

Removal of seeds from vertebrate faeces by ants: effects of seed species and deposition site

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Abstract: We investigated the removal of seeds of three species (*Philodendron corcovadense* and *Philodendron appendiculatum* (Araceae) and *Aechmea* sp. (Bromeliaceae)) from the faeces of capuchin monkeys (*Cebus apella*) by ants in a lowland Atlantic rain forest in southeast Brazil. We examined seed removal by ants in the understory and in treefall gaps, which probably differ greatly in microclimatic conditions. We examined whether seed removal varied among seed species, between understory and gaps, and also among five gaps that differed in size and age. We recorded 17 ant species (4 subfamilies, 9 genera) on the faeces, 8 of which were observed removing seeds. On average, 68% of the seeds had been removed from faecal portions containing 15 seeds each after 24 h. For both the understory versus gap and the among-gap comparisons, seed species significantly affected the proportion of seeds removed, while deposition site (i.e., understory versus gaps or among gaps) had no effect. We interpreted these results as a consequence of the equalizing effect of three myrmicine species (*Pheidole* sp. 1, *Pheidole* sp. 3, and *Pheidole* sp. 7) upon seed removal. These ant species were the most frequently recorded on faeces (63 and 44% in understory and gap sites, respectively, for all three *Pheidole* species combined) and are among the most abundant litter-foraging ants in the understory and gaps. Because of the high abundance of ants in Neotropical forests, and the flexibility of some ant species in the microclimatic gradient they use, seed removal is likely to be less affected by differences in microclimatic conditions between understory and gaps than by the seed species involved.

Résumé : Nous avons étudié le phénomène de récupération par les fourmis de trois espèces de graines (*Philodendron corcovadense* et *Philodendron appendiculatum* (Araceae) et *Aechmea* sp. (Bromeliaceae)) dans les fèces de Capucins (*Cebus apella*) dans une forêt pluvieuse des terres basses atlantiques dans le sud-est du Brésil. Nous avons observé le phénomène dans la zone sous le feuillage et dans cinq ouvertures créées par la chute d'arbres à conditions climatiques sans doute très différentes. Nous avons cherché à déterminer si le prélèvement des graines variait en fonction des espèces de graines, entre la zone sous le feuillage et les ouvertures, de même qu'entre des ouvertures de tailles et d'âges différents. Nous avons observé 17 espèces de fourmis (4 sous-familles, 9 genres) sur les fèces, dont 8 ont été vues en train de prélever des graines. En moyenne 68% des graines étaient prélevées après 24 h dans les portions fécales contenant chacune 15 graines. La comparaison des résultats obtenus dans la zone sous le feuillage et ceux obtenus dans les ouvertures et la comparaison de tous les résultats obtenus dans les ouvertures ont révélé que la nature spécifique des graines affecte la proportion de graines récoltées, alors que le site de tombée des fèces (i.e. zone sous le feuillage vs ouvertures ou ouvertures de caractéristiques différentes) n'avait pas d'effet. Nous considérons ces résultats comme une conséquence de l'effet égalisateur de trois espèces de fourmis myrmiciniées (*Pheidole* sp. 1, *Pheidole* sp. 3 et *Pheidole* sp. 7) sur la récolte des graines. Ces espèces se sont avérées les plus communes sur les fèces (63 et 44% dans la zone sous le feuillage et dans les ouvertures, les trois espèces combinées) et comptent parmi les fourmis les plus abondantes de la litière dans la zone sous le feuillage et dans les ouvertures créées par la chute d'arbres. Etant donné l'abondance considérable des fourmis dans les forêts néotropicales et la flexibilité de certaines espèces à l'intérieur du gradient microclimatique qu'elles utilisent, la récolte des graines est sans doute moins susceptible d'être affectée par les différences de conditions microclimatiques entre les zones sous le feuillage et les ouvertures créées par la chute d'arbres que par la nature des graines.

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Introduction

Faeces of frugivorous vertebrates usually contain many viable seeds (Loiselle 1990), which, if not removed from the

defecation clump by secondary seed dispersers, are subject to sibling competition (Howe 1989). Large seeds present in faeces are likely to be exploited by rodents (Janzen 1982), which eat many of the seeds but cache and lose some of them, thus effectively acting as secondary seed dispersers (Forget and Milleron 1991). However, rodents are usually not attracted by the tiny seeds present in faeces (Mittelbach and Gross 1984; Foster 1986; Kaspari 1993b), but these may be avidly exploited by harvesting ants (Byrne and Levey 1993; Kaspari 1993b). By carrying such seeds to their nests, harvesting ants rearrange the seed shadow generated by the primary seed dispersers (Roberts and Heithaus 1986; Pizo

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Table 1. Morphological characteristics of seeds embedded in monkey faeces presented to ants.

