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Sociometry and sociogenesis of colonies of the harvester ant, *Pogonomyrmex badius*: distribution of workers, brood and seeds within the nest in relation to colony size and season

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Abstract. 1. The vertical distribution in the nest of chambers, workers, callow workers, brood and seeds was studied in the harvester ant, *Pogonomyrmex badius*, in northern Florida. On each of four sample dates (May, July, October, January), six to seven colonies, chosen to represent the full range of sizes, were excavated. All chamber contents were collected and counted. Chambers were mapped and measured. In a preliminary study, two nests were excavated after preventing vertical migration by driving barriers into the wall of a pit next to the nest, severing the vertical tunnels. The vertical distribution of these barrier-nests differed little from unrestrained nests, indicating that unrestrained excavation produced a reasonable picture of vertical distributions.

2. Nest depth, chamber number and total area increased with colony size. Chamber area declined sharply with depth, as did chamber number, such that more than half of the total area was found in the upper quarter of the nest.

3. The proportion of dark-coloured (older) workers also declined strongly with depth, but this decline was weaker in the spring, and depended to a modest degree on colony size. Conversely, in the distribution of callow (young) workers, the proportion increased towards the bottom of the nest. Mean worker age was inversely related to the depth at which workers were found. The proportion of the brood also increased towards the bottom of the nest, with worker brood, sexual brood, pupae and larvae all being distributed similarly.

4. By contrast, seeds were stored at a preferred absolute depth between 40 and 100 cm. Colonies shallower than 100 cm stored seeds in their deepest chambers. Larger colonies stored most seeds in the upper third of the nest, but patterns were somewhat erratic because chambers were either filled completely with seeds or were empty.

5. Because chamber area decreased sharply with depth, the densities (individuals cm^{-2}) of all colony members, including dark workers, were lowest near the surface and highest in the deepest parts of the nest. Here, worker densities ranged from 2 to 8 cm^{-2}, and brood from 2 to 25 cm^{-2}.

6. The regularity of the patterns of distribution suggests that harvester ant colonies have considerable spatial and temporal structure, which serves or is the outcome of important colony processes. A simple mechanism that could generate several of these patterns is discussed. New workers produced deep in the nest move upwards as they age. As they leave the brood zone they change from brood care to general nest

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duties, including increased nest excavation, leading to the top-heavy pattern of nest area. As they appear at the surface, they change to guarding and foraging. Thus, age polyethism may be partly the result of this upward migration of workers.

Key words. Callow workers, nest architecture, social insects, superorganism, worker age.

Introduction

The biological functions of organisms are carried out by spatially organised structures. In social insects, two levels of organisation are present: the individual and the supra-organismal. As biological entities analogous to individual organisms, social insect colonies can be expected to have a consistent size, arrangement of parts (morphology) and pattern of development. Tschinkel (1991) suggested that the study of the morphology of colonies, which he called *sociometry*, was an essential beginning to understanding the function and evolution of social insect colonies. The challenge of social insect biology is to determine how the superorganism arises from the individual organisms of which it is composed (Wilson, 1967; Kipyatkov, 1971; Lumsden, 1982; Wilson & Sober, 1989; Hölldobler, 1991; Ratnieks & Reeve, 1992). As observed by Bonner (1974) and Sendova-Franks and Franks (1995), the parts of an organism are attached to one another to create a spatial structure, but ants in an ant colony move freely. Spatial structure of a social insect colony is thus not immediately apparent. Is there spatial structure associated with the colony's superorganismal functions? Such structure is suggested by the generally centrifugal movement of workers away from the brood, so that younger workers carry out brood care, while older workers carry out other nest tasks, eventually foraging outside the nest (Hölldobler & Wilson, 1990). The resulting association of age, location and task structures the colony spatially. For example, in laboratory colonies of *Leptothorax unifasciatus*, each worker had a limited movement zone (spatial fidelity zone), and these zones formed partially overlapping sequences from the centre of the nest to the periphery (Sendova-Franks & Franks, 1995). The tasks performed by a worker depended upon the location of its movement zone.

The subterranean nests of ants are created by the removal of soil and are often highly structured and species-typical. Although many reports on the structures of excavated ant nests exist, most published descriptions are nonquantitative, ranging from verbal descriptions to drawings (for example: McCook, 1879; Wheeler, 1910; Talbot & Kennedy, 1940; Autuori, 1942; Scherba, 1961; Talbot, 1964; Dlussky, 1968; Ettershank, 1968; Lavigne, 1969; Nielsen & Jensen, 1975; Dlussky, 1981; MacKay, 1981a; Kugler & Carmen Hincapie, 1983; McCahon & Lockwood, 1990; Bristow *et al.*, 1992). The lack of quantitative descriptions makes comparative study of nest architecture difficult. An exception is the study of Tschinkel (1987), which determined chamber area and shape in relation to depth and colony size.

Although the nest's structure may be clear, it is much less clear that the distribution of colony members and activities within the nest is spatially structured. Laboratory colonies typically show some spatial structure (Hölldobler & Wilson, 1990; Sendova-Franks & Franks, 1995), but field studies, even those based on careful excavations, usually provide no quantitative information on the distribution of ants among nest chambers (Dlussky, 1981; Conway, 1983; Darlington, 1997). Nevertheless, the literature on harvester ants suggests that there are consistent patterns of distribution within subterranean nests. In *P. occidentalis,* it has been reported that seeds are more likely to occur at some depths than at others (Lavigne, 1969). In several species of harvester ants, colony workers have been reported to be stratified by age and season – young workers were found deep in the nest and underwent an upward movement as they aged and a downward movement in winter (Chew, 1960; Golley & Gentry, 1964; MacKay, 1981a,b; Tschinkel, 1987). Porter and Jorgensen (1981) showed that the worker population of *Pogonomyrmex owyheei* is stratified, with the oldest workers occurring on or near the surface, and younger workers in deeper chambers. These observations were confirmed and expanded for workers of *P. badius* by Tschinkel (1998), who showed that callows (young workers) were found primarily in the deepest chambers, that the body fat of these callows undergoes predictable changes through the seasons, and that ageing workers move upwards in the nest. Kondoh (1968) reported that in the winter, large numbers of fat-storing workers of *Formica japonica* were packed into the lower chambers of the nest, whereas in spring and summer, workers and brood were distributed more evenly.

The nest represents an investment in colony infrastructure (Sudd & Franks, 1987), the cost of which is paid in the form of the energy and time it takes to build it, and the benefits of which are usually assumed to be such things as shelter, favourable microclimate, defence, etc. It may be assumed that the nest's architecture plays an important role in the organisation of colony function (Sudd & Franks, 1987), but this too has rarely been tested. Exceptions include the report by Brian (1956), which shows that broods are reared more efficiently when they are dispersed among several smaller chambers, rather than grouped in a single large chamber of equal total area. Porter and Tschinkel (1985) showed that small laboratory groups of fire ant workers reared broods more efficiently than did large groups. These two studies imply that nest architecture may be linked to colony function through rearing-group size. Franks and Deneubourg (1997) also

