

The flow of food in colonies of the fire ant, *Solenopsis invicta*: a multifactorial study

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ABSTRACT. A study was conducted to determine the interaction of several factors in the trophallactic distribution of food in colonies of *Solenopsis invicta* Buren. Radioactive iodine (^{125}I) was used to quantify both the ingestion of test foods by foragers and the distribution of this food to nestmates. A multifactorial design tested the simultaneous effects of: (1) food-type (sugar water, casein hydrolysate, or oil), (2) temperature during foraging and food-sharing (25, 30 or 35°C), and (3) starvation period (colonies deprived for 0, 3, 7 or 14 days). The amount of food consumed by foragers was influenced by the interaction of food-type and starvation. Foragers from severely starved colonies ingested more aqueous foods than did those from slightly starved colonies, but oil was always taken in smaller quantities and its ingestion was least affected by starvation. Ingestion was generally lowest at 35°C, probably because of mutual interference of workers while feeding. Within the colony, food sharing varied with food type and increased with starvation. The sugar solution was utilized primarily by workers. Amino acids were shared throughout the colony, but were directed preferentially to the growing larvae. Soy oil was equally shared among workers and larvae and reached more colony members per initial unit volume than did the other foods. The test factors also interacted in their influence on trophallaxis. Starvation stimulated the dispersal of labelled foods, but at different intensities for different foods. The probability of the queen's receiving food increased when the labelled food was widely exchanged among her nestmates. Casein hydrolysate reached the queen in more cases than did the other tested foods.

Introduction

Food-sharing is an activity of great importance in social insect colonies, where many members of the society cannot or do not forage but depend on their nestmates for nutrition. A number of ant species are able to store liquid food in the distensible crop of workers, and to regurgitate it (stomodeal trophallaxis) to hungry members of the society.

The trophallactic flow of fluid foods within

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ant societies can be studied by direct observation of the behaviour of colony members in artificial nests (see e.g. Wallis, 1961). Addition of radioactive tracers to the food has served as a valuable tool for quantifying food-sharing in bees, ants, wasps and termites (Wilson, 1971; Sudd, 1967; Abbott, 1978). Usually tested are the effects of individual social or environmental factors on food-sharing, while other variables are held constant. While yielding important information, such experiments cannot characterize the interactive effects of factors on food-flow.

In reality, multifactorial variety more closely approximates nature, and it is desirable to evaluate feeding responses of laboratory colonies to combinations of conditions. Recently, Brian & Abbott (1977) demonstrated the usefulness of the multifactorial approach in studying the flow of several kinds of food in colonies of the ant, *Myrmica rubra*, that had been pretreated by specifically starving workers, larvae, and/or the queen. In the present study we report on the simultaneous influence of colony starvation, type of food, and temperature during foraging and food-sharing in the ant *Solenopsis invicta* Buren.

Materials and Methods

Establishing laboratory colonies

Mature fire ant colonies were collected in northwestern Florida during sunny, winter days when the ants gathered just below the sun-warmed surface. The mound material was allowed to dry in fibreglass bins, forcing most of the colony into a damp trap-nest. Sucrose (1 M) and chopped tenebrionid beetle larvae (*Zophobas rugipes* and *Tenebrio molitor*) were provided *ad libitum* for 2–3 weeks, with the laboratory temperature at approximately 24°C.

Prior to testing, each colony was reduced to a standard size, placed in a new nest, and this in turn was placed in a large plastic box (the foraging arena). A standard colony included the queen, 10 000 workers and 1500 larvae, excluding large sexual larvae. The ants were selected by aspirating from a frequently stirred tray and were counted on a sample weight basis. Food-sharing in large, mature colonies is reasonably represented by 10 000-worker colonies (Howard & Tschinkel, 1980), and pilot tests indicated that the worker size distribution of standard colonies reflects that of the entire colony.

The unused portions of the colonies were saved as stock colonies to replace small numbers of dead ants in the experimental nests. Test colonies displaying excessive mortality were discarded.

Monitoring food flow

After being well fed for 1 week, each standard colony was assigned to a particular

combination of factorial treatments (described later). For testing, a slide containing radioactive food of known specific activity was made available until 100 foragers (1% of the worker population) had fed. Upon leaving the food, each worker was captured and dipped in water in an effort to remove external contamination. The foragers were then placed inside empty gelatin capsules and individually counted for radioactivity with a Packard Autogamma (crystal) Scintillation Counter. The volume of food ingested was determined by correcting the counts for background activity and comparing them to the radioactivity of a series of volume standards. Only foragers with counts significantly above background ($P < 0.001$) were utilized, thus excluding ants that had inspected the food but had not fed.

