

ORIGINAL ARTICLE

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Task selection by workers of the fire ant *Solenopsis invicta*

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Abstract The effects of worker size, age, and crop fullness on the flow of food into the colony were assessed using video recording and playback. Regardless of the level of colony satiation, small workers seldom had full crops and were more involved in larval grooming than in food traffic. Large workers played little role in larval care, but tended to be recruited easily to a food source and to store food in their crops. Medium workers had crops ranging from empty to full because they alternated between ingesting from and donating food to other colony members. Medium workers were the most versatile, engaging competently in food recruitment, larval grooming, and larval feeding. They displayed considerable variation in the frequency at which they fed larvae: some fed a few larvae before switching to other tasks, others fed over a hundred larvae before switching. The persistence, or lack thereof, of a worker's feeding response suggests a flexibility unaccounted for by the fixed-threshold-response hypothesis. Worker coverage of the brood pile was a dynamic equilibrium process unaffected by worker size, age, or crop fullness, or by differences in the nutritional or hygienic states of larvae. In summary, it appeared that worker size and age offered coarse regulation of task selection by workers, whereas crop fullness, flexible response, and task switching fine-tuned task selection.

Key words Formicidae · Social feeding behavior · Worker traits · Trophallaxis

Introduction

Division of labor, a defining feature of eusociality, has been investigated on three time scales: an evolutionary time scale (reviewed in Oster and Wilson 1978, p. 75; Hölldobler and Wilson 1990, p. 298; O'Donnell and Jeanne 1990; Bourke and Franks 1995, p. 400); an ontogenetic time scale (reviewed in Oster and Wilson 1978, p. 26; Wilson 1985; Tofts 1993; Tschinkel 1993; Bourke and Franks 1995, p. 400), and, lastly, a proximate time scale in which the mechanisms by which workers distribute themselves among colony tasks have been described (reviewed in Pasteels and Deneubourg 1987; Wilson and Hölldobler 1988; Detrain and Pasteels 1991; Robinson 1992; Franks and Tofts 1994; Bourke and Franks 1995, p. 400; Gordon 1996; Bonabeau et al. 1997).

Our goal was to investigate the distribution of workers among social feeding tasks to include worker recruitment to food sources, larval grooming (waste removal), and larval feeding. The majority of a worker's lifetime behavioral repertory involves within-nest activity (Hölldobler and Wilson 1990, p. 299), most of which is central to the flow of food from the environment to the larvae (Howard and Tschinkel 1981). Because fire ant larvae are immobile (O'Neal and Markin 1975; Petralia and Vinson 1979; Cassill and Tschinkel 1995), workers bear the burden of locating, transporting, processing and storing food for larval consumption (O'Neal and Markin 1973; Howard and Tschinkel 1981; Porter and Tschinkel 1985a), potentially providing workers with an avenue of control over larval development. However, despite their immobility, larvae are not passive recipients of food. When colonies are abundantly provisioned, larvae regulate meal volume (Cassill and Tschinkel 1995, 1996; Cassill et al., in press) and meal quality (D.L. Cassill and W.R. Tschinkel, unpublished data). Still, although larvae regulate the proximate distribution of food during the course of one meal, this does not necessarily mean that larvae control their ultimate developmental destiny.

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What role do workers play in social feeding and how are they distributed among social feeding tasks? In recent work (D.L. Cassill and W.R. Tschinkel, unpublished data), we addressed the first part of this question by showing that a worker's own hunger determined its tendency to forage for certain food types at certain concentrations. In this paper, we address the second half of this question, demonstrating that, in *Solenopsis invicta*, worker task selection is coarsely tuned by worker size and, to a lesser degree, by worker age, and fine-tuned by worker crop fullness and individual initiative. The results of our investigation into worker task selection are relevant to understanding the mechanisms underlying not just social feeding, but also colony nutrition, growth, and reproduction.

Methods

Stock colonies and experimental nests

All experiments were carried out on the monogyne social form of *S. invicta*. Laboratory rearing and handling methods were similar to those described by Banks et al. (1981). For some experiments, mature field colonies were collected in Tallahassee, Fla., USA during January 1995 and maintained at 28 °C in constant light for 1–3 months on a diet of tenebrionid beetle larvae and 20% sugar water. For other experiments, large, 1- to 2-year-old laboratory-reared colonies were used. These colonies were reared from newly mated *S. invicta* queens collected in Tallahassee during the spring of 1994 and were maintained in the laboratory for 1 year under the same conditions as those for field colonies. When group size, worker:brood ratio, and worker body size were experimentally standardized (D.L. Cassill and W.R. Tschinkel, unpublished data), we found no difference in the rates of feeding between laboratory-reared and field-reared colonies.

Most experiments used experimental nests made of plaster rectangles (10 × 14 × 2 cm) with a 0.3-cm-high rim around the top edge to form a brood chamber. Nests were water-saturated and sealed on the outside with paraffin wax to reduce evaporation. The brood chamber was covered with a plate of glass through which workers and larvae could be viewed by eye, microscope, or video-camera. Experimental nests were placed in plastic trays (13.5 × 12 × 2.5 cm) whose sides had been treated with Fluon to prevent worker escape.

Liquid food

When required for an experiment, food consisted of distilled water, 6% (w/v) casamino acids powder (Difco; Howard and Tschinkel 1981), 10% granulated sugar (w/v).