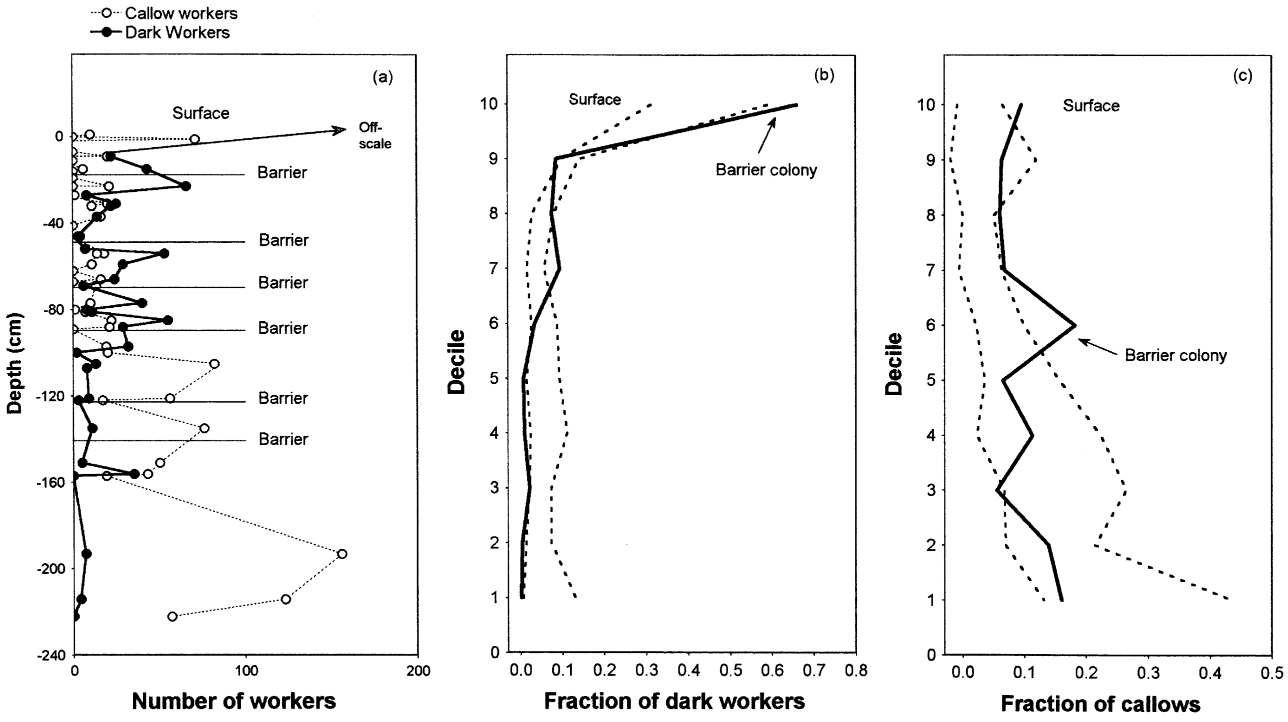

Fig. 1. (a) Barriers preventing vertical movement were placed before excavation of the nest (see text). The position of the barriers is indicated, and the number of dark workers (closed circles, solid lines) and callow workers (open circles, dotted lines) is shown. Workers did not tend to accumulate in the chambers immediately above or below the barriers, indicating that no wholesale vertical movement took place. (b) The vertical distribution of the proportion of dark workers in the barrier nest (solid line) in relation to the 95% confidence limits (dashed lines) of the mean proportions of dark workers in unrestricted nest excavations for July–October nests. (c) Similar to (b), but for callow workers.

presented evidence for links between nest architecture and colony function.

Thus, nest characteristics and within-nest distributions may be important to the normal functioning of the colony *superorganism*. The first step in testing for such relationships is to describe the architecture of ant nests in quantitative detail, and to determine the distribution of nest contents. Thereafter, a structure–function link can be sought. In this paper, some of the patterns of the nest architecture of the Florida harvester ant, *Pogonomyrmex badius,* and the spatial distribution of ants and seeds in nests are reported. This is a companion paper to Tschinkel (1998), in which worker traits in relation to colony size, season and depth in the nest are examined in detail. Papers on colony-level attributes and nest architecture will be published elsewhere.

Materials and methods

The 25-ha study site was located in the Apalachicola National Forest about 16 km southwest of Tallahassee, Florida. The soils were very well drained, almost pure, deep sands. Vegetation consisted of mostly sparse, young longleaf pines with a herbaceous ground cover containing abundant cactus (*Opuntia* sp.). The site supported a large population of *Pogonomyrmex badius* along with *Solenopsis geminata*, *Forelius pruinosus*, *Trachymyrmex septentrionalis*, *Prenolepis imparis*, *Conomyrma pyramica* and *Aphaenogaster treatae*.

Colonies were sampled and excavated four times during 1989–90 to cover a 1-year cycle: (1) 25 April–23 May; (2) 10 July–10 August; (3) 16 October–7 November; (4) 16 January–5 March. These will be referred to as the May, July, October, and January samples, respectively. At each of these times, surface features were used to choose two small, two medium, and two large colonies for excavation. Choices were haphazard and were scattered widely throughout the area.

Surface features such as crater dimensions and charcoal deposits were noted. A pit was dug next to the colony and chambers were exposed progressively in their horizontal aspect, one at a time. Depth of the chamber floor from the surface was measured and the contents of each chamber were aspirated and stored in separate containers. The outline of each chamber was traced on a sheet of acetate laid over the exposed chamber floor, and the compass orientation of the chamber noted. From these tracings, chamber perimeter and area were determined. At intervals, soil temperature was measured as the dig proceeded. Depending upon size of the colony, 1–2 days were required to complete an excavation.

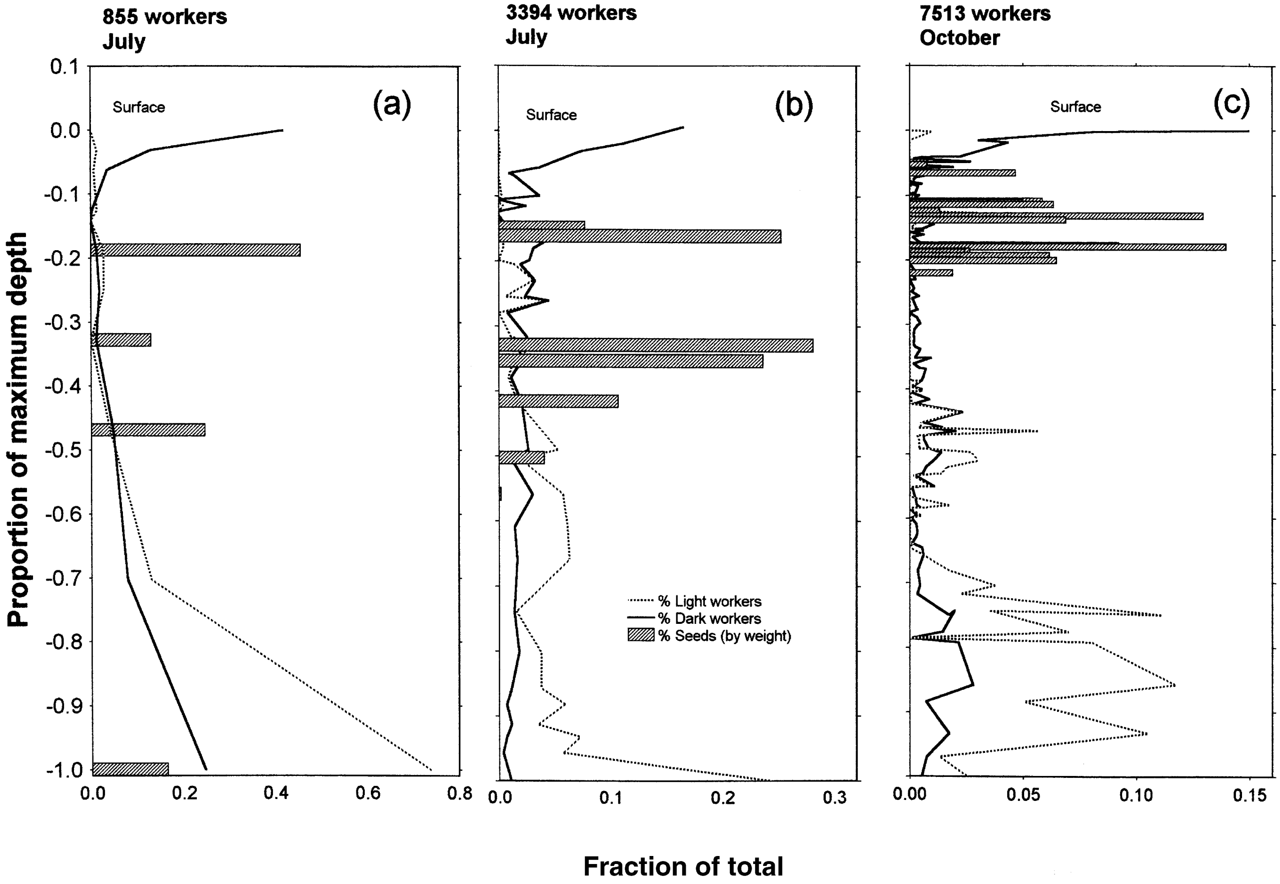

Fig. 2. Examples of chamber by chamber distribution of the proportion of dark workers, callows, and seeds. (a) Small colony, (b) medium colony, (c) large colony. Chamber number increases from (a) to (c), leading to more complex distributions.

