Research article

Nest complexity, group size and brood rearing in the fire ant, *Solenopsis invicta*

D. Cassill[1], W.R. Tschinkel[2] and S.B. Vinson[3]

[1] *Department of ESP-Biology, University of South Florida St. Petersburg, St. Petersburg, FL 33701-5016, USA, e-mail: cassill@stpt.usf.edu*
[2] *Department of Biological Sciences, Florida State University, Tallahassee, FL 32306, USA, e-mail: tschinkel@bio.fsu.edu*
[3] *Department of Entomology, Texas A&M University, College Station, TX 77843-2475, USA, e-mail: bvinson@acs.tamu.edu*

Summary. Colonies of the monogyne social form of the red imported fire ant, *Solenopsis invicta*, may contain half a million workers per nest. Spatially organizing such a large group within the confines of a single nest requires a pragmatic architectural design. The morphology of field mounds and subterranean nest chambers of *S. invicta* were determined using several cast methods. The above-ground portion of a fire ant nest, the mound, consisted of a dense matrix of narrow tunnels. Below ground level, subterranean shafts and nodes were excavated through the grass root system (10–20 cm), connecting the mound tunnels to the subterranean chambers. Chambers averaged ~ 5 cm^2 and appeared at depths from 10–80 cm below ground level. The orientation of mound tunnels and subterranean shafts was more often vertical than horizontal, probably facilitating the diurnal micro-migration of colony members back and forth from the subterranean chambers to the mound. The mean size of groups in the subterranean chambers of field nests was remarkably small relative to colony size (~ 200 individuals per chamber: 50% workers, 50% brood). In laboratory experiments, neither crowding nor nest partitioning affected brood rearing. The possibility that small group size and nest complexity generate localized or time-released communication signals is discussed.

Key words: Information flow, social organization, chamber size, mound structure.

Introduction

The nests of social insects are amongst the most sophisticated of all animal artifacts (Franks and Deneubourg, 1997; Theraulaz et al., 1998). Bees and wasps construct above-ground nests with a separate hexagonal cell for each egg. Cells can be organized into combs and each comb can be organized into distinct concentric regions for egg development, pollen storage and honey storage. In contrast, ants excavate relatively large, amorphous, subterranean chambers in which clusters of eggs and other brood stages are reared communally (Wilson, 1971; Brian, 1983; Hölldobler and Wilson, 1990). Some ant species construct simple nests consisting of a single brood chamber that is enlarged as the colony grows (e.g., *Leptothorax,* Franks and Deneubourg, 1997). When colony size is large, with thousands or even millions of members, nests are more complex (Hölldobler and Wilson, 1990). Rather than enlarging existing brood chambers, new brood chambers are excavated in soil (e.g., *Solenopsis invicta*, Markin et al., 1973; *Veromessor pergandei,* Wheeler and Rissing, 1975; *Camponotus senex*, Schremmer, 1979; *Pogonomyrmex badius*, Tschinkel, 1999) or constructed from leaves (*Oecophylla longinoda*, Hölldobler and Wilson, 1983).

Brian (1953, 1956) was the first to study the relationship between nest complexity, group size and brood rearing in the ant *Myrmica rubra*. In a series of elegant experiments, Brian discovered that workers were individually more effective in rearing offspring when group size was small, whereas groups were more effective in rearing offspring when group size was large. This paradox was resolved when Brian showed that partitioning one large group into ten smaller, interconnected groups maximized both individual and group production of offspring. Thus, nest partitioning facilitated the rearing of offspring.

In this paper, we extend Brian's work (1953, 1956, 1983) and that of Markin et al. (1973) on the form and function of nest architecture in ants by reporting on nest complexity, group size and brood rearing in the monogyne and polygyne social forms of the red imported fire ant, *Solenopsis invicta*.

