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FORAGING IN SEED-HARVESTER ANTS *POGONOMYRMEX* SPP.[1]

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Abstract. *Pogonomyrmex rugosus*, a group forager, foraged preferentially on seeds of plant species which shed large quantities of seeds at 1 time. *Pogonomyrmex desertorum*, an individual forager took seeds in relation to their availability but concentrated on grass seeds late in the growing season. *Pogonomyrmex californicus* selected seed species which allowed it to avoid contact with its congeners. During a dry year, *P. rugosus* exhibited little selectivity, supporting the idea that selectivity should be decreased under conditions of low food abundance. *Pogonomyrmex* spp. removed a significant fraction of the seed production of only 1 species, *Boutleoua barbata*. It is suggested that *Pogonomyrmex* foraging may affect the relative abundance of plant species.

Key words: Competition; harvester ants; New Mexico; Pogonomyrmex *spp.; seed production; seed selection.*

INTRODUCTION

Recently, there has been considerable interest in seeds and seed consumers in desert ecosystems. Seeds are important resources in deserts because they represent the potential vegetation (primarily annual grasses and forbs) which can flourish only during those brief periods when there is sufficient soil moisture and temperature conditions to assure growth. At the end of growth pulses and in periods between pulses, seed consumers remove an unknown fraction of the potential seed reserves. The density, species composition, and relative abundance of annuals should reflect those seeds which escape predation.

In North American deserts, ants and rodents have been suggested as the principal seed consumers (Brown et al. 1975, Whitford and Ettershank 1975, Davidson 1976, Brown and Davidson 1977). None of these studies report the relationship between seed production and utilization by consumers.

I know of only 1 study (Tevis 1958) in which the losses of seeds to ants was compared with seed production. Tevis estimated that *Veromessor pergandei* harvested only 1% of the seeds produced in a Mojave Desert area but suggested that *Veromessor* may influence the abundance of certain plant species by selective foraging on seeds. Using an indirect technique, Rogers (1974) estimated that *Pogonomyrmex occidentalis* removed 2% of the seed biomass available to them. Davidson (1977*b*) demonstrated a relationship between worker body size and seed size selected but presented no data on seed selection in relation to seed production. The suggestion that harvester ants forage selectively remains to be tested.

In the Chihuahuan Desert in southern New Mexico, 3 species of large body-size harvester ants (*Pogonomyrmex rugosus*, *Pogonomyrmex desertorum* and *Pogonomyrmex californicus*) occur at densities >200 colonies/ha with peak numbers of 180,000 foragers/ha (Whitford and Ettershank 1975). The great abundance of these large seed-harvesting ants suggested that they might have a significant effect on the seed crop and hence on the productivity and composition of the annual plant community. To examine forage selection and the effect of foraging by *Pogonomyrmex* on seed crop (input to seed reserves), I studied seed production by annual plants and seed removal by the 3 species of harvester ants.

METHODS

Studies were conducted in 1972 and 1973 on the Jornada Validation Site, a Chihuahuan Desert watershed ≈40 km NNE of Las Cruces, New Mexico. Studies of forage selection, foraging activity and fruit production were conducted on a 4-ha plot characterized by honey mesquite (*Prosopis glandulosa*), mormon tea (*Ephedra trifurca*), snakeweed (*Gutierrezia sarothrae*) and creosote bush (*Larrea tridentata*), and a sandy loam soil. The 50-yr average rainfall is 225 mm with nearly one third occurring in July through September. Summer maximum temperatures reach 40°C and freezing temperatures are recorded from mid-October through mid-April.

Harvester ants frequently carry whole fruits and remove the seed from the nonedible parts in the nest. Here I use the term "seed" to denote the item carried to the nest without distinguishing between fruits and seeds.

