

# The adaptive nature of non-food collection for the Florida harvester ant, *Pogonomyrmex badius*

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**Abstract.** 1. Many animals forage for non-food objects, such as nesting materials. In many organisms, the depots of such objects can be expansive, and are not intuitively adaptive. This study empirically explores varying theories for why these depots exist in the Florida harvester ant, *Pogonomyrmex badius*.

2. The Florida harvester ant, like its western congeners, collects and deposits large quantities of non-food objects around its nest entrance. The vast majority of objects sampled from colonies in this study population were charcoal pieces whereas most western species collect pebbles.

3. Objects in these depots can number in the millions, suggesting a large cost to this behaviour and strengthening an adaptationist argument.

4. Many hypotheses have been suggested for these depots, including temperature and water modification and territoriality. No evidence was found to support the results of a previous study which found that charcoal depots deter other ant species.

5. The depots do not appear to affect soil hydrology, but do slightly increase soil temperature at the very top of the nest. In an attempt to estimate the seasonal fitness of colonies with and without charcoal depots, no statistical difference was detected in sexual investment between treatment groups.

6. These results suggest that the charcoal depots may be selectively advantageous through temperature modification, but may serve alternate functions that are species and habitat specific.

**Key words.** Adaptation, depot, foraging, function, object, *Pogonomyrmex*.

## Introduction

Many organisms forage for items, in addition to food, such as nesting materials. Sometimes, the adaptive significance of non-food items is not obvious, such as when rodents collect shiny materials (e.g. *Neotoma* sp.; Kaufman & Kaufman, 1984), woodpeckers collect rocks and bones (Hess & James, 1998), and ants collect pebbles and twigs (Smith & Tschinkel, 2005). As some of these animals are such prolific collectors of objects it is difficult not to construe adaptationist hypotheses (Gould & Lewontin, 1979) for the existence of this behaviour. Though this behaviour may be adaptive, it need not be (e.g. neutral selection or exaptation), and requires experimental manipulation to be adequately evaluated.

Social insects can be formidable gatherers of resources because of their ability to allocate many individuals to the task of foraging. In species that collect non-food objects, the deposition of these objects around nests can be expansive and easily visible. Many ant species collect objects such as pebbles, twigs, litter, and charcoal, and eventually deposit and arrange them around the nest entrance (e.g. many *Pogonomyrmex*, *Aphaenogaster*, *Pheidole*, *Formica*, *Myrmecocystus*, and *Dorymyrmex*, etc.). The purposes the objects serve are likely to be specific to the particular type of object, the species, and the habitat. Studies have shown that objects around nests can be marked with colony recognition markers (Grasso *et al.*, 2005), or can have antimicrobial properties (Christe *et al.*, 2003). Many researchers have proposed that large heaps of objects on top of nests can change the thermal and hydrological properties of the nest (Cole, 1932, 1968).

Harvester ants are prolific collectors of seeds, with some species storing hundreds of thousands of seeds in their granaries throughout the year (Tschinkel, 1999). In addition to seed

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collection, they collect many other objects (e.g. pebbles, litter, charcoal; Smith & Tschinkel, 2005) and deposit them in a large pile around their nest entrance. For centuries, humans have exploited the pebble mounds in some *Pogonomyrmex*. Native Americans made instruments with the pebbles (Taber, 1998), geologists have used them to approximate bedrock geology (S. Paxton, pers. comm.), and archaeologists and paleontologists exploit them to find small artifacts and fossils (Hatcher, 1896; Lull, 1915). Yet it is still not known why they collect them. It is quite likely that the behaviour of object collection in North American *Pogonomyrmex* is the same across species (homologous), regardless of what objects are collected, and represents the ancestral state for the genus (Smith & Tschinkel, 2005).

This study reports experimental tests of several hypotheses for the adaptive significance of the charcoal depots of the Florida harvester ant, *P. badius*. The only published study on these charcoal depots (Gordon, 1984) proposed that they deter con- or heterospecific ants, acting as a type of territorial marker. This hypothesis was tested experimentally using an entire ant community. As nest superstructures are often implicated to affect hydrology (Laundré, 1990; Blom *et al.*, 1994; Wagner *et al.*, 1997; Green *et al.*, 1999) and temperature (Coenen-Staß *et al.*, 1980; Seeley & Heinrich, 1981; Horstmann & Schmid, 1986; Porter, 1990; Cole, 1996), hypotheses related to those abiotic factors were also tested. Finally, the effect of charcoal depots on a measure of reproductive fitness of field colonies was also tested. While this paper is essentially addressing the 'function' of charcoal depots (e.g. Tinbergen, 1963), a companion paper (Smith & Tschinkel, 2005) examines aspects of its ontogeny, causation, and evolution.

