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Seed removal by ants from faeces produced by different vertebrate species[1]

Marco A. PIZO[2], Plant Phenology and Seed Dispersal Group, Departamento de Botânica, Universidade Estadual Paulista, Caixa Postal 199, 13506-970 Rio Claro-SP, Brazil, e-mail: pizo@rc.unesp.br
Paulo R. GUIMARÃES, Jr., Programa de Pós-graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas, Caixa Postal 6109, 13083-970 Campinas-SP, Brazil.
Paulo S. OLIVEIRA, Departamento de Zoologia, Universidade Estadual de Campinas, Caixa Postal 6109, 13083-970 Campinas-SP, Brazil.

Abstract: Ants frequently harvest seeds from faeces of frugivorous vertebrates. By transporting these seeds to nests, ants may influence seed dispersal success of plants. Seed removal by ants from vertebrate faeces is influenced by the seed species involved. Faeces from different vertebrates differ in chemical composition and physical characteristics. It remains unclear, however, whether the faeces itself affects the ant-seed interaction. In this study experimental seed-containing faecal portions were prepared using defecations of birds, marsupials, and monkeys and seeds of two aroids (*Philodendron corcovadense* and *P. appendiculatum,* Araceae) and one liana species (*Schlegelia parviflora*, Bignoniaceae). Faecal portions were arranged along a transect established in the understory of a lowland rainforest in southeast Brazil. For *P. appendiculatum* the probability of detection and the proportion of seeds removed were identical between marsupial and monkey faeces. For *P. corcovadense* and *S. parviflora*, the probability of detection was affected by seed species and, apparently, also by the interaction between seed species and type of faeces ($P = 0.097$), but not by the type of faeces itself (bird or monkey). Both factors (*i.e.,* seed species and type of faeces) affected the proportion of seeds removed (faeces type was marginally significant; $P = 0.08$), whereas the interaction between them was not significant. The results indicate that seed species affects seed removal by ants, while the type of faeces probably interacts with seed traits to influence faeces detection.

Keywords: ants, Mata Atlântica, secondary seed dispersal.

Résumé : Les fourmis se nourrissent souvent des graines qu'elles trouvent dans les fèces de vertébrés frugivores. En transportant ces graines au nid, les fourmis peuvent influencer le succès de dissémination des graines des plantes. Le prélèvement des graines des fèces de vertébrés par les fourmis est influencé par l'espèce à laquelle appartiennent les graines. Comme les fèces des vertébrés présentent une composition chimique et des caractéristiques physiques différentes selon les espèces, les fèces elles-mêmes affectent-elles l'interaction entre les fourmis et les graines? Dans cette étude, nous avons préparé des amas de fèces d'oiseaux, de marsupiaux ou de singes contenant des graines de deux plantes des Araceae (*Philodendron corcovadense* et *P. appendiculatum*) et d'une espèce de liane (*Schlegelia parviflora*, Bignoniaceae). Les amas fécaux ont été placés le long d'un transect situé dans le sous-bois d'une forêt pluvieuse des basses terres du sud-est du Brésil. Pour *P. appendiculatum*, la probabilité de détection et la proportion de graines prélevées ont été identiques dans les fèces de marsupiaux et de singes. Pour *P. corcovadense* et *S. parviflora*, la probabilité de détection a été affectée par les espèces de graines et apparemment aussi par l'interaction entre les espèces de graines et le type de fèces ($P = 0{,}097$), mais pas par le type de fèces lui-même (fèces d'oiseaux ou de singes). Les deux facteurs, soit l'espèce de graine et le type de fèces, ont affecté la proportion de graines prelevées (le type de fèces n'ayant qu'un effet significatif marginal; $P = 0{,}08$), alors que l'interaction entre les deux facteurs n'était pas significatif. Les résultats indiquent que l'espèce à laquelle appartiennent les graines affecte leur récolte par les fourmis, alors que le type de fèces interagit probablement avec les caractéristiques des graines pour influencer leur détection.

Mots-clés : dissémination secondaire des graines, fourmis, Mata Atlântica.

Nomenclature: Meyer de Schauensee, 1970; Gentry, 1973; Bolton, 1994; Nadruz, 1998; Eisenberg & Redford, 1999.

