

Interactions between Fungus-Growing Ants (Attini), Fruits and Seeds in Cerrado Vegetation in Southeast Brazil¹

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ABSTRACT

We surveyed the material collected for fungus culturing by attine ants in the cerrado vegetation of southeast Brazil. Six genera of the so-called lower attines (*Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, *Sericomyrmex* and *Trachymyrmex*) collect a wide variety of plant material as fungal substrate. Plant diaspores of nonmyrmecochorous species comprise a large portion of the items brought to the nest, especially in the rainy season. Removal experiments using fruits of selected plant species revealed that attine ants (including the leaf-cutters *Atta* and *Acromyrmex*) not only actively clean the seeds (remove fruit pulp), but also carry them up to 12 m in the cerrado. Germination tests showed that removal of fruit pulp by attine ants increases germination rate in *Ocotea pulchella* (Lauraceae), *Prunus sellowii* (Rosaceae), *Ouratea spectabilis* (Ochnaceae), *Rapanea umbellata* (Myrsinaceae) and *Psychotria stachyoides* (Rubiaceae). For *P. stachyoides*, however, ants had no effect on germination if seeds had already passed the digestive tract of birds. Aril removal by attines also increases germination success of *Copaifera langsdorffii* (Leguminosae) and *Virola sebifera* (Myristicaceae) seeds. The results indicate that attine-fruit/seed interactions are particularly conspicuous in the cerrado, suggesting that fungus-growing ants may play a relevant role in fruit/seed biology in this vegetation type. Potential ant-derived benefits to diaspores of nonmyrmecochorous plants in the cerrado would include secondary seed dispersal and/or increased germination success by ant-handled seeds.

Key words: ant-plant interaction; attine ants; cerrado vegetation; mutualism; myrmecochory; seed dispersal; seed germination.

MOST ANT SPECIES HAVE A LARGE PORTION OF THEIR DIETS composed of animal protein. The subfamily Myrmicinae, however, includes a remarkable exception within the Formicidae. Members of the tribe Attini (12 genera) have a highly specialized fungivorous diet and maintain an obligate mutualism with symbiotic fungi which are cultured inside the nest on a substrate consisting mostly of plant material collected by the ants, and less often of insect corpses and feces (Hölldobler & Wilson 1990). The cultured fungus is the only food source for the larvae and probably constitutes the principal food item of the so-called lower attines, although workers of the most advanced taxa may also complement their diets with plant juice (Stradling 1991). There are 202 attine species distributed throughout the Neotropics (Schultz & Meier 1995); they are among the most dominant elements of the ant fauna in most habitats within this region (Cherrett 1986, Wilson 1986). As a consequence of their dominance, fungus-growing ants are regarded as major primary consumers within New World terrestrial ecosystems, and their impact on vegetation is greater than that provoked by any other herbi-

vore taxon (Wilson 1986). Due to these traits, attine ants are widely regarded as severe agricultural pests of several economically important plant cultures in the Neotropics (for a review, see Vander Meer *et al.* 1990).

More recently, however, new evidence from field studies in Neotropical forests have shown that attine ants may have a beneficial effect on the seed biology of higher plants. They may act as secondary dispersal agents of primarily vertebrate-dispersed seeds, and therefore rearrange the seed distribution in a potentially beneficial way for the parent plant (Roberts & Heithaus 1986; Kaspari 1993, 1996). Moreover, through the removal of fruit matter (pulp), the attines may also reduce fungal attack on fallen ripe fruits found on the ground of humid forests, and facilitate seed germination of vertebrate-dispersed plants (Oliveira *et al.* 1995). Ant effects on seed biology are well documented for typical myrmecochorous plants (Horvitz 1981, Bond & Slingsby 1983). Seeds of these species bear a differentiated food reward for ants known as an "elaiosome," which serves as an effective attractant for potential ant dispersers (Beattie 1985). However, the ecological consequence of ant activity on plant diaspores of nonmyrmecochorous plants is still poorly understood (but see Kaufmann *et al.* 1991; Pizo & Oliveira, in press).