## Methods

### Site description

All experiments were conducted in the Apalachicola National Forest (ANF), approximately 15 km south of Tallahassee, Florida, U.S.A. Two populations of harvester ants were used: Ant Heaven and Clear-cut. These sites differ in several respects, namely that Ant Heaven was logged in 1975 while Clear-cut was logged in 1999. Furthermore, the water table is typically much deeper at Ant Heaven compared to Clear-cut. As a result the vegetation and ant communities differ between the sites. Ant Heaven now has half-grown longleaf pine (*Pinus palustris*) that are heterogeneously and thinly spaced, creating many light gaps and an open floor with patchy grasses and cacti (*Opuntia* sp.), whereas the planted longleaf pines at Clear-cut are seldom more than 1 m tall, and the site is dominated by herbaceous vegetation, predominantly *Vaccinium myrsinites*. The *P. badius* population at Ant Heaven has persisted for at least 30 years (W. R. Tschinkel, pers. obs.), whereas colonies at Clear-cut likely recruited following the logging of the area and the elimination of canopy cover. Very few *P. badius* colonies are found in adjacent unlogged patches of forest. Both sites represent dense populations for the ANF, with an estimated 5.8 colonies per hectare for Ant Heaven and 2.3 for Clear-cut. The predominant ants at these sites, other than *P. badius*, are *Solenopsis geminata* (Ant Heaven

only), *Solenopsis invicta* (Clear-cut only), *Forelius pruinosus*, *Dorymyrmex bureni* and *Trachymyrmex septentrionalis*.

### Charcoal as an ant deterrent

Gordon (1984) asserted that charcoal was a territorial marker through deterring con- and heterospecific ants. If harvester ant charcoal is an ant deterrent, then fewer ants should be caught in traps surrounded by nest charcoal than by control materials. Therefore, it was hypothesised that both *P. badius* and overall ant abundance would be lower in pitfalls surrounded by *P. badius* charcoal. This experiment was conducted at Ant Heaven in late May and early June 2002.

Pitfall traps (50 ml centrifuge tubes, 3 cm diameter opening) filled with ~15 ml of either ethylene or propylene glycol were used to capture ground-foraging ants (Agosti *et al.*, 2000). Four pitfall traps spaced 1 m apart in each cardinal direction were placed at each intersection of a 9 × 5 grid (160 × 80 m), a total of 45 sets of four, or 180 traps. Each grid intersection, with all four treatments present, was used as a block to account for spatial variation in capture rates. The pitfalls were covered for 1 week to allow ants to acclimate to their presence.

Pitfalls in each block were randomly assigned to one of four treatments: charcoal collected from *P. badius* nests outside the study plot (*P. badius* charcoal); charcoal collected from the forest floor (ambient charcoal); chopped pine needles (pine); and what was naturally in the immediate area, removed and replaced (disturb) to control for manipulations and disturbance during experimental set-up. The other three treatments allow separation of the effects of the substrate (pine needles in this case), the burning of the substrate (ambient charcoal), or the ant association with the burned substrate. Approximately 200 g of charcoal was spread evenly (~1 cm deep) around a circle with 0.6 m diameter, similar to the covering on an average *P. badius* nest (Smith & Tschinkel, 2005).

One day elapsed between substrate collection and the start of pitfall trapping. Pitfall traps were collected and replaced twice at 3-day intervals. In the lab the contents of the traps were counted, sorted and identified. Species-level identifications were only made for the first collection, ants in the second collection were only counted (although several species were sorted out), and a heavy rain spoiled the third sample. Voucher specimens have been deposited in the collection of Dr M. Deyrup (Archbold Biological Station, Lake Placid, U.S.A.).

