Learning, Memory, and Foraging Efficiency in Two Species of Desert Seed-Harvester Ants

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LEARNING, MEMORY, AND FORAGING EFFICIENCY IN TWO SPECIES OF DESERT SEED-HARVESTER ANTS[1]

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Abstract. I examined seed learning and memory in the desert seed-harvester ants *Messor pergandei* and *Pogonomyrmex rugosus* to determine (1) which aspects of handling and search efficiency are learned, (2) how fast this information is learned and then forgotten, and (3) how learning and memory affect foraging efficiency. Individuals of both species learned a suite of behaviors that enhanced foraging efficiency on a novel seed species under natural conditions. Handling time per seed and return time (travel time to and from the nest and time inside the nest) decreased for both species. Each species also used specific harvest techniques that enhanced foraging efficiency. Individuals of the larger *P. rugosus* increased efficiency by increasing the number of seeds harvested per trip. As a result, the percentage of individuals that carried >1 seed per trip increased over time. The smaller *M. pergandei* decreased the number of seeds handled before harvesting one, and still harvested heavier than average seeds because they handled but did not harvest lightweight seeds. *Messor pergandei* also varied the number of seeds handled before harvesting one, such that the fewest number of seeds was handled at low natural seed densities.

Overall, foraging efficiency of *M. pergandei* and *P. rugosus* individuals, measured as seed mass harvested per unit time, increased 1.9- and 3.85-fold, respectively, within one observation period, even excluding the effect of harvesting heavier than average seeds. The difference between species arose because individuals of *P. rugosus* could carry twice as many of the test seeds as *M. pergandei*. Memory was clearly an important component of foraging efficiency for both species, as all foraging efficiency indices fell much more slowly than they rose. Tactile-associated behaviors, such as handling time per seed and number of seeds handled, were lost quickly compared to olfactory-associated behaviors such as seed recognition and acceptance.

Key words: diet selection; foraging efficiency; learning; memory; Messor pergandei; *patch selection;* Pogonomyrmex rugosus; *seed-harvester ants.*

INTRODUCTION

Foraging efficiency can be constrained by nutrient demands (Pulliam 1975, Belovsky 1978, 1981), competition (Milinski 1982), predation (Milinski and Heller 1978, Sih 1980, Werner et al. 1981, Martin 1985, Lima and Valone 1986), and characteristics of the food itself (Hespenheide 1966, Wilson 1975, Harder 1983). Yet, within these constraints, behavioral traits that enhance foraging efficiency should be favored provided they increase survival and reproduction (Schoener 1971, Pyke et al. 1977, Pyke 1984, Stephens and Krebs 1986). Learning is the modification of behavior due to experience with some stimulus in the environment (Johnston 1985), and represents a behavioral trait that can enhance foraging efficiency.

Effects of learning on foraging efficiency can potentially cause foragers to choose diets and patches that are not predicted by conventional foraging theory. For example, learning can affect recognition time and make encounter rate an important criterion in diet selection (Hughes 1979), but encounter rates are assumed to be unimportant to diet selection in traditional foraging models (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Charnov 1976).

Previous studies generally focused on the effects of learning individual feeding behaviors (e.g., handling time per seed), but learning may influence foraging efficiency through its effect on a suite of such behaviors. Memory may also influence foraging efficiency because learned associations fade from memory (i.e., decay) if they are not reinforced. This study examines learning and memory of foraging behaviors in two ecologically similar species of desert seed-harvester ants, *Messor* (=*Veromessor*) *pergandei* and *Pogonomyrmex rugosus*, to determine (1) which aspects of handling and search efficiency are learned, (2) how fast this information is learned and then forgotten, and (3) how learning and memory affect foraging efficiency.

Both ant species may coexist in the same habitat throughout much of the Sonoran and Mohave Deserts (Davidson 1978, Rissing 1981) and have similar diets when doing so (Mehlhop and Scott 1983, Rissing 1988). Additionally, both species are group foragers (Hölldobler 1976, Davidson 1977, Whitford 1978) that typically forage up to ≈30 m from the nest (Rissing 1988). The

two species differ, however, in foraging method; foraging columns of *M. pergandei* rotate around the nest with the rate of rotation dependent on seed availability (Bernstein 1975, Rissing and Wheeler 1976), while *P. rugosus* use semipermanent "trunk trails" with high individual fidelity to a trail (Hölldobler 1976).

Learning of foraging efficiency was examined in both species by placing a novel seed species across a colony's foraging column and monitoring changes in the ants' response to these seeds over time. Memory was examined by single reobservations of the response of numerous colonies to the same novel seed species at various time intervals following familiarization with that seed species.

METHODS

Study sites

Learning trials were conducted at four sites: (1) on a bajada (alluvial fan) west of the McDowell Mountains at 576 m elevation (MDM) (33°40′N, 111°52′E), (2) 2 km southwest of MDM at 527 m (MDMVP) (33°40′N, 111°53′E), (3) near the western boundary of the Tonto National Forest at 450 m (TNF) (33°35′N, 111°38′E), and (4) at the east edge of South Mountain Park at 415 m (SMP) (33°21′N, 112°00′E), Maricopa County, Arizona. Each ant species was observed at three sites, as the two ant species were sympatric at SMP and MDM, but *M. pergandei* was the only species at MDMVP and only *P. rugosus* occurred at TNF.

Habitat of all sites was typical Sonoran Desert; vegetation ranged from a *Larrea tridentata–Ambrosia deltoidea* association at MDMVP to a *Cercidium* spp.–*Carnegiea gigantea* association at MDM. Vegetation at SMP was a *Cercidium* spp.–*L. tridentata* association, while that at TNF was a *L. tridentata* association.

Learning and foraging efficiency of colonies

Learning was examined by placing an experimental patch ($\approx 20 \times 3$ cm) of Kentucky blue grass (KBG, *Poa pratensis*) seeds across a colony's foraging column 5 m from the nest entrance. KBG seeds were used because they are novel, they are harvested readily by both ant species (Rissing 1981), and their size and shape resembles the commonly harvested seeds *Schismus arabicus* and *Plantago insularis* (Rissing 1988). KBG seeds were obtained from a >99% pure seed stock marketed by Northrup King; seeds averaged 0.310 ± 0.085 mg ($\bar{X} \pm 1$ SD, $N = 200$) (this study) and were 2.62 ± 0.41 mm long and 0.62 ± 0.13 mm wide ($N = 74$) (Rissing 1981). Seeds were presented each day for 1–2 h, the time typically required to record observations, and then removed.