Family and species	No. of faecal portions		Morphology		
	Understory	Treefall gaps	Width (mm)	Length (mm)	Mass (mg)
Araceae					
<i>Philodendron corcovadense</i>	35	45	1.58±0.18	3.41±0.40	2.19±0.26
<i>Philodendron appendiculatum</i>	25	50	0.53±0.07	1.33±0.05	0.10±0.02
Bromeliaceae					
<i>Aechmea</i> sp.	64	48	0.62±0.08	2.02±0.22	0.32±0.02

Note: Ten seeds of each species were measured and weighed. Values are given as the mean ± SD.

and Oliveira 1998). Although most of the retrieved seeds are eaten by the ants, some of them escape predation and occasionally become established (Levey and Byrne 1993). Since small-seeded fruits are plentiful in tropical forests (Foster and Janson 1985), where most of the fruits are animal-dispersed (Frankie et al. 1974; Howe and Smallwood 1982), and given the impressive abundance of ants in these habitats (Hölldobler and Wilson 1990; for seed-harvesting ants see Kaspari 1996), it is reasonable to predict that “ant–seed interactions after vertebrate seed dispersal may have an important influence on the dispersal success of plants” (Byrne and Levey 1993, p. 364).

Seed harvesting by ants is spatially highly variable (Kelrick et al. 1986; Hughes and Westoby 1990). Ant patchiness on the floor of Neotropical forests creates “hot” and “cold” spots in ant foraging activity, which leads to high microsite variation in the removal of seeds from frugivore faeces (Kaspari 1993a, 1993b). Within forests, treefall gaps represent distinct habitats that differ from the surrounding undisturbed understory in light, temperature, and moisture conditions (Foster 1986; Denslow 1987). Given that ants are sensitive to the microclimatic conditions of the forest floor (Levings and Windsor 1984; Kaspari 1993a), ant–seed interactions should differ between gaps and the understory. Le Corff and Horvitz (1995), for example, suggested that the difference in the dispersal distance of ant-dispersed seeds of *Calathea micans* (Marantaceae) located in understory versus gap sites in a Costa Rican rain forest was probably due to variation in the relative abundance of ant species between these two habitats (see also Le Corff 1996). Gaps may receive a huge amount of seeds (Denslow and Gomez-Diaz 1990; Loiselle et al. 1996) and constitute important recruitment sites for small-seeded plant species (Schupp et al. 1989). Many such seeds reach gaps embedded in the faeces of frugivorous birds and bats, which seem to prefer these habitats for their foraging activities (Levey 1988; Gorchov et al. 1993).

In this paper we investigate the removal by ants of three species of seeds naturally found in faeces of capuchin monkeys (*Cebus apella*, Cebidae). Data were gathered from faeces experimentally distributed in understory and gap sites in an Atlantic rain forest in southeast Brazil. Four questions were addressed: (1) does seed removal vary between understory and gaps, or among gaps? (2) are seeds of different plant species removed in different proportions? (3) do seed-displacement distances vary with ant species (especially with ant body size) or between understory and gaps? and (4) do different colonies of the same ant species differ in seed-

exploitation pattern? We also used honey and tuna baits to correlate ant abundance in understory and gap sites with seed removal.

Study site

The study was carried out during 1996 and 1997 in the lowland forest of Parque Estadual Intervales (24°14'S, 48°04'W), a 49 000-ha reserve located in São Paulo State, southeast Brazil. The site (Saibadela Research Station, 70 m asl) received a mean annual rainfall of 4216 mm between 1994 and 1996. Rains are well distributed throughout the year and although no month receives <100 mm, rainfall is less intense and less frequent between April and August. During this period the temperature may occasionally drop below 10°C (mean ± SD = 20.8 ± 2.5°C for the study period), which contrasts with the wetter period, when the temperature may reach 42°C (25.7 ± 2.8°C). Old-growth forest (sensu Clark 1996) predominates in the study site. The understory is open and the canopy is 25 m high, with a few emergent trees reaching 30 m (Almeida-Scabbia 1996).

The area is crossed by several 1 m wide trails that were used to establish the understory transect described below. The five gaps used in the study originated from treefalls that produced well-marked openings in the canopy. Gaps were categorized according to age and size, as follows: I, 310.0 m², 2–3 years old; II, 97.6 m², >1 year old; III, 686.4 m², 1–2 years old; IV, 72.5 m², <1 year old; V, 212.5 m², 1–2 years old. This size range encompasses most of the gaps that occur in tropical forests (Brokaw 1982). The oldest gap was dominated by herbs of the family Marantaceae, while the youngest one was still a tangle formed by the branches of the fallen tree.

