Differential learning and memory by co-occurring ant species

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Abstract

Foragers of the ants *Messor pergandei* and *Pogonomyrmex rugosus* experience differing levels of variability in the distribution of seeds they harvest due to species-specific differences in foraging behavior. *Messor pergandei* foragers experience more variable seed distributions and densities, learn to recognize a novel seed faster but forget this information faster than *P. rugosus*, which experiences more constant seed distributions even in the same habitat. Rate of learning to recognize a novel seed species was negatively associated with measures of seed species diversity for both ants. *Messor pergandei* foragers respond to variation in seed density by varying number of seeds handled per seed harvested, while *P. rugosus* foragers do not. Memory of a novel seed exceeds forager longevity, due perhaps to use of seed caches as a type of information center.

Introduction

Learning allows organisms to modify their response to familiar stimuli or to associate novel stimuli with categories that elicit familiar responses. The utility of such flexible behavior should vary interspecifically, as some species inhabit environments or display behaviors that place them in contact with novel stimuli more regularly than others. If learning ability is adaptive, then species that experience more variable or unpredictable environments should learn various novel stimuli more quickly (Johnston and Turvey, 1980; Johnston, 1982; Gould and Marler, 1984). Likewise, shorter memory span should also be adaptive in more variable environments because of the relatively rapid decline in the value of previously learned information when similar conditions recur only infrequently (Shettleworth, 1984).

Learning may be modified, however, by individual experience. Speed of learning decreases in more complex environments (Bowman and Harris, 1980; Martin, 1988), possibly because additional complexity or multiple prey items overload memory

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Environmental Variability. Foraging column dynamics of *M. pergandei* and *P. rugosus* were compared near the San Tan Mountains, Pinal County, Arizona (33°11'N, 111°43'W), during July–August, 1987; this was the only known sympatric locale at which *P. rugosus* foraged regularly in mid-summer. Foraging column direction of 13 *M. pergandei* and 12 *P. rugosus* colonies was measured to the nearest 5° each day for up to 16 days. Rotation was the angular deviation of each column between successive days. Accurate measure of double columns, which occurred regularly in *P. rugosus*, was possible because both columns never shifted direction over successive days.

Learning. Learning was examined by placing an experimental patch (ca. 20 × 3 cm) of Kentucky blue grass (KBG) seeds across a colony's foraging column 5 m from the nest entrance; all colonies of both species displayed single foraging columns throughout learning and memory trials. KBG seeds were used because they are novel seeds that are harvested readily by both ant species (Johnson, 1991). All KBG seeds were removed each day following observations.

We developed two assays of learning performance, 1) %handle: the percentage of foragers encountering novel KBG seeds in the field that grasped them with their mandibles, manipulated them, and then either dropped or carried them back to the nest, and 2) %harvest: the percentage of those individuals that handled seeds that carried one back into the nest. Thus, individuals that harvested seeds were a subset of those that handled seeds. Given that the former assay directly measures a forager's ability to respond appropriately to novel stimuli, it is this parameter that we expected to be most sensitive to environmental variance as detailed above.

Both learning indices were based on observations of 100 haphazardly chosen individuals that entered an experimental seed patch. At least two colonies per site per species were observed each day until the percentage of these 100 foragers that handled seeds reached an asymptote, defined as the day on which this figure increased less than 5% over three succesive days. These data were also recorded in two different years at one site per species. Additional colonies were observed for shorter periods; overall 12929 and 9600 observations were made on *M. pergandei* and *P. rugosus*, respectively.

Learning trials for each species were conducted across three habitats that varied in perennial plant species richness to test for interference effects on learning to recognize a novel seed type. Four sites were used for these trials: 1) west of the McDowell Mountains (MDM), 2) two km southwest of MDM (MDMVP), 3) near the western boundary of the Tonto National Forest (TNF), and 4) at the east edge of South Mountain Park (SMP), all in Maricopa County, Arizona. Habitat of all sites was typical Sonoran Desert. Each ant species was observed at three sites, as the two species were sympatric at SMP and MDM, but *M. pergandei* was the only species at MDMVP and only *P. rugosus* occurred at TNF (see Johnson, 1991).

