

## The Use of Fruits and Seeds by Ants in the Atlantic Forest of Southeast Brazil<sup>1</sup>

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### ABSTRACT

Given the abundance of litter-foraging ants and fallen fleshy diaspores on the floor of tropical forests, interactions involving them should be common and may render important consequences for the biology of the diaspores. In this study, we surveyed the interactions between ants and non-mymecochorous diaspores along a 5-km transect in a lowland Atlantic rain forest of southeast Brazil. A diaspore is defined as any seed, fruit, or infructescence that constitutes the unit of dispersal of the plant. During two years of monthly samplings of naturally fallen diaspores, 886 ant-diaspore interactions involving 36 ant species and 56 different species of diaspores (range = 0.05–29.5 g) were recorded. The number of interactions was significantly and positively correlated with rainfall but not with mean temperature. The number of ant species recorded in the interactions was positively associated with both rainfall and temperature. Lipid-rich diaspores attracted a larger ant assemblage than those with lower contents of lipids. The seasonal pattern for ant-diaspore interactions in the Atlantic rain forest is predicted by well known seasonal patterns in ant activity and diaspore production. Other factors that also may affect the observed pattern are the massive and episodic fruiting of some plant species in which diaspores are especially attractive to ants, and a preference for lipid-rich arillate seeds. Interactions between ants and fallen non-mymecochorous diaspores may be especially common in lowland rain forests in which the abundance of ants is coupled with the year-round availability of fleshy diaspores.

### RESUMO

Interações entre formigas e diásporos não-mirmecocóricos são comuns em florestas tropicais devido à grande abundância de diásporos que caem das árvores e de formigas que forrageiam na serapilheira. Tais interações podem ter importantes consequências para a biologia dos diásporos. Neste estudo registramos as interações entre formigas e diásporos não-mirmecocóricos ao longo de um transecto de 5 km amostrado mensalmente em uma área de Mata Atlântica de baixada no sudeste do Brasil. Por diásporo não-mirmecocórico entende-se qualquer semente, fruto ou infrutescência que constitua a unidade de dispersão da planta e que não seja primariamente adaptado para a dispersão por formigas. Durante dois anos, 886 interações foram registradas envolvendo 36 espécies de formigas e 56 diásporos (peso variando entre 0,05–29,5 g). O número de interações registrado mensalmente esteve positivamente correlacionado com a pluviosidade, mas não com a temperatura média mensal. Ambos os fatores climáticos estiveram positivamente correlacionados com o número de espécies de formigas registrado mensalmente nas interações. O padrão de uso de diásporos pelas formigas foi em parte ditado pelos padrões sazonais de atividade das formigas e de produção de diásporos. Outros fatores que podem ter afetado o padrão de uso observado foram a frutificação massiva de algumas plantas cujos diásporos são especialmente atrativos para as formigas, e a preferência por diásporos ricos em lipídeos. Interações entre formigas e diásporos não-mirmecocóricos devem ser especialmente comuns em matas úmidas de baixada que combinam grande abundância de formigas com disponibilidade anual de diásporos.

*Key words:* ant-fruit/seed interaction; ant-plant interaction; Atlantic Forest; Brazil; seed dispersal.

ANTS USE A VARIETY OF PLANT-DERIVED FOOD RESOURCES, including fruits and seeds (hereafter broadly referred to as diaspores), that may account for an important part of their diets (Hölldobler & Wilson 1990, Rico-Gray 1993). A diverse assemblage of ants is known to exploit diaspores on a regular basis. In Neotropical forests, this assemblage includes species in the subfamilies Ponerinae, Formicinae, and especially Myrmicinae (Horvitz &

Beattie 1980, Kaspari 1996b, Leal & Oliveira 1998, Pizo & Oliveira 1998). Although ground-dwelling ants occasionally may climb plants to acquire diaspores (Lu & Mesler 1981, Wheelwright 1985), they more often encounter them on the forest floor. In southeast Brazil, the forest floor may receive up to 400 kg/ha/yr of diaspores (Morellato 1992). Fallen diaspores reach the forest floor either directly from the parent plant or indirectly through the activity of primary seed dispersers (Howe 1980, Laman 1996). Given this huge amount of fruitfall and the diversity and density of ground-dwelling ants (Hölldobler & Wilson 1990, Byrne 1994), a

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previously unsuspected range of interactions between ants and diaspores is likely to occur on the floor of tropical forests. In fact, in the past few years subtle relations involving ants and diaspores of non-myrmecochorous plants (*i.e.*, diaspores not especially adapted to dispersal by ants) have been discovered. Ants may rearrange the seed shadow generated by primary seed dispersers (Roberts & Heithaus 1986), play a role in seed bank dynamics (Levey & Byrne 1993), facilitate seed germination (Oliveira *et al.* 1995, Leal & Oliveira 1998, Pizo & Oliveira 1998), or promote seedling establishment (Levey & Byrne 1993, Farji Brener & Silva 1996) of non-myrmecochorous plants. Recent field experiments have shown that diaspore consumption by ants also can influence significantly colony dynamics, including the investment ratio of reproductive ants (Morales & Heithaus 1998).