Videotaping larval feedings

Videotaping equipment consisted of a Sony color video-camera (WV D5100) with lens (Taylor, Taylor & Hobson, 2 in, F/1.4) and 1- to 6-cm extension tubes providing × 20 to × 80 magnification on the TV monitor, a JVC videocassette recorder (HR-D600 U), a Sony Trinitron color monitor and fiber-optic lights. On tape, the camera field of view at × 40 power sampled 50–100 larvae out of the thousands placed in each treatment group. For some experiments, the camera was mounted on a horizontally movable frame so that individuals could be followed throughout the nest.

Data collection

Transcription of feeding behaviors from the videotape employed a computerized event recorder to quantify the lapsed time to the first feeding, the number of feedings, and the mean duration of these feedings for each larva for 1 h. The videotape was rewound and feeding data on a second larva were obtained. These procedures were repeated until feeding data on a sample of ten larvae for each treatment in each replicate were obtained (for transcription details, see Cassill and Tschinkel 1995). For two experiments, the rate and duration of larval grooming were also recorded and analyzed.

The density of workers on the brood pile was determined by first drawing a 10 × 10 cm grid on the monitor screen with a fine black marker. The videotape was then paused randomly five times for each treatment of each replicate. At each pause, the number of 10 × 10 cells that contained larvae and the number of cells that contained both larvae and workers were counted (a cell was considered to contain a worker if at least one of its three body sections was inside the cell boundary). Worker density was calculated as a percentage [(number of worker-larva cells/number of larva cells) × 100].

The direction of food flow during worker-worker feeding interactions was determined by the position of the workers' mandibles. Donor mandibles were spread wide open (just as they are during the delivery of food to larvae), recipient mandibles were closed. The volume of food flowing from individual to individual was estimated by the duration of feeding, assuming that the rate of swallowing by adults is comparable to the rate of swallowing by larvae (the volume of food ingested by larvae is 0.14 nl/s; Cassill and Tschinkel 1996). Because this assumption was not verified, both worker and larval ingestion data were reported in their original state as seconds in the event that, at some future date, the rate of ingestion for workers is determined.

Data analysis

To determine differences among means, data were analyzed by analysis of variance (ANOVA) or covariance (ANCOVA) with source colony as a blocking factor. To determine differences among cell means, the Duncan range test or the Tukey honest significant difference test was used (Statsoft). When appropriate, multiple regression and Student's *t*-test were employed (Ryan et al. 1985). Residual and normal score diagnostic analyses were routinely performed to check for outliers ($SD > 2.99$) and to determine if assumptions of normality and uniform variance held. When required, data were normalized using the square root transformation.

Results

Worker hunger

The crop volume of satiated through 12-day-starved workers was used to characterize worker hunger. Initially, 1 g of workers was randomly selected from the arena and brood chamber of a single laboratory-reared stock colony, placed into an experimental nest and fed to satiation (about 4 h), whereupon food was removed. Sampling began immediately after food removal and continued at various intervals for 12 days. On each sample day, ten workers of medium size were selected and their crops dissected. Head widths and crop diameters were measured using an ocular micrometer. Crop volume (V) was calculated as a sphere $V = 4/3\pi(d/2)^3$, where d = crop diameter.

Crop volume was significantly affected by starvation time (Table 1, row 1). It declined sharply during the first 2 days, then more slowly until the 12th day when mean crop volume was between 5% and 3% of its original value (Fig. 1). These results were consistent with the finding that 3-day-starved workers ingested as least as much food as 7- to 14-day-starved workers (Howard and Tschinkel 1980). Differences in crop volume were not the result of differences in worker size because dissected workers were approximately the same size (Table 1, row 2).

To assess variation in crop volume of workers of different sizes, workers were randomly selected and frozen both before and after colony satiation. The heads were cut from the body and their widths measured (Porter 1983). Gaster weight was used to estimate crop volume: the gasters were severed from the thorax (no visible fluids were lost) and weighed. A total of 120 workers were sampled from one colony, 60 from each feeding regime and 20 from each of three worker sizes.

Gaster weight was significantly affected by worker size and by feeding (Table 1, rows 3–5), increasing with both (Fig. 2). After feeding, the mean gaster weights of small workers increased 23%, that of medium workers 73%, and that of large ones 47%. Many large workers in the starved group had partially full to full crops (sug-

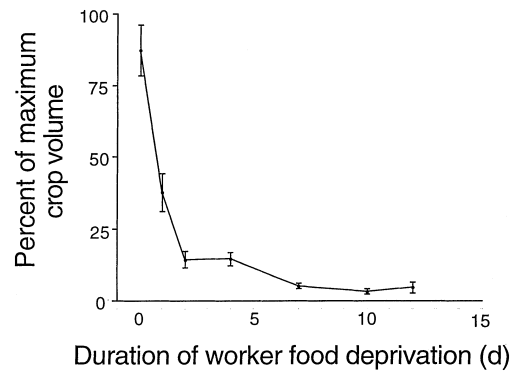


Fig. 1 Worker crop volume as a function of food deprivation (mean \pm SE). Workers were fed to satiation, then isolated without food for 12 days. Worker crop volume declined significantly within the first 48 h of food deprivation. The decline thereafter was less dramatic

gesting a storage function). When these fuller members were eliminated from the before-feeding group, the gaster weights of the remaining, truly empty workers increased 88% upon feeding.