Methods

Removal of seeds from faeces

Capuchin monkey faeces were collected beneath a bait station where a troop of monkeys regularly fed. These faeces contained mainly plant material (crushed leaves and fruit skin) with only a minor proportion, if any, of insect parts. Among the many seeds present in monkey faeces (Vieira and Izar 1999), we selected those of two species of Araceae (*Philodendron corcovadense* and *Philodendron appendiculatum*) and one species of Bromeliaceae (*Aechmea* sp.) (see Table 1), based on their availability and their small size, which permits removal by both large and small ants. From June 1996 to June 1997, as faeces containing seeds became available, we prepared small portions of faeces (1–2 cm in diameter) by embedding 15 seeds in each (using larger quantities would not have led to a significant increase in the proportion of seeds removed by ants; see Kaspari 1993b). Faeces from capuchin monkeys were found scattered on the forest floor (often in masses ≤2 cm in diameter) rather than as a single pile (P. Izar, personal observation). Seeds were first separated from the fresh faecal mass

and mixed again with seed-free portions of the same faecal load. All 15 seeds in each fecal portion were of the same species. The faecal portions were mounted on small pieces of white filter paper (4 × 4 cm) as a substrate to ensure that the ants were visible. In the field, the faeces were placed directly on the leaf litter, protected from vertebrate disturbance by wire cages (15 × 15 × 10 cm, 1.50-cm mesh) that were closed at the top, and staked to the ground. Plastic wrap placed on the top of each cage prevented the faeces and ants from being dislodged by light to moderate rains. We interrupted every trial during which intense and prolonged rains occurred. Similarly, faeces that were severely disturbed by moderate rains despite the plastic covering were not considered in the analyses. Because of these failed trials, and the limited availability of seeds, sample sizes were unequal among the three seed species used (Table 1). In the understory, faeces were placed at stations arranged 5 m apart along a transect established 1–2 m off trail. The number of stations in the understory varied from 25 to 64 according to seed species (Table 1). The transect was at least 50 m from the nearest treefall gap. In each of the five gaps, 10 experimental faeces were arranged in the center of the gap along the trunk of the fallen tree, with a minimum distance of 2 m between faeces. The number of stations in the gaps varied from 45 to 50 (Table 1). Given the ant patchiness on the floor of tropical forests (Kaspari 1993a), and the fact that most litter-foraging ant species rarely move more than 1 m from their colonies (Levey and Byrne 1993; Byrne 1994), the distances between neighboring faeces likely ensured independent discovery by different ant colonies.

Faeces were placed on the understory transect and gaps at 08:00, when low temperature favored the activity of most ant species, irrespective of body size (see Kaspari 1993a). The seeds remaining in the experimental faeces were counted after 24 h. The ant species attracted to the faeces, as well as their behavior toward the seeds (i.e., whether they removed or ignored them), were recorded in four scan samples taken at 15-min intervals from 08:00 to 09:00. During the scan samples, we visited the faeces sequentially and collected ants for identification. Voucher specimens of the ants are deposited in the Museu de Zoologia of the Universidade de São Paulo (MZUSP). We followed ants carrying seeds until they entered their nests or disappeared in the leaf litter. The seed-displacement distance was then measured. To correlate seed-displacement distance with ant body size, we measured the maximum head width (to the nearest 0.01 mm) of 10 workers of the main seed-remover species, using a dissecting microscope equipped with an ocular micrometer. The maximum head width of ants is highly correlated with body size (Kaspari 1996).

The faecal portions constituted the unit of analysis and the proportion of seeds removed after 24 h was the dependent variable. Since the data were not normally distributed, we performed Friedman's two-way tests to examine the effects of seed species and deposition site (understory versus gaps, or among gaps) on the proportion of seeds removed by ants. Data were ranked within deposition sites to examine the effect of seed species and vice versa (Sokal and Rohlf 1981).

Ant abundance in the understory and gaps

To compare the abundance of litter-foraging ants in the understory and gaps, we sampled the ants attracted to tuna and honey baits distributed along the understory transect and in the gaps in the same way as described above for faeces. In February 1997, 100 baits of each type were placed along the understory transect, and 10 baits of each type in the five gaps. Small pieces (4 × 4 cm) of white filter paper were used as substrate for baits. Bait trials were initiated at 08:00 and the species of ants attracted to the baits were recorded after 1 h. Tuna- and honey-bait trials were run on consecutive days, and the results of the two trials were pooled for the analyses. Ants of the tribe Attini, which are more

attracted to fruit baits (see Leal and Oliveira 1998), were not included in the analyses.