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In the first part of this study, we identify the material collected for fungus culturing by six genera of Attini whose natural history is poorly known—*Cyphomyrmex*, *Mycetarotes*, *Mycocarpus*, *Myrmicocrypta*, *Sericomyrmex* and *Trachymyrmex*. Since fruits and seeds from several plant species were collected frequently by the species in these genera, and also by the leaf-cutters *Atta* and *Acromyrmex*, a series of field and greenhouse experiments were conducted in the second part of the study to better describe and quantify this interaction in the cerrado. We show that fruits (entirely or in part) and seeds are actively collected by fungus-growing ants in the cerrado, and provide observational and experimental evidence for a potential benefit of attine activity on the seed biology of plant species typical of this vegetation type.

MATERIALS AND METHODS

Field work was carried out in the cerrado reserve of the Estação Experimental de Mogi-Guaçu (22°18'S, 47°13'W), southeast Brazil. The climate of the region is characterized by a cold/dry (April to September) and a warm/rainy season (October to March). The Brazilian cerrados embrace an area of 2 million km², and within their distribution present several intergrading physiognomic forms ranging from closed forest to open grassland with scattered shrubs (Goodland 1971). A detailed floristic analysis of the cerrado of Mogi-Guaçu is given by Gibbs *et al.* (1983). During March and April 1995, five trails (totalling 7 km) were selected in the cerrado *sensu stricto* and in the transitional zone between “campo cerrado” and gallery forest. Baits made of fruits and dry cereal were used to attract attine ants and locate their nests along the trails. Nests of *Cyphomyrmex* ($N = 22$), *Mycetarotes* ($N = 8$), *Mycocarpus* ($N = 197$), *Myrmicocrypta* ($N = 41$), *Sericomyrmex* ($N = 6$) and *Trachymyrmex* ($N = 39$) were then marked for a seasonal monitoring of the material being collected by the workers for fungus culturing. Ant activity in each marked nest was monitored monthly from May 1995 to April 1996, during 5 min intervals, between 0800 and 1800 h.

The interaction between attine ants and fruits/seeds (pulp or aril removal, and dispersal) from six selected plant species was studied in detail by placing groups of diaspores (fruits or seeds) along transects in the cerrado, and by periodically recording their removal by ants. The data from such removal experiments include also records of *Atta* and *Acromyrmex* workers at fruits and seeds. Plant dia-

spores were dispersed in groups of ten (‘baiting station’), at intervals of 10 m to maintain independent discoveries by different ant colonies (Byrne & Levay 1993; Kaspari 1993, 1996). The removal experiments were performed with six typical cerrado plant species whose fruits or seeds were in general highly attractive to attine ants (Table 1): *Ocotea pulchella* (Lauraceae, 310 fruits, 31 baiting stations), *Prunus sellowii* (Rosaceae, 510 fruits, 51 baiting stations), *Ouratea spectabilis* (Ochnaceae, 500 fruits, 50 baiting stations), *Rapanea umbellata* (Myrsinaceae, 300 fruits, 30 baiting stations), *Psychotria stachyoides* (Rubiaceae, 300 fruits, 30 baiting stations), and *Virola sebifera* (Myristicaceae, 300 arillate seeds, 30 baiting stations). Baiting stations were set up at 0700 h and ant-fruit/seed interactions were checked at 2 h intervals, from 1000 to 1800 h. Removal experiments for each plant species were performed on sunny days from January to April of 1996 and 1997 (fruiting season, see Mantovani & Martins 1988).

The effect of attine ants on seed germination was evaluated through germination tests in the greenhouses of the Universidade Estadual de Campinas (seeds handled by nonattine ants were not used in the tests). Seeds of *O. pulchella*, *P. sellowii*, *O. spectabilis* and *R. umbellata* were grouped into two categories for the tests: (1) seeds coated by a pulp (fruit not manipulated by the ants); (2) cleaned seeds (fruit pulp removed by attine ants).

Ant effects on seed germination were also evaluated for two plant species bearing arillate seeds, *Copaifera langsdorffii* (Caesalpiniaceae) and *Virola sebifera* (Table 1). Arillate seeds of these two species were divided into two groups for the germination tests: (1) intact seeds collected on the plant from recently opened fruits; (2) fresh-fallen seeds whose aril had been totally removed by attine ants.

