

The harvester ant (*Pogonomyrmex badius*) midden: refuse or boundary?

DEBORAH M. GORDON Department of Zoology, Duke University, Durham, N.C.

ABSTRACT. 1. *P. badius* Latreille, a harvester ant of the southern U.S.A., surrounds its nest mound with small bits of charcoal, previously believed to be incidental refuse, along with other components of the colony's midden.

2. Charcoal middens were removed from the nest mounds of colonies in northern Florida. These colonies collected new charcoal and replaced the middens within 7 days.

3. Activity rhythms, use of space, and interspecific aggression were compared in experimental and control colonies. When middens were removed, the frequency of invasions of the nest mounds by other species of ants increased. Foreign ants circled the nest mound and interfered with colony activities. Increased numbers of invading ants led to an increase in patrolling and defensive behaviour by the *P. badius* colonies.

4. The charcoal midden is not merely refuse. Instead, it acts as a boundary that deters ants of other species from coming onto the *P. badius* nest mound. Ants may use charcoal bits as a repository of a chemical substance functioning as a territorial marker.

Key words. Ants, seed-harvesting, territoriality, activity rhythms, midden, refuse pile.

Introduction

The harvester ant, *Pogonomyrmex badius* Latreille, piles bits of charcoal, small twigs, and seed husks on its nest mounds. The species is granivorous, and the ants can be seen carrying seeds into the nest and depositing their husks on the mound. *P. badius* lives at the edges of pine forests in the southeastern U.S.A. where fires are frequent. The charcoal on the nest mounds could have been encountered during the excava-

tion of the nest tunnels and then discarded outside the nest. Many ant species keep their refuse in a discrete pile in or near the nest (Wheeler, 1928). Thus the material on the nest mound often is assumed to be a refuse heap, or midden.

The effect of harvester ant middens on seed dispersal (O'Dowd & Hay, 1980; Davidson & Morton, 1981; Pulliam & Brand, 1975) and on the soil chemistry of abandoned mounds (Gentry & Stiritz, 1972; Rogers & Lavigne, 1974) has received some attention from ecologists. Curiously, however, there has been little speculation about what role the midden may play in the biology of the ant colony itself.

Correspondence: Dr D. M. Gordon, Museum of Comparative Zoology, Harvard University, 26 Oxford St., Cambridge, MA 02138, U.S.A.

One salient fact argues against the view that the *P. badius* midden is merely refuse. The ants bring charcoal bits and twigs to the nest from outside the nest mound area (pers. obs.). Other *Pogonomyrmex* species, in the western U.S.A., have been observed to bring midden objects such as pebbles to the nest (Rogers, 1974; Van Pelt, 1976; Jorgensen & Porter, 1982; Gordon, 1983a). It has been suggested that ants bringing midden objects are foragers that have made a mistake (Willard & Crowell, 1965; Porter & Jorgensen, 1981). It has also been suggested that the midden might be useful in nest construction (Rogers, 1974; Lavigne, 1969).

The present study explores the possibility that the midden may serve some function other than that of a refuse heap. This possibility was suggested by the following observations. In the laboratory, *P. badius* colonies devote a significant portion, about 20%, of the work-force outside the nest to maintaining the midden (Gordon, 1983b, c, 1984). In the field, colonies rebuild middens each spring when they re-emerge from their nests (Gentry & Stiritz, 1972). The charcoal midden is first placed in a ring around the outer edge of the nest, though in some colonies additional material is later brought in to cover the entire mound surface.

The fact that the colony devotes so much effort to the midden suggests that the midden is useful to the colony. The arrangement of the midden in the field suggests that one function of the midden may be as a territorial boundary, demarcating the edge of the nest area. The present study explores that possibility, by examining how the colony's behaviour changes when the midden is removed.

In ants of other genera that pile objects on their mounds, a thermoregulatory function of midden behaviour has been suggested (Wasmann, 1915, cited by Seeley & Heinrich, 1981; Greenslade, 1974; Ettershank, 1971). In the case of *P. badius*, heat absorption by charcoal on the mound may cause higher soil temperature underneath it. A preliminary investigation was made of this possibility.

Methods

Observations of twenty-two *P. badius* colonies were made during 18 days in May 1983, in northern Florida, near Panacea, in the St Marks

National Wildlife Refuge. The colonies were all at the edge of an old field that had been undisturbed for at least 10 years. Colonies were observed from 08.00 until about 15.00 hours, i.e. during the entire morning activity period. All colonies had charcoal arranged around the outer edges of their nest mounds and scattered on the mound itself. In some colonies there was also a discrete pile of seed husks, mostly of *Panicum* sp. seeds. The mean distance between study colonies was 20.4 m; the closest two were 9 m apart.

