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Size and lipid content of nonmyrmecochorous diaspores: effects on the interaction with litter-foraging ants in the Atlantic rain forest of Brazil

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Abstract

Ants are often attracted to diaspores not adapted for dispersal by ants. These diaspores may occasionally benefit from this interaction. We selected six nonmyrmecochorous plant species (*Virola oleifera, Eugenia stictosepala, Cabralea canjerana, Citharexylum myrianthum, Alchornea glandulosa and Hyeronima alchorneoides*) whose diaspores differ in size and lipid content, and investigated how these features affect the outcome of ant-diaspore interactions on the floor of a lowland Atlantic forest of Southeast Brazil. A total of 23 ant species were seen interacting with diaspores on the forest floor. Ants were generally rapid at discovering and cleaning the diaspore pulp or aril. Recruitment rate and ant attendance were higher for lipid-rich diaspores than for lipid-poor ones. Removal rate and displacement distance were higher for small diaspores. The large ponerine ant *Pachycondyla striata*, one of the most frequent attendants to lipid-rich arillate diaspores, transported the latter into their nests and discarded clean intact seeds on refuse piles outside the nest. Germination tests with cleaned and uncleaned diaspores revealed that the removal of pulp or aril may increase germination success in *Virola oleifera, Cabralea canjerana, Citharexylum myrianthum* and *Alchornea glandulosa*. Gas chromatography analyses revealed a close similarity in the fatty acid composition of the arils of the lipid-rich diaspores and the elaiosome of a typical myrmecochorous seed (*Ricinus communis*), corroborating the suggestion that some arils and elaiosomes are chemically similar. Although ant-derived benefits to diaspores – secondary dispersal and/or increased germination – varied among the six plant species studied, the results enhanced the role of ant-diaspore interactions in the post-dispersal fates of nonmyrmecochorous seeds in tropical forests. The size and the lipid-content of the diaspores were shown to be major determinants of the outcome of such interactions.

Introduction

Prior to most studies that investigated ant-diaspore interactions, Carroll & Janzen (1973, p. 235) noted that “seeds with an oily covering may be fed on by almost any kind of ant”. In fact, ants may disperse diaspores with a broad array of characteristics, ranging from primarily ant-dispersed (myrmecochorous) to primarily bird-dispersed (ornithochorous) diaspores (Davidson & Morton 1984; O’Dowd & Gill 1986; Bello y Bello 1997; Pizo & Oliveira 1998). Myrmecochorous plants are not common in tropical forests, but many interactions involving ants and nonmyrmecochorous diaspores can take place in such habitats as a result of both the great ant abundance (Hölldobler & Wilson 1990) and the considerable amount of fruits that become available to ants on the forest floor (Jordano 1993). Many anecdotal observations of ants exploiting fallen nonmyrmecochorous diaspores in tropical forests are reported in the literature (Motta Junior & Lombardi 1990; Mandujano et al. 1994). Although nonmyrmecochorous plants produce diaspores that lack special adaptations for dispersal by ants, recent studies reveal that ants can rearrange the seed shadow generated by primary seed dispersers (Roberts & Heithaus 1986), affect seed bank dynamics (Levey & Byrne 1993), facilitate seed germination (Oliveira et al. 1995; Leal & Oliveira 1998; Pizo & Oliveira 1998), and promote seedling establishment of nonmyrmecochorous plants (Farji Brener & Silva 1996).

The interactions between ants and myrmecochorous diaspores are influenced by diaspore traits such as size (Gorb & Gorb 1995) and the presence of a lipid-rich appendage called elaiosome (Hughes & Westoby 1992a; Mark & Olesen 1996). Myrmecochorous diaspores are usually small (< 50 mg; see Davidson & Morton 1981) and easily transported by ants. Therefore, other things being equal, ants should respond to differences in diaspore size and carry small diaspores more easily than large ones (Kaspari 1996b; Leal & Oliveira 1998). The nonmyrmecochorous diaspores with which ants interact in tropical forests have a broad range of size and lipid-content in the fleshy portion (either pulp or aril) exploited by the ants (Pizo & Oliveira 2000). How ants respond to variation in these features, and how such responses affect the biology of nonmyrmecochorous diaspores are still to be assessed.

In this paper we selected six diaspore types that contrast in size and lipid content to study their interactions with litter-foraging ants in a lowland rainforest in southeast Brazil. We investigated (1) how ants respond to the variable size and lipid content of nonmyrmecochorous diaspores, and (2) how diaspore size and lipid-content influence the outcome of the interaction with ants. To address these questions, we studied the time-to-discovery, recruitment behaviour, attendance, diaspore cleaning, removal, and displacement distance of diaspores by ants. With these set of observations we tried to cover all the stages of the interaction, from the moment the nonmyrmecochorous diaspore falls from the parent plant until it reaches the ant nest. The fate of diaspores carried to ant nests was investigated with captive ant colonies. Ant effects on seed germination were investigated in greenhouse experiments. Since fatty acids have been shown to be an important group of lipids for ant-diaspore interactions (Beattie 1985, 1991; Hughes et al. 1994), we also analyzed the fatty acid composition of the arillate diaspores studied.

Study site

The study was carried out from October 1995 to July 1997 in the lowland forest of the Parque Estadual Intervales (24°14′ S, 48°04′ W), a 490-km^2 reserve located in São Paulo state, southeast Brazil. The site (Saibadela Research Station), located at an elevation of 70 m, received a mean ± SD of 4216.2 ± 245.5 mm of rainfall between 1994–1996. Rains are well distributed through the year with no month receiving less than 100 mm. Rainfall, however, is less intense and less frequent between April and August, when temperatures may drop to nearly 10 °C (mean ± SD = 20.8 ± 2.5 °C for the study period). This period contrasts with the wetter period (September–March) when temperature may reach 42 °C (25.7 ± 2.8 °C). The vegetation is composed chiefly of old-growth forest (sensu Clark 1996) with trees reaching up to 30 m and an open understory. The area is crossed by several 1-m wide trails, which were used to establish the transects described below.

Study species

We studied the diaspores of the following ornithochorous trees: *Virola oleifera* (Schott.) A. C. Smith (Myristicaceae), *Eugenia stictosepala* Kiaersk. (Myrtaceae), *Cabralea canjerana* Vell. (Mart.) (Meliaceae), *Citharexylum myrianthum* Cham. (Verbenaceae), *Alchornea glandulosa* Endl. & Poepp. and *Hyeronima alchorneoides* Fr. All. (Euphorbiaceae) (throughout the paper we refer to them only by their generic names). These diaspores were selected for the study for two reasons. First, they represent three discrete size classes that encompass the size range of most of the fleshy diaspores produced in tropical forests (Corlett 1996). *Alchornea* and *Hyeronima* have small diaspores, *Cabralea* and *Citharexylum* have medium-sized diaspores, whereas the diaspores of *Virola* and *Eugenia* were considered large (see Table 1). Second, the selected diaspores also fit within two distinct extremes relative to the lipid content of their fleshy portions; the arils of *Virola*, *Cabralea* and *Alchornea* are lipid-rich, while the pulps of *Eugenia*, *Citharexylum* and *Hyeronima* are lipid-poor (Table 1).