Learning by colonies was examined by recording three measures of foraging efficiency: (1) number of seeds handled before harvesting a seed, (2) number of seeds harvested per foraging trip, and (3) handling time per seed all for that subset of 100 randomly observed foragers that entered the seed patch and harvested seeds). A fourth index, the percentage of individuals that harvested >1 seed, was derived for *P. rugosus* because this species regularly harvested multiple seeds. Typically, few of the 100 observed individuals harvested KBG seeds during the 1st and sometimes 2nd d of learning trials. During these periods, I continued to record the number of seeds handled by *M. pergandei* and the number of seeds harvested by *P. rugosus* until 10 individuals had been observed. Handling time per seed was time in the patch divided by number of seeds handled for individuals that ultimately harvested a seed.

At least two colonies per site per species were observed each day until the percentage of the 100 randomly observed foragers that handled seeds reached an asymptote, defined as the day in which this figure increased <5% over three successive days. Additional colonies were observed for shorter periods; overall 12 929 and 9600 observations were made on *M. pergandei* and *P. rugosus*, respectively. *Pogonomyrmex rugosus* colonies display distinct annual activity cycles and forage predictably at these sites only for various durations following rainfall (see Rissing 1987). Consequently, *P. rugosus* colonies were sometimes induced to forage by pouring water down the nest, which simulated rainfall.

Foraging efficiency may also increase by learning to selectively harvest seeds by mass, which is suggested in that foragers of both ant species harvest heavier than average seeds of a species (Rissing 1981). This aspect of foraging efficiency was examined by placing KBG seeds across a colony's foraging column 5 m from the nest entrance. I then collected 50 seeds that were harvested and 50 that were rejected (those that had been handled and dropped) by two *M. pergandei* colonies at MDMVP for at least 10 consecutive days. Unharvested seeds were removed daily. The mean mass of offered seeds was determined from 200 random seeds collected immediately after initial placement of the patch. All seeds were dried at 55°C for at least 24 h and weighed to 0.001 mg. Seed mass was not examined for *P. rugosus* because individuals regularly harvested >1 seed.

Seed density

Learning was examined relative to natural seed density by conducting learning trials at three sites per species; one site per species was used in two different years. Annual seed density is positively associated with rainfall from 1 January to 1 April, the period of maximum germination and seed set in the Sonoran Desert (Beatley 1974, Rissing 1986). Rainfall data were taken from records of the nearest weather station for TNF and SMP. Rainfall at MDM and MDMVP was the mean of the Carefree and Tempe, Arizona, weather stations, which were nearly equidistant from the sites (NOAA 1985, 1986, 1987).

Learning and foraging efficiency of individuals

Learning by individual ants was also examined. Individuals that harvested a KBG seed during their first encounter with the seed patch (i.e., the first time KBG seeds were offered to this nest) were marked with Dayglo fluorescent pigment; marking did not appear to disturb behavior. Four measures of individual foraging efficiency, i.e., (1) number of seeds handled before harvesting a seed, (2) number of seeds harvested per foraging trip, (3) handling time per seed, and (4) return time (time to and from the nest and time inside the nest), were recorded for at least 10 individuals per species (one or two per colony) over 8–15 consecutive trips to the seed patch. Observations began within 10 min of initial placement of seeds to ensure that the ants had had no experience with KBG seeds.

Colony memory and foraging efficiency

I assessed colony memory using KBG seeds. Colonies were first familiarized with KBG by placing seeds across the foraging column 5 m from the nest each day for 14 d. The percentage of 100 randomly chosen foragers that handled seeds was assessed as above (*Learning and foraging efficiency of colonies*), once per colony, on days 12 through 14; I only used colonies in which seeds were handled by at least 75 of 100 observed individuals, this percentage being typical for familiarized colonies of both ant species (Johnson 1989). Unharvested seeds were then removed. Each of 37 *M. pergandei* and 30 *P. rugosus* colonies were then re-exposed to KBG seeds once at from 2 to 100 d since the last day of conditioning. Over this time period, foraging efficiency indices could decay due to loss at the individual level or due to forager mortality. During the retest, I examined memory by recording the three measures used in learning trials (above, *Learning and foraging efficiency of colonies*) for 100 randomly selected individuals. All foraging efficiency indices fell quickly, especially for *M. pergandei*. Additional colonies were observed during the first 15 d to better determine rate of memory loss. For analyses, this period was divided into intervals from 1 to 3, 4 to 5, 7 to 9, and 11 to 14 d. Up to four colonies were observed in each interval as well as in subsequent 10-d intervals.

Data analysis

I removed the effect of variable ground temperature on ant velocity by standardizing time measurements to 30°C. Ground temperature was measured periodically to 0.3°C with a Yellow Springs Instruments telethermometer equipped with a small probe. *Messor pergandei* times were standardized using the equation $V = 0.0878T - 0.1724$ (Rissing 1982), where T is ground temperature (in degrees Celsius) and V is velocity (in metres per minute). For *P. rugosus,* this relationship was determined from field measurements taken over the temperature range encountered in learning trials (21.2°–40.6°C) using individuals that ran 20 cm without interruption. Ground temperature was measured every few minutes. Velocity of *P. rugosus* individuals was related to ground temperature ($V = 0.1914T - 1.9830$, $R^2 = 0.72$, $P < .0001$, $N = 150$).

All foraging efficiency indices changed curvilinearly through time. Consequently, I used colony residuals to compare values intraspecifically between years and among sites. Residual values were calculated for each learning trial (day) as the difference between each colony value on each day and the species mean on that day. Using data appropriate for the respective comparisons, indices were first compared between years using a *t* test; data were pooled when no differences occurred ($P > .05$). Sites were then compared using a one-way ANOVA followed by an LSD test (Sokal and Rohlf 1981). Each comparison included only data up through the last day in which observations were common to all respective sites. Data with unequal variances (Bartlett's test, $P < .05$) were $\log_{10}$ or square-root transformed. Linear regression was used to compare means of consecutive learning trials.