Eight of the twenty-two colonies were chosen as experimental colonies. For each experimental colony there was at least one control colony of a similar size with a midden of similar appearance. In these eight colonies the charcoal and other midden material was removed from the nest mound by scraping it off with a spoon. Removals were done in the morning before the colony was active. If the colony had a discrete pile of seed husks, as was the case in six out of the eight experimental colonies, the pile was left intact when the rest of the midden was removed. Material removed from the midden was placed in a pile about 0.5 m outside the edge of the nest yard. Both the eight treatment colonies and the fourteen control colonies were observed for 7 days after middens were removed. For 4 days after middens were removed the experimental colonies were photographed each afternoon, after colony activity had stopped.

All colony behaviour observed outside the nest was classified into five activity types: foraging, nest maintenance, patrolling, midden work, and convening (Table 1). An observation consisted of recording the numbers of ants engaged in each of the five activities within 1.3 m of the nest entrance. After middens were removed it was occasionally difficult to distinguish between midden workers and patrollers. In these cases an ant was counted as a midden worker if it manipulated objects on the nest mound. The sum of the five numbers of ants in each activity, called the observation sum (OS), is the total number of ants outside the nest within 1.3 m of the nest entrance. In addition, in each observation, I recorded the number of ants of any other species inside the *P. badius* colony's nest yard. A total of 1132 observations was made.

Measurements were made of the soil temperature at a depth of 3 cm, both (1) near the nest

TABLE 1. Classification of colony activities.

Foraging	A. Ants travel directly away from the nest entrance, not carrying anything, on foraging trail. B. Ants travel directly to the nest entrance carrying a seed or insect bit, on foraging trail.
Nest maintenance	A. Carrying out: ants come out of the nest entrance carrying something, put it down in the nest yard, and go back into the nest. B. Clearing vegetation: ants climb in vegetation at edge of nest yard, clip pieces of it off with mandibles. C. Ants open nest entrance at the beginning of the activity period by carrying out soil. D. Ants close nest entrance at the end of the activity period.
Patrolling	A. Ant walks with frequent stops and changes in direction (compared to foragers). Abdomen is often bent underneath the thorax. Objects and other ants encountered are frequently inspected with antennae. B. Defence: At the site of a disturbance, such as a new object in the nest yard not brought in by ants, ants gather and stand with mandibles open. When foreign ants are circling on the nest mound, ants chase them or circle in front of them, thus obstructing their path. C. After midden was removed: ants circle quickly on the nest mound, frequently inspecting other ants with antennae.
Midden work	A. Ants stand on the midden, repiling it or inspecting it with antennae. B. Ants move objects from one midden to another midden in nest yard. C. After midden was removed: ants circle slowly on the nest mound, frequently stopping and picking up objects and putting them down again.
Convening	A. Ants mill around in nest entrance. Frequent antennae contacts between workers.

entrance and not underneath the midden, and (2) underneath the charcoal midden. A YSI telethermometer and thermistor were used. A total of fifty-four measurements was made on nine colonies, in the course of 11 days, with seven to ten measurements for each hour between 08.00 and 14.00 hours.

Results

All eight experimental colonies rebuilt their middens within 7 days after the midden had been removed. For the most part, middens were replaced with charcoal bits, though some twigs were brought onto the middens as well. The numbers of ants rearranging and inspecting charcoal middens, and bringing charcoal to the middens, increased when middens were removed, while the numbers of ants rearranging seed husk middens decreased (Fig. 1). For at least 3 days after middens were removed, no ants were observed retrieving objects from the pile of their own midden material placed by me near the nest yard. Instead, most charcoal was retrieved by ants travelling farther from the nest along

nest trails. Later, recruitment trails occasionally formed to the piles I had made of midden material, but most of the replaced midden came from other places. As charcoal was brought in to replace that removed, it was often placed first around the outer edge of the mound.

The numbers of charcoal bits on the middens were counted using photographs of some of the experimental colonies (Table 2). The ants often placed charcoal bits in small piles or clusters; each of these clusters was arbitrarily counted as one bit. For this reason, the numbers in Table 2 are certainly too low (especially colony 20, days 2, 3 and 4, and colony 21, day 4). Smaller, apparently younger colonies (colonies 3, 4, 5 and 16) that had less midden material originally than older, larger ones (colonies 8, 11, 20 and 21) brought in less new charcoal than did the larger ones. In general, it is clear that the amount of charcoal on the nest surface increased considerably in all colonies in the course of 4 days.