Seeds of *Psychotria stachyoides* were tested for germination before and after dispersal by birds. In this case, seeds were grouped into four categories: (1) seeds collected on the plant from ripe fruits and having the pulp removed by us; (2) cleaned fallen seeds with fruit pulp recently removed by attine ants; (3) seeds collected by us from bird droppings; (4) seeds collected by attine ants from bird droppings. Categories (1) and (3) were included in the germination tests with *P. stachyoides* to evaluate possible effects on seed germination due to ant manipulation.

Germination tests in the greenhouse followed the same procedure for all plant species. Seeds in each category were placed in separate plastic boxes (40 × 40 cm) containing moist cerrado soil and

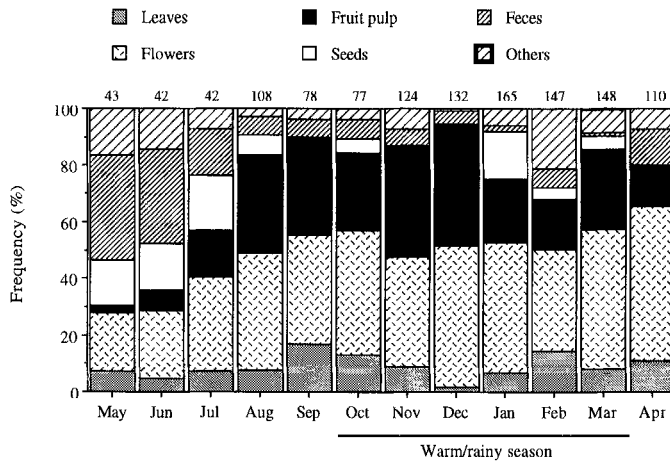


FIGURE 1. Material collected by attine ants in the cerrado of Mogi-Guaçu, southeast Brazil. Numbers above the bars refer to total number of records per month (1995 and 1996), and include the following ant genera: *Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, *Sericomyrmex* and *Trachymyrmex*.

kept in partial sun. Germination boxes were watered regularly. Seeds were buried 1 cm into the substrate, 3 cm apart from each other, and checked for germination at 3 d intervals during three months.

Since we were most concerned with the general effect of attines on seed biology in the cerrado, ants were identified only to the generic level in the present paper. Voucher specimens of all morphospecies are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP). A detailed account of the field biology of the cerrado attines, including the material collected for fungus culturing by the different genera, will be provided in a separate paper.

RESULTS

THE FUNGUS-CULTURING MATERIAL OF LOWER ATTINES.—A total of 313 nests of the so-called lower attines were marked in the study area, comprising 19 morphospecies in 6 genera (*Cyphomyrmex*, *Mycetarotes*, *Mycocepurus*, *Myrmicocrypta*, *Sericomyrmex* and *Trachymyrmex*). Attine ants collect a wide variety of plant material for fungus culturing in the cerrado, and the selection appears highly dependent on seasonal factors. Overall, the ants were observed collecting material from a total of 53 plant species from 28 families; items include leaves, flowers, fruits, seeds, mosses, lichens, feces, and insect corpses (Fig. 1). Flowers and fruits were the items most frequently collected by the ants, especially during the warm/wet season (flowering/fruiting pe-

riod). Seeds, feces and other material are more commonly collected during cold/dry months (Fig. 1). There were no records of lower attines climbing on plants to cut leaves. Records of vegetative parts were mainly (>95%) fallen foliolules of *Anadenanthera falcata* (Mimosaceae).

Table 1 lists the plant species whose fruits and/or seeds were collected by attines in the cerrado of Mogi-Guaçu, with the total number of monthly records for one year. Many plants had their fruits and/or seeds utilized by attines, especially *Rapanea umbellata*, *Ocotea pulchella*, *Prunus sellowii* and *Ouratea spectabilis*. Seeds of several species, especially in the families Melastomataceae, Myrsinaceae, Rubiaceae and Solanaceae, were also frequently collected by attine ants from bird or bat feces (Table 1). Workers of *Mycocepurus* occasionally collected seeds of *Psychotria stachyoides*, *R. umbellata* and *Siparuna guianensis* from *Acromyrmex* refuse piles. The collection of seed arils for fungus culturing was recorded for six plant species: *Copaifera langsdorffii*, *Pera obovata*, *Siparuna guianensis*, *Trichilia palida*, *Virola sebifera*, and *Xylopia aromatica* (Table 1).

