Control of food influx by temporal subcastes in the fire ant, *Solenopsis invicta*

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Summary. Temporal subcastes in the fire ant, *Solenopsis invicta* Buren were selectively starved to determine if foragers could assess the nutritional status of their nestmates and respond accordingly. We found that starved foragers increase the honey entering the colony (Fig. 1). When nurses are starved more oil and liquid egg yolk enters the colony (Figs. 2, 3) and when both reserves and nurses are starved, more egg yolk powder is brought in by the foragers (Fig. 4). When queens are starved, more liquid egg yolk and oil enters the colony (Figs. 2, 3). Starved larvae increase the oil in the colony (Fig. 2) and when held with nurses for 24 h before feeding, increase the egg yolk powder brought in and receive significantly more of it than other subcaste members (Fig. 5). We conclude that foragers can respond to the nutritional needs of their nestmates. Based on our behavioural observations, the quantity of food brought in by the foragers is regulated via discriminatory solicitation by reserves in response to the nutritional needs of the nurses.

Introduction

The exchange of liquids among members of a social insect colony, called trophallaxis, plays a key role in its social organization (Wilson 1971). In the majority of social insects trophallaxis is an open-ended system, i.e., each worker will share food with an unlimited number of nestmates (Wilson and Eisner 1957). These repeated exchanges keep the workers informed of the nutritional state of the colony as a whole and keep the needs of the colony uniform. The importance of these inter-

actions has been described in honeybee colonies (Michener 1974). The speed with which a forager can unload her nectar to house bees will determine her subsequent foraging activity. If her nectar is actively solicited, she will recruit other bees and return to the food source. If delivery time is longer she ceases to recruit to that food source. The receivers also control the quality of nectar brought into the hive and, in a similar manner, the flow of pollen. Lindauer (1961), reviewing his studies and those of Kiechle (1961), concluded that bees from the brood area are able to stimulate foragers to switch from food gathering to water gathering in response to increasing hive temperature, again by discriminatory solicitation of water laden foragers. Ohguchi and Aoki (1982) concluded that foraging selectivity in honeybees is a compromise between two conflicting colony needs, one for sugar and one for water.

In the present study we investigated the possibility that a similar exchange of information on the nutritional status of certain workers might influence foraging activity in ants. Many aspects of the distribution of food among nestmates in different ant species and the factors affecting it have been studied (Sudd 1967; Wilson 1971; Abbott 1978; Sorensen and Vinson 1981). Carbohydrates are mainly used by foragers (Wilson and Eisner 1957; Schneider 1972), lipids by workers and some larvae (Echols 1966) and proteins by growing larvae and egg laying queens (Lange 1967). Brian and Abbott (1977) confirmed, in *Myrmica rubra,* the existence of a 'gradient of hunger' from foragers to larvae via the nurses. Other studies on effects of starvation on trophallaxis in ants include those on *Formica polyctena* (Schneider 1966; 1972), *Iridomyrmex humilis* (Markin 1970), *Formica fusca* and *F. sanguinea* (Wallis 1961; 1962; 1964), *Monomorium pharaonis* (Sudd 1957), *Solenopsis invicta*

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(Howard and Tschinkel 1980) and *Tapinoma erraticum* (Meudec and Lenoir 1982). However, none of these studies compared the effects of selective starvation of temporal subcaste members on different food types. In the present study, we looked at the effects of these factors on the fire ant, *Solenopsis invicta* Buren.

S. invicta workers are weakly polymorphic (Wilson 1978) with a temporal division of labour. There are two behaviourally discrete temporal castes, nurses and foragers, and a third transitional phase, reserves (Mirenda and Vinson 1981). Workers typically progress from nursing to nest maintenance to foraging. Our previous research showed that a worker's response to food is related to its current career (Sorensen et al. 1983a). In this study we examined how the state of hunger of temporal subcaste members affected the quantity of food brought into the colony.

