19 Ants as Seed Dispersers of Fleshy Diaspores in Brazilian Atlantic Forests

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Introduction

Most studies on seed dispersal of tropical species have hitherto focused mostly on fruit consumption and seed deposition patterns generated by primary seed dispersers (Estrada and Fleming, 1986; Fleming and Estrada, 1993; Levey et al., 2002), but recent studies have emphasized the importance of post-dispersal events for seed fate and demography of plant species (see Chambers and MacMahon, 1994; Andresen, 1999). For instance, seed removal by ants from frugivore defecations has been shown to affect seed distribution in tropical forests (Roberts and Heithaus, 1986; Kaspari, 1993; Pizo and Oliveira, 1999), and this in turn may have a marked influence on seedling growth and survival (Levey and Byrne, 1993; Böhning-Gaese et al., 1999; Passos and Oliveira, 2002). Ants can transport fruits that have fallen from parent plants, acting as primary seed dispersers, or fruits and seeds dropped by vertebrate frugivores, serving as secondary seed dispersers. In either case, ant-mediated seed dispersal can affect plant recruitment (Böhning-Gaese et al., 1999; Passos and Oliveira, 2002). Fallen fruits can weigh up to 400 kg/ha/year in humid forests of south-east Brazil (Morellato, 1992).

Such considerable fruitfall applies not only on a community-wide basis, but also for individual plants. For instance, over 50% of the seed crop produced by Ficus trees in a Bornean rainforest falls beneath parent plants (Laman, 1996), and in the Brazilian Atlantic forest ≈ 30% of the diaspores taken by birds from Cabralea canjerana (Meliaceae) trees drop to the ground below the parent tree, which, for some especially fecund trees, may represent nearly 8000 diaspores over the entire fruiting season (Pizo, 1997).

The abundance and diversity of ants in the tropics are remarkable, and ground-dwelling ants are perhaps the most likely organisms to encounter diaspores on the floor of tropical forests, where ant density may exceed 800 workers/m² (Hölldobler and Wilson, 1990). For instance, in the 1500 ha of rainforest at La Selva Biological Station (Costa Rica), densities of ant colonies exceed 4 nests/m² (Kaspari, 1993), and at least 437 ant species can be encountered (Longino et al., 2002). Given the heavy fruitfall and the diversity and density of tropical ground-dwelling ants (Byrne, 1994), a wide range of interactions between ants and fleshy fruits (hereafter called diaspores, sensu van der Pijl, 1982) is expected (Kaspari, 1993; Leal

and Oliveira, 1998; Pizo and Oliveira, 2000, 2001; Passos and Oliveira, 2003). Indeed, in the past decade, subtle relations involving ants and fleshy diaspores have been documented in tropical environments (Beattie and Hughes, 2002). Even leaf-cutter ants (tribe Attine), traditionally considered pests, have been shown to positively influence the biology of seeds (Farji-Brener and Silva, 1996; Wirth et al., 2002).

We have been investigating the interactions between ground-dwelling ants and vertebrate-dispersed diaspores in the Brazilian Atlantic forest. Results from a series of field studies have both improved our understanding of these interactions and raised relevant questions for future research (Oliveira et al., 1995; Pizo and Oliveira, 1998, 1999, 2000, 2001; Passos and Oliveira, 2002, 2003). In this chapter we first provide an overview of our recent findings by describing:

1. The ant and plant species involved in these interactions.
2. The attributes of ants and diaspores that mediate the interaction.
3. The possible consequences of the interaction for plants.

We then examine how these interactions vary spatially by comparing the patterns of selected ant–diaspore interactions occurring at our two main study areas in the Brazilian Atlantic forest. Possible causes underlying such patterns are examined and discussed, and avenues of future research are suggested. Although ants may climb on to plants to gather diaspores (Lu and Mesler, 1981; Dalling and Wirth, 1998) and very often remove seeds from vertebrate defecations (Kaspari, 1993; Levey and Byrne, 1993; Pizo and Oliveira, 1999), our focus here is on interactions involving ants and fallen (either directly from plants or dropped by primary seed dispersers) diaspores on the forest floor.

Study Areas

Our studies were carried out at two sites in extensive, well-preserved Atlantic forest reserves in São Paulo State, south-east

Brazil: the lowland forest of Parque Estadual Intervales (49,000 ha) at Saibadela Research Station (hereafter PEI; 24°14′S, 48°04′W; 70 m above sea level), and the sandy plain forest (locally called 'restinga' forest) that grows on the lowest portion of Parque Estadual da Ilha do Cardoso (hereafter PEIC; 25°03′S, 47°53′W; 2–3 m above sea level), a 22,500 ha island. Separated 94 km from each other, PEI and PEIC sites differ in several aspects, including soil, annual rainfall, and fruit production (Table 19.1). Old-growth forest (sensu Clark, 1996) predominates at PEI; the understorey is open and the canopy is 25–30 m tall (Almeida-Scabbia, 1996). The vegetation at PEIC is characterized by 5–15 m tall trees forming an open canopy, with abundant bromeliads on the ground layer (Barros et al., 1991). At both sites, there is a cool and less humid season between April and August, and a warm, wet season from September to May. No well-marked dry season occurs at PEI because no month receives less than 100 mm of rainfall.

