was significantly higher in the between-species pairs (69% worker mortality for nov/long) than in the two within-species pairs (29% and 30% mortalities for nov/nov and long/long, respectively; $F=6.8$, $df=2$, $P=0.0052$; ANOVA of arcsine-transformed percentages), suggesting that greater intraspecific tolerance may have contributed to the observed greater likelihood of within-species cultivar transfers.

In the intraspecific pairings, most garden-deprived colonies moved into the neighboring nest and attempted to join or usurp the neighboring colony (Table 1). In 73% of these joining and usurpation attempts, the resident ants executed the invading queen, yet the nonresident workers remained with their neighbors and helped tend their garden. In one intraspecific case the garden-deprived workers stole the entire neighboring garden, then both colonies cohabited in a common garden, but both queens died eventually.

In six of the eight interspecies pairs, workers from the two colonies showed mutual intolerance that prevented any fungal transfer, but the two remaining cases were interesting: in one case, colonies fused and the two queens coexisted in the common garden for 36 days, at which point the host queen died, completing the takeover; in the other case, the garden-deprived workers stole the entire neighboring garden, carried it

Table 1 Cultivar transfers between Cyphomyrmex colonies after garden loss. Queenright colonies from two sibling species, C. longiscapus (long) and the undescribed Cyphomyrmex sp.nov. (nov), were paired in all combinations (long/long, nov/nov, nov/long) with respective workforces adjusted to ten versus five work- ers. The garden was removed from the larger colony to simulate pathogen-driven garden devastation as it occurs under natural conditions (Currie et al. 1999a, b). Cultivar transfers were scored after 17 days of daily observation

Mode of cultivar transfer		Intraspecific pairs		Interspecific pairs
		long/long ($n=9$)	nov/nov ($n=7$)	nov/long ($n=8$)
Colony fusion	Both queens coexist[a]	0%	0%	12.5% ($n=1$)
	Both queens dead[b]	0%	28.5% ($n=2$)	0%
Garden stealing[c]		11% ($n=1$)	0%	12.5% ($n=1$)
Usurpation	Attempted[d]	56% ($n=5$)	43% ($n=3$)	0%
	Successful[e]	11% ($n=1$)	28.5% ($n=2$)	0%
No cultivar transfer[f]		22% ($n=2$)	0%	75% ($n=6$)

[a] Workers and the queen from the garden-deprived colony move into the neighboring nest and cooperate with their neighbors in a common garden
[b] Workers and the queen from the garden-deprived colony move into the neighboring nest, but both resident and nonresident queens die, while workers from both nests continue to cooperate in a common garden
[c] Workers from the garden-deprived colony steal part of the garden from the neighboring colony and use it as a starter for a replacement garden in their original nest chamber

[d] Workers and the queen from the garden-deprived colony attempt to move into their neighbor's garden, but the nonresident queen and some of her workers are killed in the attempt, while the resident queen survives with some of her workers
[e] Nonresident workers move into the neighbor's garden, the resident queen and her workers are killed during garden usurpation, but the nonresident queen survives
[f] Nonresident ants are gradually killed one by one, the nonresident queen dies too or remains alive in the original garden chamber without reacquiring a cultivar

to their chamber, and successfully defended it against their neighbors.

Overall, 22% (long/long), 28.5% (nov/nov), and 25% (nov/long) (Table 1) of the garden-deprived colonies retained their queen *and* switched to a novel cultivar that they obtained from their neighbors. In the interspecific cases, the colonies switched to a distantly related cultivar (see above and Mueller et al. 1998). Virgin queens produced by such "switched" colonies would now take an inoculum of the novel cultivar when leaving their natal nests to found their own nests, thus passing on this cultivar to their descendents. Lateral cultivar transfer thus punctuated the more typical pattern of vertical cultivar transmissions within ant lineages (von Ihering 1898; Weber 1972; Mueller et al. 1998).

Because different attine species and genera may nest within a few cm of each other under natural conditions (Weber 1972; Mueller and Wcislo 1998; U.G. Mueller, unpublished), garden loss followed by exchanges between neighboring colonies may well be a general mechanism of cultivar transfers among other attine species. Documenting such events under natural conditions for the generally inconspicuous attine species is difficult; indeed, to our knowledge there exist no field records of fungal transfers that were triggered by garden loss. However, intraspecific raiding of small incipient colonies by large established colonies involving between-nest transfer of brood and fungal gardens has been observed in the well-studied leafcutter *Atta sexdens rubropilosa* (Autuori 1950), and similar intraspecific garden and brood raiding occurs regularly between incipient colonies of the leafcutter *Acromyrmex versicolor* (Rissing et al. 1989). Low levels of intraspecific brood raiding were also implicated in a DNA-fingerprinting analysis of the leafcutter *Atta colombica* (Fjerdingstad et al. 1998). No study has documented raiding *between* attine species or genera under natural conditions, but such events may well have escaped observation, especially for the cryptic and largely unstudied non-leafcutter species. Future fieldwork therefore should test the hypothesis of pathogen-driven cultivar transfers in the field through direct observation or experimentation with pathogens.

Pathogens frequently devastate attine gardens under natural conditions (Currie et al. 1999a, b), and garden usurpation and colony joining thus emerge as critical behavioral adaptations for coping with garden loss. These behaviors have obvious parallels in human agricultural societies. For example, dependence on productive gardens can trigger temporary joining of Yanomanö Indian villages after garden loss due to flooding (Chagnon 1997), and there exist numerous historical cases for other agriculturists where crop loss induced cultivar transfers through crop sharing, dispersal, or territorial expansion (Crosby 1994; Cavalli-Sforza and Cavalli-Sforza 1995). Indeed, much of human agricultural evolution and the fate of entire human societies appear to have been decided by a delicate balance between sharing, redistribution, and belligerent acquisition of agricultural resources (Diamond 1997). Crop sharing and aggressive crop appropriation thus appear as convergent behaviors in both ant and human farmers.

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