Memory loss was examined by regressing each foraging efficiency index (dependent variable) against days since previous exposure to KBG seeds (independent variable). Each regression included data up to and including the asymptote, which was the interval during which the mean of each index changed <5% over three successive intervals. Number of days until each foraging efficiency index decayed completely was determined by inserting the mean naive colony value (day 1 response) into the regression equation. To ensure that individual learning did not affect colony memory indices, I only analyzed the first 10 observed individuals that harvested a seed for handling time per seed, number of seeds harvested, and the percentage of individuals that harvested >1 seed.

RESULTS

Learning and foraging efficiency of colonies

Handling time per seed decreased significantly (*F* test, $P < .004$), by 36 and 53%, and reached an asymptote in 5 and 4 d for *M. pergandei* and *P. rugosus* colonies, respectively (Fig. 1A). Handling times did not differ between years (*t* test, $P > .10$) or among sites (LSD test, $P > .10$), and the data were pooled within species. Handling time per seed was consistently less for *P. rugosus* colonies (Wilcoxon paired-sample signed-ranks test, $P < .01$, $N = 10$ d).

Each species used specific harvest techniques that increased foraging efficiency. Individuals of *P. rugosus* increased efficiency by increasing the number of seeds harvested per trip (*F* test, $P < .001$). Because most individuals harvested only one seed during the first learning trial, the percentage of individuals that harvested >1 seed also increased over time (*F* test, $P < .005$) (Fig. 1B). Neither the number of seeds harvested
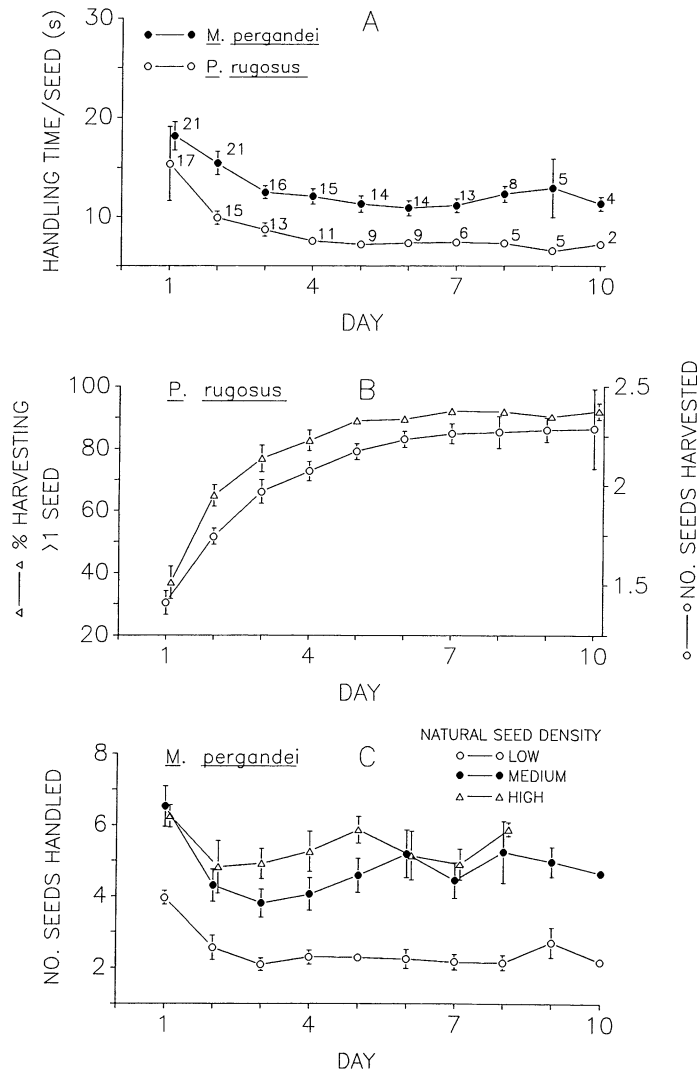
FIG. 1. Increase in foraging efficiency on Kentucky blue grass (KBG) seeds for *Messor pergandei* and *Pogonomyrmex rugosus* colonies over consecutive learning trials. Data ($\bar{X} \pm 1$ SE) come only from individuals that harvested a KBG seed. Number of colonies that were observed for each learning trial is given in (A). Data in (A) and (B) were pooled for each species because no differences occurred between years or among sites. (A) Handling time per KBG seed. (B) Mean number of KBG seeds that were harvested and the percentage of *P. rugosus* individuals that harvested >1 KBG seed per foraging trip. (C) Number of KBG seeds that were handled before one was harvested, by *M. pergandei* colonies at three natural seed densities. Natural seed density was inferred from rainfall data. $N \geq 3$ for each seed density through day 7.

per trip or the percentage of individuals that harvested >1 seed differed between years (*t* test, $P > .11$) or among sites (LSD test, $P > .25$), and the data were pooled. Both indices reached an asymptote in 5 d and thereafter maintained a steady state with individuals carrying an average of 2.25 seeds (range = 1–4 seeds); at this time ≈91% of the foragers carried >1 seed per trip. Only 1.9% of the smaller bodied *M. pergandei* harvested two seeds, and these individuals generally appeared to be larger than most other foragers. Both species picked up and handled KBG seeds along the width dimension and then manipulated the seeds until they were held near the midsection. *Pogonomyrmex rugosus,* and *M. pergandei* when applicable, carried

multiple seeds similarly by stacking them in their mandibles, either by adding seeds singly (both species) or by picking up multiple seeds simultaneously (*P. rugosus*).

Messor pergandei increased efficiency by decreasing the number of seeds handled before a seed was harvested. The number typically decreased by 1–2 seeds after the 1st d, regardless of natural seed density, and reached an asymptote by the 3rd d (Fig. 1C). This decrease was significant for all years and sites when comparing the number handled on day 1 to succeeding days (two-tailed sign test, $P < .05$), each of which represented a repeat sampling within a colony. Consistency of this decrease, however, varied among sites;

TABLE 1.   Data used to infer relative natural seed density at the study sites. Rainfall is for the period 1 January to 1 April.

