Oecologia (1993) 95:81–88

Oecologia

Removal of seeds from Neotropical frugivore droppings

Ant responses to seed number

Michael Kaspari

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson Arizona, USA

Received: 28 August 1992 / Accepted: 9 March 1993

Abstract. In a Costa Rican rain forest, the majority of tree and shrub species have their seeds dispersed by vertebrates. Over a third of the species' seeds are of a size accessible to, and primarily carried away by, ants. Frugivorous bird droppings come in sizes from a few seeds to over a thousand, with number of seeds isometric with bird body mass. Dropping size decreases as seeds are scattered by rain. Larger droppings produced from fruits of *Miconia affinis* (Melastomataceae) are discovered and recruited to more by ants, with a diverse guild of 22 ant species carrying away the seeds. Droppings with 64 and 16 seeds were used by a subset of the ant community exploiting 4-seed droppings, likely due to resource defense by aggressive species. Seeds in the smallest droppings stood the smallest chance of being removed. Although soil-nesting ants of the tribe Attini were the primary removers of seeds in this forest, a third of removal was by ants living in ephemeral litter nests. Seeds of *M. affinis* were found in litter ant nests in 8 of 28 1-m^2 plots, suggesting that seed rain was not highly localized. Since litter nests are common, contain few seeds/nest and are often abandoned by their ants, litter ants may be the best candidates for ant-plant dispersal mutualisms.

Key words: Ants – Neotropics – Seeds – Predation – Mutualism

In a neotropical rain forest over 90% of the shrubs and trees may rely on frugivores to disperse their seeds (Frankie et al. 1974). Studies of plant-frugivore interactions have focused on how the frugivore's foraging behavior and mobility affect where the seed is deposited (Howe and Smallwood 1982; Wheelwright and Orians 1982; Martin 1985; Moermond and Denslow 1985). What happens to seeds between deposition and germination?

These seeds are likely to encounter ants. Over 40 species of ants harvest seed particles at the La Selva field station in Costa Rica (Kaspari 1990), and ant densities in tropical forests may exceed 800 ants/m^2 (Hölldobler and Wilson 1990). Ants are widely recognized as important seed predators in deserts (Tevis 1958; Brown et al. 1975; Mares and Rosenzweig 1978; Davidson et al. 1985) and as dispersers in a variety of habitats (Beattie 1985). Less is known about ant diversity and impact in the tropics (Andrews 1982; Risch and Carroll 1986).

Seeds in the neotropics may be a dependable resource for an ant assemblage: 49 seeds may rain on a meter^2 of litter per month (Denslow and Gomez-Diaz 1990). If these seeds vary in local density this variation may constitute a niche axis enhancing ant species diversity (Davidson 1977; Brown 1989). So the rules used by ants to discover, recruit to, and defend droppings with different numbers of seeds may have consequences both for the seeds and the ants that feed on them.

Here I explore what determines the number of seeds/dropping in a lowland Costa Rican wet forest. I test behavioral models that predict how seeds/dropping influences seed removal by ants. Finally, I use this information to examine how variation in seeds/dropping may effect seed survival and act as a niche axis in a diverse ant community.

Sources of variation in seeds/dropping

Ants encounter bird-dispersed seeds in packages called droppings. Frugivore droppings are typically watery masses of seeds with some pulp. At least three factors may shape the distribution of seeds/dropping. First, frugivores come in a range of body sizes (Martin 1985). The average number of seeds/dropping should be a function of a species' average meal size, its gut passage rate, and its cloacal volume. Since all of these likely scale with body mass, seeds/dropping should be a function of body mass as well. Second, each frugivore meal results in a number of droppings (Levey 1987) whose size may decrease as the gut is evacuated. Finally, rain may dilute droppings before

---

Current address: M. Kaspari, Brackenridge Field Laboratory, Department of Zoology, University of Texas, Austin, Texas USA 78712-1064

ants can discover them. Habitats with greater exposure to rainfall may thus yield more and smaller droppings. The roles that body size, within-bird effects, and rainfall play in shaping seeds/dropping all remain to be explored.

Discovery and recruitment to seeds

Suppose more seeds provide a stronger sensory cue to ants. Then larger droppings should have a higher discovery rate. Picture a circular dropping with equal density of seeds throughout. Seeds/dropping, S, should be proportional to πr^2, and thus its radius proportional to $\sqrt{S}$. The *Pheidole* and small Attine ants in the forest litter appear to orient to a dropping after they bump into it (pers. obs.). If discovery results solely from a random walk, then droppings should be discovered at a rate proportional to $\sqrt{S}$, the boundary of the dropping exposed to a ground foraging ant. Quite apart from the rewards a dropping might contain, large droppings are more likely to be discovered.

