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Research article

Effects of colony-level attributes on larval feeding in the fire ant, *Solenopsis invicta*

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Summary. Do colony attributes modulate individual behavior? The effects of colony size and worker : brood ratio on the rate of worker-to-larva trophallaxis in the fire ant, *Solenopsis invicta*, were investigated. Neither colony size ranging from 100 to 10,000 nor worker : brood ratio ranging from 1 : 1 to 16 : 1 affected the density of workers on the brood pile, nor the rate or duration of worker-to-larva trophallaxis. The demands of hungry larvae were met even in groups as small as 100 workers in worker : brood ratios as small as 1. Only when the worker : brood ratio was less than 1, were larvae tended or fed at reduced rates. Under natural conditions, this occurs only in incipient colonies. Otherwise, in post-incipient colonies, the flow of food to larvae was unmodified by colony attributes. The implications of this finding are two-fold: First, it reinforces previous research demonstrating that social feeding in the fire ant emerges from localized interactions rather than mass communication. Second, it highlights the resiliency of this weedy species. Hypothetically, colonies drastically reduced by catastrophic events such as flooding should still be able to produce sexuals.

Key words: Worker : larva ratio, colony size, trophallaxis.

Introduction

For holometabolous insects, adult body size is second only to adult nutrition in determining adult fecundity (Chapman, 1982, p. 94). In social Hymenoptera, colony size is the equivalent of adult body size for predicting survival (Kaspari and Vargo, 1995) and reproductive output. Species that produce larger colonies produce more sexuals (*Myrmica*, Elmes and Wardlaw, 1982). Within species, larger colonies produce more sexuals (Hölldobler and Wilson, 1990, pp. 159; *Solenopsis invicta*, Tschinkel, 1993 a; *Harpagoxenus sublaevis*, Bourke et al., 1988; *Tetramorium caespitum*, Brian et al., 1967).

But is large colony size the trigger for sexual production? After all, a number of colony attributes change with colony size. For example, colony size is positively associated with elaborate communication systems (Hölldobler and Wilson, 1990, pp. 160); complex caste structure (reviewed in Michener, 1964; Tschinkel, 1993 a); territory size and boundary disputes (Adams, 1990); colony survival after founding (Markin et al., 1973; Tschinkel, 1993 b); and complex nest construction (Markin et al., 1973; Tschinkel et al., 1995). Colony size is associated with individual-level attributes such as the production of larger-bodied workers (*Atta cephalotes*, Wilson, 1983; *Solenopsis invicta*, Porter and Tschinkel, 1985; Tschinkel, 1988 a), more sexuals (Tschinkel, 1988 b, 1993 a) and heavier queens (Tschinkel and Howard, 1978). Because of the complexity of associations among colony-level attributes, the extent to which colony size itself actively shapes other attributes is difficult to determine.

Nevertheless, several researchers have separated the effects of colony size from other correlated variables. In *Myrmica rubra* (Brian, 1953, 1956), nest complexity and worker : brood ratio rather than colony size, produced larger larvae. When the size of nurses and worker : brood ratio of the fire ant were analyzed as covariates (Porter and Tschinkel, 1985), the effect of colony size on pupal size was no longer significant.

Recently, we characterized the individual attributes of larvae and of workers during social feeding and found that workers regulate the flow of food from the environment into the nest (Cassill and Tschinkel, 1999 a) whereas larvae regulate its distribution within the nest (Cassill and Tschinkel, 1995, 1996, 1999 b; Cassill et al., 1999). In this paper, we report on the capacity of two colony attributes, colony size and worker : brood ratio to affect the distribution of food among larvae.

Materials and methods

Source colonies and experimental nests

Mature colonies were collected in Tallahassee, FL, USA during January 1994 and again in January 1995 and were maintained on a constant diet (tenebrionid larvae and 20% sucrose water), at 28 °C in constant light. Laboratory-reared colonies were started from newly-mated queens collected in June 1994 and were maintained under the same regime. Laboratory housing and handling methods were similar to those described by Banks et al. (1981). We refer to field-reared and laboratory-reared colonies as "source" colonies throughout the rest of the paper.

