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Worker size and seed size selection by harvester ants in a Neotropical forest

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Abstract The rules ants follow when selecting seeds are important both to theories of colony organization and to the shaping of their impact as harvesters. Two Costa Rican forests yielded the most diverse harvester ant assemblages yet studied (41 and 44 ±4 species). I assayed seed size preferences within and between species using milled barley. Seed size selection varied at a number of levels. First, species differed in seed size use: small species mainly carried off small seeds; large species retrieved a broad range of seed sizes. Within species, one-third of those tested yielded inter-colony differences in preferred seed sizes. Finally, workers of polymorphic species often preferred different seeds: five of seven species tested showed significant worker/seed size correlations. Species, colony, and worker level differences are common among harvester ants. Their significance to community organization and colony ergonomics however is hotly debated and requires a better understanding of the dynamics of food limitation. From the plant's perspective, small seeds will be harvested by a wider variety of ants than large seeds.

Key words Size-matching · Ants · Granivory · Body size · Prey selection · Tropics

Introduction

Harvester ants play a major role as dispersers and consumers of seeds (Brown et al. 1979; Beattie 1985; Davidson 1985; Rissing 1986; Byrne and Levey 1993; Levey and Byrne 1993). To predict the impact of ants on plant recruitment we need to understand the patterns of ant distribution and behavior (Horvitz 1980; Horvitz and Schemske 1986; Kaspari 1993).

In a Costa Rican forest, ants are the dominant harvesters of seeds dispersed by frugivorous birds (Loiselle 1990; Kaspari 1993). Depending on the size of the dropping and time of day, the seeds are removed, stored, and consumed by an array of ant species (Byrne and Levey 1993; Kaspari 1993, 1994). A single bird dropping may contain many seed species (Loiselle 1990). Ants crawl over the dropping, choose a seed, and carry it away. What factors govern that choice?

Body size constrains the choices open to organisms (Peters 1983; Calder 1984). In ants, worker/prey size correlations (SCs) are argued to increase colony efficiency within species (Wilson 1978) and partition diets between species (Davidson 1977, 1978; Hölldobler and Wilson 1990). However, the frequent high variance in these SCs, and their patchiness in time and space, have raised doubts as to their importance in colony ergonomics or community structure (Rissing and Pollock 1989; Traniello and Beshers 1991; Schmid-Hempel 1992).

Few studies have explored seed size selection–between species, colonies, and workers–for a harvester ant assemblage. This is especially true for the tropics, where the makeup and behavior of harvester ant assemblages is poorly known. In this paper, (1) I describe the composition of the harvester ant fauna of two tropical forests; (2) I test for differences in seed size selection between and within species; and (3) I explore how body size may cause these differences.

Materials and methods

This study was performed from May through July 1990 at the Estacion Biológica La Selva (10 25′ N, 83 59′ W) on the Caribbean slope of Costa Rica. Holdridge classifies La Selva as a tropical wet forest (Holdridge et al. 1971; see Hartshorn 1983 for a further site description). May–July constitutes the early rainy season at La Selva.

I studied the ant assemblages in two forests, both recovering from disturbance, and on the same alluvial soil. The two forests were approximately 0.5 km apart. The "Closed Forest" (Sendero Atajo) was abandoned as cattle pasture 17 years before. This site had a closed canopy and a thick blanket of understory palms. The

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Table 1 Ant species collected at stations baited with barley particles in Closed (17 years old) and Open (7 years old) forest at La Selva, Costa Rica. [*OBS* The number of observations of the species, *%OBS* percentage of these observations represented by the species, *STA* the number of stations (of 30) at which the species was found]. Names in *parentheses* used in Fig. 1. Classification is given in terms of **Subfamily,** tribe and *Genus species*

Classification	Closed Forest			Open Forest		
	OBS	%OBS	STA	OBS	%OBS	STA
Ponerinae						
Ectatommini	**23**	**3**		**64**	**9**	
Ectatomma ruidum (ecru)	23	3.2	15	64	9.2	22
Myrmicinae						
Pheidolini	**231**	**33**		**118**	**17**	
Pheidole ANN	2	0.3	1	1	0.1	1
P. BI				1	0.1	1
P. CEL (pcel)	20	2.8	8	1	0.1	1
P. CU	6	0.8	4	3	0.4	3
P. DO	1	0.1	1			
P. ERE	13	1.8	4			
P. FLA (pfla)	83	11.6	17	10	1.4	8
P. IN (pint)	7	1.0	5	4	0.6	3
P. MS	3	0.4	3			
P. MI	2	0.3	2			
P. NEB (pneb)	26	3.6	11	8	1.2	6
P. NGA	2	0.3	2			
P. RUI				3	0.4	2
P. RUG	6	0.8	3	4	0.6	1
P. RA				8	1.2	6
P. RES	1	0.1	1			
P. SIM (psim)	16	2.2	10			
P. SP (pspe)	23	3.2	11	34	4.9	17
P. SS (pssp)				15	2.2	7
P. SU	1	0.1	1			
P. SUB				5	0.7	5
Aphaenogaster araneoides (apfe)	15	2.1	13	20	2.9	12
Crematogastrini	**1**	**0.1**		**4**	**0.5**	
Crematogaster HA	1	0.1	1	1	0.1	1
C. KA	1	0.1	1	2	0.3	1
Solenopsidini	**113**	**16**		**73**	**11**	
Solenopsis (Diplorhoptrum) CO (dico)	19	2.7	7	9	1.3	5
S. PL	5	0.7	5	8	1.2	5
S. PO (dipo)	13	1.8	9	2	0.3	2
S. RP (dirp)	32	4.5	9	7	1.0	5
S. SO (diso)	21	2.9	5	15	2.2	9
S. SP	1	0.1	1			
Solenopsis geminata (soge)	22	3.1	10	31	4.5	13
Blepharidattini	**29**	**4.1**		**33**	**4.8**	
Wasmannia auropunctata (waau)	29	4.1	8	33	4.8	12
Attini	**311**	**43**		**399**	**58**	
Acromyrmex octospinosus (acoc)				19	2.7	3
Apterostigma GR (apgr)	19	2.7	5	35	5.1	12
A. MI				1	0.1	1
Atta cephalotes (atce)	17	2.4	10	42	6.1	17
Cyphomyrmex cornutus (cyco)	3	0.4	3	17	2.5	11
Cy. minutus (cymi)	3	0.4	3	39	5.6	18
Cy. rimosus				2	0.3	2
Sericomyrmex aztecus (seaz)	177	24.7	21	175	25.3	21
Trachymyrmex cornetzi (trco)	57	8.0	16	12	1.7	8
T. IN (trin)	7	1.0	4			
T. saussurei (trsa)	28	3.9	8	57	8.2	11
Formicinae	7	1		1	0.1	
Lasiini	**6**	**0.9**	**5**	**1**	**0.1**	**1**
Paratrechina steinheili	4	0.6	3	1	0.1	1
Pa. BY	2	0.3	2			
Total number of species	38			35		