After counting, the 100 foragers were removed from their capsules and together introduced into the nest interior. The nest was briefly reopened 1 h later so that the queen and about 100 each of workers and larvae could be removed. Workers were aspirated from randomly predetermined sites in the nest and larvae were collected from various areas of the brood pile. The queen was encapsulated, counted quickly and returned to her nest. Seventy each of workers and larvae were selected for counting by stirring under the intake of an aspirator. The airflow was strong enough to pull in large and small ants alike. The larvae were counted first and returned to their colony but the workers were rinsed, counted and then discarded. If an individual's radioactivity exceeded background at the $P < 0.001$ level it was considered to have received the food. This conservative criterion avoided the confounding effects of residual external contamination. The volume of radioactive food in individuals was estimated by the method used for foragers. Since it is possible that the food and tracer are assimilated at different rates, the estimates are volume equivalents rather than absolute units of volume.

Factors tested

The simultaneous influence on food-distribution of three different factors was tested, as described below.

1. *Starvation.* Preceding the introduction of radio-labelled food, colonies were starved for 0, 3, 7 or 14 days. During prolonged starvation, cannibalism of the larvae was sometimes severe, requiring replacement with equally starved brood from the appropriate stock colonies several hours before testing.

2. *Food type.* Colonies were offered one of three radio-labelled foods: (a) 5% sucrose (fire ant workers are reported to disgorge stronger solution on the nest floor; Vinson, 1968); (b) a solution of casein hydrolysate (1:10 by weight, DIFCO Laboratories), reported to be widely accepted by fire ants (Lofgren *et al.*, 1961); (c) once-refined soybean oil. The aqueous foods were mixed with free, Na^{125}I , to yield a specific activity of *c.* $0.3 \mu\text{Cu}/\mu\text{l}$. ^{125}I was chemically bound to soybean oil by the method of Stanley & Thannhauser (1949) and the specific activity adjusted to *c.* $0.3 \mu\text{Cu}/\mu\text{l}$ by mixing with unlabelled soy oil. A coverslip prevented the ants from walking on the food and contaminating themselves, and aqueous foods were periodically substituted before evaporation could appreciably increase the concentration.

3. *Temperature.* From 1 h before to 24 h after presentation of the radioactive food, the arena-nest complex was placed in a constant-temperature chamber at 25, 30 or 35°C.

Factorial design

A complete factorial design required a total of thirty-six cells ($3 \times 3 \times 4$ levels). Colonies were randomly assigned to starvation and temperature treatments, but since some refused to feed on an assigned food, even after considerable periods of starvation, the colonies had to be pre-screened for food preferences and assigned food-type treatments accordingly. Colonies that would accept only one food were not used.

Testing of a single replicate colony per cell required 3 months. Since additional replicates were not run, statistical analysis followed Winer's (1962) recommendations on analysis of variance (Anova) for single replicate, multi-factorial designs. Fixed models were used with the mean square of the highest order interaction applied as an estimate of residual error. In some analyses, sample time was included as a factor.

Results

Consumption of liquids by foragers

It is unlikely that external contamination contributed significantly to the foragers' radioactivity since the workers were generally fastidious during feeding. Of the three factors, food-type had the most pronounced influence on the quantity of labelled fluid ingested by foragers. Regardless of starvation or temperature conditions, foragers consumed markedly less soybean oil than sugar or casein hydrolysate (Fig. 1). Analysis of variance (log-transformed) revealed a significant main effect for food type ($P < 0.001$). Fire ants are reported to take unsaturated lipids more readily than saturated ones (Vinson *et al.*, 1968), and we reasoned that the addition of iodine across some of the double bonds might have reduced the attractiveness of the soy oil. However, a test showed that hungry foragers would take as much of the partially iodinated oil as they would of a 1:10 mixture of the partly iodinated oil and normal oil. Although the foragers' abdomens often swelled with aqueous foods but not with oil, they nevertheless appeared to feed for longer periods on the oil.