There was a question about the effect of rearing conditions (laboratory-reared or field-reared) on social feeding behavior. Ten source colonies, five field-reared and five laboratory-reared colonies were standardized for colony size (2 g workers), worker size (medium-sized workers) and diet (15% solution of sucrose and amino acids in a 2:1 ratio). Neither the rate of trophallaxis (Table 1, line 1) nor the duration of worker-larva trophallaxis (Table 1, line 2) differed significantly between laboratory-reared and field-reared colonies. This outcome allowed us to use either colony type in our experiments without jeopardizing our ability to interpret or generalize the findings.

Observation nests consisted of water-saturated, plaster bases of variable size to standardize worker density. Nests had a 0.3 cm high rim around the top edge that, when covered by glass, formed a brood chamber through which workers and larvae could be viewed by eye, microscope or video-camera. Nests were sealed on the outside with paraffin wax to reduce evaporation. Experimental nests were placed in plastic trays of variable size to standardize worker density whose sides had been treated with Fluon (to prevent worker escape). Two entrance tunnels were available at opposite ends of the brood chamber to allow workers to move freely to and from the arena and brood chamber.

Standard experimental treatment

Because we assayed larval feeding, our experimental colony fragments consisted of workers and 4th-instar larvae (80–90% of growth occurs in the 4th-instar stage; Petralia and Vinson, 1979). Unless otherwise noted in the Results section, standard experimental treatment groups consisted of 2 g workers (~4,000) and 1 g 4th instar larvae (~ 2,000). Workers were randomly aspirated from the arena and brood chambers of source colonies, mixed, weighed, then placed into the experimental nest. Workers were deprived of food for 48 h to empty their crops prior to the experiment. Twenty-four hours before the experiment, larvae were aspirated from several source colonies, separated from workers, and mixed together in a holding chamber without food. One hour before the experiment, larvae were sub-sampled, weighed and placed into the experimental nest. In this way, each treatment contained workers and larvae of approximately the same hunger level. Eggs and microlarvae, which were sequestered away from 4th-instar larvae in a different part of the brood chamber, were never collected for experiments.

Food was placed in the arena 10 cm from the nest entrance. Scouts found the food within 60 s. The number of recruits reached its maximum within 10 min. Larvae were being fed at regular rates within 20 min. Video-taping of larval feedings began 30 min after food placement.

Food types and dyes

A standard food composed of 10% (w/v) granulated sugar and 5% (w/v) casamino acids powder (DIFCO Labs) dissolved in distilled water was used. When required for an experiment, liquid food was dyed (10–20% v/v) with over-the-counter food dyes (French's or McCormick's), usually green, sometimes red. The addition of food-dyes to solids or solutions, at concentrations between 10–30% (v/v) had no effect on the percent of larvae fed (unpubl. data).

Videotaping and transcribing larval feedings

Videotaping equipment included a Sony color video camera (WV D5100) with lens (Taylor, Taylor and Hobson, LTD, 2 in, F/1.4) and 1–6 cm extension tubes providing 20 × –80 × magnification on the TV monitor, a JVC video cassette recorder (HR-D600U), a Sony Trinitron color monitor and fiber optic lights. On tape, the camera's field of view

Table 1. Below are the analysis of variance results for the experiments reported in the Results. The dependent variables were transcribed from video tapes of larval feedings. Rate-of-trophallaxis is the mean number of feedings delivered per larva during the first hour of feeding. Duration-of-trophallaxis is the mean length of time that each feeding lasted per larva. Worker density is equivalent to the number of workers attending larvae per unit of brood pile surface area. The independent variables describe treatment types for a given experiment. Abbreviations: w = worker; l = larva; col = colony