“Open Forest” (Sendero Chanchera) was abandoned as a cacao grove 7 years before, had a broken canopy, and contained patches of grass and ferns.

In each forest, I set up transects composed of 30 sampling stations, 10 m apart and 2 m off-trail. This distance appears adequate to maintain independent discoveries by different ant colonies, since colony densities typically exceeded 4 nests/m^2, and ants rarely walked >1 m to the nest from a station (Byrne and Levey 1993; Kaspari 1993).

To generate different seed sizes, I used milled barley. By doing so one can vary seed size while keeping particles nutritionally homogeneous. Natural seeds of a variety of sizes are taken by these ants (Levey and Byrne 1993; Kaspari 1993, in preparation).

I milled pearl barley into four median particle sizes–0.35, 0.75, 1.2 and 1.7 mm-using Taylor sieves (total range: <0.35–2.2 mm). I used this size range for three reasons. First, it was close to that used by Davidson (1977) in her studies of the harvesting ants of North America. Second, in pilot experiments, larger pieces of barley (cracked and whole, minimum diameter 2.8–4.0 mm) were masticated *in situ*, but rarely carried off by ants. Finally, the particles represented 38% of the seed size range (and likely more of the total seed rain) from 271 bird-dispersed plant species at La Selva (B. Loiselle, unpublished data).

I placed milled barley baits on a platform consisting of two glass microscope slides, taped together below and scored with sandpaper above. Over each station was a foil and hardware cloth shelter to keep out light rain. Iarranged the four particle sizes in piles of equal circumference (approx. 1 cm), 2 mm apart. The resulting seed pile is similar to a large bird dropping without pulp. Upon arrival, ants typically crawled over and around seed baits. Since diameter of a seed clump–an important determinant of encounter rate (Kaspari 1993)–was held constant for all four seed sizes, the resulting seed selection is thus a test of ant preference for different sizes of seeds. Replenishing seeds kept their availabilities roughly equal over the course of the experiment.

I set the seeds out at dawn (approx. 0600 hours) and at midday (approx. 1200 hours). This corresponds to the coolest and warmest times of day at La Selva (Kaspari 1994). Starting times were approximate since dawn was often delayed by heavy cloud cover, and rains sometimes postponed or interrupted transect runs for up to 45 min. I began a day's observations by dispensing seeds at each station. Each station was then visited in sequence (beginning at either end of the transect equally) for 2 min. I collected ants harvesting seeds and placed them in a vial unique for that station visit and particle size. I ran both transects eight times: four from 0600 h to 1100 hours, four from 1200 h to 1700 hours. The first four runs included three station visits per day. The remaining runs included two station visits.

Ants were sorted to species or morphospecies. Many species in this study are unnamed or unidentified: these are referred to by genus plus a two-letter code. Vouchers are deposited at the Harvard Museum of Comparative Zoology and the Los Angeles County Museum.

I measured maximum head width of each species to 0.01 mm with an ocular micrometer mounted on a dissecting scope. I measured eight individuals, randomly selected from the collection, calculating the mean and coefficient of variation of head width. A total of 23 species met the minimum requirement of ten seeds carried away in a forest. I measured head width, thorax length and width, and hind femur length of these ant species, as described above. All measures were tightly correlated (Kaspari 1992) and I have used head width in the following analysis.

I studied within-species SCs using *Solenopsis geminata (So. geminata)* and species from the tribe Attini. These ants show varying degrees of size polymorphism (Weber 1972; Wilson 1978) and were the most size-variable members of these assemblages (see below). Because sample sizes varied across species, I only analyzed those with at least ten workers sampled per particle size. I measured head widths for up to 30 ants for each particle class, randomly chosen from those collected at baits. Within-species SCs were analyzed with linear regression.

Results

The harvester ant assemblage of La Selva, Costa Rica

Ants were active in both forests, occurring at 83% of all bait observations. Altogether, 46 species of ants harvested seed particles, including 3 subfamilies, 7 tribes, and 13 genera. I recorded 38 species in the Closed Forest and 35 species in the Open Forest (Table 1). Jackknifing (Heltshe and Forrester 1983) yielded estimates of 44 and 41 species (±4.4) in Open and Closed Forests; not statistically different. The two forests shared only 59% of their species (Table 1).

