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Removal of seeds from frugivore defecations by ants in a Costa Rican rain forest

M. M. Byrne & D. J. Levey
Department of Zoology, University of Florida, Gainesville, FL 32611, USA

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Abstract

At our Costa Rican field site, seeds defecated by frugivorous birds usually do not remain where they have been deposited. Many species of ants are attracted to frugivore defecations and remove seeds and/or pulp. *Pheidole* species selectively remove seeds, fungus-growing species (tribe Attini) remove both pulp and seeds. Seeds of many Melastomataceae have an appendage, which we hypothesized is an elaiosome. Indeed, preference trials demonstrated that two species of *Pheidole* selected seeds with the appendage over seeds of the same species in which the appendage had been removed. However, we found that these ants did not take the appendage when it was offered by itself. We conclude that the appendage is not an elaiosome. In further trials, different ant species preferentially selected different seed species. These ants consumed some seeds and deposited others unharmed in refuse piles. We conclude that because the composition of leaf-litter ant communities is highly variable between neighboring square meter plots, and the probability of seed predation depends upon the species of ant, the over-all effect of ants on seed shadows and seed banks is spatially unpredictable.

Introduction

[1]Models and theories of seed dispersal by vertebrates usually assume that dispersed seeds either germinate or die where they are first deposited; although a few studies have examined post-dispersal seed predation (Janzen 1982; Traveset 1990). To a large extent, this assumption is borne out of practicality; it is extremely difficult to map seed shadows generated by seed dispersers and even more difficult to determine the ultimate fate of dispersed seeds. Yet, two observations suggest that we reconsider this assumption for dispersed seeds in neotropical rain forests. First, the number of seeds falling onto a square meter of leaf litter, (e.g. 49 seeds/m^2/month; Denslow & Gomez-Diaz 1990, data from La Selva, Costa Rica), and the density of seeds already in the seed bank (742 seeds/m^2; Putz 1983, data from Barro Colorado Island, Panama), suggest that seeds are a plentiful resource for rainforest granivores. Second, the density of ants is equally impressive. Hölldobler & Wilson (1990) estimate 800 ants/m^2 in the Amazon; ant biomass outweighs vertebrate biomass by approximately four to one. Based on studies of congeners, many of these ants are likely to consume and/or disperse small seeds (e.g. Berg

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Addendum: The names of the two *Pheidole* emphasized in this study, *P. nebulosa* and *P. nigricula*, are unpublished names from a generic revision being prepared by E. O. Wilson and W. L. Brown. Their use here is not intended to constitute taxonomic publication but is solely for more precise identification in future ecological research of similar nature.

1975; Bond & Slingsby 1984; Beattie 1985; Horvitz & Schemske 1986).

Given the abundance of dispersed seeds and seed-carrying ants in rain forests, perhaps our emphasis on vertebrate removal of seeds from fruiting plants has been too narrow (see Janzen 1982; Chapman 1989). Ant-seed interactions after vertebrate seed dispersal may have an important influence on the dispersal success of plants. Two types of interactions are most obvious, seed dispersal ('myrmecochory') and predation. Myrmecochory is widespread, occurring in over 60 plant families (Neson 1981; Beattie 1983). Seeds of myrmecochorous species are typified by the presence of an elaiosome, a fleshy lipid-rich appendage that attracts ants. The ants usually carry the seed to their nest, eat the elaiosome, and discard the seed in viable condition (Berg 1966; Beattie 1983). Seed predation by ants is also widespread (Davidson 1977). Although seed predation appears especially prevalent in drier areas, several genera of seed-eating ants are abundant in tropical rain forests (Hölldobler & Wilson 1990).

Here we focus on the interaction between leaf-litter ants and dispersed seeds from several species of Melastomataceae, a speciose family of mostly bird-dispersed understory shrubs and treelets. Ants readily remove melastome seeds from bird defecations (Levey & Byrne 1990). Are these ants playing the role of seed predators, seed dispersers, or both? Pilot experiments and observations led us to believe that they were dispersers. In particular, we noticed that the seeds of many species had an obvious appendage. We suspected this appendage was an elaiosome, since it passed intact through frugivore guts and appeared to attract ants to the seeds. These initial experiments, however, suffered from low sample sizes and our inability to distinguish among ant species and follow the fates of seeds.

We report a series of field and laboratory preference trials designed to determine what component of a frugivore's defecation (pulp vs. seeds) attracts ants, whether the appendage is an elaiosome (which would be evidence of myrmecochory), what seed attributes influence ant preference patterns, and whether species of ants differ in their seed preferences. These trials were conducted both in the field and with captive colonies in the laboratory. They represent a first step towards teasing apart a complex interaction between small-seeded rain forest plants and leaf litter ants.