The selected plant species are common at the study site. Tree densities ranged from 5.8 individuals (dbh > 5 cm) ha^{-1} for *Eugenia* to 21.1 individuals ha^{-1} for *Hyeronima* (density not available for *Citharexylum*; Almeida-Scabbia 1996). With the exception of *Citharexylum*, which occurs in secondary-growth vegetation and edge habitats, all other species occur in the old-growth forest. We used the term diaspore to define the unit of dispersal of the plant, being either the whole fruit or the seed plus aril (van der Pijl 1982). The fruits of *Eugenia*, *Citharexylum* and *Hyeronima*, which constitute their diaspores, are drupes bearing one (*Eu-*

Table 1. Fruit maturation period, morphology, and chemical composition of the six diaspores studied. Morphological values are means ± SD. A minimum of 20 diaspores of each species were measured and weighed.

Diaspore type	Fruit maturation period	Morphology				Percent water	Chemical composition[a] (percent of dry mass)			
		Length (mm)	Width (mm)	Total weigh (g)	Fresh weight of pulp/aril (g)		L	P	TC	A
Non-arillate										
Hyeronima	Mar-Apr	5.0 ± 0.2	4.2 ± 0.2	0.05 ± 0.01	0.03 ± 0.01	85.6	7.9	6.3	–	–
Citharexylum	Feb-Mar	13.2 ± 1.0	11.6 ± 1.1	0.9 ± 0.2	0.7 ± 0.2	81.4	6.3	6.8	82.7	4.1
Eugenia	Apr-May	31.1 ± 2.3	18.3 ± 1.5	5.8 ± 1.2	2.1 ± 1.0	77.9	5.2	8.5	85.5	0.8
Arillate										
Alchornea	Oct-Nov	5.5 ± 0.4	5.3 ± 0.4	0.09 ± 0.01	0.03 ± 0.01	43.3	68.4	7.6	21.7	2.4
Cabralea	Sep-Dec	18.1 ± 1.7	11.2 ± 1.0	0.9 ± 0.3	0.09 ± 0.02	47.7	70.8	10.3	16.5	2.3
Virola	Jul-Oct	23.7 ± 1.9	15.7 ± 1.2	3.5 ± 1.2	1.1 ± 0.5	62.7	61.8	4.6	32.1	1.4

[a] L = lipids, P = protein, TC = total carbohydrate (i.e., soluble + structural carbohydrates), A = ash. Lipids, proteins, and ash were analyzed according to the methods described in Bligh and Dyer (1959), AAC (1995, method # 46-13) and AOAC (1984, method # 22027), respectively. Total carbohydrates were obtained by difference.

genia and *Hyeronima*) or two seeds (*Citharexylum*). The fruits of the remaining species are capsules that open to expose the diaspores, i. e., seeds coated by red (*Virola* and *Alchornea*) or orange (*Cabralea*) arils. Fruits of *Virola* always have a single diaspore, whereas those of *Alchornea* and *Cabralea* may contain up to two and six diaspores, respectively. All these diaspores are eaten by birds in the Atlantic forest (Galetti 1996; Galetti & Pizo 1996; Pizo 1997), but the fruits of *Eugenia* are also eaten by bats, and those of *Hyeronima* serve as food for Muriqui monkeys (*Brachyteles arachnoides*), which usually drop a huge amount of fruits while feeding in the canopy (M. A. Pizo, personal observation). The period of fruit maturation of the six plant species is presented in Table 1. With the exception of the seed fate trials with captive ant colonies, all other trials and censuses described below were performed using fresh diaspores during the period of fruit maturation of each species.

Voucher specimens of the ants and plants are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), and at the herbarium of the Universidade Estadual Paulista at Rio Claro (HBRC), respectively.

Methods

Recruitment of ants to diaspores

We investigated the recruitment of ants to diaspores by placing 20 diaspores of each species along a transect at random spots on the forest floor and, after they had been discovered by an ant, by recording the number of ants recruited at each 1-min interval during a 15-min period. Recruitment trials were performed between 08:00 and 12:00 during the maturation period of each diaspore species (see Table 1). Diaspores were observed individually and placed on small pieces (4 × 4 cm) of white filter paper to facilitate ant visualization. A previous study (Byrne & Levey 1993) has shown that the use of filter paper does not alter the behaviour of ants. To ensure independent discoveries by different ant colonies, conspecific diaspores were set at least 5 m apart. Given the ant patchiness on the floor of neotropical forests (Kaspari 1996a), and the short distances covered by ground-dwelling foraging ants (usually less than 1 m; Levey & Byrne 1993; Byrne 1994), a 5-m distance between diaspores likely ensured independent discoveries by different ant colonies of most of the attending species. Once the diaspores were placed on the paper substrate, we recorded the time-to-discovery and the first ant species attracted. In case the diaspore was first discovered by a ponerine ant, the recruitment was recorded for the next myrmicine ant discovering the diaspore. We followed this procedure because, contrasting with the relatively sophisticated mass recruitment of most myrmicines, ponerines usually recruit only a single nestmate at a time (Hölldobler & Wilson 1990). Thus, the inclusion of the few trials involving ponerines (10 out of 120 trials; the remaining invariably involved the myrmicine genera *Pheidole* and *Solenopsis*) would weaken recruitment rate comparisons between diaspores. Every time we detected any disruption of the recruitment behaviour of an ant species by another dominant species, the trial was interrupted and another diaspore was set on a different spot on the forest floor.

Censuses (24 h) of the ants attending the diaspores

We made diurnal and nocturnal censuses of the ants attending diaspores placed on the forest floor along a 250-m transect. Fifty diaspores of each species were set along the transect 5 m apart, the transect being established 1–2 m off-trail. Small pieces (4 × 4 cm) of white filter paper were used as substrates for diaspores to facilitate ant visualization. Each diaspore was protected from vertebrate removal by wire cages (15 × 15 × 10 cm, 1.5 cm mesh) closed on the top and staked to the ground. Plastic wrap placed on the top of cages protected diaspores and ants from being disturbed by light to moderate rains. No census was conducted under heavy rains for which the plastic shelters were useless. Diaspores were set on the transect at 08:00 and checked at 4-h intervals during 24 h. During each census, we recorded the number of ants from different species attending the diaspores. The time taken by attending ants to entirely remove the pulp or aril from the diaspores was also recorded.

Diaspore removal by ants and vertebrates

To compare the removal of diaspores by ants and vertebrates (mainly rodents because ground-dwelling granivorous birds are rarely seen at the study site) we established two parallel 500-m transects set 1–2 m off-trail on opposite sides of one of the trails that crossed the study site. For each species, two hundred diaspores were assigned to one of two treatments: caged (100 diaspores) and uncaged (100 diaspores). Caged diaspores (1 per station) were protected by wire cages (15 × 15 × 10 cm, 1.5 cm mesh) which excluded the rodents but permitted free access to ants (see Roberts & Heithaus 1986). No exclosure was provided to uncaged diaspores (1 per station), thus permitting free access by both ants and rodents. Caged and uncaged diaspores were paired along the two parallel transects, in such a manner that the distance within a pair was at least 2 m, and consecutive pairs were separated by 5-m intervals. Diaspores were set on the transect at 08:00 and the number of diaspores removed was checked 24 h later. A diaspore was considered removed if not found within a 15-cm radius of its original position. Since the greatest foraging activity by frugivorous birds occurs at dawn (Howe 1977), and given that birds are probably responsible for most of the diaspores dropped from trees in the study site (Pizo 1997), the period when experimental diaspores were available to ants and rodents simulated the natural availability of most fallen diaspores.

Every time we intercepted ants transporting diaspores during either the 24-h censuses, the recruitment trials, or the diaspore removal experiment, we followed them until they entered their nest or disappeared in the leaf litter. The distance of seed displacement was then measured.