Ant Attendance to Diaspores

A great variety of ant and diaspore species interact on the floor of the Atlantic forest. At PEI, 36 ant species (17 genera, four subfamilies) and 56 species of diaspores (40 genera, 28 families) are potentially involved in these interactions. At PEIC, potential ant–diaspore interactions include 48 ant species (19 genera, four subfamilies) and 44 plant species (40 genera, 26 families). Myrmicinae was the most frequently recorded ant subfamily at both sites (25 and 36 species at PEI and PEIC, respectively), followed by Ponerinae (seven and five species, respectively). The subfamilies Formicinae, Dorylinae and Dolichoderinae were also recorded, but much less frequently. Plant species whose diaspores were exploited by ants included trees, shrubs, herbs, lianas, epiphytes, hemiepiphytes and parasites. Diaspores ranged in weight from 0.02 g to 29.5 g. Complete lists of ant and plant species names for PEI and

Table 19.1. Summary of abiotic and biotic features of Parque Estadual Intervales (PEI) and Parque Estadual da Ilha do Cardoso (PEIC) related to the interactions between ants and fleshy, vertebrate-dispersed diaspores on the forest floor.

	PEI	PEIC
Soil	Alluvial, rich	Sandy, poor
Annual precipitation (mm)	4000	2200
Fruit production	High	Low
Litter depth	Thick	Thin
(mean no. of leaves ± SD)	(3.4 ± 1.1)	(1.6 ± 1.3)
Biomass of litter arthropods (g/trap)	High	Low
(mean ± SD)[a]	(0.14 ± 0.15)	(0.06 ± 0.05)
No. of ant species that exploit diaspores	36	48
No. of diaspore species exploited by ants	56	44
Frequency of interaction (interactions/km)[b]	7.4	2.2
Abundance of ponerines (%)[c]		
Pachycondyla striata	15	31
Odontomachus chelifer	6	23
Diaspores exploited by ponerines (%)		
Pachycondyla striata	38	80
Odontomachus chelifer	23	45
Interactions with ponerines (%)[d]	1	35

[a]Arthropods sampled with 50 and 41 pitfall traps (plastic cups 6.5 cm wide × 8.0 cm height) run for 24 h at PEI and PEIC, respectively; see text for details.
[b]5-km and 1.4-km trails sampled monthly during 2 consecutive years at PEI and PEIC, respectively.
[c]Percentage of tuna baits (n = 100) with each ant species.
[d]*Pachycondyla striata* and *Odontomachus chelifer* pooled.

PEIC are given in Pizo and Oliveira (2000) and Passos and Oliveira (2003), respectively.

Ants treated the diaspores in different ways. Ants were observed removing whole diaspores, tearing pieces off diaspores, or collecting liquids from them (the last two behaviours were more common). The behaviour of ants towards diaspores depended in part on the size of the diaspore relative to the size of the ant: (i) large ponerine ants (total length 1–1.5 cm, mainly *Pachycondyla striata* and *Odontomachus chelifer*) individually removed diaspores of up to 1 g to their nests (Fig. 19.1A, 19.1B); (ii) small and medium-sized ants (e.g. *Pheidole, Cremato-gaster*) recruited 1–110 workers and fed on the diaspore on the spot (Fig. 19.1C), but diaspores ≤ 0.05 g were occasionally transported; and (iii) some *Solenopsis* species covered the diaspore with soil before collecting liquid and solid food from it (Fig. 19.1D). Although large diaspores (> 1 g) were generally consumed on the spot (Figs 19.1E, 19.1F, 19.2A), heavy fruits containing small seeds (e.g. *Psidium* spp.; > 10 g fruit weight) often had the seeds removed with bits of pulp attached by *Pachycondyla* and *Odonto-machus*, or by large attines such as *Acro-myrmex* (Pizo and Oliveira, 2000; Passos and Oliveira, 2003).

The distance of diaspore displacement varied greatly, depending mostly on the relative sizes of the diaspore and the ant. Small diaspores (< 0.10 g) can be displaced up to 100 m by leaf-cutter ants (tribe Attini) (Fig. 19.2A–D; Dalling and Wirth, 1998; Leal and Oliveira, 1998), whereas medium- to large-sized diaspores were moved, if ever, for only a few metres. Large ponerines can move diaspores for 10 m or more (Fig. 19.1A; Horvitz, 1981), while small ants (< 0.5 cm) usually do not carry diaspores beyond 2 m (Pizo and Oliveira, 1999). Inside the nests of ponerines, fleshy portions of diaspores (either pulp or aril) serve as food for larvae and adults (Horvitz, 1981; Pizo and Oliveira, 2001). Residence time of seeds inside captive colonies of the ponerine ant *Pachy-condyla striata* ranged from 2 to 9 days, after
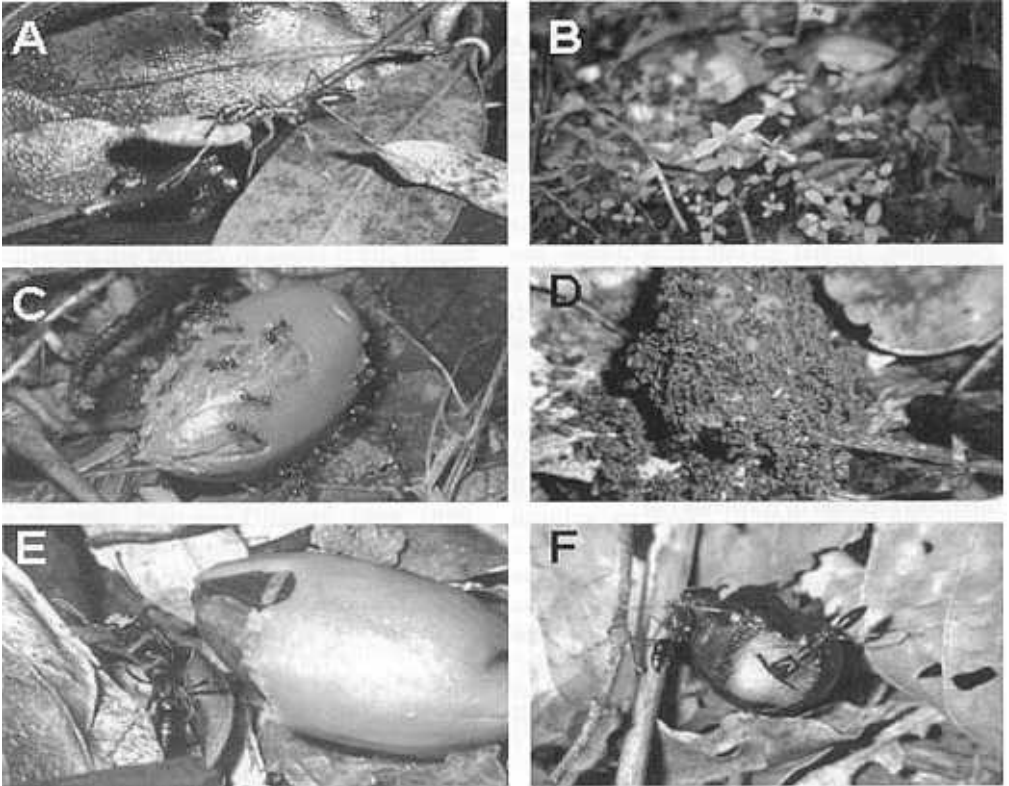
Fig. 19.1. Ponerinae and Myrmicinae ants and fleshy, vertebrate-dispersed diaspores in the Brazilian Atlantic forest. (A) *Odontomachus chelifer* carrying a fallen diaspore of *Clusia criuva* (Clusiaceae) to its nest; (B) seedlings of *Clusia criuva* (Clusiaceae), *Myrcia rostrata* and *M. bicarinata* (Myrtaceae) growing on a nest of *O. chelifer*; (C) *Pheidole* sp. removing bits of the aril of *Virola bicuhyba* (Myristicaceae); (D) a diaspore of *V. bicuhyba* covered with soil by *Solenopsis* sp.; (E) *Pachycondyla striata* removing the aril of *V. bicuhyba*; (F) *Odontomachus chelifer* exploiting a fruit of *Eugenia* sp. (Myrtaceae).