Species richness at each station was high and heterogeneous, with 4–17 (mean=8.6) ant species/station in the Closed Forest and 5–18 (mean=8.5) ant species/station in the Open Forest. The most common species [*Sericomyrmex aztecus (Se. aztecus)* in the Closed Forest *Ectatomma ruidum (E. ruidum)* in the Open Forest] were found at over two-thirds of the stations (Table 1). Species occurred at 1–21 stations (mean=6.0) in the Closed forest and 1–22 stations (mean=6.1) in the Open Forest.

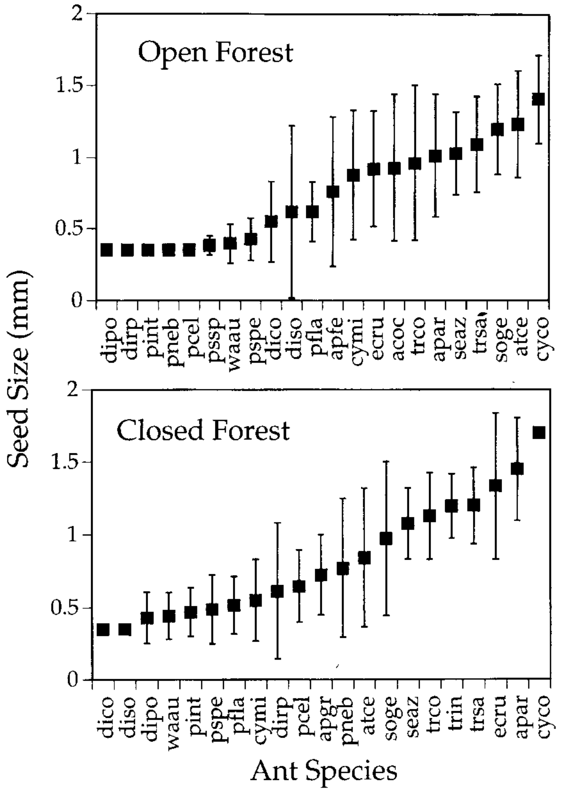


Fig. 1 Mean particle size harvested (±1 standard error) differs among ant species from two forests of La Selva, Costa Rica [acoc *Acromyrmex octospinosus*, apar, apfe *Aphaenogaster araneoides*, apgr *Apterostigma* GR, atce *Atta cephalotes*, cyco *Cyphomyrmex cornutus*, cymi *Cy. minuta*, dico *Solenopsis (Diplorhoptrum)*CO, dipo *D.* PO, dirp *D.* RP, diso *D.* SO, ecru *Ectatomma ruidum*, pcel *Pheidole* CEL, pfla *P.* FLA, pint *P.* IN, pneb *P.* NEB, psim *P.* SIM, pspe *P.* SP, pssp *P.* SS, seaz *Sericomyrmex aztecus*, soge *Solenopsis geminata*, trco *Trachymyrmex cornetzi*, trin *T.* IN, trsa *T. saussurei*, waau *Wasmannia auropunctata*]

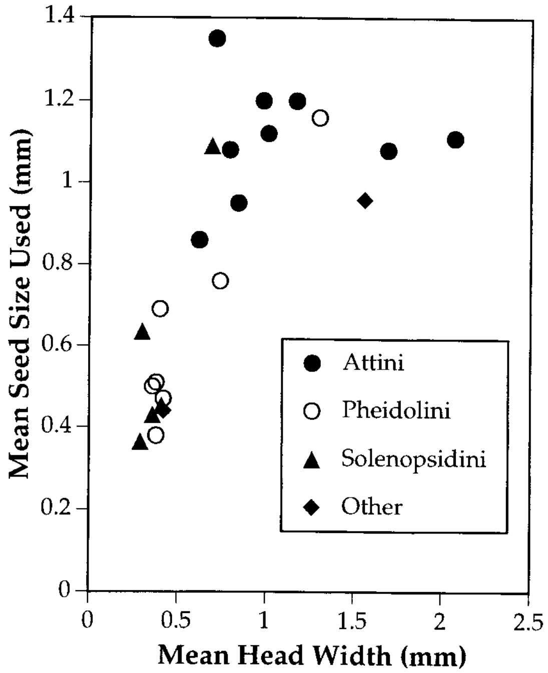


Fig. 2 The correlation between mean seed size and species mean size is positive and saturating. Symbols represent different tribes

The harvester ants at La Selva were a subset of the ground fauna. Many ant genera common on the forest floor (e.g. the tribe Dacetini, and virtually all the Ponerines) were never recorded carrying away seed baits. Likewise, harvesters are not necessarily obligate granivores (see also Wheeler 1926; Morton and Davidson 1988). For example, the Attini, the fungus-growing ants, harvested the most seeds in both forests and included two herbivores: the leaf cutters *Atta cephalotes (At. cephalotes)* and *Acromyrmex octospinosus (Ac. octospinosus).* Nests of *Apterostigma* GR (*A.* GR) and *Cyphomyrmex minuta (Cy. minuta)* contained seeds with fungus gardens (pers. obs.).

Here I focus on the 23 species removing more than ten particles from bait stations. These species accounted for 96% of seeds removed in the Closed Forest and 98% in the Open Forest. The attine *Se. aztecus* removed nearly half the seeds in both forests. The tropical fire ant *So. geminata* was active in both forests, as was the only granivorous ponerine, the generalist *E. ruidum.* The genera *Pheidole (P.)* and *Solenopsis (So.)* [subgenus *Diplorhoptrum*] were speciose but less active as seed harvesters.

