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The Effect of Colony Size and Starvation on Food Flow in the Fire Ant, *Solenopsis invicta* (Hymenoptera: Formicidae)

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Summary. Food-sharing experiments were performed with laboratory colonies of *Solenopsis invicta* containing 1000, 10,000, or 20,000 workers and starved for 0, 3, 7, or 14 days. The effect of these variables was measured on the uptake of radioactive sugar water (1 *M*) by 1% of the colony's workers and on the trophallactic flow of food from these foragers to the remainder of the colony.

Patterns of food distribution in small colonies differed significantly from those in larger nests. In 1000-ant nests, small workers more frequently received food than large workers, but in bigger colonies the opposite occurred.

Fire ants were adept at distributing sugar water, with food from a few workers rapidly reaching the majority of the colony as foragers donate their crop contents to groups of recipients and these recipients may themselves act as donors.

Foragers respond to colony starvation by individually taking up more food and sharing this fluid with a greater proportion of nestmates. Even foragers from satiated colonies can retrieve at least small amounts of liquid.

The forager's state of hunger plays an important role in regulating food distribution. In sugar-satiated nests, previously starved foragers are highly successful at passing on labelled sugar whereas previously fed foragers are not.

Introduction

In ant societies, the task of procuring food for the colony falls on only a fraction of the population; consequently food distribution among nestmates is of critical importance to colony survival. The diets of many species contain a substantial liquid content, and fundamental to food sharing in such ants is both their capacity to store food in a distensible crop (Eisner and Brown 1958) and their ability to transfer this food to others (trophallaxis; for review, see Sudd 1967; Wilson 1971; and Abbott 1978). One of the most powerful and frequently applied methods for the study of trophallaxis is to monitor the spread of radiolabelled food in artificial nests. Often, however, the colonies tested contain only a minute fraction of the number of individuals in mature field colonies, leaving open the possibility that food distribution may occur differently in larger nests. Further, factors such as starvation, temperature and type of food may affect the dispersal of liquids differently in small nests and larger nests.

We investigated the effects of colony size and starvation on food-sharing patterns within colonies of the fire ant, *Solenopsis invicta* Buren. The fire ant is catholic in its food preference, foraging mainly on insects (Hays and Hays 1959, Wilson and Oliver 1969) but also taking homopteran honeydew and a wide variety of other solid or liquid animal and plant materials (Hays and Hays 1959).

Several studies have shown that crop foods or other fluids can pass in either direction between *S. invicta* adults and larvae (O'Neal and Markin 1973). The diet of larvae differs from that of workers (Vinson 1968) and larvae receive different foods according to their ages (Petralia and Vinson 1978).

Vinson (1968) used dyes to follow the dispersal of oil, sugar and protein in large laboratory colonies, and found that these foods are distributed differentially among various fire ant castes. Toom et al. (1976) discuss the flow of food among members of incipient *S. invicta* colonies.

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Materials and Methods

Fire ant mounds were collected in Leon County, Florida. In the laboratory, the mound material was spread in large fiberglass bins to dry, and plastic petri dishes with moist plaster floors were provided as trap nests to attract the ants from the soil. Colonies remained in these temporary facilities for several weeks, with minced mealworms and sugar water supplied daily.

In preparation for testing, each colony's queen and a specified number of her workers (1000–20,000) were relocated in new nests constructed from covered plastic petri dishes with Plaster-of-Paris flooring and a water reservoir. Each nest rested in its own 30 × 24 × 9 cm plastic box which served as a foraging arena where 1 *M* sucrose and minced mealworms were provided daily. Laboratory temperatures varied from 23.5° to 28 °C and constant overhead lighting was utilized.

After a week, food was removed for a specified period. At the end of the starvation period, a drop containing radioactive 1 *M* sucrose ($Na^{125}I$ added to yield 0.1–0.3 mCu/ml of food) was placed on a glass slide in the foraging arena. This food was usually quickly discovered by foragers and remained available until 1% of the colony's worker population had fed (e.g. 100 foragers from a 10,000-ant colony). To minimize contamination of nonfeeding nestmates, foragers were captured upon departure from the radioactive bait. Even ants that did not appear to feed but simply contacted the food were collected as a precaution.

During feeding, evaporation from the food was periodically checked by removing microliter samples. Whenever the specific activity of such samples exceeded the original level by more than 10%, fresh food was substituted.

