

INTERNAL DISTRIBUTION OF LIQUID FOODS IN ISOLATED WORKERS OF THE FIRE ANT, *SOLENOPSIS INVICTA*

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Abstract—(1) Workers of different size classes of the fire ant, *Solenopsis invicta* were fed radiolabelled liquid foods and later their crop and other body parts were monitored for distribution of radioactivity. A multifactorial design was used to test the manner in which worker-size, food-type and isolation time affect internal food-storage.

(2) Large workers tend to ingest more aqueous foods than do smaller workers but on an ant-weight basis, foragers of different sizes do not differ significantly in consumption of a particular food.

(3) When isolated, foragers tend to retain ingested oil for longer periods than sugar-water or amino acid solutions.

(4) Small ants are least suited for prolonged storage of sugar-water, and their crops retain a smaller proportion of ingested amino acids than do larger workers. While this supports the hypothesis that large workers serve as a trophic caste, behavioural tests are required for confirmation.

(5) Amino acids are retained in the crop longer than sugar-water and evidence suggests that sugar passes to the midgut more rapidly.

INTRODUCTION

LIQUIDS comprise a major portion of the diet in many social insects, yet the nests of only a few feature honeycomb or similar structures for the storage of fluid foods. Ant species that rely on nectar, honeydew, or prey fluids withstand starvation by sharing liquid foods stored in distensible, non-digestive crops of colony members. Crop fluid can be passed to the worker's own midgut or may be shared with nestmates via trophallaxis (EISNER, 1957; WILSON, 1971). There is little work on physiological aspects of food storage in the crop, even though fluid storage is linked with the socially significant capacity for trophallaxis. The ability of workers to store and share liquids varies radically among ant species and is correlated with feeding habits (WILSON and EISNER, 1957; GÖSSWALD and KLOFT, 1963) and the functional morphology of alimentary structures (EISNER, 1957; EISNER and BROWN, 1958; EISNER and HAPP, 1963). Fluid storage is most highly developed in ant species with 'replete castes', workers whose gasters can swell with food far beyond the limits of their foraging sisters and whose function is limited to food storage (*sensu* WILSON, 1971). Even species lacking a true replete caste may contain groups of workers more predisposed to serve as food-storers. For example, in *Campanotus fraxinicola*, major workers store more sugar-water when it is plentiful and regurgitate it to others more readily when it is scarce than do minor workers (WILSON, 1974).

The imported fire ant, *Solenopsis invicta* Buren has

been the subject of several studies of trophallactic food flow (WILSON and EISNER, 1957; VINSON, 1968; O'NEAL and MARKIN, 1973; HOWARD and Tschinkel, 1980) but only sparse and somewhat conflicting information exists regarding the storage capabilities of workers in this species (RICKS and VINSON, 1972; GLANCEY *et al.*, 1973; WENDEL and VINSON, 1978; WILSON, 1978). *S. invicta* is a weakly polymorphic species but workers in mature colonies show considerable variation in size, with the majority of ants belonging to smaller size classes (WILSON, 1978; WOOD and TSCHINKEL, 1980). We were interested in determining whether there exists a relationship between the size of fire ant workers and their physiological ability to store fluids internally. Further, if size-related differences in food-storing do exist in this species, do such relationships vary with the type of fluid being stored? We fed radio-labelled fluids to fire ant workers and after various periods of isolation, monitored the ants' body parts for the distribution of radioactivity. A factorial design simultaneously tested the effect of three types of food, three size classes of workers, and three periods of isolation.

MATERIALS AND METHODS

Mature fire ant mounds were collected in July, 1977, near Tallahassee, Florida. The queen and 10,000 randomly chosen workers were transferred to a permanent laboratory nest enclosed within an escape proof foraging arena.

Preliminary food-preference tests on 12 colonies produced three nests whose foragers would readily accept all three test liquids. These colonies received

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1 M sucrose and chopped mealworms (*Tenebrio molitor* and *Zophobas rugipes*) *ad lib.* for two weeks, followed by a one week starvation period. Starved colonies can vary greatly in brood cannibalization, therefore the test colonies contained no brood.