Materials and methods

Nest architecture

To quantify chamber size, group size and group composition, 11 mature fire ant nests (8 in sandy soil; 3 in clay soil) were excavated and censused during June and July 1995, near the airport in Tallahassee, Florida, U.S.A. Before excavation, nest occupants were euthanized with approximately 30 to 50 ml of chloroform which was sprinkled onto the mound. A large sheet of plastic was placed over the nest to block chloroform fumes for ten minutes before excavating the subterranean chambers. Thirty randomly-selected chambers containing both brood and workers were censused per nest. Chambers were labeled according to depth (number of cm from ground level) and their sequence of excavation. Occupants were aspirated from a chamber and placed in a labeled container. Next, the outline of the chamber was traced onto an acetate sheet and labeled to match that of its occupants. The surface area of each chamber was calculated from these acetate tracings. Because weather had been dry and hot, colony members were located only in the subterranean portion of the nest.

To determine the effect of chloroform on the distribution of colony members within a nest, four laboratory colonies (~ 5000 workers and ~ 300 brood) were established in vertical, glass nests ($12 \times 4 \times 0.5$ cm). In every case, only a small portion of workers visibly reacted to the fumes. Those workers moved in erratic fashion for $5-30$ s, before succumbing to the chloroform fumes. A small fraction of workers tumbled into chambers from the vertical tunnels. Otherwise, workers succumbed in the chambers in which they had been located prior to administration of the chloroform. No brood was moved. Based upon these observations, it was assumed that chloroform would not significantly alter the distribution of workers and brood among the chambers in field colonies.

Variables recorded for each colony were: soil type, chamber depth, chamber surface area; number of workers per chamber; number of pupae per chamber; and number of larvae per chamber. Eggs were too delicate to survive the census process. Containers with colony members were held overnight at $-20\,°C$ in a laboratory freezer until the census could be completed the following day. To check reliability of census counts, colony members from ten randomly-selected chambers were recounted three times each. Differences among individual counts fell within 5% of the value of their pooled mean. Measures of the surface area of chambers were repeated three times on 20 randomly-selected chambers. Differences among individual measurements fell within 3% of the value of the pooled mean. Measurements of the diameter of plaster tunnels and nodules were repeated three times on 20 tunnels and 10 nodules. Differences among individual measurements fell within 1% of the value of the pooled mean.

The density and composition of occupants inside mounds were determined by excavating five nests in research fields at Texas A and M University, College Station, Texas, U.S.A. during November 2000. To ensure pristine architecture, mounds were censused in the afternoon on days following a ground-soaking rain. To further characterize mound architecture, plaster casts were made of three mounds and their subterranean systems up to 10 cm below ground level. The mound casts were broken apart to measure the diameter of tunnels and nodules. Lastly, a cast of one above-ground mound was made. Two longitudinal sections were cut through the dome of the mound caste perpendicular to the ground surface to estimate the length of vertical and horizontal tunnels in the mound. Freezing weather intervened before additional mounds could be excavated.

Effects of chamber size on group size

To determine the effect of nests without partitions on the size of brood groups, 3000 colony members (2 g workers and 1 g brood) from a laboratory-reared stock colony were placed in a single, large artificial chamber (145 cm²) at half the density of field chambers (21 members/cm²). The location of brood (pupae, larvae and eggs) within each chamber was mapped every other day for 9 days (five maps/chamber). These procedures were repeated for a total of five colony replicates from monogyne stock colonies.

Effects of crowding and nest partitioning on brood-rearing

To determine the effects of crowding and nest partitioning on brood rearing, three nest morphologies were tested. Each nest had the same total volume, but differed in either the size (floor area) or number of chambers (Fig. 1a, b, c). Data from a flat, single-chambered nest was the control for both crowding and partitioning treatments. Ten stock colonies were used as replicates for a 10×3 experimental design.

Each artificial nest contained 600 colony members (0.2 g or ~ 300 larvae and 0.4 g or ~ 300 workers). To randomize differences, larvae were culled from multiple stock colonies and pooled into one container. Next, 30 samples of larvae were randomly selected from the pool and placed inside each of 30 artificial nests.