Once a dropping is discovered, how should the number of seeds/dropping affect the colony's decision to harvest? We start with the assumption that colonies are food limited, and that ant colonies tend to maximize food intake rate, increasing the number of workers recruited to larger droppings. Increasing the number of workers available will tend to increase a colony's potential energy intake/time (E/T) since more workers will decrease the number of ant round trips needed to exhaust a dropping (Kaspari 1992). However increasing the number of seeds/dropping does not automatically increase E/T, it only increases E/T when the colony's worker force is adequate to harvest the seeds without an increase in total time. To see this, imagine two colonies, one with one worker, the other with ten. A 1-seed dropping will yield the same energy for the same round trip time for both colonies. For the one-worker colony, a 2-seed dropping will double the round trip time, resulting in the same E/T. For a ten worker colony, a 2-seed dropping will also double the intake, but the colony will retrieve the dropping in the same amount of time by committing 2 workers (assuming they both fetch a seed simultaneously) yielding a doubled E/T. Likewise, a 50-seed dropping yields a higher E/T to a colony of 50 or more workers than it does to a colony of 1 or 10.

So ant species with large load sizes or worker forces – either of which decreases the travel time required to deplete a dropping – should selectively recruit to large droppings. In contrast, species with small load or colony sizes should be opportunists, recruiting to small and large droppings alike.

However, increasing seeds/dropping should also make the dropping more profitable to defend (Carpenter 1987; Johnson et al. 1987). Ants will often vigorously defend local baits (Hölldobler and Wilson 1990). By adding resource defense, we get a different prediction from the above. If a subset of ants defend large droppings, then species richness will not increase and may even decrease with seeds/dropping.

We now have three predictions. First, discovery rate should increase as a square root of seeds/dropping. Second, recruitment will be higher for larger droppings. Finally, the suite of ants attracted to larger droppings should increase if dropping choice is governed purely by exploitation and stay the same or decrease if droppings with more seeds are defended by a subset of ants.

Methods

This study took place at the Estacion Biológica La Selva (10° 25′ N, 84° 01′W), located on the Caribbean slope of Costa Rica. Holdridge classifies La Selva as a tropical wet forest (see Hartshorn 1983 for a further site description). The work was conducted during the 1989 and 1990 rainy season (mean monthly rainfall 1988–90: May: 422 mm, June: 411 mm, July: 391 mm).

I performed experiments next to a 600-m stretch of the Atajo trail. Younger portions of the trail (ca. 9 years since abandonment as cattle pasture) are a patchwork of grassy swales and small trees. Tall forest canopy and sparser ground cover dominate older portions (ca. 15 years old). *Miconia affinis* (Melastomataceae) is common along the length of the trail, and is the fifth most common tree > 5 cm DBH in La Selva's second growth (Hartshorn 1983). *M. affinis* is a mid-successional tree that produces abundant, small, purple fruits. These fruits mature primarily in the rainy season (Opler et al. 1980), concurrent with this study, and contain ca. 40 small (1 × 0.5 mm) seeds per fruit. A variety of birds disperse these fruits (Loiselle and Blake 1990); and a variety of ants carry away these seeds (see below). Although I often find hollowed out *M. affinis* seeds in ant nests on the study site, the ant-*M. affinis* interaction is likely more complex than simple predation (Levey and Byrne in press, see below).

Sources of variability in seeds dropping

In June 1989 I censused the frugivorous bird community by mist-netting along the Atajo trail. *Manacus candei* accounted for 51% of captures of 11 frugivores (167 net hours). I used this species to prepare droppings for experiments, placing a dish of *M. affinis* fruits in the cage, and collecting droppings from a plastic liner after 40 min. I mixed these droppings together and fashioned them into circular droppings of 4, 16, 32, and 64 seeds for the experiments below.

To examine the range of seeds/dropping produced from a single meal, I allowed 3 *M. candei* in 1989 to feed until sated on *M. affinis* fruits. After 3 h, I removed droppings from the plastic liner and counted the number of seeds in each. I calculated mean and skew for the droppings produced by each bird.

To examine how the size of *M. affinis* droppings varied with bird mass, birds were mist-netted from second-growth around La Selva (Bette Loiselle, unpub. data) and placed in plastic boxes for ca. 5–10 min. Droppings were collected from the box (Loiselle and Blake 1990; Loiselle 1990). I supplemented Loiselle's data with droppings collected in the field from Crested Guans (*Penelope purpurascens*) observed feeding in a *M. affinis* tree. I calculated the mean number of *M. affinis* seeds/dropping for each of the six bird species. Bird mass was taken from Stiles and Skutch (1989). I regressed log bird mass against log seeds/dropping.

Rainfall and seeds/dropping

I explored the effects of raindrops on the size of *M. affinis* droppings across a second-growth mosaic. I made two 100-m transects, through adjacent young and old portions of the Atajo trail. Each transect consisted of 10 stations. At each station I estimated percentage open canopy from 1.5 m height using a spherical densiometer.

At each station I placed a rain gauge (a 2-dram vial, planted in the ground on a stiff wire) and a platform with a *M. affinis* dropping at its center. The base of the platform was the bottom half of a plastic petri dish (9.5 cm in diameter) affixed to a small rod and punctured with five holes for drainage. I fitted a piece of water-permeable cloth, Agryl®, into the bottom of the dish. I then capped the petri dish with its top half. I topped this petri dish platform with a disk of filter paper. In this way, any seed washed from the filter paper into the bottom petri dish were caught by the cloth nested between the dish halves. The rod holding up the platform was smeared with Tanglefoot® to exclude ants and pushed into the ground.

