Comparison of Diets of Two Fire Ant Species (Hymenoptera: Formicidae): Solid and Liquid Components[1]

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ABSTRACT Diets of the red imported fire ant, *Solenopsis invicta* Buren, and the native fire ant, *Solenopsis geminata* [F.], were studied in adjacent field colonies in south central Texas. A comparison of solid food diets of the two species revealed a 59% overlap of identifiable arthropods and other solid food matter. The major difference was that *S. geminata* collected eight times more seeds than did *S. invicta.* Both species collected liquid food much more frequently than solid food; in fact, an average of 70-80% of successful foragers returned with liquid. Rates of liquid collection were approximately 40% higher for *S. invicta* than for *S. geminata.* Foraging rates fluctuated with season but the percent of successful foragers returning with liquid remained relatively constant. Plants and honeydew producing homopterans are the most probable sources of this liquid based on sugar and amino acid analyses of *S. invicta* foragers. Use of liquid carbohydrate energy sources helps explain how fire ant colonies can collect sufficient food to sustain extremely dense field populations.

KEY WORDS Insecta, *Solenopsis invicta, Solenopsis geminata,* diet, foraging, liquid food, solid food.

The introduction of the red imported fire ant, *Solenopsis invicta* Buren, to North America has resulted in the competitive exclusion and range reduction of many native ant species, including the native fire ant, *Solenopsis geminata* (F.) (Porter et al. 1988; Wojcik 1983; Glancey et al. 1976; Wilson and Brown 1958; Porter and Savignano 1990). Competition for food may be one important factor in the overall interaction between these two fire ant species. Differences in types of food, food sizes, foraging times, foraging territories, and temperatures at which foraging occurs have been documented in many studies of competition between sympatric ant species (Hölldobler and Wilson 1990).

Arthropods, both alive and dead, are an important part of the diet of *S. invicta* (Hays and Hays 1959; Wilson and Oliver 1969; Morrill 1977). The red imported fire ant preys on many pests such as the pecan weevil (Dutcher and Sheppard 1981), horn fly, and lone star tick (Oliver et al. 1979; Ali et al. 1984). Liquid food is also part of *S. invicta's* diet but it has previously been considered a minor component. *S. invicta* has been observed to tend aphids and scale insects (Green 1952; Hays

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and Hays 1959; Ricks and Vinson 1972a) and to collect nectar and other excretions from plants (Agnew et al. 1982). Wilson and Eisner (1957) documented the presence of liquid in the crops of *S. invicta* foragers. *S. invicta* occasionally attacks germinating seeds and young plants (Eden and Arant 1949; Adams et al. 1983; Smittle et al. 1983), but seeds generally constitute a very small part of the diet (Hays and Hays 1959; Wilson 1978).

In contrast, seeds are important in the diet of *S. geminata* (Travis 1941; Van Pelt 1958; Carroll and Risch 1984). Wilson (1978) goes so far as to classify *S. geminata* as a seed specialist. Nevertheless, this native fire ant is omnivorous, preys on many pest insects (Risch and Carroll 1982), and, like the imported species, "attacks and eats almost everything it encounters" (Wheeler 1910). Liquid food is also a component of the diet of *S. geminata;* ants have been observed tending coccids on the roots of grasses (Wheeler 1910; Van Pelt 1958) and tending aphids (Travis 1941).

The purpose of this study was to compare diets and foraging success rates of *S. invicta* and *S. geminata*, to investigate sources of the diets, and to examine uses of different food types by the fire ant colony. We had the opportunity to study these two species side by side in the same habitat. This study is the first to make a direct dietary comparison of the two species and quantitatively investigate liquid food collection. Dietary comparisons are an important step towards explaining how the imported fire ant is able to displace its native congener.

Materials and Methods

This study was conducted at the Brackenridge Field Laboratory (BFL) of the University of Texas in Austin, TX. The first set of colonies was located in an open field of native grasses (*Croton monanthoginus, Stipa leuchotrica,* and *Sorghum halpense,* with a few invading shrubs and scattered mesquite clumps). They were studied for a total of 10 weeks, from February through April 1987. Liquid collection was monitored from March through April 1987. Observations were made between 1400 h and 1800 h on three pairs of colonies, each pair consisting of one *S. invicta* and one *S. geminata* mound. Colonies within each pair were located no more than 6 m apart in the same habitat. Species vouchers were deposited at the Brackenridge Field Laboratory and at Harvard University's Museum of Comparative Zoology in Cambridge, MA. All *S. invicta* and most *S. geminata* colonies were polygyne, containing more than one functional queen (Porter et al. 1988; personal observation).