A factorial design was adopted since it provided a method of testing for both independent effects of three test factors and for interactions of the factors. For each factor, three conditions (levels) were tested, as below:

(1) Food type

Three liquid foods (3 levels), radio-labelled with ^{125}I to yield specific activities of roughly 0.1–0.3 micro Curries/microlitre, were used: (a) 5% sucrose with Na ^{125}I ; (b) 1:10 casein hydrolysate (Casamino acids) with Na ^{125}I ; and (c) unrefined soybean oil with bound ^{125}I by the method of STANLEY and THANNHAUSER (1949) and diluted to the required specific activity with non-labelled soy oil. Fluids were placed in the foraging arena on small squares of filter paper between matching pieces of glass, thus limiting the zone of availability to the edge of the blotter and reducing external worker contamination. Each colony was offered the three foods one at a time, in random order. When necessary, the blotters were replaced with fresh ones to avoid evaporative concentration of the liquid.

(2) Worker size

Workers that had clearly fed were randomly selected as they departed the food, but all foragers contacting the labelled food were collected to prevent possible contamination of the remainder of the colony. Fed workers were classified into one of three head width groups (HW, measured as distance between lateral extremes of the compound eyes): (a) small—HW < 0.75 mm, (b) medium—0.8 < HW < 1.05 mm, and (c) large—HW > 1.10 mm.

(3) Sample time

Captured workers were briefly rinsed in water and dried between loose tissue to remove external contamination. Each ant was randomly assigned for sampling of radioactivity to one of three times after

feeding: (a) 0 hr (immediately after patting dry), (b) 6 hr and (c) 24 hr. Ants assigned to (b) or (c) were held in isolation in small stoppered test tubes containing moist hardened plaster of Paris flooring.

There was a total of 27 treatment combinations (3 foods \times 3 sizes \times 3 sample times). Each combination was initially represented by 12 worker replicates but mortality sometimes reduced the sample size of some treatment blocks (maximum loss was 4).

At the appropriate time, each worker was killed in liquid nitrogen. While still frozen, the workers were separated into head, trunk and gaster. Crop contents were recovered by gently pressing the freshly thawed abdomen towards the petiole and collecting the expressed fluid onto a small piece of filter paper. The effectiveness of this method in providing the complete, uncontaminated crop contents was limited, especially with soybean oil due to its viscosity and the lipophilicity of the cuticle.

The body parts, crop contents and isolation nests were counted separately in a Packard Autogamma Scintillation Counter. Because the specific activities of the different foods varied somewhat, all counting rates were converted into volume equivalents of originally ingested food. Volume equivalents reflect relative rather than absolute amounts of food.

After counting, body parts were dried at 80°C for two days, pooled by replicate groups, and mean weights to the nearest 10 μg were determined for each part with a Mettler balance. These weights were used to calculate specific activities (volume equivalents/unit dry weight) of body parts from different treatment groups.

The data were computer-analyzed by SPSS programme for multifactorial analysis of variance. Where appropriate, the data were treated by transformations such as log-, squareroots- and ascisin squareroot percent-transformations.

RESULTS

The quantity of labelled food ingested was estimated by summing the volume-equivalents of radioactive