The ants were rinsed in water to remove external contamination and lightly patted dry with tissue paper. Each individual was placed live inside an empty gelatin capsule (Parker, size 000) which was in turn fitted into a sample tube of a Packard 5220 Autogamma Scintillation Counter with an automatic 300-sample changer and punched paper-tape output. Each ant could move freely inside its capsule without affecting the geometry of counting.

An ant was considered radioactive if its counting rate exceeded the mean background rate at the $P < 0.001$ level. The volume of food taken by a radioactive forager was estimated by comparing its counting rate with that of a volumetric series of labelled sugar water standards. Foragers were counted only briefly to reduce the likelihood of their regurgitating labelled food inside the capsules.

As soon as the required number of radioactive foragers had been collected, the sugar water was removed from the arena. The foragers were freed from their capsules and transferred together to the nest arena. At specified sample times, food sharing was monitored by quickly aspirating samples of about 100 ants, rinsing them, and counting their radioactivity. For each sample, the queen was also captured. The queen was counted immediately and returned to her colony. Next, a random subsample of 70–100 of the collected workers was drawn and each worker counted individually. Surplus ants were returned directly to their nests and other ants were returned after counting.

The same radioactivity criterion and volume estimation were applied to the sampled ants. Because the ants may have transferred unbound tracer and sugar water at different rates, and since the labelled food might easily have been diluted with fluids already in the crop, these estimates are only rough relative indices of food volume, and the term 'volume-equivalents' is appropriate (Wilson and Eisner 1957).

Workers' headwidths were measured in the final samples after counting. The ants were assigned to one of three arbitrary size classes (there are no discrete worker size classes in this weakly polymorphic species): (a) *small* – headwidth 0.65 mm or less; (b) *medium* – 0.70–0.85 mm; (c) *large* – 0.90 mm or greater. Unless otherwise noted, statistical significance was determined by analysis of variance (ANOVA).

Results

Influence of Colony Size

Three groups of colonies were prepared, each with a mother queen and either 1000, 10,000 or 20,000 of her randomly selected workers. The smallest population roughly corresponds to field colonies that are less than a year old (Markin et al. 1973); the larger sizes approximate field colonies capable of rearing sexual castes. Three colony-replicates each were completed for the first two sizes and two replicates were obtained for 20,000-ant nests. The petri dish nests were approximately proportional in volume to the populations they held.

After one week, food was withheld for three days. At the end of this starvation period, radiolabelled sugar water was given to the required number of foragers ($n = 10$, 100, or 200, respectively). Because it took longer to collect and count larger numbers of foragers, the foragers from smaller colonies were not returned to their nests until the time needed to count 200 foragers had elapsed. Samples of ants were drawn at 6, 24, and 48 h after the workers had been replaced in their nest.

A first objective was to determine whether colony size affects the quantity of food ingested by individual foragers. Since the frequency distribution of meal volumes reflected the positively skewed distribution of worker body sizes, the volume data (in nanoliters) were normalized with the $\log_{10}(x+1)$ transformation. Marked differences among colonies were noted in their food intake, with the mean meal size for the colony's foragers ranging from 1.24 to 2.28 (log-transformed values). Although consumption appeared to increase with colony size (mean log values were, respectively, 1.72, 1.80, and 2.11), one-way ANOVA on the transformed means did not detect a significant colony size effect.

The food introduced by the few foragers was distributed rapidly to a large number of recipients. The most active phase of food dispersal was the first 6 h, and by 48 h, at least 50% of the workers had received radioactivity in six of eight test colonies (Fig. 1). The mean percentages of radioactive workers for the small, medium, and large colonies at 48 h were 46%, 63%, and 69%, respectively, suggesting that the portion of a colony that participates in sharing the radioactive food increases with colony size, but this trend was not statistically significant (two-factor ANOVA,