I estimated seed production at 2-wk intervals by multiplying the estimated density of each plant species by the average number of seeds produced by plants of that average size. I estimated density by the point-quarter method (Cottam and Curtis 1956) using >40 points selected at random. I recorded the canopy diameter, height and phenology of each plant sampled. When a species of forb or grass attained maximum fruiting, 15 individuals of varying size were measured

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TABLE 1. Seed selection by *Pogonomyrmex* spp. and availability of seed species. Seed selection and availability is based on the biomass of the different seed species. For each data set, the data are from top to bottom for *Pogonomyrmex rugosus*, *Pogonomyrmex desertorum* and *Pogonomyrmex californicus*. The monthly numbers are the ratio of relative occurrence in the diet (d_{ik}) to relative environmental availability (f_f). The selectivity coefficient is $B_s = 1/[\sum_{k=1}^{m} (d_{ik}/f_k)^2]$ (Schoener 1974)

Taxa	Fruit length (mm)	Weight/ seed (mg)	% avail- able	Jun	% avail- able	Jul	% avail- able	Aug	% avail- able	Sep	% avail- able	Oct–Nov
Allionia incarnata	2.2–3.7	2.11	...	...	...	...	...	...	9.1	...	9.1	...
				...		...		...		*		*
				...		...		...		*		...
Ammocodon chenopodioides	2.4–5.1	2.01	0.01	...	...	...	...	...	...	...	...	...
				...		...		...		...		...
				...		...		...		...		...
Aristida adscenionis	6.0–19	0.37	...	...	...	...	...	...	0.7	...	0.7	...
				...		...		...		357.9		...
				...		...		...		...		...
Baileya multiradiata	2.8–4.2	0.43	...	...	52.4	*	13.6	0.1	7.9	...	7.9	4.6
						*		1.5		0.1		...
				...		*		0.5		4.6		6.4
Boerhaavia spicata	3.5–6.2	1.51	...	...	...	...	0.5	324.0	...	...	...	...
				...		...		...		...		...
				...		...		...		...		...
Bouteloua barbata	4.0–6.5	0.03	...	...	...	...	2.6	11.9	13.6	...	13.6	...
				...		...		...		0.5		17.5
				...		...		...		...		*
Cassia bauhinioides	3.5–5.0	4.30	0.1	...	*	...	*	...	0.4	...	0.4	130.6
				...		...		...		...		...
				...		...		...		...		...
Chenopodium incanum	0.3–1.2	0.47	...	...	23.1	1.1	3.2	58.0	10.4	...	10.4	0.7
				...		*		5.6		...		0.9
				...		*		0.1		0.3		...
Croton pottsii	3.5–5.0	1.15	0.4	2.8	...	...	*	...	...	...	...	...
				...		...		...		...		...
				...		...		...		...		...
Cryptantha crassisepala	4.5–6.0	0.30	...	...	...	...	...	...	...	...	...	...
				...		...		...		...		...
				...		...		...		...		...
Descurainea pinnata	3.5–5.0	0.06	...	...	...	...	...	...	...	...	...	...
				...		...		...		...		...
				...		...		...		...		...
Dithyrea wislizenii	2.5–3.5	0.34	...	...	...	...	...	...	...	...	...	...
				...		...		...		...		...
				...		...		...		...		...
Eriogonum abertianum	2.0–3.4	0.18	79.0	0.3	19.9	7.6	4.67	0.1	7.4	...	7.4	0.2
				*		0.5		0.3		8.2		2.6
				0.2		1.8		1.2		58.2		22.7
Eriogonum rotundifolium	1.8–3.2	0.20	...	...	...	...	...	...	...	...	...	...
				...		...		...		...		...
				...		...		...		...		...
Eriogonum trichopes	2.2–3.6	0.13	19.7	3.5	4.5	0.5	23.6	0.6	9.9	...	9.9	...
				14.1		266.7		1.6		0.2		...
				9.0		110.4		1.8		0.2		4.1
Euphorbia sp.	1.5–3.2	0.50	...	...	...	...	1.2	2.8	1.9	...	1.9	235.4
				...		...		0.2		126.1		0.3
				...		...		...		41.1		41.2
Kallstroemia parviflora	2.1–3.0	1.11	...	...	...	...	0.2	4.3	...	...	...	...
				...		...		...		...		...
				...		...		...		...		...
Perezia nana	14–16	0.06	1.3	...	*	...	...	...	...	...	...	...
				...		...		...		...		...
				...		...		...		...		...
Tidestromia languinosa	<1.0	0.41	...	...	...	...	9.4	...	8.0	...	8.0	...
				...		...		...		...		...
				...		...		...		...		...
Tribulus terrestris	3.2–10.5		...	...	...	...	1.2	...	7.1	...	22.8	0.3
				...		...		...		...		*
				...		...		...		...		0.3
			B_s	0.15		0.109		0.002		...		0.003
				0.07		0.004		0.11		0.02		0.05
				0.11		0.009		0.28		0.01		0.01

(canopy height and width), excavated, returned to the laboratory and dried at 60°C. Seeds were removed, weighed and counted, and the relationship between seed number and canopy size determined. For species which produce seed continuously over much of the growing season, I placed seed traps under randomly selected plants and cleaned the traps weekly to obtain estimates of seed production.

