



Reduction in the foraging activity of the leaf-cutting ant *Atta sexdens* caused by the phorid *Neodohrniphora* sp.

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Abstract

Females of the parasitic phorid *Neodohrniphora* sp. were collected in the field and released singly inside an observation chamber placed between a laboratory colony of *Atta sexdens* (L.) and its foraging arena. The number and speed of loaded and unloaded ants returning to the nest, the weight of foragers and their loads, the number of leaf fragments abandoned by ants, and the number of small workers 'hitchhiking' on leaf fragments were measured before phorids were released, while they were in the observation chamber, and after they were removed. Relatively few ants were attacked by *Neodohrniphora* sp., but the presence of flies prompted outbound ants to return to the nest and caused a significant reduction on the number and mass of foragers. Additionally, the weight of leaf fragments transported by ants was reduced and the number of abandoned fragments increased in response to *Neodohrniphora* sp. Presence of the parasitoid caused no significant changes in the number of hitchhiking ants. The regular ants' traffic was resumed after phorids were removed, but foraging activity remained below normal for up to three hours. In the field *A. sexdens* forages mostly at night, but colonies undergo periods of diurnal foraging during which ants are subject to parasitism from several species of phorid flies. Considering that daytime foraging may be necessary for nutritional or metabolic needs, phorids may have a significant impact on their hosts by altering their foraging behavior regardless of the numerical values of parasitism.

Introduction

Phorid flies are one of the most widely distributed and diverse groups of insects, and several species are parasites of ants (Disney, 1994). Many ant species exhibit remarkably elaborate and similar types of defense behavior against phorids (Feener & Brown, 1993; Porter et al., 1995; Tonhasca, 1996), which suggests an evolutionary adaptation to parasitism. Despite the complex escape strategies displayed by ants of diverse ecological characteristics, it seems that parasitism is a less important threat to colonies than indirect processes triggered by phorids' presence, such as reduction of foraging rates (Feener, 1988; Feener & Brown, 1992; Orr, 1992; Porter et al., 1995) and interference in competitive interactions between ant species (Feener, 1988; Feener & Brown, 1992). Because of

their capability to upset the foraging rhythm of ant colonies, their specificity, and their possible evolutionary association with their hosts, phorids have been suggested as 'keystone' species for ant communities (Feener, 1995). For economically important ants such as *Solenopsis* spp., recent studies have demonstrated that phorids are potential candidates for biological control (Orr et al., 1995; Porter et al., 1995).

In Southeast Brazil, *Neodohrniphora* spp. (Diptera: Phoridae) are parasites of one of the most common leaf-cutting ant species, *Atta sexdens* (L.) (Hymenoptera: Formicidae). Leaf-cutting ants have a significant role on the fertility and structure of tropical soils (Coutinho, 1984; Farji-Brener & Silva, 1995) as well as on the establishment and regeneration of tropical forests (Nepstad et al., 1996). Moreover, *A. sexdens* is one of the most conspicuous and eco-

nominically important leaf-cutting ants (Fowler et al., 1989), and its distribution has been increasing probably in response to deforestation (Eidmann, 1935; Fowler, 1983). Tonhasca (1996) established that parasitism rates of *Neodohriniphora* sp. on *A. sexdens* were relatively low; only about 2% of the ants on foraging trails were attacked. However, as previous work on ant-phorid relationships has demonstrated, mortality rates are not sufficient for evaluating the importance of these parasitoids. In this study, we quantified responses of *A. sexdens* foragers to the presence of *Neodohriniphora* sp. under laboratory conditions. This new species was incorrectly identified as *Neodohriniphora declinata* Borgmeier in Tonhasca (1996) (B.V. Brown, personal communication).