which the intact, cleaned seeds (i.e. without the fleshy portion) are deposited on refuse piles outside the nest. Attine ants also discard intact seeds in refuse piles outside their nests (Fig. 19.2D; Dalling and Wirth, 1998; Leal and Oliveira, 1998). Other myrmicines (e.g. *Pheidole*) prey upon some of the seeds they collect, but also cache intact seeds inside their nests where germination and seedling establishment occasionally occur (Levey and Byrne, 1993; M.A. Pizo, unpublished data). For diaspores exploited by ants on the spot (Figs 19.1E, 19.1F, 19.2A), the piecemeal removal of pulp or aril usually lasts less than 24 h (Pizo and Oliveira, 2001). Further details on ant behaviour towards fleshy diaspores of a variety of Atlantic forest plant species are given by Pizo and

Oliveira (2000) and Passos and Oliveira (2003).

Ant and Diaspore Attributes Mediating the Interaction

Field observations indicate that the sizes of ants and diaspores are key factors in the way that they interact. Paralleling what happens with the interaction between ants and myrmecochorous diaspores (*sensu* van der Pijl, 1982), which is influenced not only by the size of diaspores, but also by the presence of a lipid-rich appendage called elaiosome (Hughes and Westoby, 1992; Gorb and Gorb, 1995; Mark and Olesen,
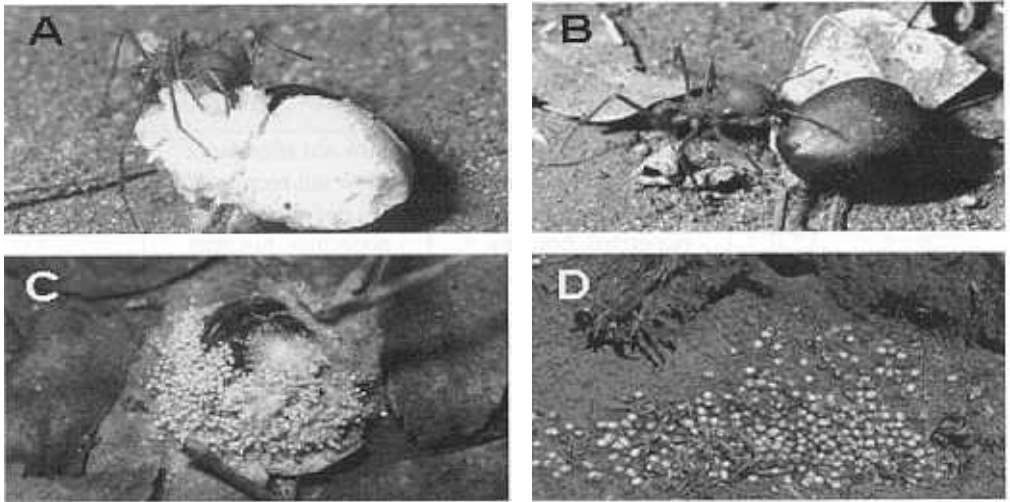
Fig. 19.2. Attini ants and fleshy, vertebrate-dispersed diaspores. (A) *Atta sexdens* removing the aril of *Copaifera langsdorffii* (Caesalpiniaceae); (B) *Atta sexdens* carrying a seed of *C. langsdorffii* to its nest; (C) fungi infestation on a diaspore of *C. langsdorffii* not exploited by attines; (D) seeds and seedlings of *Prunus sellowii* (Rosaceae) growing on a nest of *Acromyrmex* sp.