In the laboratory, the workers and brood from each chamber were sorted, counted and oven-dried at 50 °C for several days. Light-coloured workers were regarded as callows and were analysed separately from dark-coloured workers. The primary data for this study were counts of dark workers, callow workers, worker larvae, worker pupae, sexual larvae, sexual pupae, and seeds in each chamber. Analysis of worker weights, size, and fat content have been published (Tschinkel, 1998), and colony-level characteristics and nest architecture will be published elsewhere.

Seeds were oven-dried and, using standard testing sieves of decreasing mesh size, sifted into eight size categories. This paper reports only the distribution of total seed weights; analysis by seed size will be published elsewhere.

Data and data analysis

The basic data were aggregated into subdivisions of 10% of the maximum nest depth (deciles) for most analyses, and were used to calculate various totals and ratios. Data were analysed by regression and/or ANOVA using Statistica-W4.5 (Statsoft, Inc., Oklahoma City, Oklahoma). Log and arcsin transformations were applied as needed to stabilise the variance. To balance ANOVA designs, mean values were substituted for missing values, and the degrees of freedom of the *F*-ratios reduced accordingly.

Results

Are distributions derived from nest excavations accurate?

Do the results of such excavations reflect the real distribution of workers, brood, and seeds, or does the disturbance of excavation cause the ants to redistribute themselves? In one excavation, a 2-m pit was excavated rapidly next to the nest and sheets of metal were driven horizontally into the wall of the pit in order to sever the vertical tunnels of the nest and prevent worker movement between chambers. The nest was then excavated as above, taking special note of any accumulation of workers or brood above or below the metal barriers. This excavation tested the assumption that excavation did not cause significant movement of ants within the nest, and that the distribution of ants among excavated chambers represented their real distribution in undisturbed colonies.

The results indicated that there was no wholesale movement of ants in response to excavation. Ants did not pack into the blocked tunnels immediately above or below the metal barrier, as though they were trying to reach the next chamber, nor did they tend to accumulate in the chambers immediately above or below the barriers (Fig. 1a). This was tested further by calculating the relative number of dark workers, callows, and brood in the chambers immediately above and below each barrier. In the absence of any net vertical movement, this fraction should not differ much from 0.5, which indeed it did not. The mean fraction above the barriers ranged from approximately 0.3 to 0.5, and the mean ± the 95% confidence interval of the mean included 0.5 for dark workers, callows, worker larvae and worker pupae. These data thus suggest that net vertical movement in response to excavation is absent, or limited.

When the percentage of the total worker population in each decile was compared with the mean distribution of comparable nests (July and October samples, > 1000 workers), it was not greatly different. The vertical distribution of dark workers in the barrier-colonies may be somewhat more top-biased than the comparison nests (Fig. 1b), but the differences do not indicate wholesale movement. The same is true for callow workers (Fig. 1c). The vertical distribution of brood was also not obviously different from that in nonbarrier nests, and showed a similar bias towards the lower chambers.

Thus it was concluded that excavation yields a reasonable, although perhaps not perfect, picture of the true distribution of ants and seeds in the nest. MacKay (1981b) came to a similar conclusion.

Distribution of nest contents

Workers and seeds are neither uniformly nor randomly distributed within the nest. Both can be found in particular parts of the nest with high predictability. These patterns of distribution change with the season and colony size. Three examples, a small, a medium and a large colony, are shown in Fig. 2. Although there is much chamber-to-chamber variability, there are clear patterns – dark workers are found more abundantly near the top of the nest, callow workers near the bottom, and, in the two larger colonies, seeds in the upper third. Most of the patterns seemed to be referenced not to absolute depth but to a proportional position relative to the ground surface and the deepest nest chamber (maximum nest depth). Most of the distributions are thus best expressed with reference to percentage of maximum nest depth in 10% increments (deciles). The effect of colony size was removed by analysing the distribution of ants, area, and material as a percentage of the total.

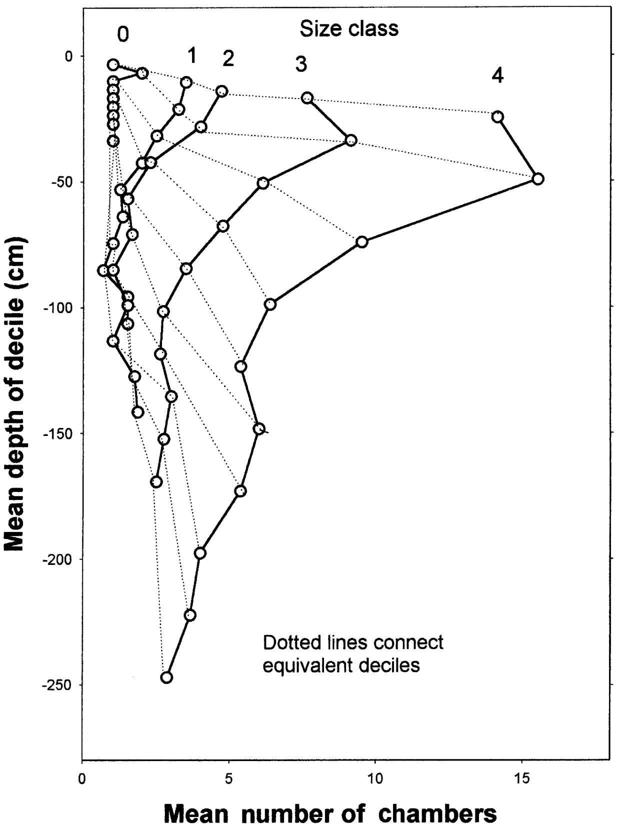

Fig. 3. As colonies grow, the nests get deeper and the number of chambers in each decile increases proportionally. Dotted lines connect each decile across all nest sizes.

Vertical distribution of chamber area

Larger colonies can be expected to excavate larger nests, but how are chamber number and chamber area distributed vertically? Figure 3 shows that maximum nest depth increased dramatically with colony size, from about 35 cm for the smallest colonies (incipient) to almost 250 cm for the largest. At the same time, the mean area of chambers increased greatly, especially in the top third of the nest. Mean chamber area in the top decile increased more than fivefold over the range of colony size (Fig. 4a). At the same time, within each colony size class the mean number of chambers in each decile decreased with decile (Fig. 3), so that the distribution of total chamber area in the nest column paralleled mean chamber area.