Seed size use between species and between colonies

Ant species harvested different seed sizes in both forests. Since most ants rarely traveled >1 m to a bait station, I treated each station as an independent sample of a species' mean seed size preference. The 20 common ant species from the Closed Forest showed mean preferences ranging from 0.35 mm to 1.7 mm [Kruskal Wallis (KW) $X^2_{20,127}=274$, $P<0.0001$, Fig. 1]. The 21 common species from the Open Forest ranged from a mean preference of 0.35 to 1.41 mm (KW $X^2_{21,149}=139$, $P<0.0001$, Fig. 1).

Some species differed in seed size preference *between* stations. To increase statistical power I compared mean seed sizes for the 13 species removing most of the seed particles from both forests, and eliminated stations for each species where only one seed was removed. Four species differed significantly between stations in seed size preference [*At. cephalotes* KW $X^2_{8,86}=15$, $P=0.05$, *P. NEB* KW $X^2_{3,39}=15$, $P=0.002$, *Se. aztecus* KW $X^2_{34,1301}=66$, $P=0.0007$, *T. saussurei* KW $X^2_{10,385}=23$, $P=0.01$), while another three species *(P. SP, So. geminata,* and *P. CEL)*] differed between stations at $P<0.10$. Colonies of half the species thus differed at least marginally in seed size preference.

Body size as a factor promoting size preferences among species

Mean head width of species in this study varied an order of magnitude in linear size, from 0.25 mm for some *Solenopsis (Diplorhoptrum)* to 2.2 mm for *Ac. octospinosus* (Fig. 2). To study overall seed use by species, I calculated a grand seed size mean for each species. Workers from the Attini were largest and most variable (head width 0.7–2.1 mm), followed by the Pheidolini (minor workers only, 0.36–1.2 mm) with the Solenopsidini the

Table 2 The ant/seed size correlation differs among three tribes of ants at La Selva, Costa Rica. Separate linear regressions show that the Pheidolini and Solenopsidini, but not the Attini, have significant, positive size correlations (*df* Degrees of freedom, *SS*=Sum of Squares)

Source	Parameter			
	df	Type III SS	F	Pr>F
Head Width	1	0.48	25.06	0.0002
Tribe	2	0.73	18.97	0.0001
Interaction	2	0.44	11.35	0.0010
Error	15	0.29		

Tribe	Parameter							
	n	Intercept	Slope	Model SS	Error SS	F	Pr>F	r^2
Attini	9	1.07	0.03	0.0016	0.1621	0.07	0.80	0.01
Pheidolini	7	0.23	0.71	0.3714	0.0489	37.96	0.00	0.88
Solenopsidini	5	0.06	1.58	0.2693	0.0776	10.40	0.05	0.78

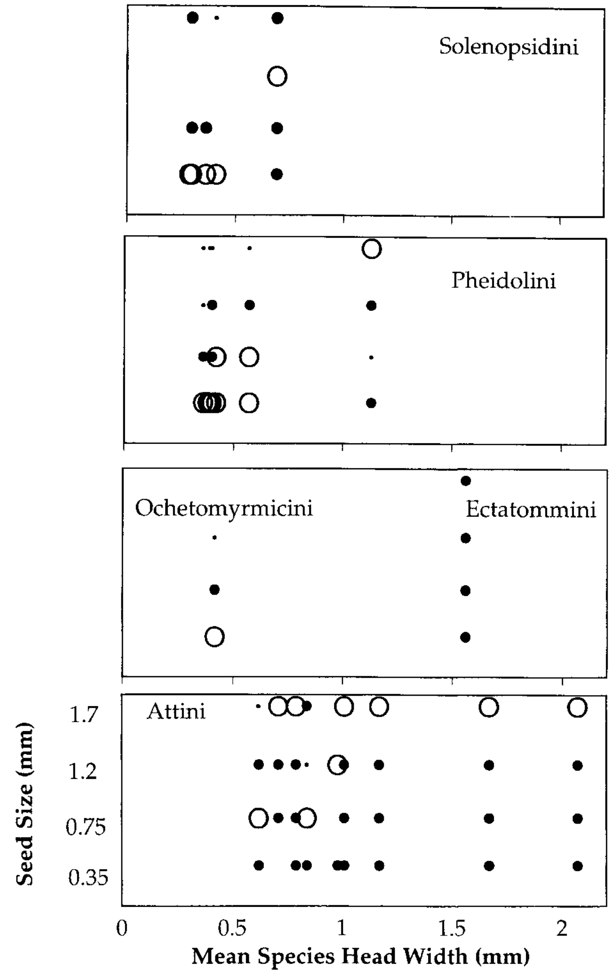


Fig. 3 The range of seed sizes used by the 23 common harvester ants at La Selva Costa Rica tends to increase with body size. Each set of 4 vertically placed *symbols* represents a species' use of the 4 particle sizes offered. *Small dots* represent <15% use, *mid-size dots* represent 15–30% use, *circles* represent >30% use

smallest and least variable (0.28–0.62 mm head width). An analysis of covariance shows that the three common tribes differed both in the slope and the intercept of their SCs (Table 2, $P<0.001$). Species from both the Solenopsidini ($r^2=0.78$, $P<0.05$) and the Pheidolini ($r^2=0.88$, $P<0.00$) but not the Attini ($r^2=0.01$, $P<0.80$, Table 2) showed significant SCs.

Collectively, Fig. 2 suggests a curvilinear relationship between seed size and body size (although it may be driven by the three largest species). This would result from the greater diet breadth of larger ant species (Fig. 3). When given a choice among four seed sizes, all but one of the small ants (head widths <0.5 mm) preferred the smallest seeds (Fig. 3) and only occasionally dragged large seeds off the platform. With increasing body size, ant species typically preferred the largest seed but retained smaller seeds in quantity. For example, among the five largest ant species, one *(E. ruidum)* was an opportunist taking seeds in proportion to their availability. The other four all preferred the largest seed size, but with the three smaller seeds making up 58% (*Aphaenogaster araneoides*), 61% (*T. saussureri*), 63% *(Ac. octospinosa)* and 64% (*At. cephalotes*) of the diet. For all species but *Cy. cornutus* 15% or more of the seeds chosen were the smallest seeds. Large species did not drop small seeds from the diet even when large seeds were readily available.