Memory. Memory was assessed at MDMVP for *M. pergandei* and TNF for *P. rugosus*. Individuals within colonies were conditioned by placing ca. 10 g of KBG seeds across the foraging column 5 m from the nest each day for 14 days. The percentage of 100 haphazardly chosen foragers that handled seeds was assessed as above on days 12

through 14; 32 *M. pergandei* and 22 *P. rugosus* colonies in which seeds were handled by $\geq 75\%$ of the observed individuals (typical for conditioned colonies of both species) were used in subsequent memory trials. Unharvested seeds were removed after this period. Individuals in each colony were subsequently re-exposed to KBG seeds once at a predetermined date 2 to 100 days after conditioning by placing seeds across the foraging column 5 m from the nest. During the retest, memory was assessed by recording the percentage of 100 haphazardly selected foragers that handled and harvested KBG seeds. Up to four colonies were observed at intervals of 2–4 days until 15 days since conditioning, and at 10 day intervals thereafter.

Over the period in which memory was examined, recognition indices could decay due to memory loss at the individual level, forager mortality, or due to consumption of all KBG seeds in the colony seed cache; the latter method of decay relates to the possibility that individual ants acquire information from their colony seed cache. To better understand these possible causal factors we estimated maximum forager longevity using 100 foragers from each of four colonies per species. Individuals were housed in laboratory containers and provided water and a dilute honey solution *ad libitum*. Longevity was measured by counting dead individuals every 1–3 days. This method provides an upper estimate of forager longevity because predation is absent and environmental extremes are minimized under laboratory conditions.

Natural Seed Density. Ability of each species to respond to variability in natural seed density was measured for foragers that harvested a seed(s) as number of KBG seeds handled per seed harvested. Typically, few of the 100 observed individuals harvested KBG seeds during the first and sometimes second day of learning trials. During these periods, we continued to record number of seeds handled per seed harvested until 10 individuals had been observed.

Annual seed density is positively associated with rainfall from 1 Jan. to 1 Apr., the period of maximum germination and seed set in the Sonoran Desert. Relative seed density was inferred from rainfall data (Johnson, 1991) at the nearest weather station (TNF and SMP) or the mean of equidistant stations (MDM and MDMVP) (NOAA 1985, 1986, 1987).

Data Analysis. Learning data were analyzed for colonies with ≥ 2 days exposure to KBG seeds using a standard stochastic learning model (Coombs et al., 1970):