Fate of seeds inside captive ant colonies

We collected four queenright colonies of *Pheidole* sp. 1 with plenty of brood; this is one of the ant species most frequently seen collecting seeds from faeces. Colonies were maintained in our laboratory at the Universidade Estadual de Campinas (UNICAMP) in plastic boxes (30 × 20 cm) under natural conditions of light and temperature. The sides of the boxes were coated with Fluon to prevent ants from escaping. One test tube covered by a dark red plastic shelter and containing water trapped behind a cotton plug was placed in the center of each box to serve as a dark, moist nest site. Colonies were fed every 2 days with artificial ant diet (Bhatkar and Whitcomb 1970) and cockroaches (*Nauphoeta* sp.), even during the trials described below.

From April to July 1997, after a 2-month minimum period of habituation to captivity, a series of seed-fate trials was performed using *P. corcovadense* and *P. appendiculatum* seeds obtained from monkey faeces. These were the largest and the smallest, respectively, of the seeds used in this study (Table 1), and the most frequently removed by ants in the field (see below). Each trial consisted of offering 15 seeds of each species to the captive colony on small pieces of white filter paper (2 × 2 cm) placed 10–15 cm from the nest entrance. The fate of the seeds was checked daily for 1 week, after which a new trial with a different seed species was initiated. We recorded whether ants ignored the seeds or carried them to refuse piles or into the nests. Each colony was offered 60 seeds of each species in four trials. At the end of the study we inspected the refuse piles outside the artificial nests for discarded seeds.

Results

Seed removal

We recorded a total of 17 species of ants (4 subfamilies, 9 genera) on the faeces, 8 of which were observed removing seeds (Table 2). Understory and gap sites had 13 and 10 ant species, respectively, with 6 species in common. The species not shared were probably responsible for a minor proportion of seed removal (Table 2). *Pheidole* sp. 1, *Pheidole* sp. 3, and *Pheidole* sp. 7 were the main seed removers, and together were recorded on 63 and 44% of the faeces in understory and gap sites, respectively (Table 2). Although the latter two species did not differ in the proportion of faeces on which they were recorded at understory and gap sites, *Pheidole* sp. 1 was more commonly recorded at faeces placed in the understory ($\chi^2 = 5.01$, $df = 2$, $P = 0.02$; Table 2). Ants removed seeds from 88.8% of the faeces ($N = 267$; understory and gap sites combined). On average, 10.2 ± 5.4 (mean \pm SD) seeds were removed from each faecal portion after 24 h (10.0 ± 5.6 in the understory and 10.4 ± 5.3 in gaps; $N = 143$ and 124 faeces, respectively). Seed removal was bimodal; 11.2% of the faeces had no seed removed, while 35.2% had all the seeds removed ($N = 267$ faeces). The proportion of faeces from which no seeds were removed, possibly because they were not discovered by seed-carrying ants, did not differ between understory and gaps (12.1 and 10.5%, respectively; $\chi^2 = 0.05$, $df = 1$, $P = 0.82$). Overall, only 2.8% of the seeds that remained in the faeces after 24 h presented clear signs of predation by the ants (e.g., hollowed out and (or) broken); the others were intact.

Table 2. Frequency, behavior, and nesting habits of ant species attracted to faeces and bait stations at understory and treefall-gap sites.

Subfamily and species	Carry seeds?	Nest site	Percentage of observations ^a			
			Faeces		Bait stations	
			Understory (N = 124)	Treefall gaps (N = 143)	Understory (N = 200)	Treefall gaps (N = 100)
Ponerinae						
<i>Ectatomma edentatum</i>	Yes	Soil	0.8	0	5.5	19.0 ***
<i>Odontomachus chelifer</i>	?	Soil	0.8	0	5.0	7.0
<i>Odontomachus meinerti</i>	Yes	Soil	0.8	0	1.0	0
<i>Gnamptogenys</i> sp.	?	Soil	0.8	0	2.5	0
Myrmicinae						
<i>Pheidole</i> sp. 1	Yes	Soil	26.6	14.6*	13.0	7.0
<i>Pheidole</i> sp. 2	?	?	0	0.7	1.5	5.0
<i>Pheidole</i> sp. 3	Yes	Twigs	11.3	9.0	6.0	3.0
<i>Pheidole</i> sp. 7	Yes	Soil	25.0	20.8	25.0	24.0
<i>Pheidole</i> sp. 9	Yes	Soil	3.2	0	3.5	5.0
<i>Pheidole</i> sp. 10	?	?	0	0.7	0	0
<i>Solenopsis</i> sp. 1	No	Twigs	7.2	5.5	26.5	15.0*
<i>Solenopsis</i> sp. 2	No	?	0.8	0	1.5	1.0
<i>Solenopsis</i> sp. 5	?	Soil	0	0.7	8.0	2.0
Myrmicinae, tribe Attini^b						
<i>Apterostigma</i> sp. 1	?	Soil	0.8	0	–	–
<i>Cyphomyrmex</i> sp.	Yes	Soil	2.4	2.1	–	–
Formicinae						
<i>Brachymyrmex</i> sp.	Yes	?	0.8	1.4	8.0	7.0
Dolichoderinae						
<i>Linepithema</i> sp. 1	No	Arboreal	0	2.1	2.5	1.0