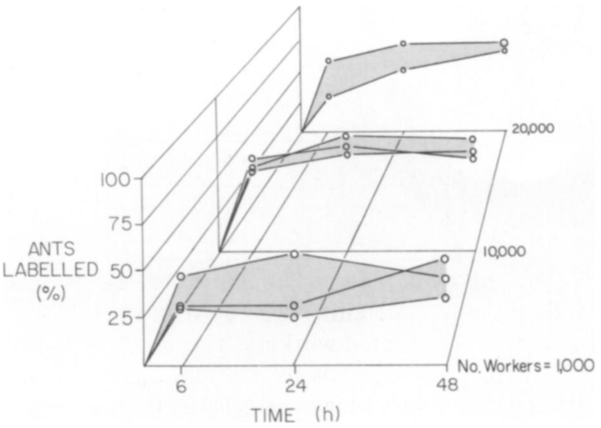

Fig. 1. Effect of colony size and sampling time on the proportion of a colony's workers receiving radioactivity. Time after introduction of radiolabel-fed foragers on the x-axis; proportion of worker population labelled on y-axis; colony size on the z-axis. *Each curve* describes an individual colony

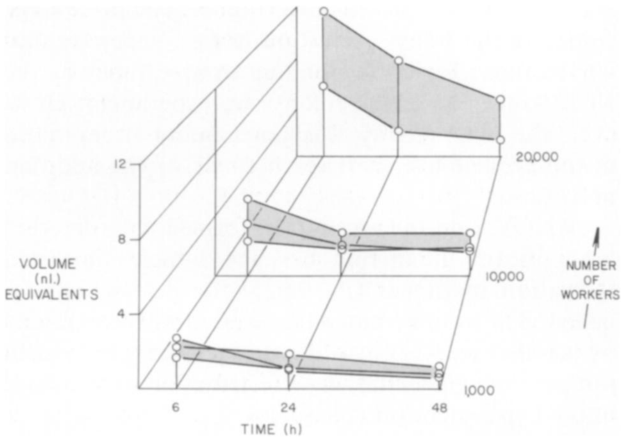

Fig. 2. Effect of colony size and sampling time on the mean volume equivalents contained by sample workers. *Axes* as in Fig. 2, except for dependent variable on y-axis

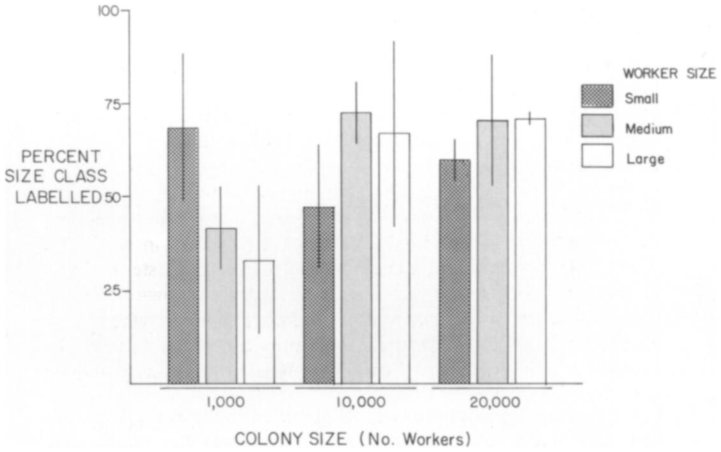

Fig. 3. Percentage of worker size classes receiving radioactivity in colonies of three sizes. *Bars* = mean ± 2 SE

arcsin $\sqrt{\%}$ transformation, repeated measure design). The radioactive proportion of the colony did increase significantly with sample time ($P<0.05$) and this effect was independent of colony size (i.e., there was no significant colony size × sample time interaction in the ANOVA). Colonies with 1000 workers displayed the greatest heterogeneity in labelled proportions and intermediate size nests the smallest (Fig. 1).

The frequency distribution of volume equivalents (VE) for sampled ants was always positively skewed. For all colonies, VE distribution tended toward uniformity with time as those ants carrying very large amounts of radioactivity became rarer. At the same time, the mean VEs in radioactive workers decreased significantly with time (Fig. 2) ($P<0.001$; two-factor ANOVA). Although Fig. 2 suggests a direct relationship between mean transformed VEs and colony size, the ANOVA narrowly failed to detect a significant colony size effect ($0.05<P<0.10$) or interaction between colony size and time.

Colony size did significantly influence food distribution among workers of different body size. At 48 h, colonies with 1000 workers had a greater proportion of labelled small workers than large ones (Fig. 3), but in colonies with 10,000 and 20,000 ants this relationship was reversed ($P<0.05$).