1996), the chemical composition of vertebrate-dispersed diaspores, particularly the lipid content, also plays a role in the interaction with ants. The importance of lipids, particularly fatty acids, as possible mediators of ant–diaspore interactions has been stressed by several authors (e.g. Marshall *et al.*, 1979; Skidmore and Heithaus, 1988; Brew *et al.*, 1989), and vertebrate-dispersed diaspores have a fatty acid composition remarkably similar to the elaiosomes of myrmecochorous diaspores (Hughes *et al.*, 1994; Pizo and Oliveira, 2001; see Mayer *et al.*, Chapter 10, this volume). The vertebrate-dispersed diaspores with which ants interact in Atlantic forests have a broad range of sizes and lipid content in the fleshy portion exploited by the ants (Pizo and Oliveira, 2000). How ants respond to variation in these features and how such responses affect the biology of vertebrate-dispersed diaspores were thoroughly investigated at PEI (Pizo and Oliveira, 2001).

We studied the interactions between ground-dwelling ants and six selected ornithochorous diaspore species at PEI: *Virola bicuhyba* (Myristicaceae); *Eugenia stictosepala* (Myrtaceae); *Cabralea canjerana* (Meliaceae); *Citharexylum myrianthum*

(Verbenaceae); *Alchornea glandulosa* and *Hyeronima alchorneoides* (Euphorbiaceae) (hereafter referred to by their generic names). These diaspores were chosen because they represent three discrete size classes that encompass the size range of most of the fleshy diaspores produced in the study site (M.A. Pizo, M. Galetti and L.P.C. Morellato, unpublished data). *Alchornea* and *Hyeronima* have small diaspores (< 0.1 g), *Cabralea* and *Citharexylum* have medium-sized diaspores (both 0.9 g), whereas the diaspores of *Virola* and *Eugenia* are much larger (3.5 and 5.8 g, respectively). Moreover, the selected diaspores also represent two extremes relative to the lipid content of their fleshy portions; the arils of *Virola*, *Cabralea* and *Alchornea* are lipid-rich (> 60% of dry mass), while the pulp of *Eugenia*, *Citharexylum* and *Hyeronima* is lipid-poor (< 8% of dry mass; lipid analysis follows Bligh and Dyer, 1959). With this set of diaspore species, we investigated the time to discovery, recruitment behaviour, attendance, diaspore cleaning, removal and displacement distance of diaspores by ants.

Results from this series of investigations are summarized in Fig. 19.3. Ants generally

Diaspore size

		Small (< 0.1 g)	Large (> 3 g)
Lipid content	Poor (< 8%)	• Low ant attendance • Slow ant recruitment • Do not attract large ponerines, but may attract attines • Seldom removed • **Moved long distances (> 10 m)**	• Low ant attendance • Slow ant recruitment • Do not attract large ponerines, but may attract attines • Never removed
	Rich (> 60%)	• **High ant attendance** • **Rapid ant recruitment** • **Attract large ponerines**, do not attract attines • **Rapidly removed** • **Moved long distances (> 10 m)**	• **High ant attendance** • **Rapid ant recruitment** • **Attract large ponerines** and, more rarely, attines • Never removed

Fig. 19.3. Summary of ant responses to fleshy, vertebrate-dispersed diaspores found by ants on the floor of the Atlantic forest at the Parque Estadual Intervales (PEI). Ant responses are categorized according to the size and lipid content (on a dry mass basis) of diaspores. Responses that are most likely to benefit diaspores are in bold.

discovered diaspores on the forest floor rapidly (on average < 8 min). Time to discover a diaspore was not influenced either by diaspore size (ANOVA: $F = 1.27$, df = 2, $P = 0.28$) or lipid content ($F = 0.227$, df = 1, $P = 0.64$). Lipid content influenced positively the recruitment rate of ants to large and medium-sized diaspores (within size class comparisons with Kolmogorov–Smirnov tests: both $P < 0.001$), and ant attendance on a daily basis. Lipid-rich diaspores were attended day and night by a greater number of ants than lipid-poor ones. Diaspore size influenced negatively both removal rate (Spearman rank correlation: $r_s = -0.93$, $n = 6$, $P < 0.05$) and displacement distance ($r_s = -0.94$, $n = 6$, $P = 0.02$). Based on these results, Pizo and Oliveira (2001) predicted that small, lipid-rich diaspores would be more likely to benefit from interactions with ants at PEI.

The attachment of the fleshy portion to the seed influences how quickly ants clean seeds. For instance, other things being equal,

a seed with a loosely attached pulp or aril is cleaned more rapidly than a seed wrapped by a firmly attached pulp. Moreover, large ants with powerful mandibles (Figs 19.1E, 19.1F, 19.2A) tend to clean seeds more rapidly than small ants (ranges 2–24 h and 8–42 h, respectively; Fig. 19.1C, 19.1D). Because most of the diaspore-exploiting ants in the Atlantic forest are attracted to the pulp or aril rather than to the seed itself, the velocity of seed cleaning affects the probability of the exploiting ant being displaced by another, competitively superior ant species.

The diet of ground-dwelling ants is also important. Carnivorous ponerines foraged more frequently on lipid-rich diaspores, whereas fungus-growing attines were more frequently recorded on lipid-poor diaspores (Fig. 19.4). As mentioned previously, the fatty acid composition of vertebrate-dispersed lipid-rich diaspores is similar to that found in the elaiosomes of myrmecochorous diaspores, which have been hypothesized to mimic insect prey (Hughes et al.,
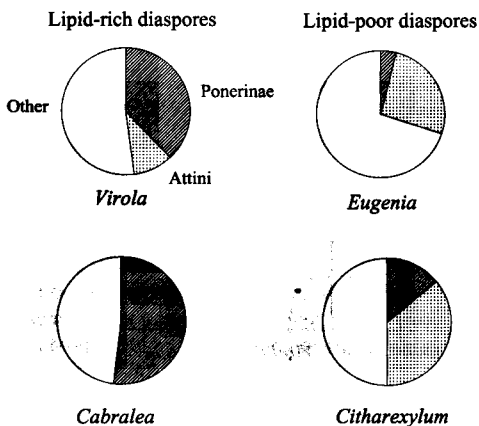
Lipid-rich diaspores   Lipid-poor diaspores

Fig. 19.4. Attendance by Ponerinae, Attini and other ants on lipid-rich (> 60% of lipids in aril dry mass; *Virola bicuhyba* and *Cabralea canjerana*) and lipid-poor (< 8% of lipids in pulp dry mass; *Eugenia stictosepala* and *Citharexylum myrianthum*) diaspores placed on the forest floor of Parque Estadual Intervales (PEI). Fifty diaspores were used for each species.

