

## INTERACTIONS BETWEEN A PARASITIC FLY, *NEODOHRNIPHORA DECLINATA* (DIPTERA: PHORIDAE), AND ITS HOST, THE LEAF-CUTTING ANT *ATTA SEXDENS* *RUBROPILOSA* (HYMENOPTERA: FORMICIDAE)

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**Abstract.** This study was conducted to examine the behavior of a parasitic phorid fly, *Neodohnrnhophora declinata* Borgmeier, and its impact on its host, the leaf-cutting ant *Atta sexdens rubropilosa* Forel, in a eucalyptus forest in Brazil. *N. declinata* perches along ants' foraging trails near tunnel entrances and tries to oviposit mostly in ants with head width of 3.0 mm or greater. Median values of attack attempts and actual attacks per 15-min. period were 5.0 and 2.0 respectively. The low success rate of *N. declinata* attacking bouts was attributed to the escape behavior of the host. *A. sexdens rubropilosa* avoided parasitism by running (45.5%), attacking the fly (43.0%), or protecting itself by raising its legs (11.5%). The frequency of parasitism of large ants (measured by emergence of adult flies) was estimated to be 10.5%, which corresponded to 2.2% of all ants on foraging trails. Dissection and rearing of ants collected immediately after an attack revealed parasitism rates of 22.7% and 32.1% respectively. Head widths of attacked ants were significantly larger than those of ants collected at random during the day, but there was no significant difference between the size of ants collected during the day and at night. There was no significant correlation between the number of ants and the number of flies on the trails, but the number of ants was positively correlated with the number of attacks and negatively correlated with percentage of ants attacked. Accepted 20 December 1996.

**Key words:** *Atta sexdens rubropilosa*, leaf-cutting ants, *Neodohnrnhophora declinata*, Phoridae, parasitism.

### INTRODUCTION

Leaf-cutting ants *Atta* spp. and *Acromyrmex* spp. are the most important "herbivores" in the Neotropical region, removing more vegetation than any other animal group (Hölldobler & Wilson 1990). These ants are among the most destructive agricultural pests in Central and South America (Weber 1972, Cherrett 1986), but they also play an important role in tropical ecosystems through organic matter fragmentation, nutrient cycling, soil fertilization and stimulation of plant growth (Haines 1978, Hölldobler & Wilson 1990). The leaf-cutting ant *Atta sexdens* (L.) is present over a wide area of subtropical South America (Kempf 1972), and is one of the most serious pests of agriculture and forestry (Gonçalves 1945). In Southeast Brazil, the subspecies *Atta sexdens rubropilosa* Forel is widespread in urban areas, crops and commercial forests, and its range and importance has increased because of the expansion of agriculture and reduction of native forests (Weber 1972). Despite the conspicuous presence of *A. sexdens rubropilosa* in tropical ecosystems, little is known about the relevance of natural enemies for this species.

Leaf-cutting ants are subject to parasitism from several species of flies in the family Phoridae (reviewed in Feener & Moss 1990). Recent work has indicated that these flies may have a significant impact on behavioral and ecological patterns of *Atta* spp. (Feener & Moss 1990, Orr 1992, Feener & Brown 1993). In this study, I observed the interactions of *A. sexdens rubropilosa* with one of its phorid parasitoids, *Neodohnrnhophora declinata* Borgmeier. The parasitic ability of *N. declinata* has long been known (Borgmeier 1925), but there is little information on the parasitoid-host relationship. Because both species overlap in a considerable part of their geographic distributions (Kempf 1972, Pires do Prado 1976, Brandão 1991), *N. declinata* may be an important natural enemy of *A. sexdens rubropilosa*.

### METHODS

The study was conducted from August 1994 to April 1995 in a forest of eucalyptus (predominantly *Eucalyptus robusta* Smith) located 35 km from Campos dos Goytacazes (21°48'S, 41°20'W), Rio de Janeiro State, Brazil. The 1307 ha forest of mostly mature

trees (> 4 years old) had little undergrowth except for scattered patches of grasses, which are rarely collected by *A. sexdens* (Gonçalves 1945). Thus, eucalyptus was the major source of vegetation for *A. sexdens rubropilosa* in the area. Based on the number of nests in the observation area ( $\approx 24$  ha), density of *A. sexdens rubropilosa* was estimated to be 0.7 colonies/ha. No other *Atta* species were found in the eucalyptus forest, but colonies of *Acromyrmex* spp. were common.