The use of plant-derived food resources by ants varies seasonally due to plant phenology and variation in abiotic conditions (Hughes & Westoby 1990, Rico-Gray 1993, Rico-Gray *et al.* 1998). Collection of fallen diaspores by ants is influenced by the availability of diaspores on the plants (Leal & Oliveira 1998), which in turn, varies seasonally in tropical forests (Frankie *et al.* 1974, Foster 1982). The abundance of ants changes seasonally as a consequence of climatic conditions (*e.g.*, a prolonged dry season), leading to population fluctuations or variation in the activity of the colonies (Levings & Windsor 1982, Levings 1983). Therefore, given the temporal variability in the abundance of diaspores and ants on the forest floor, we should expect a corresponding temporal variation in the number of interactions involving them.

This study was designed to answer the following questions: (1) which ants exploit fleshy non-myrmecochorous diaspores on the floor of a lowland Atlantic rain forest in southeast Brazil?; (2) how does the ant fauna attracted to diaspores compare to the community of generalized omnivores attracted to honey and tuna baits?; (3) which diaspores are exploited?; (4) are the chemical characteristics of the diaspores predictive of their attractiveness to ants?; (5) is there any seasonal variation in the number of ant-diaspore interactions?; and (6) is such variation, if any, a consequence of climatic conditions (*e.g.*, rainfall, temperature)? Only fleshy diaspores were surveyed since they comprise most of the local flora at the study site (Almeida-Scabbia 1996), and also because they provide a diverse array of food types (pulp, aril, endosperm) that are especially attractive to ants.

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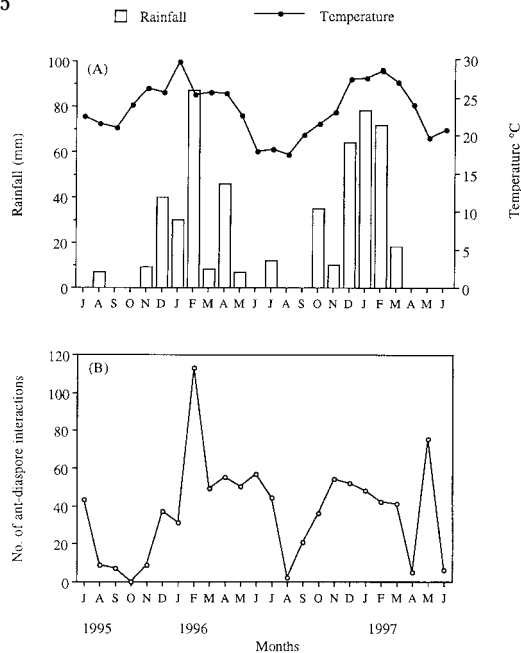


FIGURE 1. Seasonal distribution of (A) rainfall and mean temperature, and (B) number of ant-diaspore interactions recorded on the forest floor along a 5-km transect at the Parque Estadual Intervales, southeast Brazil. Weather data are from the days the ant-diaspore surveys took place.

## STUDY SITE

The study was carried out in the lowland forest of the Parque Estadual Intervales (24°14'S, 48°04'W), a 49,000-ha reserve located in São Paulo state, southeast Brazil. The site (Saibadela Research Station; 70 m elev.) received a mean annual rainfall of  $4216.2 \pm 245.5$  mm between 1994 and 1996. A cool dry season occurs between May and September, and a warm wet season between November and April (Fig. 1).

Old-growth forest (*sensu* Clark 1996) predominates at the study site; the understory is open and the canopy is 25–30 m tall. The most speciose plant families are the Myrtaceae (40 species), Leguminosae (20 species), Rubiaceae (18 species), and Lauraceae (16 species), and the most common tree species is the palm *Euterpe edulis* with a density of 255.6 individuals (DBH >5 cm) per hectare (Almeida-Scabbia 1996). The area is crossed by several 1-m wide trails that were used to carry out the surveys of ants interacting with fallen diaspores, as well as to establish the transects described below.

## MATERIALS AND METHODS

**SURVEY OF ANT-DIASPORE INTERACTIONS.**—Monthly from July 1995 to June 1997, we walked a 5-km transect along the trails that crossed the study site looking for ants on fallen diaspores. Diaspores were searched *ca* 2 m off both sides of the trail. Each time ants were found exploiting a diaspore (*i.e.*, in contact with the surface of the diaspore apparently collecting liquids or removing portions of it), an interaction was recorded and the ants were collected for identification. Additional data included the number of ants and the diaspore species. Ants were censused between 0730 and 1230 h. Voucher specimens of the ants and plants were deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP) and the herbarium of the Universidade Estadual Paulista at Rio Claro (HBRC), respectively.