Of equal importance to the capacity for increase in crop volume is the variation in crop volume within each worker group. Gaster weight varied substantially even

Table 1 Analysis of variance results for the experiments. When appropriate, source colony was analyzed as a blocking factor

Row	Dependent variable	Independent variable(s)	Effect	F-ratio	df	P	R ²
1	Crop volume	Time	Main	59.44	11,109	< 0.0001	
2	Crop volume	Head width	Main	1.04	11,109	n.s.	
3	Gaster weight	Worker size and food	Main, size	229.48	2,114	0.0001	74
4	Gaster weight	Worker size and food	Main, food	30.75	1,114	0.0001	5
5	Gaster weight	Worker size and food	Interaction	8.57	2,114	0.0003	4
6	Larval feeding rate	Worker starvation period	Main	39.34	2,114	0.0001	
7	Worker crop volume	Worker starvation period	Main	32.96	3,36	0.0001	
8	Worker antennation	Worker starvation period	Main	1.06	2,57	n.s.	
9	Worker density on brood	Worker starvation period	Main	1.35	2,33	n.s.	
10	Duration of trophallaxis	Worker starvation period	Main	0.48	2,283	n.s.	
11	Rate of trophallaxis	Worker starvation period (fed)	Main	1.35	1,119	n.s.	
12	Duration of trophallaxis	Worker starvation period (fed)	Main	0.007	1,119	n.s.	
13	Rate of trophallaxis	Worker size	Main	37.03	3,117	0.0001	
14	Rate of grooming	Worker size	Main	9.98	3,145	0.0001	
15	Worker density on brood	Worker size	Main	2.97	3,41	0.05	
16	Workers tending larvae	Worker size	Main	2.04	2,213	n.s.	
17	Duration of trophallaxis	Worker size	Main	1.58	3,117	n.s.	
18	Duration of grooming	Worker size	Main	1.15	3,88	n.s.	
19	Rate of trophallaxis	Worker size and worker age	Main, size	224.67	2,140	0.0001	50
20	Rate of trophallaxis	Worker size and worker age	Main, age	17.02	4,140	0.0001	13
21	Rate of trophallaxis	Worker size and worker age	Interaction	3.52	8,140	0.001	7
22	Rate of grooming	Worker size and worker age	Main, size	22.46	2,135	0.0001	18
23	Rate of grooming	Worker size and worker age	Main, age	11.01	4,135	0.0027	18
24	Rate of grooming	Worker size and worker age	Interaction	3.15	4,135	0.0027	10
25	Worker density on brood	Worker size and worker age	Main, size	12.23	2,30	0.004	29
26	Worker density on brood	Worker size and worker age	Main, age	4.73	4,30	0.001	23
27	Worker density on brood	Worker size and worker age	Interaction	1.28	8,30	n.s.	13
28	Recruitment	Worker size and worker age	Main, size	38.48	2,23	0.0001	47
29	Recruitment	Worker size and worker age	Main, age	10.65	3,23	0.0001	20
30	Recruitment	Worker size and worker age	Interaction	5.21	6,23	0.01	19
31	Worker size	Feeding intensity group	Main	0.97	2,52	n.s.	
32	Duration of trophallaxis	Individual nurses	Main	1.36	51,667	n.s.	9

within each worker size group, both before and after the colony was fed. For medium-sized workers, variation in gaster weight was greater after feeding [coefficient of variation (COV) = 0.554] than before feeding (COV = 0.308). Small workers demonstrated relatively small variation in weight before feeding (COV = 0.130) and after feeding (COV = 0.237). For large workers, variation in gaster weight was greater before feeding (COV = 0.363) than after feeding (COV = 0.216). This variability indicated that food was unevenly distributed among workers regardless of the general state of colony satiation, and suggested that colonies are never really satiated (in the sense that all their members are satiated).

The effect of worker hunger (duration of food deprivation) on the rate of larval trophallaxis was investigated in two experiments. In the first experiment, workers (2 g workers per treatment) and larvae (1 g per treatment) were drawn from field-reared source colonies that had been maintained in the laboratory for 1 month. Workers were fed green-dyed liquid food to satiation and then deprived of food for one of three durations – satiated, 1-day starved and 4-day starved. No food was introduced into the arena at the time that larvae were added. Videotaping began 1 h after introducing larvae and continued for 1 h. During the disturbance caused by adding larvae to the nest of each treatment, ten workers of similar size (estimated by eye) were selected and their gasters crushed against white paper. The smear area (mm²) served as an estimate for the relative volume of crop contents. Four replicates of this experiment were completed. In both experiments, worker starvation periods were staggered such that all starvation treatments were tested on the same day using the same batch of larvae.

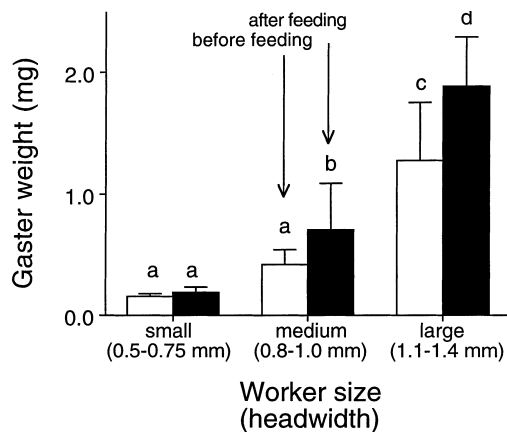


Fig. 2 Gaster weights of workers before and after feeding. The mean weight of small-worker gasters did not change significantly with colony satiation – most of their crops were empty. The mean weight and variation in gaster weight of medium workers increased with colony satiation, indicating a shift in the ratio of workers with empty or full crops. The gasters of large workers were moderately full before colony satiation and more full after colony satiation, suggesting a storage specialization. Results are shown as the mean \pm SD. Different letters indicate statistically significant differences between means as determined by the Tukey honest significant difference test