Methods

Ants used in these studies were from 18 polygynous colonies collected in College Station, Texas. Laboratory maintenance procedures were as described previously (Sorensen and Vinson 1981). In order to separate foragers, nurses, and reserves, colonies were transferred to behavioural distribution nests (Sorensen et al. 1981) and held at 28° C on a 14:10 light:dark regime and fed daily with mealworms, crickets, and honey water. Subcastes were then separated by location (Sorensen et al. 1981) and marked with fine coloured wires (Mirenda and Vinson 1979). Small splinter colonies were used for studies to permit differential marking of subcaste members. Ants to be starved were separated by subcaste and approximately 300 of these workers placed in a plastic cylinder (7 cm high, 10 cm diameter) with a dampened castone base. They were held 3 d without food. The remaining subcastes in each trial were left in the behavioural nest and fed mealworms, crickets, and honey water daily until separation immediately prior to the experiment.

The effects of selective starvation on subcaste members were tested in splinter colonies containing 20 foragers (F), 20 nurses (N), 20 reserves (R), 50 larvae (L) and 1 queen (Q). They were placed in two stacked clear plastic cylinders (7 cm high, 10 cm diameter) with the upper chamber as a foraging chamber and the lower as a brood chamber for 15 min before testing. We tested splinter colonies where one subcaste was starved while all of the remaining subcastes were well-fed. Two controls were also evaluated where all ants were well-fed or all ants were starved. In both controls, all three subcastes were separated during starvation and either starved or well fed as described previously. Three replicates of each combination were done, each time using ants from a different polygynous colony.

The responses of starved subcastes to four different food types, three liquid and one solid, were tested, each with three replications. Food was introduced into the foraging chamber on glass depression slides, either 20 mg egg yolk powder, or 20 µl of either egg yolk powder mixed with water (1:3), a 50% solution of honey water, or a mixture of sunflower oil:peanut oil:soybean oil (1:1:1). Foods were mixed with Iodide-labeled albumin as a nonvolatile radiolabel, undetectable to workers in the quantities used (Sorensen and Vinson 1981). After 1 h of feeding, the ants were killed by freezing. All ants had access

Table 1. Overall mean quantity of food retained by each subcaste member. Duncan's Multiple Range Test compares quantity of food retained by subcaste members for each food. Means followed by the same letter are not significantly different at the $P=0.05$ level, from other subcastes in that column

Subcaste	Honey µl	Oil µl	Liquid egg µl	Egg powder µg
Foragers	3.27a	0.52b	0.24a	1.46ab
Nurses	1.93b	1.31a	0.26a	1.85a
Reserves	1.86b	0.48b	0.14b	1.04b
Queens	1.84b	0.29b	0.13bc	0.56b
Larvae	0.09c	0.14b	0.05c	1.26b

to the food but only foragers and a few reserves were observed in the foraging chamber. Radioactivity was measured individually using a Searle 1195 series gamma radiation counter. To determine the quantity (µg or µl) of food consumed by each ant, we subtracted the background radiation and compared this value to that of a volumetric series of labeled food standards.

Although workers were able to quickly communicate hunger by soliciting food from returning foragers, we felt that larvae might require a longer period of time to communicate hunger to nurses. Therefore, using egg yolk powder, we held starved larvae with nurses in splinter colonies for 24 h instead of 15 min before testing and compared these with well-fed larvae held with nurses for 24 h. We also held starved nurses alone for 24 h in splinter colonies before testing since nurses may have been responding to lack of food from larvae and thus, in effect, their own hunger (Sorensen et al. 1983b). The mechanisms by which starved subcaste members could influence food flow were examined by observing the behaviour of starved nurses and contrasting it with that of well-fed nurses.