The *shapes* of these distribution curves were compared by standardising all data as a fraction of the total within each of ten equal intervals of the maximum nest depth (deciles). Because these were fractions, the data were square-root or arcsin-square-root transformed for ANOVA. Size class 0 was not analysed because it occurred only in the July sample, unbalancing the design. Size class 1 was absent from the May sample, and the appropriate mean values were substituted, followed by a reduction of the degrees of freedom in the *F*-test. In addition to the main effect of decile, the effects of interest

Dependent variable	Trans-formation	Effect	F-ratio	d.f.	P-value	R^2 of effect
% area	arcsin	decile, main	122.3	8,100	<0.001	72 %
		decile X size	4.13	24,100	<0.001	7
		decile X date	2.16	24,100	<0.01	4
		3-way inter.	1.80	64,100	<0.01	9

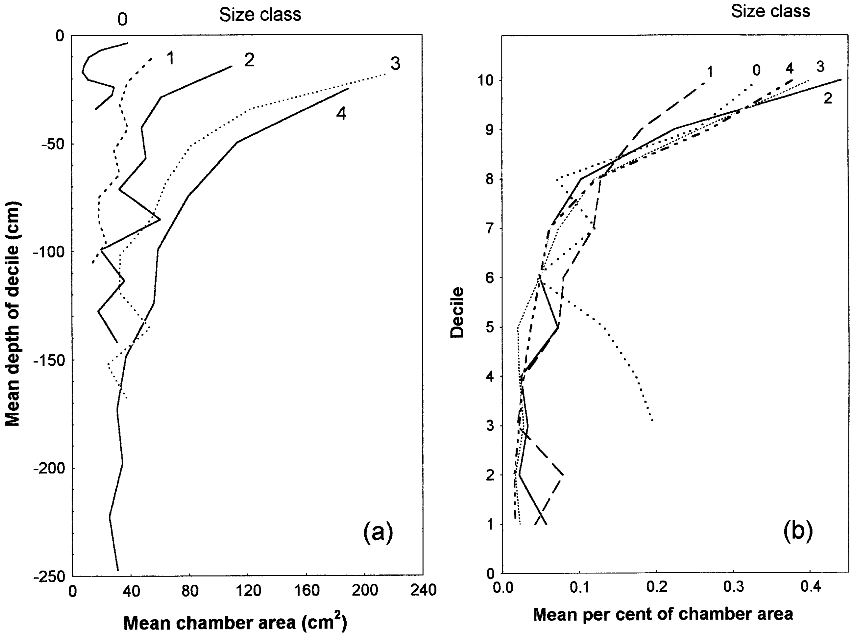

Fig. 4. (a) As colonies grow, their nests get deeper and the mean area of their chambers increases, especially in the upper parts of the nest. (b) The proportional distribution of total chamber area changed little with colony size (after the incipient stage, size 0, which was not included in the ANOVA analysis).

were the interactions of decile with colony size and/or sample date, because these indicated *differences of distributional patterns* with size or season. Most of the ANOVA outcomes can be found in the relevant figures.

Total chamber area was distributed such that it decreased strongly from the top to the bottom of the nest (Fig. 4b). The top third of the nest contained more than half of the total chamber area. The distribution was significantly different in small than in large colonies (decile–size interaction). This difference was almost entirely the result of the more even distribution of chamber area in the smallest colonies (size class 1) (Fig. 4b) (size class 0 was excluded from the ANOVA). All larger colonies proportionated their area very similarly along the nest column. The interaction with sample date and the three-way interaction were also significant, but these effects were small and lacked a clear pattern.

Total chamber number is not shown as a figure, but its pattern of distribution was very similar to that of nest area. The proportion of chambers decreased strongly with depth, and this was more pronounced for the smallest colonies [main effect of decile on proportion of total chamber number (arcsin square-root transformed): $F_{8,100} = 40.02$, $P < 0.001$; decile–size interaction: $F_{24,100} = 4.26$, $P < 0.001$]. Regression analysis showed that 86% of the variation in chamber area could be explained by chamber number, but that chamber area increased much faster than chamber number ($F_{1,38} = 233.53$, $P < 0.001$). Every tenfold increase in chamber number was accompanied by a 75-fold increase in chamber area. Chamber enlargement contributed much more to total area than did the creation of new chambers, at least partly because area increases with the square of the dimensions.

Proportional distribution of callow and dark workers

Callow (young) workers can be recognised by their lighter colouration, and were analysed separately from older, dark workers. Dark workers were very unevenly distributed with respect to depth, with much higher proportions near the surface and the bottom (Fig. 5). The middle deciles harboured relatively fewer workers. The details of this vertical distribution were different for colonies of different size (Fig. 5b) and at different times of the year (Fig. 5a). Most of the size-related difference was the result of the more even vertical distribution of workers in two of the size classes (size × decile interaction; Fig. 5b).

There were significant seasonal differences in the vertical distribution of dark workers, such that a higher proportion of them resided in the upper regions of the nest in spring and summer, and in the lower regions in autumn and winter

Dependent variable	Trans-formation	Effect	*F*-ratio	d.f.	*P*-value	R^2 of effect
% Dark workers	arcsin	decile, main	26.82	8,100	<0.001	36%
		decile X size	3.93	24,100	<0.001	16
		decile X date	4.13	24,100	<0.001	17

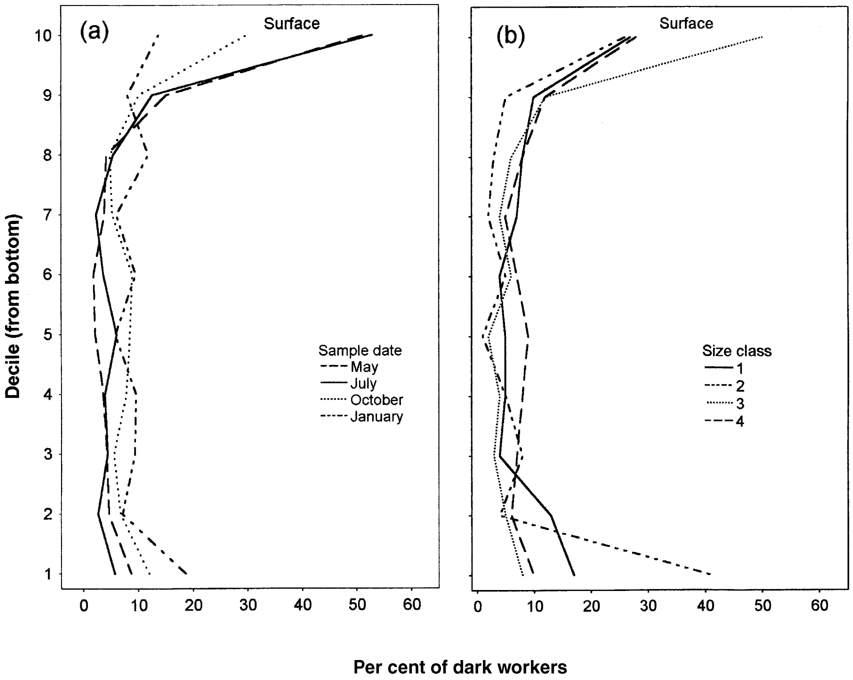

Fig. 5. A greater proportion of dark workers was found in the upper reaches of the nest, no matter what the colony size (b) or season (a). Vertical distribution of dark workers was more even in May than in other samples, and varied somewhat by colony size, although not in a regular way.

(Fig. 5a) (decile × date interaction). These movements were associated with the seasonally changing surface activity and the general inactivity during the winter.

The vertical distribution of callow workers was very different from that of dark workers; the greatest proportion of them was always found near the bottom of the nest during all three of the samples in which they were present (July–January) (Fig. 6). This distribution was somewhat different for different sizes of colonies (decile × size interaction) (Fig. 6b), but these differences were small and irregular. There were no seasonal differences in callow distribution (Fig. 6a). Thus, young workers simply accumulate near the bottom of the nest with little regard to the colony size or season.

Because the trends in the fraction of dark workers and callow workers were opposite, the frequencies of these workers must be changing in relation to one another. In other words, for any colony, what fraction of the workers in each decile was callow? When this fraction was regressed against the decile, it showed a linear increase with depth, no matter what the sample date (Fig. 7a). The fraction that was callow was higher in larger colonies, but the increase in fraction of callows with depth was similar for all colony sizes (no decile × size interaction) (Fig. 7b). The callow fraction is probably a reasonable surrogate for mean worker age. If so, the mean age of workers increased in a linear fashion between the nest bottom and the surface, i.e. workers moved upwards with age at a fairly constant rate. Under this scenario, the top-heavy and bottom-heavy distributions of workers result from their production as seasonal cohorts in the bottom of the nest. Indeed, the most even distribution of older workers and the most bottom-heavy distribution of callows occurred in January.