Within the observation area, seven mature and active colonies were chosen for observations conducted during morning hours at approximately weekly intervals. Based on the number of tunnel entrances (Bitancourt 1941), all selected colonies were estimated to be at least two years old. On each sampling date, up to five foraging trails were chosen for observations of parasitoid activity and up to ten trails were selected for collection of ants. Trails were selected according to the ants' foraging activity, which was indicated by the presence of freshly cut pieces of eucalyptus leaves along trails and around tunnel entrances. Because foraging activity and density of leaf-cutting ants were highly variable among colonies or among trails within colonies, location and number of observed trails varied during the study period. Despite this variability, there is evidence that *Atta* spp. workers are consistent regarding their foraging trails (Forti *et al.* 1984). Thus, tunnel entrances and their respective foraging trails were considered suitable experimental units.

During the study period, *A. sexdens rubropilosa* workers were active mostly at night. To enhance or establish foraging activity during each observation, a squeezed half-orange was placed on each active foraging trail, at approximately 2 m from the tunnel entrance. This distance was chosen because preliminary observations indicated that it contained most of the *N. declinata* hovering over foraging trails. Orange pulp is highly attractive to leaf-cutting ants, and a foraging path was generally established in less than 30 minutes. After the traffic of ants leaving and returning to a tunnel entrance became regular, the number of ants passing by a fixed point on the trail (flow) was counted for 5 minutes. Presence and number of phorid flies along the 2 m trail sections, the number of attacking bouts and successful attacks of *N. declinata* on leaf-cutting ants, as well as the behavior of flies and ants were recorded for 15-min. periods. An attacking bout occurred when a fly pursued an ant and elicited a defensive behavior (see results), and a successful attack was defined as a full

contact between a fly and its host. Occasionally a fly would slightly touch an ant, provoking a defensive reaction; these ants were not considered parasitized.

On 12 observation dates at approximately 3-week intervals, ants attacked by *N. declinata* were collected after an apparent oviposition ( $n = 240$ ). During the same period, samples of the larger ants ( $> \approx 3.0$  mm head width) were collected at random from trails without baits for estimation of parasitism levels ( $n = 219$ ). The size of collected ants was restricted because *N. declinata* attacks only large ants (see results). Ants were transported to the laboratory and placed individually in Petri dishes (9.0 cm diameter) containing a cotton ball imbibed with saturated sucrose solution, which was replenished daily. Petri dishes were kept in an environmental chamber in the dark at 27°C, which are the approximate conditions of *Atta* nests (Weber 1972). Some ants attacked by *N. declinata* were dissected one to six days after sampling ( $n = 97$ ). The remaining attacked ants, and ants collected at random from foraging trails, were maintained in the environmental chamber for a period sufficient for parasitoid emergence.

Samples were also collected for determination of size distributions of workers during day- and nighttime. Each sample consisted of approximately 50 ants collected randomly from foraging trails from 7:30 to 10:00 h (7 dates), and from 22:00 to 23:00 h (6 dates). Ant size was measured by the standard head width, which is the greatest width of the head viewed face on (Wilson 1980a). Measurements were taken to the nearest 0.1 mm with a dissecting microscope equipped with an ocular micrometer.

Diagnostics of studentized residuals plotted against the independent variables, and normal scores plotted against studentized residuals, indicated that data for regressions did not fit bivariate normal distributions despite transformations. Thus, these data were analyzed with the Spearman's rank correlation coefficient. Parametric analyses were not suitable for ant size data because of skewness and the presence of outlier values, therefore comparisons between two populations were made with the Mann-Whitney U-test. In the results, medians are followed by 95% confidence intervals calculated with nonlinear interpolations (Hettmansperger & Sheather 1986), and means are followed by standard deviations. Sample sizes are expressed as the number of observation periods or number of ants.

Identification of *N. declinata* was made by R.H.L. Disney, University Museum of Zoology,

Cambridge, England. Voucher specimens of *A. sexdens rubropilosa* and *N. declinata* were deposited in the collections of the Museu de Zoologia, Universidade de São Paulo.

## RESULTS

The behavior of *N. declinata* is similar to the behavior of *N. curvinervis* (Malloch), a parasite of *A. cephalotes* (L.) in Costa Rica (Orr 1992, Feener & Brown 1993). Despite the evidence provided by Brown & Feener (1991) that some phorids use olfactory cues for host location, it appears that at short range *N. curvinervis* (Feener & Brown 1993) and *N. declinata* locate their hosts visually. Flies perched on leaves and sticks overhanging the trail and turned their bodies towards passing ants as they were selecting suitable hosts. When a fly started a pursuit it would try to position itself behind the host, hovering over the target for a few seconds before attempting to oviposit in the ant's head. After an attacking bout, the fly usually returned to the same perching site. Contrary to *N. curvinervis*, which attacks only ants leaving tunnels (Feener & Brown 1993), *N. declinata* made no distinction between outgoing and incoming ants. There was also no apparent distinction between loaded and unloaded ants.