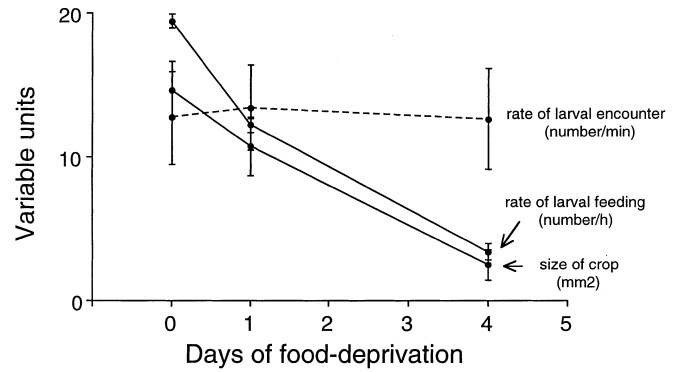


Fig. 3 Food deprivation and worker initiative. Worker crop fullness declined as a function of the duration of food deprivation. Both the rate of searching for larvae and the rate of responding to larval hunger declined in proportion to the amount of food left in the worker crop. These facts suggest that individual initiative was lowered, rendering workers less likely to donate food to hungry larvae and probably more likely to solicit food from other workers or to become inactive. Results are shown as the mean \pm SE

The rate of larval trophallaxis (Table 1, row 6) and worker crop volume (Table 1, row 7) declined proportionately with worker starvation (Fig. 3). The rate of larval encounter (Table 1, row 8) and the percentage of the brood pile that was attended by workers (Table 1, row 9; mean \pm SD = 89.3 \pm 1.2%) remained constant across worker starvation treatments. The duration of trophallaxis was unaffected by the duration of worker starvation (Table 1, row 10).

In the second experiment, 2 g of workers was aspirated from the arena and brood chamber of a laboratory-reared source colony. Workers were mixed, divided into two groups of 1 g each and each group was placed into an experimental nest. Both groups were fed to satiation. Food was then removed such that, on the day of testing, one group was 1-day starved and the other 4-day starved. On the test day, 0.5 g of larvae (starved for 24 h) was added to each nest. One hour later, food was introduced to the arena. Larval feedings were videotaped for 40 min; data were prorated to 1 h. Six replicates were completed from six source colonies.

When workers were offered food just before feeding larvae, the duration of prior food deprivation did not affect the rate of larval trophallaxis (Table 1, row 11) suggesting that crop filling canceled any effects of prior starvation. The duration of trophallaxis was also independent of the duration of prior food deprivation (Table 1, row 12).

Worker size (mixed ages)

Workers from mature field colonies, maintained in the laboratory for 2 months, were sifted into five sizes using standard testing sieves of mesh sizes no. 16, 20, 25, 30, and 35. A 100-W lamp was placed over the sieves to encourage workers to move into the lowest possible

sieve. Large workers were collected from mesh size no. 16 (mean head width = 1.35 mm, mean weight = 4.5 mg); medium workers from mesh size no. 25 (mean head width = 0.86 mm, mean weight = 1.3 mg), and small workers from mesh size no. 30 and 35 (mean head width = 0.77 mm, mean weight = 0.95 mg). Each worker size class was maintained independently in its own experimental nest. A polymorphic group of workers was established as a control by mixing the three worker sizes in equal numbers. Approximately 1500 workers per size class were sampled and tested with 1000 larvae. Before their addition to the experimental nest, workers were starved for 48 h and larvae for 12 h. Food was introduced 1 h before videotaping began. Because only a fraction of the workers in a colony attend larvae at any given time, the relative size of workers actually tending and feeding larvae was determined by measuring ten worker head widths from each of three randomly selected videotape frames on the previously calibrated monitor screen. Four replicates were completed.

Worker size had a significant effect on the rate of larval trophallaxis (Fig. 4a, Table 1, row 13.). Whereas the small, medium, and polymorphic worker groups fed larvae at about the same rate (~18/h), very few large workers fed larvae even once. The rate of larval grooming and coverage of the brood pile followed the same pattern. Large workers were the only group that groomed larvae less often (Fig. 4b, Table 1, row 14) and tended brood with slightly fewer workers (Fig. 4c, Table 1, row 15) than other worker sizes. In the polymorphic group, even though each worker size was represented in equal numbers (~500 per size class), the majority of the workers on the larval pile feeding larvae were medium sized (Fig. 5). The lack of difference in larval feeding, grooming, and coverage of the brood pile between the small, medium, and polymorphic colonies (Fig. 4a–c) was due to some overlap of worker size between groups. Those workers actually on the brood pile tending larvae were similar to each other in size (Fig. 4c) suggested that workers of a given size initiated similar tasks whether they were in polymorphic or monomorphic groups. The duration of larval trophallaxis was