Starvation also affected ingestion ($P < 0.001$) but this influence varied according to the type of food (food \times starvation interaction; $P < 0.002$). Although foragers showed a gradual increase in their intake of sugar water with starvation, those offered casein hydrolysate did not show a dramatic increase in consumption until 2 weeks without food had elapsed. The cannibalism of brood may be partly responsible for producing this pattern, for larvae were heavily depleted in nests starved from 7 to 14 days.

Unlike that of other foods, the consumption of oil by foragers was essentially independent of starvation. Other tests (Howard & Tschinkel, 1980) have shown that foragers from a starved colony will take much smaller amounts of oil than of aqueous foods, hence it is unlikely that low oil intake is due to a lack of hunger.

Temperature only subtly affected ingestion ($P < 0.01$) with intake generally lowest at 35°C. At this temperature, the ants were both active and aggressive, and feeding often terminated when a forager was jostled by a rapidly moving nestmate. Temperature's effect did

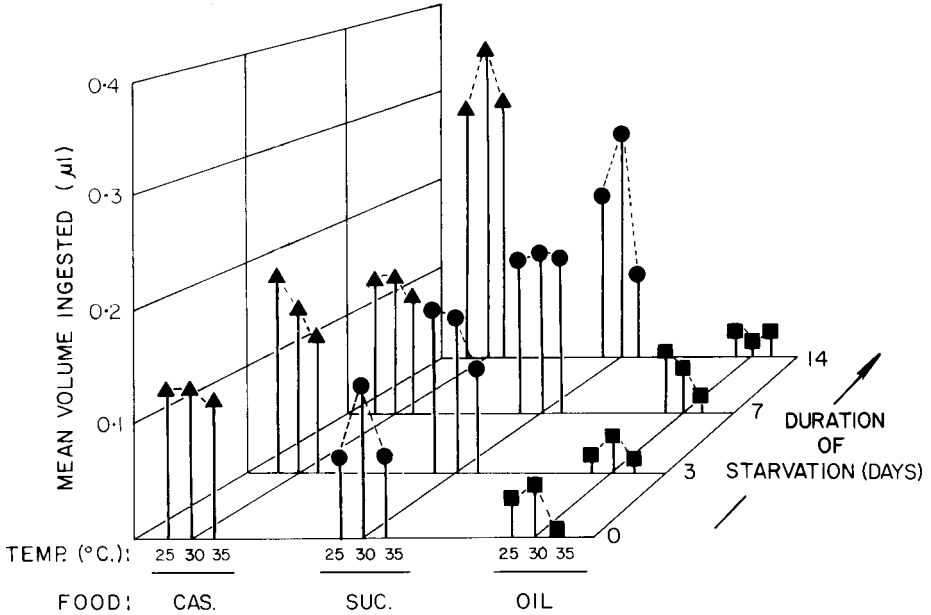


FIG. 1. Effect of three factors on the volume of food ingested by fire ant foragers. Foragers from individual colonies are arranged on the x-axis according to the food they were given and the temperature at which they fed, the y-axis indicates the mean consumption for a colony's 100 foragers, and the period for which the colony was starved is given by the z-axis.

not significantly interact with food-type or starvation.

Food distribution to workers

We now consider the influence of test factors on the trophallactic flow of the forager-introduced food to workers, larvae and the queen. The proportion of a colony's worker population that received radioactive food varied significantly according to the type of food their foragers retrieved (Anova, arcsine square root-transformed, main effect; $P < 0.001$). Colonies fed amino acids generally displayed the greatest number of radioactive workers, soy oil was the second most distributed food, and sugar water generally reached the fewest workers (Fig. 2).

The dispersal of radioactivity among workers increased with starvation (main effect; $P < 0.001$) but at different levels varying for different foods (food \times starvation interaction; $P < 0.01$). When casein hydrolysate was being shared, the number of radio-labelled workers consistently increased with starvation, but the relationship was less regular for the other two foods (Fig. 2). Sampling error may contribute