Statistical analyses were done using the Statistical Analyses System (SAS) for computer data analyses. A general linear model (GLC) procedure was used to determine whether replications could be combined and whether a significant amount of the variance could be accounted for by using amount as a dependent variable. Effects of selective starvation of subcastes on food brought back and its subsequent distribution were then assessed using an analysis of variance and Duncan's multiple range test for means.

Results

A summary of the overall distribution of food types among colony members is given in Table 1. It shows the mean quantity of food retained by each subcaste member in µg or µl regardless of state of hunger. Foragers retained significantly more honey than other subcastes with larvae receiving negligible amounts. Nurses retained significantly more oil than other subcastes and again, larvae received very little. Both liquid and powdered egg yolk were retained primarily by nurses and foragers but the latter was also given to larvae in appreciable quantities.

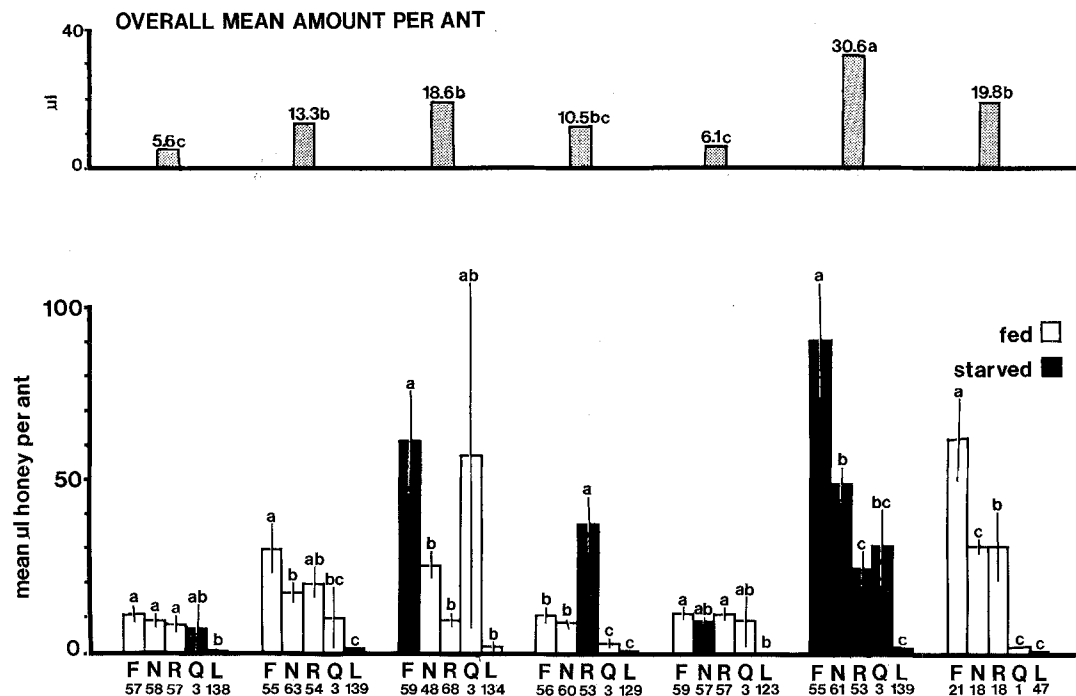Figure 1 shows the effects of selective starvation of subcaste members on honey. Foragers

Fig. 1. Results of selective starvation of temporal subcaste members on the distribution of honey. Subcastes tested were foragers (F), nurses (N), reserves (R), queens (Q), and larvae (L). The total number tested is shown below each subcaste. Black shading indicates which subcaste was starved. Bars with the same letter above them are not significantly different from other subcastes in that treatment at the $P=0.05$ level. Standard error ($+2$ SE) is given by lines. Overall mean amount per ant is given directly above in the upper graph. Bars with the same letter above them are not significantly different at the $P=0.05$ level

brought back significantly more honey when all colony members were starved than when all were fed. With the exception of splinter colonies with starved reserves, the foragers retained as much or significantly more honey than other subcaste members. When either nurses or queens were starved, the honey per ant was significantly less than when the entire colony was fed, suggesting a possible suppression of foraging activity. The queen received more honey when foragers were starved than she received in other treatments. The larvae received less than 3% of the honey regardless of the condition of colony members but starved larvae received 2% of the honey compared with 0.2% in well-fed colonies.