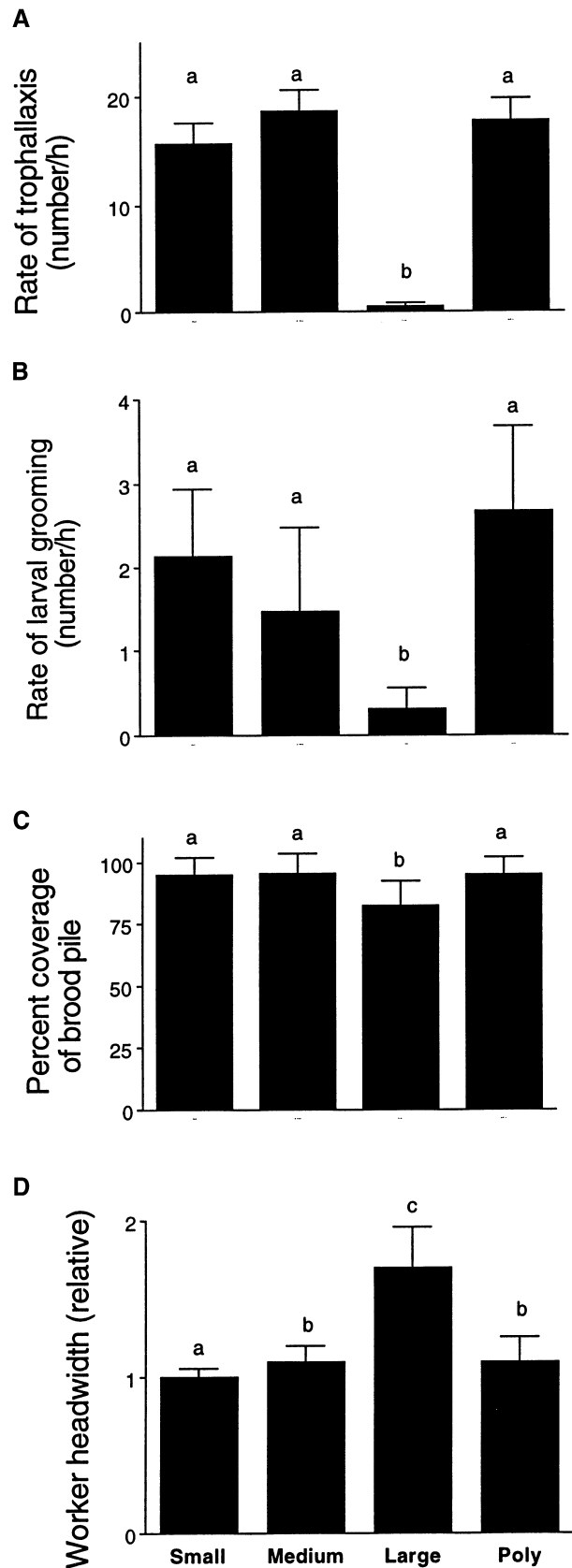
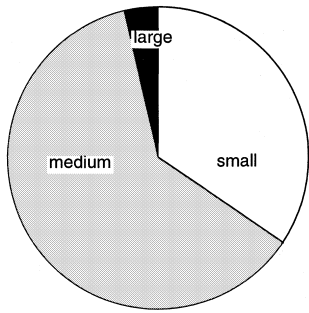


Fig. 4 Worker size and worker initiative. Results are shown as the mean \pm SE. Different letters indicate statistically significant differences between means as determined by the Tukey honest significant difference test. **A** The rate of larval trophallaxis varied with worker size. Colonies comprised of large workers responded infrequently to larval hunger relative to colonies comprised of small, medium, or polymorphic workers. **B** The rate of larval grooming varied with worker size. Colonies comprised of large workers groomed larvae infrequently relative to colonies comprised of small, medium, or polymorphic workers. **C** Coverage of the brood pile by large workers was slightly but significantly lower than that of the other worker size groups. **D** Mean worker head width (mm) per worker size group in the brood chamber (head widths were determined on a sample of 100 workers from the colony after termination of the experiment). The small, medium, and polymorphic worker groups averaged the same size indicating that our method for sizing smaller workers was ineffective



Percent of workers (by size) feeding larvae

Fig. 5 The polymorphic colony was composed of an equal number (~500) of the three worker size classes. Most of the workers actively tending and feeding larvae were medium sized. Other workers were in the brood chamber away from the brood pile or outside the nest, in the arena

unaffected by worker size (Table 1, row 17) as was the duration of larval grooming (Table 1, row 18).

Worker size and age

In a preliminary experiment on the effects of worker aging and larval feeding beginning with newly eclosed workers (unpublished data), age explained less than 10% of the variation in larval feeding behavior and less than 1% of variation in the number of workers recruiting to food. The small magnitude of these age effects was unexpected, but may have resulted from the large variation in aging rate across the large range of worker sizes, such that more slowly aging workers took over larval feeding from those workers no longer inclined to do so. These results suggested that worker size and age needed to be tested together in a multifactor experiment.

Pupae from five large field colonies were collected, combined, and sifted into five sizes. Pupae were selected from sieve no. 16, 25, and 35 (pupae from intermediate-sized sieves were discarded). Pupae were housed separately in stock nests with about 50 callow workers of the appropriate size to assist with eclosion. Each size/age cohort was tested every other week. Throughout the experiment, larvae were drawn from the same stock colony; they were removed following videotaping to prevent age contamination. This experiment was terminated at 9 weeks because of high worker mortality. One replicate of the five combined colonies was completed.

Workers of different sizes fed larvae at greatly different rates (Fig. 6a, Table 1, row 19). As small workers aged, the rate at which they fed larvae declined (Fig. 6a, Table 1, row 20), but this was not true for medium and large workers, leading to a significant age \times size interaction (Table 1, row 21). Overall, worker size and age accounted for 81% of the total variance in worker response to larval hunger. Of this, worker size accounted for 84%, worker age for 12% and the interaction between worker size and age for 4% of observed variation.