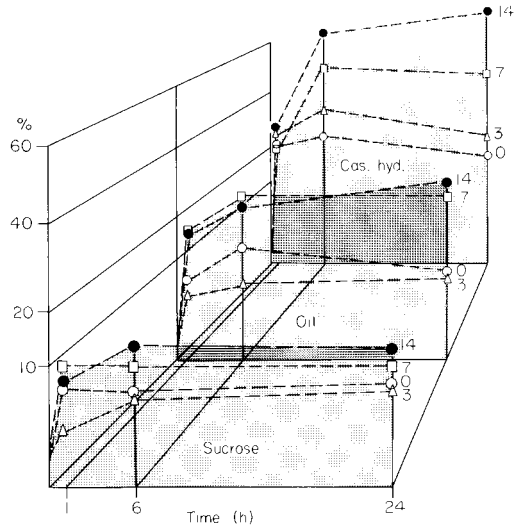


FIG. 2. Influence of sample time, starvation (0, 3, 7 or 14 days starved), and food-type on the mean per cent of sampled workers who contained radioactivity. Sample time is given on the x-axis, and the z-axis shows food-type. Each curve represents change in means for three colonies that were exposed to different temperatures but otherwise were treated equally. Starvation time is indicated by numbers to the right of each curve. The non-linear scale of the y-axis takes into account the arcsin-per cent transformation.

to this irregularity, since proportions labelled were low for sucrose and oil. Most food dispersal took place within 6 h after forager introduction (Fig. 2).

When averaged over all starvation and food-type conditions, the mean proportions of workers labelled did not vary significantly for the three temperatures (no main effect for temperature). However, elevated temperatures enhanced food distribution among workers in severely starved colonies but not in well-fed nests (temperature \times starvation interaction; $P < 0.01$). In unstarved colonies, the mean proportions of workers labelled at 25, 30 and 35°C were 0.23, 0.21 and 0.15, respectively, but for 14-day-starved colonies the corresponding proportions were 0.26, 0.32 and 0.35.

Food distribution to larvae

Many more larvae received radioactivity in colonies foraging casein hydrolysate than in those offered sucrose or oil (food effect; $P < 0.001$) and the proportions of labelled larvae generally increased with the colony's hunger (starvation effect; $P < 0.001$) (Fig. 3). Because this starvation response was more pronounced in colonies sharing casein hydrolysate than in those sharing other fluids, a significant food \times

starvation interaction was detected ($P < 0.001$). The majority of larvae receiving radioactive food did so within 1 h; thereafter the number of labelled larvae increased only slightly. Consistent relationships between temperature and other factors were not detected.

Some differences were notable in the distribution of food among workers and the flow from workers to larvae. The proportions of larvae receiving sugar or oil were slightly lower than, or equal to, the proportions for their respective workers (compare Figs. 2 and 3), but substantially greater fractions of larvae received casein hydrolysate than did workers, especially during the early phases of food-sharing. Colonies dispersing the hydrolysate were also the only ones that showed a greater response to starvation for larvae than for workers (Figs. 2 and 3), thus suggesting that workers give priority to feeding amino acids to the larvae rather than broadly distributing them among themselves. However, worker-larva priority can be better assessed by comparison of the volumes of food in each, as considered in the next session.

Volumetric flow of food in the colony

Many samples of workers or larvae included only a few radioactive individuals, whose volume equivalents may have varied by several orders of magnitude, and this even persisted to a degree when larger numbers of radio-labelled individuals were found in samples. Therefore, sample means were determined for log-transformed data but Anova was not applied.

Calculating from 24-h counts of workers and larvae, approximately 80–90% of the radioactivity introduced with oil and casein was recovered from colony members but only c. 25% of the sugar's label could be accounted for. The loss of radioactivity from colonies fed sucrose was a general phenomenon, with eleven or twelve colonies showing less than 40% recovery, and may have been partially due to workers regurgitating or excreting onto the nest or arena floor (Vinson, 1968). Differences in the biological half lives of ^{125}I mixed freely with food (as in sucrose or casein hydrolysate) or chemically bound to it (as with soy oil) may also be responsible (Sorenson *et al.*, 1980), especially if the larvae acted as a

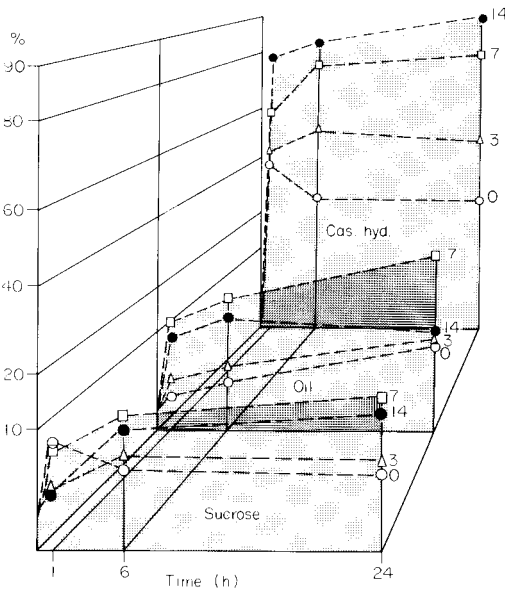


FIG. 3. Influence of sample time, starvation (0, 3, 7 or 14 days starved), and food-type on the per cent of larvae who contained radioactivity.

