Seed Dispersal of a Neotropical Myrmecochore: Variation in Removal Rates and Dispersal Distance[1]

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ABSTRACT

We investigated small-scale spatial variation in dispersal success of the ant-dispersed herb *Calathea ovandensis*, and the potential effect of seed predators on seed dispersal. We found no evidence that vertebrate seed predators influenced seed dispersal probabilities. Seeds placed in experimental seed depots which excluded vertebrate seed predators (but not ants) were removed at the same rate as those in depots accessible to both ants and vertebrates. Five ant species were attracted to the seeds, but only two, *Pachycondyla harpax* and *P. apicalis*, regularly moved seeds beyond the parent plant canopy. *P. harpax*, the most abundant ant, moved seeds about 75 cm; the rarer *P. apicalis* moved seeds 12 times further. Other ants recruited to seeds without effecting dispersal; in particular, *Solenopsis geminata* and *Wasmannia auropunctata* interfered with seed dispersal. Their frequency varied (0–36%) among sites, resulting in significant variation among sites in seed removal rates.

VARIATION AMONG POTENTIAL MUTUALISTS may constitute an important selective force in plant–animal interactions that could result in evolutionary specialization of plants to particular animals (Horvitz & Schemske 1984, Schemske & Horvitz 1984). However, there is little information on the magnitude and causes of spatial variation in mutualisms in general, and in seed dispersal systems in particular. In this paper we examine ant–seed interactions in the tropical herbaceous myrmecochore, *C. ovandensis* Matuda (Marantaceae) (Horvitz 1980, 1981; Horvitz and Beattie 1980). We conducted observations and experiments to answer the following questions concerning variation in dispersal success: (1) Do ant species vary in dispersal distance? (2) What are the frequencies of different ant species at different sites? (3) Does the percent of seeds removed vary among sites as a result of spatial variation in the ant community?

Because the probability of successful seed dispersal in myrmecochores is often affected by both ants and vertebrate seed predators (Culver & Beattie 1978, Heithaus et al. 1980, O'Dowd & Hay 1980, Heithaus 1981, Beattie 1983), we determined whether vertebrate seed predation is a contemporary selective force in *Calathea*. We compared the removal rates in seed depots open to all dispersal agents and predators with those in cages which excluded vertebrates. This experimental design does not investigate the historical selective forces that shaped the evolution of ant dispersal, but does examine the contemporary selective effects of vertebrate seed predators in an ant-dispersed species.

STUDY SPECIES AND SITE

C. ovandensis (Marantaceae) is an acaulescent tropical perennial herb that is deciduous during the dry season (see Horvitz 1980, 1981; and Horvitz & Schemske 1984 for a detailed description). Fruit capsules, containing a maximum of three seeds each, dehisce at maturity in the late rainy season, and the large (0.5 cm) seeds fall to the forest floor near the parent plant. Each seed bears a large (0.4 cm), white, lipid-rich aril that is used for food by ants. The seeds have innate dormancy and germinate at the beginning of the next rainy season, *ca.* 270–300 days after capsule dehiscence.

Our study site was located in a secondary forest at Laguna Encantada, near San Andrés Tuxtla, Veracruz, Mexico (Horvitz & Schemske 1984). *C. ovandensis* is abundant throughout this forest, varying among sites in density, population stage structure, and population dynamics (Horvitz & Schemske, pers. comm.).

MATERIALS AND METHODS

DISPERSAL CHARACTERISTICS OF DIFFERENT ANT SPECIES.—To determine how far ants carry seeds and where seeds are taken by ants, we directly observed ant–seed interactions. Each observer placed six fresh seeds on the forest floor and subsequently observed ant activity continuously for 90 min, recording which ant species came to the seeds, where seeds were taken by ants, and any interactions among ant species. Six seeds was chosen because fruit capsules contain a maximum of three seeds each and no more than two capsules per plant dehisce on the same day (Horvitz, pers. comm.); therefore, six represents a maximum number of seeds that dispersal agents are likely to find at one spot at one time. Twenty-nine such obser-

TABLE 1. *Dispersal characteristics of ant species.*

Ant species	% of ant–seed interactions[a] (N = 134)	Dispersal distance, cm $\bar{x}$ (SD, max)			Root or rock	Litter	Tunnel	Log	Crevice
					Relative frequency (%) drop-site types				
Pachycondyla harpax	54.5	76	(43)	[247]	56	23	9	3	0
P. apicalis	5.9	925	(635)	[2050]	86				14
Pheidole spp.	17.2	0							
Solenopsis geminata	19.4	7.9	(8.5)	[37]	Shallow burial *in situ*				
Wasmannia auropunctata	3.0	4.0	(2.9)	[7]					

[a] Each seed is scored for only one ant–seed interaction; see Methods.

vations were made over a 3-wk period during the fruiting season (September–October 1983) and near fruiting plants. We watched a total of 174 seeds for 90 min and recorded all ant activity at these seeds. There were occasionally visits by several ants to the same seed within the observation period. In these cases we counted the ant having the greatest effect on that seed as the relevant ant–seed interaction.