A multivariate analysis of variance (Timm, 1975) was used to test the effect of midden removal on colony activities. Data were normalized for differences in colony size (by dividing

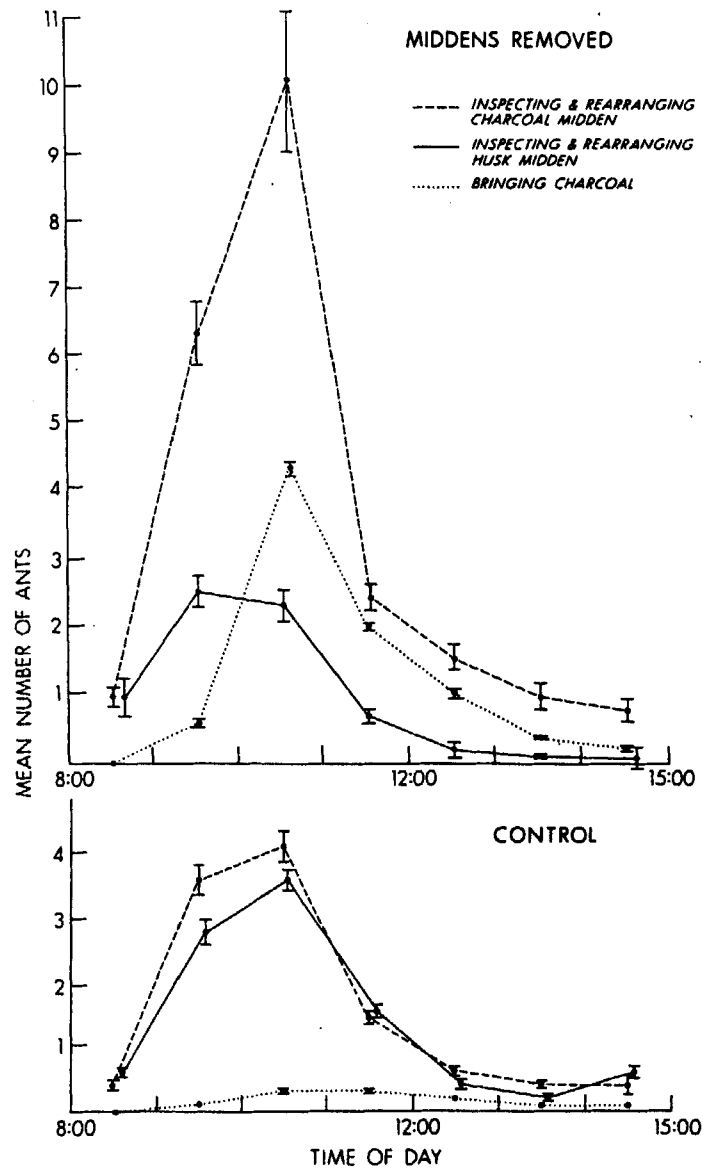


FIG. 1. The effect of removing middens on midden activities. The mean normalized numbers of ants engaged in each of several midden activities are shown as a function of time of day, for both control colonies and experimental colonies. Results are shown for 7 days of observation of each colony. Error bars show the standard error of the mean.

the data for each colony by the largest observation sum for that colony) and submitted to an arcsin transformation. Factors considered were treatment (removal of the midden) and colony nested within treatment. The results are shown in Table 3. Removal of the midden significantly affected the distribution of ants into the five activities ($P < 0.0001$). The activity rhythms of

experimental and control colonies are shown in Fig. 2. There were also significant differences among colonies within treatment ($P < 0.0001$). The univariate tests showed that when middens were removed the numbers of ants engaged in patrolling were significantly increased, while the numbers doing nest maintenance were significantly decreased. A Bonferroni comparison of

TABLE 2. Counts of charcoal bits brought on to nest mounds after middens were removed.

Day	Colony				
	21	4	11	5	20
0	373	290	298	379	494
1	669	—	600	—	937
2	797	505	794	541	1243
3	914	594	901	551	1145
4	1097	633	—	600	1081

TABLE 3. Results of manova testing effect of removing middens on colony activities.