Both ant abundance (number of ants per trap) and occurrence (presence/absence) were used to estimate ant activity. As ants are colonial organisms that recruit to resources, analyses of total abundance can often lead to a misinterpretation of results since colony size varies by orders of magnitude across species and species differ in how they forage (i.e. solitary, group, mass recruiting) and where they forage (below ground, in the litter, in the vegetation). A conservative analysis assesses the presence or absence of any given species in the trap, thus making the assumption that only a single colony of each species is present in the collection (this was not done for collection two because species were not identified).

A randomized block ANOVA, using only the main effects of treatment and block, was used to assess the effects on the

community as a whole. Tukey's Honest Significant Difference (HSD) test was used to assess all pair wise differences in the randomized block ANOVA models. To elucidate the importance of species identity in driving the overall effect, a subset of abundant species were analysed separately. Due to heterogeneous variances, a non-parametric Kruskal-Wallis test (neglecting the variance due to block) was used. To account for zeros, log base 10 ( $x + 1$ ) transformations were used in all analyses.

### Hydrology

The hypothesis that charcoal prevents the loss of soil moisture (i.e. as a mulch) was tested independently of colonies at Ant Heaven in March 2004. Four pairs of circular areas similar in size to *P. badius* nests (diameter = 0.6 m) were stripped of litter and enclosed using aluminum flashing (~8 cm deep). Plots in each pair were 0.5 m apart, and 10 m apart from any other pair. Flashing was used to prevent horizontal water loss and maintain the objective of simulating flooding. On four of these areas, one in each pair, a layer of 200 g of charcoal, similar in amount to that on *P. badius* colonies, was spread evenly, while the other four were left bare. Two litres of water from a watering can simulated rain and was enough to form small temporary pools within the enclosures. This translates into 2 mm of rain in ~2 min ('heavy rain' is > 0.75 mm per hour; Whiteman, 2000). At 0, 1, 2, and 5 days after watering, 5 cm deep soil cores (averaging 19 g of dry soil) were taken from each type of enclosure and directly outside the enclosures (unmanipulated control). The resulting holes were filled to prevent increased evaporation. Wet and dry soil weights were used to calculate the per cent of water in the soil. A two-way ANOVA, with treatment (covered, uncovered, control) and time since watering, was used to assess statistical differences. Tukey's HSD test was used to compare differences between individual treatments.

To test whether charcoal acts as a roof, protecting the upper chambers from collapse during heavy rain, six colonies at Ant Heaven (March 2004) were stripped of their charcoal and the covering was replaced in three of these. A small pit (~0.75 m deep) was excavated adjacent to the colony and slowly expanded in the direction of the colony until chambers were exposed in cross-section. The height of exposed chambers was measured and a piece of filter paper was placed inside. Three to four chambers were sampled per colony, with chambers ranging from ~1–13 cm in depth. Subsequently, the mound was evenly watered, simulating heavy rain as described above. The chambers were re-measured and the filter paper checked for dampness. It was hypothesised that a decrease in chamber height was indicative of damage due to simulated rain.

### Temperature

Temperature was measured using two types of probe. In the first method, a probe with temperature sensitive microchips placed at depths of 0, 4, 8, 16, 32, 64 cm and air was placed in the center of an area (0.6 m in diameter) covered with ~200 g of charcoal. A second probe was placed in an adjacent uncovered

area. Probes recorded data every three minutes for two 24 h cycles and then were switched, and recorded two additional 24 h cycles. Since the effective sample size was only two, these data were analyzed qualitatively, and hence no statistics are reported. Temperatures were grouped by depth and into four time categories: 'too early' = 00:01 h–06:00 h, 'morning' = 06:01 h–12:00 h, 'afternoon' = 12:01 h–18:00 h, and 'evening' = 18:01 h–00:00 h. This was carried out at Ant Heaven in late July 2002.

The second method measured temperature at 2, 4 and 8 cm depth using thermocouple sensors at nests with charcoal either removed, or removed and replaced. This was carried out in mid-April 2003 on a total of 15 colonies of each type at Clear-cut. All measurements were taken near midday because Gordon (1984) detected the biggest effect of charcoal on nest temperature at this time. *T*-tests between charcoal covered and uncovered nests, at each depth, were used to analyze these data.