We compared the ant community attracted to diaspores to the generalized omnivore community attracted to honey and tuna baits. Attini, the fungus-growing ants, were not included in the analysis due to their known dietary specialization. In December 1996, 100 tuna and 100 honey baits were distributed 5 m apart along transects established 1–2 m off-trail. To facilitate ant visualization, small pieces (4 × 4 cm) of white filter paper were used as substrates for baits. Baits were set upon the transects at 0800 h and the number and identity of ant species attracted to them were recorded after one hour. Different trails were used for tuna and honey baits, and data for both transects were pooled for analysis. Given the ant patchiness on the forest floor of Neotropical forests (Kaspari 1996a), and since most ground-dwelling ant species rarely walk more than 1 m from their colonies (Byrne & Levey 1993, Byrne 1994), a 5-m space between baits was considered adequate to insure independent discoveries by different ant colonies. We used Pearson correlations to test for the association between the number of ant-diaspore interactions recorded and the weather data (rainfall and mean temperature) from the days the surveys took place. Although we also collected ant and plant species involved in interactions recorded during nonsystematic qualitative observations, these were not included in any of the statistical analyses.

**CHEMICAL CUES TO ANT-DIASPORE INTERACTIONS.**—The relationship between chemical composition of the fleshy portion (pulp or aril) of the diaspores and the number of ant species they attracted was investigated for 26 diaspore species representing 15

families (Table 2). These diaspores were selected solely on their availability, and trials were done throughout the year during the fruiting period of each species. Fifty fresh diaspores of each species were placed along the trails 5 m apart and 1–2 m off-trail. The diaspores were placed on small pieces (4 × 4 cm) of white filter paper to facilitate ant visualization. Observations began *ca* 0800 h and ants exploiting the diaspores were recorded in four scan samples made at 15-min intervals during one hour. Pulp or arils were collected from recently fallen diaspores and frozen until chemical analyses were performed. Lipids and proteins were analyzed according to the methods described in Bligh and Dyer (1959) and the AACC (1995; method no. 46-13), respectively. Ash content was measured by incineration, and the amount of total carbohydrates was obtained by subtraction. The proportion of dry mass for each of the chemical components analyzed was arcsine transformed to perform the Pearson correlations with the number of ant species attracted to the diaspores.

## RESULTS

**PATTERNS OF ANT-DIASPORE INTERACTIONS.**—We recorded a total of 886 ant-diaspore interactions in the monthly samplings during the two-year study. Thirty-six ant species (17 genera, 4 subfamilies) and 56 species of diaspores (40 genera, 28 families) were involved in these interactions (5 additional ant species and 12 additional plant species were involved in interactions recorded in qualitative surveys; Table 1; Appendix). The Myrmicinae was the most frequently recorded ant subfamily (25 species), followed by the Ponerinae (7 species), Formicinae (3 species), and Dolichoderinae (1 species). Two species of *Pheidole* (sp. 1 and sp. 7) and one species of *Solenopsis* (sp. 1) together accounted for 64.1 percent of the ant-diaspore interactions recorded at the study site (Table 1). Ants were observed removing diaspores, tearing off pieces of diaspores, and collecting liquids from them (the last two behaviors were more common). In general, different ants treated the diaspores in different ways: (1) large ponerine ants (*Pachycondyla* and *Odontomachus*) individually moved diaspores of up to 1.0 g to their nests; (2) small and medium-sized ants (*Pheidole*, *Crematogaster*) recruited workers and fed on the diaspore on the spot (diaspores  $\leq 0.05$  g were occasionally transported); and (3) *Solenopsis* (sp. 4 and sp. 5) covered the diaspore with soil before collecting liquid and solid food from it.

TABLE 1. *Ant species recorded exploiting diaspores on the forest floor of Parque Estadual Intervales, southeast Brazil. Ant species followed by an asterisk were not recorded in the 5-km transect.*