Figure 2 shows the response of colony members to oil following selective starvation. Significantly more oil was brought back to the colony in response to starved nurses, queens, and larvae than in other treatments. Oil in the colony following starvation of all members was not significantly higher than that in well-fed colonies. Starved reserves retained more oil than reserves in well-fed colonies or in starved colonies. When either nurses, queens, or larvae were starved, oil in the nurses was higher than in other subcastes. Starved queens received negligible amounts of the oil compared

with those in well-fed colonies, or in colonies where nurses or larvae were starved. Starved larvae received 19% of the oil but less than 4% of the oil in the other treatments.

The distribution of liquid egg is shown in Fig. 3. Compared with all other treatments, starved nurses significantly increased the mean liquid egg yolk per ant. The least liquid egg yolk per ant was observed in colonies with starved reserves. Starved foragers contained more liquid egg yolk than foragers in well-fed colonies or in starved colonies. Starved nurses also contained more liquid egg yolk than nurses in well-fed colonies or in starved colonies. In contrast, starved queens received less liquid egg yolk than queens in colonies where all subcastes were well-fed or starved. Starved larvae received 7% of the liquid egg yolk but only 3% in well-fed colonies.

Figure 4 shows the effects of selective starvation on the distribution of egg yolk powder. Again, starved nurses significantly increased the mean egg yolk per ant compared with all other treatments. The mean egg yolk per ant in response to starved reserves was significantly greater than that found in the remaining treatments. The foragers contained as much or more egg yolk than other subcaste members in colonies where all subcastes were
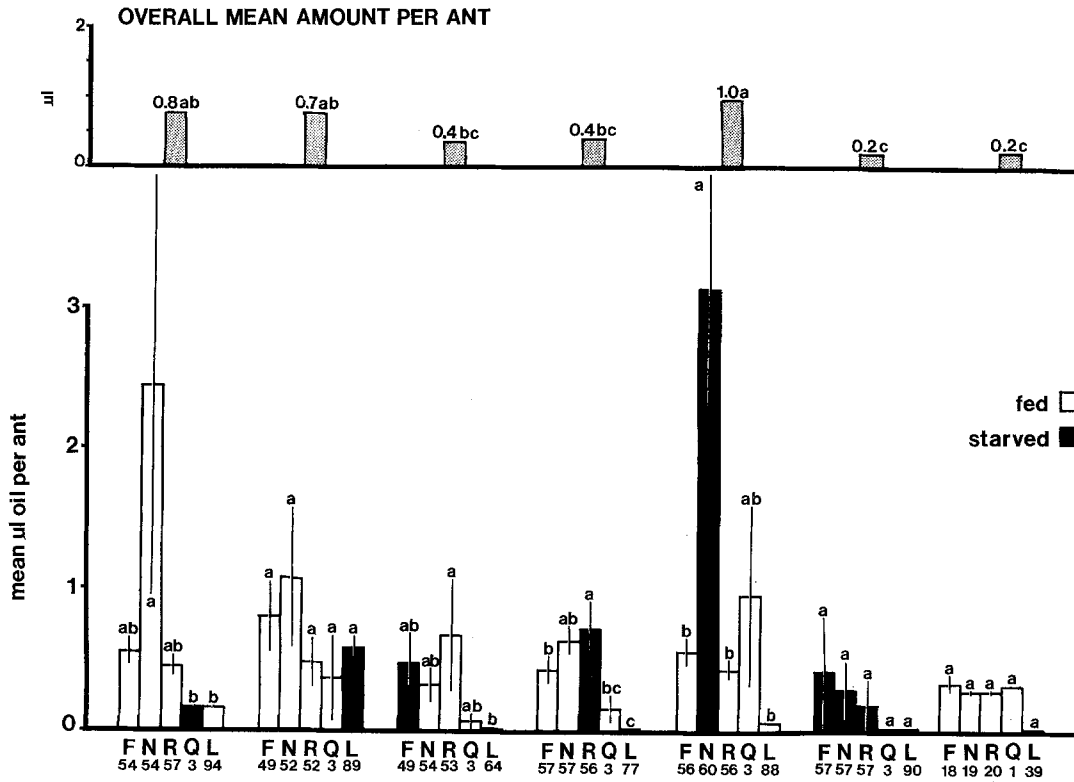
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Fig. 2. Results of selective starvation of temporal subcaste members on the distribution of oil. See Fig. 1 for description
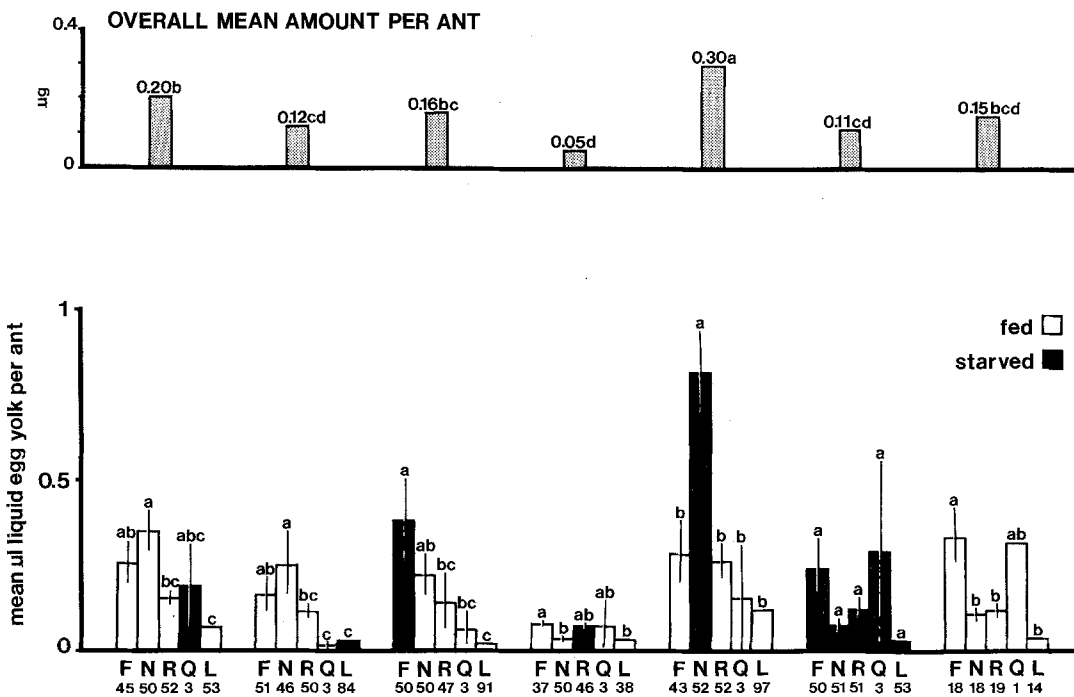