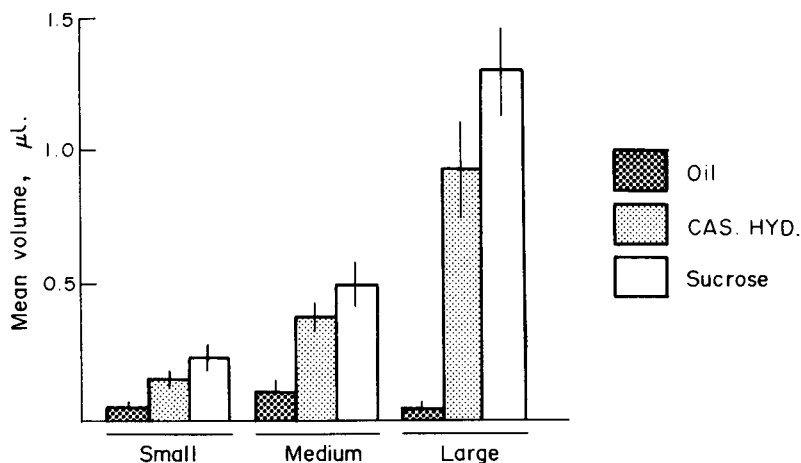


Fig. 1. Mean consumption of liquid food by *S. invicta* workers of three sizes. Each value shown is the mean for ants assigned to three sample times (\pm 2 S.E.).

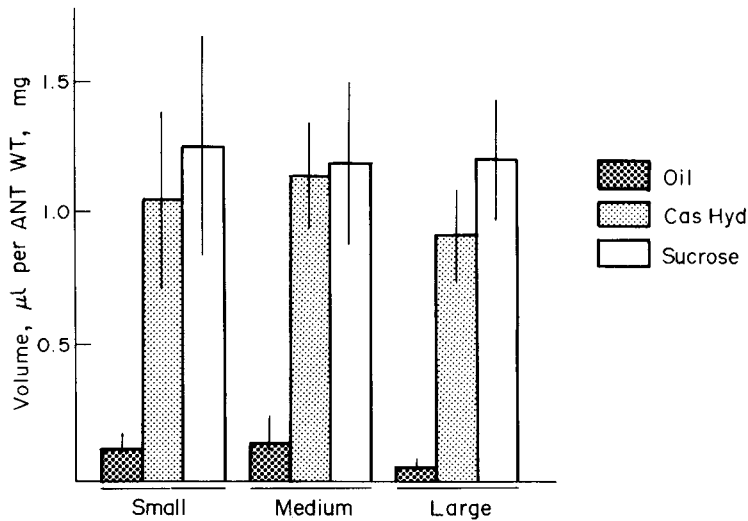


Fig. 2. Mean consumption of liquid food based upon the mean dry weight of foragers. Data are from the 0-hour sample only. Bars = ± 2 S.E.

food in an ant's crop and body parts and adding the volume-equivalents eliminated during isolation in the test-tube nest. A pilot study showed that this method of estimation generally agreed ($\pm 15\%$) with more direct, but less convenient methods of meal volume determination. The mean consumption values were obtained by averaging over the three sample times.

Foragers consistently ingested slightly greater amounts of sugar-water than casamino acids, and both aqueous foods were taken in much greater quantities than was oil (Fig. 1). The workers spent as much or more time feeding on oil as they did ingesting aqueous foods, yet oil consumption was comparatively small. The volume of aqueous meals increased markedly with worker size but oil consumption remained relatively low for workers regardless of their size (Fig. 1) Analysis of variance (ANOVA) indicated significant effects for food-type and worker size as well as a significant size \times food interaction ($P < 0.001$, for each).

The dramatic increase in meal volume with worker size suggested that large workers might be capable of ingesting a disproportionate amount of aqueous food. This was tested by comparing the ratio of volume ingested to dry weight of ant for different size-classes of workers in the 0 hour sample. Ants from this sample time were chosen because: (a) the ingested food was generally more available for drainage from the crop than at later times, thus the weight of the meal itself could be more easily separated, and (b) ants isolated for 6 and 24 hr might lose weight at different rates according to their size class, thus confounding estimations of their weight at ingestion. As shown in Fig. 2, the comparison on an ant-weight basis reveals that workers of all sizes ingested similar amounts of a given food. Thus, large workers do not take up disproportionately more fluid than do small workers.