Methods

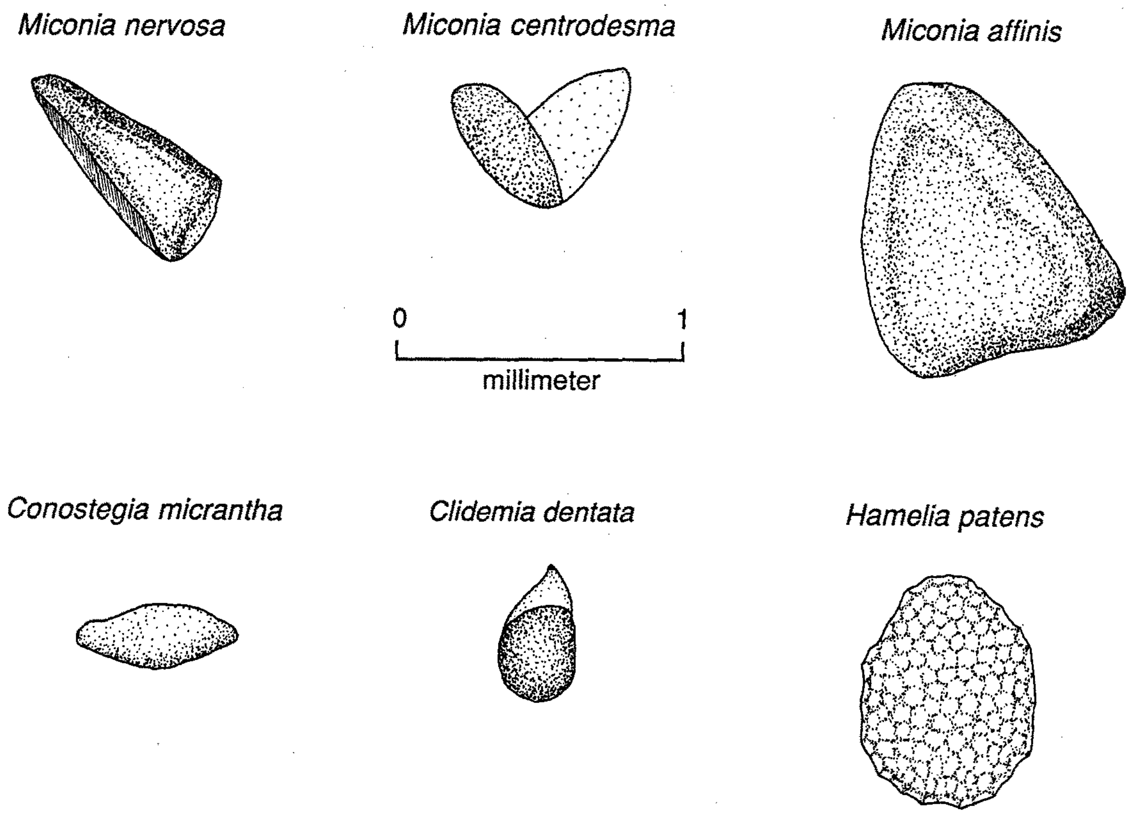
Study site and species

The study was conducted in May to July of 1989 and 1990 at Estación Biológica La Selva in Heredia province, Costa Rica. Field experiments were performed in an area of primary forest near the intersection of the 'Camino Central' and the 'Camino Circular Lejano' trails. Laboratory experiments made use of colonies collected from the field and maintained in the lab.

Captive ant colonies were established by removing all ants and brood from a single nest and placing them in a clear plastic petri dish (9 cm diameter) with a layer of Plaster of Paris on the bottom. The Plaster of Paris was kept moist by periodically adding water. Holes in the sides of the dishes allowed ants to enter and exit their 'nest'. Each plate was covered with two layers of red cellophane, and placed in an open plastic box (approximately 35 l × 20 w × 10 h cm). Ants were prevented from escaping by a band of Fluon™ (a slippery, teflon-like substance) painted around the inner sides of the box. They were fed small insects and cookie crumbs, and provided with a cotton-stoppered vial of water.

The ant species used in the laboratory trials, *Pheidole nigricula* and *P. nebulosa*, are abundant in the leaf litter at La Selva (1.32 and 0.37 colonies/m^2, respectively, Byrne 1991). They are small (minor worker size 1–3 mm), and generally live in rotting twigs. Eight colonies of each species were maintained in the laboratory for use in choice experiments. Average size of the colonies was 50 workers for *P. nigricula*, and 90 workers for *P. nebulosa*. All captive colonies contained one queen.