SEED REMOVAL BY VERTEBRATES AND ANTS.—We quantified removal rates of seeds by simultaneously stocking seed depots with seeds and subsequently censusing these depots. We used two experimental treatments: A, seeds accessible only to ants, and B, seeds accessible to ants and vertebrates. If vertebrates remove seeds, we expected the removal rate in treatment B to be greater than that in treatment A. In treatment A, vertebrates were excluded by surrounding seeds with a 5-sided wire enclosure (14 × 14 × 7 cm; 2-cm mesh) that was closed on top and staked to the ground. In treatment B, to control for the possible negative effects of the wire cage on ant foraging, seeds were surrounded by a 4-sided (14 × 14 × 2.5 cm) short wire fence that was open on top, presenting no barrier to vertebrates. To sample ant and vertebrate activity throughout the local habitat, we set up five pairs of cages at each of four sites where *Calathea* was present. Within each pair, treatment A cages were 1.5 m from treatment B cages. The distance among pairs within sites was at least 4 m. The distance among sites was 80–250 m ($\bar{x}$ = 200). In total there were 40 cages, 20 for each treatment (2 treatments/pair × 5 pairs/site × 4 sites). The experiment was repeated on two nights, one morning, and two afternoons during the peak fruiting period (October 1983). For the night trials, cages were stocked (6 seeds/cage) at dusk (1700–1800 hr), and the next morning we recorded the number and conditions of seeds remaining and the ant species present. For the day trials we stocked cages (6 seeds/cage) at 0800 hr (morning experiment) and at noon (afternoon experiment) and censused each cage after 4 hr. The same data were recorded as in the night experiments. In all, including morning,

afternoon and night trials, 200 groups of seeds, or a total of 1200 seeds, were placed in the cages, including 300 seeds at each of the 4 sites.

RESULTS

DISPERSAL CHARACTERISTICS OF ANT SPECIES.—During the direct observations of ant–seed interactions, we observed five ant species from two subfamilies at seeds of *C. ovandensis* (Table 1), and 77 percent of the seeds (N = 174) were discovered by ants. *P. harpax* was the most frequent ant, accounting for 54 percent of ant–seed interactions, and moved seeds a mean distance of 76 cm (Table 1). *P. apicalis* accounted for only 6 percent of ant–seed interactions, but moved seeds 12 times farther, a mean distance of 925 cm (Table 1). Both these species foraged individually or by tandem running (*sensu* Wilson 1971). Individuals often returned to the seed depots several times to obtain additional seeds. Seeds carried away by *P. harpax* or by *P. apicalis* were primarily taken under rocks or tree roots. Seeds were also deposited (in descending order of frequency) in decomposing litter, soil tunnels, under rotting logs, and into rock crevices (Table 1).

The other three ant species did not move seeds an appreciable distance. *S. geminata, W. auropunctata,* and *Pheidole* spp. recruited large numbers of workers to the seeds. The most frequent of these ants, *Solenopsis,* accounted for 19 percent of ant–seed interactions (Table 1). We occasionally observed interactions between ant species. Individual foragers of *Pachycondyla* spp. were successfully repelled by groups of aggressive *Solenopsis* workers on seeds in 5 of 6 observed encounters. In contrast, *Pachycondyla* spp. were undisturbed by encounters (N = 8) with *Pheidole* spp. No encounters were observed between *Pachycondyla* spp. and *Wasmannia auropunctata,* but other data indicated that *W. auropunctata* lowered the probability of seed removal (see below).

For *Pachycondyla, Solenopsis,* and *Wasmannia,* the microsite to which we tracked the seed was the final point of deposition. In contrast, ant–seed interactions with *Pheidole* were regularly followed by a dispersal event involving

TABLE 2. *Results of exclosure experiments.*

| Time of day | Repli-cate | Percent of seeds removed[a] | | χ^2 |
		Uncaged	Caged	
Night	1	88	88	0.04, n.s.
	2	91	90	0.18, n.s.
Afternoon	1	77.5	86.7	3.43, n.s.
	2	79.2	84.2	1.00, n.s.
Morning	1	91.7	90.1	0.05, n.s.