$$C_{n+1} = C_n(1 - m) + \theta[P - C_n(1 - m)]$$

where C_{n+1} is number of foragers in the conditioned state on a given day, i.e. they handled/harvested KBG seeds that day, C_n is the number in that state on the previous day, and m is the 24 hour mortality rate. Theta (θ), the rate of learning, is the proportion of the previously unconditioned forager population (the base population [P] minus the number of remaining foragers that had been conditioned on preceding days) that on any given exposure learns to handle/harvest KBG seeds. This model formalizes the assumption that each exposure conditions a fixed portion (θ) of the unconditioned population $[P - C_n(1 - m)]$. The population is assumed steady-state so that births cancel deaths, keeping P constant. We divide by the unknown, P,
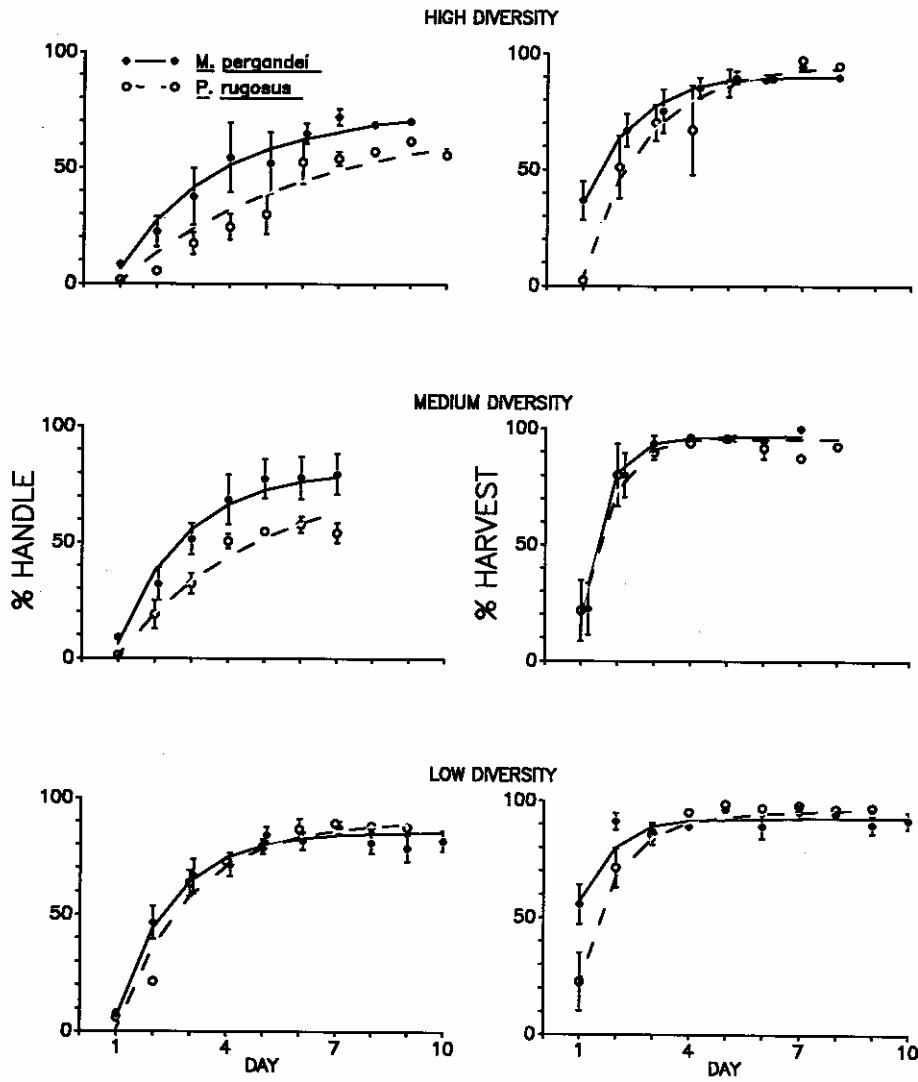
Figure 1. Percentage of *Messor pergandei* and *Pogonomyrmex rugosus* foragers that handled seeds (left) and harvested seeds given they had handled them (right). The first exposure was on day 1. Each data point is the mean (± 1 SE) of all colony values recorded for that learning trial (day). Data for each colony are based on 100 haphazardly observed individuals per trial. Dashed and dotted lines are predicted values for each species (see text). Interspecific comparisons are valid for only the high and medium diversity sites

convert to proportions, and rearrange to derive the predicted form of the learning curve

$$p_{n+1} = p_n(1 - \theta)(1 - m) + \theta$$

where $p = C/P$ is the proportion of the population that is conditioned. The asymptote is 1.0 when trained foragers are not lost through mortality or task reassignment ($m = 0$) and proportionately lower as mortality increases. Theta sets the rate of approach to the asymptote. These curves are thus determined by three parameters, m, θ, and p_1, the probability of "recognition" on day 1. For both %handle and %harvest, p_1 was set to the observed value on the first day across the three tested habitats per species in which learning trials were conducted. Thetas were compared between species at the two sites of sympatry using a Mann-Whitney U test and within each species across the three levels of environmental diversity using the Jonckheere test for ordered alternatives (Hollander and Wolfe, 1973).

Memory was examined by regressing %handle and %harvest against days since previous exposure to KBG seeds. Each regression included data up to and including the asymptote, which was the interval during which the mean of each index changed less than 5% over three successive intervals. Number of days until each recognition index decayed completely was determined by inserting the mean naive colony value (day 1) into a best fit line obtained from an iterated linear regression using the memory data. Rate at which recognition scores decayed was compared interspecifically by comparing regression lines. Recognition scores were compared similarly with forager survival data.
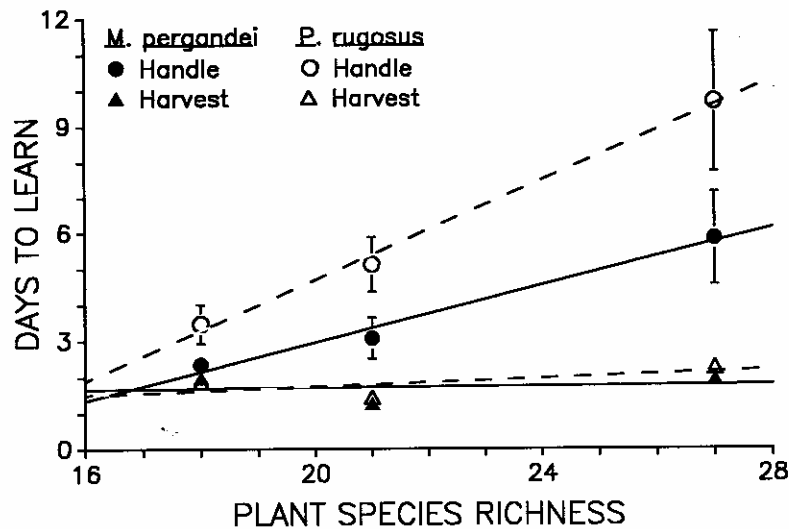