The experimental colony fragments were incubated for one week under constant light at $30\,°C$ and were fed an over-abundance of frozen crickets and 30% sugar water (w/v) on a daily basis. Nests were moistened daily to prevent larval or worker desiccation. The experiment was terminated when > 90% of the larvae had pupated. Nests were placed in a freezer with a minimum of disturbance of colony members. Data were recorded the following day.

The total mass of workers per nest and the total mass of pupae per nest were determined. From each nest, twenty pupae were randomly selected and weighed individually to determine mean live body weight per pupa per nest. Worker mortality per nest was determined by counting the heads and the gasters of ant carcasses piled in the foraging area. If the numbers did not agree, a recount was conducted until the difference in the number of heads was < 2% of the number of gasters. Density per nest was calculated as the number of workers and brood per cm² of nest floor area. The worker:brood ratio per nest (i.e., available labor for brood rearing) was calculated as the number of workers inside the nest divided by the number of pupae inside the nest. The number of workers residing outside the nest was also counted to determine a correlation between worker exposure and worker mortality.

Data analysis

Data were analyzed using JMP software (Sall and Lehman, 1996). In all cases, the stock colony of origin was analyzed as a blocking factor or covariate. Chamber surface area and group size per chamber were transformed using common logarithms. Differences and associations were reported as significant at $\alpha < 0.05$. The tunnel diameter was reported in "mm" units whereas chamber floor area was reported in "cm²" units.
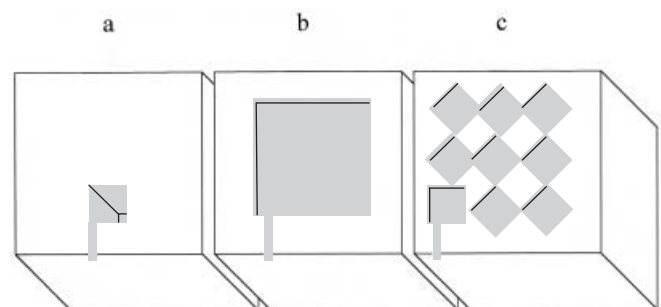

Figure 1. Artificial nest morphology. Nests contained chambers of the same total volume (1 cm³) but of different shapes. Nests were made of plaster poured over 1 cm³ clay that had been shaped into one of three chamber morphologies: **a**) a cubic chamber with 1 cm² floor area; **b**) a flattened chamber with 9 cm² floor area; and **c**) nine flat chambers with 1 cm² floor area per chamber). After the plaster hardened, the clay was removed, leaving a chamber in which workers and brood resided

The subterranean chamber data were from monogyne colonies whereas mound data were from polygyne colonies. Casual observation suggested that the architecture between these two fire ant forms was similar. However, because mean worker size in polygyne colonies is smaller, it is possible that mound tunnels and subterranean chambers are smaller. Additional excavations are needed to resolve this issue.

Results

Nests

The mound portion of the nest was a dense matrix of tunnels and nodules (Fig. 2) constructed from soil pellets of varying size (Fig. 3). The curvature of some pellets suggested that soil was shaped into a ball by the curvature of the mandibles – much as an ice cream scoop shapes ice cream. The length of vertical tunnels was twice that of horizontal tunnels ($F_{1,54}$ = 25.626; $p < 0.0001$). The mean diameter of tunnels in the mound was 4.4 mm (range = 3.0 mm to 8.0 mm). The mean density of colony members in the mound was 70 individuals per cm^2 (range = 48/cm^2 to 90/cm^2). Density was positively correlated with number of brood ($F_{1,101}$ = 108.7; $p < 0.0001$) but was not correlated with worker: brood ratio ($F_{1,101}$ = 0.430; $p = 0.513$) or mound temperature ($F_{1,101}$ = 1.326; $p = 0.0162$). The composition of colony members in the mound varied from nest to nest. In two nests, the majority (70%) of colony members located in the mound were workers whereas, in the remaining three nests, the majority (75%) of colony members located in the mound were brood. In three mounds, 70% of brood was pupae and prepupae whereas in two mounds, 80% of brood was larvae. Thus, mounds appear to serve as an incubator for all stages of brood.