	M. pergandei sites*				P. rugosus sites*			
	MDMVP 1985	MDMVP 1986	SMP† 1987	MDM 1986	SMP 1987	TNF 1986	SMP 1986	MDM 1986
Rainfall (cm)	4.2	8.1	5.2	8.1	5.2	9.2	8.1	8.1
Inferred relative natural seed density	low	medium	medium	high	low	medium	high	high

   * Site abbreviations: MDM, McDowell Mountains; MDMVP, 2 km southwest of the McDowell Mountain site; TNF, Tonto National Forest; SMP, South Mountain Park.
   † Natural seed density is inferred only across sites within each species. Consequently, relative density at the same site can differ between ant species.

the percentage of succeeding days in which the number handled was lower than on day 1 was significantly higher at the lowest natural seed density tested (percentage test, $P < .01$, $N = 61$), at which time the fewest seeds were handled (Fig. 1C).

In contrast, the number of seeds handled by *P. rugosus* increased with experience (Friedman two-way layout, $n = 4$, $k = 7$, $P < .025$, where n is sites [replicates] and k is days [learning trials] [Hollander and Wolfe 1973: 139–146]). Values were the means of all colonies at a site for each day. However, number of seeds handled per seed harvested did not change with time ($P > .10$), indicating that additional seeds were assessed only because the ants harvested more seeds on each foraging trip.

Handling of seeds by *M. pergandei* facilitated harvesting heavier seeds. Even when seed density and number of seeds handled were lowest, harvested seeds averaged 18 and 5% heavier than those rejected ($P < .005$, $N = 21$, Wilcoxon paired-sample rank-sum test) and offered ($P < .005$), respectively, and rejected seeds were lighter than offered seeds ($P < .005$). Mass of rejected or harvested seeds did not change with experience at either nest (runs test; $P > .10$; Sokal and Rohlf 1981). Thus, the decrease in number of seeds handled with experience and lack of difference in mass of harvested seeds shows that the ants learned to identify and choose heavier seeds more rapidly and with less handling time.

Seed density

The SMP and MDM sites were on bajadas and had a coarser soil texture (Johnson 1989) and a higher available soil moisture than alluvial basin sites (Yang and Lowe 1956, MacMahon and Wagner 1985) such as MDMVP. Consequently, these coarse-textured sites should produce more annual seeds for a given rainfall. Thus, a priori, I inferred that natural seed density at *M. pergandei* sites was low at MDMVP in 1985, intermediate at the same site in 1986 and SMP in 1987, and high at MDM (Table 1). Based on rainfall data at *P. rugosus* sites and the more fine-textured soil at TNF, I inferred, a priori, that natural seed density was low at SMP in 1987, intermediate at TNF, and higher at SMP in 1986 and at MDM (Table 1).

Number of seeds handled before one was harvested was positively associated with natural seed density for *M. pergandei*, but not for *P. rugosus*. This number differed among sites (LSD test, $P < .001$) for experienced *M. pergandei* colonies (>3 learning trials), and was lowest at low seed densities (Fig. 1C; $P < .05$, $\bar{X} = 2.24$ seeds), intermediate at medium densities (MDMVP 1986: $\bar{X} = 4.55$ seeds; SMP: $\bar{X} = 4.64$ seeds), and highest at high densities ($\bar{X} = 5.27$ seeds). Number of seeds handled per seed harvested by *P. rugosus* was not associated with natural seed density; the number was lowest at intermediate seed densities (LSD test, $P < .002$) and did not differ between 2 yr (t test, $P > .9$, data pooled) in which rainfall differed by $> ⅓$.

Learning and foraging efficiency of individuals

Most patterns of individual learning within one observation period paralleled those of colony learning for foraging indices that could be compared. Handling time per seed decreased for 9 of 10 *M. pergandei* and all of 10 *P. rugosus* individuals (Fig. 2A); both species reached an asymptote on the sixth trip. Experience reduced handling time per seed significantly (F test, $P < .003$), by 57.3 and 59.8% for *M. pergandei* and *P. rugosus* individuals, respectively. The mean time of *P. rugosus* individuals was significantly less across all visits to the patch (Wilcoxon paired-sample signed-ranks test, $P < .01$, $N = 15$).

Number of seeds harvested per trip increased through the fifth trip to the seed patch for 13 of 15 *P. rugosus* individuals (Fig. 2B). The number then levelled off for several trips and finally reached an asymptote on the 13th trip, as did the percentage of individuals that harvested > 1 seed. Both indices increased significantly with experience (F test, $P < .001$), rising from all individuals harvesting one seed on the first trip to an asymptote of 2.02 seeds harvested per trip and 73.7% of the individuals harvesting > 1 seed after the 13th trip. However, these values were still considerably lower than the 2.24 seeds and 90.8% for experienced *P. rugosus* colonies.