During isolation, workers released only a small portion of their radioactivity into their nests, probably through regurgitation and/or excretion. Worker size was not significantly related to radioactivity retention, either as a main effect or in combination with other

factors. Thus, the degree of radioactivity retention was averaged for workers of different size classes. After 6 hr, on the average only 2–5% of the ant's radioactivity had been voided (Fig. 3). By 24 hr it became clear that radioactivity was being lost more rapidly from sugar- and amino acid-fed workers than from those fed oil (10–15% lost versus *ca* 5% lost, respectively). This contributed to a weak, but significant ($P < 0.05$) food \times time interaction.

An auxiliary experiment was conducted to determine whether a relationship between worker size and radioactivity retention would develop with a longer period of isolation. Various sizes of workers who had been starved for one week were fed a mixture of 1 M sucrose, 0.5% methylene blue and $NA^{125}I$. After counting their radioactivity, the fed workers were isolated for four days in small petri dishes with moist filter paper. Despite considerable scatter,

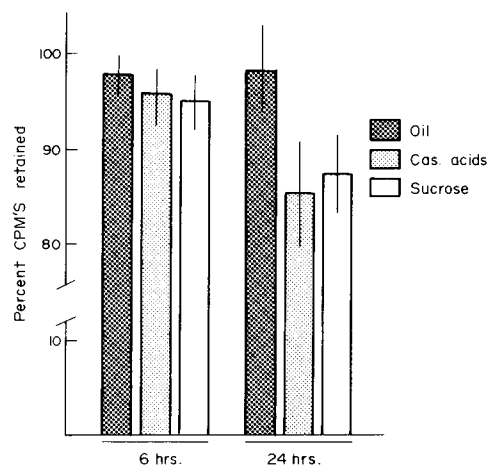


Fig. 3. Percentage of ingested radioactivity retained by isolated foragers. Percentages calculated as: (Volume Equivalents of food in ant at sample time) $\times 100$ divided by (Volume Equivalents in ant + Volume Equivalents recovered from nest).

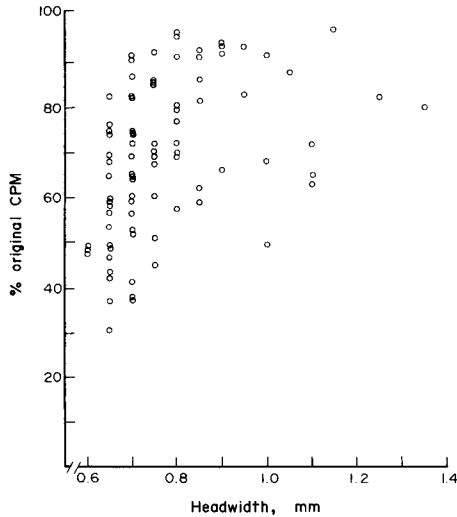


Fig. 4. Percentage of ingested radioactivity remaining in individual foragers of various sizes after 4 days in isolation.

workers displayed increased tracer retention with body size between headwidths of 0.6–0.8 mm (Fig. 4). The slope of the relationship is lower for larger workers. At least some of the food was regurgitated, for soon after isolation, some workers wiped droplets of blue liquid from their mouth parts onto the nest floor.

In order to study food storage in the crop, it was first necessary to determine the effectiveness of our crop-draining procedure. We assumed that immediately after an ant feeds (0 hour sample), most of the radioactivity in its abdomen is located in the crop. We

can estimate emptying efficiency by comparing radioactivity in the abdomen before and after draining the crop. For workers fed casamino acids, a mean of 84% of the abdomen's radioactivity was collected onto filter paper. For sugar- and oil-fed workers it was 71% and 60% respectively. Some of this residual radioactivity undoubtedly represented liquid we failed to remove from the crop. Oil is more viscous than aqueous food and therefore leaks less rapidly from the ruptured crop and is more difficult to squeeze from the crop. A portion of the residual radioactivity may be material that passed from the crop to the midgut and therefore not readily removable. In summary, the quantities of radioactive sugar or amino acids stored in the crop are adequately characterized by our method, but estimates of oil volume are less reliable and possibly low.