Shafts and nodules continued through the grass root system 5 cm to 10 cm below ground level. The mean diameter of shafts was 6.0 mm (3.0 mm to 9 mm); nodules were 14.0 mm in diameter (8.0 mm to 19 mm), both significantly larger than mound tunnels and nodules (Tukey-Kramer $q = 0.566$; $p < 0.05$). We were unable to collect data on group size or density in these shafts because the dense root system disrupted our ability to census colony members.

True chambers did not appear within the nest until just below the grass root system, 10 cm – 80 cm from ground level (Fig. 4 a, b). The mean floor area of subterranean chambers was 4.6 cm^2 ± 2.4 cm^2 (± SD; range = 3.0 cm^2 to 9.9 cm^2; n = 243). Chamber depth was not measured. The floor area of subterranean chambers did not vary significantly with sandy versus clay soil type ($F_{1,239}$ = 2.536; $p = 0.113$) or chamber depth ($F_{1,239}$ = 1.399; $p = 0.238$). The amoeboid shape of large brood chambers suggests that they may actually be conjoined chambers (Fig. 5). Chambers were inhabited by 185 ± 10 individuals, 92 individual brood and 93 workers, for a mean worker:brood ratio of 1:1. Of the 92 brood individuals, 48 were pupae and 44 were larvae for a mean pupa:larva ratio of 1:1. Nests in sandy soil changed more abruptly from the mound's tunnel system to the subterranean chamber system than did nests in clay soil. The difference may have been the lack of a thick, grass root system in the sandy soil.

Figure 2. A hydrostone mold of a nest mound (side view). Mounds were composed of a labyrinth of tunnels and nodules constructed from soil pellets excavated from the subterranean portions of the nest. Shafts and nodules continued through the grass root system, connecting mound tunnels to subterranean chambers below the root system. Photo by Walter R. Tschinkel
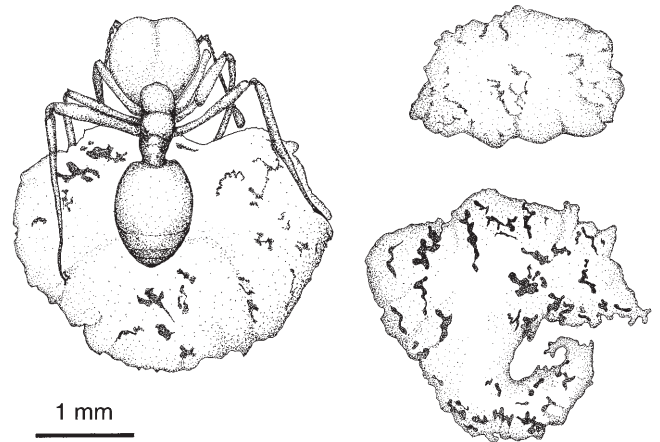

1 mm

Figure 3. Soil pellets from a mound. The worker is a major from a polygyne colony. Soil pellets varied in size. Many pellets showed a curled formation, suggesting that rain-dampened soil might be excavated by a worker's mandibles in much the same way that ice-cream is excavated by an ice-cream scoop