Figure 2. Average number of days for each species to learn to handle or harvest novel seeds, as a function of environmental diversity. These data, which are the reciprocals of theta, give the mean number of days required to condition the foraging population

Results

Messor pergandei colonies experience higher levels of environmental variability while foraging than do sympatric colonies of *P. rugosus*. Over a 15 day period at one of our field sites, 88% of *M. pergandei* columns (N = 161) changed direction on the succeeding day, compared to only 12% of *P. rugosus* columns (N = 188) (percentage test, P < 0.001; Sokal and Rohlf, 1981). Four of 12 *P. rugosus* colonies did not change direction in two weeks, while all *M. pergandei* colonies changed direction at least five times in 12 days. Foraging columns of *M. pergandei* colonies also travelled in more directions over that time than did those of *P. rugosus* (Wilxoxon two-sample rank test, P < 0.001, no overlap).

As predicted from differences in foraging column direction change, *M. pergandei* foragers learned to handle KBG seeds more quickly and had a higher asymptotic probability of doing so at both sites tested where the ants co-occurred, i.e., the high and medium diversity sites (Fig. 1; one-tailed Mann-Whitney U test, MDM; P = 0.05, N = 10: SMP; P = 0.05, N = 11). These differences became more pronounced when pooling data at both sites (P < 0.01, N = 21), despite habitat variability in these values for both species (see below). Percent handling did not differ between years at the same site for either species (P > 0.20, two-tailed Mann-Whitney U test). Percent harvesting seeds, a behavior contingent upon %handling, did not differ interspecifically at either site (P > 0.10) as predicted. Recognition indices (%handle and %harvest) for both species increased with conditioning following the characteristic negative exponential growth curve (Fig. 1) (Coombs et al., 1970).

Average number of days needed by each species to learn to handle novel seeds, measured as the reciprocals of theta (θ), varied as a function of environmental diversity. Number of days to learn to handle the novel KBG seeds took significantly longer for both species in more diverse environments (Jonckheere test, P < 0.005; Fig. 2), and as expected *M. pergandei* was less affected by this apparent sensory load than was *P. rugosus*. Learning to harvest a seed once it was handled was quicker than learning to handle it and was similar between species and across the three levels of environmental diversity (Fig. 2).

Rate of decay for both recognition indices was also faster for *M. pergandei* than *P. rugosus* (F test, P < 0.001, Fig. 3). Further, percent handling KBG seeds decayed more quickly than percent harvesting seeds in both species (%handle: *Messor:* Y = $-1.1\,X + 91.4$, N = 30; *Pogonomyrmex:* Y = $-0.5\,X + 91.6$, N = 22: %harvest: *Messor:* Y = $-0.9\,X + 104.5$, N = 30; *Pogonomyrmex:* Y = $-0.15\,X + 98.4$, N = 22). Memory for handling a novel seed was retained significantly longer than maximum estimated forager longevity for either species (F test, P < 0.001). Percent handling decayed to the level of naive colonies in 75 days for *M. pergandei* and was still decreasing after 82 days for *P. rugosus*, while all laboratory-housed foragers died within 52 days (mortality: *Messor:* Y = $-2.1\,X + 86.0$, N = 99; *Pogonomyrmex:* Y = $-2.4\,X + 89.6$, N = 77; Fig. 3).