We were able to distinguish several important relationships between storage of food in the crop and the test factors. The fraction of a radioactive meal retained in a worker's crop depends on the type of food it has ingested (Fig. 5) (food main effect, $P < 0.001$). Workers fed casamino acids contained a greater fraction of the radioactive meal in their crop than did sugar-fed workers over the 24 hr sample period. Less oil appeared to be stored in the crop than in other regions of the body (Fig. 5). However, sampling may have underestimated the crop's oil content.

With increasing isolation time, the crop tended to retain diminishing proportions of the total body radioactivity (Fig. 5). For workers fed sugar or amino acids, a rapid decline in the crop's fraction of body radioactivity was noted between 0 and 6 hr, followed by only a slight-to-moderate decrease. All but the small, oil-fed workers showed a greater fraction of oil in the crop than did the 0 or 24 hr samples, contributing

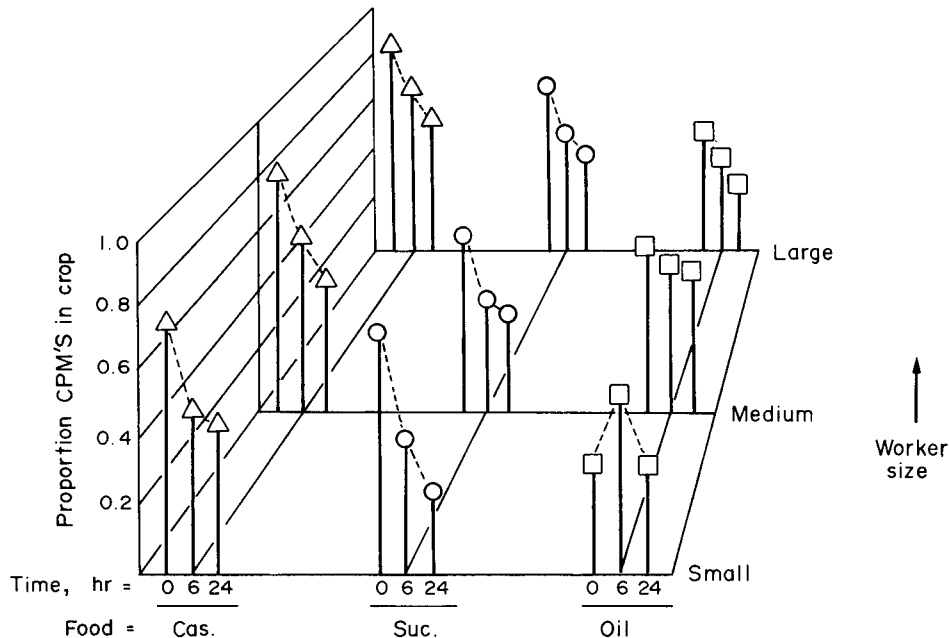


Fig. 5. Effect of three factors on the mean proportion of total ant radioactivity recovered from the crop. Sample times are sequentially arranged on the x-axis, the y-axis represents the dependent variable (proportion of radioactivity) and increasing size classes or workers are arranged along the z-axis. Triangles = casamino acid-fed workers; circles = sucrose; squares = oil.