Fig. 3. Results of selective starvation of temporal subcaste members on the distribution of liquid egg yolk. See Fig. 1 for description
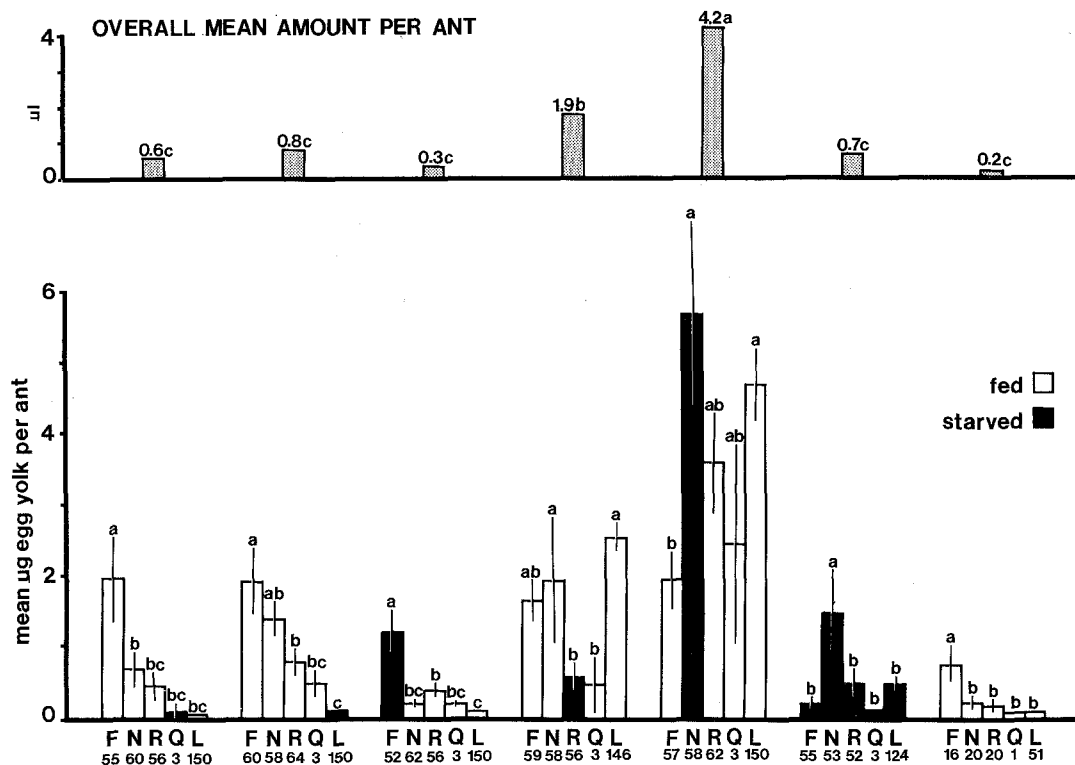
Fig. 4. Results of selective starvation of temporal subcaste members on the distribution of powdered egg yolk. See Fig. 1 for description

fed or where foragers, larvae, or queens were starved. Larvae received more egg yolk when reserves or nurses were starved than in all other treatments. Queens received none of the egg yolk when all subcastes were fed but received appreciable amounts when either nurses, foragers, or larvae were starved.

When starved larvae were held with workers for 24 h instead of 15 min, the egg yolk powder entering the colony was equivalent to that solicited by starved nurses (Fig. 5). In addition, the starved larvae received significantly more egg yolk than reserves, nurses, or foragers in their colonies.

We observed the behaviour of well-fed and starved nurses in splinter colonies which received egg yolk powder. In colonies with well fed nurses, the nurses remained inside the brood chamber during the foraging activity, which lasted only 10 min. The nurses received some food from reserves who contacted them after feeding on egg yolk powder brought back and left on the nest periphery by the foragers. They did not actively solicit food from the reserves. Returning foragers remained in the nest after depositing the egg yolk and groomed themselves. In contrast, when nurses were starved, they left the brood chamber and actively solicited food from both reserves and foragers. Food from returning foragers was immediately taken by either
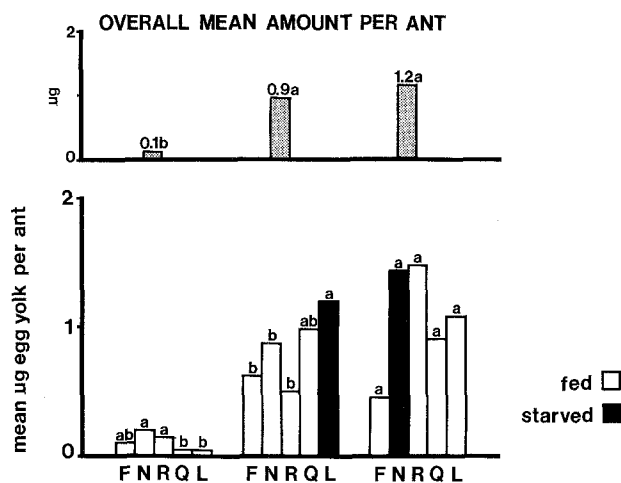