Nine large *S. invicta* colonies were studied at four additional sites around the Austin area in June 1989. The first site (three colonies) was monitored at four different time periods during the day: between 0600-0700, 1000-1100, 1600-1800, and 2200-2400 h. in order to investigate diel changes in diet. This site was another grassland at BFL dominated by *Stipa leuchotrica, Bothriochloa ischeum,* and *Solidago* sp. The next site (two colonies) was a rocky oak and juniper forest at BFL with a grassy edge of little bluestem and *Setaria* sp. The third and fourth sites (two colonies each) were located in Zilker Park; the first in a disturbed grassy field of *Sorghum halpense, Cynodon dactylon,* and *Bothriochloa ischeum* and the second in a well estblished native grassland of *Buchloe dactlyoides, Leptaloma* sp., and *Solanum* sp. Only *S. invicta* colonies were sampled because *S. geminata* had been virtually eliminated from the area by 1989.

Fire ants forage in underground tunnel systems which radiate out from the mound (Markin et al. 1975). These tunnels were exposed by digging a trench around the colony (20 - 40 cm from the mound and approximately 25 cm deep). A sheet of metal flashing (22 cm wide) was inserted vertically into the trench to prevent ants from digging new tunnels through the soil. The trench was then refilled with soil and capped with cement. This procedure forced foragers to form their trails over the top of the cement from which ants were easily observed and collected. Ceramic tiles were placed over the trails on the concrete to protect them from environmental exposure. Several trails per colony were sampled at least once a week for a period between 5 and 10 minutes. Incoming foragers passing a fixed reference point on the trail were carefully examined and the number returning with solid or liquid food was tallied. Air and soil temperatures were measured at each sampling.

Solid Food. The type of solid food material gathered was determined by collecting returning foragers carrying particles to the mound for one or two 30 minute collection periods each week. Foragers and particles from various foraging trails were collected with an aspirator and placed in 70% ethyl alcohol for later separation from the ants and identification. Prey were examined under a binocular microscope and identified to family whenever possible. All particles were visually classified into five size classes: (average length × width in mm ± standard deviation): I (1.3 ± 0.4 × 0.5 ± 0.2), II (2.0 ± 0.5 × 0.9 ± 0.4), III (2.7 ± 0.7 × 1.4 ± 0.3), IV (3.2 ± 0.5 × 1.9 ± 0.5), V (5.1 ± 1.4 × 2.8 ± 1.1). Mean weights of each class are shown in parentheses in Figure 3.

Liquid Food. Foragers carrying liquid were identified by a visibly enlarged gaster, which appeared "striped" because the abdomen was distended, exposing the intersegmental membranes. Dissection of the incoming foragers proved that those with enlarged gasters did indeed have a crop full of aqueous liquids. No outgoing ants exhibited an enlarged gaster nor contained liquid in the crop.

To measure the amount of liquid stored in the crop, outgoing ants with non-extended gasters and incoming foragers with enlarged gasters were collected from the three *S. invicta* and two of the *S. geminata* colonies. These ants were weighed on a microbalance (nearest 0.01 mg) and their head widths were measured with an ocular micrometer (nearest 0.02 mm). Dry body weights were also taken after foragers were dried for 24 hours at 65°C.

In June 1989, areas surrounding the nine study colonies were examined for root coccids and aphids by digging up 10 samples of vegetation (15 cm in soil diameter) in a circle around each colony and examining roots for homopterans and fire ants.

Analysis of Liquids. Liquid collected by *S. invicta* foragers from 15 field samples was analyzed for sugar content by using thin layer chromatography (Stahl 1969) to detect the presence and relative concentrations of fructose, glucose, and sucrose. Liquid in the crop was extracted by gently squeezing the gaster with forceps which forced the ant to regurgitate the crop contents. Liquid was collected in micro-capillary tubes, which were then sealed at both ends and refrigerated until analysis. Thirteen samples were taken from three field colonies. Nine samples were each composed of liquid from approximately ten small workers and four samples were each made up of liquid from ten large workers. To estimate concentrations and to test whether surcrose may have been broken down in the crop, 0.25, 0.5 and 1.0 M solutions of sucrose were fed to one field colony and three laboratory colonies. The crop contents were collected at least 20 minutes after feeding. Two samples of each concentration were analyzed for sugar contents.