Ant subfamilies/species	Number of diaspore species used <sup>a</sup>	Number of records in the 5-km transect
<b>Ponerinae</b>		
1. <i>Ectatomma edentatum</i>	19	7
2. <i>Gnamptogenys</i> sp.	17	5
3. <i>Hypoponera</i> sp. 1	1	2
4. <i>Hypoponera</i> sp. 2	1	1
5. <i>Odontomachus chelifer</i>	13	3
6. <i>O. affinis</i> *	2	0
7. <i>O. meinerti</i>	5	1
8. <i>Pachycondyla striata</i>	21	5
9. <i>P. apicalis</i> *	4	0
<b>Myrmicinae</b>		
10. <i>Crematogaster</i> sp. 1	5	2
11. <i>Crematogaster</i> sp. 2	9	4
12. <i>Pheidole</i> sp. 1	45	117
13. <i>Pheidole</i> sp. 2	14	30
14. <i>Pheidole</i> sp. 3	41	49
15. <i>Pheidole</i> sp. 7	58	254
16. <i>Pheidole</i> sp. 8	2	5
17. <i>Pheidole</i> sp. 9	32	27
18. <i>Pheidole</i> sp. 10	4	4
19. <i>Pheidole</i> sp. 11	16	19
20. <i>Pheidole</i> sp. 12	2	2
21. <i>Solenopsis</i> sp. 1	49	197
22. <i>Solenopsis</i> sp. 2	19	20
23. <i>Solenopsis</i> sp. 4	9	4
24. <i>Solenopsis</i> sp. 5	22	46
25. <i>Hylomyrma</i> sp.*	1	0
26. <i>Octostruma</i> sp.	2	1
<b>Myrmicinae (Attini)</b>		
27. <i>Apterostigma</i> sp. 1	8	4
28. <i>Apterostigma</i> sp. 2	1	2
29. <i>Acromyrmex subterraneus</i>	22	5
30. <i>Acromyrmex</i> sp. 1	7	1
31. <i>Acromyrmex</i> sp. 2	14	8
32. <i>Acromyrmex</i> sp. 4*	1	0
33. <i>Trachymyrmex</i> sp. 1	1	1
34. <i>Trachymyrmex</i> sp. 2	2	1
35. <i>Cyphomyrmex</i> sp.	7	6
36. <i>Sericomyrmex</i> sp.	11	21
<b>Dolichoderinae</b>		
37. <i>Linepithema</i> sp. 1	8	2
<b>Formicinae</b>		
38. <i>Brachymyrmex</i> sp. 1	21	22
39. <i>Brachymyrmex</i> sp. 2	1	1
40. <i>Paratrechina</i> sp. 1*	1	0
41. <i>Paratrechina</i> sp. 2	1	1

<sup>a</sup> Includes records made during the monthly surveys on the 5-km transect, records from the feeding trials used to investigate chemical cues in the attraction of ants, and incidental records of diaspores being explored by ants.

Large diaspores ( $\gg 1.0$  g) always were consumed on the spot, irrespective of the ant species. Virtually all the ants were recorded on diaspores in a ripe or pre-ripe condition. The number of ants recorded on diaspores ranged from 1 to 80. The number of interactions recorded for each non-attine ant species was highly correlated with their frequencies on tuna and honey baits (Spearman's rank correlation:  $r_s = 0.77$ ,  $N = 34$ ,  $P < 0.001$ ), indicating that the use of fallen diaspores by these ants occurred according to their relative abundance on the forest floor. With the exception of one arboreal species (*Linepithema* sp. 2), all the non-attine ants attracted to baits also were recorded on diaspores, while ten of the species recorded on diaspores were not recorded at baits.

Ants were observed exploiting diaspores of trees (46 species), hemiepiphytes (5 species), lianas and epiphytes (2 species each), and shrubs (1 species). Myrtaceae was the family with the largest number of species (16) exploited by ants, as it is the most speciose family at the study site (Appendix). Ants exploited arils of 12 diaspores and the pulp of the remaining ones. In only two instances were ants also observed digging on the endosperm of seeds. Diaspores varied enormously in size, ranging from 0.05 g (*Hyeronima alchorneoides* and *Tetrorchidium rubrivenium*, Euphorbiaceae) to 29.5 g (*Astrocaryum aculeatissimum*, Arecaceae). Some diaspores were exploited only after being crushed by primary dispersers, thus permitting ant access to the fleshy parts (Appendix).

There was great intra- and interannual variation in the number of ant-diaspore interactions recorded monthly, ranging from 0 to 113 ( $\bar{x} \pm SD = 36.9 \pm 2.7$  interactions/mo). Months with low numbers of interactions were followed immediately by months rich in interactions and vice versa (Fig. 1B). The number of interactions was significantly correlated with rainfall on the days of the survey ( $r = 0.55$ ,  $N = 24$ ,  $P = 0.005$ ) but not with mean temperature ( $r = 0.18$ ,  $N = 23$ ,  $P = 0.40$ ). The number of ant species recorded in the interactions, however, was associated with both rainfall ( $r = 0.59$ ,  $N = 24$ ,  $P = 0.002$ ) and mean temperature ( $r = 0.41$ ,  $N = 23$ ,  $P = 0.04$ ). A maximum of 11 ant species was recorded during the dry/cold months, while up to 19 species exploited diaspores in the remaining period.

THE CHEMICAL COMPOSITION OF DIASPORES AND ITS EFFECT ON ANT ATTRACTION.—The lipid, protein, and carbohydrate contents of the pulp or aril of the 26 diaspores used in the feeding trials are listed

TABLE 2. Number of ant species attracted to the diaspores and the chemical composition (percent dry mass) of their pulp or aril. Plant species followed by an asterisk have arillate diaspores.