None of the 10 *M. pergandei* individuals exhibited a decrease in number of seeds handled, nor did the mean number of seeds handled change significantly within one observation period (F test, $P > .6$) (Fig.
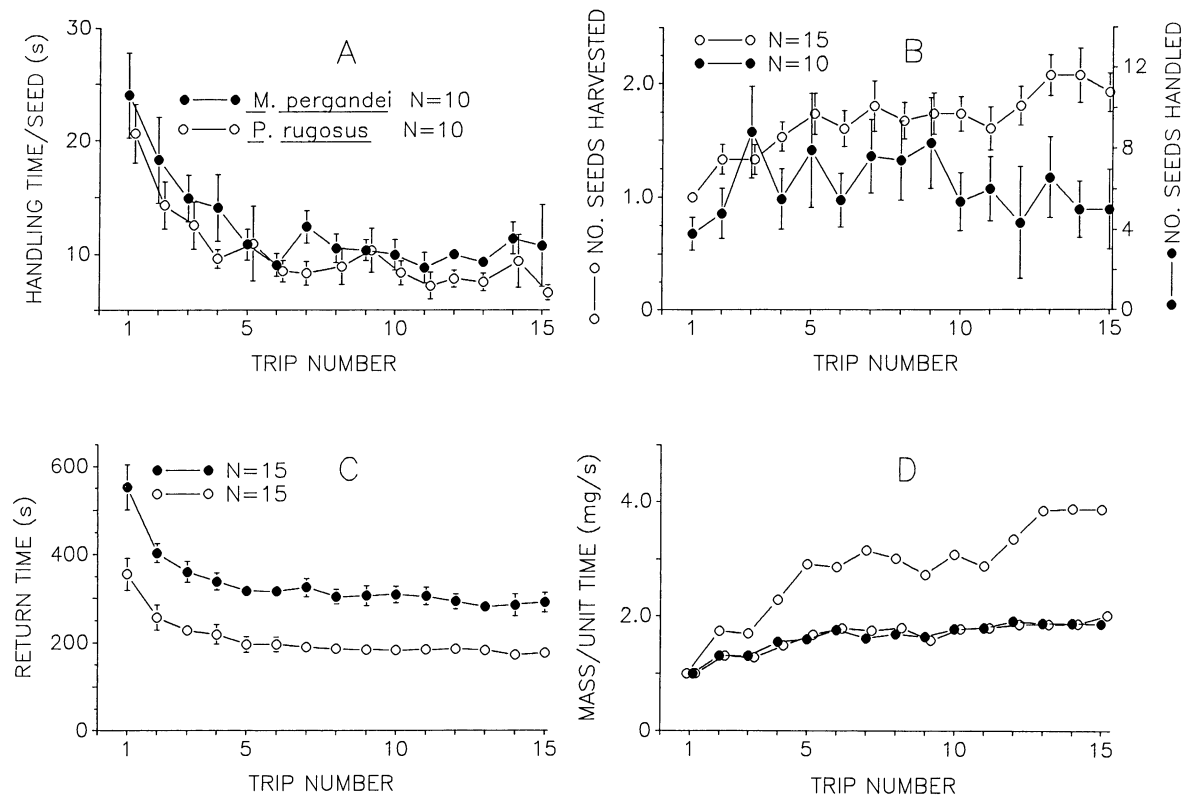
FIG. 2. Increase in foraging efficiency for marked individuals observed over 15 consecutive foraging trips to a patch of Kentucky blue grass (KBG) seeds. *Messor pergandei* was observed at MDMVP and *Pogonomyrmex rugosus* was observed at SMP and MDM (see *Methods: Study sites*). Data ($\bar{X} \pm 1$ SE) come only from individuals that harvested a KBG seed. (A) Handling time per KBG seed. (B) Number of KBG seeds handled before harvesting one by *M. pergandei,* and number of KBG seeds harvested per foraging trip by *P. rugosus*. (C) Return time, defined as travel time to and from the patch of KBG seeds and time inside the nest. Trip 1 is the return time following an individual's first encounter with the seed patch. (D) Overall increase in foraging efficiency, calculated using time in the seed patch (A and B) and return time (C), for *M. pergandei* and *P. rugosus*. The bottom two lines reflect the increase due only to a decrease in total trip time (in and out of the patch), while the upper line also includes harvesting of multiple seeds by *P. rugosus*.

2B). Consequently, this was the only foraging efficiency index measured for this species in which changes within one observation period did not parallel colony level changes.

Return time was examined only for individuals, and it decreased for all observed individuals (Fig. 2C), reaching an asymptote on the fifth trip for both species. Return time decreased significantly with experience (*F* test, $P < .002$), by 45.2 and 47.8% for *M. pergandei* and *P. rugosus,* respectively, due to individuals moving faster, taking more direct routes, and spending less time in the nest. For *M. pergandei,* the extra burden of harvesting seeds that averaged 5% heavier than offered seeds should have decreased travel velocity <0.2% (Rissing 1982). Hence, the increase in travel time was small relative to the gain in seed mass.

Travel time from the patch to the nest, and vice versa, were compared for the effects of learning on individual search strategies (Rissing 1982) using those individuals in which these subsets of return time were measured. Times from the patch to the nest were significantly less than times from the nest to the patch for

two *M. pergandei* individuals (Wilcoxon paired-sample signed-rank test, $P < .05$), were significantly greater for one, and did not differ for seven other individuals ($P > .10$). Similarly, times from the patch to the nest were less for one *P. rugosus* individual, were significantly greater for one, and did not differ for five other individuals. Return times across all visits were significantly less for *P. rugosus* (Wilcoxon paired-sample signed-rank test, $P < .01$), but these differences were similar to those expected based on relative travel velocity.

Patch time (handling time per seed × number of seeds handled) decreased 42–61% for *M. pergandei* depending on the number of seeds handled, and 23% for *P. rugosus,* with this lower decrease due to individuals handling more seeds with experience. However, a decreased handling time per seed accounted for little of the overall increase in foraging efficiency, as time in the patch 5 m from the nest was ≈⅙ of the return time for both species.