Methods

This study was conducted between November 1996 and August 1997 with *A. sexdens* colonies maintained in a rearing room at the Departamento de Biologia Animal, Universidade Federal de Viçosa, Brazil. Colonies consisted of 3-l glass containers interconnected with plastic tubes and linked to a foraging arena (Della Lucia et al., 1993). For this study, an observation chamber (100 cm long, 45 cm wide, 40 cm high) was placed between an adult colony (three years old) and the foraging arena. Temperature, humidity, and photoperiod in the laboratory were kept at 23 ± 1 °C, $85 \pm 5\%$, and L10:D14, respectively. To reduce possible disturbances to the colony, the study started four days after moving the nest to the laboratory. During the study, the colony was supplied with leaves from a single plant species (*Acalypha wilkesiana* M. Arg.) because plant quality affects foraging characteristics of *Atta* spp. (Nichols-Orians & Schultz, 1989).

Our first experiment was conducted to evaluate the impact of *Neodohriniphora* sp. on the foraging rhythm of *A. sexdens*. Female flies hovering over *A. sexdens* foraging trails were collected daily from several nests located near the university campus. Flies were taken to the laboratory, where they were kept singly in glass tubes containing a cotton ball saturated with a 10% honey solution until they were released in the observation chamber. Before the flies were released, we measured ants' traffic by counting the number of loaded and unloaded ants passing by a marked point on the plastic tube connecting the observation chamber to the nest. Each observation consisted of five three-minute counts taken at 7 min intervals. Because

illumination affects the rhythm of *Atta* spp. colonies in the laboratory, observations started at least 2 h after the lights were turned on. We then released one female *Neodohriniphora* sp. in the observation chamber and after 5 min measured ants' traffic as described. Phorids usually started to search for their host as soon as they were released. If a fly did not start the pursuit within 5 min, it was replaced with another one. Occasionally a phorid was killed by ants, in which case another fly was released for the remaining observation period. After 55 min in the chamber, the phorid was removed and ants' traffic was again measured. The first trial of this experiment consisted of six parasitoid releases over a 5-day period (releases with no parasitoid attack were not considered). Because of a possible carryover effect of phorids on the colony, we made no more than two releases per day, and they were at least 7 h apart.

Results of the first trial suggested that *Neodohriniphora* sp. affected the traffic of foraging ants even after flies were removed from the observation chamber (see Results). Therefore, we conducted three additional trials to measure a possible prolonged response of ants to phorids. We followed the protocol used in the first trial, except that now the five three-minute counts after phorid removal were made consecutively, and there were four additional samples every 45 min after flies were removed. Trial 2 consisted of 12 parasitoid releases over a 7-day period, and trial 3 consisted of five daily releases. After the last release in trial 3, the nest was replaced by another *A. sexdens* colony of similar characteristics and trial 4 was conducted, which consisted of four daily releases.

During trials 1 and 4, we collected at random up to ten foragers returning to the nest and their respective loads immediately after each count of the number of ants before phorids were released, while they were in the observation chamber, and after they were removed. Foragers and their leaf fragments were weighed to the nearest 0.1 mg on a precision balance. The relative load capacity of foragers was evaluated with burden, computed as $(M_a + M_l)/M_a$, where M_a and M_l are ant and leaf fragment masses, respectively (Rissing, 1982). During trials 3 and 4, we measured ant speed immediately after each count of the number of ants and before collecting ants. Speed was calculated from the time taken by up to ten loaded and ten unloaded ants randomly chosen to cover 20 cm of the plastic tube connecting the observation chamber to the nest. To assess the parasitic potential of *Neodohriniphora* sp. in the laboratory, we recorded the number of successful attacks of 26 additional flies manipulated as described