Plant families/species	Number of ant species	Percent of dry mass			
		Lipids	Protein	Total carb. <sup>a</sup>	Ash
Annonaceae					
<i>Rollinia sericea</i>	13	9.0	6.3	78.7	6.0
Arecaceae					
<i>Euterpe edulis</i>	4	19.7	7.5	69.5	2.7
<i>Geonoma pauciflora</i>	5	2.2	4.9	—	—
Cecropiaceae					
<i>Pouroma guianensis</i>	10	1.8	7.5	85.5	5.1
Celastraceae					
<i>Maytenus robusta*</i>	5	1.1	5.0	92.2	1.7
Clusiaceae					
<i>Garcinia gardneriana</i>	8	5.0	5.0	86.6	3.4
Euphorbiaceae					
<i>Alchornea glandulosa*</i>	10	68.4	7.6	21.7	2.4
<i>Hyeronima alchorneoides</i>	6	7.9	6.3	—	—
Lauraceae					
<i>Cryptocarya moschata</i>	8	4.2	8.0	84.0	3.8
Meliaceae					
<i>Cabralea canjerana*</i>	16	70.8	10.3	16.5	2.3
Myristicaceae					
<i>Virola gardneri*</i>	11	88.8	4.9	5.3	1.0
<i>V. oleifera*</i>	13	61.8	4.6	32.1	1.4
Myrtaceae					
<i>Campomanesia xanthocarpa</i>	7	1.6	8.6	—	—
<i>Eugenia melanogyna</i>	8	2.5	4.7	88.1	4.6
<i>E. multcostata</i>	6	3.5	9.7	—	—
<i>E. oblongata</i>	4	18.7	9.1	67.4	4.7
<i>E. stictosepala</i>	8	5.2	8.5	82.3	4.0
<i>Eugenia</i> sp. 2	5	17.4	10.9	67.2	4.5
<i>Eugenia</i> sp. 5	12	3.7	12.2	80.7	3.3
<i>Gomidesia spectabilis</i>	5	5.6	6.1	84.2	4.1
<i>Myrceugenia reitzii</i>	9	8.0	8.5	77.4	6.0
Olacaceae					
<i>Heisteria silvianii</i>	16	29.7	12.8	52.4	5.1
Quiinaceae					
<i>Quiina glaziovii</i>	8	8.0	2.9	69.5	19.6
Sapotaceae					
<i>Pouteria venosa</i>	7	11.0	8.7	76.6	3.8
Verbenaceae					
<i>Citharexylum myrianthum</i>	11	6.3	6.8	82.7	4.1
<i>Vitex</i> sp.	6	1.1	4.1	—	—
CV (%)		140.4	34.5	38.6	84.3

<sup>a</sup> Total carb. = Total carbohydrate.

in Table 2. Lipid content was the most variable component (CV = 140.4%), being generally higher in arils ( $58.1 \pm 33.4\%$  dry mass,  $N = 5$ ) than in pulp ( $8.2 \pm 7.4\%$ ,  $N = 21$ ). A significant positive correlation was detected between lipid content and the number of ant species attracted to the diaspores ( $r = 0.50$ ,  $N = 26$ ,  $P = 0.01$ ). In contrast, a significant negative correlation was found for carbohydrates ( $r = -0.48$ ,  $N = 23$ ,  $P = 0.02$ ). No correlation was detected for proteins ( $r = 0.28$ ,  $N = 26$ ,  $P = 0.16$ ).

## DISCUSSION

Ants exploiting fallen diaspores are commonplace to those who pay attention to the floor of tropical forests. Diaspores represent part of the diet of many ant species (Hölldobler & Wilson 1990), and even predominantly carnivorous species have been observed collecting them (Horvitz & Beattie 1980, Pizo & Oliveira 1998). Moreover, fleshy diaspores are plentiful on the floor of tropical forests, and if not taken away by secondary dispersers or predators, they rot in a few days (Augsburger 1990, Oliveira *et al.* 1995). To our knowledge, this is the first study to systematically document the use of fallen diaspores by the ground-dwelling ant community of a tropical forest. Rico-Gray (1993) has recorded, among many other plant-derived resources, the use of fallen diaspores by ants in the dry vegetation (which included forest, sand dunes, and mangroves) of Mexico. Only rarely, however, did Rico-Gray (1993) observe ant-diaspore interactions, in contrast to the present study which reports on average > 30 such interactions per month in a 5-km transect. This difference between the two studies may be due to two nonexclusive factors. First, ours was more focused on finding ants on fallen diaspores than was Rico-Gray's (1993) study, which emphasized the diversity of plant material used by ants. Second, interactions between ants and fallen diaspores may be more common in rain forests than in drier vegetation. Ants are sensitive to moisture conditions (Levings & Windsor 1984, Kaspari 1993) and usually have their abundance limited during prolonged dry seasons (Levings & Windsor 1982). Additionally, fleshy fruit production generally is positively correlated with rainfall (Jordano 1993). Compared to rain forests, dry forests tend to have a greater proportion of species with dry fruits that lack fleshy parts (Frankie *et al.* 1974), and perhaps are likely to attract a less diverse ant assemblage. Analyzing the interactions between ants and diaspores of *Calathea* species (Mar-

antaceae) at La Selva Biological Station and at Corcovado National Park of Costa Rica, Bello y Bello (1997) observed that ant-diaspore interactions were more frequent at the former site. Although both sites receive roughly the same amount of annual rainfall, Corcovado experiences a longer and well-marked dry season that may have accounted for the difference (Bello y Bello 1997).