Group size was associated with chamber size (R^2 = 50.5%; $F_{1,238}$ = 326.9; $p < 0.0001$; Fig. 6) and varied marginally among colonies ($F_{1,238}$ = 3.937; $p = 0.048$). Group size did not vary with soil type ($F_{1,238}$ = 0.124; $p = 0.726$) or chamber depth ($F_{1,238}$ = 1.909; $p = 0.168$). The number of brood individuals per chamber was unaffected by soil type ($F_{1,190}$ = 0.199; $p = 0.656$) or chamber depth ($F_{1,190}$ = 1.8995; $p = 0.170$). The mean density of colony members within chambers was 40.2 ± 2.4 individuals per cm^2 (± SD; range = 4/cm^2 to 95/cm^2). The density of colony members increased significantly with group size ($F_{1,237}$ = 328.6; $p < 0.0001$), decreased
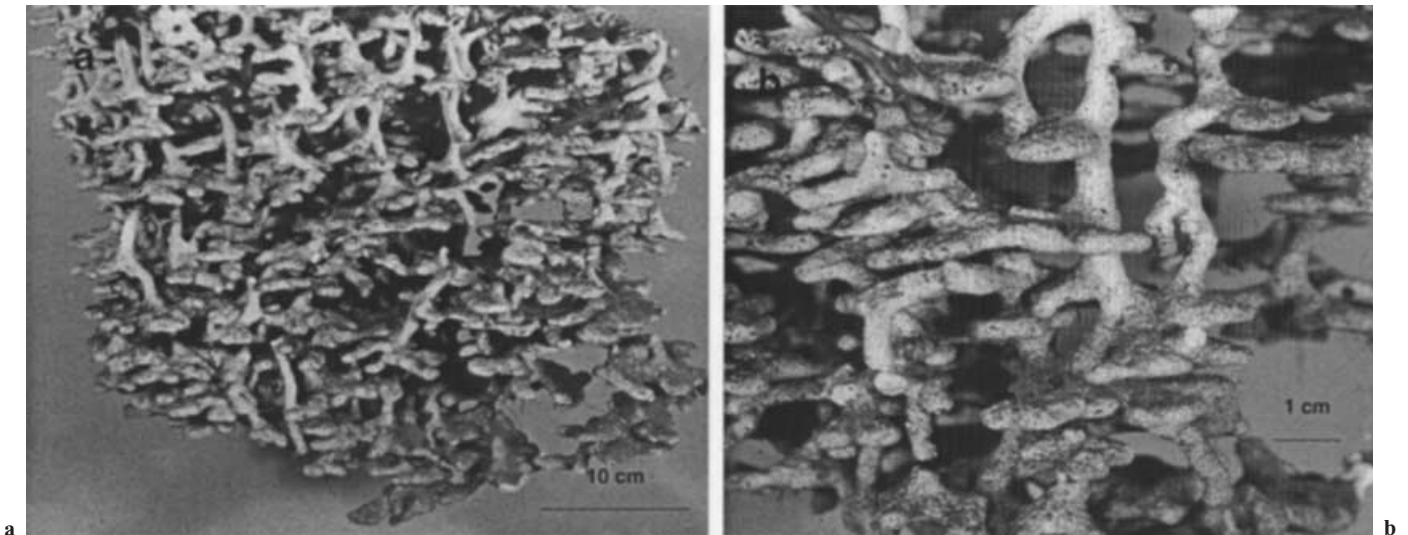
Figure 4. A hydrostone mold of the subterranean chambers of a nest (side view). (**a**) Horizontal chambers branch from verticle shafts. (**b**) Most chambers were skewered by multiple shafts. Photos by Walter R. Tschinkel
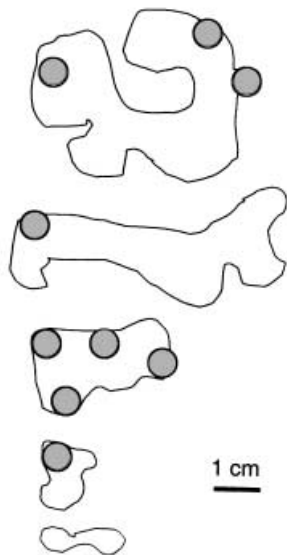