Effect	DF	Foraging			Nest maintenance			Patrolling		
		SS	F	P	SS	F	P	SS	F	P
Model	(21)									
Error	(1110)									
Treatment	(1)	0.00	0.0	NS	0.18	5.59	0.03	0.16	20.9	0.0002
Colony within treatment	(20)	0.43	1.34	NS	0.63	5.08	0.0001	0.15	4.10	0.0001
Bonferroni comparison of means			NS		Control > Experimental $P < 0.05$			Experimental > Control $P < 0.05$		

Effect	DF	Midden work			Convening			Manova		
		SS	F	P	SS	F	P	SS	F	P
Model	(21)							0.17	4.16	0.0001
Error	(1110)							2.13		
Treatment	(1)	0.03	3.76	NS	0.0001	2.24	NS			0.0001
Colony within treatment	(20)	0.14	3.56	0.0001	0.001	1.39	NS			0.0001
Bonferroni comparison of means		Experimental > Control $P < 0.05$			NS					

means (Timm, 1975) showed that the mean number of ants engaged in midden work increased significantly when middens were removed. The numbers in other activities did not change significantly.

A similar manova comparing experimental and control colonies for 7 days before middens were removed showed no significant differences ($P > 0.05$) in the numbers of ants engaged in any of the five activities.

The effects of removing the middens on the temporal pattern of patrolling, and of invasion by other species, are shown in Figs. 3 and 4. The numbers patrolling inside the nest yard, where foreign ants were, increased more than numbers patrolling outside the nest yard edge (Fig. 4).

Removing middens significantly increased the numbers of invading ants (anova, $ss = 219.6$, $F = 7.01$, $P = 0.0084$). The numbers of the following species of ants on *P. badius* nest yards were included in this analysis: *Conomyrma flavopecta* Smith, *Paratrechina* sp., *Iridomyrmex pruinosus* (Roger) and *Aphaenogaster floridana* M. R. Smith. Members of these species were invariably chased by *P. badius* patrollers. Though ants of another species, *Trachymyrmex septentrionalis* (McCook), were frequently observed on *P. badius* mounds, they were invariably seen foraging in the seed husk middens and never went closer to the nest entrance. In fifty-nine observations of visits by a total of 389 *T. septentrionalis* foragers, I saw no

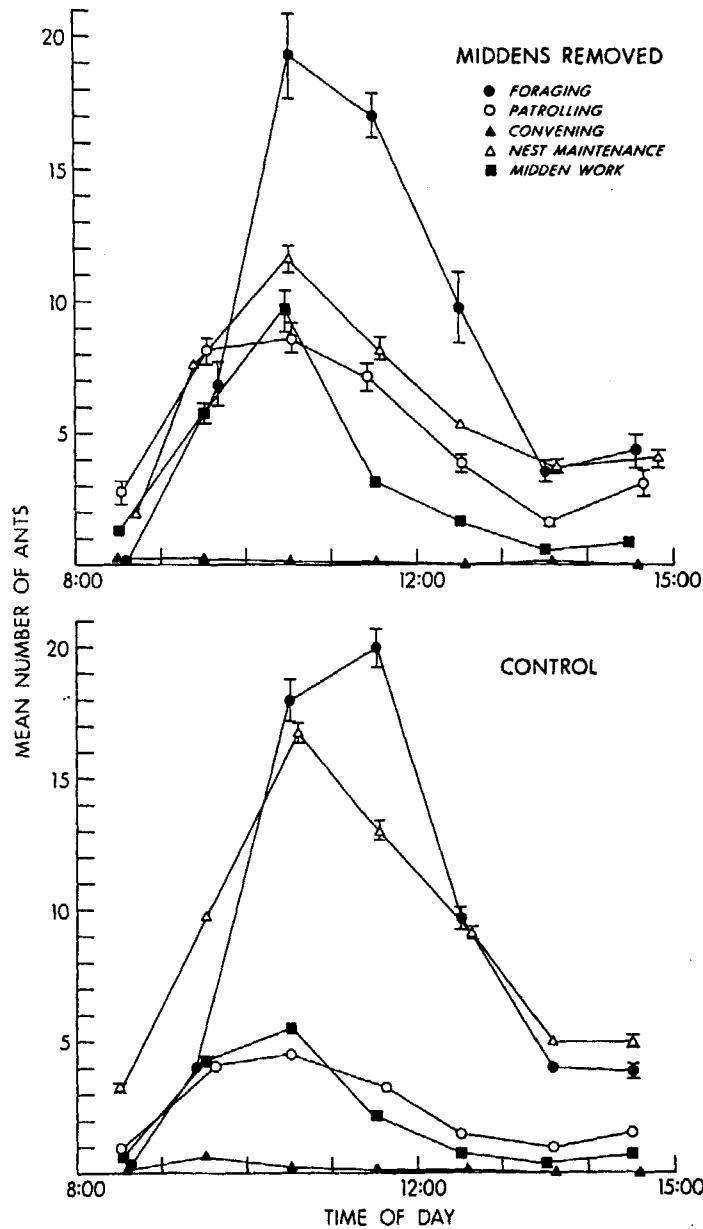


FIG. 2. The effect of removing middens on colony activities. The mean normalized numbers of ants engaged in each of five activities are shown as a function of time of day, for both control and experimental colonies. Results are shown for 7 days of observation of each colony. Error bars show the standard error of the mean.

chasing, attacking, or other agonistic behaviour. For that reason, the numbers of *T.septentrionalis* ants on the nest yards were omitted from this and subsequent analyses.