I studied forage selection by collecting all foragers and their booty returning to a colony over a 5-min period. I sampled 5 or more colonies of each species, each month, 4 times during the day, to insure sampling at peak activity times for all species. Forage items were identified to species, counted and stored in vials. Using the estimated density figures and seed production figures to estimate abundance (environmental availability) of the seed species, I calculated a coefficient, B_s (Schoener 1974), for each species. The preference coefficient B_s compares occurrence in the diet with environmental availability.

For each plant species, forage removal (FR) per hectare is estimated by the following equation:

$$FR = \sum_{i=1}^{3} HR_i \times N_{Fi} \times 0.5 \times D_i \times F_P,$$

where HR_i is the estimated number of hours per month that a harvester ant species was active, N_{Fi} is the mean number of foragers per colony of the ith species active during that month, D_i is the number of colonies of the ith species per hectare, F_P is the ratio of the number of seeds of the forage species under consideration to the total number of seeds foraged by a particular species of ant. HR_i and N_{Fi} were obtained from data in Whitford and Ettershank (1975). The 0.5 is an empirical forager success correction factor: when collecting forage from returning workers the number of foragers with and without booty were tallied indicating a percent success ranging between 15 and 91% with a mean of 49.6%. These data were collected over the entire study period and were consistent throughout, i.e., high variance ranging between 15 and 91%. Also, there was no correlation between foraging success and soil surface temperature, saturation deficit or time of day ($N = 42$, $r < .3$).

Results and Discussion

Pogonomyrmex spp. exhibited a marked preference for certain seeds. This preference was not simply a function of seed size (Table 1). *Pogonomyrmex rugosus* preferred seeds of selected plants which reflected the phenology of the plant. *Pogonomyrmex rugosus* concentrated its foraging on species which shed large quantities of seeds in a short time interval. Although the numbers of *Eriogonum* spp. seeds which were available remained relatively constant from June through September, *P. rugosus* switched to other species when they became available; for example, seeds of *Chenopodium incanum*, which matured and were shed in August, were selected despite the small seed size of this species when compared with others available at that time (Table 1). However, in August, *P. rugosus* also exhibited a marked preference for *Boerhaavia spicata* seeds, the heaviest (hence the most energy efficient) seed available at that time (Table 1). These data suggest that forage selection in *P. rugosus* is not simply a function of energy efficiency (Pulliam 1974), abundance, or of seed size as suggested by Davidson (1977*a*). This pattern of switching preference to a species which shed large quantities of seeds at 1 time is predicted for an ant that engages in group foraging (Davidson 1977*b*). Davidson (1977*b*) presented experimental evidence demonstrating the importance of clumped seeds in the foraging of *P. rugosus*. This study and that of Davidson (1977*b*) clearly indicate that group-column foraging is an adaptation to exploit clumped resources.

Pogonomyrmex desertorum exhibited no selectivity in early summer, taking seeds in relationship to their abundance on the soil surface but as the grasses matured, *P. desertorum* concentrated on these grasses (Tables 1 and 2). In August, when *P. rugosus* selected *Bouteloua barbata*, *P. desertorum* took other seed species but not *B. barbata*. However, later in the season when *P. rugosus* switched its preference to other species, *P. desertorum* selected *B. barbata*. This pattern of forage selection suggests that when highly preferred seeds are not available, *P. desertorum* takes seeds as they are encountered without regard to weight, size or chemical composition. Although *P. desertorum* apparently prefers the seeds of the annual grama grass, *B. barbata*, it avoids *B. barbata* when *P. rugosus* is concentrating on that species. Although I have not observed aggressive interactions between these species, this behavior strongly suggests that interference competition has occurred in the past and that aggressive encounters are avoided now by shifts in resource utilization in time and space by *P. desertorum*.