^aThe significance level of the χ^2 tests applied to comparisons of understory and treefall gaps is indicated as follows: *, $P < 0.05$; ***, $P < 0.001$.

^bAttine ants were not sampled at bait stations.

Table 3. Friedman's block tests for the effects of seed species and deposition site (understory \times treefall gaps and among gaps) on the proportion of seeds removed from monkey faeces by ants.

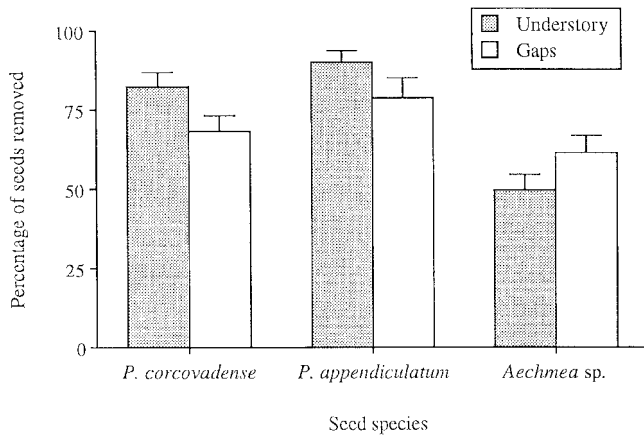
Test	Effect	Understory \times gap				Among gaps			
		df	Mean square	F	P	df	Mean square	F	P
Seed blocked by deposition site	Seed	2	21864.67	16.71	0.0001	2	217.30	3.41	0.03
	Error	264	1308.16			142	63.68		
Deposition site blocked by seed	Deposition site	1	928.63	1.21	0.27	4	348.32	1.93	0.11
	Error	265	767.82			140	180.18		

Ants differed in the way they interacted with the faeces. While most species were only interested in the seeds, picking them up from the faeces and carrying them individually to nests, species belonging to the Myrmicinae (tribe Attini) exploited the whole faecal mass, including the embedded seeds (see also Byrne and Levey 1993). Other ants such as *Solenopsis* sp. and *Linepithema* sp. seemed to be interested mostly in the liquids present in the faecal mass, since we never observed them removing either seeds or faeces. Given that six out of eight ant species nest in the soil (including two of the three main seed removers; see Table 2), most of the seeds removed from the faeces were likely transported into soil nests.

The proportion of seeds removed was significantly influenced by seed species, while deposition site had no effect (Table 3, Fig. 1). Similarly, seed removal from the different

gaps was affected by seed species but not by gap (Table 3, Fig. 2). The proportion of *P. appendiculatum* seeds removed was the highest (89.8 and 78.8% in the understory and gaps, respectively), followed by *P. corcovadense* (82.3 and 68.1%) and *Aechmea* sp. (49.7 and 61.5%) (Fig. 1). The tiny seeds of *P. appendiculatum* were the only seeds removed by *Pheidole* sp. 7, the most abundant (Table 2) and one of the smallest (approximately 2 mm total body length) litter-foraging ants at the study site. Faeces containing *P. corcovadense* seeds attracted the largest assemblage of ants (14 species); faeces containing seeds of the other two species, *P. appendiculatum* and *Aechmea* sp., attracted 7 and 8 ant species, respectively. *Philodendron corcovadense* seeds retain a fleshy, juicy coat after passing through the monkey's gut and this seems to be very attractive to ants. Seven of the 16 ant species recorded on faeces, including the predominantly carniv-

Fig. 1. Percentages of seeds of *Philodendron corcovadense*, *Philodendron appendiculatum*, and *Aechmea* sp. removed from capuchin monkey faeces by ants at understory and treefall gap sites in the Atlantic forest of southeast Brazil. Vertical lines correspond to standard errors.



orous *Ectatomma edentatum*, *Odontomachus chelifer*, and *O. meinerti* (subfamily Ponerinae), were only recorded on faeces containing *P. corcovadense* seeds.