There was no clear relationship between colony size and the tendency for queens to become radioactive. Within 48 h, all but two queens had received labelled food. Generally, queens from colonies with a large proportion of labelled workers became radioactive more often. The number of radioactive queens in the eight test colonies increased with sample time, from three at 6 h to six at 48 h. In all cases where the queen was radioactive, she was much less so than the majority of her radioactive workers.

Effects of Colony Starvation

Mealworms and sugar water were withheld from queenright, 10,000-ant colonies for different periods of time prior to the introduction of radioactive food. After one week of ad libidum feeding, three colonies each were starved for either 3, 7, or 14 days. During this time, dead ants were removed from the arena to reduce cannibalism, and replicates showing excessive mortality were replaced. An unstarved control group was also included, giving a total of 12 test colonies.

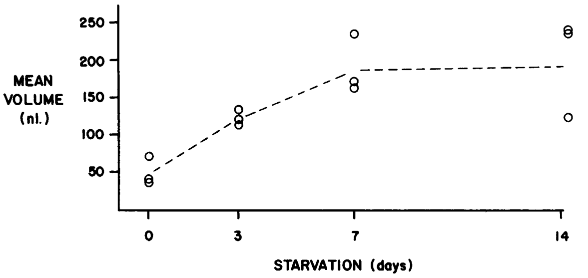

Fig. 4. Average consumption of radiolabelled sugar water from differently starved colonies. Each point represents the log-derived consumption (*nl*) of an individual colony. *Curve* is the mean transformed ingestion for each of the three replicates

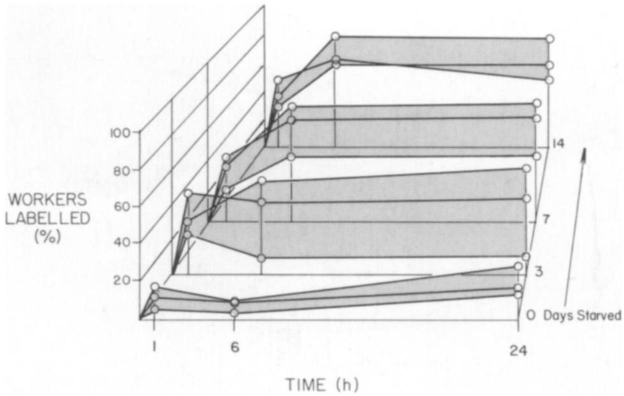

Fig. 5. Percentage of workers receiving radiolabelled sugar water after their colonies were starved for various periods of time. *Axes* as in Fig. 1, except for substitution of starvation period on *z*-axis

Radiolabelled sucrose was given to 1% of each colony, as before, but for the present test nonradioactive sucrose solution (the 'chaser') remained available for the duration of the food-sharing period. Samples of workers ($n = 70$) and the queen were withdrawn at 1, 6, and 24 h.

Foragers from starved colonies consumed considerably more radiolabelled food than did their well-fed counterparts (Fig. 4), reaching a plateau at 7 days of starvation. Dissection of several foragers from 7- and 14-day-starved nests revealed that their crops were collapsed but not completely empty. Rather, they contained droplets of yellow oily material and often also small quantities of aqueous fluids. Since meal volume frequency distributions were again positively skewed, the data were log-transformed. There were significant differences among the means of the four groups (one-way ANOVA; $P < 0.001$), with intake by the control group significantly lower than that of all starved groups.

Early samples disclosed that liquid food can be distributed very rapidly, and that the rate of distribution depends upon colony starvation. Since chaser was available to the colonies, it is likely that by monitoring the distribution of radioactivity, we are essentially charting the general flow of sugar water. Food flow in unstarved colonies was rather low and no more than 30% of the sampled ants become radioactive within 24 h (Fig. 5). However, for colonies starved for 1–2 weeks, after only 1 h the radioactivity had spread to 20%–50% of the workers, and had equilibrated within 6 h when the majority of the colony had become radioactive (Fig. 5). The intensity of food exchange in 3-day-starved colonies was fairly heterogeneous and was intermediate between control and 7- to 14-day-starved nests (Fig. 5). The percentage values for the 3-day-starved group were generally similar to those for corresponding sample times in the 10,000-ant nests of the colony-size experiment. However, the heterogenity was much more pronounced in the present test, perhaps because of the addition of a chaser.