Not only were the interactions between ants and diaspores common at our study site, they also involved a considerable part of the ground-dwelling ant community and even some arboreal species (*e.g.*, *Linepithema* sp. 1, *Crematogaster* spp.). The absence of *Camponotus* and *Pseudomyrmex* species is noteworthy given that both genera are generally well represented in Neotropical forests (Wilson 1987). In fact, some species in these two genera could be seen at our study site. *Camponotus* ants, however, seem to prefer feeding on extrafloral nectar and homopteran honeydew (Oliveira & Brandão 1991, Rico-Gray 1993, Del-Claro & Oliveira 1999), while most *Pseudomyrmex* species are arboreal (Ward 1991) and rarely descend to exploit fallen diaspores.

The use of fallen diaspores occurred throughout the year, following a pattern significantly associated with rainfall but not with temperature. Seasonal fluctuation in insect abundance is positively associated with rainfall in tropical forests (Wolda 1978). Ant activity and ant species abundance are reported to vary seasonally in tropical moist forests, and are positively correlated with rainfall (Levings 1983). Increased moisture availability on the forest floor leading to more appropriate conditions for ant activity probably accounts for this pattern (Levings & Windsor 1984, Kaspari 1993). Seasonal variation in the use of plant-derived food by ants can be associated with rainfall and temperature in Mexican habitats, but the effect of these environmental parameters has differed among habitats (Rico-Gray 1993, Rico-Gray *et al.* 1998). Although the seasonal pattern reported here for ant-diaspore interactions in the Atlantic Forest corroborates the general tendency found in other Neotropical areas, other factors also may be affecting the pattern found at our study site. First, the massive and episodic fruiting of some species produced pulses of especially attractive diaspores (*e.g.*, *Garcinia gardneriana* in February 1996, and *Posoqueria latifolia* in May 1997; Fig. 1B). Once these diaspores become available, a great number of ant species exploit them irrespective of the time of year. Second, the study site lacked a pronounced dry season which may have accounted for the relative

uniformity of fleshy fruit production throughout the year (Frankie *et al.* 1974). It has been demonstrated that the production of fleshy fruits usually is depressed during prolonged dry periods (Frankie *et al.* 1974, Foster 1982). A simultaneous study on the phenology of 380 fleshy fruit trees (*ca* 115 species) has shown a pattern of continuous fruit production at our study site (L. P. C. Morelato & V. Zipparro, pers. comm.). Therefore, fleshy diaspores are available for ants on a year-round basis.

Although ants as a whole exploited the diaspores opportunistically as they appeared on the forest floor, lipid-rich diaspores attracted a larger assemblage of ants than those with lower contents of lipids. A possible confounding effect of this result is related to the time of year when different diaspores were presented to ants, which as we have observed, can influence the number of ant species interacting with them. Since only fresh diaspores were used, feeding trials necessarily were run in the months when ripe diaspores were available; however, only 8 out of the 26 different diaspores were tested in the potentially ant-poor period (May–September), thus with minor effects on the trend observed. Many studies have shown experimentally that ants are especially attracted by lipids, which are either of important nutritional value to some ants, or function as behavioral releasers for others (Marshall *et al.* 1979, Skidmore & Heithaus 1988, Brew *et al.* 1989). Elaiosomes (the food bodies of myrmecochorous diaspores) are typically rich in lipids (Beattie 1985). Moreover, lipid-rich non-myrmecochorous diaspores attracted a large number of ant species at our study site (Pizo & Oliveira 1998). Given that different ant species are likely to provide different treatments to diaspores (Horvitz & Beattie 1980, Hughes & Westoby 1992, Leal & Oliveira 1998), lipid-rich diaspores potentially may benefit from a diverse array of fates provided by the ants (*e.g.*, removal to the nests, cleaning of pulp or aril, covering with soil particles; Pizo & Oliveira 1998). The negative correlation between carbohydrate content of the diaspores and number of ant species attracted is an artifact rather than an actual cue to diaspore “preference” by ants. Lipids and carbohydrate contents were highly negatively cor-

related in our sample ( $r = -0.96$ ,  $N = 23$ ,  $P < 0.001$ ), as they usually are for diaspores (Jordano 1993). There is no reason to suspect that ants avoided carbohydrate-rich diaspores. On the contrary, seed selection by harvesting ants has been demonstrated to be positively associated with the carbohydrate content of the seeds (Kelrick *et al.* 1986); however, there is no doubt that lipid-rich diaspores are preferred more than carbohydrate-rich ones.