Fig. 5. Results of holding starved larvae with nurses 24 h prior to feeding. See Fig. 1 for description

reserves or nurses and relayed into the brood chamber. Foragers repeatedly returned to the foraging chamber for a 1 h period. Nurses that did not actively solicit food fed on egg yolk that had been deposited in the brood chamber.

Discussion

The food entering a social insect colony is brought in by a small percentage of its workers (Abbott

1978). For maximum efficiency of food utilization, these foragers must continually assess the nutritional status of the colony. In honeybees this is accomplished by the discriminatory solicitation of returning foragers by the house bees (Michener 1974). In ants, workers may be either active or passive donors or receivers of food (Sudd 1967). The probability of a worker being a donor or receiver is based partly on its age (Wilson 1971; Meudec and Lenoir 1982) and partly on the response of its nestmates (Sudd 1967). Whether a donor or acceptor initiates an exchange depends on the relative strengths of the motivation of the two participants (Wallis 1961). Howard and Tschinkel (1980) showed that food donors can play the active role in trophallaxis depending on the relative degree to which the donor and its respective colony have been starved. Wilson (1971) felt that the selection of food type is determined by the acceptor rather than the donor. A study by Brian and Abbott (1977) later showed this assumption was correct. We studied the selective starvation of temporal subcastes to determine how responsive fire ant foragers were to colony needs.

We found differences in the overall distribution of food types that indicated that foragers might be responding to the needs of nestmates. These differences agreed with those found by other researchers (Howard and Tschinkel 1980, 1981a; Sorensen and Vinson 1981; Sorensen et al. 1981). Howard and Tschinkel (1980) showed that colony size affects the distribution of food and that extrapolation from studies on small colonies might not be applicable to larger colonies. Mirenda and Vinson (1981) found that smaller colonies send out proportionately more foragers than larger colonies because their workers are more accessible to recruitment signals. Since we used small splinter colonies we cannot conclusively state that all of our results are applicable to very large colonies.

We found that foragers contained significantly more honey overall than other subcastes. When starved they contained less honey than foragers in well-fed colonies but this was due to differential feeding of queens. Howard and Tschinkel (1981b) found that sugars are shunted quickly into the forager's midgut. Shunting was probably of limited significance here since workers could make repeated forays to food. However, the retention of honey by foragers may have been reinforced by their passive behaviour. In a related study we found that foragers, in reponse to honey, were largely passive donors (Howard and Tschinkel 1980) and would often try to donate honey only

to give way to more aggressive workers and accept it instead (authors, unpublished data). The effect of foragers on oil was minimal. They showed only a slight tendency to retain oil in response to their own hunger, bringing in significantly more oil in response to starved nurses, larvae, or queens. They also showed a slight tendency to retain liquid egg yolk when starved, but again brought in significantly more egg in response to starved nurses. With egg yolk powder they transferred more egg when starved than their controls in well-fed colonies, indicating that they might have been responding to their own hunger by transferring more egg yolk to colony members. Brian and Abbott (1977) found that sugar-starved foragers of Myrmica rubra give priority to providing prey-hungry larvae with prey juice rather than sugar.