Fate of diaspores in captive ant colonies

Although myrmicines were the most abundant ants recruiting to the diaspores, these tiny ants usually collect liquid and solid food from diaspores on the spot (Pizo & Oliveira 1998, 2000). Since large ponerine ants frequently transport diaspores in the field, we used captive colonies to investigate the fate of diaspores inside their nests. We excavated and collected seven colonies of five of the most common ponerine ants occurring at the study site (two colonies of each *Odontomachus affinis* Guérin and *O. meinerti* Forel, one colony of *Pachycondyla striata* Fr. Smith, *O. chelifer* Latreille and *Ectatomma edentatum* Roger). With the exception of *P. striata*, all colonies were queenright and included brood. Colonies were maintained at 25 °C in our laboratory at the Universidade Estadual de Campinas in plastic boxes (40 × 30 cm) kept under natural light conditions. The sides of the boxes were coated with Fluon to prevent ants from escaping. Two or three glass test tubes covered by dark red plastic shelters and containing water trapped behind a cotton plug were placed in the center of the boxes to serve as dark moist nest sites. Colonies were fed every two days with cockroaches and synthetic ant diet (Bhatkar & Whitcomb 1970), even during the experimental trials described below.

Diaspore-fate trials with captive ant colonies were performed from April to July 1997 after a minimum period of habituation to captivity of two months. Since the arillate diaspores were removed by ants in greater quantities in the field than non-arillate ones, captive experiments were performed only with the former. We used frozen – preserved arillate diaspores that had been collected directly from the trees, or as recently fallen diaspores in the previous year. The process of freezing usually does not affect the attractiveness of diaspores to ants (see Ruhren & Dudash 1996). Each trial was initiated by placing two diaspores of each *Cabralea* or *Alchornea*, or one diaspore of *Virola*, 10–15 cm from the nest entrances. The fate of the diaspores was recorded daily, during two days. We recorded whether the ants ignored the diaspores, transported them to refuse piles, or carried them into the nests. Once the diaspores were transported to the nests we recorded the residence time of diaspores inside the nests. The three different diaspores were used sequentially in the diaspore-fate trials totaling 20 trials for each diaspore with each ant colony.

Germination

To test if diaspore cleaning (i.e., pulp or aril removal) had any effect on seed germination, we sowed intact diaspores (control), as well as diaspores having their pulp or arils removed by us (treatment), in plastic trays containing regularly moistened vermiculite. A total of 50 (*Eugenia* and *Alchornea*) or 100 diaspores (the remaining species) were used in each treatment. Diaspores in the two treatments were placed in separate trays which were kept in the greenhouse of the Universidade Estadual de Campinas. Radicle protrusion was checked at 15-day intervals until seeds presented clear decay signs (see Table 5). Given that some ants may secrete fungicidal substances from their metapleural glands (Beattie et al. 1986), thus potentially rendering an additional benefit for seed germination, we believe that the cleaning of diaspores by us represented in fact a conservative simulation of the services provided by the ants.

Fatty acid composition of the arils

The lipid fraction was separated from the arils of *Virola*, *Cabralea* and *Alchornea* according to the method described by Bligh & Dyer (1959). Fatty acid methyl esters prepared from the lipid fraction (Hartman & Lago 1973) were analyzed using a Perkin Elmer Sigma 3B gas chromatographer equipped with a 4.0 m × 1/8″ Silar 10C column. Peak areas were calculated with reference to standard mixtures. To compare the composition of the arils with the elaiosome of a myrmechocorous diaspore, elaiosomes of *Ricinus communis* L. (Euphorbiaceae) – a common diplochorous herb (Webster 1994) in the early secondary-growth vegetation at the study site – were separated from recently released diaspores and also analyzed for fatty acid composition.

Statistical analyses

We performed a two-way ANOVA using the SAS GLM procedure (SAS 1988) to test for the effects of size and type of fleshy portion (pulp or aril) of the diaspores (independent variables) on the time-to-discovery and number of ants after the 15-min recruitment period (dependent variables). The two dependent variables were log- and $\log(n + 1)$-transformed, respectively, prior to the analyses to achieve uniformity of variances. Kolmogorov-Smirnov tests were used to compare the rates of ant recruitment within size classes, and the rate of seed germination between intact and cleaned seeds of *Eugenia*. Non-parametric statistics (Spearman's rank correlation and Mann-Whitney U-test) were employed when the data departed from the assumption of normality. All χ^2 tests are reported using Yates correction.

Results

Recruitment of ants to diaspores

Ants rapidly discovered diaspores placed on the forest floor. On average, an ant was attracted to the diaspore in < 8 min. However, great interspecific variation occurred in the time-to-discovery (range 0.1–28.4 min), which was not significantly affected by the size or type of fleshy portion (pulp or aril) of the diaspore, or the interactions between these two variables (Table 2). Once the diaspores had been discovered, however, recruitment rates differed between arillate and non-arillate diaspores in all but the two smallest diaspores (Figure 1). At the end of the 15-min recruitment period, arillate diaspores attracted significantly more ants than their similar-sized non-arillate counterparts (12.5 ± 16.6 vs 5.0 ± 7.9 ants, respectively; see Table 2). The size, as well as the interaction between size and type of fleshy portion, did not affect significantly the number of attending ants at diaspores after 15 min (Table 2).

Table 2. Two-way ANOVA table for the effects of size and fleshy portion type (pulp or aril) of the diaspores on time-to-discovery and number of ants attending the diaspores at the end of the 15-min recruitment period. Time-to-discovery and number of attending ants were, respectively, log- and log(n+1)-transformed prior to the analysis.

Effects	df	Time-to-discovery			Number of attending ants		
		M S	F	*P*	M S	F	*P*
Model	5	0.203	0.86	0.51	0.563	1.94	0.09
Size	2	0.302	1.27	0.28	0.065	0.22	0.80
Fleshy portion	1	0.051	0.22	0.64	2.390	8.25	0.004
Size × fleshy portion	2	0.181	0.76	0.46	0.147	0.51	0.60
Error	114	0.237			0.290		