Body size as a factor promoting size preferences among workers

When seeds were locally abundant, five of seven polymorphic species tested showed positive SCs (Table 3, Fig. 4). Workers of each size class overlapped greatly in the size of particle collected, yielding regression coefficients (r^2) from 0.06 to 0.19. Significant SCs were not a simple function of polymorphism, since two of the strongest SCs (r^2 values=0.16, 0.19) came from species with the least size variable workers (CV of head width=6, Fig. 4).

Discussion

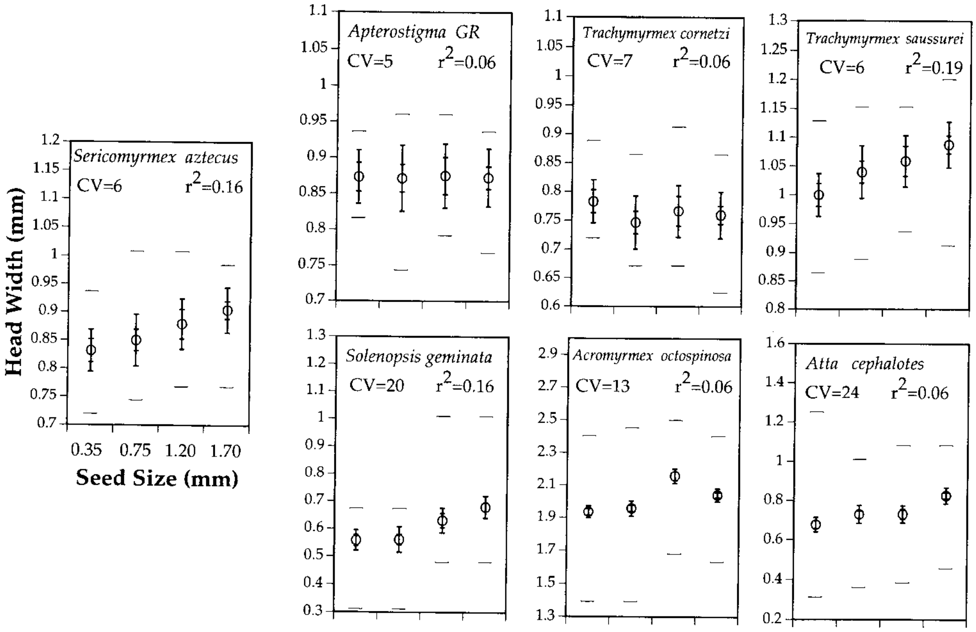
Ants are the primary predators and dispersers of small seeds in a variety of habitats (Beattie 1985; Horvitz and Schemske 1986; Rissing 1986; Roberts and Heithaus 1986; Levey and Byrne 1993; Kaspari 1993). In two Neotropical forests at La Selva Costa Rica, there were more harvester ant genera (13 versus 6 and 5) and species (42 versus 9 and 5) than any assemblage yet reported from the harvester ant assemblages of Australia and North America (Davidson 1977; Morton and Davidson 1988).

Seeds falling to the forest floor at La Selva thus find a diverse set of potential consumers/dispersers. Which seed(s) are chosen depends upon the species of ant, in

Table 3 Five of seven polymorphic species (indicated by asterisk) tested show significant, positive correlations between seed size and mean head width of workers

Species	Parameter						
	n	Intercept	Slope	Model SS	Error SS	F	Pr>F
Apterostigma GR	73	0.872	0.000	0.000	0.124	0.0	0.991
Trachymyrmex cornetzi	75	0.768	−0.006	0.001	0.188	0.3	0.583
Trachymyrmex saussurei	107	0.987	0.060	0.087	0.390	23.5	0.0001*
Sericomyrmex aztecus	120	0.811	0.054	0.090	0.472	22.5	0.0001*
Solenopsis geminata	80	0.511	0.098	0.196	1.020	15.0	0.0002*
Acromyrmex octospinosa	72	1.896	0.127	0.264	4.375	4.2	0.044*
Atta cephalotes	117	0.639	0.100	0.297	4.107	8.3	0.005*

Fig. 4 Of seven species tested, five show significant ant/seed size correlations. *Error bars* are standard deviations and 95% confidence intervals, *brackets* represent maximum and minimum head widths of ants using each size particle. (*CV* Coefficient of variation of head width for that species)



some cases the particular colony, and in polymorphic species, the size of the worker. I treat each in turn.

Species differences

In both the closed and open canopy forests at La Selva, species took different seed sizes (Fig. 1) and the SC was positive (Fig. 2). Seeds larger than those in this study were rarely carried off by ants in the pilot experiment. Thus the relatively small seed size values from the largest species in Fig. 2 were not likely an artifact of the limited range of seed sizes in this study. Rather, the larger ants, while preferring large seeds, still included small seeds as 50% of their diet (Fig. 3). Other factors may have contributed to broad diets of large species. The attines *Cy. cornutus* and *Cy. minutus* were both adept at bundling small seeds (see also Johnson 1991). *E. ruidum,* a monomorphic opportunist, grabbed the first seed it found and walked off.

Species carry away seeds of different sizes in many assemblages (Davidson 1977; Morton and Davidson 1988). Do these differences enhance species coexistence by decreasing diet overlap? At La Selva, probably not, since colony growth and reproduction are not density dependent (Kaspari in press).