Introduction

Secondary dispersal of seeds plays a major role in the spatial pattern of some plant species (Forget & Milleron, 1991; Chambers & MacMahon, 1994). In tropical habitats, ants are important secondary dispersers of seeds embedded in faeces of frugivorous vertebrates (Levey & Byrne, 1993; Kaspari, 1993b; Leal & Oliveira, 1998; Pizo & Oliveira, 1999). Although the most common outcome for the retrieved seeds is to serve as food for ants, some seeds escape predation and may develop into an established seedling (Hughes & Westoby, 1992; Levey & Byrne, 1993). Given the impressive abundance of ants in tropical forests (Hölldobler & Wilson, 1990) and the frequency with which they interact with seed-containing faeces (Kaspari, 1993b; Pizo & Oliveira, 1999), ants can play a key role in the seed dispersal process of some plant species (Levey & Byrne, 1993). By removing seeds from the faeces and transporting them to their nests, ants can rearrange the seed shadow generated by primary seed dispersers (Roberts & Heithaus, 1986), influence seed

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[2] Author for correspondence.

bank dynamics, and promote seedling establishment (Levey & Byrne, 1993; Passos & Oliveira, 2002).

Seed removal by ants from vertebrate faeces is influenced by the number of seeds (Kaspari, 1993b) and the seed species involved (Pizo & Oliveira, 1999). What remains unclear, however, is whether the faeces themselves also influence the ant-seed interaction, and how they interact with seed species to shape the outcome of these interactions. Faeces from different vertebrates differ in nutrient and moisture content, texture, and consistency (Macqueen, 1975; Gittings & Giller, 1998), which may in turn influence their attractiveness to ants and the ease with which ants bore into them to collect seeds. Such an influence has been demonstrated for dung beetles (Scarabaeidae); faeces from different vertebrates attract different species of dung beetles (Estrada *et al.,* 1993).

In this study we investigated the removal by ants of seeds of three plant species (*Philodendron corcovadense* and *P. appendiculatum,* Araceae; and *Schlegelia parviflora*, Bignoniaceae) embedded in bird, marsupial, and monkey faeces in a tropical rainforest of southeast Brazil. Our main goal was to address the question of whether seed removal by ants is influenced by the seed species and the type of faeces into which seeds are embedded.

Methods

STUDY SITE

The study was carried out from June 1996 to June 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 a.s.l.) received a mean annual rainfall of 4,216 mm between 1994 and 1996, with rains well distributed throughout the year (no month receives < 100 mm). There is, however, a drier-cooler period between April and August when the temperature may occasionally drop below 10 °C (mean ± SD = 20.8 ± 2.5 °C for the study period) and a wetter-hotter period from September to March when 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.

SEED REMOVAL TRIALS

Bird faeces were obtained from captive individuals of two frugivorous species found in forest edges and second-growth vegetation at the study site, *Manacus manacus* (Pipridae) and *Tachyphonus coronatus* (Emberezidae, Thraupinae). Captive birds were fed a synthetic diet composed of bananas, wheat germ, soy protein isolate, vegetable oil, and minerals (Denslow *et al.,* 1987). Fruits were offered to captive birds in conjunction with the regular diet, and the seed-containing faeces were collected daily. Marsupial faeces were obtained from individuals of *Didelphis aurita* (Didelphidae) trapped in the study site during a simultaneous study carried out by Vieira (1999). Captured animals usually defecate inside the trap. Marsupial faeces were predominantly composed of material of animal origin, especially arthropod remains. Monkey faeces were collected beneath a bait station where a troop of Capuchin monkeys (*Cebus apella,* Cebidae) regularly fed. These faeces contained mainly plant material (crushed leaves and fruit skin), with only a minor proportion, if any, of arthropod parts.

Seed selection for this study was constrained by seed size (only small seeds removable by most ant species were used), by seed occurrence in marsupial and monkey faeces collected in the field, and by the availability of fruits for captive birds. Such constraints restricted the studied species to two hemiepiphytic aroids (*P. corcovadense* and *P. appendiculatum*) and one liana species (*S. parviflora*), all of which produce fleshy fruits. *Philodendron appendiculatum* had the smallest seed size (1.3 mm length × 0.5 mm width, 0.1 mg mass; 10 seeds were measured and weighed for each species), followed by *S. parviflora* (2.8 × 1.1 mm, 1.5 mg) and *P. corcovadense* (3.4 × 1.6 mm, 2.2 mg). Seeds of *P. corcovadense* and *S. parviflora* occurred in bird and monkey faeces, whereas *P. appendiculatum* seeds were found in marsupial and monkey faeces.