Number of seeds handled prior to harvesting one varied as a function of *a priori* determined natural seed density for *M. pergandei* but not for *P. rugosus:* in habitats inferred to have low natural seed density *M. pergandei* foragers handled fewer KBG seeds while *P. rugosus* foragers displayed no such response (Fig. 4).
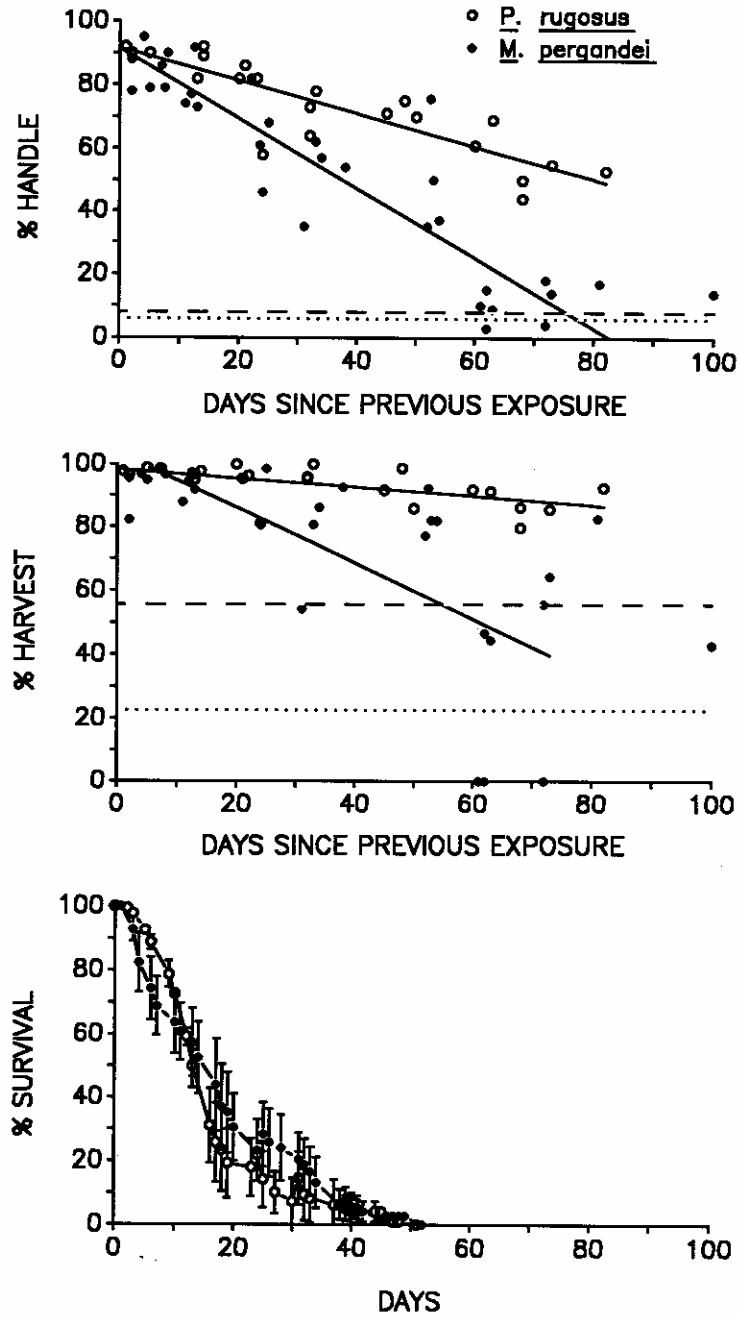
Figure 3. Percentage of foragers that handled (top) or harvested seeds given that they had handled seeds (middle) as a function of days since the last day of conditioning. Each colony contributed one data point per panel. Data for each colony are based on 100 haphazardly observed individuals that entered the seed patch. The dashed and dotted lines are scores for percent handling and percent harvesting by naive *Messor pergandei* and *Pogonomyrmex rugosus* colonies, respectively. Survival of foragers for each species (bottom) was estimated using 100 field-collected individuals from each of four colonies per species that were housed in the laboratory
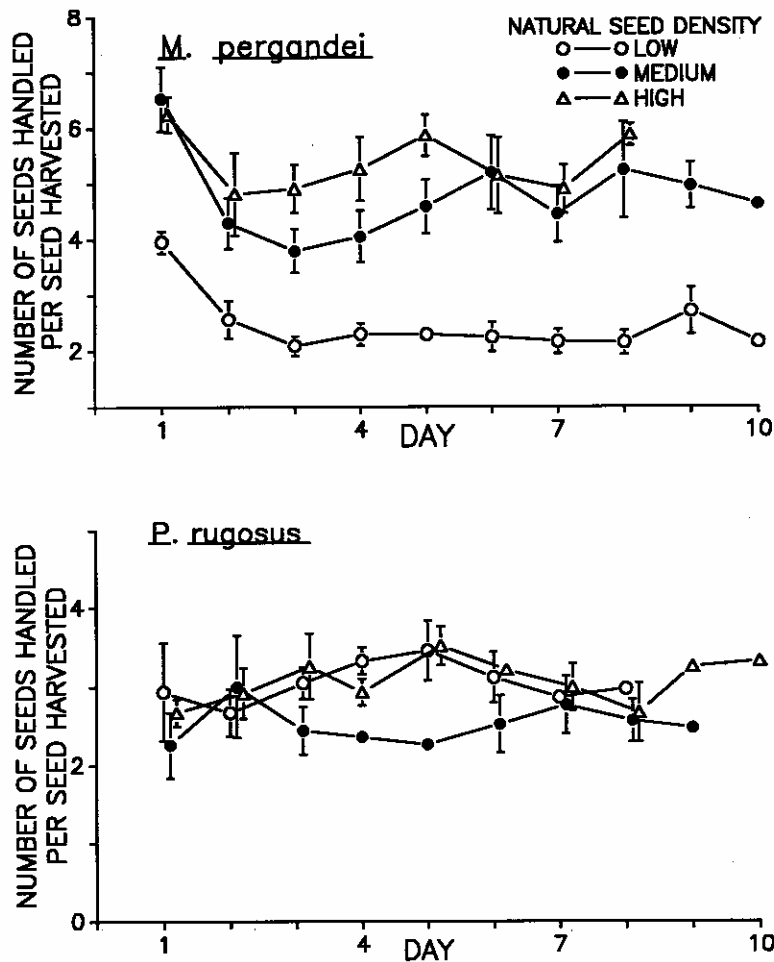
Figure 4. Variation in number of Kentucky blue grass (KBG) seeds handled by *Messor pergandei* and *Pogonomyrmex rugosus* colonies. Data include only individuals that harvested a seed. Each data point is the mean (± 1 SE) of all colony values recorded for that learning trial. Sample sizes are N ≥ 3 colonies per seed density through days 6 and 7 for *M. pergandei* and *P. rugosus*, respectively, except for N ≥ 2 for *P. rugosus* at medium seed densities