Overall, foraging efficiency was a function of time in the patch, return time, number of seeds harvested, and
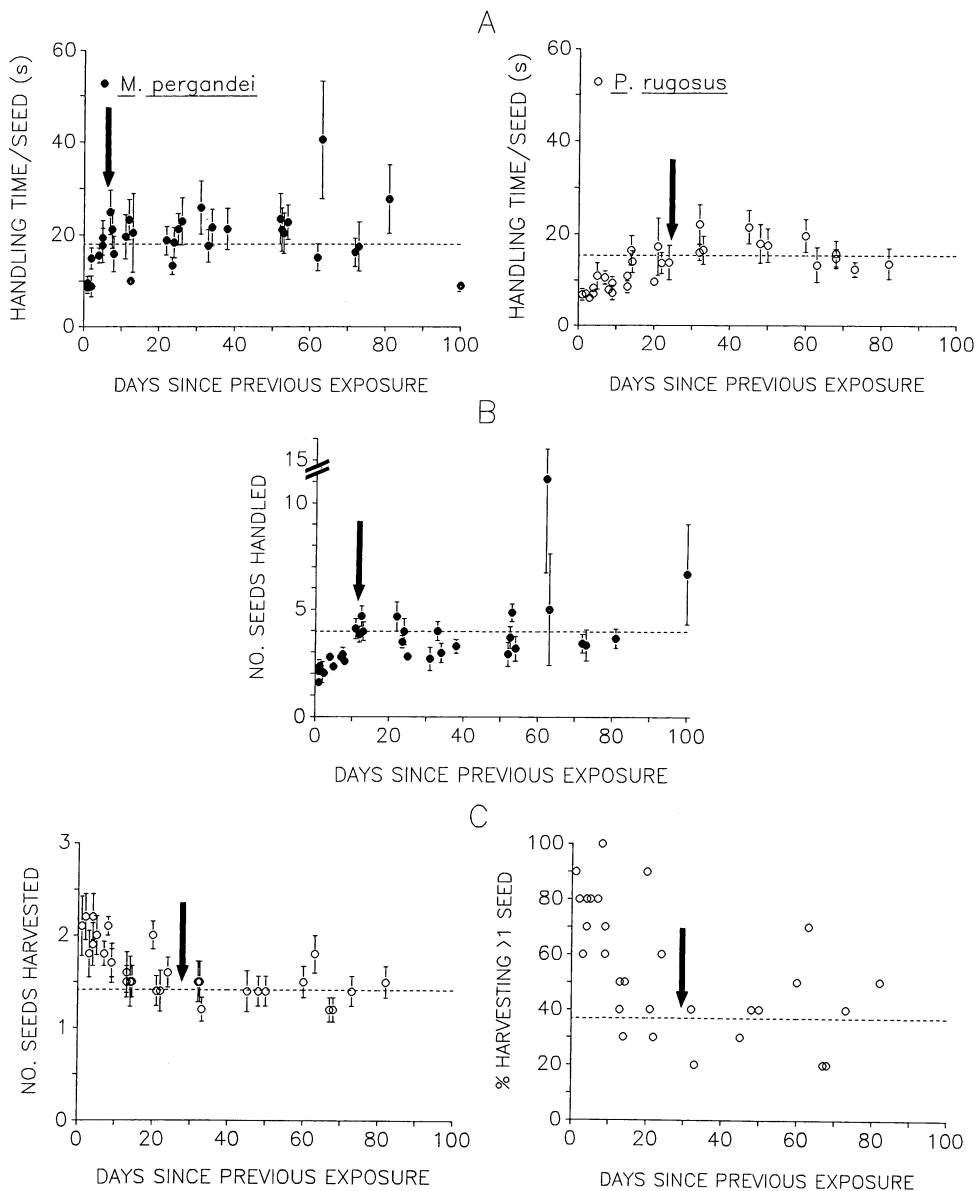
FIG. 3. Decrease in foraging efficiency on Kentucky blue grass (KBG) seeds for *Messor pergandei* and *Pogonomyrmex rugosus* colonies at MDMVP and TNF, respectively (see *Methods: Study sites*), following a familiarization period with KBG seeds. Data ($\bar{X} \pm 1$ SE) come only from individuals that harvested a KBG seed. Each dot represents the first 10 (A and C) or all (B) observed individuals in each colony that harvested a KBG seed (see *Methods: Data analysis*). Arrows indicate when indices returned to the level of naive colonies. Dashed lines are the values of each index for naive colonies (see Fig. 1). (A) The decay curve for handling time per KBG seed by *M. pergandei* (left) and *P. rugosus* colonies (right). (B) The decay curve for number of seeds handled per seed harvested by *M. pergandei* colonies at low natural seed densities. (C) The decay curve for number of KBG seeds harvested (left) and percentage of individuals that harvested >1 KBG seed per foraging trip (right) for *P. rugosus* colonies.

seed mass harvested. Foraging efficiency of *M. pergandei* and *P. rugosus* individuals increased ≈1.9- and 3.85-fold (F test, $P < .0001$) (Fig. 2), respectively, within one observation period, even excluding the effect of harvesting heavier than average seeds. Individuals of both species realized an ≈1.9-fold increase due to a decreased time per foraging trip (time in the patch plus return time). The difference between species was caused

by *P. rugosus* achieving an additional twofold increase due to harvesting multiple seeds.

Colony memory and foraging efficiency

Colonies of *M. pergandei* and *P. rugosus* eventually forgot all learned elements of foraging on KBG seeds. When indices returned to the level of naive colonies, I assumed learned traits had been forgotten. Handling

time per seed increased to an asymptote $\approx$7–9 d since previous exposure for *M. pergandei,* and reached the level of naive colonies after 5.7 d (Fig. 3; $Y = 1.71X + 8.38$, $R^2 = 0.71$, $N = 11$ colonies, $P < .01$). Handling time for *P. rugosus* increased to an asymptote $\approx$32–33 d since previous exposure, and reached the level of naive colonies after 24.8 d ($Y = 0.36X + 6.44$, $R^2 = 0.71$, $N = 21$ colonies, $P < .0001$), significantly longer than for *M. pergandei* (F test, $P < .005$) (Neter and Wasserman 1974).

Number of seeds handled increased to an asymptote $\approx$11–14 d since previous exposure for *M. pergandei* and reached the level of naive colonies after 12.1 d (Fig. 3; $Y = 0.2X + 1.7$, $R^2 = 0.85$, $N = 14$ colonies, $P < .0001$). For *P. rugosus,* number of seeds harvested and the percentage of individuals that harvested >1 seed fell to an asymptote $\approx$32–33 d since previous exposure and declined to the level of naive colonies in 28.4 (Fig. 3; $Y = -0.22X + 2.02$, $R^2 = 0.57$, $N = 21$ colonies, $P < .0001$) and 29.4 d (Fig. 3; $Y = -1.52X + 81.4$, $R^2 = 0.48$, $P < .0001$), respectively. After complete memory loss, none of the indices differed from the levels of naive colonies (Mann-Whitney test, $P > .10$).

