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Interference competition between ants (Hymenoptera: Formicidae) in Amazonian clearings

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Resumen. *El primer caso en Sud América de competencia por interferencia debido al llenado del orificio del nido con partículas de suelo es documentado para* Ectatomma quadridens *y* Pheidole fallax *en claros de bosques amazónicos. Las obreras de* E. quadridens*, activas sólo durante el día, llegan a los nidos de* P. fallax *al amanecer, y comienzan a llenar los orificios del nido con partículas de suelo. Durante el día, obreras de* E. quadridens *quedan encima del nido como guardas, y vuelvan a llenar con suelo los orificios si éstos comienzan a abrirse. Colonias de* P. fallax *distantes de nidos de* E. quadridens *están activas durante todo el día, pero colonias próximas están limitadas a una actividad nocturna. Este patrón no fue visto a distancias mayores del lugar donde se depositaban desechos alimenticios, de acuerdo a la predicción que postula que la concentración del recurso es importante en la organización de la competencia por interferencia. Próximo a los restos alimenticios y nidos de* E. quadridens*, las colonias de* P. fallax *solamente consigueron 60% de los recursos de colonias de* P. fallax *que estuvieron activas durante todo el día.*

Abstract. *The first case of interference competition through soil dumping in South America is documented between* Ectatomma quadridens *and* Pheidole fallax *in Atnazonian forest clearings. Workers of the diurnaly active* E. quadridens *arrive at nests of* P. fallax *at dawn, and begin to fill up nest entrances with soil. During the day,* E. quadridens *workers remain stationary on the closed nest of* P. fallax*, and fill soil at the first signs of nest openings. Colonies bf* P. fallax *distant from* E. quadridens *nests are active for 24 hrs, while those near E. quadridens nests are limited to foraging nocturnally after opening nest entrances. This pattern was not found between heterospecific colonies at greater distances from the camp middett, according with the prediction that interference competition is more probable as resources become more concentrated. Colonies of* P. fallax *near* E. quadridens *nests located near the camp middett were calculated to have net forage intake of 60% of those located in areas without* E. quadridens.

Introduction

Interference competition is quite common among ants (Holldobler 1986, Holldobler and Wilson 1990. Fowler et al. 1991). Interference competition is hypothesized to become more prevalent with increased concentration of resources (Osier and Wilson 1978). As distances between nests of potential competitors decrease, interference competition which is not evidenced in the absence of concentrated resources is marked with decreasing distances to concentrated resources (Osier and Wilson 1978). Among the most obvious, yet rarely reported, forms of interference competition are soil or stone dumping in the nest entrances of potential heterospecific competitors (Moglich and Alpert 1979, Holldobler 1982, Gordon 1988), and the complete covering of smaller nests through the expansion of nest *tumuli* by larger colonies (Samways 1982, 1983). All documented cases of soil dumping have been from semi-arid regions of North America and Australia, and all involve species pairs from different genera, and, with the exception of Gordon (1988), species pairs are from different subfamilies. Whether the rarity or this behavior is due to lack of studies, or is indeed rare, is at present impossible to ascertain. However, I present evidence for interference competition by soil

dumping in clearings of the Amazon Basin and show that this phenomenon is not limited to arid and semi-arid zone ants. Furthermore, I show a significant depression of foraging activity associated with soil-dumping.

Materials and Methods

Study site

Observations and experiments were carried out in a clearing used as a campsite (Colosso) of a forest reserve approximately 70 km north of Manaus, Amazonas, Brazil (2° 25'S, 59° 48'W). The area is principally *terra firme* forest, with average annual precipitation of 2100 mm, varying seasonally between a rainy period from November through May, and a dry period from June through October (Ribeiro 1976). The 1000 m^2 campsite was cleared of all but ruderal vegetation and a limited number of fruit trees used by project personnel. Studies were conducted in December 1991 (rainy season).