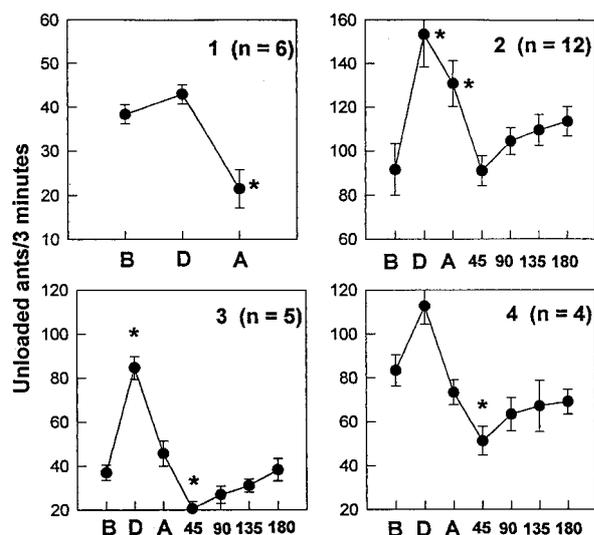


Figure 1. Mean numbers of *A. sexdens* without loads returning to the nest in trials 1–4 before *Neodohrniphora* sp. were released (B), during *Neodohrniphora* sp. presence in the observation chamber (D), and immediately after (A) to 180 min of phorids removal. Bars represent standard errors, *n* is the number of parasitoid releases, and * indicate means significantly different ($P < 0.05$) from means of 'before' according to the Dunnett's test.

above and released at different occasions during the period of trials 1 to 4.

Small leaf-cutting ants oftentimes 'hitchhike' on leaf fragments carried by larger workers, and this behavior has been considered as a defense method against phorids (Eibl-Eibesfeldt & Eibl-Eibesfeldt, 1967; Feener & Moss, 1990). In our experimental setting, we have observed that foragers oftentimes abandon their loads when they detect *Neodohrniphora* sp.. Consequently, the number of hitchhikers on leaf fragments and fragment-dropping behavior may be associated with the presence of *Neodohrniphora* sp.. To evaluate these possibilities, we conducted a second experiment with the second *A. sexdens* nest. Sampling procedures were similar to the first trial of the previous experiment, but this time the variables measured were number of loaded ants, number of foragers with hitchhikers, and number of hitchhikers. After sampling ants, we counted the number of fragments in a 0.25-m² area demarcated at the center of the observation chamber. The experiment consisted of 15 parasitoid releases over a 10-day period.

Results of these experiments were subject to analyses of variance after a $\log(x+1)$ transformation to homogenize variances. Because activity level of *A. sexdens* colonies vary considerably between days and

between mornings and afternoons of the same day (unpubl.), data for foraging rhythm and speed were analyzed separately for each trial. For the foraging rhythm data in trials 2, 3 and 4, we compared seven stages of parasitoid presence: before *Neodohrniphora* sp. were released, during *Neodohrniphora* sp. presence in the observation chamber, and 0, 45, 90, 135 and 180 min after phorids were removed. For the remaining data, we compared before, during and after. For the analyses, time of parasitoid releases was treated as blocks of random effect, and the five measurements taken in each stage of parasitoid presence were averaged. Therefore, each release of *Neodohrniphora* sp. resulted in one sample of before, during and after. Thus we are making a reasonable assumption that interactions between stage of parasitoid presence and time of release were not significant. When F-tests for stage were considered significant ($P < 0.05$), we used Dunnett's (1955) test to compare means obtained before the release of *Neodohrniphora* sp. with the subsequent means to determine which ones were different from pre-release levels.

Results

Similar to field observations (Tonhasca, 1996), *Neodohrniphora* sp. in the laboratory made no distinction between outgoing and incoming ants or between loaded and unloaded ants when searching for a host. The 26 flies released to estimate parasitism rates had a mean ± 1 s.d. of 20.1 ± 10.5 successful attacks per 60-min period. The average traffic of ants during these releases was 119.3 ± 58.6 ants per 3-min period. Thus, the probability of an ant being parasitized while in the observation chamber was less than 1%. This value is just an approximation, as *Neodohrniphora* sp. discriminates ant sizes, which are not equally represented on foraging trails (Tonhasca, 1996).