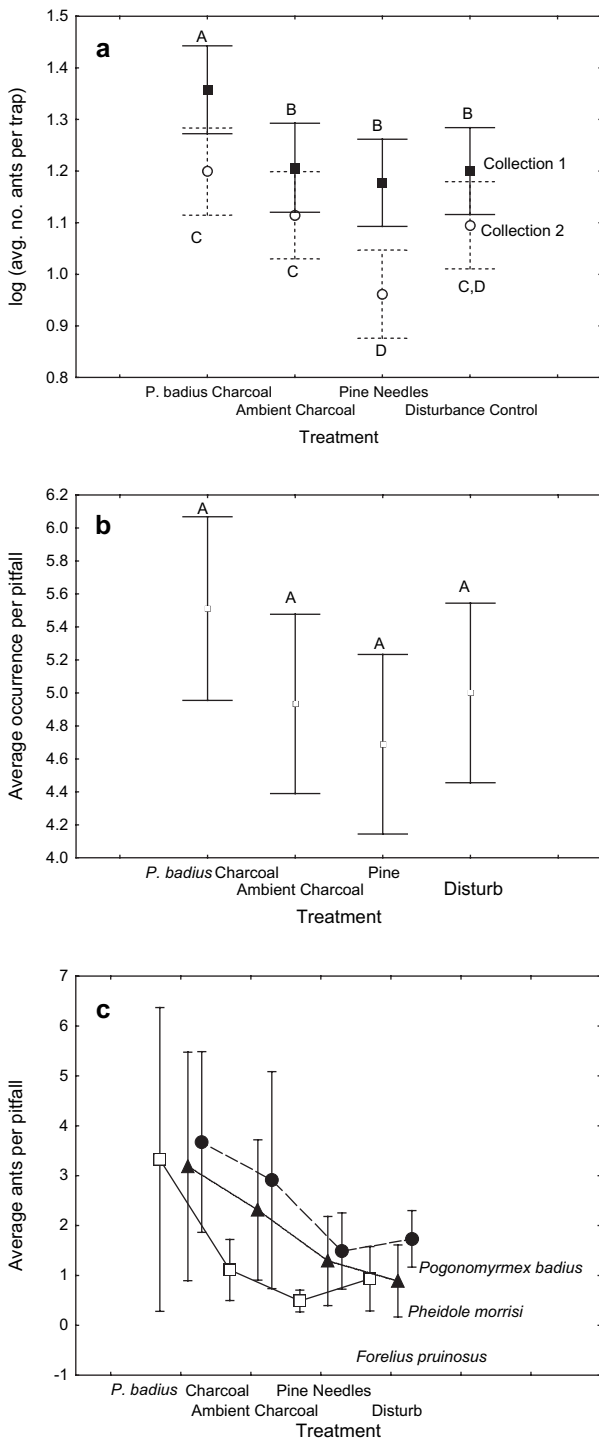
### Fitness

The reproductive output of colonies (adjusted for colony size) over one reproductive season was used as a proxy for true fitness. At Clear-cut in early March 2003, 30 *P. badius* colonies were randomly assigned to a treatment, either charcoal removal or removal-and-replacement. The ideal third treatment group, unmanipulated colonies, was not included in the design due to constraints in our ability to excavate colonies prior to nuptial flights (but after all sexuals had been produced). This was a foreseen tradeoff; although including a control for nest disturbance was more valuable than having the unmanipulated control. Every 2–3 weeks treatments were maintained as colonies continuously collected charcoal (Smith & Tschinkel, 2005). When reproductive flights seemed imminent in late May/early June, the largest 18 of the original 30 colonies were fully excavated as in Tschinkel (1998). In the lab, colonies were sorted and the number and weights of workers and winged reproductives (male and gyne adults and pupae) were determined. An ANCOVA was used to analyze these data where the number of dark (mature) workers was the covariate.

## Results

### Charcoal as an ant deterrent

A total of 6257 ants of 29 species were trapped. More ants were collected in the first compared to the second collection (an average of 20 vs. 15 ants per trap respectively). More individual ants were collected in pitfall traps surrounded by *P. badius* charcoal than all other treatments in both collections (Tukey's HSD test: *P. badius* charcoal was different to all other groups,  $P < 0.05$ ; other groups were not different from each other; Fig. 1a). There were no differences between groups in the occurrence data (Tukey's HSD test:  $P > 0.05$  in all cases; Fig. 1b). If *P. badius* is eliminated from the abundance data, the overall pattern does not change (more ants collected in pitfalls surrounded by *P. badius* charcoal), and is still statistically significant ( $F_{3,130} = 5.42$ ,  $P < 0.01$ ).