Most of the seed species used were from the


Miconia nervosa

Miconia centrodesma

Miconia affinis

Conostegia micrantha

Clidemia dentata

Hamelia patens

Fig. 1. Seed species used in the preference trials. Except for *Hamelia* (Rubiaceae), all seeds come from Melastomataceae.

family Melastomataceae. The seeds chosen differed in presence and size of the appendage (Fig. 1). However, they also varied in overall size (0.5–1.2 mm). The appendages on most species were firm in texture. The one exception, *Miconia nervosa*, had a fluid-filled appendage. Because this appendage tended to desiccate quickly and we were unsure of whether ants would respond equally to fresh and desiccated appendages, we substituted *Clidemia dentata* and *M. centrodesma* for *M. nervosa* in our 1990 trials.

General methods

All seeds used in the choice experiments were collected daily from fresh bird feces. We fed fruits of the desired species to captive White-collared Manakins (*Manacus candei*), and then removed the seeds from their defecations. For some trials, we removed the seed appendages, being careful not to damage the seed coat. The seeds, appendages, and/or defecated pulp were placed on damp squares (approximately 1.5 × 1.5 cm) of Whatman No. 1 filter paper. Filter paper was chosen as a substrate because it allowed us to see the seeds and ants easily. The ants did not appear to distinguish the filter paper from nearby leaf litter (i.e., ants generally did not pause when they first encountered a piece of filter paper). The seeds were positioned side by side (for two-way choices) or in a triangle (for three-way choices) such that the distance between the seeds was less than the length of an ant's body. We placed the seeds in such close proximity to ensure that ants would be aware of their choices before picking up a seed. Indeed, the ants usually antennated all seeds before selecting one.

The pieces of filter paper were placed on the leaf litter (in the field experiments) or in the bottom of the plastic boxes (in the laboratory experiments). If the filter paper became dry during the experiment, water was added with an eyedropper. We always handled seeds and filter paper with forceps to avoid introduction of human carried scents.

Ants often picked up and then dropped a seed while on the filter paper. However, once the ant had moved off the filter paper with a seed, it rarely dropped it. Thus, in order for an ant to 'select' a given seed, it had to move it completely off the filter paper. After removal of a seed, the paper was replaced by a new one with a complete set of seeds. During the field experiments, all ants that removed seeds were collected and preserved in 70% ethanol. *Pheidole nigricula* and *P. nebulosa* were the most common seed-takers (77% of the collected ants) in the first field experiments, and so were subsequently used in the laboratory trials. *P. nebulosa* is bigger than *P. nigricula* and is thus able to carry slightly larger seeds.

Specific trials

We performed four types of preference tests. The trials were spread equally among the eight captive colonies of each species. Thus, the preferences we report are not artifacts of a single colony's behavior but are likely to represent species-wide preferences (at least at our study site). A minimum of 80 independent choices were obtained in the laboratory trials for each seed and ant species. Sample sizes in the field experiments were lower because we lacked control over which species took seeds, and rates of removal were lower.

Experiment 1

What component of a fruit-eating bird's defecation attracts ants? And, are all ant species attracted to the same component?

To test the assumption that ants were attracted to frugivorous birds' defecations because of the seeds they contained, we first examined an alternative hypothesis that the pulpy matrix adhering to the seeds was the attractant and thus that seeds are removed incidentally by ants. This second hypothesis gains plausibility when one considers that fruit pulp is high in carbohydrates and frugivorous birds have unusually low digestive efficiencies (Levey & Karasov 1989; Karasov & Levey 1990). Thus, defecated pulp may still contain a relatively high density of nutrients.

We ran a three-way choice test with *Miconia nervosa* seeds and pulp. In addition to offering a choice between a seed and a small (approximately 1.5 × 1.5 mm) clump of defecated pulp, we included a seed whose appendage had been removed. Thus, we tested whether ants preferred seeds or pulp, and if they preferred seeds, whether they preferred them with or without an appendage. These trials were done in the field in 1989.

Experiment 2

Do ants prefer seeds with appendages intact over those with appendages removed?

The field trials described in experiment 1 addressed this question but were limited in scope, lacked control over ant species, and made use of a species with an atypical (fluid-filled) appendage. To avoid these problems, in 1990 we ran two-way choice tests with *P. nigricula* and *P. nebulosa* laboratory colonies using *Miconia centrodesma* seeds with and without appendages.

Experiment 3

Does the appendage itself act as an attractant?