Starved reserves contained honey and, to some extent, oil and liquid egg yolk. However, they transferred egg yolk powder to other subcaste members. Reserves act as a relay system for food brought into the colony, soliciting food from returning foragers and transferring it to nurses (Sorensen et al. 1981). This relay system is especially evident in response to solid protein. In a division of labour study, we found that reserves were more active (versus passive) in donating and receiving food than were other subcastes, reflecting this role in relaying food (A. Sorensen, unpublished data). Since they are the most likely workers to encounter returning foragers (Mirenda and Vinson 1981; Sorensen et al. 1981), they must respond to both their own hunger and that of nurses by soliciting the necessary food items. Older reserves will also forage to a limited extent (Mirenda and Vinson 1981). We have found that up to 25% of marked reserves will respond to colony needs by actively foraging for food (A.A. Sorensen and S.B. Vinson, unpublished data).

We found that starving the nurses resulted in increasing the quantity of liquid egg yolk, egg yolk powder, and oil brought into the colony, foods used by growing larvae (Sudd 1967). After 1 h, the nurses contained most of these foods. Howard and Tschinkel (1981a) suggested that workers retain amino acids either for energy or for forming glandular secretions as well as feeding them directly to larvae. Our study showed nurses largely controlled the flow of proteins and oil in the colony, either for their own use or to feed to the larvae. Starved nurses and queens appeared to suppress foraging activity for honey, although this may have been an artifact of experimental design since different colonies were used for replications. A colony's

preference for food type can change with time (Glunn et al. 1981) and is influenced by differences in foragers' food preferences (Lenoir 1979).

Starved queens had a noticeable effect on liquid egg yolk and oil entering the colony. Since these foods were also actively solicited by nurses, this may indicate that nurses were responsive to the queens. Queens also received more honey when starved than their controls in well-fed colonies. Brian and Abbott (1977) found that queens influence the passage of food in *Myrmica*. However, Howard and Tschinkel (1981a) found that fire ant queens are not fed preferentially but are more likely to be fed in colonies with extensive food sharing than in colonies with limited food exchange. Our results may merely reflect extensive food sharing.

Starved larvae increased the oil entering the colony as did queens and nurses. In each treatment they received slightly more food than did their controls in well-fed colonies. They received significantly more food when they were held for a longer period of time with the nurses. Brian and Abbott (1977) found that hungry *Myrmica rubra* larvae induce nurses to demand and receive prey juices from foragers. The head of a larva elicits some foraging activity but most is due to the larva's ability to continually absorb prey liquids. In fire ants, larval feeding is encouraged by positive feedback from well-fed larvae in the form of larval secretions (Sorensen et al. 1983b). Our results indicated that the response of nurses to starved larvae was rapid and increased with time.

In three of the four foods tested, the unstarved and starved controls were similar. This finding was not expected since selective starvation of subcastes did result in increased uptake of food. It may indicate that 3 d was not sufficient to decrease the overall food retained by colony members. It is possible that the reserves, which act as short term food storers for the colony (Sorensen et al. 1983a) actively exchanged food during this period and kept the level of food high enough among subcaste members so that increased food solicitation was not necessary.

In summary, our studies showed that fire ant foragers responded to the nutritional needs of their nestmates. Nurses were never observed in the foraging chamber during this study so that they were not responding directly to the needs of nestmates by foraging themselves. Mirenda and Vinson (1981) and Sorensen et al. (1981) found that fire ant nurses never forage and our other studies have confirmed this (authors, unpublished data). Older reserves in transition to a foraging career will re-

spond to colony needs by foraging to a limited extent although in most instances they are recruited and do not forage on their own initiative (Mirenda and Vinson 1981). Our behavioural observations showed that starved nurses actively solicited food from reserves and that this resulted in increased food solicitations by reserves and increased foraging activity by foragers. This leads us to speculate that quantities of food brought in by the foragers were regulated via discriminatory solicitation by reserves in response to the nutritional needs of the nurses.

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