Discussion

Learning ability in the desert seed-harvester ants *M. pergandei* and *P. rugosus* is a trait influenced proximately by individual experience (habitat differences) and ultimately by the environment experienced by each species (interspecific differences). Differences in learning and memory observed between *M. pergandei* and *P. rugosus* are consistent with species-specific differences in foraging methods and the resulting differences in environmental variation experienced. While laboratory studies have

demonstrated faster learning in species that possess greater behavioral flexibility (Sasvàri, 1979; Greenberg, 1984; Laverty and Plowright, 1988), this is the first study to examine multiple aspects of learning ability in the field.

The learning equation of Coombs et al. (1970), designed for simple conditioning experiments, successfully models colony learning whether the phenomenon governing rate of learning is due to consolidation of individual memory or to recruitment of individuals to these seeds. Observations suggest both processes occur as some individuals consistently harvest KBG seeds after their first exposure, others handle seeds and exit the patch without a seed, while others ignore the seeds. Regardless of the underlying mechanism of learning by individuals in a colony, interspecific differences in learning rate at both sites suggest this rate is a consequence of the species' ecology.

Learning rate was also inversely associated with environmental diversity, which suggests that increasing numbers of seed types progressively interfered with recognition of a new seed species (Kintsch, 1977). Such results would arise from ants having a limited learning capacity for seed types, a phenomenon that may also occur in birds (McGregor and Avery, 1986). Such interference is one of the most robust findings in studies of memory and might explain memory differences between species, as the foraging column rotation of *M. pergandei* exposes them to a more variable diet. But such interference works against learning and memory, making the faster learning by *M. pergandei* even more impressive.