1994; Beattie and Hughes, 2002). Thus it is not surprising that carnivorous ponerines would prefer lipid-rich diaspores. Why attine ants, in contrast, exploit lipid-poor diaspores more often than lipid-rich ones should be investigated in greater detail (see Beattie, 1991).

Effects of Ants on Seeds and Seedlings

We have shown that ground-dwelling ants frequently interact with a plethora of vertebrate-dispersed diaspores in the Brazilian Atlantic forest. A key issue for this interaction is whether ants have any significant impact on population recruitment of these plants (see Horvitz and Schemske, 1986). Potential benefits to vertebrate-dispersed diaspores secondarily dispersed by ants are similar to benefits to myrmecochorous diaspores primarily dispersed by ants (Beattie and Hughes, 2002), and include enhancement of germination success, escape from predation and directed dispersal (*sensu* Howe and Smallwood, 1982), i.e. the placement of seeds in sites where

seedlings find better conditions for establishment and development than the surrounding environment.

By removing the pulp or aril from fleshy diaspores, ants reduce fungi infestation of seeds (Fig. 19.2C) and can increase germination success by 19 to 63% (Oliveira *et al.*, 1995; Leal and Oliveira, 1998; Pizo and Oliveira, 1998, 2001; Passos and Oliveira, 2002, 2003). When ants remove the seeds from beneath parent plants, they help the seeds escape from density- or distance-oriented seed predators (Janzen, 1970; Pizo and Oliveira, 1998). Using exclosure experiments to compare the removal rates of caged (no access to vertebrates) and uncaged diaspores (free access to vertebrates and ants), we have shown that: (i) ants removed from 0 to 91% of the diaspores in 24 h (small, lipid-rich diaspores experienced the highest removal rates), and (ii) removal attributed to vertebrate seed predators (estimated by the difference in diaspore removal between caged and uncaged treatments) increased with the size of the diaspore (up to the threshold represented by the size of *Eugenia* (5.8 g), which is too big to be exploited by most of the rodents at PEI; Vieira *et al.*, 2003) because large diaspores are not transported by ants, thus becoming available to rodents (Fig. 19.5; Pizo and Oliveira, 2001). Therefore, if escape from seed predators is a benefit accrued by vertebrate-dispersed diaspores as a result of their interaction with ants, this benefit is greatest for small, lipid-rich diaspores, which are rapidly removed by ants (especially primarily carnivorous, ponerine ants).

Directed dispersal of *Clusia* and *Guapira* seeds to ponerine ant nests

The lipid-rich, arillate diaspores of *Clusia criuva* (Clusiaceae; diaspore mass = 0.10 ± 0.05 g, *n* = 150; 83.4% lipids on a dry mass basis; Passos and Oliveira, 2002), and the protein-rich fruits of *Guapira opposita* (Nyctaginaceae; 0.25 ± 0.04 g, *n* = 30; 28.4% protein; Passos, 2001) are dispersed by many bird species in the Atlantic forest
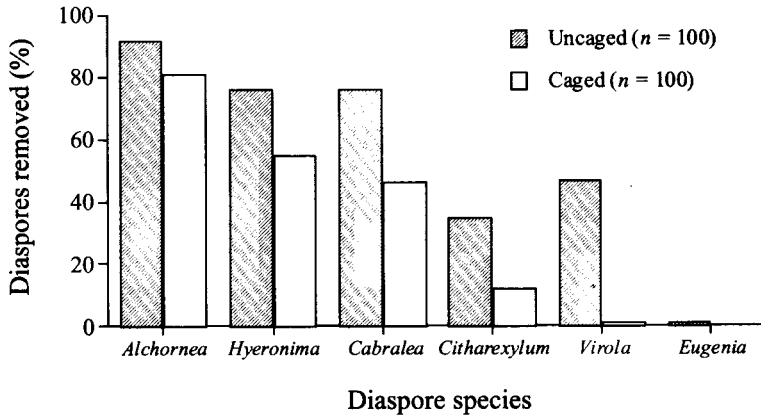
Fig. 19.5. Percentage of caged (access to ants only) and uncaged (access to ants and vertebrates) diaspores removed in a 24-h period from the forest floor of Parque Estadual Intervales (PEI). Diaspores are arranged from left to right according to their size: small (*Alchornea glandulosa* and *Hyeronima alchorneoides*; < 0.1 g), medium (*Cabralea canjerana* and *Citharexylum myrianthum*; 0.9 g), and large (*Virola bicuhyba* and *Eugenia stictosepala*; > 3.5 g).

(M.A. Pizo, unpublished data). However, once on the ground, either dropped directly from the parent plant or dispersed by birds, *Clusia* and *Guapira* diaspores are exploited by a diverse assemblage of ground-dwelling ants, but most especially by two primarily carnivorous ponerines – *Pachycondyla striata* and *Odontomachus chelifer* (Fig. 19.1A; Passos, 2001; Passos and Oliveira, 2002). We investigated the effects of these two ponerines on seedlings of *Clusia* and *Guapira* at PEIC in 1998 and 2000, respectively. The number of *Clusia* and *Guapira* seedlings growing on nests of these ant species was compared to control areas (without nests) by establishing paired experimental plots (0.5 m × 0.5 m). *Clusia* seedlings within plots were marked and monitored every 2 months for a year. Additionally, soil samples from ponerine nests and from control plots were analysed for nutrients and physical properties. Further methodological details are given in Passos and Oliveira (2002) and Passos (2001).