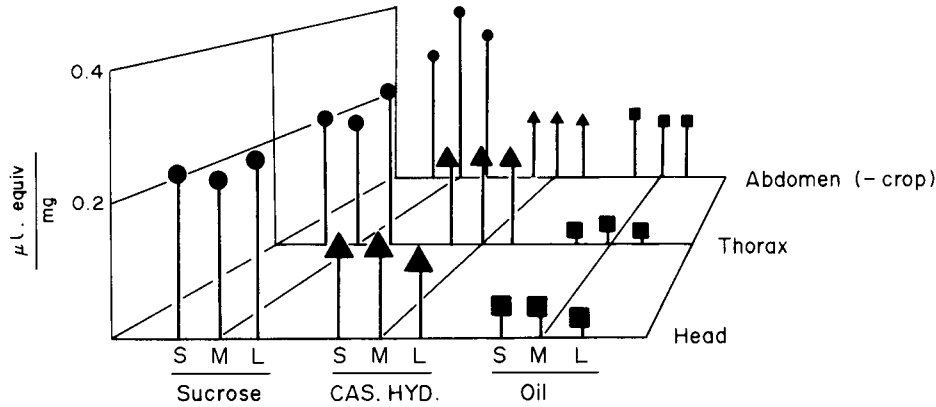


Fig. 6. Effect of food-type and worker size on the specific activity of three regions of the isolated body of the forager. Food types and worker size are arranged on the x-axis, the dependent variable is plotted on the y-axis, and the bodily regions are represented on the z-axis. Sucrose casamino acids, and soy oil are represented by circles, triangles and squares, respectively.

to a significant food \times time interaction ($P < 0.001$). The 6 hr group of small workers had originally ingested approx. twice as much oil as ants in the other time samples, and this may partially account for this discrepancy.

The crop's share of total body radioactivity also depended on worker size, but this relationship varied according to the type of food being stored (food \times size interaction, $P < 0.05$). For sugar, the relative amount in the crop was independent of worker size (Fig. 5). In the casamino acid-fed group, it increased gradually but consistently with worker size suggesting again that large workers can serve preferentially as a food storing class. For oil-fed ants the proportion in the crop was slightly greater for medium workers but these originally consumed more and this may be partly responsible for the higher proportion of label in the crop. In general, the influence of worker-size was less marked than was food type or sample time.

Workers held proportionately less sugar-water ^{125}I in their crops than casamino acids, even immediately after feeding on approx. equal volumes of these. We measured the distribution of labelled food in the head,

thorax, and abdomen after collecting crop fluid. Counting rates were normalized to volume equivalents per milligram dry worker. For convenience this measure will be referred to simply as 'specific activity'. Separate ANOVA tests were conducted for each of the three body regions.

Worker size was found to be the least consequential of three factors related to the specific activity of body parts. The head's specific activity did not vary significantly with worker size (Fig. 6), but thorax and abdomen did. The nature of this relationship varied for different foods (food \times size interactions, $P < 0.01$). The specific activities of these parts increased with worker size in sugar-fed ants and tended to either decrease slightly with size or remain equal in ants fed casamino acids or oil (Fig. 6). These relationships were stable with sample time and no significant sample time \times size interaction was found.

The specific activity of a body part depended on the type of ingested food. For each body region, the main effect for food was $P < 0.001$. Whole-body specific activity was always highest for sugar-fed workers, moderate for casamino acids and lowest for the oil.

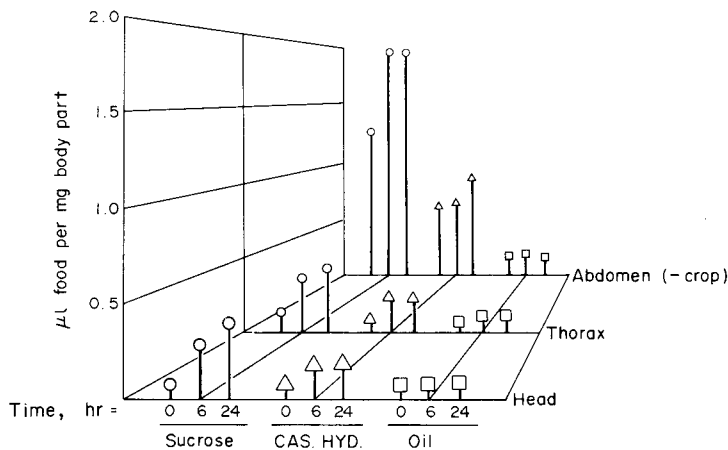


Fig. 7. Effect of food-type and sample-time on the specific activity of three body regions. Variables arranged as in Fig. 6, except sample-times are substituted along x-axis for worker size.