The experimental faecal portions were prepared by first separating the seeds from the fresh faecal mass and then mixing them again with seed-free portions (1-2 cm in diameter) of the same faecal load. Each faecal portion received 15 seeds of one plant species. This quantity was chosen because it was shown that greater quantities of seeds would not necessarily result in a significant increase in the proportion of seeds removed by ants (Kaspari, 1993b). The faecal portions were mounted on small pieces of white filter paper (4 × 4 cm) used as a substrate to facilitate visual location. Faecal portions were placed directly on the leaf litter at stations 5 m apart along a transect established 1-2 m off trail. Each station received only one faecal portion. Given the patchiness of ant distribution on the floor of tropical forests (Kaspari, 1993a), and that most litter-foraging ant species rarely walk more than 2 m from their colonies (Levey & Byrne, 1993; Byrne, 1994), the distances between neighbouring faeces likely ensured independent discoveries by different ant colonies. Each faecal portion was protected from vertebrate disturbance by wire cages (15 × 15 × 10 cm, 1.5 cm mesh) closed at the top, covered by translucent plastic shelters, and staked to the ground. Every trial subjected to intense and prolonged rains was interrupted. Similarly, faecal portions which were severely modified by moderate rains were not considered in the analyses. These cancelled trials, and the limited availability of seeds, resulted in unbalanced sample sizes among seed species and faeces types used (Table I).

Faeces were set on transects at 0800, when the low temperature was favourable for the activity of most ant species (Kaspari, 1993a). The number of seeds remaining in the experimental faeces was counted after 24 h. The ant species attracted to the faeces, as well as their behaviour toward the seeds (*i.e.,* whether they removed or ignored the seeds), were recorded in four scan samples taken at 15-min intervals from 0800 to 0900. During the scan samples, the faeces were visited sequentially and ant

Table I. Number of records of ant species attracted to bird, marsupial, and monkey faeces containing seeds of *Philodendron corcovadense*, *P. appendiculatum* (Araceae), and *Schlegelia parviflora* (Bignoniaceae). Numbers of faecal portions are in parentheses.

	Seed species / faeces types						
	P. appendiculatum		*P. corcovadense*		*S. parviflora*		
Ant subfamily/species	marsupial (30)	monkey (25)	bird (47)	monkey (35)	bird (16)	monkey (37)	Total number of records
Ponerinae							
Ectatomma edentatum	0	0	2	1	0	0	3
Gnamptogenys sp.	0	1	1	0	0	0	2
Odontomachus chelifer	0	0	0	1	1	0	2
Odontomachus meinerti	0	0	0	1	0	0	1
Pachycondyla striata	0	0	3	0	0	0	3
Myrmicinae							
Crematogaster sp. 2	0	0	2	0	0	0	2
Pheidole sp. 1	7	5	21	8	6	15	62
Pheidole sp. 3	2	7	1	2	1	0	13
Pheidole sp. 7	11	6	13	14	6	8	58
Pheidole sp. 9	0	0	2	2	0	0	4
Pheidole sp. 10	0	0	1	0	0	0	1
Solenopsis sp. 1	5	2	3	4	0	4	18
Solenopsis sp. 2	0	1	0	0	0	1	2
Myrmicinae - tribe Attini							
Acromyrmex subterraneus	0	0	2	0	0	0	2
Apterostigma sp. 1	0	0	1	1	0	1	3
Cyphomyrmex sp.	0	2	0	1	0	0	3
Trachymyrmex sp. 1	0	0	1	0	0	0	1
Formicinae							
Brachymyrmex sp.	0	0	0	1	0	0	1
Dolichoderinae							
Linepithema sp. 1	0	0	2	0	0	0	2
Probability of detection	1.0	1.0	0.96	0.97	0.94	0.59	
Proportion of seeds removed (mean ± SE)	0.90 ± 0.04	0.90 ± 0.04	0.86 ± 0.04	0.82 ± 0.05	0.75 ± 0.09	0.43 ± 0.07	

specimens were collected for identification. Voucher specimens of the ants are deposited in the Museu de Zoologia of Universidade de São Paulo (MZUSP).

Two components of seed removal were considered: 1) probability of detection (*i.e.,* probability of at least one seed being removed from a faecal portion), and 2) proportion of seeds removed (*i.e.,* the number of seeds removed/number of seeds originally present in the faecal portion). The effects of faeces type, seed species, and the interaction between them were statistically evaluated only for *P. appendiculatum* and *S. parviflora* seeds, which had been tested with the same two types of faeces (bird and monkey). Differences in the probability of detection were assessed using logistic regression (Dobson, 2002). Seed-removal data were not normally distributed, but characterized by a bimodal distribution in which the peaks were 1) no seed was removed and 2) all seeds were removed. As a consequence, we coded faeces in which less than 50% of the seeds were removed as "low seed removal" and faeces in which more than 50% of the seeds were removed as "high seed removal". Differences in the probability of seed removal were also assessed using logistic regression (Dobson, 2002).