During the 1st week, small workers fed larvae at high rates even though recruitment to food was low.

The rate of larval grooming differed significantly with worker size (Fig. 6b, Table 1, row 22) and age (Fig. 6b, Table 1, row 23), although small and medium workers groomed larvae at about the same rate when averaged over the 9-week test period ($t_{23} = 0.76$, n.s.). The interaction of worker size and age was significant (Table 1, row 24). Medium and large workers groomed larvae at a declining rate with age; small workers did not show such a decline.

Worker coverage of the brood pile varied only slightly with size and age (Fig. 6c; Table 1, rows 25–27) suggesting that larvae attracted workers whether or not those workers were inclined to feed or groom them.

Worker recruitment to food differed significantly with worker size (Fig. 6d, Table 1, row 28). Small workers showed little tendency to be recruited at any time during the experiment. Recruitment also varied with age (Fig. 6d, Table 1, row 29) for medium workers but not for large or small workers (interaction: Table 1, row 30). Overall, worker size and age accounted for 88% of the total variance in the number of workers being recruited to food. Of this, worker size accounted for 78%, worker age 17%, and the interaction between worker size and age was 5%.

Flexible worker feeding response

To determine the degree of variation in worker responsiveness to larval hunger, 2 g of workers was selected from a source colony and placed in an experimental nest. Workers were starved 48 h before hungry larvae were introduced into the nest and food placed in the arena. One hour later, focal workers were selected, one at a time, while feeding larvae (to assure that each worker was a nurse) and were followed with the camera at $\times 40$ magnification for periods ranging from 15 to 60 min. We quantified the frequency and duration of worker-larva trophallaxis, worker-worker trophallaxis (both donating and ingesting), the proportion of time spent on or off the brood pile, and the percentage of active time during the observation period. All data were prorated to 1 h. An average of nine workers was sampled from each of six colony replicates ($n = 53$).

Larval feeding

Ninety percent of the observed workers (48 of 53) were active more than 75% of the time. Of these, approximately 80% (31 of 48) spent the majority of their time on the brood pile. A histogram of individual feeding responses suggested a Poisson distribution, with many nurses delivering few feedings rather than few nurses delivering many feedings. Nurses were somewhat subjectively classified into three categories of feeding response (Fig. 7). High-response nurses (4 of 53) deliv-

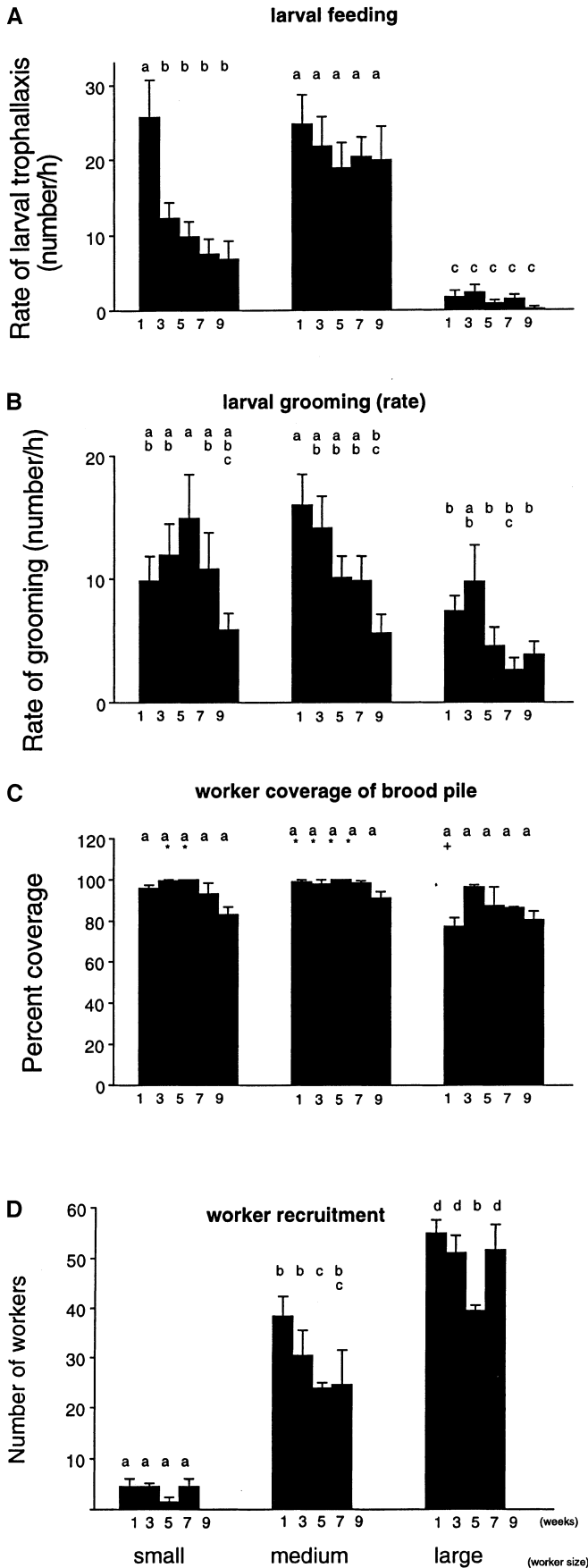


Fig. 6 Worker size/age and worker initiative. Newly eclosed workers were observed every other week for 9 weeks. Worker sizes were tested independently. Results are shown as the mean \pm SE. Different letters indicate statistically significant differences between means as determined by the Tukey honest significant difference test. **A** The rate of larval trophallaxis varied by worker size (medium-sized workers fed larvae more frequently than small or large workers) and worker age (small workers fed larvae less often as they aged; there was no age-related decline in larval feeding for medium or large workers). **B** Large workers groomed larvae far less often than small or medium workers. Only medium workers groomed larvae less often as they aged. **C** In general, coverage of the brood pile was unaffected by worker size and age. Only newly eclosed large workers distributed themselves less densely on the brood pile than did workers of other sizes or ages. The single + mean was statistically different than the * means. **D** The rate of worker recruitment to food varied by worker size (large workers recruited the most strongly, small workers recruited weakly). Only medium workers recruited less strongly as they aged