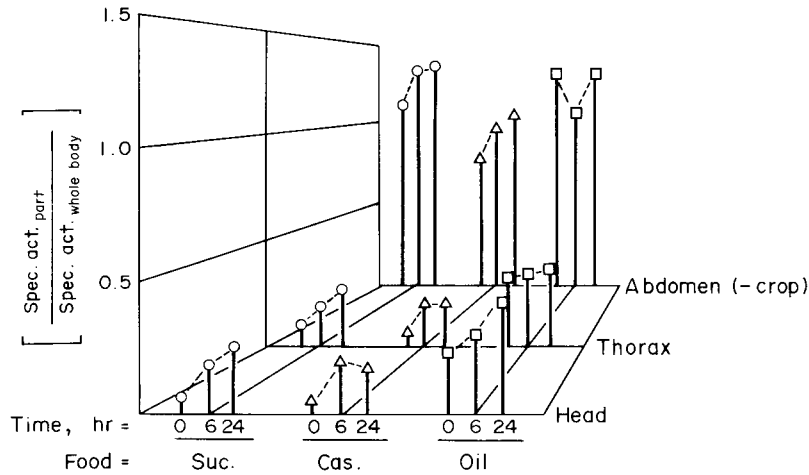


Fig. 8. Effect of type of food and sample-time on the normalized concentration of radiolabel in three regions of the body of the forager. Normalized concentration is the ratio of the specific activity of body part to the specific activity of the whole body. Food type and sample time are on the x-axis, and concentration is measured on the y-axis. Symbols as in Fig. 6.

(Fig. 6). This ranking is not surprising since the foods were ingested in the same order (see Fig. 1). However, in comparison to sugar-fed workers, the specific activities of the body parts of casamino acid-fed workers tended to be lower than could be accounted for by differences in ingestion and loss by regurgitation.

Sample time influenced specific activities of body parts in different ways for different foods (food \times time interactions: head- $P < 0.001$; thorax- $P < 0.001$; abdomen (minus crop)- $P < 0.02$). The level of radioactive oil changed very little with time in the three body areas (Fig. 7). The specific activities of all body parts increased with time for workers receiving aqueous foods, but at an appreciably higher rate for sugar-fed than for amino acid-fed ants. Generally, specific activity increased rapidly between 0 and 6 hrs and gradually thereafter.

All together these results suggest that workers internally store and distribute sugar-water in a different manner than casamino acids. Simple differences in consumption or loss cannot account for the disparity in specific activities between these two foods. The radioactivity decreased with time while that of the bodies increased, indicating that tracer is being absorbed (presumably via the midgut) and distributed to other areas of the body. That the rates of this increase are different for the two foods suggests: (a) that the tracer does in fact accompany food for part of its journey though the body and (b) that sugar-water is more readily used than amino acids. Finally, the 0 hr samples show that sugar-water may actually enter the midgut during or within a few seconds of ingestion.

To determine where in the body the tracer is concentrated, we compared the specific activities of each body part with the whole body specific activity. Values for this ratio, referred to as 'normalized concentration,' would be highest for ants with the weakest tendency to utilize their crops for storage and in those body parts which contain proportionately more label.

Normalized concentration was generally highest in the abdomen regardless of food type (Fig. 8). Uncollected crop fluid could account for part of this, but the increase in normalized concentration with time indicates that transfer of label from the crop is also responsible. Tracer concentration was higher in the heads and thoraces of oil fed workers than in those receiving aqueous foods. Oil accumulated at a greater rate in the head than the thorax.

DISCUSSION

Study of the digestive anatomy and physiology of trophallactic participants can give insight into physiological division of labour in ant societies. Although we have worked with isolated workers, there is little doubt that the fate of ingested food is affected by isolation or grouping. For example, the biological half-life of radioactive iodine is longer in grouped *Formica* workers than in isolated (GÖSSWALD and KLOFT, 1960). Despite the social importance of such 'group effects' much can also be learned about food-storage in isolated individuals.