Although *Erioneuron pulchellum* produced mature fruits in October and November, it made up 36% of the foraging of the *P. desertorum* the following May (Table 2). Of the species not listed in Table 2, but which were taken by *P. desertorum* in May 1973, 60% were grass seeds from the previous year. Although seeds of spring annual forbs were abundant and *P. rugosus* was not active (Whitford and Ettershank 1975), *P. desertorum* selected scattered grass seeds which had ripened the previous year.

The selection of grass seeds over the larger and/or more abundant seed species suggests that in late summer, *P. desertorum* is selecting a diet based on quality rather than maximizing energy intake per unit time when a choice is available and a dominant congeneric competitor is not active. Pulliam (1974) states that maximizing energy intake per unit time may only be adaptive at times of extreme hunger and that a pred-

TABLE 2. Seeds harvested by 3 species of *Pogonomyrmex* harvester ants expressed as percent of total number of items foraged. R indicates *Pogonomyrmex rugosus*; D indicates *Pogonomyrmex desertorum*, C indicates *Pogonomyrmex californicus*. (Seeds harvested by *Pogonomyrmex desertorum* in 1973 indicated by *)

	May			Jun			Jul			Aug			Sep			Oct		
Plant species	R	D	C	R	D	C	R	D	C	R	D	C	R	D	C	R	D	C
Baileya multiradiata	...	9	...	...	<1	...	3	2	1	5	27	10	...	21	...	17	12	20
Bouteloua barbata	...	...	...	...	...	...	9	...	...	1	...	...	...	10	...	...	57	...
Chenopodium incanum	...	...	...	...	...	1	24	2	1	29	9	1	...	...	6	9	10	...
Cryptantha sp.	40	11*	...	5	14	...	...	...	...	...	...	...	...	...	...	...	...	...
Descurainea pinnata	10	13*	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Eriogonum abertianum	14	9*	...	43	<1	32	55	16	27	17	27	46	...	21	56	11	12	35
Eriogonum trichopes	4	...	...	37	74	59	3	55	47	19	29	32	...	4	5	0	0	20
Erioneuron pulchellum	...	36*	...	1	...	...	<1	8	...	<1	<1	...	...	6	...	12	1	7
Euphorbia sp.	...	...	...	...	...	...	6	...	11	2	<1	...	...	21	12	29	1	12
Other seeds	30	25	...	9	...	...	...	27	8	18	3	7	...	15	15	16	4	1
Termites	...	...	...	1	10	3	1	...	1	1	1	2	...	2	...	...	...	...
Miscellaneous	2	6	...	4	...	2	1	...	4	4	3	2	...	...	6	5	5	...

ator might do better to specialize on a prey with a high amount of some needed nutrient. With regard to seed-harvesting ants, this might be modified to state. . . some needed nutrient or with few, if any, toxins. Although there are no data for the seed species used by *Pogonomyrmex*, Rhoades and Cates (1976) calculated that $\approx$15% of annual and herbaceous perennial dicot species contain tannins. Thus, it is possible that seeds of some nongrass species contain tannins or other toxins.

Pogonomyrmex californicus, also an individual forager species, selected *Eriogonum trichopes* in early summer and *Eriogonum* and *Euphorbia* in the early fall (Tables 1 and 2). The activity of both *P. rugosus* and *P. desertorum* was reduced in September and October (Whitford and Ettershank 1975). In early summer, *P. californicus* climbed into the canopy of *E. trichopes* to collect fruits and in August and September exhibited similar behavior in *Euphorbia* spp. *Pogonomyrmex californicus* avoids contact with its congeners by this behavior and seasonally concentrating its foraging in early spring and late autumn (Whitford and Ettershank 1975, Schumacher and Whitford 1976, Whitford 1977).