On 16 July 1990, at the onset of a rain shower, I placed twelve 64-seed droppings and eight 16-seed droppings randomly at the 20 stations (with equal replication in old and new second growth). I collected the stations at the conclusion of the 2-hour shower. At each station, I recorded distance moved by each seed in the dropping. Based on observations of seeds splashed off the plate, I assigned seeds washed into the lip and splashed off the plate a distance 1.5 times the distance from the center to the lip (67.5 mm).

Ant-dropping interactions

In 1989 and 1990, I measured rates of dropping discovery, ant recruitment, and survivorship of *M. affinis* seeds as a function of seeds/dropping. In 1989, I ran an 80-station transect, each station 6 m apart. The night before, I prepared 4, 16,32 and 64-seed droppings and stored them, refrigerated, on moistened filter paper in a petri dish. I chose the levels of seeds/dropping for two reasons. First this range of seeds/dropping spans 72% of that produced by *M. candei*, the most common frugivorous bird at the site. Second, the densities of 4, 16, and 64 seeds/dropping represent doublings of dropping circumference. The discovery model predicts a corresponding increase in proportion of droppings discovered.

On the morning of the experiment, I placed the droppings in the center of a glass microscope slide, one slide/station. The slide was covered with masking tape (sticky-side down). To prevent seed dispersal by rain, I sheltered droppings with a 20 × 20 cm clear plastic bag affixed to a wire frame. The plastic did not reach the ground and so did not interfere with ants approaching the slide. The size treatments were laid out in a stratified randomized design. The droppings were placed out at 0800 h and collected 24 h later over 2 days, July 1989.

In 1990, I ran a similar experiment on a 30-station transect through the same second growth, each station separated by 10 m. I set out 3 dropping treatments (4, 16, 64) on glass slides scoured with sandpaper. A small (12 × 8 cm by 6 cm high) wire mesh cage topped with aluminum foil sheltered the dropping from rain. Holes between the wire legs allowed free access to the dropping. These small cages, if disturbed, would indicate the activity of a larger vertebrate predator (e.g., rodents of the genus *Oryzomys* or *Heteromys*, R. Timm, pers. comm.).

I ran the experiment on 5 days spread over the month of July. I randomized dropping across stations, with 16 daily replicates of the 4-seed dropping, 8 replicates of the 16-seed dropping and 6 replicates of the 64-seed dropping. By the end of each experiment each station received at least one 4-seed treatment, 29 stations received a 16-seed treatment, and 27 received a 64-seed treatment.

Placing the droppings out took 20 min. In 1990, I made 4 circuits of the transect, stopping for 10 s at each station. Each circuit took about 20 min. I collected a representative of any ants carrying or mandibulating droppings. Removing ants in this way likely skewed estimates of recruitment and seed removal downward. Twenty-four hours later I counted the remaining seeds.

Where do ants move *M. affinis* seeds? I collected all litter nests (small twigs and wood, and between leaves) from 28 1-m^2 plots in a transect parallel to and 5 meters from the 1990 transect (the other two plots were in the middle of an army ant raid on the day of collection). Nests were returned to the lab stored in plastic bags. There I recorded the nest type (twig, rotten wood, between-leaves) and number of *M. affinis* seeds therein.

In this study 6–10 meters separated experimental stations. Litter nesting ants rarely forage > 30 cm from their nest (Byrne and Levey 1993). I followed soil-nesting ants from 12 bait stations back to their nest entrance. Distances averaged 45 cm (range 15–72 cm). Taken together, these data suggest it is unlikely that ants from one colony ever exploited more than one station. To reduce the possibility that ants would set up long-term foraging trails to a station (and violate the assumption of temporal independence) I never ran experiments two days in a row.

Results

Sources of variation in seeds/dropping: Birds and Rainfall

M. affinis seeds were in 21–37% of the droppings collected from the 5 netted species (*P. purpurascens* droppings were collected beneath *M. affinis* trees). Seeds/dropping was isometric with bird body size (# *M. affinis* seeds = 0.308 mass (g)$^{1.02}$, standard errors = 0.487, 0.227; $p = 0.011$, $r^2 = 0.836$, $n = 6$). The distribution of seeds/dropping was right-skewed in the 4 of 6 bird species with sample sizes adequate for a statistical test ($n > 25$, $g > 1.5$, $p < 0.01$). Right skew concentrates most of the seeds in a minority of droppings: 15% of the *M. candei* droppings contained 45% of the seeds.

Rainfall dispersed and diluted droppings. The 15 year old second growth was more closed (4–24% open canopy) than the 9 year old second growth (31–100% open canopy). Across stations, rainfall ranged from 0.2–5.0 mm of rain during the two-hour experiment. Seeds were scattered farther with increasing rainfall (Spearman $r = 0.45$, $p = 0.0438$, $n = 20$). After the rain, 40% of 16-seed droppings and 62% of 64-seed droppings contained fewer than 10 seeds.