Effects of ants on seeds and seedlings of *Clusia* and *Guapira* are summarized in Table 19.2. Overall, ants behaved similarly towards seeds and seedlings of both species, but the plants were not equally affected by the two ponerines. Seedlings of *C. criuva* were more abundant in the vicinity of nests

of *P. striata* (Wilcoxon paired-sample test, $Z = -3.869$, $P < 0.0001$, $n = 21$) and *O. chelifer* ($Z = -2.964$, $P = 0.003$, $n = 20$) than in areas without nests (Fig. 19.1B). Early survival (1 year) of *Clusia* seedlings was greater in nests of *P. striata* than in control areas ($\chi^2 = 14.18, P = 0.0002$), but was not affected by *O. chelifer* ($\chi^2 = 1.31$, $P = 0.2526$). *Guapira* seedlings, on the other hand, are more frequent close to *O. chelifer* nests than in sites without such nests ($Z = -4.947$, $P < 0.0001, n = 40$; Passos, 2001). This inter-specific variation may have been influenced by differences in soil properties around ant nests, in nutrient requirements of the seedlings of both plant species, or by unknown temporal factors. The results with *Clusia* and *Guapira* indicate that, as reported for myrmecochorous diaspores in xeric environments (Davidson and Morton, 1981; Culver and Beattie, 1983; Beattie, 1985), the directed dispersal provided by ponerine ants at the sandy plain forest of PEIC involves the deposition of vertebrate-dispersed diaspores in nutrient-enriched soil close to their nests. Soil enrichment near the nests probably results from the deposition of organic material on adjacent refuse piles (Beattie, 1985). Similar effects of seed dispersal by *Odontomachus* have been shown for seedlings of other vertebrate-dispersed

Table 19.2. Summary of the effects of two ponerine ant species, *Pachycondyla striata* and *Odontomachus chelifer*, on seeds and seedlings of *Clusia criuva* and *Guapira opposita* in the sandy forest of Cardoso Island (PEIC), south-east Brazil. Data with *C. criuva* and *G. opposita* were obtained in 1998 and 2000, respectively. A dash indicates that the ant activity or ant effects were not tested with that particular plant species. Further details in Passos and Oliveira (2002) and Passos (2001).

| | *C. criuva* | | *G. opposita* | |
Ant activity and ant effects on plants	*P. striata*	*O. chelifer*	*P. striata*	*O. chelifer*
Remove fallen diaspores	Yes	Yes	Yes	Yes
Remove diaspores from bird faeces	Yes	Yes	–	?
Discard intact seeds outside nest	Yes	Yes	Yes	Yes
Removal of fleshy portion increases germination[a]	Yes	Yes	–	–
Increased seedling recruitment near nest[b]	Yes	Yes	–	Yes
Increased seedling survival (1 year) near nest[b]	Yes	No	–	–
Increased soil nutrients near nest[b]	Yes	Yes	–	Yes
Higher soil penetrability near nest[b]	–	–	–	Yes
Potential herbivore deterrence near nest[b,c]	–	–	–	Yes

[a]Although the effects of cleaning activity were not assessed for *Guapira*, pulp removal by the authors increased germination in this species.
[b]Compared to random control plots without nests.
[c]Evaluated by recording attack rates by ants on dipteran larvae placed on seedlings growing near the nests and in control plots.

plants such as *Anthurium* sp. (Araceae), *Myrcia rostrata* and *Psidium catleyanum* (Myrtaceae) in the same area (Fig. 19.1B; Passos and Oliveira, 2003).

Spatial Variation in Ant–Diaspore Interactions

Patterns

Although the interactions between ants and vertebrate-dispersed diaspores occur at PEI and PEIC and involve a variety of ant and plant species at both places, there are important differences between the sites (Table 19.1). One difference is the frequency of ant–diaspore interactions, as revealed by the monthly surveys carried out during 2 consecutive years along 5-km and 1.4-km trails at PEI and PEIC, respectively. Any instance of one or more ants in contact with a given diaspore either removing it or collecting material from it was recorded as an interaction. A total of 886 interactions (7.4 interactions/km) were recorded at PEI (Pizo and Oliveira, 2000), whereas only 75 interactions (2.2 interactions/km) were

recorded at PEIC (Passos and Oliveira, 2003).

The between-site difference in the participation of the two most common ponerine species at both sites (*Pachycondyla striata* and *Odontomachus chelifer*) was marked. While these species were responsible for only 1% of the interactions recorded at PEI, they accounted for 35% of the interactions at PEIC. This difference may reflect the abundances of these ants at each site. A survey with 100 tuna fish baits used to evaluate the abundance of ant species at PEI detected *P. striata* and *O. chelifer* in 15% and 6% of the baits, respectively. The same procedure employed at PEIC revealed that *P. striata* is twice as abundant (31% of the baits), while the abundance of *O. chelifer* is almost four times greater (23% of the baits). However, abundance alone is not sufficient to explain the difference found in the number of interactions with fallen diaspores because *O. chelifer* and *P. striata* were apparently more selective towards diaspores at PEI than at PEIC. In the former site, these two ant species exploited 13 and 21 diaspore species, representing respectively 23% and 38% of all plant species used by ants (Pizo and Oliveira, 2000). In contrast, at PEIC

O. chelifer and *P. striata* utilized 20 and 35 diaspore species, which comprise respectively 45% and 80% of all plant species used by ants at this site (Passos and Oliveira, 2003). When we compare the number of interactions involving the two ponerines and selected diaspores shared by both sites, the between-site difference holds not only for lipid-rich, but also for lipid-poor fleshy diaspores (Table 19.3). Therefore, *O. chelifer* and *P. striata* use a greater variety of diaspores at PEIC than at PEI.