Traffic of ants returning to the nest without loads was significantly affected by the introduction of *Neodohrniphora* sp. in the observation chamber in all four trials (1: $F_{2,10} = 6.92$, $P = 0.01$; 2: $F_{6,63} = 2.22$, $P = 0.05$; 3: $F_{6,24} = 14.91$, $P < 0.001$; 4: $F_{6,18} = 5.15$, $P = 0.003$). The number of nestbound unloaded ants increased while *Neodohrniphora* sp. were in the chamber, but it was reduced as soon as the parasitoids were removed (Figure 1). A lag effect of the diminished number of ants in the foraging arena following the introduction of *Neodohrniphora* sp. reflected on the significant traffic reduction up to 45 min after the

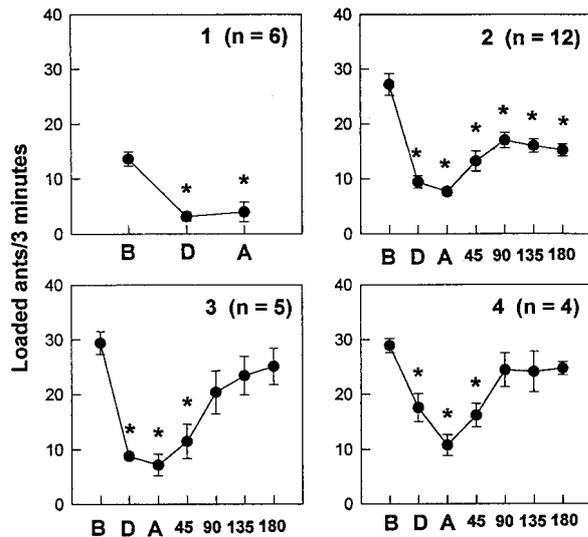


Figure 2. Mean numbers of *A. sexdens* with leaf fragments returning to the nest in trials 1–4 before *Neodohriniphora* sp. were released (B), during *Neodohriniphora* sp. presence in the observation chamber (D), and immediately after (A) to 180 min of phorids removal. Bars represent standard errors, *n* is the number of parasitoid releases, and * indicate means significantly different ($P < 0.05$) from means of 'before' according to the Dunnett's test.

parasitoid was removed in trials 3 and 4. As for forager traffic, it was sharply reduced when *Neodohriniphora* sp. were introduced (Figure 2). This effect was significant for all trials (1: $F_{2,10} = 11.79$, $P = 0.002$; 2: $F_{6,63} = 15.48$, $P < 0.001$; 3: $F_{6,24} = 11.76$, $P < 0.001$; 4: $F_{6,18} = 8.59$, $P < 0.001$). For all trials, forager traffic did not return to normal for at least 45 min after flies were removed. For trial 2, forager activity remained below normal for the duration of the observations (Figure 2). The statistical significance of comparisons between means should be viewed with caution, as repeated tests could inflate error rates. Nonetheless, the pattern of reduction of forager traffic is clear for all four trials. The increase of nestbound traffic in response to *Neodohriniphora* sp. was accompanied by an increase in speed, although results were statistically significant only for loaded ants in trial 4 (Table 1).

Results for forager and leaf fragment mass from trials 1 and 4 were combined because there is little variation in these variables as long as colonies are supplied with the same plant substrate (unpubl.). In fact, *t*-tests demonstrated that there were no significant differences between colonies on forager mass ($t = 0.98$, $P = 0.37$, $DF = 8$) or fragment mass ($t = 2.34$, $P = 0.06$, $DF = 8$) before they were exposed to

Neodohriniphora sp.. The introduction of parasitoids in the observation chamber significantly reduced the mass of foragers and leaf fragments transported (Table 2). Although the mass reduction was relatively greater for leaf fragment than for forager mass, there was no significant reduction in foragers load capacity (Table 2).

The total number of hitchhikers remained practically constant during the experiment, but their relative percentage on fragments increased in the presence of *Neodohriniphora* sp. (Table 3). This was the result of the lower availability of foragers, which were negatively affected when the parasitoid was introduced (Table 3). Only 11.5% of leaf fragments with minima had more than one hitchhiker, thus differences between numbers of hitchhikers could not be evaluated. The reduced number of foragers was followed by a significantly higher number of fragments abandoned in the observation chamber after the introduction of *Neodohriniphora* sp. (Table 3).