Colony differences

The colonies of one-third of the common species in this study were carrying away different size seeds from identical baits. Between-colony variation in foraging is common in harvester ants (Davidson 1977, 1978; Rissing 1987). Its occurrence is humbling to community ecologists focusing on species means. Its causes are little explored.

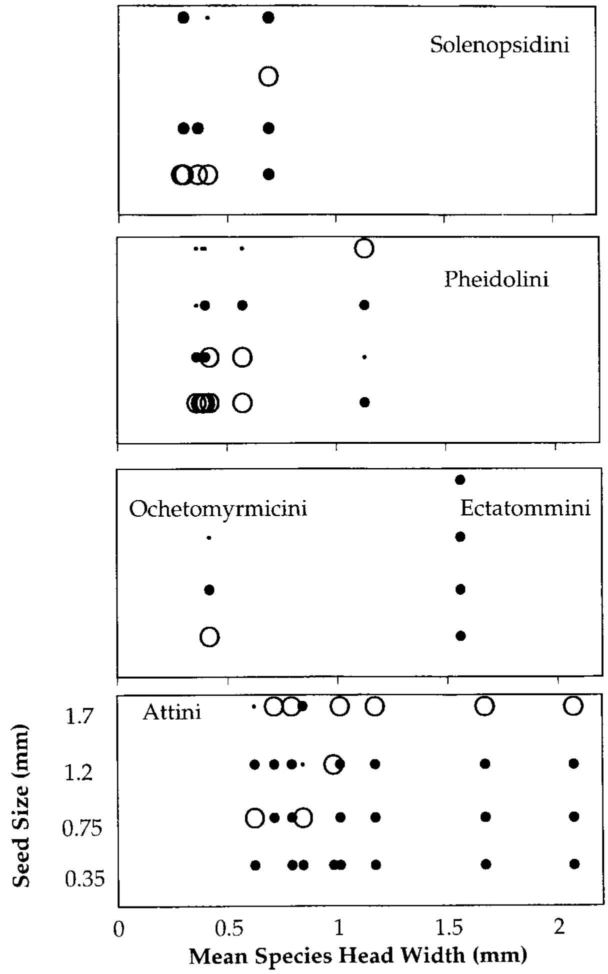
Two factors may contribute to between-colony variation in seed size selection. Colonies may vary in the size of their worker force. Worker size tends to increase with colony age (Porter and Tschinkel 1985; Wilson 1985) and vary with production constraints (Rissing 1987; Tschinkel 1988). Differences in seed size selection may also result from interspecific interactions at baits, though these were rare at La Selva (Kaspari 1993).

Worker differences: size correlations and colony ergonomics

The functional significance of worker size variation within ant colonies has long been pondered (Wheeler 1907; Wilson 1953, 1978; Wheeler 1991). Nowhere has study led to such divergent results as among harvester ants. So far, in nine harvester ant species, worker body size accounts for 1–25% of the variance in prey size (this study, Davidson 1978; Rissing and Pollock 1989; Feener and Lighton 1991; Traniello and Beshers 1991). Other polymorphic species show much stronger SCs [*At. cephalotes,* Wetterer 1990b; *Eciton burchelli (Ec. burchelli),* Franks 1986]. What accounts for the divergence in SCs among species, and sometimes within species (*Messor pergandei,* Davidson 1978; Rissing and Pollock 1989; Feener and Lighton 1991)?

One can envision three models for SCs in polymorphic harvester ant species. Each assumes a size limit–the maximum size seed an ant can lift and carry–that increases with ant size (Fig. 5). If a narrow range of plants are setting seed, one size of seed is nutritionally superior to the rest, or the range of available seeds never taxes the species' size limit, then all ants may take the same range of seed sizes. This produces a weak to non-existent SC, as is found for two of five species at La Selva (Fig. 5A).

In contrast, a range of palatable seed sizes may tax the size limit of a colony's workforce. If workers pick up any seed they can carry, this will produce a scatterplot of seed/worker size that mimics a right triangle (Fig. 5B) and yields a weak positive SC.



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When seeds were locally abundant, five of seven polymorphic species tested showed positive SCs (Table 3, Fig. 4). Workers of each size class overlapped greatly in the size of particle collected, yielding regression coefficients (r^2) from 0.06 to 0.19. Significant SCs were not a simple function of polymorphism, since two of the strongest SCs (r^2 values=0.16, 0.19) came from species with the least size variable workers (CV of head width=6, Fig. 4).

Discussion

Ants are the primary predators and dispersers of small seeds in a variety of habitats (Beattie 1985; Horvitz and Schemske 1986; Rissing 1986; Roberts and Heithaus 1986; Levey and Byrne 1993; Kaspari 1993). In two Neotropical forests at La Selva Costa Rica, there were more harvester ant genera (13 versus 6 and 5) and species (42 versus 9 and 5) than any assemblage yet reported from the harvester ant assemblages of Australia and North America (Davidson 1977; Morton and Davidson 1988).