Ant activity at droppings

I recorded 22 species of ants on *M. affinis* droppings in 1990. These included 2 subfamilies (Ponerinae, Myrmicinae), 5 tribes, and 9 genera (Table 1). The tribes Pheidolini and Attini – both Myrmicinae – accounted for 46 and 39% of species. More species of ant likely carry off *M. affinis*. I base this conclusion on two pieces of evidence. First, 46 species were recorded at barley particles in this habitat (Kaspari in review). Second, a plot of species against sample effort suggests that the curves have not saturated (Fig. 1).

The attine *Sericomyrmex aztecus* removed seeds from droppings in 29% of the observations. *S. aztecus* and two *Pheidole* species accounted for 50% of the seed removal observed. None of the 150 aluminum foil cages in 1990 was disturbed. This suggests that the small seeds of *M. affinis* were not used by vertebrates like rodents. Gryllids and Opilionids were sometimes observed on the droppings.

Ants responded to droppings in a variety of ways. I recorded 15 ant species carrying away seeds during this study's 10-second observation periods. Ants touched the dropping with their antenna for seconds or minutes. They then picked up a seed or cut loose some pulp attached to the seed and walked away. The species not observed carrying seeds here did carry seed particles in a study with longer observation periods (Kaspari 1992). However, while some of these ants were just slow to pick up a seed

Table 1. Ant species observed in 106 focal samples of 4, 16 and 64-seed *Miconia affinis* droppings. " %-Obs" is the percentage of total ant observations by this species. Carry is "yes" if ants were observed removing *M. affinis* seeds. Nest site refers to substrate where ants were observed to nest

Tribe/Genus species	Number at 4	16	64	% Obs	Carry	Nest Site
Ectatommini				2.4		
Ectatomma ruidum	1	2	0	2.4	Yes	Soil
Solenopsidini				7.3		
Solenopsis geminata	0	0	1	0.8	Yes	Soil
S. Diplorhoptrum CO	1	1	1	2.4	No	Twigs
S.D. RA	0	0	1	0.8	No	Twigs
S.D. RP	1	1	1	2.4	No	Twigs
S.D. SO	0	0	1	0.8	No	Twigs
Ochetomyrmicini				5.6		
Wasmannia auropunctata	4	1	2	5.6	No	Twigs
Pheidolini				46		
Pheidole CU	0	0	1	0.8	No	Soil
P. IN	3	2	2	5.6	Yes	Twigs
P. MI	2	3	6	8.7	Yes	Soil
P. nebulosa	3	5	1	7.1	Yes	Twigs
P. SP	1	2	0	2.4	Yes	Twigs
P. UN	1	0	0	0.8	No	Soil
P. OP	2	2	4	6.3	Yes	Soil
P. MG	0	1	0	0.8	Yes	Twigs
P. nigricula	1	0	0	0.8	Yes	Twigs
P. simsoni	4	8	4	12.7	Yes	Soil
Attini				38.9		
Sericomyrmex aztecus	7	7	12	28.6	Yes	Soil
Trachymrymex cornetzi	2	0	0	1.6	Yes	Soil
T. sausseri	1	0	0	0.8	Yes	Soil
Apterostigma MI	1	0	0	0.8	Yes	Soil
Cyphomyrmex cornutas	2	2	5	7.1	Yes	Soil

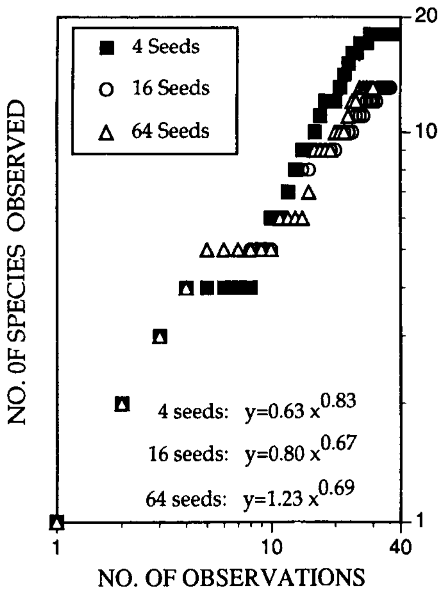

Fig. 1. The number of species recorded decreases with the number of seeds/dropping. Curves plot number of species recorded at each size dropping against number of ant observations at that dropping (see Table 2)

(e.g., *Wasmannia auropunctata*), *Solenopsis* of the subgenus *Diplorhoptrum* behaved differently. *S. Diplorhoptrum* stood on droppings for minutes, their heads lowered and abdomens raised. They may have been externally digesting the seeds, pulp, or both (Went et al. 1972). Raised abdomens, "gaster flagging", in Solenopsis is often used to defend a local resource (Hölldobler and Wilson 1990).

Conflict at droppings was difficult to detect in the short 10 s focal samples. However, observations at *M. affinis* droppings and other seed baits suggest it does occur. *S. aztecus* was often aggressive and would charge and drive away other ants. Also, the large-headed soldier caste of the species *Pheidole MI* appeared to defend laden workers, accompanying them back to the nest. Both *S. aztecus* and *P. MI* were most common at 64-seed droppings. Resource defense may thus affect dropping use by the ant community.