Displacement distance

Seeds were removed for distances that ranged from 1 to 117 cm (27.0 ± 22.1 ; $N = 99$). The three main seed removers (*Pheidole* sp. 1, *Pheidole* sp. 3, *Pheidole* sp. 7) differed in seed-displacement distance (one-way ANOVA applied to log-transformed data, $F_{[2,85]} = 15.18$, $P < 0.001$). The difference was due to the shorter displacement distance for *Pheidole* sp. 7 (11.5 ± 8.6 cm; $N = 18$) than for *Pheidole* sp. 1 (26.8 ± 17.8 cm; $N = 48$) and *Pheidole* sp. 3 (34.3 ± 20.5 cm; $N = 22$) (Tukey's multiple-comparison test, $q_{crit} = 3.37$, $P < 0.05$). In fact, *Pheidole* sp. 7 has the smallest body of the three species (head width 0.34 mm for *Pheidole* sp. 7 and 0.57 mm for *Pheidole* sp. 1 and *Pheidole* sp. 3). Overall, displacement distances did not differ between understory (28.6 ± 24.0 cm; $N = 70$) and gap sites (22.2 ± 16.2 cm; $N = 29$; t test, $t = 1.29$, $df = 97$, $P = 0.19$).

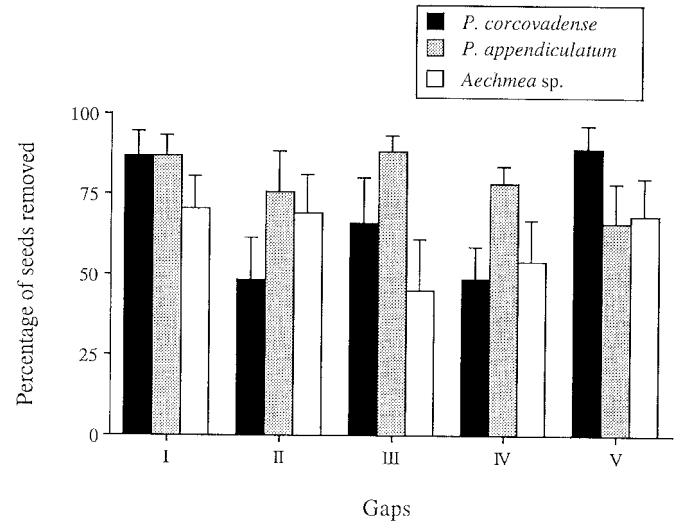
Ant abundance

The ant fauna attracted to the faeces was very similar to that recorded on the baits (Table 2). With the exception of *E. edentatum* and *Solenopsis* sp. 1, the frequency of occurrence of seed-carrying ants at bait stations at understory and gap sites did not differ (Table 2). Similarly, the frequency of the three main seed removers (*Pheidole* sp. 1, *Pheidole* sp. 3, and *Pheidole* sp. 7) combined did not differ among the five gaps ($\chi^2 = 3.87$, $df = 4$, $P = 0.42$). *Pheidole* sp. 1 and *Pheidole* sp. 7 were among the most abundant ant species in both understory and gaps (Table 2).

Fate of seeds inside captive ant colonies

The four colonies of *Pheidole* sp. 1 differed in the proportion of *P. corcovadense* and *P. appendiculatum* they carried to nests (range 0–63.3 and 13.3–85.0%, respectively; Kruskal–Wallis test, $\chi^2 \geq 7.60$, $df = 3$, $P \leq 0.05$). Seeds carried to nests were offered to the larvae and, after a few days,

Fig. 2. Percentages of seeds of *P. corcovadense*, *P. appendiculatum*, and *Aechmea* sp. removed from capuchin monkey faeces by ants at five treefall-gap sites in the Atlantic forest of southeast Brazil. Ten seed-containing faecal portions were tested in each gap. Vertical lines correspond to standard errors. Gap sizes and approximate ages are given in the text.



they were cached, i.e., deposited intact inside the nest. None of the seeds that were carried were found in refuse piles outside the nests at the end of the study (i.e., 3 months after the first seeds were collected by the ants).