ANT BEHAVIOR TOWARD FRUITS AND SEEDS.—None of the plant species listed in Table 1 have a typical elaiosome-bearing seed to attract ants; their primary dispersal agents in the cerrado are birds or bats which are attracted to the aril or pulp of their diaspores. The fruit pulp of these plants is frequently rich in carbohydrates (*Prunus sellowii*, *Miconia* spp. and *Psychotria* spp.) or lipids (*Ouratea*

TABLE 1. Plant species whose fruits and/or seeds were collected by attine ants in the cerrado of Mogi-Guaçu, southeast Brazil. Values refer to number of records during 12 monthly censuses of marked colonies of *Cyphomyrmex*, *Mycetarotes*, *Mycocarpus*, *Myrmicocrypta*, *Sericomyrmex* and *Trachymyrmex*, and nonsystematic observations of *Acromyrmex* and *Atta*.

Plant species	Plant family	No. of records	
		Fruits	Seeds
<i>Rapanea umbellata</i>	Myrsinaceae	75	5 ^c
<i>Copaifera langsdorffii</i>	Caesalpinaceae	—	48 ^a
<i>Ocotea pulchella</i>	Lauraceae	36	—
<i>Prunus sellowii</i>	Rosaceae	36	—
<i>Ouratea spectabilis</i>	Ochnaceae	27	—
<i>Miconia albicans</i>	Melastomataceae	17	4 ^b
<i>Didymopanax vinosum</i>	Araliaceae	15	—
<i>Miconia rubiginosa</i>	Melastomataceae	13	3 ^b
<i>Cordia sellowiana</i>	Boraginaceae	12	—
<i>Miconia ligustroides</i>	Melastomataceae	12	—
<i>Pera obovata</i>	Euphorbiaceae	—	14 ^a
<i>Byrsonima intermedia</i>	Malpighiaceae	7	—
<i>Rudgea viburnioides</i>	Rubiaceae	6	2 ^b
<i>Qualea grandiflora</i>	Vochysiaceae	5	—
<i>Zanthoxylum rhoifolium</i>	Rutaceae	4	—
<i>Psychotria stachyoides</i>	Rubiaceae	3	12 ^b
<i>Trichilia palida</i>	Meliaceae	—	3 ^a
<i>Siparuna guianensis</i>	Monimiaceae	—	3 ^a
<i>Ficus citrifolia</i>	Moraceae	2	—
<i>Rapanea ferruginea</i>	Myrsinaceae	1	—
<i>Anadenanthera falcata</i>	Mimosaceae	—	8
<i>Palicourea rigida</i>	Rubiaceae	—	6 ^b
<i>Solanum</i> sp.	Solanaceae	—	4 ^c
<i>Psychotria barbiflora</i>	Rubiaceae	—	2 ^b
<i>Xylopia aromatica</i>	Annonaceae	—	2 ^a
<i>Virola sebifera</i>	Myristicaceae	—	2 ^a

^a Aril-bearing seeds.

^b Seeds also collected from bird feces.

^c Seeds also collected from bat feces.

spectabilis and *Ocotea pulchella*), which presumably makes them attractive to ants. Seed carrying by the ants, especially *Atta* and *Acromyrmex*, occurred mainly when the fruit pulp was more strongly attached to the seeds. In these cases the diaspore may possess structures that facilitate their transport by the ants, as seen in fruits of *Rapanea* spp., *Didymopanax vinosum* and *Prunus sellowii*, which retain the peduncle after falling to the ground. Removal by ants is also facilitated by seed structures such as the caruncle in *Xylopia aromatica*, thorns and aril in *Siparuna guianensis*, hairs in *Solanum* sp., and the carbohydrate-rich aril in *Copaifera langsdorffii* (Galetti 1996). While transporting the diaspores to their nests, attine ants may occasionally drop them along the trail. Entirely cleaned seeds are seen on the refuse piles near the nest entrance, especially for *Atta* and *Acromyrmex*.