[a] $N = 120$ for each treatment and replicate.

other ant species. Because many of the undiscovered seeds are eventually dispersed (see below) and because seeds discovered first by *Pheidole* are often later dispersed by other ant species, the distribution in Table 1 does not completely characterize the ultimate dispersal distances of seeds. However, the dispersal characteristics and relative frequencies of *Pachycondyla* spp., *S. geminata,* and *W. auropunctata* would determine in large part the distribution of seed distances. Using these data, we estimated a mean seed dispersal distance of 113 cm ($N = 111$; SD = 264).

Fifty-one percent of seeds were moved beyond 50 cm, the canopy radius of mature reproductives of *C. ovandensis,* suggesting that approximately half the seeds are likely to experience negative interactions with the maternal plant. Only *Pachycondyla* spp. regularly moved seeds beyond the parental canopy (Table 1).

Seed removal by vertebrates and by ants.—Our results from censusing the seed depots indicate that the frequency of seed removal was extremely high (89.2%). There was no significant effect of the exclosure treatment on the frequency of seed removal at night or at any other time of day (Table 2). Thus, vertebrate seed predators did not influence seed removal at Laguna Encantada. Since the cage treatments did not affect seed removal rates, we

combined the data from both treatments to examine spatial and diurnal patterns of seed removal by ants. In this context, each stocking of each seed depot represents a replicate seed trial (6 seeds/trial) irrespective of cage type, and there were 50 seed trials at each of the four sites.

In 18 percent of the seed trials ($N = 200$), we observed either *S. geminata* or *W. auropunctata* (Table 3). These ants recruited large numbers of workers to the seeds and swarmed over the seed arils. *S. geminata* constructed thin (<3 mm) soil tunnels over the seeds and gradually removed the seed arils by bits. *W. auropunctata* did not remove the arils. Generally, neither of these ants moved seeds more than 20 cm away from the initial seed deposition spot. There were significant differences among the four sites in the frequency that seed trials were covered by these ants ($\chi^2 = 22.2$, df = 3, $P < 0.001$), ranging from 0 to 36 percent (Table 3). Seed trials that were covered by *S. geminata* or *W. auropunctata* had a significantly lower proportion of seeds removed (53.7 vs 93.8%) than trials without these species ($\chi^2 = 245$, df = 1, $P < 0.001$) (Table 3). This effect did not differ significantly among the three sites where these ants occurred ($\chi^2 = 4.6$, df = 2, n.s.) (Table 3).

There was significant heterogeneity among sites in the proportion of seeds removed for seed trials that were free of *S. geminata* or *W. auropunctata* ($\chi^2 = 63.5$, df = 3, $P < 0.001$) (Table 3). These differences presumably reflect differences in activity of *Pachycondyla* spp. among sites.

There were significantly fewer seeds removed in the afternoon trials (81.9%) than either the night (88.9%) or morning (91.2%) trials ($\chi^2 = 16.0$, df = 2, $P < 0.001$) (Table 2).

DISCUSSION

The seed removal frequencies we observed were much higher than those reported for temperate forest myrmecochores (Culver & Beattie 1978, Beattie *et al.* 1979,

TABLE 3. *Effects of site and ant activity on seed removal. At each site there were 50 seed trials (6 seeds/trial). Seeds covered by numerous workers of* Solenopsis *or* Wasmannia *were removed significantly less frequently (P < 0.005) than other seeds (54% vs 94%).*

| | Site | | | | |
	1	2	3	4	All sites
Percent of seeds removed					
Trials with *Solenopsis* or *Wasmannia*[a]	67	—	52	47	54
Trials without *Solenopsis* or *Wasmannia*[b]	84	100	98	92	94
All trials[b]	82	100	81	80	86
Percent of seed trials					
With *Solenopsis* or *Wasmannia*[a]	16	0	36	20	

[a] Only three trials were covered by *Wasmannia,* all at site 1.
[b] Significant heterogeneity among sites, $P < 0.01$.

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Heithaus 1981). At our site, *Pachycondyla* spp. were the largest ants attracted to the seeds and were also the only species that regularly moved seeds beyond the radius of the parent plant canopy. The most frequent disperser ant, *P. harpax*, moved the seeds short distances (<1 m), whereas the rarer disperser, *P. apicalis*, moved seeds an order of magnitude farther (≤20 m). Long-distance dispersal of seeds may be important in colonizing new sites. In addition, the difference in dispersal distances between *P. harpax* and *P. apicalis* may influence the genetic structure of populations.

Some ants that use *Calathea* arils for food did not displace seeds away from the parent plant. Activities of these ants reduced the dispersibility of seeds. To the extent that undispersed seeds experience lower survival and germination or result in seedlings with lower growth and survival, the observed small-scale spatial variation in the activities of these ants may contribute to small-scale variation in plant demographic parameters. Two other studies have investigated spatial variation in myrmecochory. Pudlo *et al.* (1980) reported that large-scale spatial differences in ant communities and dispersal quality of ant species had important population consequences for the temperate myrmecochore *Sanguinaria canadensis*. In contrast, Heithaus (1986) found no spatial variation in ant communities or components of dispersal quality among six sites within a West Virginia forest for the temperate myrmecochore *Asarum canadense*.