Line	Dependent variable	Independent variable(s)	F-ratio	d.f. n,d	$p \leq 0.05$
1	rate of trophallaxis	lab vs field	1.46	1,99	n.s.
2	duration of trophallaxis	lab vs field	2.21	1,99	n.s.
3	worker density	larvae vs pupae	0.96	1,56	n.s.
4	worker density	brood pile areas	0.97	4,53	n.s.
5	worker density	time (12 h)	2.10	23,46	n.s.
6	rate of trophallaxis	colony size	0.85	2,77	n.s.
7	duration of trophallaxis	colony size	2.05	2,77	n.s.
8	worker density	colony size	2.87	2,77	n.s.
9	rate of trophallaxis	w:l ratio	49.46	6,313	0.0001
10	duration of trophallaxis	w:l ratio	9.88	6,267	0.0001
11	worker density	w:l ratio	15.33	6,33	0.001
12	rate of trophallaxis	col size; w:l ratio (size)	1.95	1,36	n.s.
13	rate of trophallaxis	col size; w:l ratio (ratio)	31.3	1,36	0.0001
14	rate of trophallaxis	col size, w:l ratio (interaction)	1.55	1,36	n.s.
15	duration of trophallaxis	col size; w:l ratio	1.18	1,36	n.s.
16	duration of trophallaxis	col size; w:l ratio	0.67	1,36	n.s.

at 40 magnification sampled 50–100 larvae out of the thousands placed in each treatment group. One larva was selected randomly for data collection. The tape was started and the duration of each worker-larva trophallactic event during 1 h to that larvae was recorded using a computerized event recorder. The videotape was rewound and feeding data on a second larva were obtained. These procedures were repeated until feeding data on a sample of 10 different larvae for each treatment in each replicate were transcribed (for details, see Cassill and Tschinkel, 1995). The frequency and mean duration of trophallactic events were compiled on each larva for analysis. Larval feedings are independent events (Cassill and Tschinkel, 1995); therefore, degrees of freedom were based on number of larvae rather than number of source colonies used to replicate experiments.

During trophallaxis, food is ingested by 4th-instar larvae at a rate of 0.135 nl/s (Cassill and Tschinkel, 1996). This rate can be used as a conversion factor to estimate the volume of liquid food consumed by larvae over a specified time period (0.135 nl/s × mean duration of trophallaxis × number of feedings).

Data type and analysis

Throughout this paper, the term "experiment" refers to the sum total of all treatments. The term "replicates" refers to the total number of source colonies employed for each experiment. To determine the density of workers on the brood pile, a grid with 25 cm^2 cells was drawn on the monitor screen. While the videotape was paused at random times, cells containing only larvae and cells containing both larvae and workers were counted (a cell was considered to contain a worker if at least half of its body was inside the cell's boundaries). Worker coverage of the brood pile was calculated as a percentage [(number of worker-larva cells/number of larva cells) × 100]. Worker density was based on the surface area covered by workers and brood rather than the number of workers and brood because of large size variation in both life stages. On average, every five seconds, one worker could police one sexual larva or two-to-three 4th-instar larvae or twenty 2nd-instar larvae. In other words, the same number of workers assessed each square centimeter of brood whether that centimeter contained 50 2nd-instar larvae or 5 4th-instar larvae. Coverage of the brood pile was sampled randomly 5 times per treatment.

Data were analyzed using regression (Ryan et al., 1985) or analysis of variance (ANOVA) with Tukey's honest significance tests for post-hoc comparisons. A randomized block design was employed with source colony as the blocking factor to reduce error variance. The significance level threshold was $\alpha = 0.05$. Diagnostic analyses were routinely performed to determine if assumptions of normality and uniform variance held and to check for outliers. Data points exceeding a standard deviation >2.99 were deleted from the final analysis. Degrees of freedom sometimes reflected this reduction of data.

Experiments and results

Preliminary experiments: worker density on the brood pile

When a treatment required large numbers of brood, combinations of pupae and 4th instar larvae were used. To assure ourselves that the density of workers tending pupae was the same as that for larvae, we compared worker density between pupae and larvae. Additionally, we measured worker density over time and among different sectors of the brood pile. Density was measured as the percent of the brood pile covered by workers. Each experiment (brood type, time or brood pile sector) was replicated using a total of four source colonies.