FRUIT/SEED REMOVAL BY ANTS.—Table 2 presents the results from the field experiments evaluating ant

attraction to baiting stations containing fruits of *O. pulchella*, *P. sellowii*, *O. spectabilis*, *R. umbellata*, *P. stachyoides*, and arillate seeds of *V. sebifera*. The data show that several attine ants not only actively clean the seeds (*i.e.*, remove fruit pulp or aril), but also remove them to distances of nearly 12 m. The larger *Atta* and *Acromyrmex*, in general, carried the diaspores to longer distances than the other attine genera (Table 2). Small fruits tended to be removed from the baiting stations in greater proportions than large ones—62 percent of the fruits of *R. umbellata* (fruit diameter = 0.40 ± 0.03 cm, $N = 50$) were removed by ants against only 38 percent of *O. spectabilis* (1.26 ± 0.08 cm, $N = 50$). Medium-sized fruits, such as *P. sellowii* (0.81 ± 0.04 cm, $N = 50$), *P. stachyoides* (0.89 ± 0.23 cm, $N = 50$) and *O. pulchella* (0.95 ± 0.14 cm, $N = 50$) were removed by the ants at intermediate rates (52%, 43%, and 48%, respectively). Despite their large size (1.23 ± 0.52 cm, $N = 50$), 44 percent of the arillate seeds of *V. sebifera* were removed by

TABLE 2. Ant occurrence at baiting stations containing diaspores (fruits or seeds) of six selected plant species (10 diaspores per station) in the cerrado of Mogi-Guaçu, southeast Brazil.