**Fig. 1.** (a) The effect of treatments on the total number of ants captured in traps in experiment 1. Treatments with shared letters were not different in a Tukey's HSD test ( $P > 0.05$ ), A–B and C–D pertain to collections 1 and 2 respectively. (b) The average ant occurrence (presence of a species) in pitfalls across treatments. Letters indicate groups that were not significantly different ( $P > 0.05$ ) in a Tukey's HSD test. (c) The average number of ants per pitfall across treatment groups for three species of ant: *Pogonomyrmex badius*; *Pheidole morrisi*, and *Forelius pruinosus*. All error bars denote 95% confidence intervals.

Taking the identity of individual species into account suggests that the effect is driven by a subset of species. Three species in particular cause this greater abundance in the *P. badius* charcoal treatment: *P. badius*, *Pheidole morrisi*, and *F. pruinosus* (Fig. 1c). These data were heteroscedastic and required non-parametric statistics. Although trends were apparent for several species ( $P \sim 0.1$ ), only *P. badius* showed a significant effect of treatment, where more were collected in the *P. badius* charcoal treatment (Kruskal–Wallis test:  $H_{3,178} = 9.3, P < 0.05$ ). In multiple comparisons, the *P. badius* charcoal group was only significantly higher in *P. badius* abundance than pine needles ( $P < 0.01$ ), and not differentiable from the other groups.

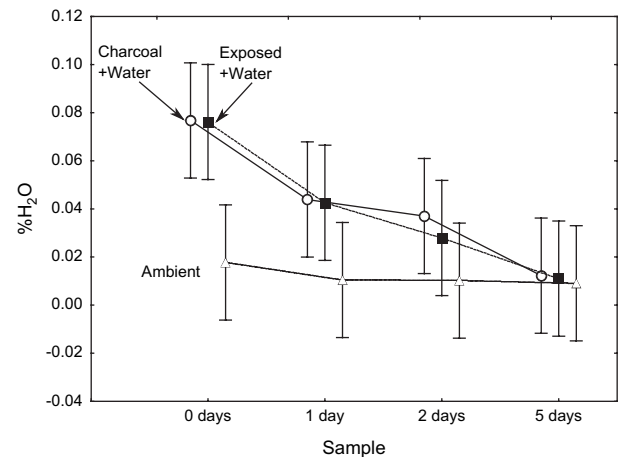
*Hydrology*

The simulated heavy rain increased soil moisture by approximately 6% within 10 min in the top 5 cm of soil. Charcoal had no effect on the ability of soil to retain this water – charcoal covered soil dried at the same rate as bare soil (Fig. 2) (ANOVA: treatment,  $F_{2,36} = 8.17, P < 0.005$ ; sample,  $F_{3,36} = 8.00, P < 0.001$ ) (Tukey's HSD test for treatment: covered and uncovered plots were not different, but both were greater than unwatered plots until the 5th day). After 5 days both treatments were not differentiable from the ambient soil moisture, which remained constant throughout the experiment.