Figure 5. Dorsal view of subterranean chambers (actual size). Chambers were amorphous and varied in size and number of tunnels (shaded area)
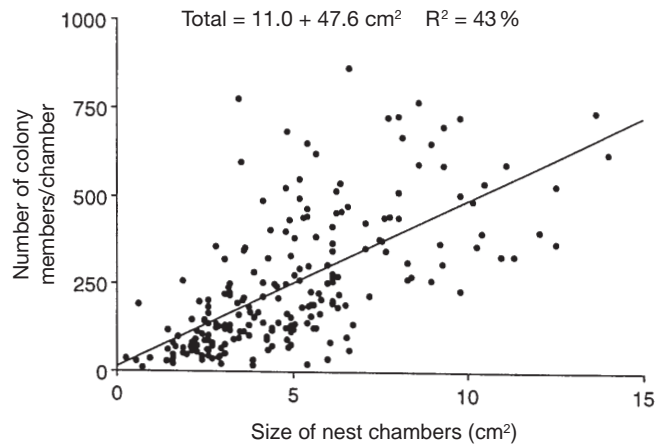

Figure 6. Within field nests, group size was correlated with chamber size

significantly with chamber size ($F_{1,237} = 147.3$; $p = < 0.0001$), but was unaffected by soil type ($F_{1,237} = 2.907$; $p = 0.090$), chamber depth ($F_{1,237} = 0.031$; $p = 0.859$) or colony ($F_{1,237} = 1.299$; $p = 0.256$). The ratio of workers to brood was unaffected by chamber size ($F_{1,236} = 2.222$; $p = 0.137$, chamber depth ($F_{1,236} = 0.077$; $p = 0.782$) or group density ($F_{1,236} = 0.401$; $p = 0.527$).

Effects of chamber size on group size

Within an artificially enlarged chamber, workers partitioned brood into small groups (Fig. 7) in a bi-modal distribution.

Half the groups contained fewer than 10 brood individuals – mostly large larvae; the other half contained a mean of 120 brood individuals. Brood individuals were segregated into clusters of pupae, larvae and eggs (Fig. 7). Eggs were associated with pupae – both are non-feeding brood stages. Pupae were packed more densely than larvae ($66/cm^2$ versus $37/cm^2$). More than likely, the curvature and pilosity of larvae precluded dense packing, allowing workers easy access to them for feeding and grooming. Thus, workers maintained brood in small groups even without the constraints of nest walls. The groups containing ten or fewer larvae may have resulted from workers unintentionally pushing larvae away from the main cluster in the process of feeding them.

Figure 7. The distribution of brood within an artificial nest without partitions (five different nests are shown). Brood individuals were sorted into small clusters of pupae (white areas), larvae (black areas) and eggs (dotted area). The distribution of clusters was bi-modal with half the clusters containing fewer than 10 larvae; the other half contained a mean of 120 larvae

Effects of crowding on brood-rearing

Even though the density of colony members was 10-fold greater in cubic nests than in flat nests (494 colony members/cm² versus 50.2 colony members/ cm² of floor area), crowding did not affect total pupal mass per nest ($F_{1,19}$ = 0.816; p = 0.389) or mean mass of individual pupae per nest ($F_{1,19}$ = 0.267; p = 0.616; 0.74 mg and 0.73 mg live weight per pupae). Nor did crowding affect the number of workers tending brood ($F_{1,19}$ = 2.095; p = 0.181), the worker: brood ratio inside the chamber ($F_{1,19}$ = 0.003; p = 0.957) or worker mortality (percent of total workers that were dead: $F_{1,19}$ = 0.306; p = 0.595). Chamber volume rather than floor area may be the more meaningful metric of nest architecture. Varying the height of chambers rather than the floor area may produce different results.

Effects of nest partitioning on brood-rearing

Partitioning had no effect on total pupal mass ($F_{1,19}$ = 0.54; p = 0.481), or the mean mass of individual pupae ($F_{1,19}$ = 2.869; p = 0.125; 0.73 mg and 0.76 mg live weight per pupa). Moreover, partitioning did not affect the density of colony members ($F_{1,19}$ = 0.92; p = 0.363; 50.2 and 47.0/cm² respectively), the number of workers tending brood ($F_{1,19}$ = 0.182; p = 0.681), the worker:brood ratio ($F_{1,19}$ = 0.001; p = 0.932) or worker mortality ($F_{1,19}$ = 0.31; p = 0.592). Regardless of chamber surface area or partitioning, 53% of workers and 100% of larvae resided inside the nest in a 1 : 1.6 worker: brood ratio. The remaining workers (40.5%) resided outside the chamber, huddled together in a single cluster. Thus, workers rather than brood suffered exposure in crowded conditions. In nature, exposed workers would have excavated new chambers for themselves (Cassill, unpubl. data).