Proportional distribution of brood

The January sample was excluded from the brood distribution analysis because no brood was present. Larvae and pupae were not distributed differently from one another (i.e. worker larvae and pupae were highly correlated, $r = 0.7$), nor were sexual broods and worker broods. Figure 7 therefore shows all broods together. The vertical distribution of broods was strongly biased towards the lower chambers, with a minimum number (often none) in the middle range. Many nests had more than half of their brood in the bottom decile or two. For worker broods, decile explained 31% of the variation and a decile × size interaction explained another 16%. This interaction resulted

Dependent variable	Trans-formation	Effect	F-ratio	d.f.	P-value	R^2 of effect
% Callows (excl. May)	arcsin	decile, main	15.97	8,80	<0.001	52%
		decile X size	2.07	24,80	<0.02	18

Fig. 6. A greater proportion of callow workers was found in the lower regions of the nest, no matter what the colony size (b) or season (a). There were small colony-size differences in the vertical distribution, but they were not regular.

from a less bottom-concentrated distribution of the worker broods of the largest size class (Fig. 8a). There were no seasonal differences in worker-brood distribution (Fig. 8b).

Patterns were less strong for sexual broods (not shown as a figure), because these were much less abundant, but were generally similar to worker broods. Only the May sample had enough sexual broods for an ANOVA. The fraction of sexual broods increased with depth [main effect of decile on proportion (transformed): $F_{3,35} = 10.3$, $P < 0.001$, $R^2 = 69\%$]. There were no seasonal or colony-size differences in the vertical distribution of sexual broods (no significant interactions). Like worker broods, they were mostly kept near the bottom of the nest.

In view of the similar vertical distribution of callow workers and broods, the two may be correlated on a very local scale. When the fraction of all broods that were found in each decile of each colony was regressed against the fraction of the callows found in that decile (Fig. 9), the relationship was isometric (slope = 0.98) and very tight (January sample excluded: $F_{\mathrm{brood}} = 0.0011 + 0.98(F_{\mathrm{callow}})$, $F_{1,97} = 640$, $r = 0.932$, $R^2 = 87\%$). This high correlation was also seen when numbers were used instead of fractions. Two explanations suggest themselves. First, callows may be aggregated near the brood because they care for brood, or, second, the association may simply result from the fact that the brood become callows, and callows remain where they eclose. The latter is supported by the observation that the number of brood per callow worker was much higher in July than in October or May.

Vertical location of queens in the nest

All but three of the 26 recovered queens were found in the bottom third of the nest, and 17 of these were in the bottom chamber. No clear seasonal differences in location were apparent.

Proportional distribution of seeds and seed size

Workers store seeds at a preferred depth below the surface, between approximately 40 and 90 cm (Fig. 10a). In small nests where the total depth was less than the preferred seed-storage depth, seeds were simply stored in the deepest chambers (note size classes 0 and 1 in Fig. 10a). The proportional vertical distribution of seeds was most strongly associated with depth, peaking at 20–40% of the maximum nest depth, and explaining 24% of the variance (Fig. 10b). Proportional seed distribution was somewhat lower in May (decile × date interaction), but this

Dependent variable	Trans-formation	Effect	F-ratio	d.f.	P-value	R^2 of effect
Fraction callow	log-log	size, main	6.73	3,79	<0.001	17%
		decile, main	6.86	9,79	<0.001	53

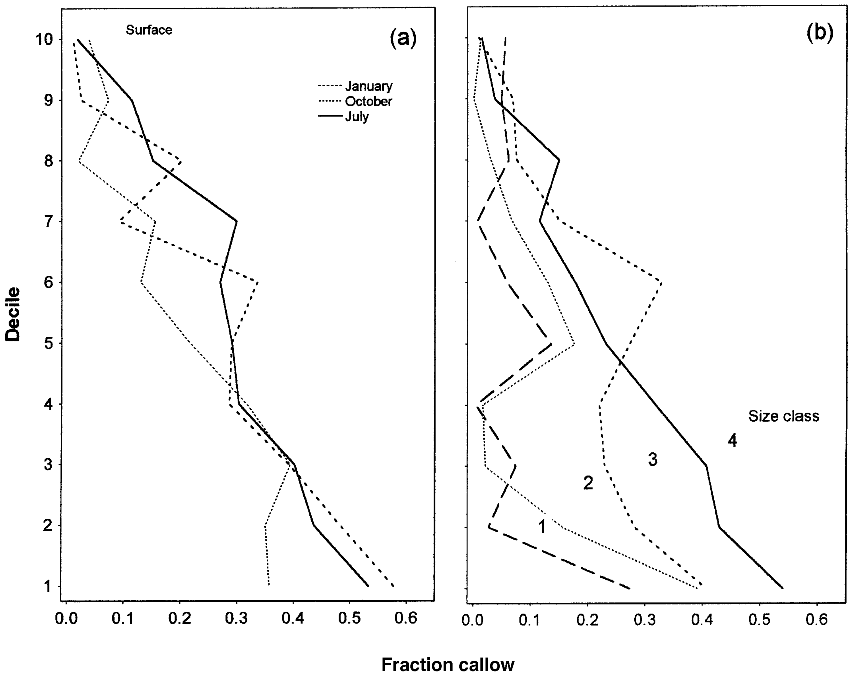

Fig. 7. (a) The fraction of the workers in each decile that was callow decreased in a linear fashion from the bottom of the nest to the surface. This fraction is a reasonable surrogate for mean worker age. (b) As colony size increases, the fraction of workers that is callow increases, but the vertical distribution of this fraction does not vary in relation to size class.

effect was barely significant. Because small, shallow colonies store seeds proportionally deeper, there was a significant decile–size interaction that added 16% to the explained variance. Also, because chambers tended to be either filled with seeds or have none, the pattern was rather erratic, leading to an uninterpretable three-way interaction. A total of 66% of the variance was explained by significant effects.

Seeds from each chamber were passed through a series of sieves to separate them into 10 size classes. The number of seeds of each size was summed within each decile, and these distributions were converted into percentages using the total number of seeds in each decile as the divisor. These data were used to test possible differences in seed size distribution by season, depth, and colony size. Neither sample date nor colony size affected the seed size distribution (ANOVA $P > 0.5$), but a significant decile × seed size interaction ($F_{81,780} = 2.64$, $P < 0.00001$, $R^2 = 34\%$) indicated that seed size distributions were different at different depths. Inspection of the distributions indicated that some of this variation may have been capricious and erratic, but it also seemed that May, and to a lesser extent July, colonies had mostly very large seeds in the top decile. This and the other variations in seed size distributions probably represent local and seasonal availability, rather than changing worker preferences.

Vertical distribution of densities

Because chambers decreased in size towards the bottom of the nest, but all ants except dark workers increased, the density of ants (individuals cm^{-2}) increased strongly in the lower parts of the nest. Even dark workers, although there were proportionally more in the top of the nest (Fig. 5), occurred at their highest densities in the bottom (Fig. 11). The greatest proportion (28%) of the variance in dark-worker density was explained by decile. The erratic vertical distribution of density in size class 2 of the May sample (Fig. 11) resulted in significant interactions of decile with size and date. However, these patterns were difficult to interpret and may be anomalous. Each contributed approximately 10% to the explained variance. The density of dark workers was consistently lower in the July sample before worker emergence was in full swing (Fig. 11a), resulting in the main effect of date that explained 9% of the variance. Surprisingly, colony size had only a small direct effect on density, accounting for 3% of the variance. Apparently, nest enlargement slows down the worker population very little. Overall, 61% of the variance in dark-worker density was explained by significant effects.