An analysis of covariance was used to examine the relationship between the numbers patrolling and the numbers invading. The number of

foreign ants on the nest yard in each observation (called 'number of invaders') was compared with the variable $\log (P/1-P)$, where P is the normalized number of ants engaged in patrolling, in that same observation. This transformation of the number of patrollers was used to approximate a linear curve for the function

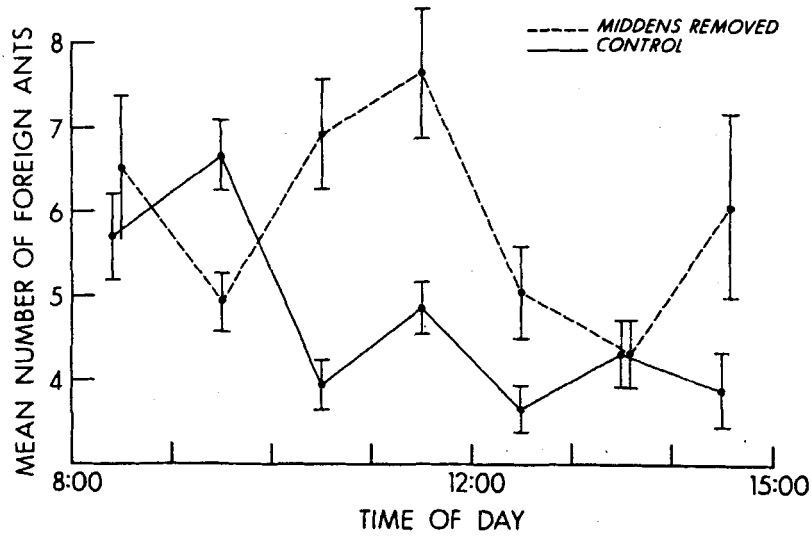


FIG. 3. The effect of removing middens on numbers of foreign ants in *P. badius* nest yards. The mean numbers of foreign ants (see text for species) on *P. badius* nest yards are shown as a function of time of day, for both control and experimental colonies. Results are shown for 7 days of observation of each colony. Error bars show the standard error of the mean.

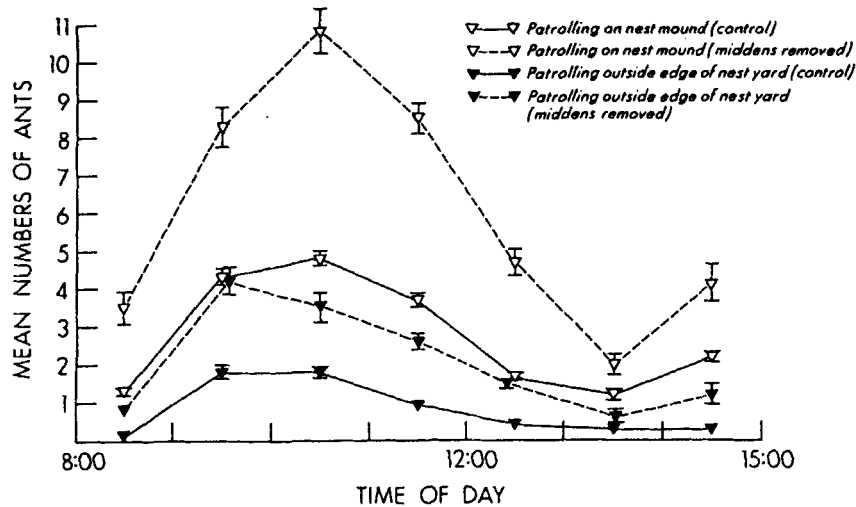


FIG. 4. The effect of removing middens on numbers and location of *P. badius* patrollers. The mean normalized numbers of patrollers both inside and outside the nest mound are shown as a function of time of day, for both control and experimental colonies. Results are shown for 7 days of observation of each colony. Error bars show the standard error of the mean.

relating numbers patrolling to numbers of invaders. The transformed number of patrollers was used as the dependent variable, and factors considered were treatment, colony nested within treatment, and time of day (grouped by hours) as main effects. Interaction effects considered were number of invaders \times treatment and number of invaders \times colony within treatment.