Seeds falling to the forest floor at La Selva thus find a diverse set of potential consumers/dispersers. Which seed(s) are chosen depends upon the species of ant, in

Table 3 Five of seven polymorphic species (indicated by asterisk) tested show significant, positive correlations between seed size and mean head width of workers

Species	Parameter						
	n	Intercept	Slope	Model SS	Error SS	F	Pr>F
Apterostigma GR	73	0.872	0.000	0.000	0.124	0.0	0.991
Trachymyrmex cornetzi	75	0.768	−0.006	0.001	0.188	0.3	0.583
Trachymyrmex saussurei	107	0.987	0.060	0.087	0.390	23.5	0.0001*
Sericomyrmex aztecus	120	0.811	0.054	0.090	0.472	22.5	0.0001*
Solenopsis geminata	80	0.511	0.098	0.196	1.020	15.0	0.0002*
Acromyrmex octospinosa	72	1.896	0.127	0.264	4.375	4.2	0.044*
Atta cephalotes	117	0.639	0.100	0.297	4.107	8.3	0.005*

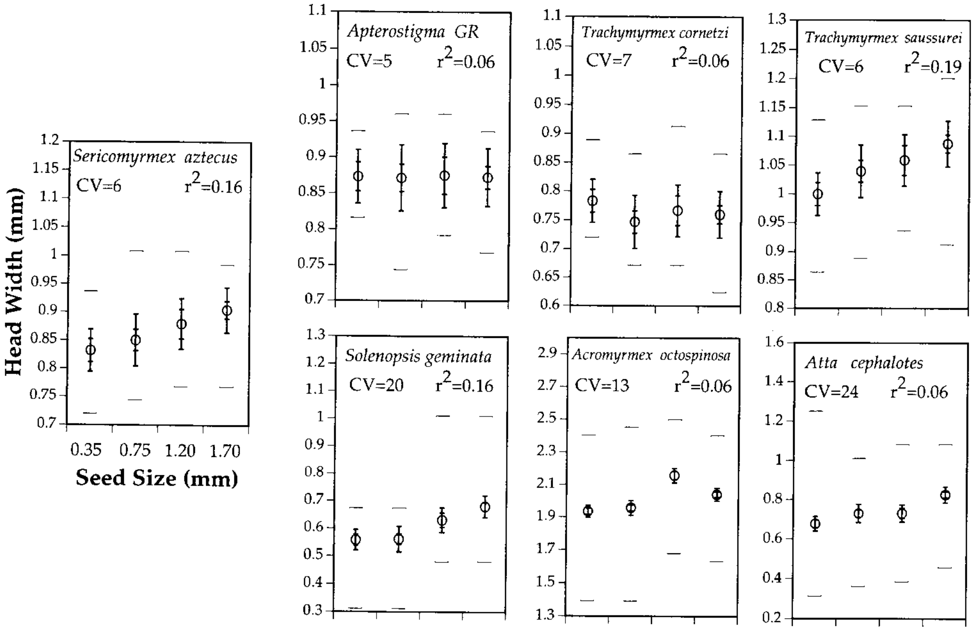

Fig. 4 Of seven species tested, five show significant ant/seed size correlations. *Error bars* are standard deviations and 95% confidence intervals, *brackets* represent maximum and minimum head widths of ants using each size particle. (*CV* Coefficient of variation of head width for that species)

some cases the particular colony, and in polymorphic species, the size of the worker. I treat each in turn.

Species differences

In both the closed and open canopy forests at La Selva, species took different seed sizes (Fig. 1) and the SC was positive (Fig. 2). Seeds larger than those in this study were rarely carried off by ants in the pilot experiment. Thus the relatively small seed size values from the largest species in Fig. 2 were not likely an artifact of the limited range of seed sizes in this study. Rather, the larger ants, while preferring large seeds, still included small seeds as 50% of their diet (Fig. 3). Other factors may have contributed to broad diets of large species. The attines *Cy. cornutus* and *Cy. minutus* were both adept at bundling small seeds (see also Johnson 1991). *E. ruidum,* a monomorphic opportunist, grabbed the first seed it found and walked off.

Species carry away seeds of different sizes in many assemblages (Davidson 1977; Morton and Davidson 1988). Do these differences enhance species coexistence by decreasing diet overlap? At La Selva, probably not, since colony growth and reproduction are not density dependent (Kaspari in press).

Colony differences

The colonies of one-third of the common species in this study were carrying away different size seeds from identical baits. Between-colony variation in foraging is common in harvester ants (Davidson 1977, 1978; Rissing 1987). Its occurrence is humbling to community ecologists focusing on species means. Its causes are little explored.

Two factors may contribute to between-colony variation in seed size selection. Colonies may vary in the size of their worker force. Worker size tends to increase with colony age (Porter and Tschinkel 1985; Wilson 1985) and vary with production constraints (Rissing 1987; Tschinkel 1988). Differences in seed size selection may also result from interspecific interactions at baits, though these were rare at La Selva (Kaspari 1993).

Worker differences: size correlations and colony ergonomics

The functional significance of worker size variation within ant colonies has long been pondered (Wheeler 1907; Wilson 1953, 1978; Wheeler 1991). Nowhere has study led to such divergent results as among harvester ants. So far, in nine harvester ant species, worker body size accounts for 1–25% of the variance in prey size (this study, Davidson 1978; Rissing and Pollock 1989; Feener and Lighton 1991; Traniello and Beshers 1991). Other polymorphic species show much stronger SCs [*At. cephalotes,* Wetterer 1990b; *Eciton burchelli (Ec. burchelli),* Franks 1986]. What accounts for the divergence in SCs among species, and sometimes within species (*Messor pergandei,* Davidson 1978; Rissing and Pollock 1989; Feener and Lighton 1991)?

One can envision three models for SCs in polymorphic harvester ant species. Each assumes a size limit–the maximum size seed an ant can lift and carry–that increases with ant size (Fig. 5). If a narrow range of plants are setting seed, one size of seed is nutritionally superior to the rest, or the range of available seeds never taxes the species' size limit, then all ants may take the same range of seed sizes. This produces a weak to non-existent SC, as is found for two of five species at La Selva (Fig. 5A).