I measured discovery rate in two ways. In 1989 I estimated discovery rates using number of droppings with seeds removed in a day. As predicted, discovery rate increased with seeds/dropping from 30 to nearly 80% after 24 h ($\chi^2=21.0$, 1-tailed $p<0.0001$, Fig. 2). In 1990 I estimated discovery rate using the number of ants at droppings after 20 min. Discovery rate increased with seeds/dropping from 21% up to 47% after 20 min. in the field (Fig. 3, $\chi^2=5.4$, df$=2$, 1-tailed $p<0.05$).

Although I fashioned droppings to double dropping circumference from 4 to 16 to 64 seeds/dropping, this did not result in a consistent doubling of discovery estimates. Discovery rate increased faster from 4 to 16-seed droppings (108% in 1989 and 76% in 1990) than from 16 to 64-seed droppings (24% in both years, Fig. 2).

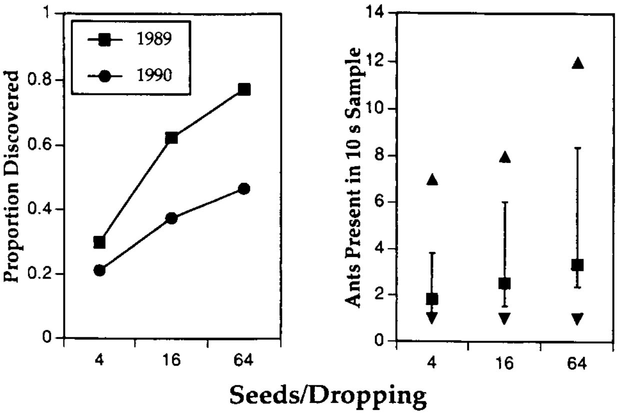

Fig. 2. Discovery and recruitment increases with the number of seeds per dropping. Left: Discovery rate is measured in 1989 as number of droppings with seeds removed after 24 hours (value for 32 seed treatment (0.72) omitted for clarity). In 1990, discovery rate measured as proportion of droppings with ants after 20 minutes. Right: Recruitment rate for discovered droppings measured as number of ants present in 10 s focal samples. Squares are means, error bars are quartile 1 and 3, triangles are minima and maxima

For those droppings that were discovered, I compared the maximum number of ants that appeared at that station day's 10-s sample. Ant numbers at droppings were skewed right for all three treatments (Fig. 2). This measure of recruitment increased with seeds/dropping (Kruskal Wallis $\chi^2 = 6.09$, 1-tailed $p < 0.024$, Fig. 2). This effect does not appear to result from increased independent discoveries of the droppings. First, colonies of different species used a dropping together in only 8% of the observations. Second, I never observed individuals of the same species coming and going along different recruitment trails, suggesting independent discovery and recruitment.

I recorded a total of 13 ant species at 16- and 64-seed droppings and 18 species at 4-seed droppings. Power functions explained between 96 and 98% of the variation in the species/observation curves (Fig. 1). I compared the slopes of the curves using an ANCOVA (Table 2). The significant interaction between dropping size and number of observations ($p < 0.001$) suggested that treatments accumulate species at different rates. The slope of the species accumulation is significantly greater at 4-seed droppings (0.83) than either the 16-seed dropping (0.67) or 64-seed dropping (0.69) using 95%-confidence intervals.

In sum a variety of ants used droppings, with recruitment and discovery rates increasing with dropping size. However, fewer species used 16 and 64-seed droppings than 4-seed droppings. Combined with observations of conflict at droppings, this is consistent with a model of resource defense.

Seed harvesting and ant nesting habits

I sampled litter for nests in the study area, with more thorough studies in 1991 (Kaspari in review). Ten of 22 ant species in this study nest in the forest litter with the remainder nesting in the soil (Table 1). Weighting the number of each ant species at each dropping size, 36% of 4- and 16-seed droppings and 22% of 64 seed droppings wind up in litter nests.

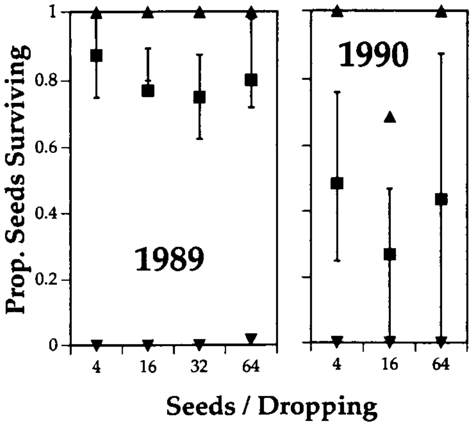

Fig. 3. Proportion of seeds remaining in a dropping decreases with number of seeds per dropping in two years of study. Squares are mean probabilities, error bars are quartile 1 and 3, triangles are minima and maxima. Large quartile range due to bimodality centered around proportions of 0's and 1.0's

Table 2. The number of species observed at a dropping decreases with dropping size, increases with number observations, with the rate of accumulation varying between dropping size (see Fig 1)

Source	df	Type III SS	Pr>F
Seeds/dropping	2	0.0211	0.0146
Log(observations)	1	7.431	0.0001
Interactions	2	0.0769	0.0001

Of 133 nests collected on 28 1-m^2 plots, 81% were in small rotten twigs, 14% between leaves, and the remainder in bits of wood. I found *M. affinis* seeds in 11% of these nests. Four of 11 leaf nests and 9 of 107 twig nests had seeds. However, there were few seeds in these nests, less on average than even the smallest seeds/dropping treatment (mean 2.5, range 1–8). Many seeds were partially hollowed out.