The analysis of covariance showed a significant relationship between number of invaders and numbers patrolling ($P < 0.0001$) (Table 4). There was a highly significant treatment effect ($P = 0.0067$). This result shows that the linear dependence of numbers patrolling on numbers of invaders accounts for a considerable part, though not all, of the treatment effect in the

TABLE 4. Results of analysis of covariance of numbers patrolling and numbers invading.

Effect	DF	SS	F	Error mean square	P
Model	49	252.06	12.06	0.43	0.0001
Error	1082	461.63			
Time	6	142.9	55.82	0.43	0.0001
Treatment	1	11.6	9.14	1.27*	0.0067
Colony within treatment	20	25.4	2.98	0.43	0.0001
Invaders	1	10.4	24.50	0.43	0.0001
Invaders × treatment	1	4.1	11.77	0.35†	0.0026
Invaders × colony within treatment	20	7.0	0.82	0.43	0.6898

* Error mean square based on mean square for colony within treatment.

† Error mean square based on mean square for invaders × colony within treatment.

manova discussed above, in which numbers of invaders were not included in the model. There was also a significant colony within treatment effect ($P < 0.0001$).

The invaders × treatment interactions ($P = 0.0026$) showed that the slope of the function relating numbers patrolling to numbers of invaders is significantly higher for control colonies (0.0533) than the slope of the same curve for experimental colonies (0.0296). When middens are removed and the numbers of invaders increase, there are fewer patrollers for each invading ant.

In summary, the relationship between increase in patrolling and increase in number of invaders when middens are removed can be attributed largely to the linear dependence of numbers patrolling on numbers invading.

The results of the temperature measurements (Fig. 5) suggest that soil under the charcoal midden is warmer than uncovered soil at the same depth, but inspection of the error bars suggests that the difference may not be statistically significant.

Discussion

It seems clear that charcoal middens are not mere refuse piles. If midden material were mere refuse, it would be difficult to see why colonies replace it with such alacrity when it is removed.

Territorial behaviour in *P. badius* is concentrated around the nest yard, not around the rest of the foraging range (Harrison & Gentry, 1981). When middens were removed, the incidence of patrolling and the numbers of invading ants of other species inside the nest yard were both increased. Invading ants tended to circle around on the nest yard until they were driven away by *P. badius* ants. Such circling

interfered with *P. badius* nest yard activities, such as nest maintenance, and with the passage of foragers onto foraging trails and back into the nest. In some cases, when the number of invaders was large, overall activity of *P. badius* ants seemed to decrease. This kind of interference behaviour has been observed in other species (Hölldobler, 1982; Hölldobler & Lumsden, 1980).

On seven occasions, ants of some of the invading species (especially *Conomyrma flavopecta*) were observed taking dead or even live, apparently injured ants off *P. badius* nest yards and into their own nests. Thus, middens may deter predation by other species, at least predation on injured *P. badius* ants in their own nest yards, by decreasing the number of predatory ants of other species in the nest yard.

In some ways, then, the midden acts as a territorial marker (*sensu* Gosling, 1982) for other species of ants. There may be a chemical marker contained in midden objects. A porous material like charcoal would serve well as a repository for chemical substances (Komarek *et al.*, 1973). When *P. badius* midden workers are observed in the laboratory under a microscope, they can be seen to lick midden objects, turn them around with their mandibles, and inspect them with their antennae. Ants also deposit faecal droplets at the midden. Ants doing midden work may be maintaining the chemical status of midden objects.

Experimental colonies did not prefer their own midden material to other charcoal in the area. This suggests that if the charcoal does contain a chemical marker that elicits midden work (as opposed to a territorial marker, which may not elicit midden work), its active life is not very long, or the process of moving the middens changes it beyond recognition. Several ant

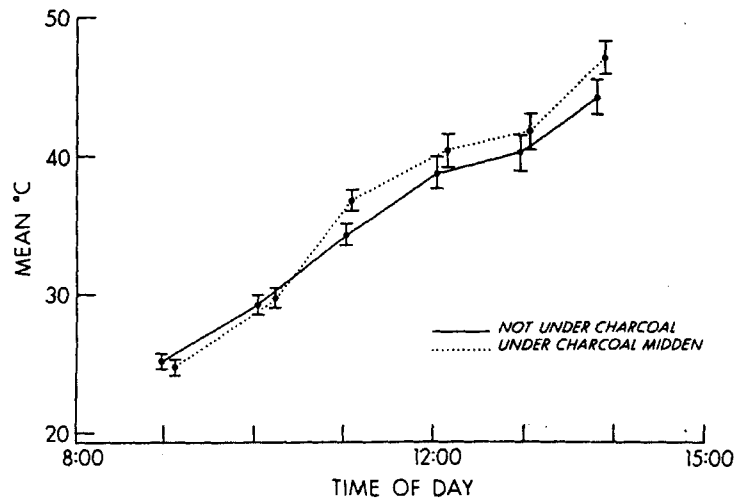


FIG. 5. The effect of charcoal midden on soil temperature in nest mound. Soil temperatures at a depth of 3 cm both under charcoal middens and not under them are shown as a function of time of day. Error bars show standard error of the mean.