During the 15-min. observation periods ( $n = 31$ ), median values of attacking bouts and successful attacks were 5.0 (4.0–7.3) and 2.0 (2.0–3.3), respectively. Thus, the ratio of successful attacks to flight bouts was approximately 1:3. The low success rate of *N. declinata* attacks was probably due to the strong evading behavior of the host. Sometimes the hovering fly would go unnoticed, but generally the fly's presence elicited one of following reactions from the ant: running away (45.5%), attacking the fly (43.0%), or defending itself by crouching and raising its legs (11.5%). The percentages of responses were obtained from 200 unsuccessful bouts. The ants' aggressive behavior, whose patterns were described by Weber (1972), was not a major risk to the fly. In almost 8 h of observations there were only 2 instances where an ant captured a fly. In one of these cases the fly was grabbed by an ant walking behind the threatened ant. Thus, it appears that the defensive behavior deters oviposition mostly because the host is not in an adequate position. The crouching strategy was the least common; as the ant sensed the fly's approach it would stop, raise all legs over its back and become motionless. The ant sometimes remained inert for a

few minutes after the fly had abandoned the pursuit, even when occasionally other ants started to remove it from the trail.

The flow rate of ants on trails ranged from 30 to 1335 workers/15 min, with a median value of 258.0 (205.6–495.7) ( $n = 48$ ). *N. declinata* were present in 75% of the observation periods, with a range of 1 to 6 and a median of 1.0 (1.0–2.0) fly/2 m trail sections ( $n = 48$ ). There was no significant correlation between flow and the number of flies on trails ( $r_s = 0.133$ ,  $P > 0.05$ ,  $n = 48$ ). Flow was significantly correlated with the number of attacking bouts ( $r_s = 0.653$ ,  $P < 0.01$ ,  $n = 27$ ) and with the number of successful attacks ( $r_s = 0.386$ ,  $P < 0.05$ ,  $n = 27$ ) (Fig. 1). However, there were negative correlations between flow and the percentage of ants threatened by attacking bouts ( $r_s = -0.831$ ,  $P < 0.01$ ,  $n = 27$ ) and between flow and percentage of attacked ants ( $r_s = -0.488$ ,  $P < 0.01$ ,  $n = 27$ ) (Fig. 1). These results indicate that the number of attacks increased with greater traffic of ants, although ants on more crowded trails had a greater probability of escaping parasitism.

The minimum head width of an ant attacked by *N. declinata* was 1.8 mm, but 93.7% of attacked ants had a width greater than 3.0 mm (Fig. 2). The frequency of parasitism of ants collected at random from foraging trails (measured from emergence of adult flies) was 10.5%. Considering an average of 21.4% of ants most likely to be attacked by *N. declinata* (head width  $\geq 3.0$  mm), the parasitism rate can be estimated as being 2.2% of all ants on foraging trails. For ants collected immediately after an attack, dissection and rearing methods revealed parasites in 22.7% and 32.1% of the cases respectively. The traumatic effect of oviposition is not usually measured in parasitism studies, but it may represent a significant source of host mortality (Day 1994). Thus, the number of parasites found in ants could underestimate the importance of *N. declinata* parasitism. Head widths of parasitized ants, 4.8 (4.5–4.9) mm ( $n = 46$ ), were not significantly different ( $P = 0.31$ ) from those of ants attacked but not successfully parasitized, 4.5 (4.3–4.7) mm ( $n = 97$ ). These results suggest that head size was not a likely cause for oviposition failure. Head width of attacked ants was significantly larger than head width of ants collected randomly during the day ( $P < 0.001$ ), but there was no significant difference ( $P = 0.67$ ) regarding the size of foragers between day and night (Fig. 2).

Dissection and rearing always indicated a single *N. declinata* individual in the head capsule. Most ant-