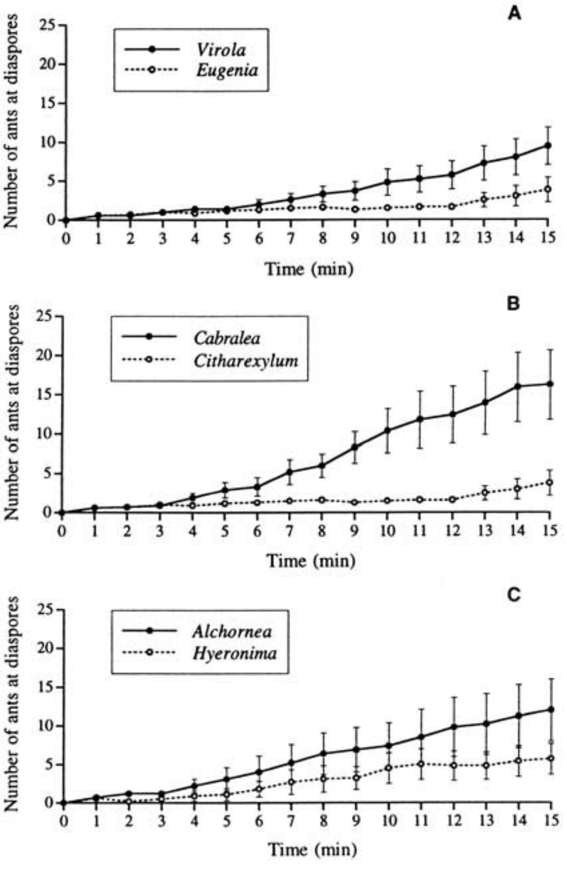


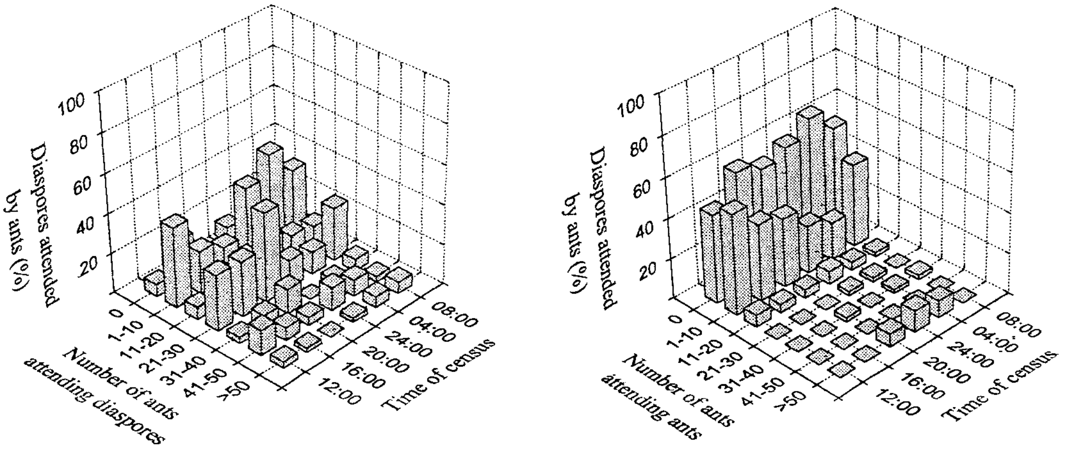
Figure 1. Number of ants attracted to large (A), medium (B), and small (C) nonmyrmecochorous diaspores (n = 20 diaspores for each species). Recruitment rates of arillate (black circles) and non-arillate diaspores (open circles) were compared within each size class using Kolmogorov-Smirnov tests (*Virola* vs *Eugenia*: $D_{\max} = 0.15$, $P < 0.001$; *Cabralea* vs *Citharexylum*: $D_{\max} = 0.13$, $P < 0.001$; *Alchornea* vs *Hyeronima*: $D_{\max} = 0.02$, $P = 1.00$). Vertical lines refer to standard errors.

Censuses of the ants attending the diaspores

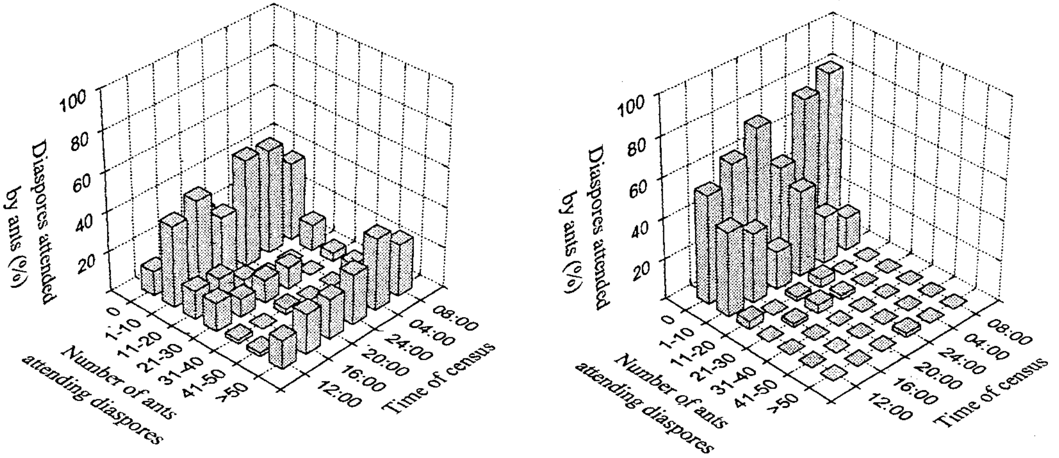
During the 24-h censuses, a greater number of ants was recorded attending arillate than non-arillate diaspores (Figure 2). The great number of ants on arillate diaspores was combined with a round-the-clock attendance by ants during which the arils were removed piecemeal. The great number of ants (> 50 individuals) attending some diaspores of *Eugenia* in the nocturnal censuses was due to the presence of a single species, the nocturnal leaf-cutting ant *Acromyrmex subterraneus* Forel. *Cabralea* diaspores were constantly attended by many ants (> 50 individuals; see Figure 2), mainly *Pheidole* sp. 7, *Solenopsis* sp. 5 and *Linepithema* sp. 1 (see also Table 3). At the end of the census period, 100% of the arillate diaspores of *Virola* and *Cabralea*, and 96% of *Alchornea*, had been attended by ants. For the non-arillate diaspores of *Eugenia*, *Citharexylum* and *Hyeronima* the proportions of attended diaspores were 88%, 86% and 74%, respectively (Table 3).

Table 3 summarizes the 23 ant species recorded during the censuses. Myrmicine ants in the genera *Pheidole* and *Solenopsis* were the most commonly seen attending the diaspores. The number of ant species that attended the diaspores ranged from 7 in *Alchornea* to 17 in *Cabralea* and *Citharexylum*. However, some species may have passed unnoticed on diaspores of *Alchornea* and *Hyeronima* simply because many of these diaspores were removed by ants prior to the first census (34% and 22%, respectively). While some individual diaspores did not attract any ant species during the entire census period, others were attended by up to five different species. In one extreme case, four ant species simultaneously attended a *Cabralea* diaspore. Ponerine and attine ants differed in the proportion of arillate and non-arillate dias-

Virola oleifera — *Eugenia stictosepala*



Cabralea canjerana — *Citharexylum myrianthum*



Alchornea glandulosa — *Hyeronima alchorneoides*

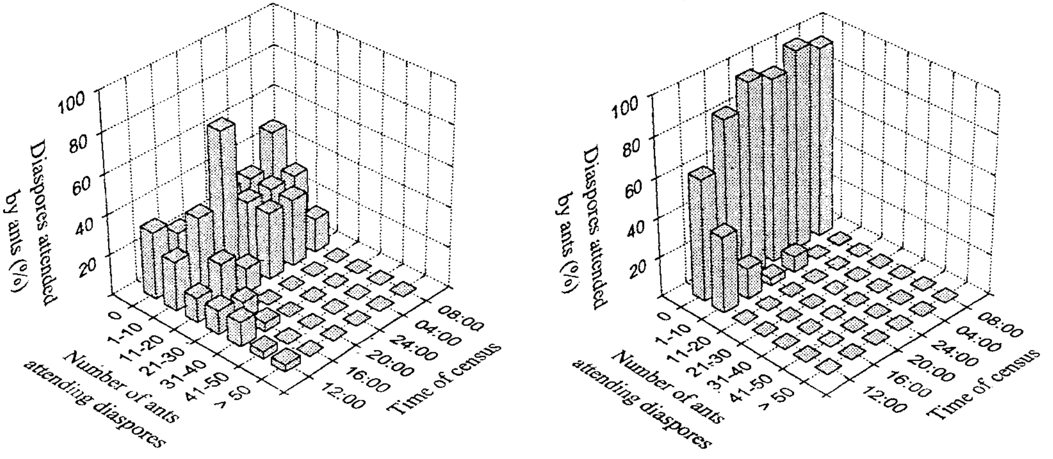


Figure 2. Number of ants attending the diaspores recorded in censuses conducted at 4-h intervals during a 24-period. Arillate and non-arillate diaspores are represented on left and right graphs, respectively.