If ants prefer seeds with appendages, it becomes important to determine why. We suggest two non-exclusive explanations: the appendage is nutrient-rich (most elaiosomes are lipid-rich; e.g., Horvitz & Beattie 1980) or it functions as a 'handle' necessary to carry the seed (O'Dowd & Hay 1980). The appendages were too small to collect sufficient quantities for nutrient analyses and our attempts at staining them for lipids yielded inconclusive results. The possible role of a 'handle' is an important one, given that many ant species had difficulty lifting and carrying Melastomataceae seeds (D. Levey & M. Byrne, pers. observation).

To distinguish between these hypotheses, we offered our laboratory colonies two-way choices between either *M. centrodesma* or *Clidemia dentata* seeds with appendage removed and the removed appendage.

Experiment 4

Do ants show significant preferences among different seed species? Does appendage size influence preference? Do preferences differ between *P. nebulosa* and *P. nigricula*?

The above experiments each involved a single species of seed. Here we offered ants either two or three species. We selected species of approximately equal seed size (except for *Miconia affinis* and *Conostegia micrantha*, which were slightly larger and smaller, respectively) but with different appendage size. All species except *Hamelia patens* were in the Melastomataceae. In 1989 we ran two sets of experiments in the field. A two-way preference trial between *Hamelia patens* and *Miconia centrodesma* tested a species with a large appendage (M.c.) against a species without an appendage (H.p.). A three-way trial with *M. centrodesma*, *M. nervosa*, and *C. micrantha*, gave ants a choice among seeds with a large appendage (M.c.), a moderate-sized appendage (M.n.), and no appendage (C.m.).

In 1990 we ran a similar set of trials with laboratory colonies. A two-way test between *M. centrodesma* and *M. affinis* paired species with and without obvious appendages. A three-way test with *M. centrodesma*, *Clidemia dentata*, and *Conostegia micrantha* was similar to the 1989 three-way test among seeds with different appendage sizes (C.d. replaced M.n.).

Table 1. Number of ants of each species chosing *M. nervosa* pulp, seed with appendage, and seed with appendage removed (field trial, 1989).

Ant species	Pulp	Seed with appendage	Seed without appendage
Pheidolini			
Pheidole nigricula	2	32	13
P. nebulosa	0	12	15
P. la selva	0	1	3
P. lancifer	0	0	1
Attini			
Apterostigma	2	0	1
Cyphomyrmex	5	0	0
Trachymyrmex A	1	0	0
Trachymyrmex B	1	0	0

Results

Experiment 1

Both *P. nigricula* and *P. nebulosa* displayed nonrandom choices ($\chi^2 = 29.3$, d.f. $= 2$, $n = 47$, $P < 0.001$, and $\chi^2 = 14.0$, d.f. $= 2$, $n = 27$, $P < 0.001$, respectively). Individuals of *P. nigricula* removed intact *M. nervosa* seeds more than twice as often as seeds with the appendage removed (Table 1). They only removed pulp twice. *P. nebulosa* never removed pulp but took the two types of seeds with nearly equal frequency (Ta-

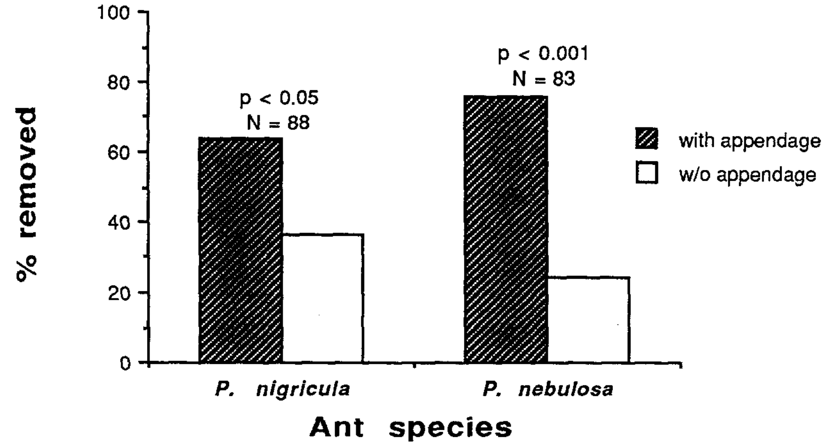


Fig. 2. Laboratory preference trials in which ants chose between *Miconia centrodesma* seeds with and without appendages.