'sink' for amino acids and prolonged their half life relative to that of sucrose.

The average volume equivalents for radioactive workers are greater than those for larvae when sucrose or oil were being shared but less than for the casein hydrolysate (Fig. 4). Because the average weight of larvae was close to that of workers (*c.* 1 mg) the relationships also hold on a volume equivalent per unit and weight basis. The mean decrease in larval volumes from 1 to 6 h was probably mainly due to their receiving smaller amounts of food as time progressed, but the backflow of label from larvae to workers (through larval secretions or excreta, or by cannibalism of larvae) cannot be ruled out.

Calculations for the total volume of the three foods recovered at 24 h indicated that larvae as a group contained approximately 30% or their colony's accountable casein hydrolysate, 10% of the oil, and 5% of the sugar water. Since the biomass of standard colonies consisted of 10–15% larvae, we conclude that amino acids are distributed with priority to the larvae, that sugar remains primarily among workers, and that oil is divided equally between the two groups.

While both sample-time and food-type were important factors in determining the mean volume equivalents in larvae and workers, con-

sistent effects of starvation or temperature were not apparent.

A comparison can be made of the volume of a particular food taken by foragers and the proportion of larvae and workers who subsequently receive it. In Fig. 5 the points represent individual colonies, each tested under a different factorial combination. Casein hydrolysate and sucrose were consumed in similar quantities, yet the former tended to reach a much greater proportion of the colony's workers and larvae than did the sugar. Furthermore, even though much less oil was brought into colonies than was sugar, overall, oil was distributed to as many workers and brood. Hence, on the basis of ants labelled per volume ingested by foragers, oil is much more widely spread than the aqueous foods. Fig. 5 also indicates that the colony's proportions of recipients, workers and brood alike, tend to increase with increasing uptake by foragers.

The flow of food to the queen

As for workers and larvae, the factor which most clearly determined whether or not the colony's queen became radioactive was food-type. Table 1 summarizes the effects of food type, starvation, and sample time on the feeding of queens. Casein hydrolysate was most

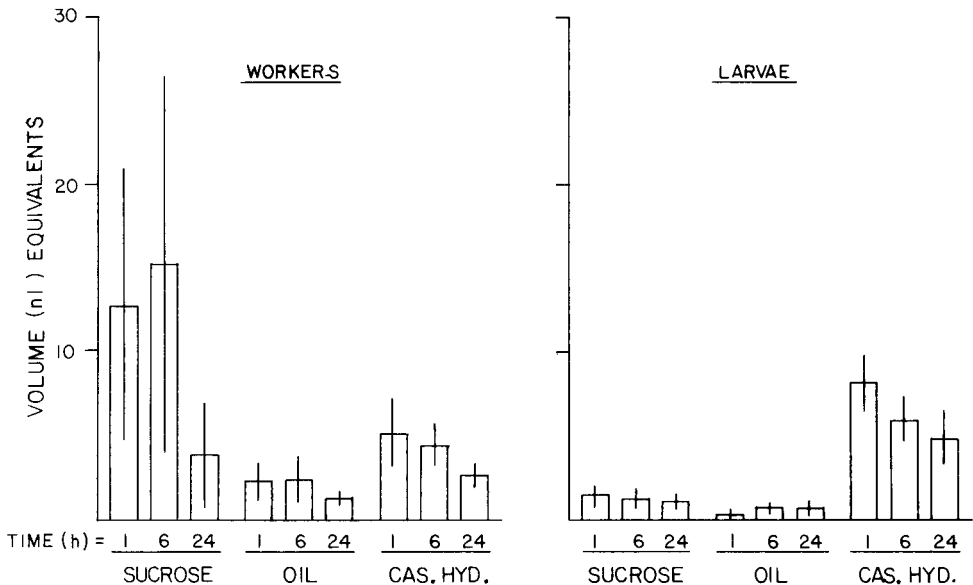


FIG. 4. Mean volume equivalents (log-derived) in radioactive workers and larvae. Each bar represents mean for twelve colonies (three temperatures \times four starvation) \pm 2 SE.