species employ chemical secretions to mark their territories (Cammaerts *et al.*, 1977; Hölldobler & Wilson, 1980; Jaffe *et al.*, 1979). I know of no other case, such as this one may be, of ants using collected objects as repositories of the marking substance.

Other possible functions of the charcoal midden remain to be investigated. The charcoal may raise soil temperatures in the nest mound. Some other *Pogonomyrmex* species devote considerable effort to midden work (Gordon, 1983a). The middens of these species may have a thermoregulatory or territorial function.

The role of the charcoal midden in the intraspecific territoriality of *P. badius* was not clear. I saw thirty instances of intraspecific aggression in the eight experimental colonies, and nineteen instances in fourteen control colonies. Other research suggests that the nest material (Hangartner *et al.*, 1970) and foraging trails (Hölldobler, 1976; Hölldobler & Lumsden, 1980) of *Pogonomyrmex* colonies are marked with colony-specific odours; this may be true of midden objects as well. However, Harrison & Gentry (1981) reported that *P. badius* workers rarely venture inside the foraging ranges of other conspecific colonies, and thus would rarely arrive at the nest yards of other colonies. Whether the *P. badius* midden functions in intraspecific territoriality remains to be investigated using marked ants.

Dead ants are seen rarely on *P. badius* middens in the field. Dead ants are usually taken up to 6 m outside the nest yard and then dropped (pers. obs.). Thus the literature on the reactions of *P. badius* to dead ants (Wilson *et al.*, 1958; Gordon, 1983c) may not be relevant to the behaviour associated with the charcoal and twig middens. The piles of seed husks on the mounds do seem to function as refuse heaps, since the husks are brought out of the nest, and foraging on these piles is uncontested by *P. badius* (see also MacKay, 1981). The results of the present study, linking midden work and territorial behaviour, help to explain previous reports that the same workers that do midden work also do patrolling (Gordon, 1984) or nest defence (Porter & Jorgensen, 1981).

In conclusion, an examination of colony behaviour when middens were removed sheds new light on a hitherto ignored aspect of harvester ant behaviour. Clearly, the charcoal midden has functions other than that of mere refuse-disposal. Careful investigation of the midden behaviour of other ant species may lead to surprising results.

Acknowledgments

The work was supported by the Peter Nikolic Award of the T. C. Schneirla Research Fund. I

thank J. D. Gordon, F. Oncay and J. Apstein for their help during my stay in Tallahassee; W. R. Tschinkel and S. Porter for valuable discussions and advice; D. S. Burdick and M. Rausher for statistical advice; T. Nuhn, at the U.S. National Museum, for identifying the ants; two anonymous reviewers for helpful comments on the manuscript; and J. Gregg and R. Palmer for their help with all stages of the project.