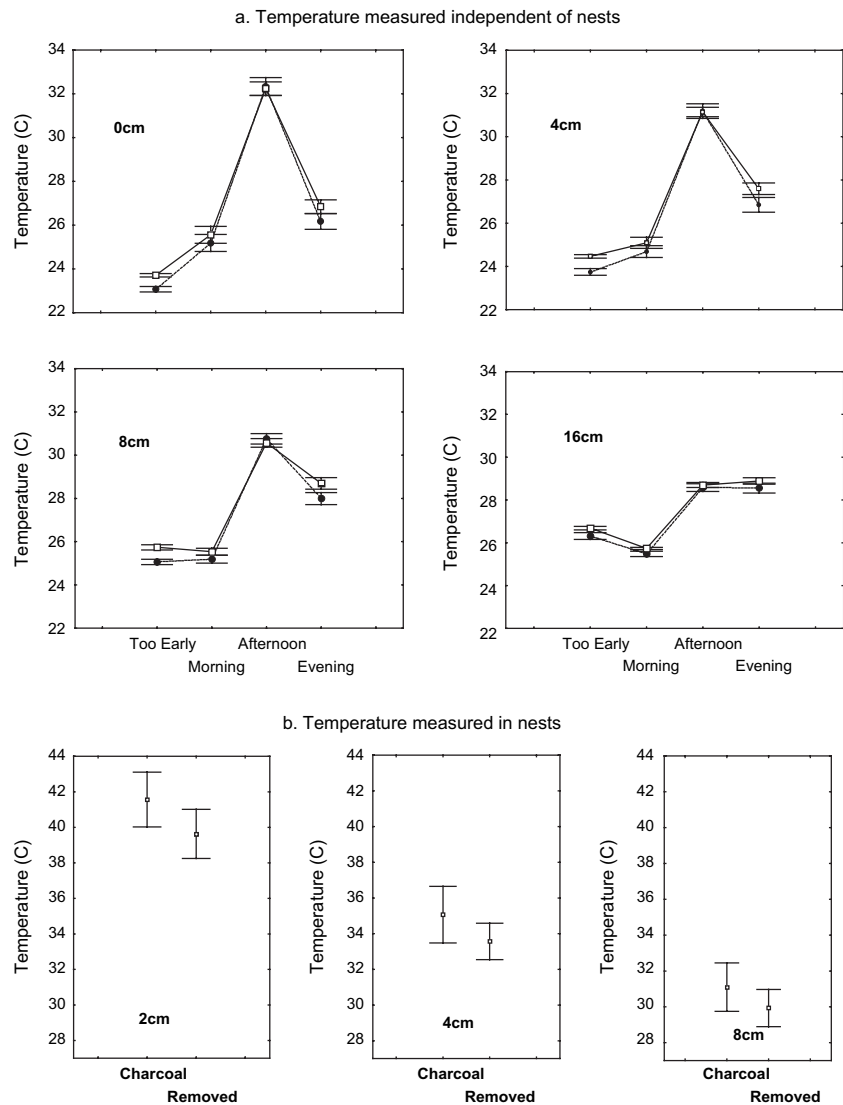
No chambers collapsed after simulated rain. There was not even a change in chamber height afterwards ( $t_{19} = 0.56, P > 0.4$ ). Chambers that were nearer the surface were marginally more likely to get wet than deeper chambers ( $t_{19} = 1.8, P < 0.1$ ). The average depths of wet vs. dry chambers were 3.2 and 5.3 cm respectively.

*Temperature*

Independent of nests, a covering of charcoal, compared to bare soil, increased temperature up to a depth of 16 cm (Fig. 3a),



**Fig. 2.** The effect of charcoal on soil moisture over time. Error bars denote 95% confidence intervals. Charcoal did not affect the rate of soil drying.



**Fig. 3.** The effect of charcoal on soil temperature across depth. (a) Soil temperatures independent of nests. In all graphs, open squares represent temperature probes surrounded by a layer of charcoal, whereas solid circles represent untreated probes. Time intervals are each 6 h where ‘Too early’ = 00:01 h–06:00 h, ‘Morning’ = 06:01 h–12:00 h, ‘Afternoon’ = 12:01 h–18:00 h, and ‘Evening’ = 18:01 h–00:00 h. Error bars denote 95% confidence intervals. (b) The effect of charcoal on nest temperature at 2, 4, and 8 cm. Error bars are 95% confidence intervals. Treatments were not statistically different at any depth, although there is a consistent trend indicating that charcoal does increase nest temperature. Temperatures were taken in the afternoon in late spring at nests at Clear-cut. Error bars denote 95% confidence intervals.

but only in the morning and evening. Moreover, temperature differences were all small ( $< 1^{\circ}\text{C}$ ).

The second method measured temperature directly in nests with and without charcoal coverings during midday heat. Although no significant temperature differences were found between treatments at any depth, there is an obvious trend (all values were marginally significant and had the following ranges,  $1.3 < t_{28} < 1.8$ ,  $0.05 < P < 0.2$ ) for charcoal covered colonies to have higher temperatures at all depths. Charcoal covered colonies had higher average temperatures at all depths. At 2 cm the difference between treatments was  $2^{\circ}\text{C}$ , at 4 cm  $1.5^{\circ}\text{C}$ , and at 8 cm  $1^{\circ}\text{C}$  (Fig. 3b).