The vertical distribution of callow worker density was simpler (Fig. 12), increasing primarily with depth (the May

Dependent variable	Trans- formation	Effect	F- ratio	d.f.	P- value	R^2 of effect
Per cent brood (excl. Jan)	arcsin	decile, main	11.75	8, 84	<0.001	31%
		decile X size	1.98	24, 84	<0.05	16

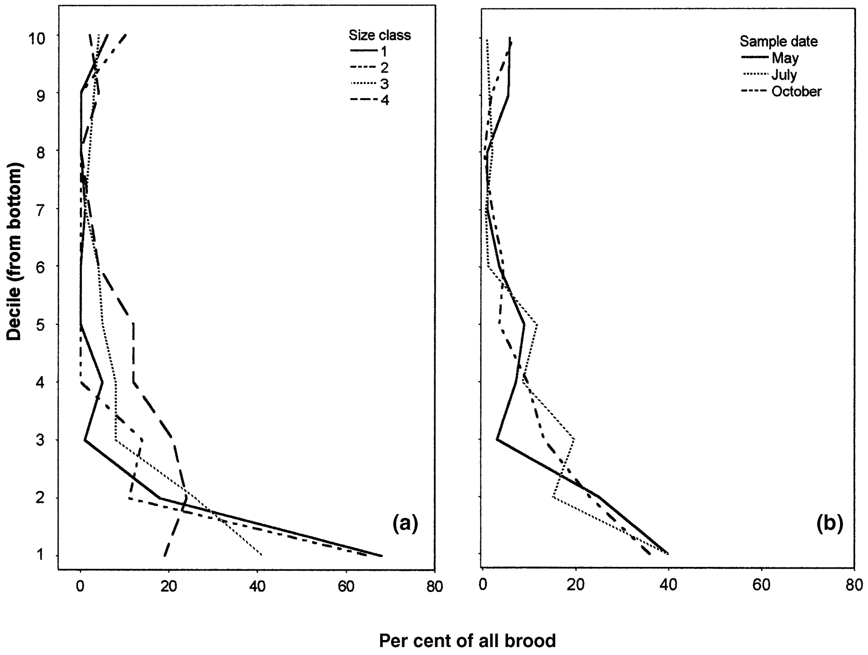

Fig. 8. (a) Broods were much more prevalent near the bottom of the nest, and were somewhat more evenly distributed in the largest colonies, giving rise to a significant decile × size interaction. (b) Vertical distribution of broods did not change across the seasons (broods were absent in January).

sample was excluded because callows were absent). Thus, decile accounted for 36% of the variation. The overall density of callows was consistently greater in the two larger size classes (Fig. 12b), giving rise to a significant main effect of colony size. The density did not differ by date, nor did the effect of decile vary among the sample dates (Fig. 12a). It appears that callows distributed themselves simply in relation to depth in the nest, with space being somewhat scarcer in the larger colonies.

The distribution of worker-brood density was also simple (Fig. 13). The strong increase in worker-brood density with decile accounted for 30% of the variance. The January sample was excluded from the analysis because worker-broods were absent. Worker-brood density did not change significantly with colony size or sample.

Sexual brood was abundant only in the May sample, and, by chance, was absent in size class 2. Analysing only those colonies in the May sample in which sexual brood was present, sexual-brood density simply increased with depth in the nest, so that decile accounted for 73% of the variance (main effect of decile, log-transformed data: $F_{8,18} = 7.88$, $P < 0.001$). Like worker broods, sexual broods were arranged simply in reference to the bottom of the nest. The sharply decreasing chamber area coupled with the increased number of broods and callows created very high densities in the bottom of the nest. Because the patterns were similar for worker and sexual broods, Fig. 13 shows the density of total broods in relation to decile. The discrepancy between the ANOVA results and the apparent interactive effect between decile and season or decile and size that is seen in Fig. 13 is a consequence of using log-transformed data for the ANOVA and for plotting the arithmetic values in the figure.

Discussion

This analysis of ant, seed, and chamber distribution is essentially a morphometric one; by transforming all counts and measures to a proportion of the total, all data are standardised and made *size-free*. The relationships among two or more such standardised variables amount to *shape* variables, in the sense used in morphometric analysis of shape. For example, the relationship of the proportion of total nest area to the proportion of maximum depth describes the size-free, vertical *shape* of nest area. Similarly, the proportion of dark workers in relation to the proportion of maximum nest depth is the size-free, vertical *shape* (spatial structure) of the dark-worker population. Comparisons among such standardised variables also allow the detection of *differences* in the *shapes* of colony attributes. Shape differences show them-

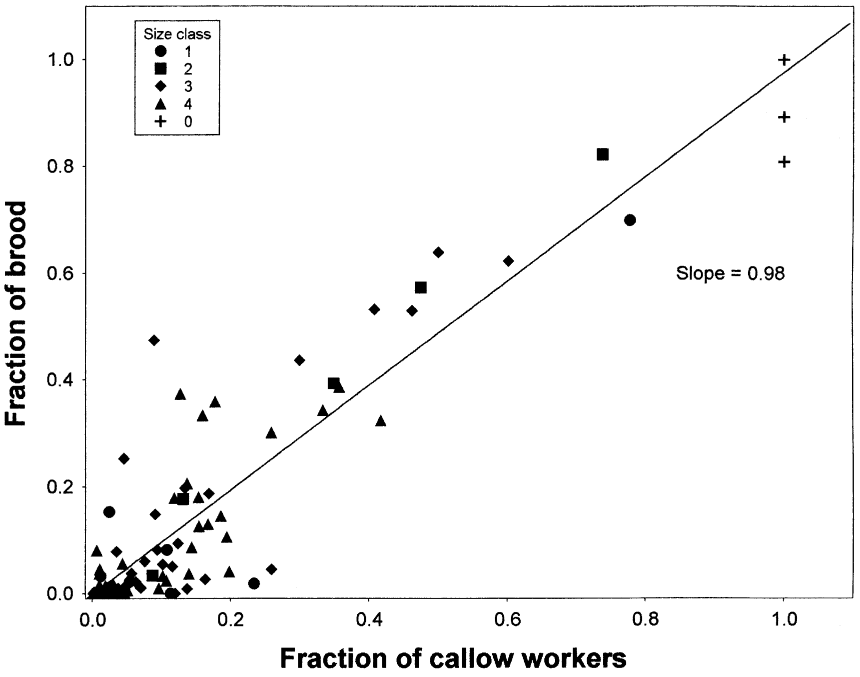

Fig. 9. The fraction of the brood and the fraction of the callow workers were isometric. Each point represents one decile of one colony. Deciles without brood and callows are undifferentiated at 0,0.

Dependent variable	**Trans-formation**	**Effect**	***F*-ratio**	**d.f.**	***P*-value**	**R^2 of effect**
Per cent seeds	arcsin	decile, main	13.20	8,100	<0.001	24%
		decile X size	2.83	24,100	<0.001	16
		decile X date	1.80	24,100	=0.05	10
		3-way inter.	1.78	64,100	<0.01	26

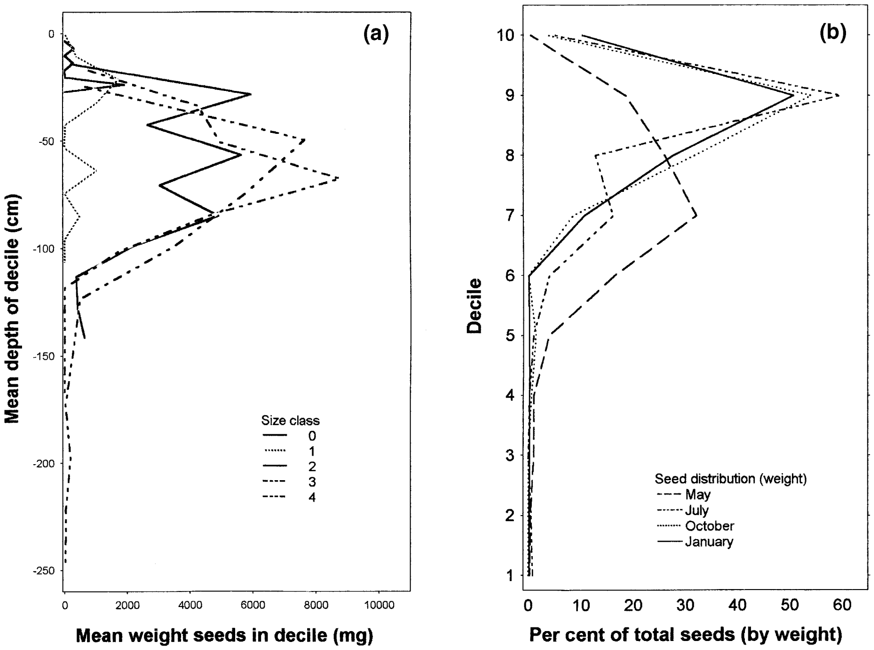

Fig. 10. The vertical distribution of seeds (a) as the mean weight of seeds by chamber depth and (b) by decile as a percentage of the total weight of seeds. Seeds were stored at a preferred depth between 40 and 100 cm, rather than a preferred percentage of total depth. Colonies with shallower nests than this stored seeds near the bottom of the nest.