DISCUSSION

Learning and foraging efficiency

Messor pergandei and *P. rugosus* learned a suite of species-specific behaviors that improved foraging efficiency on a novel seed species under natural conditions. When the seed was withdrawn, both species forgot all learned behaviors, although tactile stimuli were forgotten faster than olfactory stimuli (Johnson 1989). Other studies have also shown that ants can improve foraging efficiency via learning (Rissing 1981, Schmid-Hempel and Schmid-Hempel 1984, Traniello 1988), although each study only examined isolated aspects of foraging behavior. Habitat had little effect on learning foraging efficiency indices except that seed density influenced the number of seeds handled by *M. pergandei.*

Messor pergandei and *P. rugosus* apparently learned information on seed mass by handling several seeds initially. This experience influenced future decisions for the number handled, number harvested, and mass harvested, but the two species differed in the behaviors that they modified. *Pogonomyrmex rugosus* used information gained from handling several seeds initially to increase the number of seeds harvested per trip. Moreover, the value of this behavior was signalled by increases in the percentage of individuals that harvested multiple seeds. *Messor pergandei* used information gained from handling several seeds to determine an acceptable seed mass and to reduce the number of seeds handled while still obtaining heavier seeds.

Consistently greater mass of harvested than rejected or offered seeds by *M. pergandei* (this study, Rissing 1981, Rissing and Pollock 1984) and *P. rugosus* (S. W.

Rissing, *unpublished data*) indicates that handling several seeds functions to harvest a seed of acceptable mass. Handling multiple seeds may function similarly in other seed-harvester ants; though mass appears unimportant in selecting a seed species (Rissing 1981, 1988), it apparently is the primary physical attribute used to select seeds within a species (Hansen 1978, Chew and De Vita 1980, Rissing 1981).

Mass provides a quick and easy assay of seed quality when foraging time is limited, as it is for both ant species (Bernstein 1974), while other criteria may be used in the nest. For *M. pergandei* colonies, number of seeds handled decreased on the 2nd d even though few individuals handled seeds on day 1. Additionally, *M. pergandei* individuals did not learn to decrease the number of seeds handled nor did *P. rugosus* individuals learn to harvest their full potential of seeds within one observation period. These results suggest that both species fully learn seed characters either by handling numerous seeds while foraging or that individuals become familiar with seed characters by processing seeds in the nest. The lack of short-term change in these foraging indices was probably not related to overcoming caution in dealing with a novel stimulus since another index, handling time per seed, decreased quickly within one observation period.

For both species, learning information on seed characters also decreased the handling time needed to assess seed mass. Other studies document that experience reduces prey handling time (Laverty 1980, Wiegl and Hanson 1980, Werner et al. 1981, Cunningham and Hughes 1984, Hughes and Dunkin 1984, Laverty and Plowright 1988), but my study shows that experience can also reduce the time needed to assess quality of a food item.

Variation in natural seed density affected the number of seeds handled before harvesting a seed for colonies of *M. pergandei,* but not *P. rugosus.* For *M. pergandei,* number of seeds handled was positively associated with natural seed density. Because mass of harvested seeds was examined at only one seed density it is not known if the number of seeds handled affected selection of seeds by mass. However, another study (Rissing and Pollack 1984) showed no relation between number of seeds handled and seed mass harvested. Consequently, number of seeds handled by *M. pergandei* at a given distance from the nest is likely related to the probability of finding a heavier seed (see also Elner and Hughes 1978). This probability increases at high seed densities, when ease of locating and assessing other seeds can outweigh additional search costs. Conversely, the first seed encountered of acceptable mass may be harvested at low seed densities, which may explain why the number of seeds handled decreased most consistently at the lowest natural seed density tested.

The $\approx$50% decrease in return time for both species was probably due to individuals learning the seed patch location and richness rather than recruitment to the

patch because marked individuals were usually one of few individuals to harvest KBG seeds during initial observations. Learning seed patch location and richness also modified individual search behavior. Outgoing ants typically walk slower and search for seeds along the path compared to ants returning to the nest with seeds (Rissing 1982). Similar travel times for ingoing and outgoing foragers indicate that the ants changed this behavior quickly by taking more direct routes and rarely searching for seeds en route. Individuals may also have learned and followed landmarks (Hölldobler 1976), as marked foragers often passed the same points along the path and arrived at the same location in the seed patch.

Return time was the largest time component of a foraging trip. This may explain the benefit of handling several seeds, as the gain in mass due to assessing additional seeds and subsequently harvesting a heavier than average seed more than offsets the relatively small increase in total trip time. However, few seeds should be handled at low seed densities because the increased search time relative to travel time greatly decreases the value of locating several seeds to obtain one of slightly greater mass (Charnov 1976, Orians and Pearson 1979).

Individuals and colonies differed in the time required for foraging efficiency to reach an asymptote due to slow seed recognition by colonies; the percentage of observed individuals that handled KBG seeds did not reach an asymptote until 7 and 9 d for *M. pergandei* and *P. rugosus* colonies, respectively (Johnson 1989). This difference suggests that enhancement of foraging efficiency by learning at the colony level was slowed by inexperienced individuals that began to harvest KBG seeds after the 1st d.

Body size and foraging techniques

Use of species-specific techniques that increase foraging efficiency may be a function of worker size relative to seed size. When seed size is small relative to worker size, as it was for *P. rugosus,* then foraging efficiency may be greatly improved by harvesting multiple seeds. This same strategy was employed by the smaller *M. pergandei* when harvesting the small *Sisymbrium irio* seeds (R. A. Johnson, *personal observation*). Though no data are available, *P. rugosus* may also decrease the number of seeds handled when harvesting larger seeds. Thus, both techniques for improving foraging efficiency might be employed by both species, but use of either or both techniques may depend on seed size relative to body size. These results do not suggest that body size differences in foraging efficiency affect partitioning of seed species, but rather demonstrate that foraging efficiency may improve via different techniques that correlate with body size. Species differences in foraging efficiency were due to *P. rugosus* carrying >1 seed.

Body size also affected travel time and handling time per seed, which were both consistently less for *P. ru-*

gosus. Travel time was related to the larger body size of *P. rugosus,* which had a faster travel velocity over the range of temperatures used in learning trials. The lower handling time per seed by *P. rugosus* was also probably due to a larger body size relative to seed size (Hespenheide 1966, Schluter 1982, Martin 1985), leaving more variance for learning effects of handling time in *M. pergandei.*

Memory and foraging efficiency

Memory was clearly an important part of foraging efficiency for both ant species, as all foraging efficiency indices (handling time per seed, number of seeds handled, number of seeds harvested) fell more slowly than they were acquired. All indices fell to the level of naive colonies within 12 d for *M. pergandei* and 29 d for *P. rugosus.* Differences between the two species may be due to differences in memory, greater longevity of *P. rugosus* foragers, or length of cue availability, e.g., presence of seeds in the nest.