In conclusion, a great part of the ground-dwelling ant community at the study site exploited diaspores at least occasionally. They did so opportunistically as the diaspores became available on the floor. As a result, a variety of fleshy diaspores was exploited, and lipid-rich diaspores in particular attracted a broad array of ant species. Evidently, we should not expect that all ant–diaspore interactions observed in this study will render some benefit to the plants; however, interactions involving the removal and/or cleaning of fleshy diaspores by ants may benefit the plants by promoting escape from seed predators and/or an increased germination success (*e.g.*, O’Dowd & Hay 1980, Bond & Slingsby 1984, Pizo & Oliveira 1998, Leal & Oliveira 1998). The kind of ant–plant interaction investigated in this study may be especially rich and common in lowland rain forests in which the diversity of ants (Olson 1994) is coupled with the abundance and year-round availability of fleshy diaspores.

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APPENDIX. *Plant diaspores exploited by ants on the forest floor of Parque Estadual Intervales, southeast Brazil. Data were gathered during monthly surveys along a 5-km transect, from feeding trials used to investigate the chemical cues involved in ant attraction, and from qualitative surveys of diaspores being explored by ants. Plant species followed by an asterisk were not recorded in the 5-km transect. Plant species and families are arranged in alphabetical order. Ant species numbers as in Table 1.*

Plant families/species	Growth form <sup>a</sup>	Ant species	Months
<b>Annonaceae</b>			
<i>Rollinia sericea</i>	T	1, 2, 5, 8, 9, 11, 12, 14, 15, 17, 21, 27, 29, 37	Feb.
<b>Arecaceae</b>			
<i>Astrocaryum aculeatissimum</i> <sup>b</sup>	T	12	Dec.
<i>Euterpe edulis</i>	T	14, 12–16, 18, 19, 21–25, 27, 30	Apr.–Aug.
<i>Geonoma pauciflora</i> *	S	12, 14, 15, 17, 21	May
<b>Araceae</b>			
<i>Heteropsis oblongifolia</i>	H	15, 17	Mar.
<i>Monstera adansonii</i>	H	12	Oct.
<i>Philodendron corcovadense</i>	H	1, 9, 11–14, 21, 29	Jan.–Dec.
<i>P. appendiculatum</i> *	H	1, 8, 12, 15, 17, 21, 38	Feb.
<b>Bromeliaceae</b>			
<i>Aechmea nudicaulis</i>	E	1, 2, 10–15, 17, 21	Jan.–Dec.
<b>Burseraceae</b>			
<i>Protium widgrenii</i>	T	1, 13, 15, 21, 39	Nov.–Dec.
<b>Caesalpinaceae</b>			
<i>Copaifera trapezifolia</i>	T	12, 14, 15, 17, 21, 22, 29, 31, 36	July–Sept.
<b>Cecropiaceae</b>			
<i>Cecropia glaziovii</i>	T	5, 8, 12, 14, 15, 21, 22, 31	Jan.
<i>Pouroma guianensis</i>	T	2, 3, 13–16, 18, 22, 23, 30, 31, 32, 36, 39	Feb.–Mar.
<b>Celastraceae</b>			
<i>Maytenus aquifoliaum</i>	T	15	Nov.–Dec.
<i>M. robusta</i>	T	12, 14, 15, 17, 21, 36	July
<b>Chrysobalanaceae</b>			
<i>Parinari excelsa</i>	T	1, 12, 14, 15, 17, 21, 22, 29, 36, 38	Nov.–Jan.
<b>Clusiaceae</b>			
<i>Clusia parviflora</i>	H	11, 12, 15, 21, 22	Dec.–Feb.
<i>Garcinia gardneriana</i> <sup>b</sup>	T	1–3, 5, 7, 8, 10–15, 17, 21–24, 26, 29, 30, 31, 35, 36, 38	Feb.–Mar.
<b>Commelinaceae</b>			
<i>Dichorisandra</i> sp.*	B	1, 5, 7, 8, 11, 12, 14, 15, 21, 22, 27, 37, 38	Feb.–Mar.
<b>Elaeocarpaceae</b>			
<i>Sloanea guianensis</i>	T	14, 15, 21, 22, 24, 36	Jan.
<b>Euphorbiaceae</b>			
<i>Alchornea glandulosa</i> *	T	1, 8, 9, 12, 14, 15, 17, 19–23, 28	Oct.–Nov.
<i>A. triplinervia</i>	T	1, 8, 14, 15, 21, 24, 31	Jan.
<i>Hyeronima alchorneoides</i> *	T	1, 2, 8, 12, 14, 15, 17, 19, 21, 22, 27, 29, 31, 38	Feb.–Mar.
<i>Tetrorchidium rubrivenium</i>	T	11, 15, 21	Dec.–Jan.
<b>Hippocrateaceae</b>			
<i>Salacia</i> sp. <sup>b*</sup>	L	19, 24, 32, 34	Nov.–Dec.
<b>Lauraceae</b>			
<i>Cryptocarya moschata</i>	T	6, 11, 13, 15, 16, 18, 20, 22, 23, 25, 27, 30, 38, 39	May–July
<b>Marcgraviaceae</b>			
<i>Marcgravia polyantha</i>	E	12, 15	Sept.–Nov.
<b>Melastomataceae</b>			
<i>Clidemia blefarodes</i>	L	15	Mar.