Escape from seed predation by rodents has been suggested as an important selective force favoring the mutualism between ants and seeds in some habitats (Heithaus *et al.* 1980, O'Dowd & Hay 1980, but see Davidson & Morton 1981). We found no evidence that vertebrate seed predators influenced seed dispersal probabilities of *C. ovandensis*. This result contrasts sharply with data on seed removal rates obtained from experiments similar to ours, *i.e.*, seed-predator exclosures vs no exclosures (Culver & Beattie 1978, Heithaus 1981). The animal most likely to have a negative effect on *Calathea* seeds is the ant *Solenopsis geminata*, which removed seed arils without displacing seeds away from the parent plant and reduced the probability that seeds were removed by *Pachycondyla* spp. This result contrasts with previous conclusions based on laboratory studies of seed-handling that *Solenopsis* was a disperser (Horvitz 1981).

Our results emphasize that the benefits of mutualistic interactions to a particular recipient often vary substantially among mutualists. In *C. ovandensis*, some ants are clearly more effective dispersers than others. For plant–animal mutualisms, variation among animal taxa in the selective effects on plant fitness is probably the rule rather than the exception (Howe 1984, Schemske & Horvitz 1984). Such variation can have important ecological consequences, *e.g.*, the effects on host demography, and may influence the opportunity for coevolutionary specialization between mutualists (Schemske 1983).

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LITERATURE CITED

BEATTIE, A. J. 1983. Distribution of ant-dispersed plants. Sonderbd. naturwiss. Ver. Hamburg 7: 249–270.
———, D. C. CULVER, AND R. J. PUDLO. 1979. Interactions between ants and the diaspores of some common spring flowering herbs in West Virginia. Castanea 44: 177–186.
CULVER, D. C., AND A. J. BEATTIE. 1978. Myrmecochory in viola: dynamics of seed–ant interactions in some West Virginia species. J. Ecol. 66: 53–72.
DAVIDSON, D. W., AND S. R. MORTON. 1981. Myrmecochory in some plants (F. Chenopodiaceae) of the Australian arid zone. Oecologia 50: 357–366.
HEITHAUS, E. R. 1981. Seed predation by rodents on three ant-dispersed plant species. Ecology 62: 136–145.
———. 1986. Potential demographic consequences of variation in dispersal. *In* A. Estrada and T. H. Fleming (Eds.). Symposium on frugivores and seed dispersal. Dr. W. Junk Publishers, The Hague.
———, D. C. CULVER, AND A. J. BEATTIE. 1980. Models of some ant–plant mutualisms. Am. Nat. 116: 347–361.
HORVITZ, C. C. 1980. Seed dispersal and seedling demography of *Calathea microcephala* and *Calathea ovandensis*. Dissertation, Northwestern Univ., Evanston, Illinois, U.S.A.
———. 1981. Analysis of how ant behaviors affect germination in a tropical myrmecochore, *Calathea microcephala* (P. & E.) Koernicke (Marantaceae): microsite selection and aril removal by neotropical ants: *Odontomachus, Pachycondyla* and *Solenopsis* (Formicidae). Oecologia 51: 47–52.
———, AND A. J. BEATTIE. 1980. Ant dispersal of *Calathea* (Marantaceae) seeds by carnivorous ponerines (Formicidae) in a tropical rain forest. Am. J. Bot. 67: 321–326.
———, AND D. W. SCHEMSKE. 1984. Effects of ants and an ant-tended herbivore on seed production of a neotropical herb. Ecology 65: 1369–1378.

Howe, H. F. 1984. Constraints on the evolution of mutualisms. Am. Nat. 123: 764–777.

O'Dowd, D. J., and M. E. Hay. 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. Ecology 61: 531–540.

Pudlo, R. J., A. J. Beattie, and D. C. Culver. 1980. Population consequences of changes in an ant–seed mutualism in *Sanguinaria canadensis*. Oecologia 146: 32–37.

Schemske, D. W. 1983. Limits to specialization and coëvolution in plant–animal mutualisms. In M. H. Nitecki (Ed.). Coevolution, pp. 67–109. Univ. of Chicago Press, Chicago.

———, and C. C. Horvitz. 1984. Variation among floral visitors in pollination: a precondition for mutualism specialization. Science 225: 519–521.

Wilson, E. O. 1971. The insect societies. Cambridge Belknap, Harvard.