Discussion

The number of successful attacks of *Neodohriniphora* sp. in the laboratory was similar to the values obtained in the field (Tonhasca, 1996), which indicates that artificial conditions in these experiments did not impair the parasitoid's ability to search for its host. Moreover, parasitoids were able to complete their development in ants attacked in the laboratory (unpubl.). The number of ants successfully attacked suggests that parasitism by *Neodohriniphora* sp. is an unlikely event. Nonetheless, hovering and attacking attempts were sufficient to elicit the vigorous defensive behavior from ants described by Tonhasca (1996), or, in most cases, to induce threatened and nearby ants to quickly return to the nest. In fact, the characteristic defense and escape behavior displayed by *A. sexdens* can be used as signs of the presence of phorids in the field.

In a field study, Tonhasca (1996) failed to detect a significant reduction in *A. sexdens* activity in response to *Neodohriniphora* sp.. Those observations were made on artificially baited trails, a situation that may have masked responses to the parasitoid. This study, on the other hand, demonstrated a clear disruption of foraging patterns of *A. sexdens*. Reduction in the number of foragers returning to the nest, increase in the number of abandoned leaf fragments, and a less evident increase in ant speed are consequences of the escape behavior of *A. sexdens*

Table 1. Means \pm 1 s.d. for speed of loaded (S_l) and unloaded (S_u) *A. sexdens* before *Neodohrniphora* sp. were released in the observation chamber (before), while they were in the chamber (during), and immediately after they were removed (after); * indicate means significantly different ($P < 0.05$) from means of 'before' according to the Dunnett's test

	S_l (cm/s)	S_u (cm/s)
Trial 3 ($n = 5$):		
Before	1.86 \pm 0.07	2.30 \pm 0.14
During	1.92 \pm 0.38	2.53 \pm 0.41
After	1.76 \pm 0.19	2.10 \pm 0.15
	$F_{2,8} = 0.53, P = 0.61$	$F_{2,8} = 3.59, P = 0.07$
Trial 4 ($n = 4$):		
Before	1.19 \pm 0.06	1.65 \pm 0.12
During	1.35 \pm 0.11	1.82 \pm 0.19
After	1.46 \pm 0.15 *	1.76 \pm 0.15
	$F_{2,6} = 10.45, P = 0.01$	$F_{2,6} = 2.89, P = 0.13$

Table 2. Means \pm 1 s.d. ($n = 10$) for ant mass (M_a), leaf fragment mass (M_1), and burden ($B = [M_a + M_1]/M_a$) of *A. sexdens* before *Neodohrniphora* sp. were released in the observation chamber (before), while they were in the chamber (during), and immediately after they were removed (after); * indicate means significantly different ($P < 0.05$) from means of 'before' according to the Dunnett's test

	M_a (mg)	M_1 (mg)	B
Before	10.4 \pm 0.9	17.9 \pm 2.9	2.7 \pm 0.3
During	9.5 \pm 1.4	13.3 \pm 3.2 *	2.4 \pm 0.4
After	9.2 \pm 1.7 *	11.9 \pm 3.0 *	2.3 \pm 0.5
	$F_{2,18} = 3.50, P = 0.05$	$F_{2,18} = 10.62, P = 0.001$	$F_{2,18} = 2.69, P = 0.09$

Table 3. Means \pm 1 s.d. of the percentage of *A. sexdens* foragers with hitchhikers (%hitch.), number of hitchhikers (#hitch.), number of foragers (#for.) per 3-min period and number of fragments abandoned (#frag.) before *Neodohrniphora* sp. were released into the observation chamber (before), while they were in the chamber (during), and immediately after they were removed (after); * indicate means significantly different ($P < 0.05$) from means of 'before' according to the Dunnett's test