Plant species & ant genera	Occurrence at baiting stations	Fruits or seeds cleaned per station	Fruits or seeds removed per station	Distance (cm) $\bar{x} \pm SD (N)$
<i>Ocotea pulchella</i>				
(N = 31 baiting stations)				
<i>Acromyrmex</i>	9	6.1 ± 2.4	8.6 ± 2.5	738.1 ± 275.1 (78)
<i>Atta</i>	1	7	10	358.0 ± 0.0 (10)
<i>Cyphomyrmex</i>	4	4.0 ± 0.8	0.2 ± 0.5	23 (1)
<i>Mycocepurus</i>	10	4.7 ± 2.4	0.5 ± 0.7	74.8 ± 35.3 (5)
<i>Myrmicocrypta</i>	7	4.1 ± 1.7	0.7 ± 1.1	257.0 ± 80.3 (5)
<i>Sericomyrmex</i>	1	5	2	230 (2)
<i>Trachymyrmex</i>	6	6.3 ± 3.0	7.8 ± 3.5	648.8 ± 333.3 (47)
<i>Prunus sellowii</i>				
(N = 51 baiting stations)				
<i>Acromyrmex</i>	9	6.9 ± 2.7	7.9 ± 3.1	1152.4 ± 569.9 (103)
<i>Atta</i>	5	8.2 ± 2.5	10.0 ± 0.0	954.2 ± 666.1 (50)
<i>Cyphomyrmex</i>	3	4.0 ± 1.0	0	0
<i>Mycocepurus</i>	16	5.0 ± 2.9	0.5 ± 0.7	159.2 ± 133.0 (8)
<i>Myrmicocrypta</i>	6	5.7 ± 1.9	0.5 ± 0.6	311.0 ± 88.5 (3)
<i>Sericomyrmex</i>	1	5	1	45 (1)
<i>Trachymyrmex</i>	7	7.5 ± 2.9	8.3 ± 3.9	615.7 ± 273.0 (100)
<i>Ouratea spectabilis</i>				
(N = 50 baiting stations)				
<i>Acromyrmex</i>	8	7.4 ± 3.7	8.7 ± 2.3	960.0 ± 516.5 (70)
<i>Atta</i>	3	10.0 ± 0.0	10.0 ± 0.0	1231.0 ± 677.7 (30)
<i>Mycocepurus</i>	8	5.2 ± 3.3	0.1 ± 0.3	348 (1)
<i>Myrmicocrypta</i>	1	1	0	0
<i>Sericomyrmex</i>	2	2.0 ± 0.0	0	0
<i>Trachymyrmex</i>	11	7.8 ± 2.7	7.9 ± 2.7	669.0 ± 262.9 (87)
<i>Rapanea umbellata</i>				
(N = 30 baiting stations)				
<i>Acromyrmex</i>	9	2.5 ± 2.1	5.0 ± 2.7	714.8 ± 410.9 (45)
<i>Atta</i>	6	4.8 ± 2.8	5.3 ± 3.1	492.0 ± 211.1 (32)
<i>Cyphomyrmex</i>	3	4.0 ± 1.0	3.7 ± 1.1	317.4 ± 117.1 (11)
<i>Myrmicocrypta</i>	4	4.0 ± 1.8	3.2 ± 1.2	314.6 ± 102.1 (13)
<i>Mycocepurus</i>	10	5.3 ± 2.7	5.3 ± 2.9	359.2 ± 165.6 (55)
<i>Trachymyrmex</i>	7	3.4 ± 2.0	4.3 ± 2.0	528.7 ± 242.5 (30)
<i>Psychotria stachyoides</i>				
(N = 30 baiting stations)				
<i>Acromyrmex</i>	5	5.0 ± 3.2	5.0 ± 2.7	846.6 ± 256.0 (25)
<i>Atta</i>	8	6.0 ± 2.9	5.7 ± 2.9	895.7 ± 428.9 (46)
<i>Cyphomyrmex</i>	4	3.2 ± 0.7	2.0 ± 1.4	295.7 ± 159.0 (8)
<i>Mycocepurus</i>	8	3.0 ± 1.6	2.9 ± 1.7	350.6 ± 154.4 (23)
<i>Myrmicocrypta</i>	2	4.0 ± 1.4	3.0 ± 0.0	500.0 ± 21.9 (6)
<i>Trachymyrmex</i>	6	5.3 ± 2.4	3.8 ± 1.5	623.3 ± 276.0 (23)
<i>Virola sebifera</i>				
(N = 30 baiting stations)				
<i>Acromyrmex</i>	7	3.3 ± 2.4	4.3 ± 2.1	672.7 ± 415.7 (30)
<i>Atta</i>	3	6.3 ± 3.2	7.3 ± 3.0	450.9 ± 182.0 (22)
<i>Cyphomyrmex</i>	2	3.5 ± 0.7	2.0 ± 1.4	415.0 ± 136.9 (6)
<i>Mycocepurus</i>	10	5.0 ± 1.8	3.4 ± 1.5	397.0 ± 194.4 (34)
<i>Myrmicocrypta</i>	3	4.0 ± 1.0	2.7 ± 1.5	458.7 ± 158.5 (8)
<i>Sericomyrmex</i>	1	5	5	721.0 ± 0.0 (5)
<i>Trachymyrmex</i>	8	3.4 ± 1.2	3.6 ± 1.6	643.3 ± 241.5 (29)

TABLE 3. Germination tests of seeds whose fruits were manipulated (treatment group) or not (control group) by attine ants in the cerrado of Mogi-Guaçu. Tests with *C. langsdorffii* and *V. sebifera* evaluated the effect of ants removing (treatment group) or not removing (control group) the seed aril.

Plant species	No. of seeds planted		Germination success (%)		Significance of difference (χ^2 tests)
	Control	Treatment	Control	Treatment	
<i>Ocotea pulchella</i>	110	110	10.9	73.6	$P = 0.0001$
<i>Prunus sellowii</i>	120	120	15.0	51.7	$P = 0.0001$
<i>Oouratea spectabilis</i>	200	200	10.5	34.0	$P = 0.0001$
<i>Rapanea umbellata</i>	168	168	12.5	57.1	$P = 0.0001$
<i>Copaifera langsdorffii</i>	144	144	63.9	82.6	$P = 0.0005$
<i>Virola sebifera</i>	88	88	25.0	51.1	$P = 0.0006$

the ants, and this is probably due to the lipid-rich aril typical of the species in this genus (Galetti 1996).