ered 90–110 feedings/h, intermediate-response nurses (44 of 53) delivered an average 40 feedings/h and low-response nurses (5 of 53) averaged 3 feedings/h to larvae. Two of the five low-response nurses were active and on the brood pile 100% of the observation time, but their activity was primarily grooming and moving larvae rather than feeding them. The other three spent most of their active time walking about the brood chamber away from the brood pile. None of the nurses in any of the three categories donated food to other workers and only one stopped for a refill (41 s). The head width of nurses in the three groups was measured from the TV monitor and they did not differ significantly in size (Table 1, row 31). Variation among individuals in the duration of worker-larva trophallaxis was not significant (Table 1, row 32). Of note was the observation that workers frequently interrupted their bouts of larval feeding to groom themselves, groom other workers, or to offer food to other workers (donor display). Individual workers switched tasks often; the mechanism generating task switching, task persistence or task selection were not apparent.

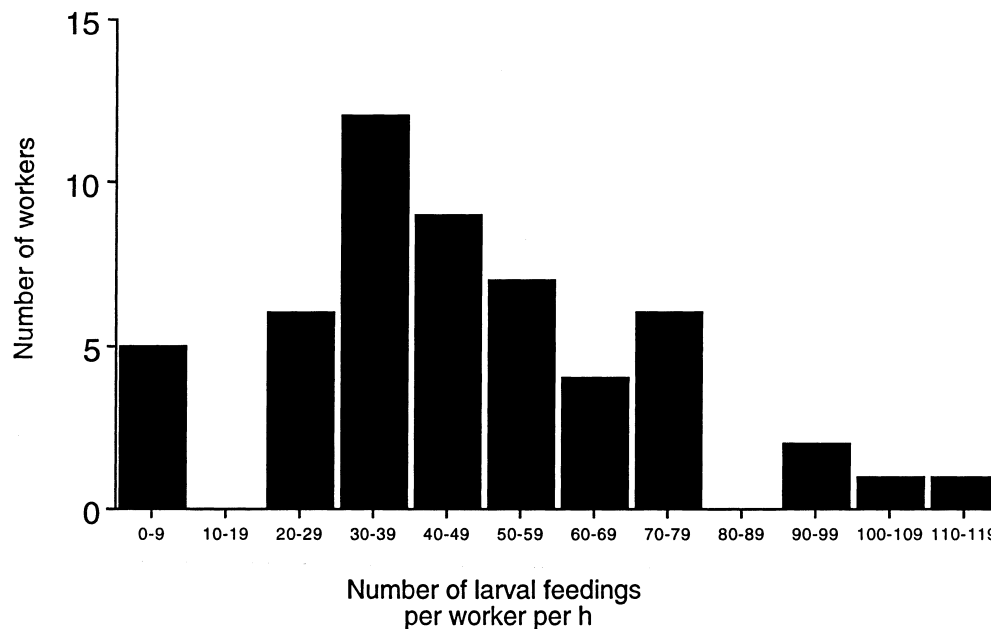
Nurse-to-worker trophallaxis

The majority of nurses (80%) did not donate food to other workers. Of the 20% that did (11 of 53), 10 nurses donated less than four times and only when they were away from the brood pile. The exceptional nurse spent 70% of her time off the brood pile, donating to other workers (19 times/h) or receiving food from other workers (14 times/h). Because the rate of larval feeding by nurses far exceeded the rate of donation to other workers, the net flow of food was one way, from nurses to larvae.

Worker-to-nurse trophallaxis

Only half of the nurses refilled their crops during the observation period, probably because most worker-nurse trophallaxis occurred during the hour just before

Fig. 7 Frequency distribution of the number of times an individual nurse responded to larval hunger. Some workers responded only once during the hour of observation, others as many as 110 times.



observations were made. Of these, about 50% refilled just once; the others refilled 2–6 times. One nurse fed 31 larvae and refilled 19 times. Assuming that her rate of swallowing was equivalent to that of larvae (0.14 nl/s), this nurse donated a total of 51 nl (40 nl to larvae, 11 nl to one other worker) and ingested 83 nl for a net gain of 32 nl of food.

The duration of worker-worker trophallaxis varied in a Poisson distribution (mean = 34.7 s, median = 13.5 s, range = 1–247 s, skewness = 2.0) with the vast majority of workers exchanging food for relatively short periods of time. Variability in the duration of worker-worker trophallaxis may be the mechanism by which variation among workers in crop fullness is established.