Worker density on the brood pile did not vary significantly with brood type (pupae = 86.3% ± 11% SD; larvae = 84.7% ± 9% SD; Table 1, line 3). Neither did worker density vary among different sectors of the brood pile (85.1% ± 9% SD; Table 1, line 4) nor over time (83.1% ± 11% SD; Table 1, line 5). These facts demonstrated that brood composed of both larvae and pupae was unlikely to confound the effects of worker:brood ratio on larval feeding.

Colony size, with constant worker:brood ratio

Experimental nests with a constant worker:brood ratio of 2, but with variable numbers of workers (10, 100, 1000, or 10000) were established. Plaster nest size and tray size varied in proportion to worker number so that the average density of group members in the brood chamber and the foraging area was constant across treatments. A mixture of pupae and larvae was used in this experiment because of the demand for large numbers of brood in the 10,000 worker treatment. After the standard food-deprivation period for both workers and larvae, brood were added to the experimental nests 2 h (rather than 1 h) before food introduction to allow workers sufficient time to sort brood by type. Videotaping lasted 1 h for each treatment. This experiment was replicated using a total of three source colonies.

In groups ranging from 100 to 10,000 workers, no significant difference was found in the rate of trophallaxis (Table 1, line 6), the duration of trophallaxis (Table 1, line 7), or worker density on the brood pile (Table 1, line 8). In the treatment with ten workers, worker recruitment to food introduced outside the nest did not occur and larvae were neither groomed nor fed. Because of the total lack of worker behavior toward larvae, this treatment was replicated using six additional source colonies. Again, workers did not recruit to food or tend larvae suggesting that a critical mass of workers or larvae is required to elicit social feeding behavior.

Worker: larva ratios at constant colony size

The effects of worker: larva ratio and brood tending on worker-larva trophallaxis were tested in three experiments. In each, worker number was held constant (2 g or ~4000 workers) and larval number was varied. Worker:larva ratios were 16, 4, 1, and 1/8 in the first experiment (one source colony); 8, 1/2, 1/4, and 1/8 in the second experiment (replicated using a total of four source colonies); and 8, 4 and 1 in the final experiment (replicated using a total of three source colonies). Standard food-deprivation periods were established prior to videotaping each experimental treatment.

Worker: larva ratio had a significant plateau effect on the rate of trophallaxis (Fig. 1a; Table 1, line 9), the duration of trophallaxis (Fig. 1b; Table 1, line 10) and worker density on the brood pile (Fig. 1c; Table 1, line 11). Larval feeding rates were equally high, duration time was equally low and worker density was equally high at ratios ≥1. At ratios <1, feeding rates declined, duration time of trophallaxis increased and worker density declined. At ratios equal to or above unity, excess workers clustered in inactive groups away from the brood