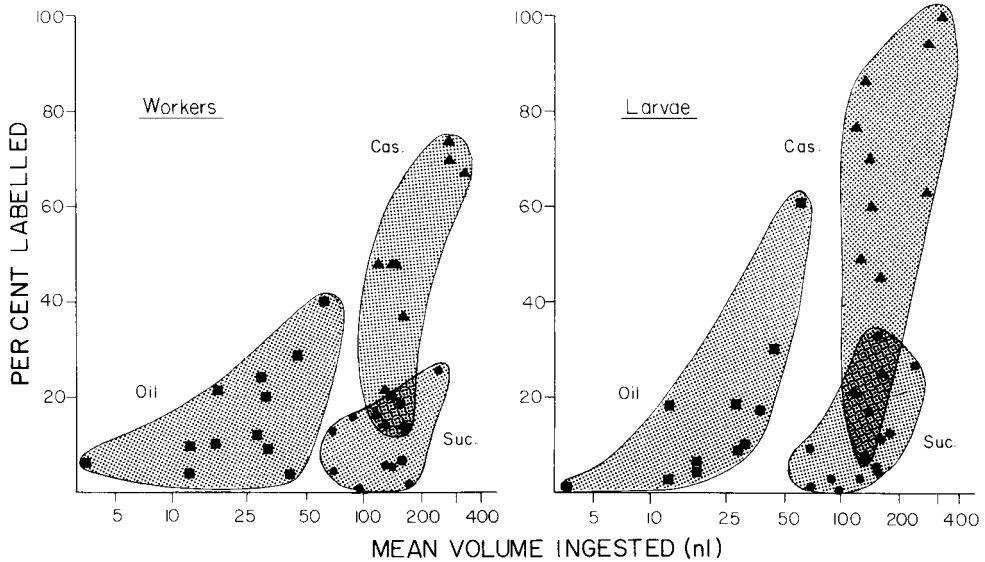


FIG. 5. Per cent of colony's workers and larvae containing radio labelled food at 24 h versus mean volume of food (log-derived) ingested by their foragers.

TABLE 1. Number of queens with significant levels of radioactivity. Maximum possible score in each cell is six queens.

Food	Days starved	Sample time (h)		
		1	6	24
Sucrose	0-3	0	2	2
	7-14	0	2	2
Casein hydrolysate	0-3	0	5	5
	7-14	3	5	6
Oil	0-3	2	2	0
	7-14	0	2	2

frequently fed to queens, for eleven of twelve queens became radioactive within 24 h, but only four queens became radioactive when sucrose was fed, and only six received radioactive oil.

Several of the oil-fed queens lost their label with subsequent samples, an effect we suspected to be due to external contamination until subsequent tests in which queens were rinsed with chloroform indicated that they carried their radioactivity inside their bodies.

The queen's volume equivalents were about the same as those of an average colony member's. The queen held more than the mean worker in only two of eight sucrose samples, three of eight oil samples, and thirteen of

twenty-four casein hydrolysate samples. For the last group, her volume equivalents exceeded the larval mean in only eleven of twenty-four cases. Since the queen outweighs individual larvae or workers by more than an order of magnitude, the volumetric data suggest that she did not receive preferential feeding. In general, the probability of a queen's receiving food was highest in colonies showing extensive food-sharing and was low in colonies showing limited food exchange.

Discussion

Food distribution in social insect colonies has usually been studied either by *ad libitum* feeding under test conditions, or by giving small test colonies a uniform 'pulse' of labelled food, via a single forager. Our study draws on both of these methods by subjecting the entire colony to treatment combinations and following the distribution of a small but forager-varied pulse of food in the nest.

The between-colony heterogeneity in food preferences meant that colonies could not be randomly assigned food treatments. Although colonies with different food preferences might be differently predisposed in their food-sharing behaviour, all colonies we utilized accepted at least two foods in preference tests and many

took all three. Further, many of our findings parallel those of other studies where heterogeneous food preferences did not present a problem.

That *S. invicta* foragers ingest more aqueous foods with increasing colony starvation agrees with Brian & Abbott's (1977) work on *Myrmica rubra*, and also indicates that individual foragers can manifest the effects of colony starvation on their first visit to a source of food. It is also clear that even in well-fed colonies, foragers may accept at least small quantities of preferred foods (Howard & Tschinkel, 1980).