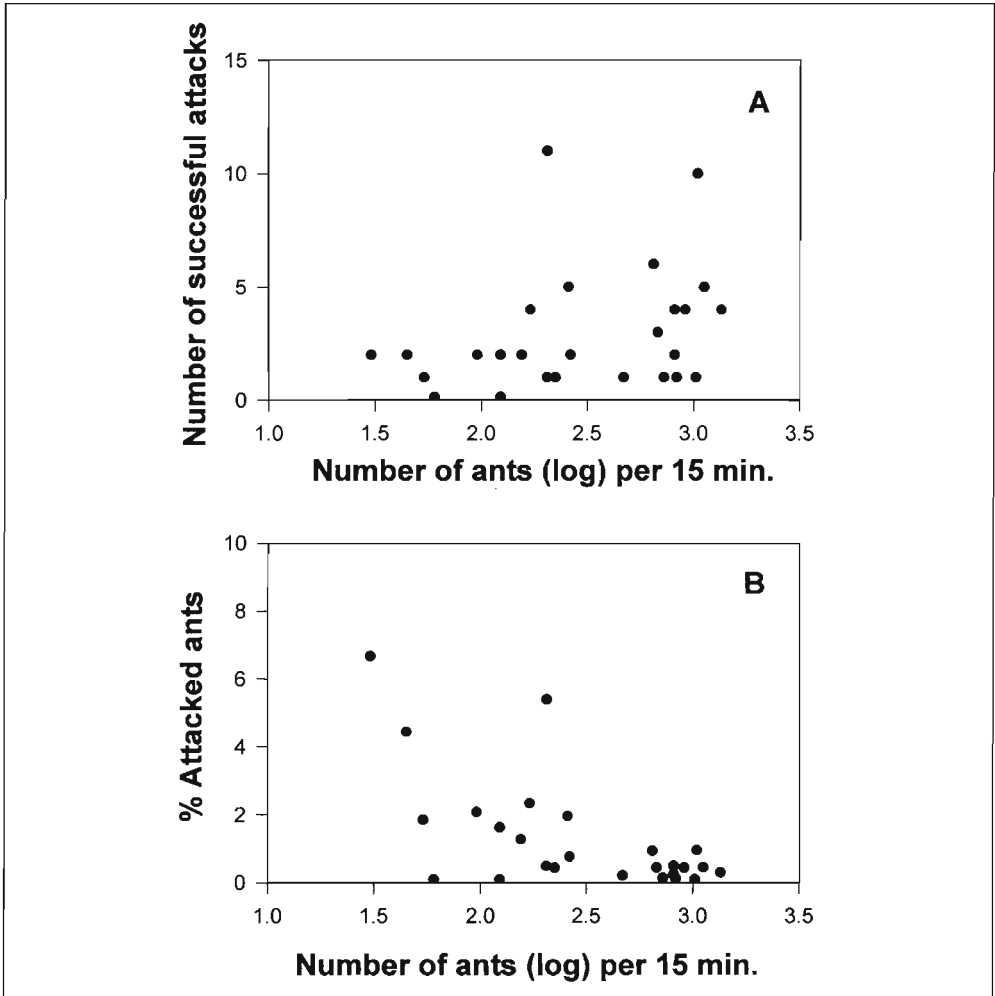


FIG. 1. Number (A) and percentage (B) of *A. sexdens rubropilosa* individuals successfully attacked by *N. declinata* in relation to the flow of ants on foraging trails.

parasitoid phorids lay a single egg per host (Brown *et al.* 1991), so it appears that superparasitism does not occur for *N. declinata*. The anecdotal description provided by Borgmeier (1928) of *N. declinata* oviposition in the ant's abdomen was not observed in this study; all attacking bouts were aimed at the posterodorsal extremity of the ant's head. Maggots were found on ants' mandibular muscles during early stages of parasitism (one to three days after the attack), so it appears that larvae migrate from the oviposition site to their developmental site. Mandi-

bular muscles represent up to 50% of the head mass and 25% of total body mass of *Atta* spp. (Roces & Lighton 1995), therefore *N. declinata* maggots have a relatively large supply of food. A maggot eventually completely occupies the ant's head cavity, but there were no noticeable behavioral or morphological differences between parasitized and non-parasitized live ants in the laboratory or in the field; parasitism could be detected only by dissection or after the ant's death. The lack of detectable signs of parasitism on live ants and the apparent inability of ants to recognize para-