Table 3. Number of arillate (*Alchornea glandulosa*, Ag; *Cabralea canjerana*, Cc; *Virola oleifera*, Vo) and non-arillate (*Hyeronima alchorneoides*, Ha; *Citharexylum myrianthum*, Cm; *Eugenia stictosepala*, Es) diaspores attended by different ant species during the 24-h censuses. Fifty diaspore of each species were used in the censuses. Under each subfamily, ant species are arranged in alphabetical order.

Ants	Arillate			Non-arillate		
	Ag	Cc	Vo	Ha	Cm	Es
Ponerinae						
Ectatomma edentatum	0	1	2	0	1	0
Gnamptogenys sp.	0	1	1	0	1	2
Odontomachus chelifer	0	3	2	0	1	0
Odontomachus affinis	0	1	1	0	0	0
Odontomachus meinerti	0	1	0	0	0	0
Pachycondyla striata	0	19	13	0	4	0
Myrmicinae						
Crematogaster sp. 1	0	1	0	0	0	0
Pheidole sp. 1	3	6	30	3	3	11
Pheidole sp. 2	0	3	4	0	3	0
Pheidole sp. 3	3	6	7	3	7	7
Pheidole sp. 7	12	20	17	7	13	20
Pheidole sp. 9	1	8	1	0	2	1
Pheidole sp. 11	0	0	1	1	0	0
Solenopsis sp. 1	5	8	6	4	5	2
Solenopsis sp. 2	1	3	1	0	1	1
Solenopsis sp. 4	0	1	0	0	0	0
Solenopsis sp. 5	3	10	14	0	0	1
Myrmicinae – Attini						
Acromyrmex subterraneus	0	0	5	0	6	9
Acromyrmex sp. 1	0	0	0	0	2	0
Acromyrmex sp. 2	0	0	0	0	2	3
Cyphomyrmex sp.	0	0	0	0	8	1
Formicinae						
Brachymyrmex sp.	0	0	4	1	6	5
Dolichoderinae						
Linepithema sp. 1	0	1	0	0	1	0
Number of attending ant species	7	17	16	6	17	12
Number of diaspores attended by ants	48	50	50	37	43	44

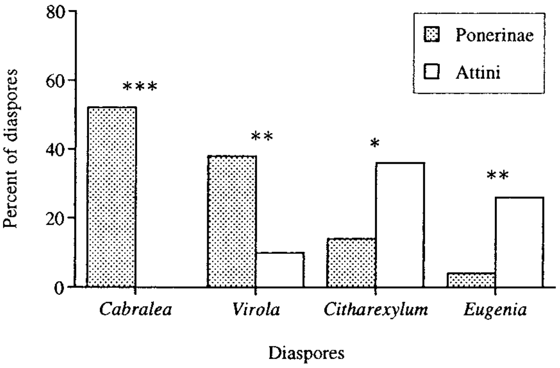


Figure 3. Percent of diaspores of *Cabralea canjerana, Virola oleifera, Citharexylum myrianthum*, and *Eugenia stictosepala* attended by ponerine and attine ants during the censuses. The former two species are arillate, while the latter two are non-arillate diaspores. Significance level for the χ^2 tests using Yates correction: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

pores they attended. Ponerines were more frequently recorded at diaspores of *Virola* and *Cabralea*, whereas attines were more common at diaspores of *Eugenia* and *Citharexylum* (Figure 3). As the small diaspores of *Alchornea* and *Hyeronima* were rapidly removed by ponerines and attines, thus precluding the record of these ants, no conclusion regarding the exploitation of small arillate vs non-arillate diaspores by attine and ponerine ants could be made.

Ants were rapid at cleaning the diaspores. The median time necessary for the total removal of the pulp or aril ranged from 8 h in *Alchornea* and *Citharexylum* to 15 h in Virola (Table 4). These figures should be viewed as rough estimates due to the low accuracy of the 4-h spaced censuses and the fact that diaspores cleaned in more than 24 h were not considered. No association was found between the amount of pulp or aril and the mean time necessary for their complete removal by the ants ($r_s = 0.60$, $n = 6$, $P > 0.20$). However, this probably results from the wide variety of ants considered in the overall removal time, many of which had marked differences in the time necessary to entirely clean the diaspores. The large ponerine *Pachycondyla striata* (body length 12 mm), for example, removed the arils of some *Cabralea* diaspores in $<$ 8 h, whereas the tiny myrmicines (e.g., *Pheidole* sp. 7, body length 2 mm) took $>$ 24 h to entirely clean such a seed. To eliminate this interspecific variation in the ant component, we compared the time necessary for *P. striata* ants to entirely remove the arils of *Virola* and *Cabralea*, the only two diaspores for which we have enough data for comparison. As a consequence of the higher amount of aril in *Virola* diaspores (see

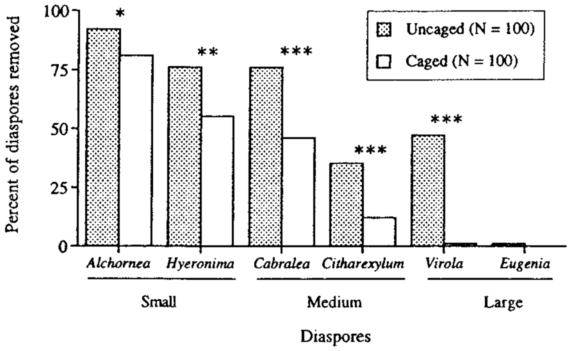


Figure 4. Percent of diaspores removed after 24 h in the caged and uncaged treatments. From left to right diaspores are arranged in the horizontal axis from the smallest to the largest diaspore. Significance level for the χ^2 tests using Yates correction: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Table 1), *P. striata* spent more time cleaning them (14.2 ± 9.0 h, $n = 12$), compared to the diaspores of *Cabralea* (9.3 ± 2.0 h, $n = 9$; U = 2.09, $P = 0.03$).

Diaspore removal by ants and vertebrates

Small and medium-sized diaspores were removed in significantly greater proportions in the uncaged than in the caged treatment, indicating that both ants and rodents removed them (Figure 4). Except for one caged diaspore, all the removal of *Virola* diaspores may be attributable to rodents. Surprisingly, only one uncaged diaspore of *Eugenia* was removed. Removal of caged diaspores by ants was negatively associated with the weight of the diaspores ($r_s = -0.93$, $n = 6$, $P < 0.05$). While the large ponerine (*P. striata* and *Odontomachus* spp.) and attine ants (*Acromyrmex* spp.) were observed transporting the small and medium-sized diaspores, the tiny myrmicines (e.g., *Pheidole* sp. 1. *P.* sp. 3) were only able to displace small diaspores. As a result, small diaspores as a whole were removed by ants in greater proportion than medium-sized diaspores ($\chi^2 = 59.34$, $P < 0.001$), which in turn were displaced in greater numbers than large diaspores ($\chi^2 = 73.53$, $P < 0.001$; Figure 4).

A significant negative correlation was found between the weight of the diaspores (Table 1) and the mean distance they were displaced by the ants ($r_s = -0.94$, $n = 6$, $P = 0.02$; Table 3). For instance, the large workers of *P. striata* were unable to move *Virola* diaspores for more than 15 cm, while the small diaspores of *Hyeronima* were transported up to 29 m by the leaf-cutting ant *Acromyrmex* sp. 2. When ants were unable to transport the diaspores to their nests, they removed the pulp or aril on the spot.