Discussion

Seed removal from faeces is influenced by several variables, including the seed and ant species involved (Byrne and Levey 1993) and the number of seeds in the faeces (Kaspari 1993b). Given that ants are sensitive to temperature and moisture level and adjust their activities accordingly (Levings and Windsor 1984; Kaspari 1993a), an additional source of variation is likely to come from the microclimatic conditions on the forest floor. By contrasting ant activity between closed and open forests at La Selva, Kaspari (1993a) found that small ants tend to be more active in cooler, moister microclimates, while large ants tend to be microclimate generalists. Although understory and gaps possibly differ in microclimate at the litter layer (Foster 1986; Denslow 1987), our results show that seed removal from faeces was affected only by seed species and not by deposition site (i.e., understory versus gaps, or among gaps). Two factors may have contributed to this. First, the main seed removers (*Pheidole* sp. 1, *Pheidole* sp. 3, and *Pheidole* sp. 7) are among the most abundant species at all sites, which exerted an equalizing effect upon seed removal. In fact, some small ant species are flexible with respect to microclimatic gradient and are able to forage in both moist and dry microclimates (Kaspari 1993a). Second, differences in microclimatic conditions between understory and gaps are greater during the hotter hours of the day but conditions are similar at dawn and probably overnight (Kaspari 1993a), when many seed-carrying ants are active (M.A. Pizo and P.S. Oliveira, unpublished data). Le Corff and Horvitz (1995) also observed that

the removal rates of the ant-dispersed seeds of *Calathea micans* did not differ significantly between understory and gap sites in the forest of La Selva. Such an understory versus gap pattern, however, should not override the importance of microsite variation in ant activity as a determinant of seed removal by ants (Kaspari 1993a, 1993b).

Le Corff and Horvitz (1995) also found that seed-dispersal distances were greater in the understory than in gaps, probably because the most common ant disperser in the understory carried seeds for longer distances than the most common disperser in gaps. We did not detect any difference in dispersal distance either between understory and gap sites or among different seed species, simply because the same three *Pheidole* species were the most important seed removers at both sites. In any case, dispersal distance per se is of minor importance for seeds removed from faeces. From the seed's perspective, what matters is the net benefit, if any, of being removed to an ant nest, irrespective of the distance between the nest and the defecation clump (see below).

Seed species emerged as the main determinant of seed removal between understory and gaps and among gaps. Seed-harvesting ants have been shown to favor some seeds over others (Gross et al. 1991; Byrne and Levey 1993; Pizo and Oliveira 1999). Seed size and nutrient content are among the characteristics that govern selection by these ants (Davidson 1977; Kelrick et al. 1986). Seed size determines not only which ants are physically able to lift and carry a seed, but also the profitability of carrying it to the nest, based on the energy balance involved (Hughes and Westoby 1992a). The nutrient content of a collected seed dictates the energy return from it. Ants have been observed selecting seeds according to their overall nutritional value (Kelrick et al. 1986). The two most frequently removed seed species (*P. appendiculatum* and *P. corcovadense*) differ greatly in size (Table 1) and probably also in nutrient content. The high removal rate of *P. appendiculatum* seeds is undoubtedly related to their small size, which permits removal by the tiny *Pheidole* sp. 7, the most abundant litter-foraging ant at the study site; it was present in 24–25% of the bait stations (Table 2). The overall removal rate of *P. appendiculatum* seeds (84%) is close to that of similar-sized *Miconia affinis* (Melastomataceae) seeds (1 × 0.5 mm) presented to ants in 16-seed bird droppings at La Selva, Costa Rica (ca. 75%; Kaspari 1993b). Tiny seeds are not exclusively exploited by small granivorous ants, but are exploited by large species as well (Kaspari 1996), thus contributing to their high removal rate. In contrast, the high removal rate of *P. corcovadense* seeds was possibly due to the attractiveness of the fleshy coat that remains on the seeds even after their passage through the gut of monkeys, marsupials, and birds (M.A. Pizo, personal observation). These seeds were removed by a large assemblage of ants, including large ponerines, which, although predominantly carnivorous (Hölldobler and Wilson 1990), are known to exploit lipid-rich diaspores (Horvitz and Beattie 1980; Pizo and Oliveira 1998). Ponerine ants usually do not eat the seeds they collect but deposit intact seeds in refuse piles outside their nests after feeding on the fleshy portion of the diaspores, thus permitting seed germination and establishment (Horvitz 1981; M.A. Pizo and P.S. Oliveira, unpublished data). Moreover, because ant species differ in the way they treat seeds, and