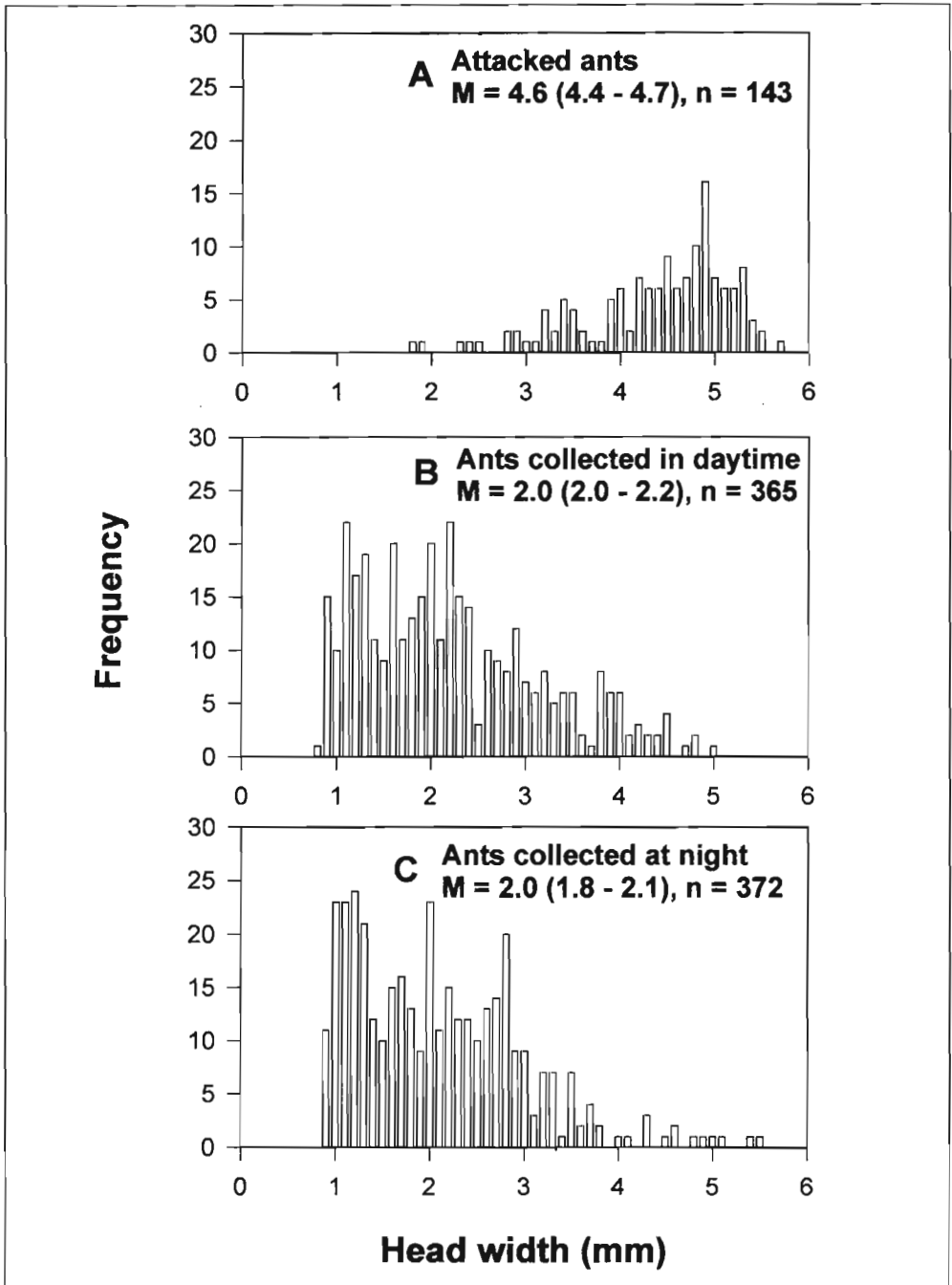


FIG. 2. Size distributions of *A. sexdens rubropilosa* individuals attacked by *N. declinata* (A), collected randomly in daytime from foraging trails (B), and collected randomly at night from foraging trails (C). Medians are followed by 95% confidence intervals.

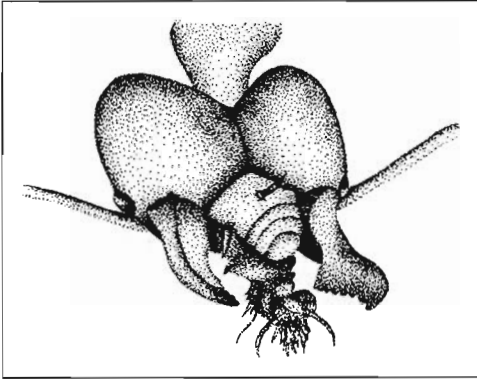


FIG. 3. Ventral view of the head of *A. sexdens rubropilosa* with a *N. declinata* puparium between the ant's mandibles.

sitized individuals is noteworthy, considering that odors originating from the head may be in great part responsible for nestmate recognition in *Atta* spp. (Whitehouse & Jaffé 1995).

Because there were no significant differences regarding parasitoid development between parasitized ants collected at random and ants collected after *N. declinata* attacks, these data were combined ( $n = 60$ ). Whereas non-parasitized ants become stiff after they die, dead parasitized ants appeared to be decomposing, with limp body parts and coalescent mouthparts. Pupariation occurred  $0.7 \pm 0.6$  (mean  $\pm$  standard deviation) days after the ant's death ( $n = 54$ ), when its mouthparts were pushed forward as a single mass to make room for the puparium (Fig. 3). The pupariation process of *N. declinata* is similar to that of *Pseudacteon litoralis* Borgmeier, a phorid parasitoid of *Solenopsis saevissima* (F. Smith) in Brazil (Porter *et al.* 1995). Respiratory horns appeared  $4.4 \pm 0.8$  days after the death of the ants ( $n = 49$ ), and adult flies emerged  $24.1 \pm 1.2$  days after ( $n = 43$ ). The relatively long time for adult emergence suggests that pupariation occurs inside ants' nests, as dead *A. sexdens rubropilosa* are readily picked up by scavenger ants such as *Solenopsis* spp. and *Ectatomma brunneum* (F. Smith), which is widespread in the study area and particularly efficient at locating dead leaf-cutting ants (personal observation). Of 46 flies that emerged in the laboratory, 19 were  $\sigma$ . These values indicated that the sex ratio of *N. declinata* was not significantly different ( $P = 0.15$ ) from 1:1, according to the binomial test (Siegel 1956). Descriptions of *N. declinata*  $\sigma$  and  $\eta$  are given by Disney (1996).