Seed memories persist longer than the individual foragers possessing them (Fig. 3). It is unlikely that foragers live as long as colonies retain information about seeds, especially since workers in most social insects display age polyethism and assume the relatively risky task of foraging near the end of their lives (Wilson, 1985). Additionally, our longevity estimates were made under ameliorated laboratory conditions that lacked environmental extremes and are longer than those for foragers of similar species under field conditions (Porter and Jorgensen, 1981).

The mechanism that promotes such long-term memory may be extensive seed caches, which could serve to prolong memory of individuals within a colony by providing chemical cues to seeds currently available in the environment. Seed cache longevity for these species is unknown, but could apparently serve such a function as caches of *P. rugosus* support colonies over several months of inactivity. For most social insects, workers that process food in the nest and consequently experience its physical and chemical characteristics will soon forage outside the nest. Younger workers will also experience chemosensory aspects of currently exploited food sources as they are spread through mutual feeding, with amount of exposure dependent on recency and richness of that food in the environment.

Use of seed caches for obtaining information is also supported by different decay rates for other learning indices. Handling indices such as handling time per seed, number of seeds handled, and number of seeds harvested decreased to the level of naive colonies in less than one-third the time required for complete decay of the recognition indices %handle and %harvest (Johnson, 1991). These differences can only be explained in that handling indices involve tactile cues to assess physical characteristics of seeds while recognition indices involve olfactory cues. Tactile cues for handling indices were probably unavailable once seeds had been processed in the

nest, while olfactory cues were available as long as seeds were in the granary or being spread through mutual feeding (Johnson, 1991).

Messor pergandei displayed an increased ability to discriminate and respond to variation in natural seed density, as the number of seeds handled per seed harvested was positively associated with natural seed density for this species but not for *P. rugosus*. Such differences may arise because "trunk trails" restrict *P. rugosus* foragers primarily to experiencing temporal variation in seed density, and even this variation is probably low as *P. rugosus* colonies often cease foraging for several months.

Several explanations for these interspecific differences in learning ability can be evaluated. Differences are not due to seed attractiveness or palatability as both recognition indices for KBG seeds overlapped interspecifically across sites; additionally palatability differences should be manifested by converse patterns of learning and memory, i. e., a faster learning and slower decay rather than faster learning and faster decay as occurred for *M. pergandei*. Neither is the faster learning by *M. pergandei* due to faster return of the same individuals to the seed patch as seed handling times and travel time to and from the nest were faster for *P. rugosus* (Johnson, 1991). It is also unlikely that KBG seeds are more similar to a food already familiar to one of the ant species, and thus preferred, because diets of sympatric colonies of both species overlap strongly (Rissing, 1988). Lastly, learning might be faster in *M. pergandei* if such ability increases as experience is gained on more prey types, i. e., learning to learn. However, learning rates for both species were negatively rather than positively associated with perennial plant species richness as this alternative would predict.

Learning rate may also vary due to species differences in recruitment rate over the 7–10 days typically required to condition colonies to KBG seeds. This idea views recruitment as a long- rather than the more typical short-term response that occurs over several hours and functions to exploit resources before competitors do (Hölldobler, 1976). Such behavior may involve recruitment of individuals from other tasks (Gordon, 1986), but changes in the absolute number of foragers could not affect our dependent variables, which were measured as percentages. Species differences due to recruitment rate or scaling recruitment to the number of seeds previously brought into the nest are further ruled out as causal factors by comparing learning and memory curves for each species; if a higher recruitment rate causes learning to be faster in *M. pergandei* then that higher rate should persist into the memory phase and lead to a slower, rather than the observed faster memory decay.

The causal mechanism for the observed interspecific differences may be genetic, developmental, or related to seed cache usage. Interspecific differences in memory may also be an example of interference of earlier memories (KBG) by later ones (Kintsch, 1977), or differential rate of replacement of initially trained animals. These potential mechanisms cannot be separated at present. An evolutionary basis for some of these differences is suggested by genetic variability and selective modification of learning in insects such as *Drosophila* and honey bees *(Apis mellifera capensis)* (Dudai, 1977; Brandes et al., 1988).

Acknowledgment

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