### Fitness

Queens were found in 17 of the 18 excavated colonies, indicating that excavations were on the whole complete; the ‘queen-less’ colony was included in analyses as it was otherwise normal in its composition, and it is likely that the queen was

among the very few ants not captured. One colony in the charcoal replacement group did not produce any sexuals. This colony had the smallest worker population and may not have produced sexuals due to its immaturity, and was therefore not included in the analysis.

Removal of charcoal had no effect on the production of sexuals after accounting for colony size (number of mature workers). Least squares means were 422 and 361 sexuals per colony for charcoal replacement and removal colonies respectively ( $F_{1,15} = 0.66$ ,  $P > 0.4$ ). The required sample size to detect an effect was eight times that used in this study.

### Discussion

From this experiment it appears very unlikely that *P. badius* charcoal deters ants, least of all conspecifics. In fact, ants were attracted to *P. badius* charcoal over other groups. It was initially thought that the attraction observed was due to the delay in



substrate collection (loss of deterrent properties over time) and pitfall trapping, but a follow-up experiment showed no consistent indications of deterrence despite the elimination of this delay (C. R. Smith, unpublished data). These results are not necessarily contradictory to those of Gordon (1984). The effect of ant deterrence detected in Gordon (1984) may in fact be due to the exclusion of some ants by others at *P. badius* nests (e.g. interference competition for resources at *P. badius* nests). The results of this study and observations suggest that many ant species forage for food, including discarded waste and dead *P. badius* workers, on these nests (see also Cole *et al.*, 2001). The same species seen most often on nests (e.g. *F. pruinosus*, *P. morrisi*, and *D. bureni*) were also those most often attracted to *P. badius* charcoal in our experiment. Moreover, the attraction of *P. badius* to charcoal of other *P. badius* nests is persuasive evidence that charcoal is not a territorial marker (*sensu stricto*, deterrent to conspecifics).

Gordon's (1984) observed result of ant deterrence may have had little to do with the charcoal depot *per se*, but instead with the observed increase in ant surface activity (e.g. patrolling and midden work) once depots were removed; there was no control for charcoal removal. It has been shown that foragers of other *Pogonomyrmex* species know the locations of neighboring nests (Harrison & Gentry, 1981; Gordon & Kulig, 1996), and foraging ranges seldom overlap. Therefore, a territorial marker at an individual nest would not be a relevant cue for deterring neighboring conspecifics.

There was no effect of charcoal on the hydrology of nests, either in terms of water retention or protection from heavy rain. Some authors note a 'crust' formed from the soil at the top of the mound (and sometimes including objects on top of the soil, e.g. pebbles). It is possible that the treatment of charcoal removal and replacement unduly damaged the structural integrity of the mound underlying the charcoal, and biased our results toward non-detection of an effect.

Perhaps, under more extreme conditions, charcoal can affect soil hydrology. The increased moisture in chambers near the surface was likely to be through water percolation instead of bulk water flow through the nest since no chambers showed any signs of damage. Pebbles may be important in protecting the uppermost chambers of western (North America) *Pogonomyrmex* nests during heavy seasonal rains. In these species the need for a protective covering may be greater, especially since these species have more permanent nests than *P. badius*. Colonies of various western species have rarely or never been documented to move whereas *P. badius* typically moves once or twice per year (Carlson & Gentry, 1973; Van Pelt, 1976; Keeler, 1993).

Charcoal affected temperature in nests up to  $\sim 2$  °C, but only in the top few centimeters of the nest soil and only during certain hours of the day (also see similar results in Gordon, 1984). Charcoal may increase the total available activity time for the colony by elevating temperatures in the morning and evening above the minimum necessary for ant activity, and also increase temperature throughout the day, increasing the range of temperatures in the soil column available to the ants (especially for developing brood). Whether or not *P. badius* can detect and track this small temperature difference is not known (but see Anderson & Munger, 2003). Three potential effects of tracking a temperature difference are that higher temperature could decrease ant development time, increase queen egg lay-