## DISCUSSION

*Atta sexdens rubropilosa* displayed a strong defensive behavior against *N. declinata*, which seems to be a general characteristic of ants attacked by phorids (Brown 1993). Nonetheless, there was no significant reduction in the flow of ants in response to presence or number of flies. Except for those ants directly threatened by a hovering fly and a few ants nearby, there were no visible changes in the rhythm of ant foraging activity during attack attempts. The lack of significant correlation between the number of ants on foraging trails and the number of flies suggests that *N. declinata* parasitism has no impact on ant foraging activity. However, these results should be viewed with caution. Baits near nest entrances may represent a more valuable and readily available resource than eucalyptus, thus eliciting ants to forage despite the risk of parasitism.

Parasitism rates were relatively low, although actual mortality resulting from *N. declinata* attacks could be higher than the estimated values because of oviposition trauma. Regardless of the parasitism rates, it is difficult to evaluate the importance of *N. declinata* for *A. sexdens rubropilosa* because numerical responses alone are not sufficient for evaluation of parasitism (Luck *et al.* 1988). Furthermore, the complex division of labor according to body size exhibited by leaf-cutting ants (Wilson 1980a, 1980b) is likely to influence the outcome of parasitism on the colony. *Neodohrniphora declinata* displayed a strong preference for large ants, a characteristic found in other ant-parasitoid phorids (Feener 1987, Feener & Brown 1993, Porter *et al.* 1995). Large *Atta* spp. individuals are responsible for cutting tough plant materials and defending the colony (Wilson 1980b, Nichols-Orians & Schultz 1989). Because *Atta* spp. preferentially cut young leaves (Nichols-Orians & Schultz 1990), larger ants may be expendable to a certain extent regarding the colony's foraging dynamics. Moreover, a large fraction of inbound *Atta* spp. workers do not carry loads (Cherrett 1968, Lugo *et al.* 1973, Littledyke & Cherrett 1976). These apparently idle ants may be doing trail maintenance (Lugo *et al.* 1973), returning from feeding (Littledyke & Cherrett 1976) or scouting incursions (Lewis *et al.* 1974), or they may represent a reserve force ready to substitute lost individuals (Wilson 1983). In this case, under normal circumstances the loss through parasitism of some of the large workers would not be crucial for the colony's survival. However, *N. declinata* parasitism may be more important for *A. sexdens rubropilosa* colonies that exploit mo-

nocultures of tough vegetation such as eucalyptus, when large individuals are necessary for cutting and transporting leaf parts. It could also be argued that parasitism may have other ecological implications besides worker mortality. Feener (1981) and Feener & Brown (1992) have demonstrated that phorid flies may interfere with ant foraging behavior and therefore influence the outcome of competition between species.

Foraging activity of *A. sexdens rubropilosa* in the eucalyptus field and surrounding areas is predominantly nocturnal throughout the year, probably because of cooler temperatures and higher humidity at night. *Atta sexdens* is more sensitive to dry conditions than other *Atta* species (Pereira da Silva 1975), and its foraging activity ceases at temperatures over 30°C (Fowler & Robinson 1979). Because *N. declinata*, like other parasitic phorids (Feener 1988, Orr 1992), occurs only in daytime (personal observation), nocturnal foraging offers limited opportunities for parasitism. Orr (1992) and Feener & Brown (1993) proposed that *Atta cephalotes* shifts its foraging force to smaller workers during daytime to reduce parasitism by *N. curvinervis*. In this study, there was no significant diel shifts in size distribution of *A. sexdens rubropilosa* workers. Diel differences between *A. cephalotes* and *A. sexdens rubropilosa* worker size could result from the relative importance of ant size. Wilson (1980a) established that the most efficient *A. sexdens rubropilosa* foragers have a head width between 1.8 and 2.6 mm, and this optimal range was assumed to be the same for *A. cephalotes* (Wilson 1983). The median size of parasitized *A. cephalotes* was within the range of greatest foraging efficiency (Feener & Brown 1993; this value was estimated, as those authors used a different head measure), but the median head width of attacked *A. sexdens rubropilosa* was approximately twice as large as the median head width of attacked *A. cephalotes*. Thus, *N. declinata* parasitism could be less important than *N. curvinervis* parasitism for their respective hosts.