	%hitch. ($n = 13$)	#hitch. ($n = 15$)	#for. ($n = 13$)	#frag. ($n = 15$)
Before	8.8 \pm 6.7	4.3 \pm 3.5	49.4 \pm 5.7	10.3 \pm 9.5
During	11.7 \pm 6.1 *	4.4 \pm 2.4	38.4 \pm 7.4	17.5 \pm 12.9 *
After	17.9 \pm 5.1 *	4.9 \pm 2.8	25.6 \pm 9.8 *	15.9 \pm 12.4 *
	$F_{2,24} = 5.69$ $P = 0.001$	$F_{2,28} = 0.64$ $P = 0.53$	$F_{2,24} = 19.95$ $P < 0.001$	$F_{2,28} = 6.52$ $P = 0.005$

in response to phorids. However, as in *Solenopsis* spp. (Feener & Brown, 1992; Porter et al., 1995), the disruption of *A. sexdens* foraging rhythm lingered even after the parasitoid was removed. Moreover, the consequences of *Neodohrniphora* sp. presence went further, with a significant reduction in foragers and leaf fragment mass. This effect on mass might be attributed to the preference of *Neodohrniphora* sp. for larger foragers (Tonhasca, 1996), which carry larger loads (unpubl.). As larger ants are more likely to be pursued by *Neodohrniphora* sp., they may be more likely to drop their loads before returning to the nest.

As *A. sexdens* foraging activity is mostly nocturnal, and considering that phorids probably are not active at night (Orr, 1992), *Neodohrniphora* sp. would have limited parasitism opportunities. However, occasional daytime foraging occurs during short periods of intense activity. These sporadic but quite evident bursts of diurnal foraging may be required because of nutritional or metabolic needs of leaf-cutting ants (Lewis et al., 1974). Thus, *Neodohrniphora* sp. and other phorids may have a significant impact on *A. sexdens* colonies because they may interfere with leaf transport during limited but essential foraging periods.

Feener & Moss (1990) attributed different levels of hitchhiking among species of leaf-cutting ants to behavioral adaptations against phorid flies that attack only leaf carriers or need to land on leaf fragments to oviposit. However, at least two other phorid species (*Myrmosicarius grandicornis* Borgmeier and *Apoccephalus atrophilus* Borgmeier) parasitize *A. sexdens* in the field besides *Neodohrniphora* sp., and none of these species were ever observed selecting leaf carriers or landing on fragments. Nevertheless, hitchhiking for *A. sexdens* is common particularly at night, when phorids probably are not present. In this study, hitchhiking did not increase in the presence of *Neodohrniphora* sp., and this could be the result of the relatively low numbers of hitchhikers under laboratory conditions. On the other hand, it is possible that hitchhiking is a stereotyped defense behavior, or minima riding on leaf fragments have other roles besides defending leaf carriers.