Results

A total of 19 ant species (4 subfamilies, 13 genera) were recorded on the faeces (Table I). Two myrmicine ants, *Pheidole* sp. 1 and *Pheidole* sp. 7, were the main seed removers, together accounting for 66.5% of the 188 ant records. Overall, ants removed seeds from 90% of the faecal portions (n = 190), which had from none to all the seeds removed within 24 h. Ants removed fewer *S. parviflora* seeds than *P. corcovadense* and *P. appendiculatum* seeds when all faeces types were pooled (proportions of seeds removed: 0.53, 0.84, and 0.90, respectively; H = 27.86, P < 0.001; Table I).

For *P. appendiculatum,* both the probability of detection and the proportion of seeds removed were identical between marsupial and monkey faeces (Table I). For *P. corcovadense* and *S. parviflora*, the probability of detection was affected by seed species (χ^2 = 4.61, P = 0.032), a consequence of higher visitation by ants on faeces containing *P. corcovadense* seeds (odds ratio = 5.90). There is no evidence that the type of faeces affected the probability of detection (χ^2 = 1.34, P = 0.247). However, the interaction between faeces type and seed species was nearly significant (χ^2 = 2.75, P = 0.097). Seed species also affected the proportion of seed removal (χ^2 = 7.64, P = 0.006), due to the higher probability of high removal of *P. corcovadense* seeds when compared to *S. parviflora* seeds (odds ratio = 3.48). There was also evidence that the type of faeces mattered (χ^2 = 2.91, P = 0.088), with monkey faeces being less likely to have high seed removal than bird faeces (odds ratio = 0.463). There was no evidence that the interaction between the type of faeces and seed species affected the proportion of seed removal (χ^2 = 1.78, P = 0.182).

Discussion

Ants are sensitive to the nutrient content (Kelrick *et al.,* 1986) and size (Anderson & Ashton, 1985; Byrne & Levey, 1993) of seeds, and, as a result, some seeds are collected at higher rates than others (Gross, Whalen & Andrew, 1991; Gorb & Gorb, 1995). In this study, seeds of *S. parviflora* were removed less often than seeds of *P. corcovadense* and *P. appendiculatum*. In fact, seeds of *P. corcovadense* and *P. appendiculatum* are very attractive to ants (Pizo & Oliveira, 1999). These differences can be explained by certain seed traits. *Philodendron corcovadense* seeds retain their nutrient-rich fleshy coat even after their passage through vertebrate guts (M. A. Pizo, pers. observ.), and the small size of *P. appendiculatum* seeds permits a high removal rate by the tiny *Pheidole* sp. 7, the most abundant litter-foraging ant at the study site (Pizo & Oliveira, 1999). In contrast, *S. parviflora* seeds have no nutrient-rich coat and are too large for some ant species.

The intensity of recruitment by ants depends on the quality of the food (Hölldobler & Wilson, 1990). When faced with less preferred seeds, such as those of *S. parviflora*, ants may be more selective with respect to the characteristics of the faeces in which the seeds are embedded, such as moisture and consistency. For instance, bird faeces usually have a soft consistency, which may have acted as a cue for ant attraction and facilitated seed removal. In contrast, the monkey faeces used in this study were much more fibrous, full of undigested plant material. The difference in consistency may have acted in conjunction with seed traits to produce the difference observed in the removal of seeds.

This is the first study to show that in addition to being attracted to bird (Kaspari, 1993b; Levey & Byrne, 1993) and monkey faeces (Pizo & Oliveira, 1999), ants are attracted to marsupial faeces to collect seeds. Marsupials eat fruits frequently, especially those containing small seeds (*e.g., Cecropia*, *Ficus*, *Philodendron*; Atramentowicz, 1988; Vieira & Izar, 1999), which are exploited by the small harvesting ants (*e.g., Pheidole*) that abound on the floor of neotropical forests (Roberts & Heithaus, 1986; Pizo & Oliveira, 1999). Future studies focusing on the seed shadow produced by marsupials in such habitats have to take into account the role played by ants in reshaping the initial seedfall.

In conclusion, our results point to the possibility that faeces characteristics do matter and that they probably affect, together with seed traits, seed detection and removal by ants. As a result, some faeces-type–seed-species combinations are less likely to be exploited by ants than others.

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