Liquid collected by *S. invicta* foragers during June 1989 was quantitatively analyzed for amino acid content using a Beckman 121-MB Amino Acid Analyzer. Twelve samples were collected from five field colonies, three samples were collected from laboratory colonies fed 0.5 M sucrose solution, and three samples were from laboratory or field colonies fed freshly killed crickets or annelids. Each sample consisted of liquid from 1-15 ants (see Figure 4).

Results

Success Rates. Rates of liquid collection differed significantly between the two species despite the small number of paired samples (n = 3). *S. invicta* foragers returned more frequently with liquid than did *S. geminata* foragers (Fig. 1; $F = 18.6$; df = 1,2; $p < 0.05$; ANOVA blocked by pair; data square root-arcsine transformed). In contrast, the percent of workers returning with solid particles did not differ significantly between the three paired *S. invicta* and *S. geminata* colonies (Fig. 1; $F = 0.18$; df = 1,2; $p > 0.05$; analysis as above).

In both species, liquid food was retrieved much more frequently than was solid food (Fig. 1). An average of 40% of all incoming *S. invicta* foragers in the February - April time period were carrying liquid food compared to only 8% carrying solid food particles ($F = 176$; df = 1,2; $p < 0.01$; ANOVA blocked for colony, data square root-arcsine transformed). For *S. geminata,* rates of liquid retrieval averaged 28% versus 6% for solid food ($F = 13.2$; df = 1,2; $p > 0.05$; ANOVA as above). This was not significant due to the low number of degrees of freedom in the ANOVA. Between 50% and 70% of foragers of both species returned without any detectable food. In June 1989, average liquid collection by *S. invicta* dropped to 19% of incoming foragers and solid food collection to 4%. However, liquid collection was still five times as great as solid food collection and liquid constituted 78% of successful foraging trips ($F = 4.05$; df = 1,7; $p < 0.001$; ANOVA as above).

Temperature strongly affected the number of foragers on the trails; the average (during 10 minute count periods) increased gradually from zero at temperatures below 12°C to greater than 200 at temperatures near 35°C. The number of foragers per trail differed between the two fire ant species. Numbers of active *S. geminata* foragers per trail were always much less than those on *S. invicta* trails. Colony size may be one factor affecting these numbers, since *S. invicta* colonies were larger on the average than *S. geminata* colonies (Porter et al. 1988). Differences in the windows of suitable foraging temperatures of these two species needs to be further investigated since *S. geminata* seemed less likely to forage at cooler soil temperatures (<20°C) than *S. invicta* (Porter and Tschinkel 1987).

In contrast to forager numbers, foraging success rates of both species were basically independent of temperature. Liquid and solid food success rates were consistent for both species over the 7 week period (Fig. 1). However, success rates for both food types were lower in colonies sampled during June 1989 (Fig. 1), indicating variability between years, sites, and perhaps seasons. Although success rates were lower, rates of liquid collection were consistently higher than rates of solid food collection.

The ratio of *S. invicta* foragers collecting liquid to those with solid food was consistent between the different trails of each colony in June 1989 samples. Further-