Dependent variable	**Trans-formation**	**Effect**	***F*-ratio**	**d.f.**	***P*-value**	**R^2 of effect**
Dark worker density	log-log	size, main	4.20	3, 100	<0.005	3%
		decile, main	17.9	8, 100	<0.001	28
		date, main	14.5	3, 100	<0.001	9
		decile X date	7.07	8, 100	<0.001	11
		date X size	2.06	24, 100	<0.02	10

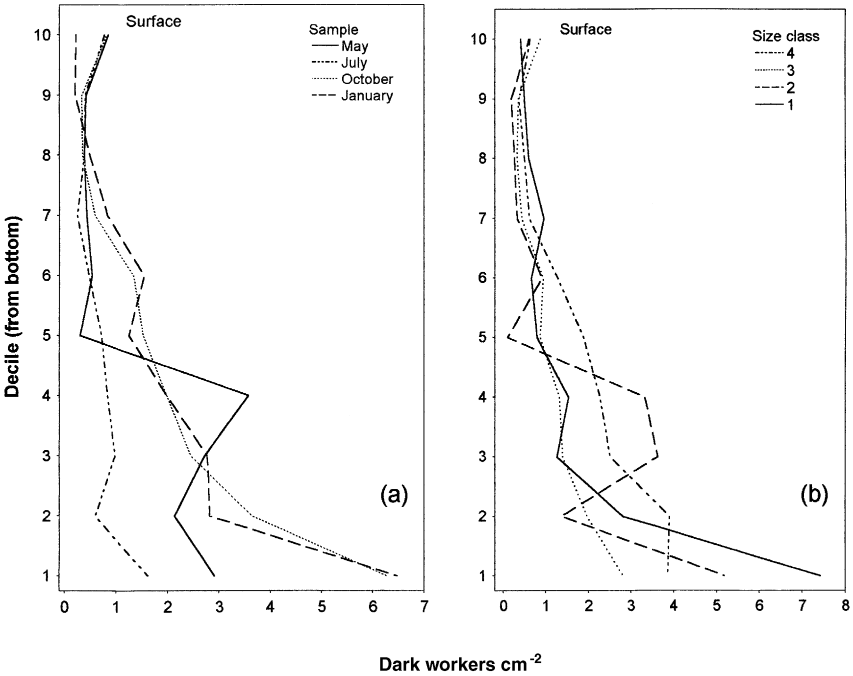

Fig. 11. (a) Although the number of dark workers was higher in the upper parts of the nest, their density was highest at the bottom. This was because chamber area was high near the surface and low near the bottom of the nest. (b) Size class had no effect on this density gradient.

selves as significant interactions between nest decile and the proportion in question, or sample date and the proportion.

This analysis shows that colonies were very top-heavy with respect to dark workers, and bottom-heavy with respect to callows and broods. The distribution of workers of all ages was decidedly more even throughout most of the nest column, and much more top-heavy than bottom-heavy at the extremes (not shown in the figures). These ant-distribution shapes only changed to a minor degree with season (January was more bottom- and less top-heavy) or with colony size. The excavated nest also showed little shape change during colony growth – the percentage area and percentage chamber number decreased smoothly and similarly from the surface to the bottom of the nest (only the smallest colonies were slightly less top-heavy). For both the percentage area and percentage chamber number, decile explained ten times more variance than did the decile × size interaction, emphasizing the minor changes of *shape* that occur during colony growth.

This is not true of seeds, the distribution-shapes of which changed with colony size. Here the interactions of decile with colony size and sample date explained twice as much variance of seed distribution as did decile alone. The size × decile interaction alone predicted two-thirds as much of the seed distribution as did decile. The reason for this was that seeds were stored preferentially between approximately 40 and 100 cm below the ground. Until nests are substantially deeper than 100 cm, the ants store seeds in the deepest chambers, i.e. proportionally deeper in shallow nests than in deep nests.

Do colony *shapes* have functional significance? Are spatial organisation and social organisation linked? Worker, brood and worker-age distributions are probably both created by and affect the geography of reproduction in harvester ant nests (MacKay, 1981b; Porter & Jorgensen, 1981; Tschinkel, 1998). Thus, larvae are reared preferentially in the lower nest chambers, accounting for the abundance of callows there. Early in their adult lives, these callows engage mostly in brood and queen care, which usually takes place in the nest region in which they eclosed. As they age, they move upwards in the nest, taking on more general nest duties, eventually becoming defenders (Porter & Jorgensen, 1981) as they begin to spend more time in the upper nest chambers. During the last few weeks of their lives they leave the nest to forage, a high-risk activity that ends with their death (Porter & Jorgensen, 1981). A number of laboratory studies have found only weak correlations between worker age and worker tasks. It is possible that, in nature, the correlation is strengthened by the upward movement of workers away

Dependent variable	Trans-formation	Effect	*F*-ratio	d.f.	*P*-value	R^2 of effect
Callow density (excl. May)	log	size, main	6.16	3, 74	<0.001	8%
		decile, main	10.43	8, 74	<0.001	36

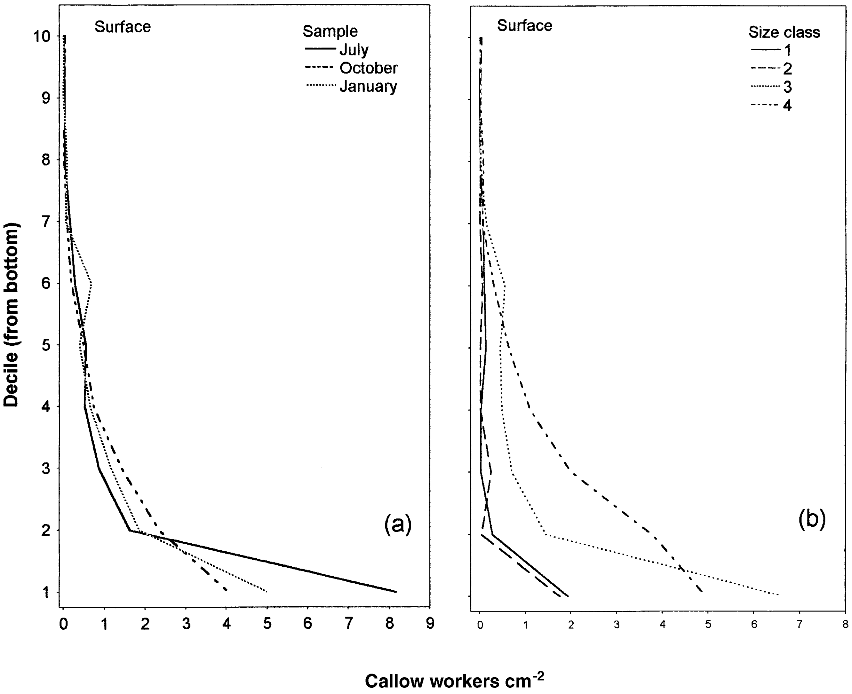

Fig. 12. The density of callow workers was highest (a) at the bottom of the nest in all samples in which they were present (excluding May), and (b) at all colony sizes. The density of callows also increased with colony size (main effect of size).

from brood. In this respect, age polyethism would be partly the consequence of the upward movement of workers, rather than a change in the preference for different tasks. Upward migration would bring workers into contact with different types of tasks. Sendova-Franks and Franks (1995) proposed a similar mechanism leading to the division of labour in *Leptothorax unifasciatus* – workers tended to restrict their activity to discrete zones (*spatial fidelity zones*) of the nest where they performed appropriate labour. Although these workers did not segregate on the basis of age, task performance was associated with location in the nest, as it was in harvester ants. Strickland and Franks (1994) also found evidence that the spatial distribution of behaviour may be important to the social structure of the colony.