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References

- Coutinho, L. M., 1984. Aspectos ecológicos da saúva no cerrado – a saúva, as queimadas e sua possível relação na ciclagem de nutrientes minerais. *Boletim de Zoologia* (São Paulo) 8: 1–9.
- Della Lucia, T. M. C., E. F. Vilela, N. Anjos & D. D. O. Moreira, 1993. Criação de formigas cortadeiras em laboratório. In: T. M. C. Della Lucia (ed.), *As Formigas Cortadeiras*. Folha de Viçosa, Brazil, pp. 151–162.
- Disney, R. H. L., 1994. *Scuttle flies: the Phoridae*. Chapman & Hall, London.
- Dunnett, C. W., 1955. A multiple comparison procedure for comparing several treatments with a control. *Journal of the American Statistical Association* 50: 1096–1121.
- Eibl-Eibesfeldt, I. & E. Eibl-Eibesfeldt, 1967. Das Parasitenabwehren der Minima-Arbeiterinnen der Blattschneider-Ameise (*Atta cephalotes*). *Zeitschrift für Tierpsychologie* 24: 278–281.
- Eidmann, H., 1935. Zur Kenntnis der Blattschneiderameise *Atta sexdens* L. insbesondere ihrer Ökologie. *Zeitschrift für Angewandte Entomologie* 22: 185–241.
- Farji-Brener, A. G. & J. F. Silva, 1995. Leaf-cutting ant nests and soil fertility in a well-drained Savanna in Western Venezuela. *Biotropica* 27: 250–253.
- Feener, D. H., Jr., 1988. Effects of parasites on foraging and defense behavior of a termitophagous ant, *Pheidole titanis* Wheeler (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 22: 421–427.
- Feener, D. H., Jr., 1995. Headless hosts, legless guests. *Nature* 378: 129.
- Feener, D. H., Jr. & B. V. Brown, 1992. Reduced foraging of *Solenopsis geminata* (Hymenoptera: Formicidae) in the presence of parasitic *Pseudacteon* spp. (Diptera: Phoridae). *Annals of the Entomological Society of America* 85: 80–84.
- Feener, D. H., Jr. & B. V. Brown, 1993. Oviposition behavior of an ant-parasitizing fly, *Neodohrniphora curvinervis* (Diptera: Phoridae), and defense behavior by its leaf-cutting ant host *Atta cephalotes* (Hymenoptera: Formicidae). *Journal of Insect Behavior* 6: 675–688.
- Feener, D. H., Jr. & K. A. G. Moss, 1990. Defense against parasites by hitchhikers in leaf-cutting ants: a quantitative assessment. *Behavioral Ecology and Sociobiology* 26: 17–29.
- Fowler, H. G., 1983. Distribution patterns of Paraguayan leaf-cutting ants (*Atta* and *Acromyrmex*) (Formicidae: Attini). *Studies on Neotropical Fauna and Environment* 18: 121–138.
- Fowler, H. G., M. I. Pagani, O. A. da Silva, L. C. Forti, V. P. da Silva & H. L. de Vasconcelos, 1989. A pest is a pest is a pest? The dilemma of Neotropical leaf-cutting ants: keystone taxa of natural ecosystems. *Environmental Management* 13: 671–675.
- Lewis, T., G. V. Pollard & G. C. Dibley, 1974. Micro-environmental factors affecting diel patterns of foraging in the leaf-cutting ant *Atta cephalotes* (L.) (Formicidae: Attini). *Journal of Animal Ecology* 43: 143–153.
- Nepstad, D. C., C. Uhl, C. A. Pereira & J. M. C. da Silva, 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. *Oikos* 76: 25–39.

- Nichols-Orians, C. M. & J. C. Schultz, 1989. Leaf toughness affects leaf harvesting by the leaf cutter ant, *Atta cephalotes* (L.) (Hymenoptera: Formicidae). *Biotropica* 21: 80–83.
- Orr, M. R., 1992. Parasitic flies (Diptera: Phoridae) influence foraging rhythms and caste division of labor in the leaf-cutter ant, *Atta cephalotes* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 30: 395–402.
- Orr, M. R., S. H. Seike, W. W. Benson & L. E. Gilbert, 1995. Flies suppress fire ants. *Nature* 373: 292–293.
- Porter, S. D., R. K. Vander Meer, M. A. Pesquero, S. Campiolo & H. G. Fowler, 1995. *Solenopsis* (Hymenoptera: Formicidae) fire ant reactions to attacks of *Pseudacteon* flies (Diptera: Phoridae) in Southeastern Brazil. *Annals of the Entomological Society of America* 88: 570–575.
- Rissing, S. W., 1982. Foraging velocity of seed-harvester ants, *Veromessor pergandei* (Hymenoptera: Formicidae). *Environmental Entomology* 11: 905–907.
- Tonhasca Jr., A., 1996. Interactions between a parasitic fly, *Neodohrniphora declinata* (Diptera: Phoridae), and its host, the leaf-cutting ant *Atta sexdens rubropilosa*. *Ecotropica* 2: 157–164.