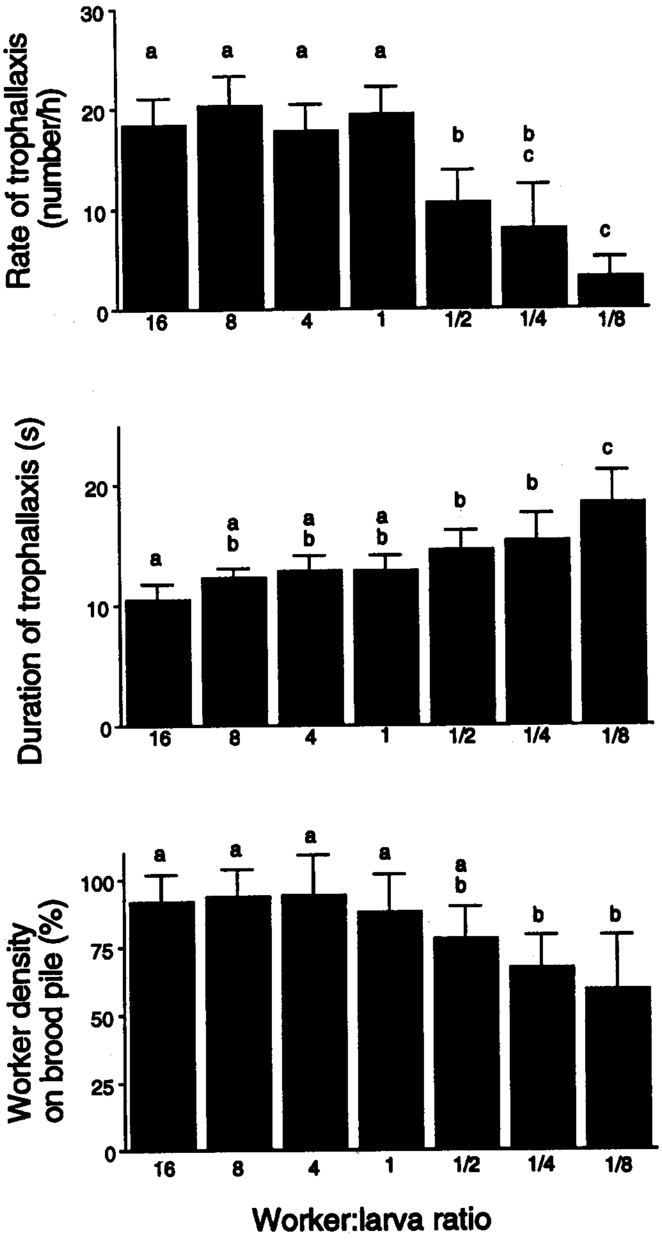

Figure 1. Worker : larva ratio and larval care. (a) Rates of worker-larva trophallaxis decreased in a non-linear fashion with the decline in the worker: larva ratio suggesting a plateau effect below which, not enough workers were available to meet the demands of hungry larvae. (b) Workers regurgitated to larvae for longer durations as crowding on the brood pile declined. (c) Worker coverage of the brood pile decreased significantly but not linearly suggesting a plateau effect above which, more workers did not result in greater coverage. For all three variables, significant effects generally occurred when ratios fell below 1. The worker brood ratio for nature colonies is > 1; the ratio for incipient colonies is ≤ 1. Bars = mean ± SE. N = 320. Bars marked with the same letter are not significantly different

pile. At ratios less than unity, workers could not keep up with the demands of larvae for food and, when they did respond with a feeding, workers lingered longer, perhaps because the probability of interruption by another worker was reduced.

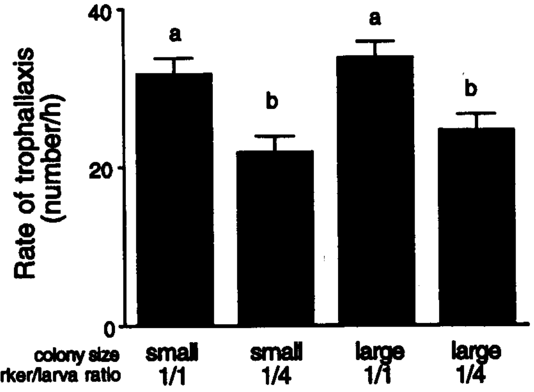

Figure 2. Colony size and worker : larva ratio on larval care. Worker: larva ratios, but not colony size, affected the rate of worker-larva trophallaxis. There was no interaction effect. Bars = mean ± SE. N = 40. Bars marked with the same letter are not significantly different

Colony size and worker : larva ratio

It is possible that colony size and worker : larva ratios interact in their effect on larval feeding. To test for this possibility, an experiment consisting of two colony sizes (100 or 10,000 workers) and two worker : larva ratios (1 or 1/4) was conducted. Workers were housed in nests proportional in size to worker numbers to eliminate density differences. Workers and larvae were starved for the standard period. Larvae were introduced 2 h and food 1 h before videotaping began. This experiment was completed on only one source colony.