Others have noted differential food flow in ant colonies (see Sudd, 1967, Wilson, 1971, and Abbott, 1978, for reviews). Markin (1970) indicated that sugars circulate mainly among workers while proteinaceous foods are directed toward the larvae and queen. Such a pattern suits the nutritional needs of the recipients, since larvae and the queen require proteins for structural growth and egg production, respectively, whereas workers need mostly carbohydrates for energy (Sudd, 1967).

In our tests, sucrose did not pass far beyond the foragers and the larvae received much less sugar per individual (and per unit weight) than did the workers. Sorenson & Vinson (1981) have conducted similar experiments which confirm this trend. Even though comparatively more radioactive honey-water was spread in their *S. invicta* colonies, there was a delay in the flow of this material to the larvae and less accumulated in them than in the workers. On the other hand, Vinson (1968) found that, in colonies that are well supplied with sugar water, the larvae can contain at least twice as much sugar water per unit weight as the foragers. Perhaps Vinson's nests included more late larval instars, which are known to be fed more sugar more frequently than are younger instars (Petralia & Vinson, 1978).

While the casein hydrolysate was preferentially fed to the larvae, the question remains as to why so many workers also received this liquid. One possibility is that the workers use the amino acids as a source of energy or for the formation of glandular secretions (see below). Sorenson *et al.* (1981) have shown that egg yolk protein is shunted preferentially to workers who tend the larvae and this prob-

ably occurs also for the protein hydrolysate. Hungry *Myrmica rubra* larvae can induce nurses to demand and receive prey juices from foragers (Brian & Abbott, 1977) and it is also possible that some of our fire ant workers received radioactivity by cannibalizing the larvae.

Soy oil has been widely used in control programmes as an attractant in insecticide baits (see Lofgren *et al.*, 1975, for a review). Our colonies showed equal but limited sharing of oil among workers and larvae, but considering the small volume made available by foragers, it was actually a rather 'spreadable' food. Sorenson & Vinson (1981) find that the initial distribution of oil is heavily biased towards workers, but after a delay it begins to accumulate in larvae. We found no delay, perhaps because few individuals received oil in our tests.

Our results suggest that colony starvation enhances the priority of larvae over workers when amino acids are being shared, but no starvation effect on priority could be detected for the other foods tested. Brian & Abbott (1977) determined that for *M. rubra* the worker-to-larvae flow of prey juices, but not of sugar, increases after larval starvation. Even when sugar is plentifully supplied, sugar-starved workers give priority to providing prey-hungry larvae with prey juice rather than sugar.

The temperature to which an ant society is exposed may have a strong shaping effect on its pattern of food flow. In *Iridomyrmex humilis* colonies that have been starved at different temperatures, food is most rapidly circulated among workers at 30–32.5°C (Markin, 1970). Worker mortality sets in at slightly higher temperatures though even near this upper thermal limit, *I. humilis* colonies still exhibit pronounced food distribution. Food-sharing among workers of several *Formica* species has been shown to be optimal near 25°C, the same nest temperature at which peak brood production occurs in field colonies (Gösswald & Kloft, 1960; Kneitz, 1963). In contrast, Khamala & Buschinger (1971) did not find significant evidence for temperature effects on food flow in several temperate species. Our results indicate that temperature's effect on food flow may vary with starvation.

Although we have discussed food flow as if only the crude, labelled contents of the crop

were being shared, it should be noted that the labelled food or the tracer alone could be assimilated or incorporated into glandular secretions. Such secretions, particularly those of the worker postpharyngeal glands, play an important role in feeding of the larvae and queen (Naarman, 1963; Gosswald & Kloft, 1960, 1963; Sudd, 1967; Markin, 1970). Ant larvae and the queen are also capable of producing liquid foods. *S. invicta* workers solicit from larvae both saliva and a milky fluid produced near the anal region (O'Neal & Markin, 1973). Such fluids may serve as food supplements for the workers. If the larval fluids include radioactive tracers that were originally fed to them by the workers, the larvae could contribute significantly to the trophallactic pattern in their colony. Queens may also participate as donors (Markin, 1970). Perhaps our observation of transient labelling of fire ant queens with radioactive oil is attributable to such donating behaviour.

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