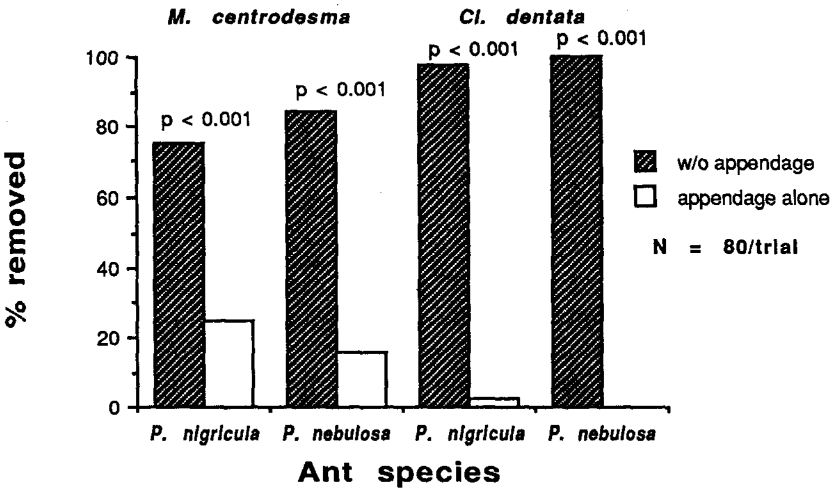


Fig. 3. Laboratory trials in which ants chose between a seed with the appendage removed and the appendage alone. ($n = 80$ for all preference tests)

ble 1). Two other species of *Pheidole*, *P. laselva* and *P. lancifer*, also removed items from the filter paper. Note that they, too, never removed pulp. In contrast, species from the tribe Attini (*Apterostigma* sp., *Cyphomyrmex* sp., and *Trachymyrmex* spp.) almost exclusively removed pulp (Table 1).

Experiment 2

Both species significantly preferred *M. centrodesma* seeds with an appendage over those in which the appendage had been removed (*P. nigricula*: $\chi^2 = 6.54$, d.f. = 1, $n = 88$, $P<0.001$; *P. nebulosa*: $\chi^2 = 22.28$, d.f. = 1, $n = 83$, $P<0.001$) (Fig. 2). This behavior contrasts to *P. nebulosa*'s choices

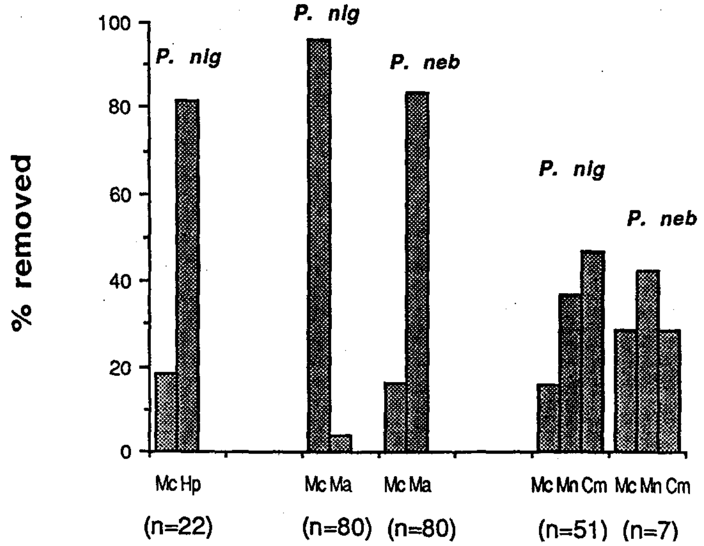


Fig. 4. Preference trials in which ants chose between two or among three seed species. Ant species: *Pheidole nigricula* (P. nig) and *P. nebulosa* (P. neb); and seed species: *Miconia centrodesma* (Mc), *Hamelia patens* (Hp), *M. affinis* (Ma), *M. nervosa* (Mn), and *Conostegia micrantha* (Cm).

in experiment 1, where it showed no preference between seeds with and without their appendage.

Experiment 3

When offered a choice between a *M. centrodesma* seed without the appendage and the appendage itself, both *P. nigricula* and *P. nebulosa* significantly preferred the seed ($\chi^2 = 20.0$, d.f. = 1, $n = 80$, $P < 0.001$; and $\chi^2 = 37.35$, d.f. = 1, $n = 81$, $P < 0.001$, respectively; Fig. 3). They showed the same pattern for *Clidemia dentata* ($\chi^2 = 72.7$, d.f. = 1, $n = 80$, $P < 0.001$; and $\chi^2 = 80.0$, d.f. = 1, $n = 80$, $P < 0.001$, respectively; Fig. 3). Thus, these ants appear to be attracted more to the seed than to the appendage.