We selected recruited foragers as test subjects. The behavioural roles of workers change with age, beginning as attendants to the brood (nurses), then shifting to other domestic chores, and gradually assuming duties outside the nest such as scouts or recruited foragers. Physiological and behavioural aspects of food-usage can change with age. For example, SCHREINER (1952) demonstrated that pollen is transferred from the crop to the midgut at a faster rate in foraging honeybees than in the younger nest bees. In incipient colonies of the ant, *Tapinoma erraticum*, older foragers may seek out and share sugary solutions whereas younger foragers tend to forage for and crop-store insect haemolymph (LENOIR, 1979). Workers of *Formica polyctena* who tend the brood crop-store prey haemolymph whereas the non-nursing workers store sugar solutions (LANGE, 1967).

Thus the results we obtained for recruited foragers may not characterize all the colony's workers.

Is worker-size important to the ability of fire ants to store food internally? Answers have been somewhat conflicting. RICKS and VINSON (1972) could find no evidence that either large or small workers are specialized for food storage, but GLANCEY *et al.* (1973) concluded that large fire ant workers serve as an oil-storage subcaste (described by them as a 'replete caste'). WENDEL and VINSON (1978) found that large *S. invicta* workers retain a greater proportion of juvenile hormone analogue in their crops than do the smaller workers, providing circumstantial evidence for the hypothesis of GLANCEY *et al.* (1973). However, WILSON (1978) points out that disproportionate survival of larger workers in long-term tests of GLANCEY *et al.* (1973) could create the illusion that they are better storers of oil than are small workers. A preliminary short-term experiment by WILSON (1978) indicated that small workers store the most sugar-water on an ant-weight basis. Overall then, food-storage in fire ant workers is far from clearly understood.

Our experiments suggest that both a worker's size and the type of food it eats are important to its ability to retain food. The rate at which sugar-water is lost is slower for large isolated workers than for smaller ants. Workers of all sizes lose ingested oil less rapidly than they do sugar- or amino acid-solutions, possibly because much less oil is ingested to begin with.

It was interesting to find that fire ant workers apparently stored a smaller proportion of ingested sugar-water in their crops than casamino acids. The effect may have been due primarily to differences in the volume of food ingested. Sugar-water was consistently taken in slightly larger amounts than amino acids, and perhaps through increased pressure on the crop, this surplus sugar was shunted into the midgut. Sugar- and amino acid-fed ants hold very similar volumes in their crops, despite differences in the total amount ingested.

A second hypothesis revolves around qualitative differences in the foods. *S. invicta* workers tend to share sugar solutions mostly among themselves but tend to regurgitate proteins (VINSON, 1968; SORENSON and VINSON, personal communication) and casamino acids to the larvae (HOWARD and TSCHINKEL, unpublished). It may be that workers refrain from utilizing casamino acids for their own nutritional needs preferring to store it for the larvae.

The ambiguity concerning the internal distribution of labelled soy oil was disappointing. Workers in different groups consumed minute but variable quantities of oil and these were difficult to harvest from the crop. The tendency for isolated workers to retain a greater fraction of labelled oil than aqueous foods may be due to the small amount of oil ingested. Foragers routinely consume less oil than aqueous foods, probably because the viscosity renders it difficult to swallow (HOWARD and TSCHINKEL, unpublished). Other preliminary studies in our laboratory have demonstrated a weakly positive relationship between forager-size and the volume of oil consumed. Lack of evidence for such a correlation in the present investigation is probably due to small sample size.

We found that oil becomes concentrated in the head possibly in the post-pharyngeal glands. These glove shaped structures connect with the buccal cavity and are known preferentially to absorb ingested oils or secrete lipids into their lumen (PEREGRINE and MUDD, 1974; DELAGE-DARCHEN, 1976; PHILLIPS and VINSON, 1980). Radiophosphate introduced with sugar-water can travel through the haemolymph and accumulate in these glands. Their secretions can drain into the crop and thus become available for eventual feeding to other colony members.

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