Nonattine ants were also observed removing fruits and seeds from the baiting stations. Species in the myrmicine genera *Pheidole*, *Pogonomyrmex* (= *Ephebomyrmex*), *Solenopsis*, and *Zacryptocerus* were occasionally registered removing fruit pulp. Ponerine ants in the genera *Ectatomma* and *Odonotomachus* removed nearly 50 percent of the arillate seeds of *V. sebifera*.

ANT EFFECTS ON SEED GERMINATION.—Pulp removal by the ants significantly increased the germination success of the five selected plant species bearing fleshy fruits, as measured by greenhouse tests with experimental seeds collected in the field (Table 3). Germination tests with *C. langsdorffii* and *V. sebifera* revealed that aril removal by attine ants also significantly increases the germination success in these plant species (Table 3). Results with *Psychotria stachyoides* further indicate that ant handling during pulp removal significantly increases seed germination as compared to control seeds whose pulp was removed by ourselves. Attine ants, however, had no effect on germination if seeds of *P. stachyoides* had already passed through the digestive tract of a bird disperser (Table 4).

DISCUSSION

Although it is well known that fungus-growing ants may collect a wide variety of items to use as fungal substrate inside their nests (Hölldobler & Wilson 1990), very little is known about the material collected by attines in the Brazilian cerrados, especially for those genera not regarded as agricultural pests. Ecological studies of attines in Brazil (and the Neotropics in general) have usually focused on economically important taxa (*Atta* and *Acromyrmex*), such as in the recent works by Schroeder and Coutinho (1990, 1991), Andrade (1991) and Vasconcelos (1990).

The current study is the first to provide a quantitative account of the diversity in plant material (as well as nonplant items) collected by lower attines for fungus culturing in cerrado vegetation. The results revealed that a wide variety of material is used by the ants as fungal substrate, and that plant diaspores comprise a large portion of the items brought to nests by lower attines, especially from August to the middle of the warm/rainy season (December; Fig. 1), when most cerrado plants produce flowers and fruits (Mantovani & Martins 1988).

These findings are relevant in view of the previously little-recognized effect that attine ants may

TABLE 4. Germination tests with *Psychotria stachyoides*. Tests before bird dispersal involved fresh seeds from ripe fruits whose pulp was manipulated (treatment group) or not manipulated (control group) by attines; after bird dispersal, experimental seeds were categorized as removed by attine ants (treatment group) or by the authors (control group) from bird droppings.

Seed condition	No. of seeds planted		Germination success (%)		Significance of difference (χ^2 tests)
	Control	Treatment	Control	Treatment	
Before bird dispersal	80	80	0	15.0	$P = 0.001$
After bird dispersal	78	70	48.7	58.6	$P = 0.3008$

have on fruit and seed biology of cerrado plants. Plant species whose fruits and/or seeds are used by attines in the cerrado (Table 1) do not bear an elaiosome, which is the specialized seed organ that attracts ants in "true" myrmecochorous plants (Beattie 1985). Instead, the plant diaspores collected by the ants in the cerrado are mostly associated with vertebrate dispersers, especially birds (Gottsberger & Silberbauer-Gottsberger 1983, Motta & Lombardi 1990).

Seeds and fruits may constitute a large portion of the litter on the floor of tropical ecosystems (Denslow & Gomez-Diaz 1990). Fallen plant diaspores may comprise up to 400 kg/ha/yr in humid forests of southeast Brazil (Morellato 1992); in cerrado vegetation this figure is estimated as 70 kg/ha/yr. In tropical areas, large amounts of fleshy fruits may reach the floor spontaneously or by being dropped by vertebrate frugivores (Howe 1980). Many of the original vertebrate dispersers of cerrado plants are either rare or absent in most of the southern section of the cerrado distribution in São Paulo, where the vegetation occurs in small and vulnerable vestiges (Gottsberger & Silberbauer-Gottsberger 1983, Gibbs *et al.* 1983). Therefore, it is reasonable to suppose that a large portion of vertebrate-dispersed plant diaspores may end up falling to the ground in such areas, becoming available for soil arthropods such as ants, and rodents. The results from the current study support this view.