Examining the overall selectivity of *Pogonomyrmex*, all were highly selective (all B_s values <0.3, Table 1) and seed size appears to be only 1 factor in this selectivity. Indeed, fruit size and morphology have an effect on handling efficiency as suggested by Brown et al. (1975) and Pulliam and Brand (1975). *Pogonomyrmex* remove the bracts, calyxes, and florets from the seeds and pile them outside the nest. Thus, these ants have expended the energy to transport the large fruit rather than the smaller seed to the nest, plus expended energy to remove the nonedible parts. This energy cost should be more than equal to the energy costs of handling small smooth seeds (Pulliam 1974, Pulliam and Brand 1975). Thus, small seeds in large fruits, e.g., *Eriogonum* spp., have an associated cost that is paid by the workers in the nest after the fruit has been located and carried to the colony. Variables like oil content (Levin 1974), energy content and presence or absence of chemical toxins may also play a role in this selectivity.

In July and August of 1971, there was little foraging activity by *Pogonomyrmex* spp. (Whitford and Ettershank 1975). There were no summer annuals in 1971 due to inadequate precipitation. Forage collected from *P. rugosus* on 6 sampling dates consisted of: 9% seeds of 3 perennial shrubs, 17.1% insects, 3.6% feces, and 70.3% seeds of *Hilaria mutica*, a perennial grass. The percentage of seed harvested was similar to the percentage of cover of the various species in the area sampled. Although the shrubs and perennial grasses produced larger numbers of seeds in 1972 and 1973, they were avoided or taken in extremely low quantities. This provides partial support for MacArthur and Pianka (1966) and Schoener's (1971) contention that

TABLE 3. Estimated numbers of seeds produced by selected species of annuals and harvested by ants of the genus *Pogonomyrmex* in a Chihuahuan Desert ecosystem during 1972. PROD = seeds produced; FOR = seeds harvested by *Pogonomyrmex* spp.; % = percentage of seeds harvested by *Pogonomyrmex* spp.

	June			July			August			September		
Plant species	PROD	FOR	%	PROD	FOR	%	PROD	FOR	%	PROD	FOR	%
Baileya multiradiata				5.0×10^8	6.4×10^5	1.3	2.1×10^7	1.8×10^6	8.6	3.2×10^6	5.6×10^5	1.6
Bouteloua barbata							1.9×10^6	1.9×10^6	100	2.1×10^6	6.9×10^5	32
Chenopodium incanum				2.2×10^8	4.2×10^6	0.2	4.1×10^8	5.1×10^6	1.3	7.5×10^7	4.2×10^6	0.5
Eriogonum abertianum	2.2×10^7	7.3×10^6	33	1.9×10^8	1.7×10^7	8.8	1.1×10^8	4.9×10^6	4.6	7.1×10^7	3.2×10^6	4.5
Eriogonum trichopes	1.5×10^7	1.3×10^7	86	3.3×10^8	1.6×10^6	4.8	2.8×10^7	5.4×10^6	19.3	–0–	1.7×10^6	...

there should be decreased selectivity under conditions of low food abundance.

Pogonomyrmex spp. removed a significant fraction of the seed production of only 1 species: *Bouteloua barbata* (Table 3). Although *Eriogonum trichopes* represented a significant fraction of the forage of *Pogonomyrmex* for most of the season of active foraging, >22% of the estimated seed production of that species remained uncollected by these harvester ants. In 1973, the densities of annuals were higher than in 1972 and *P. rugosus* did not forage during most of 1972 (Whitford and Ettershank 1975). Based on these data, I estimated that the seed harvest by *Pogonomyrmex* in 1973 was 60% lower than 1972. Thus, the seed reserves of the most heavily exploited species could be replenished during a 2nd year of high annual plant production. Tevis (1958) found that *Veromessor pergandei* harvested <1% of the available seeds in a Mojave Desert area, but suggested that the ants could have a significant effect on preferred species. Although *Pogonomyrmex* spp. harvest large quantities of grass seeds and seeds of *Eriogonum* spp., it is estimated that even in a year like 1972, when seed harvesting was intense, $>10^6$ seeds/ha escape predation by these ants. Other ants, such as *Pheidole* spp., as well as heteromyid rodents and gramnivorous birds, take seeds, so the quantitative effect of *Pogonomyrmex* spp. on the seed reserves could not be estimated. These data suggest that *Pogonomyrmex* spp. may have a qualitative effect on the vegetation, i.e., on the relative abundance of plant species.

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