Leaf-cutting ants are a significant ecological component of tropical forests, but their diversity and economic importance are greater in subtropical South America (Fowler & Claver 1991). Most research on ants of the genus *Atta* has focused on *A. cephalotes* and *Atta colombica* Guérin, and a considerable part of those studies was conducted in natural forests. There is much less information about leaf-cutting ants more closely associated with human activity such as *Atta capiguara* Gonçalves and *A. sexdens rubropilosa*. This aspect is relevant because there are con-

siderable differences in ecological patterns among *Atta* species (Gonçalves 1945). Phorid parasitism has been demonstrated to be an important factor on colony dynamics of fire ants (Orr *et al.* 1995), *A. colombica* (Feener & Moss 1990), and *A. cephalotes* (Orr 1992, Feener & Brown 1993). This study is an initial exploration of the association between *A. sexdens rubropilosa* and *N. declinata*. Considering the ecological and economic importance of that leaf-cutting ant species in the subtropical Neotropics, further investigations should be worthwhile.

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## REFERENCES

- Bitancourt, A.A. 1941. Expressão matemática do crescimento de formigueiros de "*Atta sexdens rubropilosa*" representado pelo aumento do número de olheiros. Arch. Inst. Biol. (São Paulo) 12: 229–236.
- Borgmeier, T. 1925. Novos subsidios para o conhecimento da família Phoridae. Arch. Mus. Nac. (Rio de Janeiro) 25: 85–281.
- Borgmeier, T. 1928. Nota prévia sobre alguns phorideos que parasitam formigas cortadeiras dos gêneros *Atta* e *Acromyrmex*. Bol. Biol. (São Paulo) 14: 119–126.
- Brandão, C.R.F. 1991. Adendos ao catálogo abreviado das formigas da região Neotropical (Hymenoptera: Formicidae). Revta. Bras. Entomol. 35: 319–412.
- Brown, B.V. 1993. Convergent adaptations in Phoridae (Diptera) living in the nests of social insects: a review of the New World Aenigmatiinae. Mem. Entomol. Soc. Can. 165: 115–137.
- Brown, B.V., & D.H. Feener, Jr. 1991. Behavior and host location cues of *Apocephalus paraponerae* (Diptera: Phoridae), a parasitoid of the giant tropical ant, *Paraponera clavata* (Hymenoptera: Formicidae). Biotropica 23: 182–187.
- Brown, B.V., Francoeur, A., & R.L. Gibson. 1991. Review of the genus *Styletus* (Diptera: Phoridae), with description of a new genus. Entomol. Scand. 22: 241–250.
- Cherrett, J.M. 1968. The foraging behaviour of *Atta cephalotes* L. (Hymenoptera, Formicidae). I. Foraging pattern and plant species attacked in tropical rain forest. J. Anim. Ecol. 37: 387–403.
- Cherrett, J.M. 1986. History of the leaf-cutting ant problem. Pp. 10–17 in Lofgren, C.S., & R.K. Vander Meer (eds.). Fire ants and leaf-cutting ants – biology and management. Colorado.