Experiment 4. In the field test between *M. centrodesma* and *H. patens*, *P. nigricula* removed *H. patens* significantly more often than *M. centrodesma* ($\chi^2 = 8.91$, d.f. = 1, $n = 22$, $P < 0.01$; Fig. 4). *P. nebulosa* only removed two seeds, both *H. patens*. When offered the three-way preference test in the field, *P. nigricula* displayed nonrandom choices ($\chi^2 = 7.88$, d.f. = 2, $n = 51$, $P < 0.01$; Fig. 4). *C. micrantha* was taken most often, *M. nervosa* slightly less often, and *M. centrodesma* much less often. Removal of seeds by *P. nebulosa* was much less common and more evenly distributed among the three seed species (Fig. 4).

In the laboratory trials, *P. nigricula* significantly preferred *M. centrodesma* over *M. affinis* ($\chi^2 = 68.5$, d.f. = 1, $n = 80$, $P < 0.001$; Fig. 4). *P. nebulosa*, however, showed the opposite pattern, preferring *M. affinis* over *M. centrodesma* ($\chi^2 = 36.5$, d.f. = 1, $n = 80$, $P < 0.001$, Fig. 4).

For the three-way trials in the lab, we analyzed both first and second choices (Fig. 5), which we were unable to do for the field trials due to the slow rate of the ants' return to make a second choice. *P. nigricula* showed nonrandom seed removal choices ($\chi^2 = 73.01$, d.f. = 2, $n = 162$, $P < 0.001$), with *C. micrantha* being chosen first 65% of the time. There was no difference in second choice preferences if *M. centrodesma* or *Cl. dentata* were taken first ($\chi^2 = 0.76$, d.f. = 1, $n = 36$, $P > 0.05$; and $\chi^2 = 0.67$, d.f. = 1, $n = 24$, $P > 0.05$, respectively). When *C. micrantha* was taken first, however, ants significantly chose *M. centrodesma* over *Cl. dentata* ($\chi^2 = 5.04$, d.f. = 1, $n = 105$, $P < 0.05$).

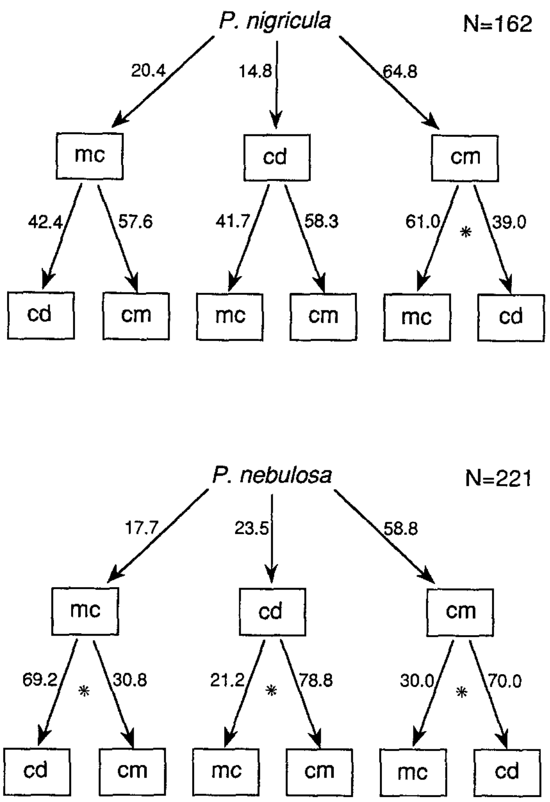


Fig. 5. First and second choice of ants in trials among three seed species. First arrows represent percentage of ants chosing a seed species as a first choice. Second arrows represent percentage of ants chosing each of remaining seed species after first choice had been made. Seed species as in Fig. 4. * Indicates a significant difference in number of ants chosing each seed species.

P. nebulosa ($n = 221$) also removed seeds nonrandomly ($\chi^2 = 65.75$, d.f. = 2, $n = 221$, $P < 0.001$), choosing *C. micrantha* first 59% of the time. All second seed selections showed significant differences in seed removal choices. *C. micrantha* was significantly preferred after either *M. centrodesma* and *Cl. dentata* were removed ($\chi^2 = 5.77$, d.f. = 1, $n = 39$, $P < 0.05$; and $\chi^2 = 17.31$, d.f. = 1, $n = 52$, $P < 0.001$, respectively). After *C. micrantha* was taken as a first choice, *Cl. dentata* was most frequently selected second ($\chi^2 = 20.8$, d.f. = 1, $n = 140$, $P < 0.01$).

Discussion

Seed preferences

Influence of appendage

Defecations of fruit-eating birds in the La Selva rain forest were visited by a wide diversity of ants – 13 species of 7 genera. The attine species appeared to have little interest in seeds, they carried away pulp almost exclusively, presumably for their fungus 'gardens'. Although no seeds were associated with pulp in our experiments and hence these ants transported no seeds, seeds and pulp are normally well-mixed and attines usually carry many seeds from defecations (Levey & Byrne, unpubl. data).