The seed-removal experiments with selected plant species from the cerrado of Mogi-Guaçu corroborate previous studies which have shown a positive effect of ant activity (including attines) on the seed biology of nonmyrmecochorous plant species. Acting as secondary dispersal agents of nonmyrmecochorous plants, attine ants were demonstrated to markedly rearrange seed distribution in rain forests, not only affecting plant reproductive success but also the spatial structure of plant populations (Roberts & Heithaus 1986, Byrne & Levey 1993; Kaspari 1993, 1996). Our study in the cerrado suggests that attine activity on plant diaspores may result in the removal of fruits and/or seeds to several meters from the experimental baiting stations. However, even if not carried to an ant nest, seeds may benefit from being dropped by ants in safe spots beneath the leaf litter where more appropriate microconditions such as moisture, temperature, and nutrients may favor seed germination (Harper 1977, Horvitz 1981). This would be particularly important in the cerrado, where soil fertility is characteristically low (Eiten 1972).

Fungal pathogens may constitute an important source of mortality to seeds on the soil of tropical habitats (Augsburger 1990). Ripe fruits of many vertebrate-dispersed plant species fall and lie intact on the ground (Galetti & Pedroni 1994). If not eaten or carried away by an animal, such fruits frequently rot during the rainy season (Janzen 1983) and seed germination success may decrease significantly after this (Augsburger 1990). The removal of fruit matter (pulp, aril) by attine ants recently has been demonstrated to play a key role for seed establishment in the Neotropical leguminous tree *Hymenaea courbaril* (Oliveira *et al.* 1995). Activity by attine ants was shown to positively affect seed germination by reducing fungal attack on fallen ripe fruits of *Hymenaea*. Similarly, the germination tests with selected cerrado plants support the hypothesis that seed cleaning by attine ants can be beneficial for the plants. Pulp removal by attines from fruits of *Ocotea pulchella*, *Prunus sellowii*, *Ouratea spectabilis*, *Rapanea umbellata* and *Psychotria stachyoides*, and aril removal from fruits of *Copaifera langsdorffii* and *Virola sebifera*, resulted in increased germination success for these species. Since ant-handled seeds of *P. stachyoides* germinated in greater proportion than control ones (pulp removed by ourselves), it is possible that ant-induced mechanical and/or chemical factors facilitate seed germination in this species. Although ant activity had no effect on germination in *P. stachyoides* seeds found in bird droppings, it is possible that seed removal from feces may decrease intra- (Roberts & Heithaus 1986, Byrne & Levey 1993; Kaspari 1993, 1996) and interspecific competition (Loiselle 1990) during seed establishment. We have no quantitative data for fungal attack on fallen plant diaspores in the cerrado, but we observed several uncleaned seeds (*i.e.*, aril not removed) of *C. langsdorffii* attacked by fungi in the study area. Indeed, Pedroni (1993) reports that attack by fungi on fallen fruits of *C. langsdorffii* accounts for a lower germination success in this plant species.

Although seeds may comprise a large portion of the diet of many ant genera in the subfamilies Formicinae, Myrmicinae and Ponerinae (Kaspari 1996), the importance of this food item varies greatly across different ant taxa (Hölldobler & Wilson 1990). Although ant-fruit/seed interactions are well documented for myrmecochorous species living in arid zones of the globe (Berg 1975, O'Dowd & Hay 1980, Bond & Slingsby 1983) and mesic environments (Beattie & Lyons 1975, Handel 1976, Beattie & Culver 1981), their ecological relevance for the dynamics of plant populations (myrmeco-

chorous or not) in South American environments is still poorly understood (but see Davidson & Epstein 1989; Moutinho 1991; Pizo & Oliveira, in press). The current study indicates that attine-fruit/seed interactions are particularly conspicuous in cerrado vegetation, suggesting that ants may play a relevant role in fruit/seed biology. The greenhouse and field data support the beneficial effect of attines as promoters of seed germination and/or secondary seed dispersers of nonmyrmecochorous plants in the cerrado. We hope that future research on the natural history and ecology of this interaction will shed more light on its relevance in Neotropical habitats.

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