It is unlikely that decay of handling efficiency indices was due to forager death as laboratory-housed foragers of both species, provided water and a dilute honey medium ad libitum, lived up to 52 d (R. A. Johnson, *unpublished data*). Additionally, field-marked *M. pergandei* foragers lived over 20 d (R. A. Johnson, *personal observation*), which was nearly twice as long as the time taken for memory indices to fall to the level of naive colonies, and mortality of *P. rugosus* foragers was low over a 1-mo period (Gordon and Hölldobler 1988).

Species differences in memory or length of cue availability cannot be separated at this time. However, the dramatic increase in *M. pergandei* foragers harvesting seeds on day 2 compared to day 1 can only be explained by naive individuals using seed caches as "informative centers" (Seeley 1985, Brown 1986, 1988) to become familiar with physical and chemical characteristics of KBG seeds. This result suggests that duration of cue availability may be involved in memory of foraging behaviors.

Handling efficiency indices fell more quickly in both species than did two discrimination indices, recognition and acceptance, the percentage of foragers that picked up and handled seeds and of that subset the percentage that harvested a seed, respectively. Seed recognition and acceptance reached the level of naive colonies in 75 and 53 d, respectively, in *M. pergandei.* Both indices were still decreasing after 82 d in *P. rugosus* and were estimated to decay to the level of naive colonies in ≈180 d (Johnson 1989). These data suggest involvement of two sensory systems, olfactory and tactile, one used in recognizing seeds and the other in handling them. Memory differences between the two sets of indices were likely related to cue availability; handling efficiency indices probably fell quickly since tactile cues were unavailable after seeds had been processed in the nest. In contrast, olfactory cues were avail-

able as long as seeds were in the granary or being spread trophallactically throughout the nest.

Learning and diet and patch selection

These results suggest that learning and memory are important components in diet and patch selection, especially for species such as these seed-harvester ants, which have limited time available to forage. The value or rank of a food type is determined by its net energy content divided by its handling time. Learning alters the value of a food type, from two- to fourfold in these seed-harvester ants; this effect is independent of recognition, which may also alter prey ranking (Hughes 1979). Consequently, prey density becomes important as foraging efficiency is a dynamic balance between learning and memory; at low prey densities forgetting occurs faster than relearning, and foraging efficiency is comparatively low.

Memory constraints may also favor prey specialization. This is especially true for prey types in which learning greatly increases their profitability because gains in foraging efficiency due to learning are only realized in the absence of interference from the simultaneous learning of other prey types (Pietriwicz and Kamil 1979, Stanton 1984, Persson 1985, Lewis 1986, Waser 1986).

Memory constraints may also similarly favor task specialization by individual ants. However, the colony dynamics of these tasks is flexible, which allows for efficient response to environmental stimuli such as territorial intrusion or rich food patches. Foraging is a high priority task within the colony (Gordon 1986). Consequently, location of rich seed patches likely results in recruitment of individuals from other tasks, such as nest maintenance, so as to more quickly exploit a food source that has been deemed worthy by numerous other colony mates (Gordon 1986, 1987).

Learning affects patch selection through decreases in search and travel time, the latter being the largest time component in a seed-harvester ant foraging trip. In this study, learning altered search behavior of outgoing foragers such that a more distant patch of known location was visited in preference to searching for nearer seed sources en route. Thus, patch distance becomes less important because the decrease in travel time to a far patch outweighs search time for a nearer patch. Large decreases in travel time should also select for foraging in patches until the patch quality is well below the habitat mean, especially for species such as these ants that utilize clumped resources (Bernstein 1975).

Overall, this study demonstrates the potential importance of learning and memory relative to diet and patch selection. The results also emphasize that a suite of learned behaviors contributes to gains in foraging efficiency, and that these learned foraging techniques are species-specific traits that correlate with body size relative to seed size.

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ERRATUM

In an article by C. T. Garten, Jr. ("Foliar leaching, translocation, and biogenic emission of ^{35}S in radiolabeled loblolly pines," Ecology **71**(1):239–251), part of the data in Table 3 (p. 244) and Fig. 2 (p. 245) were found to be miscalculated. Although the conclusions presented in the paper did not change because of these errors, the corrected data for Table 3 and Fig. 2 are published here for future reference. Data for monthly rainfall amounts, which appeared in Table 3 on p. 244, were correct as published and are not reproduced here.

TABLE 3. Mean ($\pm$SD) monthly SO_4^{2-}-S concentrations in net throughfall (NTF), and specific activity in NTF beneath each study tree.

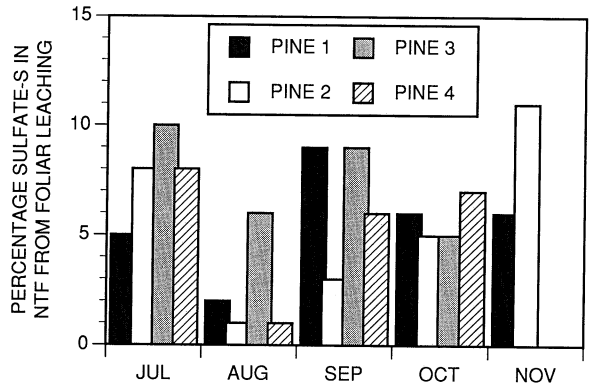| Month	Mean NTF SO_4^{2-}-S (mg/L)	Sulfur-35 specific activity in NTF (Bq/mg S)			
		Tree 1	Tree 2	Tree 3	Tree 4
July	0.72 ± 0.09	8.1	10	18	16
August	2.01 ± 0.25	3.1	1.9	12	3.0
September	0.85 ± 0.05	15	4.1	17	13
October	1.38 ± 0.46	10	6.3	8.9	14
November	0.56 ± 0.11	10	14	...	...

FIG. 2. Contribution of foliar leaching to net throughfall (NTF) sulfate concentrations beneath loblolly pines during each month of the experiment.