As before, colony size did not affect the rate of worker-larva trophallaxis (Fig. 2; Table 1, line 12) whereas worker: larva ratio did (Fig. 2; Table 1, line 13). There was no interaction between the two colony attributes (Table 1, line 14). The duration of trophallaxis did not differ significantly with colony size (Table 1, line 15) nor with worker : larva ratios (Table 1, line 16).

Discussion

Neither larvae nor workers integrated information on colony size to modulate their feeding behavior. In contrast, workers did modify their feeding response based on worker : brood ratio. An ever-larger proportion of workers resisted transferring food to larvae as ratios increased from 1 to 16 (mature colony ratios). These workers aggregated in inactive clusters away from the brood pile. The result was that the density of workers on the brood pile and the rate of larval feeding was constant for ratios equal to or greater than 1. We speculate that the mechanism regulating worker density may be time between worker contact. Workers that contact too many other workers on the brood pile, are repelled and either leave the chamber or find another task in which to participate within the chamber. Workers were unable to keep up with larval demand for food only when group size and worker : brood ratio were pushed well below the natural range for mature colonies. Thus, colony size and worker: brood ratio were "plateau" phenomena.

The point of plateau or smallest group size and worker: brood ratio at which effective larval feeding occurred was 100 workers and 100 larvae (ratio = 1). This corresponds well to the median group size and worker: brood ratio found in the brood chambers of mature field colonies (84 workers and 80 brood; unpublished data). Apparently, nest architecture in fire ants reflects the division of colony members into the largest possible number of small functional units. We can now envision colony growth as a "budding" of additional brood chambers housing small, functional units. In this respect, colony growth in fire ants resembles the growth of modular organisms such as coral or sponges.

Brood care is labor-intensive. When larvae outnumbered workers, the group's ability to fill hungry larvae was adversely affected. In incipient colonies, brood often outnumber workers until a colony is well into its fourth month of development (unpublished data). This initial lack of sufficient labor to meet larval demand for food may contribute to the small size of minim and minor workers (Tschinkel, 1988 a).

The total lack of parental behavior in artificially small groups consisting of 10 workers and 10 larvae suggested that either a larger number of brood is required to stimulate worker behavior (unpublished data on incipient colonies), or that the small sample size precluded the selection of competent nurse workers. In the fire ant, nurses represent about 1/6th of colony members and the variation in their level of competence is large (Cassill and Tschinkel, 1999 a). In the termite, *Reticulitermes flavipes*, 5% of colony members do 90% of the work on gallery construction (Robson, 1995).

For the ant, *Myrmica rubra*, the optimal worker: larva ratio for larval growth and survival was 1 (Brian, 1953), with a natural range of 1/2 to 1.5 (Brian, 1950). When the *M. rubra* worker: larva ratio was experimentally reduced to 1/4, larval growth suffered (Evesham, 1985) probably because of the substantial decrease in the number of worker-laid trophic eggs that are fed to larvae. However, when worker:larva ratios were equal to or greater than 1, regardless of colony size (Brian, 1953), larval growth remained constant, resulting in same-sized adults. The similarity of the smallest effective ratio of 1 for the fire ant and *M. rubra* hints at a potentially widespread phenomenon among ants.

There are several important implications to the fact that colony size and worker: larva ratio were plateau phenomena. First, it reinforces previous findings that food flow is regulated at the local level by individual interactions (unpubl. data) rather than mass communication of colony-level attributes. Second, the point of plateau may represent a colony's emergence into reproductive maturity. Below this point, the demands of hungry larvae are not met, resulting in nutritional castration (Wheeler, 1994). Beyond this point, colony size and worker: brood ratio can fluctuate without loss of reproductive potential. In spite of intra- and inter-seasonal oscillations in size (Tschinkel, 1988 a, 1993 a), stress-reduced colonies could still produce sexuals.

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References

Adams, E.S., 1990. Boundary disputes in the territorial ant *Azteca trigona*: effects of asymmetries in colony size. *Anim. Behav. 39*: 321–328.