Processes

The overall higher frequency of ant–diaspore interactions at PEI compared with PEIC may be related to inter-site differences in the abundance and composition of the ant fauna and/or in the availability of fruits. The abundance of ants (all species pooled), as revealed by the number of ants captured in pitfall traps (see below), did not differ between PEI and PEIC (*t*-test on log(n + 1)-transformed data: $t = -0.91$, df = 89, $P =$ 0.36). It is possible, however, that the high abundance of ponerines at PEIC (see above) may lead to the rapid disappearance of fallen diaspores, thus precluding diaspore use by other ants. Although comparative data on fruit availability at the two sites are lacking, the sandy plain forest at PEIC grows on poor-quality soils probably sustaining a lower annual fruit production compared to the forest at PEI that grows on rich alluvial soils. Therefore, it is possible that the higher frequency of ant–diaspore interactions at PEI may result from the greater fruit abundance at this area than at PEIC. Moreover, the rapid removal of fallen fleshy fruits by common ponerines at PEIC can make this resource unavailable to other small, slow-moving ants.

We developed two non-exclusive hypotheses to explain the broader use of diaspores by *P. striata* and *O. chelifer* at PEIC compared to PEI: (i) ant populations from each site may differ in food preferences ('food preference hypothesis'), and (ii) availability of arthropod prey may differ between the two sites ('arthropod availability hypothesis'). If the food preference hypothesis is to explain the observed difference in diaspore use, we predicted that, given the opportunity to choose between fruit and arthropod food items, the ants would choose fruits more frequently at PEIC than at PEI. On the other hand, if the arthropod availability hypothesis is valid, we predicted that leaf litter arthropod biomass would be higher at PEI than at PEIC, thus leading ground-dwelling *P. striata* and *O. chelifer* to rely more frequently upon fleshy diaspores at PEIC to complement their predominantly carnivorous diets.

To test the food preference hypothesis, we performed choice experiments using guava fruits (*Psidium guajava*, Myrtaceae) and cockroaches. Member of a dominant plant family in the Atlantic forest (Mori

Table 19.3. Number of interactions between ants and selected diaspore species recorded at Parque Estadual Intervales (PEI) and Parque Estadual da Ilha do Cardoso (PEIC). Lipid content of the diaspores' fleshy portion (either pulp or aril), total number of interactions with ants and number of interactions involving *Pachycondyla striata* (Ps) and *Odontomachus chelifer* (Oc) are presented.

Diaspore species (family)	Lipid content[a] (dry mass (%))	Interactions at PEI			Interactions at PEIC		
		Total	Ps	Oc	Total	Ps	Oc
Aechmea nudicaulis (Bromeliaceae)	–	25	0	0	43	8	4
Alchornea triplinervia (Euphorbiaceae)	68	39	2	0	15	5	2
Clusia criuva (Clusiaceae)	83	8	0	0	79	20	7
Euterpe edulis (Arecaceae)	20	191	0	0	9	4	0
Maytenus robusta (Celastraceae)	1	45	0	0	9	3	0

[a]Unpublished data for *A. triplinervia*, *E. edulis* and *M. robusta*; data for *C. criuva* from Passos and Oliveira (2002).

et al., 1983; Oliveira-Filho and Fontes, 2000), the guava fruit is a typical lipid-poor fruit like many others with which ants interact (see Pizo and Oliveira, 2000). We used tuna baits to locate five nests of *P. striata* and four of *O. chelifer* at each site. Around the nest entrances, we offered the ants a two-choice food source composed of equivalent pieces (< 1 cm in length) of guava and cockroach placed side by side on a white filter paper (4 cm × 4 cm). The two types of food items were < 1 cm apart. A trial was initiated after the location of the food items by a foraging ant, and terminated after the removal of one item by the ant. A choice was recorded only if the ant antennated both food items prior to selecting one of them. To ensure independence of trials, every tested ant was collected. The filter paper had no apparent effect on ant behaviour (Levey and Byrne, 1993; Pizo and Oliveira, 2000; Passos and Oliveira, 2002).

A frequency test performed using the procedure PROC CATMOD of the SAS Statistical package (SAS Institute, 1987) revealed that ants differed in their food choices ($\chi^2 = 21.54$, df = 1, $P < 0.0001$), although choices were consistent across areas ($\chi^2 = 0.09$, df = 1, $P = 0.76$). *Pachycondyla striata* consistently selected cockroaches in both areas (guava was never chosen first), whereas the results for *O. chelifer* were less clear and revealed intercolony variation (seven colonies chose cockroaches more frequently – 69–87% of choices – while one colony at PEI preferred guava fruits – 56% of choices). Despite this variation, a *t*-test applied to *O. chelifer* pooled data (PROC TTEST, SAS Institute, 1987) showed that cockroaches were selected more frequently than fruit ($t = 4.71$, df = 8.34, $P = 0.0014$). Therefore, we rejected the food preference hypothesis as an explanation for the differences in diaspore use observed between PEI and PEIC.

To test the arthropod availability hypothesis, we compared the biomass of litter arthropods in January–February 2002 at PEI and PEIC by setting 50 and 41 pitfall traps in each area, respectively. Traps consisted of plastic cups (6.5 cm wide × 8.0 cm height) half-filled with alcohol 70%, placed ≥ 10 m

apart from each other along one trail in each site. Traps were set over a period of 24 h, after which the arthropods were collected and dried to constant weight in an oven set at 55°C. Total arthropod biomass collected at each trap was then weighed to the nearest 0.01 g.