Consequences for seeds in droppings

Removal by ants was heterogeneous in time and space. In one third of the stations, a seed had <29% chance of remaining in the dropping after 24 h, a 30–51% chance in the next third, and a 60–85% chance in the final third. This represents significant microsite variability in seed removal (Kruskal Wallis $\chi^2 = 45.7$, df = 29, $p = 0.0252$). The five days of the experiment also differed in the probability of a seed remaining at a station (17, 35, 39, 58 and 63%; Kruskal Wallis $\chi^2 = 20.97$, $p = 0.0003$).

Seed removal was strongly bimodal: 0 and 100% removal were the most common fates in each seed/dropping treatment. This left a large portion of the droppings only partially depleted after 24 h. For example, in 1990 11% of the 4-seed droppings, 46% of the 16-seed droppings and 62% of the 64-seed droppings collected 24 h later were partially depleted.

Despite bimodality, and variation in time and space, a seed's probability of remaining after 24-hours declined significantly across the four seeds/dropping treatments in 1989 (Kruskal Wallis $\chi^2 = 10.2$, 2-tailed $p = 0.02$, Fig. 3). Mean probability of a seed remaining peaked at 0.88 in 4-seed droppings – all six pair-wise Kruskal Wallis comparisons supported a difference between 4 seeds and 16, 32, and 64 (p's < 0.03, 0.0054, 0.003) and no differences among the other treatments (p's > 0.6). In 1990 the survivorship pattern was similar across the three seeds/dropping treatments, but only marginally significant (Kruskal Wallis $\chi^2 = 5.58$, df $= 2$, 2-tailed $p = 0.061$). Pair wise comparisons supported differences between 4 and 16 seed treatments ($p = 0.017$), but not the other two ($p > 0.14$). The 1990 24-hour survivorship rate was also about half that of 1989.

Discussion

An array of factors interacts to shape the distribution of seeds/dropping. First, larger frugivores produce on average larger droppings. This relationship appears to be isometric: the mean number of seeds in a bird dropping is consistently proportional to that species' mass, although larger birds consume a greater range of fruit sizes (Wheelwright 1985). The majority of these droppings contained a minority of the seeds. Seeds are further scattered and diluted from droppings by rainfall. These patterns would suggest small birds in open second growth would produce small droppings, while large birds in closed canopy forest would present ants with larger droppings.

M. affinis seeds rained over a third of the plots in this habitat and were not, as often suggested, highly clumped (Harper 1977; Levin 1979; see also Murray 1988). Eight of 28 (29%) of the plots along a 300-m transect had litter nests with *M. affinis* seeds. This is likely an underestimate of the dispersion of *M. affinis* seeds for two reasons. First some plots do not contain granivorous litter ants and thus would not show *M. affinis* even if it fell there. Second, this estimate ignores the 70% of the seeds harvested by soil-nesting ants. Both factors suggest that *M. affinis* rains on over 29% of the plots along the Ataho trail.

Seeds/dropping and ant behavior

In the regenerating rain forest of La Selva Costa Rica, ants are the primary removers of dispersed *Miconia affinis* seeds: none of the flimsy aluminum shelters over the droppings were disturbed, suggesting little rodent activity. These tiny (1 × 0.5 mm) seeds may not be profitable to the rodents of the forest floor; the high discovery rates by ants (21–47% in the first 20 min, 30–80% after 24 h) may make them unreliable resources for rodents. The rodent *Liomys* is a voracious predator of *Enterolobium cyclocarpum* seeds in a tropical dry forest (Janzen 1982). However, these seeds are much larger than *M. affinis* (300–1100 mg), so that seed size may segregate ants and rodents in this as in other communities (e.g., Mittelbach and Gross 1984).

Miconia affinis seeds attracted a diverse assemblage of ants: 2 subfamilies, 5 tribes, 8 genera and 22 species in this study. The majority of these ants were rare or occasional granivores – 57% of the observed removal was by four species. In the same two years, Levey and Byrne (in press) were placing out droppings from the same *M. candei* birds, fed fruits of various Melastomes, in the primary forest of La Selva. In the primary forest, 13 species of 7 genera collected seeds from droppings, with two *Pheidole* species representing 77% of seed removals. This suggests that at La Selva, the granivore community in a primary forest may be simpler than that found in second growth.

Once harvested by the ants, at least 70% of *M. affinis* seeds are carried to soil nests – over half of these go to nests of the 5 fungus gardening attines. The suitability of seeds for fungus cultivation, which would determine if the seeds are substrate or are discarded, deserves further investigation. The remaining third of *M. affinis* seeds go to nests that are often no more than a space between two leaves or the inside of a rotten twig. Of the 133 nests sampled in this habitat from 28 m^2 plots, 11% contain a small number (1–8) of *M. affinis* seeds. Extrapolating, over 5000 litter nests in a hectare of second growth rain forest may contain small numbers of *M. affinis* seeds.