ing rate, or increase worker activity levels, and each could increase colony fitness. This predicted effect on fitness assumes that the ants will track temperature despite the energetic costs of doing so. In many species of ant the effect of nest superstructures, such as mounds, on temperature has been demonstrated (Coenen-Staß *et al.*, 1980; MacKay & MacKay, 1985; Horstmann & Schmid, 1986; Porter, 1990; Cole, 1996), and furthermore affects the distribution of workers and brood in the nest. It is not known to what extent *P. badius* moves brood within the nest, but there does exist a consistent and curious bimodal distribution of brood across depth where  $\sim 1/3$  is kept near the surface and  $\sim 2/3$  at the bottom (Tschinkel, 1999; W. R. Tschinkel, pers. obs.). No difference in brood or ant distributions, over depth, however, were found between treatments in the colonies excavated in the fitness experiment (C. R. Smith, unpublished data), although colonies had recollected large amounts of charcoal immediately preceding excavations, perhaps obscuring this relationship.

Testing the effect of anything on fitness in a long-lived perennial organism requires either very long-term data or an estimate (proxy) for fitness. In this experiment, the effect of charcoal on reproduction was estimated over a single season. The presence of charcoal on the nest had no effect on reproduction after accounting for colony size. Furthermore, data on worker production showed no effect of treatment indicating that charcoal does not affect colony growth, and by extension, future reproduction (C. R. Smith, unpublished data). More reproductives and workers, however, were produced in colonies that retained their charcoal (although not statistically so). This may indicate that the effect of charcoal on colony fitness is manifested over the lifetime of the colony and through the slight reproductive and growth benefits gained by having charcoal.

Data on charcoal collection rates, including these same colonies, indicated that colonies whose charcoal was removed recollected charcoal at a higher rate than control colonies, although they did not differ in stored seed levels (Gordon, 1984; Smith & Tschinkel, 2005). This indicates that treatment colonies were not penalised, in terms of fitness, despite their increased investment into recollection.

Although additional hypotheses of adaptive significance abound, it is possible that the extended phenotype of charcoal depots, or the object depots of many *Pogonomyrmex*, is not maintained through effects of the nest superstructure (Smith & Tschinkel, 2005). Instead, a seemingly more parsimonious explanation is that these depots are the result of foraging and consequently are maintained through selection on foraging efficiency. This theory does not preclude any derived benefits (exaptive) of having the depots, which in turn may be species or habitat specific. The behaviour of object collection, and the resulting depot, is tightly linked to many other tasks in the colony, and can feasibly have resulted as a byproduct of selection on other pathways (including foraging and trash disposal). The behaviour of object depot formation is present in all species complexes of the North American *Pogonomyrmex* and at least three South American *Pogonomyrmex* species and is thus likely ancestral for *P. badius* (Smith & Tschinkel, 2005). Therefore, its persistence in *P. badius* may be due, in larger part, to its integration into foraging and trash disposal behaviours, and not for its

direct effect on temperature and hydrology. This non-adaptive (or exaptive) hypothesis predicts that the object depot will increase as a fixed proportion of colony size (i.e. colony size and the depot are isometric), which is indeed the case (Smith & Tschinkel, 2005). If objects were removed from the nest, this hypothesis would predict that the rate of object collection would not be affected. However, when the depot is removed, objects are recollected at a higher rate than in colonies where the depot was removed and replaced (Smith & Tschinkel, 2005). In another experiment, foragers from nests of *P. barbatus*, a species that has pebble depots, were recruited to piles containing both seeds and objects (toothpick pieces). The non-adaptive hypothesis would predict that objects and seeds would be collected in the same ratio that they were offered, and that all ants would be equally likely to collect a seed or object. Seeds were collected in numbers far exceeding their relative abundance, and objects were collected by a subgroup of recruits older (measured by fat content and mandible wear) than those collecting seeds (C. R. Smith, unpublished data). Together, these results indicate that the non-adaptive hypothesis is not altogether supported, but cannot be outright rejected. Instead, colony-level selection may have favoured variability in the foraging force, which in turn resulted in the accumulation of objects at the nest and the potential for this depot to benefit the colony.

Regardless of the evolutionary origins of the behaviour, it provides an interesting system in which to evaluate task integration and overall colony optimisation. Revisiting optimal foraging theory in harvester ants, and incorporating the collection of non-food objects, is necessary and will greatly improve our knowledge of task optimisation vs. colony-level optimization (ultimately through fitness).

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