Banks, W.A., C.S. Lofgren, D.P. Jouvenez, C.E. Stringer, P.M. Bishop, D.F. Williams, D.P. Wojcik and B.M. Glancey, 1981. Techniques for rearing, collecting and handling imported fire ants. *USDA and SEA Agric. Technol. Southern Ser. 21*: 1–9.

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., 1950. The stable winter population structure in species of *Myrmica*. *J. Anim. Ecol. 19*: 119–123.

Brian, M.V., 1953. Brood-rearing in relation to worker number in the ant *Myrmica*. *Physiol. Zool.* 355–66.

Brian, M.V., 1956. Group form and causes of working inefficiency in the ant *Myrmica rubra* L. *Physiol. Zool.* 173–194.

Brian, M.V., G. Elmes and A.F. Kelly, 1967. Populations of the ant *Tetramorium caespitum* Latreille. *J. Anim. Ecol. 36*: 337–342.

Cassill, D.L., A. Stuy and R.G. Buck, 1999. Emergent patterns in liquid food distribution among fire ant larvae. *J. Theor. Biol. 195*:371–381.

Cassill, D. L. and W.R. Tschinkel, 1995. Allocation of liquid food to larvae via trophallaxis in colonies of the fire ant, *Solenopsis invicta*. *Anim. Behav. 50*: 801–813.

Cassill, D.L. and W.R. Tschinkel, 1996. A duration constant for worker-larva trophallaxis in ants. *Insectes soc. 43*: 149–166.

Cassill, D.L. and W.R. Tschinkel, 1999 a. Task selection by workers of the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol. 45*: 301–310.

Cassill, D.L. and W.R. Tschinkel, 1999 b. Social feeding and self organization in the fire ant, *Solenopsis invicta*. *Information Processing in Social Insects* (C.T. Detrain and J.M. Pasteels, Eds.), Birkhäuser Verlag, Basel, (in press).

Chapman, R.F., 1982. *The Insects: Structure and Function*. Harvard Press, Cambridge. 919 pp.

Elmes, G.W. and J.C. Wardlaw, 1982. A population study of the ants *Myrmica sabuleti* and *Myrmica scabrinodis*, living at two sites in the south of England, I: A comparison of colony populations. *J. Anim. Ecol. 51*: 651–664.

Evesham, E.J.M., 1985. The interaction of food distribution and the caste composition of an ant colony (*Myrmica rubra* L.) *Zool. soc. Lond. 207*: 241–250.

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

Kaspari, M. and E.L. Vargo. Colony size as a buffer against seasonality: Bergmann's rule in social insects. *Am. Nat. 145*: 610–632.

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. and W.R. Tschinkel, 1985. Fire ant polymorphism (Hymenoptera: Formicidae): factors affecting worker size. *Ann. Entomol. soc. Am. 78*: 381–386.

Robson, S.K., 1995. Individuals and groups: behavioral integration and organization in the social insects. Dissertation. Boston University. 186 pp.

Ryan, B.F., B.L. Joiner and T.A. Ryan Jr., 1985. *Minitab Handbook*. Boston: PWS-KENT Publishing Co. 355 pp.

Tschinkel, W.R., 1988a. Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol. 22* :103–115.

Tschinkel, W.R., 1988b. Social control of egg-laying rate in queens of the fire ant, *Solenopsis invicta*. *Physiol. Entomol. 13*: 327–350.

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

Tschinkel, W.R., 1993b. Resource allocation, brood production and cannibalism during colony founding in the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol. 33*: 209–223.

Tschinkel, W.R., 1995. Stimulation of fire ant queen fecundity by a highly specific brood stage. *Ann. Entomol. soc. Am.* 876–882.

Tschinkel, W.R., E.S. Adams and T. Macom, 1995. Territory area and colony size in the fire ant *Solenopsis invicta*. *J. Anim. Ecol. 64*: 473–480.

Tschinkel, W.R. and D.F. Howard, 1978. Queen replacement in orphaned colonies of the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol. 3*: 297–310.

Wilson, E.O., 1983. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). IV. Colony ontogeny of *A. cephalotes*. *Behav. Ecol. Sociobiol. 14*: 55–60.

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