The ant species

The most abundant ant species present at the campsite were *Ectatomma quadrideus* (Fabr.) (Ponerinae) and *Pheidole fallax* Mayr (Myrmicinae), both of which actively foraged on the kitchen middens as well as upon abundant termites (*Nasutitermes* sp.). In previous years, preliminary observations had indicated that *E. quadridens* dumped soil in the characteristic nest entrances of *P. fallax,* and that *E. quadrideus* workers were regularly seen inmobile upon closed *P. fallax* nests. Both species have been described as characteristic of forest clearings and degraded lands in the Amazon (Kempf 1961), and both species are relatively uncommon within the forest. *E. quadrideus is* a relatively large ant (2 mm long) with moderate sized colonies (Overal 1986), while the major workers of *P. fallax* are less than half this size, although colonies are large and the proportion of soldiers in the colonies is on the estimated order of 10-20%, based upon foraging groups.

Measurements

All nests of both species within the 1000 m^2 campsite were mapped. Nests of *P. fallax* have only one characteristic narrow, sinuous and long entrance. Nests of *E. quadrideus* often have 3 to 4 nest entrances within a 2 m radius. For nests of *P. fallax* plugged by workers of *E. quadrideus,* the distance between the two nests was measured, and frequent observations were taken on the activity and behavior of both species. Distances between active *P. fallax* nests and the closest *E. quadrideus* nests were also taken to determine if proximity affected nest plugging. Additionally, distances from the camp midden pile were used to examine the effect of resource concentration on nest plugging. Because previous observations indicated that *E. quadridens* workers forage a mean of 12 m from the nest, data were grouped into less than or equal to 12 m and more than 12 m, both between neighboring nests and with respect to the camp midden to permit comparisons. Daily foraging activities of both species were taken for 3 *P. fallax* nests plugged by *E. quadridens* and for 3 nests not plugged, as well as for nests of *E. quadrideus.* Assessment was based on the number of entering or departing workers at 2 min hourly intervals throughout a 24 hr period. Workers of *E. quadridens* were individually removed as they arrived at one nest of *P. fallax* which had been plugged daily. The *P. fallax* colony activity pattern associated with removal of *E. quadrideus* workers was compared with that of the previous day using 2 min counts every 30 min.

Table 1. Distribution and fate of nests of *Pheidole fallax* with respect to position from midden pile and *Ectatomma quadridens* nests (n=9). Also given is a proportional z test for frequencies found open and closed with respect to distance from the midden pile.

		Distance (m) from midden pile			
		<12		>12	
		open	closed	open	closed
Distance (m) from *E. quadridens* nest	<12	0	4	3	0
	>12	1	0	3	0
Totals		1	4	6	0
z		1.677		3.646	
P		0.0468		0.0003	

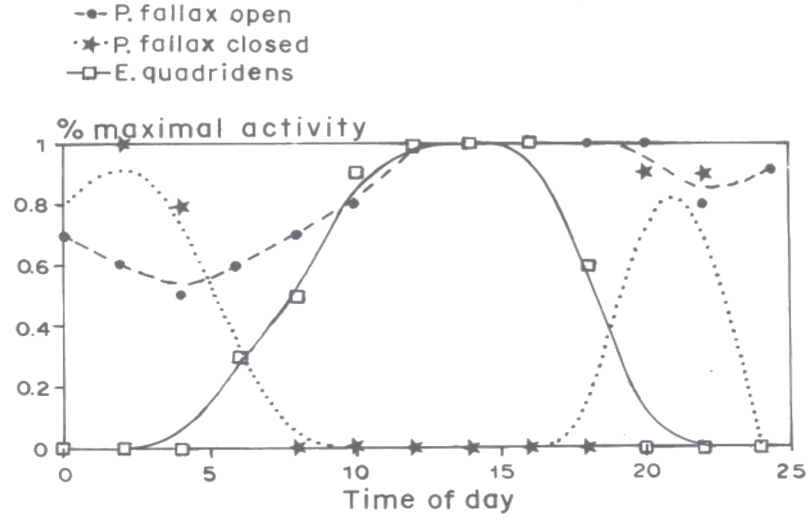

Figure 1. Activity cycles of *E. quadridens* and *P. fallax* colonies with and without nest plugging.

Results and Discussion

Behavior of nest plugging by E. quadridens

At dawn, numbers of *E. quadridens* workers aggregated at the nest entrances of *P. fallax* (Figure 1). *E. quadridens* workers began dropping soil particles in the nest entrance, while others stood with open mandibles and upraised antenna on the *P. fallax* nest *tumulus.* Complete nest entrance plugging occurred within 1 hr (Figure 1). During the rest of the day, a 2 to 5 *E. quadridens* workers stood stationarily near the plugged nest entrance. These workers returned to nest at dusk (Figure 1). No aggressive interactions were observed to counter nest entrance plugging by *P. fallax* workers. At the beginning of soil-dropping behavior, *P. fallax* workers grouped at the nest entrance, and workers neither left or entered the entrance once soil dumping by *E. quadridens* had commenced (Figure 1). The behaviors of both species are very similar to those reported for other cases of soil-dumping, nest-plugging interference studies (Moglich and Alpert 1979, Holldobler 1982, Gordon 1988).