Discussion

The nests of mature colonies of the fire ant, *S. invicta*, were composed of three distinct architectures: an above-ground mound containing a labyrinth of narrow tunnels and amorphous nodules, a subterranean set of shafts and nodules through the grass root system, and a deeper subterranean portion below the root system composed of flattened chambers skewered by vertical shafts.

Like stems in a bouquet of flowers, shafts radiated vertically from the subterranean portion of the nest, to horizontal tunnels near the crust of the mound. Such an orientation would facilitate the flow of workers and brood back and forth from the safety of subterranean chambers to the warmth of the mound (Porter, 1988; Porter and Tschinkel, 1993). Two notable features of a mound's tunnel system were the narrow diameter of tunnels and the thinness of their walls. Combined, these features would maximize the surface area-to-volume ratio that, in turn, would maximize the number of brood that could be exposed to warmer incubation conditions to accelerate brood development. As a point of fact, we found that the density of colony members in the mound was nearly twice the density of colony members in subterranean chambers. The rules of excavation employed by workers to produce a high surface area-to-volume ratio in nest mounds will be an interesting area of future research.

The size of brood groups in artificial nests without partitions was approximately the same as the size of brood groups residing in partitioned field nests. The concentration of CO_2 (Kleineidam and Tautz, 1996; Burkhardt, 1998) and the rate of contact (Gordon et al., 1993) are two possible candidates for cues that workers could use to regulate the size of brood groups. However, neither cue, by itself, would inform a worker whether she should enlarge an existing chamber or excavate a new chamber as the size of a brood group increases. Thus, the cues limiting brood group size and the decision to excavate a new chamber rather than enlarge an existing chamber are still unknown.

Our findings demonstrated that brood rearing was unaffected by chamber size or crowding (see also Cassill and Tschinkel, 1999). So why do *S. invicta* workers build nests with so many small chambers? It is known that complex nests provide workers a choice of temperature and humidity gradients for rearing eggs, larvae and pupae (Porter, 1988, Porter and Tschinkel, 1993). Moreover, complex nests promote division of labor by separating workers and tasks in space (Strickland and Franks, 1994; Franks and Deneubourg, 1997). Because temperature gradients and division of labor can occur just as well in nests composed of hundreds of larger chambers rather than thousands of small chambers, we speculate that small groups in small chambers benefit colony communication rather than brood development. First, it is known that small groups promote decision-making (Cruz et al., 1997). Second, nest complexity might modulate a colony's response to communication signals by promoting a localized or time-release response to chemical signals. In other words, nest partitioning might prevent an overreaction of mass hysteria and traffic jams. The potential relationship between nest partitioning and colony communication will be an exciting avenue for future research.

In conclusion, biologists readily recognize body size and colony size as attributes of significant biological importance to insect societies (Michener, 1964; Rissing, 1987; Gordon et al., 1993; Tschinkel, 1993; Bourke, 1988; Bonabeau et al.,

1999). Our study suggests that group size and nest complexity might be important social attributes as well. Certainly, both deserve consideration in future studies of insect societies.

Acknowledgments

References

Bonabeau, E., L. Dagorn and P. Freon, 1999. Scaling in animal group-size distributions. *Proc. Natl. Acad. Sci. USA. 96*: 4472–4477.

Bourke, A.F.G., T.M. van der Have and N.R. Franks, 1988. Sex ratio determination and worker reproduction in the slave-making ant *Harpagoxenus sublaevis. Behav. Ecol. Sociobiol. 23*: 233–245.