Seed removal results from two nested behaviors. To exploit a dropping, an ant colony must first discover the dropping, then the discovering ant must decide whether to recruit her sisters. Using a range of seeds/dropping that encompassed 72% of that produced by the habitat's dominant frugivore, I found both processes at work in this ant community.

If individual workers randomly encounter prey, then doubling dropping circumference should double discovery rates. This prediction is approximated for small droppings, but discovery rate fails to double in larger droppings (Fig. 2). This may be due to the implicit assumption of equal ant densities at all stations, an assumption invalidated over the course of this study: there can be no removal by ants at stations where there are no ants. Better understanding of the behavior and distribution granivores should allow us to better understand how the discovery process works.

Once discovered, the number of seeds/dropping may affect the profitability of that dropping to the colony. A model of energy maximization assumes ant colonies will invest more workers at larger droppings. Colonies dispatched more workers to richer droppings (Fig. 2); some species like *Sericomyrmex aztecus*, *Pheidole OP*, and *P. MI* recruited up to 12 workers at a time. However fewer, not more, species used droppings with more seeds (Fig. 1), consistent with the energy maximization model with resource defense. Conflict at droppings was common at La Selva and characterizes many interactions of ants at baits (Hölldobler and Wilson 1990).

Smaller colonies are predicted here to profitably exploit even the smallest droppings. Larger colonies in turn, can quickly exploit and defend large patches, but at the cost of maintaining those extra workers. This scenario corresponds well to J.S. Brown's (1989) equilibrial model of competitive coexistence with an interesting spatial twist. Because the discovery rate and profitability of seeds decrease with distance to the colony (Orians and Pearson 1979), large colonies may be opportunists near their nest, efficiently depleting even the smallest droppings and become selective as they forager farther away. This may help explain the partial preferences for small droppings of aggressive recruiters like *Sericomyrmex aztecus*, whose nest entrances were often only cm's from the bait. More study of the foraging economics of colonies – foraging speed, colony size and efficiency – will clear up this coexistence mechanism.

Implications for dispersed seeds

Upon falling to the forest floor, what factors regulate the removal of *Miconia affinis* seeds by ants? This study suggests two: microsite and seeds/dropping. The precise microsite in which the dropping falls may largely override any intrinsic quality of the dropping. Variation in removal rates across 20 × 20 m grids explained 56% of the seed survival in an Australian heath (Hughes and Westoby 1990), more than seed species, time of day or year, or seeds/aggregate. In this study, stations varied in mean removal rates, ranging from 0 to 85%. A visual inspection of stations found no apparent habitat differences to account for this variance. However, if soil colonies of granivorous ants are as patchy as their litter-nesting counterparts (Byrne 1991; Kaspari 1992; in review), then patchiness in ant colonies may help explain patchiness in seed removal.

At La Selva, a seed's chance of removal tended to increase with seed number, a pattern often reported (Willson and Whelan 1990). However, in both years there was a tendency for seeds in 64 seed droppings to have a lower removal rate, suggesting that larger droppings may swamp the ability of ants to deplete droppings. Ants left seeds behind at a dropping 11–62% of the time. Ants may depart useful droppings for a number of reasons, including changes in the preferred microclimate at the bait site (Levins et al. 1971) and the attraction of predators to recruiting ants (Feener 1981). In this system, the small colony sizes (mean = 59 workers, range = 8–362, unpub. data) and tiny nests of litter-nesters may limit the need or ability to store harvested seeds, giving multiple nests access to a single large dropping.

To better understand the role of ants in plant recruitment, perhaps the next steps lie in better understanding the biology of litter ants. A quarter of *M. affinis* seeds wind up in flimsy litter nests, with only 0–8 seeds per nest. Litter ant species at La Selva abandon nests every 37–136 days (Byrne 1991), and it is not uncommon to find seeds sprouting in abandoned twigs full of refuse piles (pers. obs., Levey and Byrne 1993). If ant mutualists of *M. affinis* exist, perhaps the candidates are the small, uncommon granivores (e.g., *Pheidole MG* and *nigricula*) of La Selva's litter community. If so, small birds are likely to produce the small droppings that will most efficiently deliver these seeds.

Acknowledgments. This project got its start because of the field course OTS 88-3 and the Arizona drought of 1989. B. Loiselle and B. Alverson were largely responsible for the former, and I thank them. This project was startable due to the fine efforts of Dr. Thomas Miller and the staff of the Arizona Cancer center. M. Byrne, D. & D. Clark, D. Levey, B. Loiselle, J. Longino, and L. McDade provided help and logistical support in the field. Ants are deposited in the Los Angeles County Museum and the Harvard Museum. J. Bronstein, D. Davidson, M. Donoghue, B. Loiselle, M. Rosenzweig, S. Russell, P. Smallwood and D. Vleck read various versions of the manuscript and improved it enormously. Funding was graciously supplied by the Organization for Tropical Studies, Sigma Xi, and the Roosevelt Fund. And thanks to the ants and manakins.