Results showed that biomass of ground-dwelling arthropods is twice as great at PEI than at PEIC (0.14 ± 0.15 and 0.06 ± 0.05 g per trap, respectively; *t*-test on log-transformed data: $t = 2.15$, df = 88, $P = 0.03$). Between-site difference in leaf litter thickness possibly accounts for the observed difference. By counting the number of leaves intersected by a wood stick inserted into the leaf litter at 63 random points at each site, we found that the litter is twice as thick at PEI than at PEIC (3.4 ± 1.1 and 1.6 ± 1.3 leaves, respectively; *t*-test on $\log(n + 1)$-transformed data: $t = 8.27$, df = 124, $P < 0.001$). Therefore, the arthropod availability hypothesis cannot be rejected. Ponerine ants appear to increase the consumption of fleshy diaspores when faced with a low supply of preferred arthropod prey, producing the between-site difference in diaspore use here reported for PEI and PEIC.

Consequences

Biotic interactions are typically variable in space, and the interactions between ants and vertebrate-dispersed diaspores are not exceptions (Thompson, 1994; Garrido *et al.*, 2002). For instance, although ants commonly consume fallen diaspores and increase seedling establishment of ornithochorous *Commiphora* trees (Burseraceae) in Madagascar, this interaction is absent in South Africa (Böhning-Gaese *et al.*, 1999; Bleher and Böhning-Gaese, 2001). Several factors may account for spatial variation in ant–diaspore interactions. In the *Commiphora* study, the difference in ant communities between Madagascar and South Africa is an underlying reason for the between-site differences observed (Voigt *et al.*, 2002). In the Brazilian Atlantic forest,

we suggested that low fruit availability rather than low ant abundance was responsible for the overall lower frequency of interactions recorded at PEIC compared with PEI, and decreased availability of litter arthropods at PEIC might have led predominantly carnivorous ants to use a greater variety of fleshy diaspores at this site than at PEI. As a consequence, diaspore features hypothesized as important for determining the outcome of the interactions with ants at PEI (i.e. small size and high lipid content; Fig. 19.3; see Pizo and Oliveira, 2001) may not necessarily hold for PEIC. For instance, while *Clusia* diaspores fit into these characteristics (mass = 0.10 g, 83.4% lipids; Passos and Oliveira, 2002), *Guapira* fruits are rich in protein, but poor in lipids (28.4% and 0.5%, respectively; Passos, 2001). The same holds true for *Myrcia rostrata* and *Psidium cattleyanum* (10.3% and 1.7% lipids, respectively; M.A. Pizo, unpublished data), whose seedlings are also clustered around *O. chelifer* nests at PEIC (Fig. 19.1B; Passos and Oliveira, 2003).

Therefore the relevance of ponerine ants as seed dispersers of vertebrate-dispersed plants at PEIC can be attributed to a combination of factors: (i) high abundance of *P. striata* and *O. chelifer* ants; (ii) low availability of litter arthropod prey; (iii) great longevity of ponerine nests (one nest of *O. chelifer* tagged in 1995 was still active in 2002; M.A. Pizo, personal observation); and (iv) nutrient-poor sandy soil. While the great longevity of ponerine nests contributes to the establishment of nutrient-enriched sites around ant nests, the nutrient-poor soil increases their relative importance as plant recruitment foci (see Hughes, 1990; Passos and Oliveira, 2002).

Concluding Remarks and Perspectives

The impact of ants on the reproductive output of vertebrate-dispersed tropical plants may be very important. A large percentage of the diaspores produced by such plants is dropped by vertebrate seed dispersers (Böhning-Gaese *et al.*, 1999; Passos and Oliveira, 2002). We demonstrate that in the Brazilian Atlantic forest ground-dwelling ants interact frequently with fallen vertebrate-dispersed diaspores and that this may render recruitment benefits for some plant species. We are just beginning to understand the complexity of such interactions, and more natural history studies are needed before one can assess the intricacy of plant dispersal systems in tropical forests. It is crucial to weigh the importance of secondary seed dispersal by ants against primary seed dispersal by vertebrates in what concerns seedling establishment and, ultimately, population recruitment (see Böhning-Gaese *et al.*, 1999). In this context, it is important to consider that the spatial scale of seed dispersal provided by ants is usually smaller than that provided by vertebrate seed dispersers, which has important consequences for population recruitment and spatial distribution (Horvitz and Le Corff, 1993; Horvitz *et al.*, 2002). Short-distance dispersal provided by ants may be sufficient if appropriate recruitment sites are located close to the parent plant, which seems not to be rare in tropical forests given the frequency of adult clumped distribution among tree plant species (Hubbell, 1979).

Available evidence indicates that the outcome of the interaction for the plants varies spatially, and therefore we should make progress by studying the interaction in a variety of habitats that differ both in abiotic (e.g. soil nutrient content) and biotic features (e.g. diaspore and animal prey availability, floristic composition, ant fauna). Recently, Garrido *et al.* (2002) stressed the importance of studying different localities for a better understanding of the intricacies involved in the interactions between ants and diaspores, and their possible evolutionary pathways. Data on spatial and intercolony variation in the dietary requirements of ants are also needed. Can predominantly carnivorous ants sustain their colonies on a diet comprised mostly of fleshy fruits? What kinds of benefits, if any, do ants gain by exploiting vertebrate-dispersed diaspores? Working with myrmecochorous diaspores, Morales and Heithaus (1998) showed that elaiosomes positively affected the

reproductive potential of ant colonies. Does the same hold true for ants feeding on lipid-rich tissues derived from vertebrate-dispersed diaspores?

Finally, the interaction between ants and vertebrate-dispersed diaspores is not free from human-caused disturbance (Carvalho and Vasconcelos, 1999). Guimarães and Cogni (2002) have recently demonstrated that reduced ant activity at fallen ornithochorous diaspores of *Cupania vernalis* (Sapindaceae) in the edge of a Brazilian forest fragment results in increased seed predation. The study of ant–diaspore interactions in disturbed habitats can add insights to the growing body of knowledge on the effects of habitat disturbance on biotic interactions.

Acknowledgements

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