- Day, W.H. 1994. Estimating mortality caused by parasites and diseases of insects: comparisons of the dissection and rearing methods. *Environ. Entomol.* 23: 543–550.
- Disney, R.H.L. 1996. A key to *Neodohrniphora* (Diptera: Phoridae), parasites of leaf-cutter ants (Hymenoptera: Formicidae). *J. Nat. Hist.* 30: 1377–1389.
- Feener, D.H., Jr. 1981. Competition between ant species: outcome controlled by parasitic flies. *Science* 214: 815–817.
- Feener, D.H., Jr. 1987. Size-selective oviposition in *Pseudacteon crawfordi* (Diptera: Phoridae), a parasite of fire ants. *Ann. Entomol. Soc. Am.* 80: 148–151.
- Feener, D.H., Jr. 1988. Effects of parasites on foraging and defense behavior of a termitophagous ant, *Pheidole titianis* Wheeler (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 22: 421–427.
- Feener, D.H., Jr., & K.A.G. Moss. 1990. Defense against parasites by hitchhikers in leaf-cutting ants: a quantitative assessment. *Behav. Ecol. Sociobiol.* 26: 17–29.
- Feener, D.H., Jr., & B.V. Brown. 1992. Reduced foraging of *Solenopsis geminata* (Hymenoptera: Formicidae) in the presence of parasitic *Pseudacteon* (Diptera: Phoridae). *Ann. Entomol. Soc. Am.* 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). *J. Ins. Behav.* 6: 675–688.
- Forti, L.C., Pereira da Silva, V., & V.F.B. Gulli. 1984. Distribuição e atividade de operárias marcadas de *Atta capiguara* Gonçalves, 1944 (Hymenoptera, Formicidae) no murundo e nas trilhas. Abstracts of the 9th Brazilian Entomological Meeting.
- Fowler, H.G., & S.W. Robinson. 1979. Foraging by *Atta sexdens* (Formicidae: Attini): seasonal patterns, caste and efficiency. *Ecol. Entomol.* 4: 239–247.
- Fowler, H.G., & S. Claver. 1991. Leaf-cutter ant assemblies: effects of latitude, vegetation, and behaviour. Pp. 51–59 in Huxley, C.R., & D.F. Cutler (eds.). *Ant-plant interactions*. Oxford.
- Gonçalves, C.R. 1945. Saúvas do Sul e Centro do Brasil. *Bol. Fitoss. (Rio de Janeiro)* 2: 183–218.
- Haines, B.L. 1978. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. *Biotropica* 10: 270–277.
- Hertmansperger, T.P., & S.J. Sheather. 1986. Confidence intervals based on interpolated order statistics. *Stat. Prob. Letters* 4: 75–79.
- Hölldobler, B., & E.O. Wilson. 1990. *The ants*. Cambridge, Mass.
- Kempf, W.W. 1972. Catálogo abreviado das formigas da região Neotropical (Hymenoptera: Formicidae). *Stud. Entomol.* 15: 3–344.
- Lewis, T., Pollard, G.V., & G.C. Dibley. 1974. Micro-environmental factors affecting diel patterns of foraging in the leaf-cutting ant *Atta cephalotes* (L.) (Formicidae: Attini). *J. Anim. Ecol.* 43: 143–153.
- Littledyke, M., & J.M. Cherrett. 1976. Direct ingestion of plant sap from cut leaves by the leaf-cutting ants *Atta cephalotes* (L.) and *Acromyrmex octospinosus* (Reich) (Formicidae, Attini). *Bull. Entomol. Res.* 66: 205–217.
- Luck, R.F., Shepard, B.M., & P.E. Kenmore. 1988. Experimental methods for evaluating arthropod natural enemies. *Annu. Rev. Entomol.* 33: 367–391.
- Lugo, A.E., Farnworth, E.G., Pool, D., Jerez, P., & G. Kaufman. 1973. The impact of the leaf cutter ant *Atta colombica* on the energy flow of a tropical wet forest. *Ecology* 54: 1292–1301.
- 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.
- Nichols-Orians, C.M., & J.C. Schultz. 1990. Interactions among leaf toughness, chemistry, and harvesting by attine ants. *Ecol. Entomol.* 15: 311–320.
- 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). *Behav. Ecol. Sociobiol.* 30: 395–402.
- Orr, M.R., Seike, S.H., Benson, W.W., & L.E. Gilbert. 1995. Flies suppress fire ants. *Nature* 373: 292–293.
- Pereira da Silva, V. 1975. Contribuição ao estudo das populações de *Atta sexdens rubropilosa* Forel, e *Atta laevigata* (Fr. Smith) no Estado de São Paulo (Hym.: Formicidae). *Stud. Entomol.* 18: 201–250.
- Pires do Prado, A. 1976. Records and descriptions of phorid flies, mainly of the Neotropical region (Diptera; Phoridae). *Stud. Entomol.* 19: 561–609.
- Porter, S.D., Pesquero, M.A., Campiolo, S., & H.G. Fowler. 1995. Growth and development of *Pseudacteon* phorid fly maggots (Diptera: Phoridae) in the heads of *Solenopsis* fire ant workers (Hymenoptera: Formicidae). *Environ. Entomol.* 24: 475–479.
- Roces, F., & J.R.B. Lighton. 1995. Larger bites of leaf-cutting ants. *Nature* 373: 392–393.
- Siegel, S. 1956. *Nonparametric statistics for the behavioral sciences*. New York.
- Weber, N.A. 1972. Gardening ants: the attines. *Mem. Am. Philos. Soc.* 92: 1–146.
- Whitehouse, M.E.A., & K. Jaffé. 1995. Nestmate recognition in the leaf-cutting ant *Atta laevigata*. *Ins. Soc.* 42: 157–166.
- Wilson, E.O. 1980a. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). I. The overall pattern in *A. sexdens*. *Behav. Ecol. Sociobiol.* 7: 143–156.
- Wilson, E.O. 1980b. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). II. The ergonomic optimization of leaf cutting. *Behav. Ecol. Sociobiol.* 7: 157–165.
- Wilson, E.O. 1983. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). III. Ergonomic resiliency in foraging by *A. cephalotes*. *Behav. Ecol. Sociobiol.* 14: 47–54.