Brian, M.V., 1953. Brood-rearing in relation to worker number in the ant *Myrmica. Physiol. Zool. 26*: 355–366.

Brian, M.V., 1956. Group form and causes of worker inefficiency in the ant *Myrmica rubra* L. *Physiol. Zool. 29*: 173-194.

Brian, M.V., 1983. *Social Insects: Ecology and Behavioural Biology*. Chapman and Hall. New York, NY. 377 pp.

Burkhardt, J.F., 1998. Individual flexibility and tempo in the ant, *Pheidole dentata*, the influence of group size. *J. Insect Behav. 11*: 493–505.

Cassill D.L. and W.R. Tschinkel, 1999. Effects of colony-level attributes on larval feeding in the fire ant, *Solenopsis invicta. Insectes soc. 46*: 261–266.

Cruz, M.G., F.J. Boster and J.I. Rodriguez, 1997. The impact of group size and proportion of shared information on the exchange and integration of information in groups. *Commun. Res. 24*: 291–313.

Franks, N.R. and J.L. Deneubourg, 1997. Self-organizing nest construction in ants: individual worker behavior and the nest's dynamics. *Anim. Behav. 54*: 779–796.

Gordon, D.M., R.E.H. Paul and K. Thorpe, 1993. What is the function of encounter patterns in ant colonies? *Anim. Behav. 45*: 1083–1100.

Hölldobler, B. and E.O. Wilson, 1983. The evolution of communal nest-weaving in ants. *Am. Scientist 71*: 490–499.

Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Harvard University Press, Cambridge, 732 pp.

Kleineidam, C. and J. Tautz, 1996. Perception of carbon dioxide and other "air condition" parameters in the leaf cutting ant *Atta cephalotes. Naturwissenschaften 83*: 566-568.

Markin, G.P., J.H. Dillier and H.L. Collins, 1973. Growth and development of colonies of the red imported fire ant, *Solenopsis invicta. Ann. Entomol. Soc. Am. 66*: 803–808.

Michener, C.D., 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. *Insectes soc. 11*: 317–341.

Porter, S.D., 1988. Impact of temperature on colony growth and developmental rates of the ant, *Solenopsis invicta. J. Insect Physiol. 34*: 1127–1133.

Porter S.D., and W.R. Tschinkel, 1993. Fire ant thermal preferences: behavioral control of growth and metabolism. *Behav. Ecol. Sociobiol. 32*: 321–329.

Rissing, S.W., 1987. Annual cycles in worker size of the seed-harvester ant *Veromessor pergandei* (Hymenoptera: Formicidae). *Behav Ecol. Sociobiol. 20*: 117–124.

Sall, J., and A. Lehman, 1996. *JMP Start Statistics: A Guide to Statistical and Data Analysis Using JMP and JMP IN Software*. Duxbury Press. Albany. 521 pp.

Schremmer, F., 1979. Die nahezu unbekannte neotropische Weberameise *Camponotus (Myrmobrachys) senes* (Hymenoptera, Formicidae). *Zool. Anz. 203*: 273–378.

Strickland, T.R. and N.R. Franks, 1994. Computer image analysis provides new observations of ant behaviour patterns. *Proc. R. Soc. Lond. B 257*: 279–286.

Theraulaz, G., E. Bonabeau and J.L. Deneubourg, 1998. The origin of nest complexity in social insects. *Complexity 3*: 15–25.

Tschinkel, W.R., 1993. Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. *Ecol. Monog. 63*: 425–457

Tschinkel, W.R., 1999. Sociometry and sociogenesis of colony-level attributes of the Florida harvester ant (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am. 92*: 80–89.

Wheeler, J. and S.W. Rissing, 1975. Natural history of *Veromessor pergandei*, I: The nest (Hymenoptera: Formicidae). *Pan-Pacific Entomol. 51*: 205-216.

Wilson, E.O., 1971. *The Insect Societies*. The Belknap Press of Harvard University Press. Cambridge, Mass. 548 pp.

To access this journal online:
http://www.birkhauser.ch