ANOVA on the arcsin-transformed data detected a significant interaction between sample time and starvation treatment ($P < 0.025$) for proportions labelled. The volume equivalents of radioactivity held by labelled workers also decreased significantly with sample time ($P < 0.05$), an effect similar to that seen in the experiment on colony size.

Trophallactic Behavior

We monitored trophallactic behavior visually in hungry colonies before and after feeding. Four queenright, 1000-ant colonies (with about 100 larvae each) were housed in horizontal, glass nests and observed through a dissecting microscope on sliding mounts. The colonies were starved for four days. Randomly selected areas of the nests were observed for 30 s each and scored for the numbers of workers present and the numbers performing trophallaxis. The number of participants in each trophallactic exchange was noted. When five 30-s samples had been completed for each of the four hungry colonies, they were given 20% sucrose and again observed at 9 min, 1 h, and 3 h (five samples/colony/time).

Before food was supplied, fewer than 5% of the workers were engaged in trophallaxis (Fig. 6), and these exchanges usually involved only two partici-

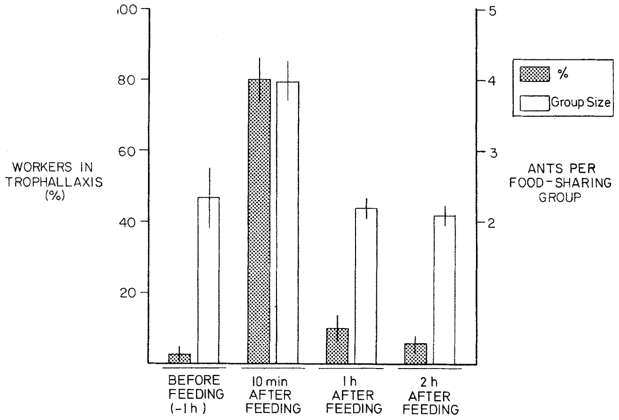

Fig. 6. Changes in trophallactic activity with time as a response to incoming food in 4-day-starved colonies. Data are means (± 2 SE) for four observation colonies. *Group size* refers to number of workers participating in each observed instance of food sharing

pants (maximum: three workers). The return of sugar-laden foragers to the nest, however, signalled the onset of a period of frenzied food exchange. Just minutes after the food was given to the colony, approximately 80% of the workers were either donating or receiving food. Donors could be identified by their characteristic open mandibles. The numbers of workers in trophallactic groups ranged from two to as many as eight, and the average group size rose to about four ants per exchange. It is unlikely that foragers alone were acting as donors, for supplementary observations revealed that food recipients can subsequently donate a portion of their meal to other workers.

The food-sharing scenario changed dramatically again by the time the 1-h sample was taken. Now, only 10% of the worker population was involved in food exchange and the majority of exchanges involved only two participants (maximum: three workers). In many cases, workers were seen standing alone with a droplet of fluid extruded between their mandibles (soliciting recipients). In some instances they wiped the fluid on the nest floor. The 2-h sample was similar to the 1-h sample (Fig. 6).

An additional test was conducted to insure that the responses were in fact due to the addition of food. In hungry colonies, a dish of tap water elicited no obvious change in trophallactic behavior. When a dish of sugar water was substituted, food-sharing activity increased markedly. Thus, we are confident that it was the influx of sugar water into the nest which evoked the increase in trophallaxis.

These behavioral observations help to explain the rapid flow of radioactivity in large, starved test colonies. Shortly after the radiolabelled foragers entered the nest, many large recipient groups formed around the donors. These recipients also passed along a part of their windfall to other workers so that the proportion of radiolabelled workers in the nest increased rapidly.

Effect of Worker Size

Returning to our radioactivity assays, it was determined that the likelihood of a worker's receiving radioactivity after 24 h depended on the worker's body size. Independently of starvation, large workers consistently contained a greater proportion of radioactive recipients than did smaller ones. Significant effects for worker size ($P<0.025$) and starvation ($P<0.001$) were found by ANOVA, but there was no evidence for an interaction betweeen these factors. It seemed possible that the enhanced labelling of large ants was due to a tendency for these individuals to consume more food than smaller workers, therefore making them more likely to exceed the counting criterion. If this were so, a positive correlation between worker size and the VEs could be expected. However, by regression analysis, only two of the 12 colonies displayed a significant positive relationship between these two variables (and transformed variations) and in both cases, the relationship was not robust (7-day-starved: $r=0.38$; 14-day-starved: $r=0.39$). Thus, an explanation based on greater consumption by large workers is not totally satisfactory.