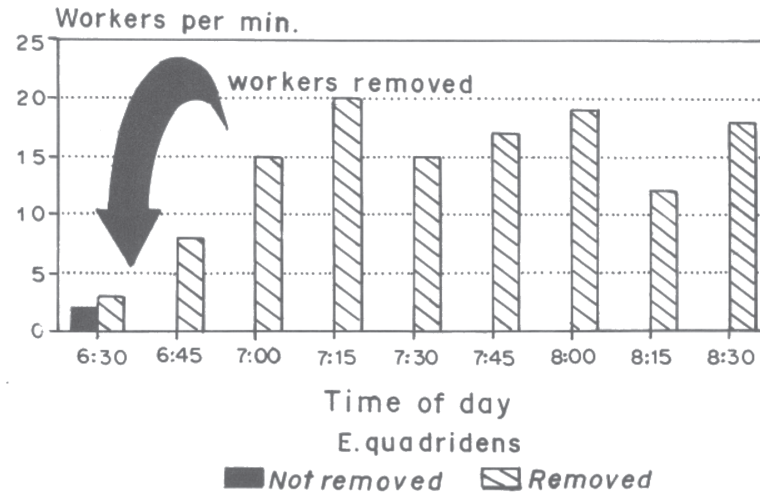

Figure 2. The effect of removal of arriving *E. quadridens* workers on activity patterns of *P. fallar. E. quadridens* workers were individually removed as they arrived at the *P. fallar* nest.

Distance effects

A strong inverse relationship was found between the number of plugged *P. fallax* nests and distance from the nearest *E. quadridens* nest (Table 1). *P. fallax* nests closer to extant *E. quadridens* nests were almost always plugged if these were located in the proximity of the camp midden pile (Table 1). *E. quadridens* colonies located at greater distances from the midden piles were not observed to dump soil in the entrances of *P. fallax* colonies, which exhibited no differences in foraging activity (Table 1).

None of the previous studies on interference by nest-plugging (Moglich and Alpert 1979, Holldobler 1982, Gordon 1988) have reported the effect of distance from concentrated resources. However, Adams and Traniello (1981) have demonstrated its use in chemical interference in other ant systems. Whether this can be generalized to the arid systems previously examined is not clear. However, these results are in accordance with the predictions of Oster and Wilson (1978).

Daily activity of P. fallax *and* E. quadridens

E. quadridens exhibited a strictly diurnal pattern of activity (Figure 1), which began at dusk and ended at dawn. Even in the campsite dining area with gas lighting at night. *E. quadridens* was never observed during the night. Nests of *P. fallax* which were not plugged exhibited a uniform foraging activity throughout the day (Figure 1). However, nests which had been plugged were restricted to foraging once the nest entrance workers appeared (Figure 1). Although these nests apparently foraged at a greater intensity during those periods free of interference competition, their observed activity was only 60% of the activity of unplugged nests (Figure 1).

When individual *E. quadridens* workers were prevented from reaching the nest entrance of a *P. fallax* nest by removal, the activity of the *P. fallax* nest was unaffected (Figure 2). Nest-plugging behavior by *E. quadridens* reduced the foraging period of *P. fallax* colonies, as has been previously demonstrated for the nest-plugging of *Myrmecocystus mimicus* nests by *Forelius* (= *Iridomyrmex*) *pruinosum* (Holldobler 1982)and by *Conomyrma bicolor* (Moglich and Alpert 1979) workers in North American deserts.

These results accord with the theory of Oster and Wilson (1978) that interference competition is strongly dependent upon resource concentration. The only other evidence in accord with this theory is in the form of chemical interference competition and not by nest plugging (Adams and Traniello 1981). 1 have also shown that interference competition, in the form of nest-plugging behavior, is not limited to arid portions of the world, and that they occur within the Amazon forest system.

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