References

Andrews AN (1982) Seed removal by ants in the mallee of northwestern Victoria. In: Junk W, Buckley RC (eds.) Ant-Plant Interactions in Australia. The Hague, pp. 31–44.

Beattie AJ (1985) The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, New York, USA

Brown JS (1989) Desert rodent communities: a test of 4 mechanisms of coexistence. Ecol Monogr 59: 1–20

Brown JH, Grover JJ, Davidson DW, Lieberman GA (1975) A preliminary study of seed predation in desert and montane habitats. Ecology 56: 987–992

Byrne MM (1991) Ecology and coexistence mechanisms of tropical twig-dwelling ants. M.S. Thesis, University of Florida, Gainesville, Florida, USA

Carpenter FL (1987) Food abundance and territoriality: to defend or not to defend. Am Zool 27: 387–400

Davidson DW (1977) Species diversity and community organization in desert seed-eating ants. Ecology 58: 711–724

Davidson DW, Samson DA, Inouye RS (1985) Granivory in the chihuahuan desert: interactions within and between trophic levels. Ecology 66: 486–502

Denslow JS, Gomez-Diaz AE (1990) Seed rain to treefall gaps in a Neotropical rain forest. J Can For Res 20: 642–648

Feener, DH Jr (1981) Competition between ant species: outcome controlled by parasitic flies. Science 214: 815–817

Frankie GW, Baker HG, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J Ecol 62: 881–919

Harper JL (1977) Population biology of plants. Academic Press, London, England

Hartshorn GS (1983) Introduction to Plants. In: Janzen D (ed) Costa Rican Natural History, University of Chicago Press, Chicago

Hölldobler B, Wilson EO (1990) The Ants. Belknap Press, Cambridge Mass

Howe HF, Smallwood J (1982) Ecology of Seed Dispersal. Annual Rev Ecol System 13: 201–228

Hughes L, Westoby M (1990) Removal rates of seeds adapted for dispersal by ants. Ecology 71: 138–148

Janzen DH (1982) Removal of seeds from horse dung by tropical rodents. Ecology 63: 1887–1900

Johnson LK, Hubbell SP, Feener DH Jr (1987) Defense of food supply by eusocial colonies. Am Zool 27: 347–358

Kaspari M (1992) Niche relationships in an assemblage of neotropical granivorous ants. Ph.D. Dissertation. University of Arizona. Tucson

Levey DJ (1987) Seed size and fruit handling technique of avian frugivores. Am Nat 29: 471–485

Levey DJ, Byrne MM (1993) Complex ant-plant interactions: *Pheidole* as secondary dispersers and post-dispersal seed predators of rain forest plants. Ecology □: □–□

Levin DA (1979) The nature of plant species. Science 204: 381–384

Levins R, Pressic ML, Heatwole (1973) Coexistence patterns in insular ants. Am Sci 61: 463–472

Loiselle BA (1990) Seeds in droppings of tropical fruit-eating birds: importance of considering seed composition Oecologia 82: 494–500

Loiselle BA, Blake JG (1990) Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. In: Morrison ML, Ralp CJ, Verner J (eds) Food exploitation by terrestrial birds. Cooper Ornithological Society

Mares MA, Rosenzweig ML (1978) Granivory in North and South American deserts: rodents, birds, and ants. Ecology 59: 235–241

Martin, TE (1985) Resource selection by tropical frugivorous birds. Oecologia 66: 563–573

Mittelbach GG, Gross KL (1984) Experimental studies of seed predation in old-fields. Oecologia 65: 7–13

Moermond TC, Denslow JS (1985) Neotropical frugivores: patterns of behavior, morphology, and nutrition with consequences for fruit selection. In: Buckley PA, Foster MS, Morton ES, Ridgley RS, Smith NG (eds.) Neotropical Ornithology. Ornithological Monographs No. 6, pp. 865–897

Murray KG (1988) Avian seed dispersal of three neotropical gap dependent plants. Ecol Mon 58: 271–298

Opler PA, Frankie GW, Baker HG (1980) Comparative phenological studies of treelet and shrub species in tropical wet and dry forest in the lowland of Costa Rica. J Ecol 68: 167–188

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds.) Analysis of Ecological Systems. Ohio State University Press, Columbus, pp. 154–177

Risch SJ, Carroll CR (1986) Effects of seed predation by a tropical ant on competition among weeds. Ecology 67: 1319–1327

Stiles FG, Skutch AG (1989) A guide to the birds of Costa Rica. Comstock Press. Cornell

Tevis L (1958) Interrelations between the harvester ant *Veromessor pergandei* (Mayr) and some desert ephemerals. Ecology 39: 695–704

Wheelwright NT, Orians GH (1982) Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. Am Nat 119: 402–413

Went FW, Wheeler J, Wheeler GC (1972) Feeding and digestion in some ants (*Veromessor* and *Manica*). Bioscience 22: 82–88

Wheelwright NT (1987) Fruit size, gape width, and the diets of fruit-eating birds. Ecology 66: 808–818

Willson MF, Whelan CJ (1990) Variation in postdispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, seasonal and species. Oikos 57: 191–198