Generally, queens received radioactive food earlier in starved colonies than in well-fed ones, and their volume equivalents tended to increase with both sample time and duration of starvation. As in the colony-size test, radioactive queens were most often found in samples containing large proportions of labelled workers. While queens gained volume equivalents, the average worker's VEs decreased. As a consequence the percentage of labelled workers with VEs smaller than those of their radioactive queen grew from 9.5% at 1 h to 64.8% at 24 h.

Forager Starvation

In well-fed colonies, attenuated food sharing could have been the result of foragers' providing smaller amounts of food. How would satiated colonies respond if these workers supplied more food? To answer this question, two groups (three replicates each) of queenright, 10,000-worker colonies were established which differed only in the level of starvation of their foragers. In one group of colonies (the 'forager-starved' group) approximately 200 foragers from each colony were isolated as a group without food

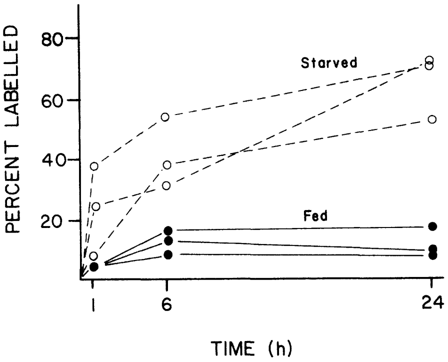

Fig. 7. Distribution of radioactivity from foragers who had been separated from their parent colonies with or without food. Distribution is the percent of workers in the parent colony receiving radioactivity

in moist petri dish nests. In the other group ('forager-unstarved') similarly isolated foragers were fed a surplus of mealworms and sugar water. In both groups, the parent colonies were unstarved.

After three days of isolation, the groups of 200 foragers were offered radioactive sugar water until 100 had become significantly radioactive. A chaser of sugar water was then placed in the well-fed parent nest and the labelled foragers were reunited with their respective colonies. The extra, nonfeeding foragers were discarded. Samples were drawn at 1, 6, and 24 h.

Isolated foragers who were starved consumed almost ten times more radioactive food ($P < 0.001$) than those who had been isolated but well fed (mean log-transformed consumption, 2.46 and 1.52, respectively). In fact, the 3-day-starved foragers ingested at least as much food as foragers from 7- and 14-day-starved colonies in the previous starvation test. Body-size difference among forager groups was not detected and cannot be the cause of the meal-volume differences.

The radioactive food in unstarved-forager colonies was distributed similarly to that in well-fed controls in the colony-starvation experiment (Fig. 7). Thus, only a small segment of the worker population received food within 24 h (9%–17%) and the proportions labelled changed little with sample time (contrast Figs. 5 and 7). However, a markedly different pattern emerged from colonies with starved foragers. Despite the well-fed condition of the parent colonies, food sharing was pronounced and by 24 h, 53%–73% of the workers had received food (Fig. 7).Further, the proportion of labelled individuals had not reached equilibrium by 6 h as it had in the colony-starvation experiment, but continued to increase. The difference in distribution patterns was statistically significant, as indicated by the forager starvation-sample time interaction ($P < 0.025$) in two-factor ANOVA.

Finally, none of the queens in control colonies became radioactive whereas all three queens from the forager-starved group received food within 6 h. The volume equivalents held by queens were generally smaller than those of radioactive workers, but the VE trends were again opposite.

Discussion

We have shown that the pattern of food flow in a colony depends both on the foragers' inclination to collect and donate food and on the tendency of nest ants to distribute it. It is helpful to consider separately the effects of starvation on these components of food dispersal.

When the colony's nutritional needs increase, as during starvation, the foragers intensify their food-retrieving activities. Thus, foragers from hungry colonies of *Formica fusca* are more easily stimulated to join in excursions from the nest (Wallis 1962) and foragers from hungry *Solenopsis invicta* (*S. saevissima saevissima*) colonies mass-recruit to food more quickly and to a greater magnitude than do those from satiated colonies (Wilson 1962). Our observation that starved *S. invicta* foragers increase their consumption of sugar water is similar to Wallis' (1964) on *F. fusca* foragers. The importance of the foragers' role in the colony response to starvation is further established by the forager-starvation experiment. Food sharing in these satiated colonies is more pronounced when labelled, previously starved foragers are introduced than when previously satiated ones are added. Wallis' (1964) data on *F. fusca* indicate that previously starved foragers in satiated colonies have a lower success rate in regurgitating than previously satiated foragers, but because the former attempt many more transfers, their overall success is greater. Such behavior may in part explain our results.