In contrast to the attines, all other species (mostly *Pheidole*) removed seeds almost exclusively. These ants generally preferred seeds with appendages over identical seeds whose appendages had been removed. Other studies have documented that many ant species display the same preference for seeds with appendages (i.e., elaiosomes; O'Dowd & Hay 1980; Davidson & Morton 1981; Drake 1981; Lu & Mesler 1981; Bond & Breytenbach 1985). In these studies ants were assumed to be attracted to the appendage. Few experiments have actually tested this assumption, however. Gates (1943) and Kjellsson (1985) did so by offering the ants a choice between an intact seed and an appendage that had been cut from another seed. They found that ants were attracted to and preferred the appendage over the seed. When we conducted the same experiment with *Pheidole nigricula* and *P. nebulosa*, we found they significantly preferred the seed. Thus, despite the preference for seeds with appendages, these ants are not attracted to the appendage itself.

Why do *Pheidole* prefer seeds with appendages if the appendages are not attractive? We offer three explanations. First, like other granivorous ants they may simply prefer larger seeds (Hölldobler 1976; Hansen 1978; M. Kaspari, pers. comm.) – the seeds with the appendage are larger than those without. We reject this explanation because it is inconsistent with our three-way choice trials, in which the smallest seed, *Conostegia micrantha*, was consistently preferred. Second, ants may have taken the seeds with the appendage because they were easier to carry (i.e., the appendage functioned as a 'handle'; O'Dowd & Hay 1980). Although ants had difficulty carrying the seeds of several *Miconia* species, the presence of an appendage did not seem to make the task easier. In fact, the species with the largest appendage, *Miconia centrodesma*, was one of the most difficult to carry and removal of the appendage seemed to make it easier to handle. Third, perhaps the ants detected that our removal of the appendage had damaged the seed and they were simply displaying a preference for undamaged seeds. A fourth explanation is developed and presented below.

Influence of seed and ant species

Many ant species show strong preferences for different types of seeds (Tevis 1958; Mott & McKeon 1977; Culver & Beattie 1978; Whitford 1978; Buckley 1982; Risch & Carroll 1986). The bases of these preferences are complex and not well understood. Seeds may be taken or rejected because of compounds that attract (e.g., Ashton 1979; Marshall *et al.* 1979) or repel (e.g., Buckley 1982), or because of physical attributes such as shape, size, and type of seed coat (O'Dowd & Hay 1980; Hölldobler 1976; Hansen 1978).

P. nigricula and *P. nebulosa* displayed strong preferences among seed species. Our relatively small number of experiments prevents us from generalizing about why they preferred the species they did. We note, however, that both ant species preferred the smallest seed, *Conostegia micrantha*, in three-way choice tests. Also, in a two-way choice test, *P. nebulosa* preferred *M. affinis* over the smaller *M. centrodesma* seed. Because *M. centrodesma* and *C. micrantha* were the only species without an appendage and were preferred over all other species (with the exception of *P. nigricula*'s choice of *M. centrodesma* over *M. affinis* which it could not lift), we speculate that the appendage found on Melastomataceae seeds may contain a compound that deters ants.

Why then did ants prefer seeds with an appendage over seeds that had their appendage removed? We could not remove appendages completely without damaging the seed. So, the manipulated seeds had a small freshly-cut surface of appendage. Any repellent compound may have been more readily volatilized from this surface than from an intact appendage. If so, this could explain why the ants preferred intact seeds; they were not attracted to the appendage on the intact seed but rather repelled by the freshly-cut surface on the seed without an appendage. This explanation is also consistent with the ants' refusal to take appendages when they were offered alone. Presence of a repellent could be tested by determining if ants are repelled or attracted to elaisome extract offered on an inert substrate (e.g., Skidmore & Heithaus 1988).

P. nigricula and *P. nebulosa*'s preferences among seed species were different. In two-way choice tests, *P. nebulosa* preferred *M. affinis* over *M. centrodesma* whereas *P. nigricula* showed the opposite preference. In three-way choice tests, although both species preferred *C. micrantha*, *P. nebulosa* typically chose *Cl. dentata* second whereas *P. nigricula* chose *M. centrodesma* second.

Seed dispersal and predation

Although seed dispersal and seed bank composition have been extensively studied (Howe 1986; Murray 1986; Garwood 1989), they have largely been examined independently. Thus, causes of discrepancies in species composition and abundance between seed rain and seed banks have remained for the most part unexplored (Rabinowitz 1981; Denslow & Gomez-Diaz 1990; Garwood 1989). Such discrepancies are almost certainly due to predation or scattering of seeds after they have been dispersed. These processes will alter seed shadows created by dispersers and affect demography and species composition of seed banks (Janzen 1982; Price & Jenkins 1986; Roberts & Heithaus 1986; Clifford & Monteith 1989; Garwood 1989; Louda 1989).