In contrast, a range of palatable seed sizes may tax the size limit of a colony's workforce. If workers pick up any seed they can carry, this will produce a scatterplot of seed/worker size that mimics a right triangle (Fig. 5B) and yields a weak positive SC.

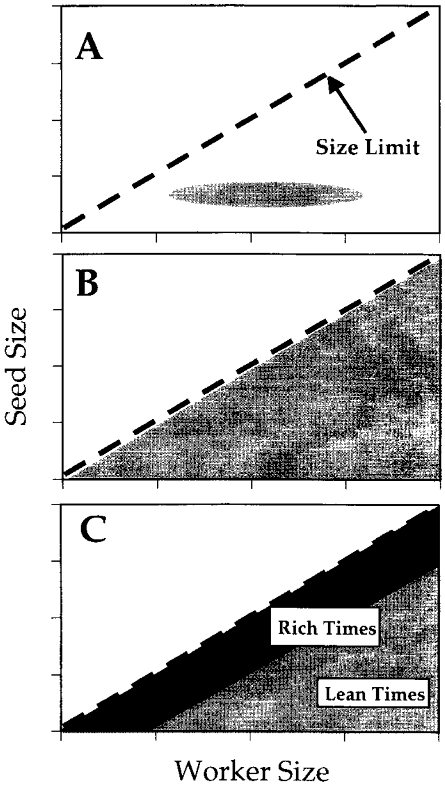

Fig. 5A–C Three models of the relation between worker polymorphism and seed size selection by ants. *Gray clouds* represent seed selection scatterplots. There is always an upper limit to the capacity of a worker to carry a seed. **A** Where a narrow range of seeds is available (or nutritionally available), the upper limit is never taxed. **B** When a range of seed sizes is available, then larger workers should harvest an increasing range of seeds. **C** When the optimum seed size increases with body size (and food intake is limiting) then diets should expand when food is rare, and contract when food is common (i.e. size matching). Note that **B** and **C** make the same prediction when food is scarce

Finally, seed intake may limit colony growth and reproduction, and the seed size that yields the highest rate of energy return may increase with worker size. If so, the optimal diet model predicts that workers will ignore smaller seeds if larger seeds closer to the optimum are sufficiently abundant (Fig. 5C, MacArthur and Pianka 1966; Stephens and Krebs 1986). This best represents the ideas of Wilson (1978) on the adaptiveness of colony polymorphism.

The jury is still out on this adaptive model of size variation in harvester ants (Schmid-Hempel 1992). To date, there have been: (1) few scatterplots of seed size against body size, (2) no tests for tighter SCs when large profitable seeds are more abundant, and (3) few convincing tests that food limits ant populations. Tests of food limitation for any ant species are rare; food supplements failed to increase alate production (at $P<0.05$) in two desert harvester ant species (Ryti and Case 1988; Munger 1992). At La Selva, litter ants appear to be less constrained by food than by nest site availability and frequent disturbance [in review, Kaspari (in press); Kaspari and Byrne (1995)].

The importance of tailoring your load: cutters can be choosers

In this study, a range of seed sizes mimicking a frugivorous bird dropping yielded weak SCs (r^2 values=0.06–0.19). This is not the case for studies of the leaf cutting ant *At. cephalotes* (r^2=46%, Wetterer 1990b) and the army ant *Ec. burchelli,* (r^2=52%, Franks 1986). Why the difference?

One answer is that *At. cephalotes* (cutting leaves) and *Ec. burchelli* (shredding animals) can tailor their load by carving it themselves, perhaps better matching loads to their own capacity. If so, we should expect weak SCs when these species are provided pre-cut prey than when they cut their own. Two leaf-cutters show precisely this pattern. *At. cephalotes* has a weaker SC matching pre-cut seeds (r^2=0.07, this study) and pre-cut leaves (0.09–0.14, Wetterer 1990a) than cutting its own leaf fragments (0.46, Wetterer 1990b). Similarly, *Ac. octospinosus* shows an SC with an r^2=0.06 when collecting seeds, but a stronger r^2 of 0.16 when observed both cutting and collecting bits of vegetation (Wetterer 1991).

Seed size and ant/plant interactions

Many factors undoubtedly contribute to the decision of a worker ant to carry off a seed and recruit her nestmates, including the number of seeds in the dropping (Kaspari 1993), and their nutritional quality (including the presence of elaiosomes Kelrick et al. 1986; Levey and Byrne 1993; Horvitz and Schemske 1994). This study shows that when seeds are provided in size batches similar to those encountered in natural frugivore droppings (Loiselle 1990; Kaspari 1993) the seed's size strongly influences the number and size of ant species that carry it off. These results have implications for the study of plant/ant interactions in the tropics.

First, large seeds will likely be preyed upon and/or dispersed by a smaller suite of ants than small seeds. Studies of ant dispersers/consumers of three Neotropical plants reported five species attracted to the 5-mm-long *Calathea* seed (Horvitz and Schemske 1986) compared to 14 and 22 species carrying off 2-mm seeds from *Miconia nervosa* (M.M. Byrne personal communication) and *M. affinis* (Kaspari 1993). Thus the hypothesis that plants may escape harvesting by down-sizing their seeds (Janzen 1971; Foster 1986) may not always be true, at least for this size range of seeds where ants are dominant, thorough harvesters (Kaspari 1993).

Finally, a seed's size may help determine its final microsite. Most large ants in this study (including all the common polymorphic species in Fig. 4) carry their seeds below ground. In contrast, most of the small ants at La Selva nest in the twigs and between leaves of the forest litter. Seeds transported to (and often abandoned in) litter nests may survive better there than in the soil (Byrne and Levey 1993; Kaspari 1993; Levey and Byrne 1993). Further studies of ant plant interactions may benefit from a focus on seed size.

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