also in their microhabitat nesting preferences (Hölldobler and Wilson 1990; Hughes and Westoby 1992b), *P. corcovadense* seeds may benefit from being exploited by a large ant assemblage and have a wide array of fates. The possibility of a two-phase dispersal mechanism in this aroid species, involving primary dispersal by vertebrates and secondary dispersal by ants, similar to that described for *Ficus microcarpa* (Moraceae) by Kaufmann et al. (1991), should be investigated. The lower removal rate of *Aechmea* sp. seeds may have been due to the lack of an especially attractive fleshy coat like that of *P. corcovadense* seeds, as well as to the size of the *Aechmea* sp. seeds, which exceeds the carrying ability of the abundant *Pheidole* sp. 7. Alternatively, the reason for the low removal rate of *Aechmea* sp. seeds may lie in some unassessed physical (e.g., shape) and (or) chemical properties of these seeds (Byrne and Levey 1993).

This study confirmed the important role of species of the subfamily Myrmicinae, especially the genus *Pheidole*, in removing seeds from the faeces of frugivorous vertebrates inhabiting Neotropical forests (Roberts and Heithaus 1986; Byrne and Levey 1993; Kaspari 1993b). Although these ants prey on most of the seeds they collect, some seeds escape predation and may germinate (Briese and Macauley 1981; Hughes and Westoby 1992b). Levey and Byrne (1993) observed that some seeds deposited in twig nests by *Pheidole* sp. at La Selva may germinate after nest abandonment and decay. Many seeds are likely to have had the same fate at our study site because the only twig-nesting seed-carrying ant species recorded on faeces, *Pheidole* sp. 3, frequently collects seeds. Eight out of 10 nests of this species collected in the field contained cached seeds. Nevertheless, the majority of seeds collected from the faeces were deposited in soil nests (see also Kaspari 1993b). Based on the observation that captive colonies of *Pheidole* sp. 1 do not deposit intact seeds outside the nest, but keep them in refuse piles inside the nest, it is still unclear whether these seeds also have the opportunity to germinate and establish. Hughes and Westoby (1992b) observed that a soil-nesting *Pheidole* species found in Australian sclerophyll vegetation cached seeds in galleries within the nest, and suggested that seeds that are “lost” as a result of damage and (or) structural changes in the nest may occasionally germinate. The depth of the seed cache, however, is likely to play a crucial role in the emergence and success of the seedlings that develop inside soil nests (see Dalling et al. 1994). It is important to emphasize that not all seeds collected in the field by *Pheidole* sp. are carried all the way back to the nest. Some may be cached in the leaf litter (Roberts and Heithaus 1986), where they eventually encounter conditions suitable for germination and seedling growth (Horvitz 1981). Although *Philodendron* sp. seeds found in monkey faeces can germinate in less than 1 week (P. Izar, personal observation), we have no information on *Aechmea* sp. seeds.

Attine ants form another important group of seed removers in Neotropical forests (Roberts and Heithaus 1986; Kaspari 1993b, 1996). In this study, attine ants represented the second most frequent group recorded on faeces. In the “cerrado” (savanna-like vegetation) of São Paulo State in Brazil, attine ants were frequently observed collecting seeds from bird and bat droppings (Leal and Oliveira 1998), and at La Selva these ants carried away approximately 35% of the

M. affinis seeds contained in bird faeces (Kaspari 1993b). Like those collected by other myrmicine species, some of the seeds collected by attines may not be used for fungus cultivation, and may establish around their nests (Farji Brener and Silva 1996). It is possible that the seeds which eventually germinate in caches made by myrmicines (including attines) will be subject to the same sort of sibling competition that they would suffer in a defecation clump (Howe 1989). This possibility should be considered in order to properly assess the actual impact of seed-harvesting ants on seeds collected from frugivore faeces.

In conclusion, removal of small seeds by ants from the faeces of birds (Byrne and Levey 1993; Kaspari 1993b), monkeys, and marsupials (M.A. Pizo, unpublished data) is common in Neotropical forests. Because of the high abundance of ants in these forests (Hölldobler and Wilson 1990; Byrne 1994), and the utilization of both moist and dry microclimates by some ant species (Kaspari 1993a), seed removal may be affected less by differences in microclimatic conditions among habitats than by the seed species involved. Seed size (Gorb and Gorb 1995) and nutrient content (Kelrick et al. 1986) are among the traits that vary from one plant species to another and influence seed displacement by ants. The discovery of faeces by ants, however, is not sufficient to guarantee the removal of the seeds because ant colonies vary in the proportion of seeds they collect. This variation interacts with a complex array of other factors (e.g., ant species, season, seed number; see Anderson and Ashton 1985; Kaspari 1993b) to determine the proportion of seeds removed from the faeces of frugivorous vertebrates.

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