Ants and rodents are responsible for much seed predation and secondary dispersal (Janzen 1982; González-Espinosa & Quintana-Ascencio 1986, Hallwachs 1986). Rodents are generally considered seed predators (Brown *et al.* 1979; Price & Jenkins 1986). Until recently, most seed harvesting of defecated seeds by ants was also assumed to be predation (e.g., Roberts & Heithaus 1986). Several species of ants are now known to remove seeds from frugivore defecations but not damage the seeds of certain plant species (Clifford & Monteith 1989). For both rodents and ants, it is important to note that even seed 'predators' are often seed dispersers as well. Many species, for example, will cache seeds but leave a small number of them intact (Berg 1966; Bullock 1974; Beattie & Lyons 1975; Beattie 1985; Price & Jenkins 1986). These seeds presumably enter the seed bank.

Are *Pheidole nigricula* and *P. nebulosa* predators or dispersers of small seeds in frugivore defecations? They appear to be both. Although they readily consume most seeds that they take, they often deposit viable seeds on refuse piles and leave caches of seeds when they abandon their nests (Levey & Byrne, unpubl. data). These seeds have, in effect, been dispersed by the ants (e.g., Roberts & Heithaus 1986; Rissing 1986). The probability that a seed will be eaten or moved and then abandoned depends upon the species of ant and seed. The ant-seed interaction at La Selva represents a complex continuum between predation and dispersal (see also Andersen 1982; Buckley 1982; Majer 1982).

It is unclear whether secondary dispersal of seeds from frugivore defecations is advantageous to the parent plant. The seeds may benefit because they are placed under ground or in a twig, which could protect them from other seed predators or pathogens (Beattie & Culver 1982). Also, the seeds could benefit from reduction in sibling competition (as they are removed from the defecation clump), which would be intense if the hundreds of seeds in each defecation were not scattered (Howe 1989). On the other hand, seeds might suffer increased levels of interspecific competition if the ants collect many species of seeds and cache them in a common place.

Even if we knew the ultimate effect of secondary seed movement by a given species of ant, predicting the fate of dispersed seeds would still be extremely difficult. Numerous species of ants harvest seeds from bird defecations and the effect of their behavior on seed survivorship varies (Heithaus 1986; Pudlo *et al.* 1980; Levey & Byrne, unpubl. data). Furthermore, the probability that a given ant species will find a defecation is largely unpredictable because ant species composition changes dramatically between nearby areas. For example, at La Selva, the species composition and abundances of twig-dwelling ants changed significantly among three 25 m^2 plots, all within 100 m of each other (Byrne 1991). In addition, primary forest and second growth areas at La Selva overlap very little in composition of the twig-dwelling ant fauna (M. Kaspari & M. Byrne, unpubl. data). Since most of the seed-harvesting species typically forage within 30 cm of their nest (Levey & Byrne, unpubl. data), placement of the defecation relative to ant nests will play a major role in determining which species finds and removes the seeds. Even a 10 cm difference in placement can affect which species discovers the defecation and thus alter the probability of what will happen to the seeds.

One evolutionary implication of this high degree of uncertainty is that any selective forces by frugivores on plant traits may be swamped by the unrelated and highly unpredictable interactions between seeds and ants (see also González-Espinosa & Quintana-Ascencio 1986). This may be one factor contributing to the general lack of tight evolutionary interactions between rain forest frugivores and small-seeded fruiting plants (Herrera 1986).

Another implication of high spatial variation in ant-seed interactions is that interspecific competitive interactions among seedlings may be highly microsite-specific. For example, two of the most common leaf litter ant species at La Selva (*P. nigricula* and *P. nebulosa*) differ in their preferences for two species of abundant seeds (*M. centrodesma* and *M. affinis*). If both seeds are deposited near a *P. nigricula* nest, the treatment of each is likely to be very different than if they had fallen near a *P. nebulosa* nest. These differences will likely affect the species composition and number of seeds that enter the seed bank at each site (González-Espinosa & Quintana-Ascencio 1986). Thus, when conditions for germination are met, the competitive interactions among seedlings will probably vary from one square meter to the next.

Obviously, we are just beginning to uncover the complexity of post-dispersal ant-seed interactions. We suggest that understanding this interaction is necessary for explaining seed bank dynamics and the evolutionary relationship between frugivores and fruiting plants.

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