Fate of arillate diaspores in captive ant colonies

Although ants invariably inspected the diaspores placed in the foraging arena of the captive colonies and occasionally transported them to refuse piles, only *P. striata* treated the diaspores as observed in the field, i.e., transported the diaspores to the nest. Thus, only the behaviour of *P. striata* is reported here. These ants removed the aril of *Virola* and carried 25.5% and 87.5% of the diaspores of *Cabralea* and *Alchornea* ($n = 20$ species for both species), respectively, to the nest. The residence time of diaspores inside the nest was on average 3.2 ± 0.9 days ($n = 4$, range 2–4 days) and 4.4 ± 1.6 days ($n = 18$, range 3–9 days) for *Cabralea* and *Alchornea*, respectively. *Pachycondyla striata* workers fed on the arils and deposited the cleaned intact seeds on refuse piles outside the nest.

Germination

With the exception of *Eugenia* and *Hyeronima*, the removal of pulp or aril significantly increased the germination success of the seeds (Table 5). Although no difference was detected in the final germination success between intact and cleaned diaspores of *Eugenia*, seeds in the latter group germinated significantly faster than intact seeds ($D_{\max} = 0.56$, $P < 0.005$). For *Hyeronima*, on the other hand, the greenhouse conditions were apparently inadequate to trigger germination, since no seed germinated in either treatment group. These seeds possibly need scarification and/or a different light regime to germinate.

Fatty acid composition of the arils

The fatty acid composition of the arils of *Virola*, *Cabralea* and *Alchornea* was closely similar to that of the elaiosome of *Ricinus communis* (Table 6), as well as to the elaiosomes of other twelve myrmecochorous species reviewed by Hughes et al. (1994). Although the elaiosome of *R. comunis* has a more diverse array of fatty acids than the arils, the unshared portion represents a minor part of the elaiosome's fatty acids. The fatty acids of the arils consisted primarily of unsaturated to polyunsaturated chains with 16 to 18 C units. The most abundant fatty acids found in arils were oleic (47.6 ± 13.3%), palmitic (25.1 ± 2.7%) and linoleic (20.0 ± 9.8%) acids, together comprising 87 to 96% of the total. The most important differences among the

Table 4. Time necessary for complete removal of the pulp or aril and displacement distances of arillate (*Virola oleifera, Cabralea canjerana, Alchornea glandulosa*) and non-arillate (*Eugenia stictosepala, Citharexylum myrianthum, Hyeronima alchorneoides*) diaspores grouped into three size classes.

Diaspores	Time for complete removal of pulp or aril (h)		Displacement distance (m)	
	Median (*n*)	Range	Mean ± SD (*n*)	Range
Small diaspores				
Alchornea	8.0 (7)	8–24	0.76 ± 1.45 (16)	0.06-5.20
Hyeronima[a]	–	–	4.73 ± 10.44 (12)	0.01-29.00
Medium diaspores				
Cabralea	10.2 (17)	8–24	0.20 ± 0.30 (50)	0-1.80
Citharexylum	8.0 (3)	8	0.15 ± 0.16 (31)	0-0.73
Large diaspores				
Virola	15.0 (16)	4–24	0.03 ± 0.04 (14)	0-0.15
Eugenia[b]	12.0 (2)	12	–	–

[a] None of the *Hyeronima diaspores* had their pulp completely removed during the census period.
[b] Ants did not displace *Eugenia* diaspores.

arillate diaspores is the higher amount of oleic acid in the aril of *Virola*, which in contrast bears the lowest concentration of linoleic acid. On the other hand, the elaiosome of *R. communis* had a higher amount of stearic acid than the arils of the three other plant species.

Discussion

It is highly unlikely that any diaspore that falls to the ground at Parque Intervales passes unnoticed by litter-foraging ants. In the present study, only 9.3% of the diaspores censused ($n = 300$, all diaspores combined) were not attended by ants. This figure, however, is certainly an overestimate because only six scan samples were taken during the 24-h census period, a schedule that left the diaspores unobserved for most of the time. Litter-foraging ants are plentiful in tropical forests (Hölldobler & Wilson 1990; Byrne 1994), especially in lowland rainforests (Olson 1994; Pizo & Oliveira 1998). In addition, ants are known to exploit a variety of diaspores. At the study site, litter-foraging ants were observed exploiting 68 different nonmyrmecochorous diaspores found on the forest floor on a year-round basis (Pizo & Oliveira 2000). Once the diaspore has been discovered by an ant, the outcome of the interaction will depend on the behaviour of the ant (Horvitz 1981; Hughes & Westoby 1992b; Pizo & Oliveira 1998), as well as on the characteristics of the diaspore (Hughes & Westoby 1992a).

Factors mediating ant-nonmyrmecochorous diaspore interactions

Diaspore morphology

No significant effect of the presence of a lipid-rich aril, the size of the diaspore, or the interaction between these two factors, was found on the time-to-discovery. In fact, difference in time-to-discovery between arillate and non-arillate diaspores should not necessarily be expected since detection of prey by foraging ants is usually visual rather than chemical (Hölldobler & Wilson 1990). According to Gorb & Gorb (1995), the general size of the diaspores is particularly important in the stage of ‘finding’ by the ants. However, time-to-discovery in the field is greatly influenced by the patchiness in ant foraging, which creates ‘hot’ and ‘cold’ spots for diaspore finding and displacement (Hughes & Westoby 1990; Kaspari 1996a). The great intraspecific variation in time-to-discovery for all the diaspores studied corroborate this hypothesis and indicate that a larger sample size would be required to detect any trend in time-to-discovery related to diaspore size.

Arillate diaspores attracted a greater number of ants for a longer period of time than non-arillate ones, causing a round-the-clock attendance by ants (Fig-

Table 5. Germination experiments with intact (control group, C) and cleaned (treatment group, T) diaspores. Cleaned diaspores had their pulp or aril removed by the authors to simulate cleaning by ants.

Diaspores	Duration of the experiment (months)	Number of diaspores		Germination success (%)		*P* (χ^2 tests[a])
		C	T	C	T	
Non-arillate						
Hyeronima	5	100	100	0	0	–
Citharexylum	5	100	100	41.0	74.0	<0.001
Eugenia	8	50	50	36.0	50.0	0.22
Arillate						
Alchornea	6	50	50	13.6	48.0	<0.001
Cabralea	1	100	100	45.0	100	<0.001
Virola	5	100	100	41.0	60.0	0.01

[a] χ^2 tests using Yates correction.

Table 6. Fatty acid composition (%) of the lipids extracted from the arils of *Virola oleifera* (Myristicaceae), *Cabralea canjerana* (Meliaceae) and *Alchornea glandulosa* (Euphorbiaceae), and from the elaiosome of *Ricinus communis* (Euphorbiaceae). Fatty acids are designed by chain length: number of double bonds followed by their common names.