The upward movement of harvester ants within the nest is a specific example of the general movement of ageing workers away from the brood area (Hölldobler & Wilson, 1990). This upward movement and the production of broods in the bottom of the nest may be the basis for several collective patterns in harvester ants. A simulation model was run (W. R. Tschinkel, unpubl. obs.) in which new harvester ant workers were produced seasonally in the bottom of the nest, and workers in each decile moved upwards to the next decile with a fixed probability during each time interval. This model produced vertical distributions of workers similar to those observed in this study. It obviously also produced a linear increase in mean worker age from the bottom of the nest to the surface, a pattern supported by the data (Fig. 7). Other features may also be explained by this simple upward movement of older workers – if workers are more likely to excavate chambers as they age, there would be more and larger chambers in the upper nest regions, as is indeed observed. It seems that the movement is a large part of the mechanism in this superorganismal regulatory process.

Other examples of persistent *localness* include *Ortstreue* (site fidelity) and the route fidelity of several species of ant (Otto, 1958; Rosengren, 1971; Porter & Jorgensen, 1980; Porter & Bowers, 1982; Cosens & Toussaint, 1985; Rosengren & Fortelius, 1986; Rosengren & Sundström, 1987; McIver & Loomis, 1993). These, the spatial fidelity zones, and the centrifugal movement away from broods may all be related phenomena linked through the more basic phenomenon of home range (the author is grateful to J. McIver for pointing this out). A great many animals typically occur within limited areas, their home ranges. When aphid-tending foragers restrict their movements to particular routes and locations, these define their home range. Across animal species, the size of home ranges increases with body size. Larger ant workers may have larger home ranges by virtue of their larger size, and thus forage to greater distances, as has been observed. Sendova-

Dependent variable	Trans-formation	Effect	*F*-ratio	d.f.	*P*-value	R^2 of effect
Brood density (July, October only)	log	decile, main	5.77	9,50	<0.001	30%

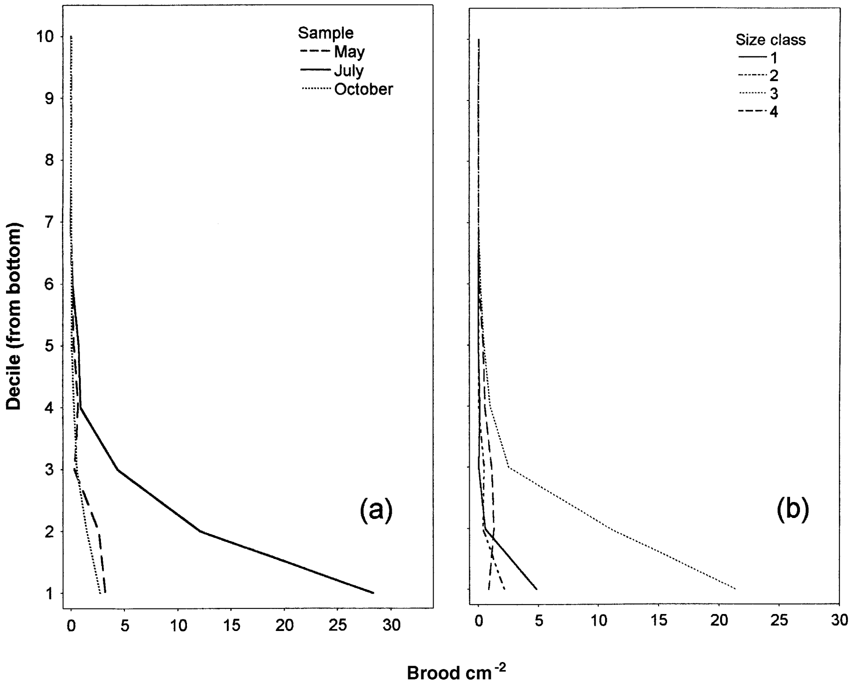

Fig. 13. The density of the brood was highest (a) at the bottom of the nest in all samples in which brood was present (excluding January), and (b) at all colony sizes. The figure shows the distribution of all broods, but the ANOVA results are for worker broods, which made up the great majority of the broods.

Franks and Franks (1995) and Strickland & Franks (1994) indicated that the size of the spatial fidelity zones of nest workers increases as they move away from the brood pile. Continued expansion of this zone as the workers move to the exterior of the nest would result in phenomena such as *Ortstreue* and route fidelity. However, spatial fidelity zones are not simply referenced to location, but are clearly also a social phenomenon – workers reconstruct their spatial fidelity zones relative to one another when they move to a new nest (Sendova-Franks & Franks, 1994).

It is difficult to understand the functional value of the large amount of nest area in the upper regions of harvester ant nests. The density of all stages was typically low in this region, whereas crowding of all stages was great in the lower nest chambers. It was common to find empty chambers in the top half of the nest. In light of the enormous effort involved in these excavations, the relative vastness of the upper nest region is unlikely to be an epiphenomenon without functional meaning.

In harvester ant nests, the lowest chambers contain the most broods and brood-tending workers (the callows), but are also the most crowded with respect to all stages and ages. Brian (1956) suggested that crowding of brood-tending workers in *Myrmica* leads to inefficiency in brood care. Little is known about the space requirements of *P. badius*, but the self-imposed nature of the crowding would suggest that even this degree of crowding is not above the optimum, because workers need only move broods a few chambers higher in the nest to relieve crowding.

It is tempting to conclude that the ants were driven into the lower regions by the excavation, but evidence from the barrier nest excavation failed to support this. Furthermore, it would require that callows move down and older workers move up in response to disturbance. Workers were rarely observed rushing out of the tunnels, as though moving upward in the nest. MacKay (1981b) also argued that excavation caused only minor vertical movement. With the exception of the defenders responding to disturbance in the uppermost chambers, workers seem to remain in chambers until exposed to daylight. This tendency seems to be widespread among *Pogonomyrmex* species, but without testing this cannot be assumed to be generally true of ant species.

The present findings on *P. badius* generally confirm those of MacKay (1981b) on three western North American species of *Pogonomyrmex*. In all cases, older workers were more abundant in the upper nest regions, younger workers in the middle and bottom regions where broods were also found. Like MacKay, no difference was found in the distribution of larvae and pupae. The colder winters experienced by the western species resulted in stronger seasonal differences in distribution, especially of the older workers. However, all species, including *P. badius*, showed strongly seasonal brood production limited to the warmer months. The first brood of the year in all species was the sexual brood. This pattern seems to be widespread in temperate ants, and is associated with the expenditure of stored fat (Tschinkel, 1987, 1993, 1998). Following the production of sexual broods, colonies only produce workers for the remainder of the year.

Although this study and that of MacKay are similar in many respects, MacKay (1981b) chose his samples differently. MacKay sampled stable populations of long-lived colonies haphazardly, so that most of the colonies were mature. This sampling regime weakens any tests of the effects of colony size, and, indeed, MacKay detected no relationship between worker number and nest depth in any of the three species he studied. In the present study, the full range of available sizes was sampled deliberately in order to be able to determine the effect of colony size on several dependent variables. Colony size was thus found to affect nest depth and total area, chamber number, seed distribution, worker-brood distribution, and callow density.

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