References

- Cammaerts, M.C., Morgan, E.D. & Tyler, R. (1977) Territorial marking in the ant *Myrmica rubra*. *Biology of Behavior*, **2**, 263–272.
- Davidson, D.W. & Morton, S.R. (1981) Myrmecochory in some plants (*F. chenopodiaceae*) of the Australian arid zone. *Oecologia*, **50**, 357–366.
- Ettershank, G. (1971) Some aspects of the ecology and microclimatology of the meat-ant *Iridomyrmex purpureus* (Smith). *Proceedings of the Royal Society of Victoria*, **84**, 137–152.
- Gentry, J.B. & Stirtz, K.L. (1972) The role of the Florida harvester ant, *Pogonomyrmex badius*, in old field mineral nutrient relationships. *Environmental Entomology*, **1**, 39–41.
- Gordon, D.M. (1983a) Species-specific patterns in the social activities of harvester ant colonies (*Pogonomyrmex*). *Insectes Sociaux* (in press).
- Gordon, D.M. (1983b) Daily rhythms in the social activities of harvester ant colonies. *Psyche*, **90**, 413–423.
- Gordon, D.M. (1983c) Dependence on necrophoric response to oleic acid on social context in the ant, *Pogonomyrmex badius*. *Journal of Chemical Ecology*, **9**, 105–111.
- Gordon, D.M. (1984) The persistence of role in exterior workers of the harvester ant, *Pogonomyrmex badius*. *Psyche*, **91** (in press).
- Gosling, L.M. (1982) A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie*, **60**, 89–118.
- Greenslade, P.J.M. (1974) Some relations of the meat-ant *Iridomyrmex purpureus* with soil in south Australia. *Soil Biology and Biochemistry*, **6**, 7–14.
- Hangartner, W., Reichson, J.M. & Wilson, E.O. (1970) Orientation to nest material by the ant *Pogonomyrmex badius*. *Animal Behavior*, **18**, 331–334.
- Harrison, J.S. & Gentry, J.B. (1981) Foraging patterns, colony distribution and foraging range of the Florida harvester ant *Pogonomyrmex badius*. *Ecology*, **62**, 1467–1473.
- Hölldobler, B. (1976) Recruitment behavior, home range orientation, and territoriality in harvester ants, *Pogonomyrmex*. *Behavioral Ecology and Sociobiology*, **1**, 3–44.
- Hölldobler, B. (1982) Interference strategy of *Iridomyrmex pruinosus* during foraging. *Oecologia*, **52**, 208–213.
- Hölldobler, B. & Lumsden, C.J. (1980) Territorial strategies in ants. *Science*, **210**, 732–739.
- Hölldobler, B. & Wilson, E.O. (1980) Colony-specific territorial pheromone in the African weaver ant *Oecophylla longinoda* (Latreille). *Proceedings of the National Academy Sciences of the United States of America*, **74**, 2072–2075.
- Jaffe, K., Bazire Benazet, M. & Howse, P.E. (1979) An integumentary pheromone-secreting gland in *Atta* sp.: territorial marking with a colony-specific pheromone in *Atta cephalotes*. *Journal of Insect Physiology*, **25**, 833–839.
- Jorgensen, C.D. & Porter, S. (1982) Foraging behavior of *Pogonomyrmex owyheeii* in southwest Idaho. *Environmental Entomology*, **11**, 381–384.
- Komarek, E.V., Komarek, B.B. & Carlyle, T.C. (1973) *The ecology of smoke particulates and charcoal residues from forest and grassland fires: a preliminary atlas*. Tall Timbers Research Station Miscellaneous Publication No. 3, Tallahassee, Florida.
- Lavigne, R. (1969) Bionomics of nest structure of *Pogonomyrmex occidentalis*. *Annals of the Entomological Society of America*, **62**, 1166–1175.
- MacKay, W. (1981) A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants. *Psyche*, **88**, 25–74.
- O'Dowd, D.J. & Hay, M.E. (1980) Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. *Ecology*, **61**, 531–540.
- Porter, S.D. & Jorgensen, C.D. (1981) Foragers of the harvester ant, *Pogonomyrmex owyheeii*: a disposable caste? *Behavioral Ecology and Sociobiology*, **9**, 247–256.
- Pulliam, H.R. & Brand, M.R. (1975) The production and utilization of seeds in plains grassland of southeast Arizona. *Ecology*, **56**, 1158–1166.
- Rogers, L.E. (1974) Foraging activity of the western harvester ant in the shortgrass plains ecosystem. *Environmental Entomology*, **3**, 420–424.
- Rogers, L.E. & Lavigne, R.J. (1974) Environmental effects of western harvester ants on the shortgrass plains system. *Environmental Entomology*, **3**, 994–997.
- Seeley, T.D. & Heinrich, B. (1981) Regulation of temperature in the nests of social insects. In: *Insect Thermoregulation* (ed. by B. Heinrich). Wiley and Sons, New York.
- Timm, N.H. (1975) *Multivariate Analysis*. Brooks/Cole Publishing Co., Monterey, California.
- Van Pelt, A. (1976) Nest relocation in the ant *Pogonomyrmex barbatus*. *Annals of the Entomological Society of America*, **69**, 493.
- Wasmann, E. (1915) *Das Gesellschaftsleben der Ameisen*. Munster, Aschendorfsche.
- Wheeler, W.M. (1928) *The Social Insects: their Origin and Evolution*. Kegan Paul, London.
- Willard, J. & Crowell, H. (1965) Biological activities of the harvester ant, *Pogonomyrmex owyheeii*, in central Oregon. *Journal of Economic Entomology*, **58**, 484–489.
- Wilson, E.O., Durlach, N.I. & Roth, L.M. (1958) Chemical releasers of necrophoric behavior in ants. *Psyche*, **65**, 108–114.