Species	Fatty acids												
	12:0 lauric	14:0 miristic	14:1 miristoleic	16:0 palmitic	16:1 palmitoleic	18:0 estearic	18:1 oleic	18:2 linoleic	18:3 linolenic	20:0 arachidic	22:0 behenic	22:1	24:0 linoceric
Elaiosome													
Ricinus communis	0.17	0.27	0.20	25.05	1.84	11.87	35.96	19.86	2.08	0.96	0.83	0.52	0.21
Arils													
Virola oleifera	0	0.34	0	22.99	0.98	2.38	62.55	9.30	0.54	0	0	0	0.16
Cabralea canjerana	0	0.02	0	24.27	1.52	2.01	43.30	28.68	0.14	0	0	0.01	0
Alchornea glandulosa	0	0.26	0	28.21	1.71	7.07	37.07	22.08	2.25	0.64	0.15	0.21	0

ure 2). In this sense, the difference between arillate and non-arillate diaspores was not restricted to the early stages of the interaction with ants but extended for the whole period during which the diaspores were attractive to ants. As a result, one would expect arillate diaspores to be cleaned more rapidly than non-arillate ones. The relationship between amount of pulp or aril and time to its complete removal by the ant assemblage may not be proportional because the way pulp and arils are attached to seeds differ among diaspores. The aril of *Virola*, for example, is loosely attached to the seed, whereas in *Cabralea* the aril is so firmly wrapped around the seed that it takes a long time to remove it completely. Moreover, the time necessary for the cleaning of diaspores will depend on the ant species. Large ponerines and attines take large portions of the pulp or aril at a time, while the myrmicines, albeit usually more numerous, take only small bits. Irrespective of ant species and aril/pulp attachment to the seed, however, diaspores were generally cleaned in less than 24 h with important consequences for seed germination (see below). Oliveira et al. (1995) also observed that a few hours of intense cleaning activity by the small *Mycocepurus goeldii* Forel (Attini) could result in the complete removal of the pulp around the huge seeds of *Hymenaea courbaril* L. (Caesalpiniaceae).

The size of the diaspores was a key factor for their displacement by ants. With the exception of some *Solenopsis* species which only drink liquids from the diaspore surface, the ants apparently transport to the nest all the diaspores that fall below a given size limit. Above this limit, however, the ants remove the pulp/aril on spot without displacing the diaspore. Obviously the size limit for diaspore displacement varies from one ant species to another (Davidson 1977).

For example, large ponerines (e.g., *Pachycondyla striata* and *Odontomachus chelifer*) and attines (e.g., *Acromyrmex subterraneus*) displaced medium-sized and small diaspores but failed to carry large diaspores. The 0.9-g diaspore of *Cabralea* is probably close to the upper size limit for these ants because they took a long time to displace it through the forest floor (Pizo & Oliveira 1998). On the other hand, the small myrmicines could only displace small diaspores through group retrieval. The displacement distance of the small diaspores of *Alchornea* and *Hyeronima* by the large ponerines and attines on one side and the myrmicines on the other, however, differed greatly in scale. *Acromyrmex* sp. 2 (Attini), for example, was observed displacing *Hyeronima* diaspores for a distance of 29 m. Small myrmicines rarely forage beyond 1 m from their nests (Levey & Byrne 1993; Byrne 1994), and the greatest displacement distance recorded in the present study was 19 cm (see also Horvitz & Schemske 1986a). Although the maximum displacement distance observed for *P. striata*, the larger and most abundant ponerine in the study site (M. A. Pizo & P. S. Oliveira, unpublished data), was only 78 cm, this figure is possibly an underestimate because once these ants picked up a diaspore, they rapidly disappeared into the leaf litter (see also Pizo & Oliveira 1998). Medeiros (1997) recorded workers of *P. striata* foraging up to 4.5 m from the nest in a semideciduous forest in southeast Brazil, which suggests that these ants can displace diaspores for distances greater than those recorded in this study. In fact, *Pachycondyla* and *Odontomachus* ants are known to transport seeds of *Calathea* species (Marantaceae) for 10–20 m (Horvitz & Beattie 1980; Horvitz & Schemske 1986a).

Although ponerines and attines can potentially displace diaspores for considerable distances, the current study showed that they forage for diaspores with different attributes. Ponerines attended arillate diaspores more frequently than attines which, in turn, were more frequently recorded on non-arillate diaspores. Carnivorous ponerines have dietary requirements different from fungivorous attines and, as a consequence, search for different diaspores. In fact, Beattie (1991) suggested that these two ant subfamilies may respond differently to the chemical composition of the food bodies offered by the plants.

Diaspore chemistry

Many authors have pointed out the importance of lipids as a mediating factor in ant-diaspore interactions (Marshall et al. 1979; Skidmore & Heithaus 1988; Brew et al. 1989). Lipids are an important food resource for ants, serving a variety of purposes that include nutrition, physiological constituents and behavioural releasers (Beattie 1985 and references therein). Lipids are the ant attractant in elaiosomes of myrmecochorous diaspores (Brew et al. 1989; Lanza, Schitt & Awad 1992), and are important constituents of extrafloral nectar and honeydew (Forrest & Knights 1972; Beattie 1985; Koptur 1992). Therefore, it is not surprising that ants responded differently to lipid-rich (arillate) and lipid-poor (non- arillate) diaspores in the present study. This difference becomes evident as soon as the diaspore is discovered by a foraging worker ant on the forest floor. The number of ants recruited to diaspores was positively influenced by the presence of a lipid-rich aril. In addition, recruitment rate of nestmates was significantly higher for medium-sized and large arillate diaspores than for non-arillate, similar-sized counterparts. Although recruitment may be influenced by factors that were not controlled for (e.g., the distance from the diaspores to ant nests), the higher number of attending ants on arillate diaspores, and the consistently higher recruitment rate toward arillate as compared with non-arillate diaspores is indicative of the role of the lipid content of nonmyrmecochorous diaspores in shaping the foraging behaviour of ants. The size of the diaspore, however, also affects the foraging behaviour of ants (Andersen & Ashton 1985; Gorb & Gorb 1995), which may account for the similarity in the recruitment rates recorded for the small arillate and non-arillate diaspores. Small diaspores are likely to elicit less recruitment pheromone and tactile signaling among nestmates, leading to a less precise and less intense recruitment (Hölldobler & Wilson 1990).

Although lipid-rich diaspores were represented in this study by arillate diaspores, this may not always be the case since not all arillate diaspores are lipid-rich. For instance, the arils of *Copaifera trapezifolia* Hayne (Caesalpiniaceae) and *Protium* sp. (Burseraceae) have < 3% of lipids (Pizo & Oliveira 2000). On the other hand, the pulp of some diaspores may be rich in lipids as well, as for example the diaspores of *Heisteria silvianii* Schwacke (Olacaceae) whose pulp has almost 30% of lipids. Notwithstanding, *Virola*, *Cabralea* and *Alchornea* are members of plant families (Myristicaceae, Meliaceae and Euphorbiaceae, respectively) whose diaspores are characteristically lipid-rich (see Jordano 1993). Moreover, the arils of these three species have a fatty acid composition closely similar to the elaiosome of *Ricinus communis* and of many other myrmecochorous species, with a marked predominance of palmitic, oleic and linoleic acids (O'Dowd & Gill 1986; Hughes et al. 1994). The latter two fatty acids may be especially important dietary substances for ants (Marshall et al. 1979; Beattie 1991; but see Midgley & Bond 1995). The variation we detected between the fatty acid composition of the arils and the elaiosome of *R. communis* is similar to the variation found by Hughes et al. (1994) among the 12 elaiosome-bearing species they analyzed. O'Dowd & Gill (1986) have also found similarities in the fatty acid composition of the arils and elaiosomes of Australian *Acacia*. These authors noted that the diaspores exploited by ants have a broad range of seed size and food body structure, including some typically bird-dispersed diaspores (see also Davidson & Morton 1984). Hughes, Westoby & Johnson (1993) found a similarity in terms of nitrogen and potassium between the arils and elaiosomes of five arillate and 22 elaiosome-bearing species in Australia. In fact, the distinction between arils and elaiosomes is functional rather than anatomical. Both are morphologically similar structures with the same embryological origin (van der Pijl 1982; Beattie 1985). The boundary separating arils as food bodies of ornithochorous diaspores from elaiosomes is frequently subtle, and some authors rely upon subjective parameters such as colour to tear them apart (Davidson & Morton 1984; O'Dowd & Gill 1986). Therefore, aside from the behavioural differences imposed by the size of the diaspores (and perhaps shape of the fleshy portion, see O'Dowd & Gill 1986), there is no reason to expect that the treatment given by ants to elaiosome-bearing diaspores would differ from the treatment given to lipid-rich nonmyrmecochorous diaspores. Even the manner through which these two groups of diaspores become available to ants is similar in certain cases. Many diaspores adapted to dispersal by ants (including *R. communis*) reach the floor after being released from the parent plant either ballistically or by other means of dispersal (i.e., diplochory sensu van der Pijl 1982). In the case of nonmyrmecochorous diaspores, it is the action of vertebrates that most frequently makes them available to ants on the forest floor, although they may also fall spontaneously from the parent plant (see Howe 1980; Pizo 1997; Pizo & Oliveira 1999).