APPENDIX. *Continued.*

Plant families/species	Growth form <sup>a</sup>	Ant species	Months
<b>Meliaceae</b>			
<i>Cabralea canjerana</i>	T	1, 2, 5–15, 17, 21–24, 29, 36–38, 40, 41	Sept.
<i>Guarea macrophylla</i> *	T	14	June
<b>Menispermaceae</b>			
<i>Abuta selloana</i> <sup>b</sup>	L	12, 14, 15, 24	July–Dec.
<b>Moraceae</b>			
<i>Brosimum</i> sp.	H	2, 8, 12, 15, 29	Jan.
<i>Ficus gomelleira</i> *	T	1, 15, 17, 24, 36	Jan.
<i>Ficus</i> sp. 1	T	15, 19, 21, 23	Jan.–Dec.
<i>Ficus</i> sp. 2	T	21, 24	Feb.
<b>Myristicaceae</b>			
<i>Virola gardneri</i>	T	1, 2, 7, 8, 12, 14, 15, 17, 19, 21, 24, 29, 37	Sept.–Dec.
<i>V. oleifera</i>	T	1, 2, 5, 6, 8, 12–15, 17, 19–24, 29, 38	July–Nov.
<b>Myrtaceae</b>			
<i>Campomanesia xanthocarpa</i>	T	3, 13–16, 18–20, 22–25, 37	Jan.–Feb.
<i>C. nerifolia</i>	T	12, 14, 15, 18, 21, 24, 35	Mar.
<i>Eugenia cuprea</i>	T	5, 15	Mar.
<i>E. melanogyna</i>	T	8, 11, 12, 14, 15, 17, 21, 29, 31	Nov.–Dec.
<i>E. mosenii</i>	T	21	May
<i>E. multcostata</i>	T	14, 15, 17, 21, 27, 28, 30, 36	Mar.
<i>E. oblongata</i>	T	12–15, 21, 22, 24, 31	Nov.
<i>E. stictosepala</i>	T	1, 2, 8, 9, 12, 14, 15, 17, 21, 22, 29, 30, 31, 35, 38	Apr.–May
<i>Eugenia</i> sp. 1*	T	21, 36	June
<i>Eugenia</i> sp. 2	T	12, 14, 15, 17, 19, 21	July–Sept.
<i>Eugenia</i> sp. 4	T	19	Nov.
<i>Eugenia</i> sp. 5	T	1, 5, 8, 11, 12, 14, 15, 21, 24, 29, 31, 37, 38	Dec.
<i>Gomidesia spectabilis</i> *	T	12, 14, 15, 17, 21	July–Aug.
<i>Marihiera tomentosa</i>	T	14	Aug.
<i>Myrceugenia myrcioides</i>	T	12	May
<i>M. reitzii</i>	T	1, 8, 12, 14, 15, 17, 21, 29, 31, 38	Mar.
undetermined 1	T	15	Aug.
undetermined 2	T	15	Sept.
<b>Nyctaginaceae</b>			
<i>Guapira opposita</i>	T	12, 15	Oct.
<b>Olaceae</b>			
<i>Heisteria silviani</i>	T	1, 4, 7, 11–14, 16–20, 22, 23, 26, 28, 36, 37	Jan.
<i>Tetrastylidium grandifolium</i>	T	10, 14, 16, 18, 20–22, 26, 30, 33, 37	Nov.
<b>Quiinaceae</b>			
<i>Quiina glaziovii</i>	T	5, 7, 8, 12, 14, 15, 17, 21, 29, 38	Jan.–Mar.
<b>Rubiaceae</b>			
<i>Posoqueria latifolia</i> <sup>b</sup>	T	2, 5, 8, 12–17, 21, 24, 36, 38	May
<i>Psychotria suterella</i>	S	15, 21	Jan.–Apr.
<b>Sapindaceae</b>			
<i>Cupania oblongifolia</i>	T	8, 12, 14, 19, 21, 24	Dec.–Jan.
<b>Sapotaceae</b>			
<i>Chrysophyllum viride</i>	T	14, 15, 17, 19, 21, 24, 29, 31, 35, 38	Mar.–Apr.
<i>Pouteria venosa</i>	T	14, 15, 21, 24, 27, 29, 31	Feb.
<b>Ulmaceae</b>			
<i>Trema micrantha</i> *	T	2, 12, 14, 15, 17, 21, 35, 38	Mar.
<b>Verbenaceae</b>			
<i>Citharexylum myrianthum</i>	T	1, 2, 6, 9, 13–16, 18, 22, 30–32, 36, 38–40	Feb.
<i>Vitex</i> sp.*	T	12, 14, 15, 21, 29, 38	Mar.

<sup>a</sup> Habits: T = tree, S = shrub, L = liana, H = hemiepiphyte, E = epiphyte, B = herb.

<sup>b</sup> Diaspores exploited by ants only after being crushed by primary dispersers, thus permitting ant access to the fleshy parts.