Discussion

We found that, in fire ants, task selection depended upon a worker's crop fullness, flexibility in task switching, worker size and, to some degree, worker age. We showed that the volume of food among workers' crops was quite variable (in contrast to the even distribution of food among larvae; Cassill and Tschinkel 1995; Cassill et al., in press), generated in part by variation in the duration of worker-worker trophallaxis. Variation in the level of crop fullness among workers persisted regardless of the general state of colony satiation, suggesting that colonies are never really satiated (in the sense that all their members are satiated). On average, small workers unloaded their crops quickly or were engaged in non-feeding tasks, large workers stored food for extended periods, and medium workers shunted food among colony members by alternately filling and donating.

Individual variation, minute by minute, in crop fullness may be the mechanism generating task selection,

task switching and task persistence. The dynamic variation in crop fullness among workers of different sizes and ages would guarantee a dynamic division of labor among tasks, with empty workers inclined to seek food from the environment or other workers and full workers inclined to recruit, store, or donate food inside the nest. Thus, the interaction between crop fullness and worker size may be a major factor organizing division of labor and social feeding.

Somewhat surprisingly, worker age affected the tendency to feed larvae much less than did worker size and crop fullness. This contrasts with the report by Miranda and Vinson (1981) who found that age affected task selection more than size. We measured the age of the group rather than of individuals, which would lessen an age effect if slow-aging workers took over brood care from fast-aging workers. Why Miranda and Vinson did not find a strong size effect is a mystery. Perhaps differences between our studies in task categories or range of worker sizes are factors. When the range of worker sizes is small, age rather than size has a greater influence on task selection (e.g., the monomorphic *Trachymyrmex septentrionalis*; Beshers and Traniello 1996).

In the polymorphic species of *Camponotus* (Sanders 1964), *Pheidole dentata* (Wilson 1976; Calabi and Traniello 1989), *P. hortensis* (Calabi et al. 1983), *Atta sexdens* (Wilson 1980a,b) and *Formica perpilosa* (Brandaö 1978), medium-sized workers are generalists (generalists are also referred to as behaviorally totipotent, flexible, or versatile), performing nearly all colony tasks. In *S. invicta* too, medium-sized workers were behaviorally the most versatile. Wilson (1980a) suggested that generalists represented the ancestral, monomorphic condition, retained over evolutionary time to successfully continue the life of the colony single-handedly if circumstances warranted.

The proportion of the worker population that displays behavioral versatility in task selection is an important question (reviewed in Pasteels and Deneubourg 1987). Our work and that of Porter and Tschinkel (1985a,b) suggest distinct limits to behavioral versatility, with limited overlap in the tasks performed by large workers. Such limits to versatility must have important consequences for the labor economy of colonies, because as colonies grow, the worker population shifts to an ever-larger fraction of large workers (Tschinkel 1988, 1993). This in turn should shift the relative labor availability from the tasks performed by small and medium workers (brood care and food sharing) to those performed by large workers (food retrieval, food storage). Such shifts in the labor economy could be important to colony growth and reproduction. This idea merits further research.

Task selection was expressed as the bias of a worker for one particular set of tasks rather than another. This bias depended on both intrinsic and extrinsic conditions. Although workers of all sizes were observed engaging in all tasks, the type of worker most likely to be grooming larvae was small, any age, with an empty crop. The type of worker most likely to be off the brood pile and recruiting to a food source was large, of any age, with a partially empty to empty crop. The type of worker most likely to be patrolling the brood pile feeding larvae was medium sized, young to middle-aged, with a full crop.

What might be the mechanisms behind worker task selection? Task selection could be regulated at a gross level by fixed-response thresholds (Calderone and Page 1992; Robinson 1992) that varied in a pattern correlated with worker size such that no amount of cue strength would trigger a response from workers that were inherently insensitive to that cue. For example, a significant proportion of large workers was insensitive to larval hunger no matter how empty the larvae, an observation also made by Porter and Tschinkel (1985a). Among more versatile workers, however, the variable and transitory (non-fixed) nature of worker response to cues such as larval hunger is problematic for the response-threshold hypothesis. Currently, it is unclear whether this is simply variation in worker versatility, or whether there is another, as yet unrecognized, dimension (e.g., physiological or genetic) to task choice when many cues are perceived.

Crop fullness, governing an individual's tendency to forage, donate, or ingest food, was itself the outcome of a worker's tendency to feed, to retain food in the crop, or to donate food to nestmates. In addition, workers donate to soliciting larvae or soliciting workers depending upon whether their crops contain solutions of protein or sucrose (D.L. Cassill and W.R. Tschinkel, unpublished data). We speculate that an effective distribution of labor emerges from a population of workers that are coarsely tuned (e.g., constrained) by worker size and age and finely tuned by the ever-changing state of their crop volume and crop content. Further, we propose that the organization of social feeding in the fire ant

is a dynamic, decentralized, non-random process in which workers respond to one of many competing cues immediately surrounding them by active choice (task selection) rather than by mandate from a higher authority (task allocation) or by random amplification (self-organized task participation; Bonabeau et al. 1997).

In support of our proposal, we recently demonstrated that food flows via a chain of demand initiated by hungry individuals soliciting food from full donors rather than a chain of transfer initiated by full workers pressing food upon passive individuals (D.L. Cassill and W.R. Tschinkel, unpublished data). No single worker possesses an overview of the nutritional status of either larvae or other workers. Rather, food flow is the product of thousands of diverse individuals independently adjusting their behavior based upon the demands of other colony members and their motivation to respond to those demands. The individual transactions of this chain of demand, governed by differences in larval characteristics and conditions (Cassill and Tschinkel 1995; Cassill et al., in press) and in worker characteristics and conditions, are the foundation of colony nutrition, growth, and reproduction.

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