In short, the distinction we made between lipid-rich and lipid-poor diaspores was worthwhile because ants indeed responded differently to the two types of diaspores in many ways. Ants recruited more rapidly and in greater numbers to lipid-rich diaspores, which were attended for a longer period and by a different set of ant species than lipid-poor diaspores. Similarly, the diaspore size gradient also represented a fine tuning to our understanding of the interactions between ants and nonmyrmecochorous diaspores. Small diaspores were removed in greater numbers, to greater distances, and by a more diverse ant assemblage than medium-sized or large diaspores. Therefore the outcome of the interaction between ants and fleshy diaspores appears largely determined by the size and lipid content of the diaspores.

Possible consequences for the plants

By removing the pulp or aril of the diaspores studied, ants enhanced the germination success in four out of the six plant species studied. Fallen diaspores that lay on the forest floor with intact fleshy parts usually die due to fungi infestation (Augspurger 1990; Oliveira et al. 1995). With respect to seed predators, however, plants would achieve no net benefit if their diaspores, despite being cleaned by the ants, were not displaced to safe microsites. Seed predation is often severe in tropical forests, especially beneath parent plants where the high density of seeds is highly attractive to seed predators (Janzen 1970, 1971; Connell 1971). After a 6-day experiment at Parque Intervales, for example, 96% and 83% of the diaspores of *Cabralea* set beneath parent trees were preyed upon by insects and rodents, respectively (Pizo 1997). In this respect, the small diaspores that are displaced by large ponerines and attines for large distances may escape from the predation-prone zone beneath parent plants (Pizo & Oliveira 1998). In addition, by being promptly displaced by litter-foraging ants, small diaspores become rapidly unavailable to rodent and insect predators. As noted by Hughes & Westoby (1990), if seeds are subjected to intense predation on the ground, the speed at which they are located and removed by ants may be crucial. The exclosure experiment gave support to the importance of ant removal of small diaspores to avoid post-dispersal seed predators. The number of diaspores taken by rodents, as estimated by the difference between caged and uncaged treatments, was lower for the small arillate diaspores of *Alchornea*, compared to the other diaspores tested.

Observations with captive colonies of *Pachycondyla striata* showed that the ants remove the arils of *Cabralea* and *Alchornea* and after a few days discard intact seeds on refuse piles outside the nest, where they eventually germinate. The same behaviour was observed by Horvitz (1981) for other *Pachycondyla* species and *Odontomachus laticeps* toward diaspores of *Calathea* spp. (Marantaceae). The fact that the captive *O. chelifer* and *Ectatomma edentatum* did not treat the diaspores in the manner they usually do in the field may be related to the stress caused by the captivity conditions or, alternatively, by the avoidance of frozen diaspores. Indeed, Horvitz also reported that the behaviour of captive *Parathechina* species toward *Calathea* diaspores 'was quite unlike their behaviour in the field' (Horvitz 1981, p. 49). Although some myrmicines (including attines) possibly destroy many of the diaspores carried to nests (Hughes & Westoby 1992b; Levey & Byrne 1993), some diaspores may escape predation and occasionally end up successfully established. Farji Brener & Silva (1996) observed that *Atta laevigata* (Attini) promote the establishment of the seeds of *Tapirira velutinifolia* (Anacardiaceae) in a Venezuelan savanna, and Leal & Oliveira (1998) demonstrated that aril/pulp removal by attine ants increases the germination success of several nonmyrmecochorous plant species of the Brazilian 'cerrado'. Likewise, Levey & Byrne (1993) observed that seeds carried to *Pheidole* nests became established after the nest is abandoned by the ants in a Costa Rican forest.

According to Levey & Byrne (1993), the removal by ants of tiny nonmyrmecochorous seeds, such as those of *Miconia* species (1–1.5 mm; Melastomataceae), should not be assumed to be seed predation because ants do not destroy all the seeds they collect. Similarly, nonmyrmecochorous diaspores dropped by vertebrate seed dispersers should not be viewed as a complete 'waste' or subjected only to secondary dispersal by rodents (Forget & Milleron 1991). Ants intensively interact with fallen diaspores and may have a positive rather than a detrimental effect upon many of them (Oliveira et al. 1995; Leal & Oliveira 1998). It is possible that small lipid-rich diaspores such as those of *Alchornea* benefit from the interaction with ants. We have shown that these diaspores are removed not only by ponerine and attines but also by myrmicine ants, sometimes to large distances. Because ant species differ in their microhabitat nesting preferences (Hölldobler & Wilson 1990; Hughes & Westoby 1992b), diaspores displaced by such a large ant assemblage are likely to be deposited in a diverse array of microsites, some of which may happen to be adequate for seed germination and establishment. Nonetheless, even if not transported all the way to the nest by a foraging ant, small diaspores may be abandoned in safe spots under the leaf litter, where conditions for germination may be appropriate (Horvitz 1981; Pizo & Oliveira 1998).

A key issue for the interaction examined here is whether ants, which play at best a secondary role in the dispersal process, have any significant impact on population recruitment (see Horvitz & Schemske 1986b). Although secondary, the impact of ants on a plant's crop may not be trivial. A great percentage of the diaspores produced by some nonmyrmecochorous tropical trees is dropped by vertebrate seed dispersers (Howe 1980; Pizo 1997). Laman (1996) estimated that $> 50\%$ of the seed crop produced by *Ficus* trees in a Bornean rainforest end up on the floor beneath parent plants. In a study of the seed dispersal of *Cabralea* by birds, Pizo (1997) observed that the five main seed dispersers dropped approximately 30% of the diaspores they took from the plants, which may represent for some especially fecund trees over 8000 diaspores during the entire fruiting season. Obviously, even considering the high abundance of litter-foraging ants in tropical forests (Hölldobler & Wilson 1990; Byrne 1994), we should not expect ants to entirely exploit such a huge amount of fallen diaspores. As suggested by Davidson & Morton (1984), there is no necessary correlation between the number of seeds dispersed by a given agent and the value of that agent for the plant's fitness. Moreover, as stated by Levey & Byrne (1993), the fact that the benefits accrued from a particular component of a dispersal system may be rare does not mean that they are unimportant. Given the growing body of information on the interactions between ants and nonmyrmecochorous diaspores (Roberts & Heithaus 1986; Levey & Byrne 1993; Oliveira et al. 1995; Farji Brener & Silva 1996; Bello y Bello 1997; Leal & Oliveira 1998; Pizo & Oliveira 1998), it seems appropriate to carefully consider these interactions as an important factor for population recruitment of some plant species.

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