Starvation-induced food sharing occurs in the nonforaging population of the nest as well as among foragers. We have shown that colony starvation boosts the frequency of trophallaxis following the entry of food-laden foragers and also increases the ratio of recipients to donors in such exchanges. Related responses have been noted for *Lasius niger* (Lenoir 1974) and *F. fusca* (Wallis 1962, 1964). The size of food-exchanging groups must figure significantly in the rate of food flow, since it has been shown that recipients can subsequently serve as donors (Gösswald and Kloft 1960).

Studies on the food-sharing roles of foraging and nonforaging workers under various starvation conditions have produced somewhat conflicting results (Kneitz 1963; Schneider 1966, 1972; Markin 1970). Sudd (1957) and Wallis (1961, 1962, 1964) explained that apparent discrepancies in whether a donor or an acceptor play the active role in trophallaxis may be resolved if the overall condition of food availability is considered. Thus, results may pivot not simply on whether a forager or its colony is starved or fed, but on the relative degree to which these conditions apply. The trophallactic ability of the fire ant may have been previously misjudged. In their pioneering study of food sharing in several ant species, Wilson and Eisner (1957; Eisner and Wilson 1958) monitored the dispersion of labelled honey-water from a single fire ant forager in a colony fragment consisting of a queen and 42 workers. After three days, approximately 67% of the workers were labelled. Eisner and Wilson (1958) concluded that in fire ants 'the transmission of sugars appears to be quite incomplete, at least under laboratory conditions ...". Other authors interpreted this study (which, after all, was ultimately based on the donating tendencies of a single fire ant) as indicating 'slow' sugar distribution in fire ants, where radioactivity 'does not spread beyond a few workers' (Sudd 1967; Vinson 1968). Our observation that sugar can spread within 6 h from 100 foragers to more than 5000 nestmates suggests that such interpretations underrate the food-sharing ability of fire ants.

Food distribution can vary markedly according to the body size of the recipients. In 10,000- and 20,000-ant colonies, regardless of starvation conditions, a smaller proportion of small workers is labelled than large workers. Vinson's (1968) data on sugar dispersal in large fire ant colonies indicate a similar trend (not statistically tested). A preliminary study on the transfer of dyed oil in *S. invicta* colonies led Glancey et al. (1973) to conclude that large workers function as a replete caste, capable of storing oil in their crops for long periods and later regurgitating it to their nestmates under the stress of starvation. However, Wilson (1978) pointed out that the evidence of Glancey et al. (1973) could be otherwise interpreted. Wilson (1978) found that when a starved fire ant colony is permitted to feed to satiation, it is the small workers rather than the large ones who hold a proportionately greater amount of sugar water. Thus, he argued that small workers appear more specialized for storage, at least where sugar is concerned. Based on available evidence we feel that it is premature to label one worker size class as food-staring specialists, especially in light of our finding that the food-sharing roles of workers can change with colony size.

Our data revealed that patterns of food flow in fire ant colonies can change with the number of workers present. It is thus evident that certain inferences on the dynamics of food distribution in large colonies may not necessarily be extrapolated from studies on much smaller colonies. Although we are confident that 10,000-ant colonies are more appropriate models of mature colonies than are the smaller ones, we caution that our colonies lacked the brood and sexuals typical of mature, field colonies. Our study also does not eliminate the possibility that colony size effects may change when starvation conditions are varied.

Several studies on other species have shown that workers tend not to feed sugars directly to the queen (Wilson and Eisner 1957; Gösswald and Kloft 1960, 1964) but that labelled food can be synthesized into glandular secretions which are subsequently fed to the queen (Gösswald and Kloft 1963; Naarman 1963; Markin 1970). Our finding that *S. invicta* queens gain over their workers in radioactivity may indicate glandular transfer, but as pointed out earlier, a simple statistical effect could also be responsible.

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