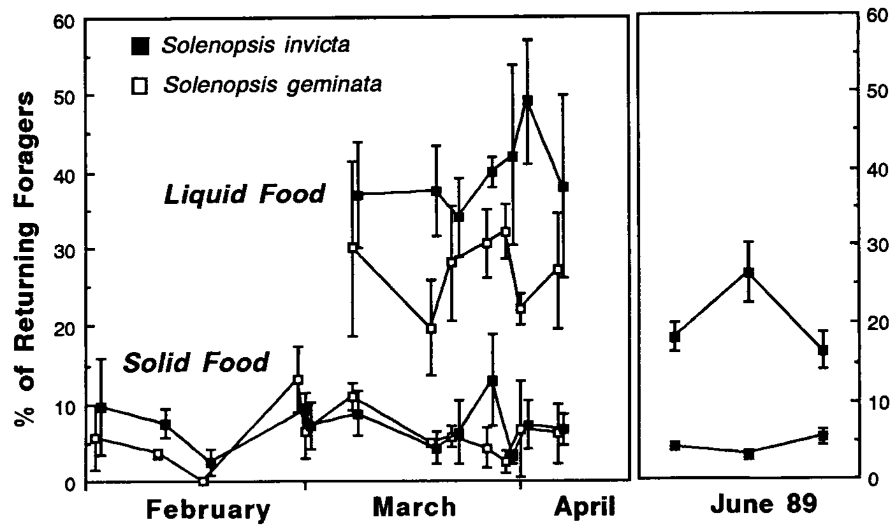

Fig. 1. Percentages of *Solenopsis invicta* and *Solenopsis geminata* foragers returning with liquid and solid food. Each point is the mean of three colonies. Standard errors are indicated for each sample date. Observations of liquid collection began in March.

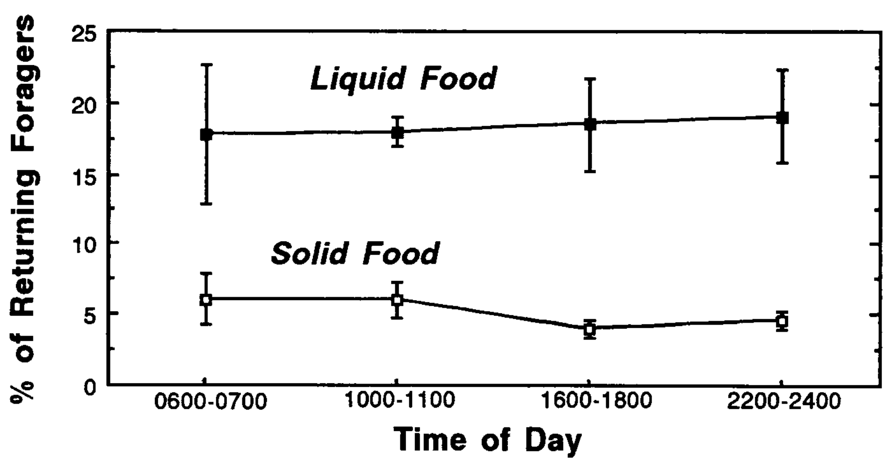

Fig. 2. Percentages of *Solenopsis invicta* foragers returning with liquid and solid food during four daily time periods in June 1989. Each point is the mean of three colonies. Standard errors are indicated for each sample time.

more, foraging success rates did not change over the course of a day (Fig. 2; two-factor ANOVA blocked for time; liquid: $F = 0.60$, $df = 1,6$, $p > 0.05$; solid: $F = 1.23$, $df = 1,6$, $p > 0.05$).

Solid Food. Overall, *S. geminata* collected larger food particles than did *S. invicta* (Fig. 3). Eighteen percent of the particles collected by *S. geminata* were of the two largest size classes compared to 7% in these size classes for *S. invicta* (Fig. 3). The average weight of particles retrieved by *S. invicta* was approximately 0.12 mg compared to 0.17 mg for *S. geminata* (calculated from Fig. 3). This difference is most likely due to the larger size of *S. geminata* foragers (average head width of 0.8 ± 0.1 mm versus 0.7 ± 0.08 mm for *S. invicta*) and to the greater number of large seeds in the diet of *S. geminata*.

For *S. invicta*, animal matter consituted 93.9% of the total solid food diet while plant material made up only 6.1% (Table 1). Seeds made up 78% of the plant material. Of the 521 items collected by *S. invicta*, the most abundant identified item was Collembola making up 11.4%. The second largest category was Coleoptera larvae, which in total constituted 4.8% of the solid diet.

Also important in the composition of foraging material were pieces of annelids, accounting for 4.2% of the collected matter. Spider parts (3.3%), Lepidoptera larvae (3.1%), Diptera larvae (2.3%), and Homoptera nymphs (1.9%) constituted the bulk of the remaining identified material. Unidentifable material made up 47.2% of the diet of *S. invicta*, most of which was probably composed of pieces of insects which were too large to be retrieved intact.

Solid food collected by *S. geminata* consisted of 68.6% animal material and 31.4% plant material (Table 1). In contrast to *S. invicta*, seeds comprised 94.3% of

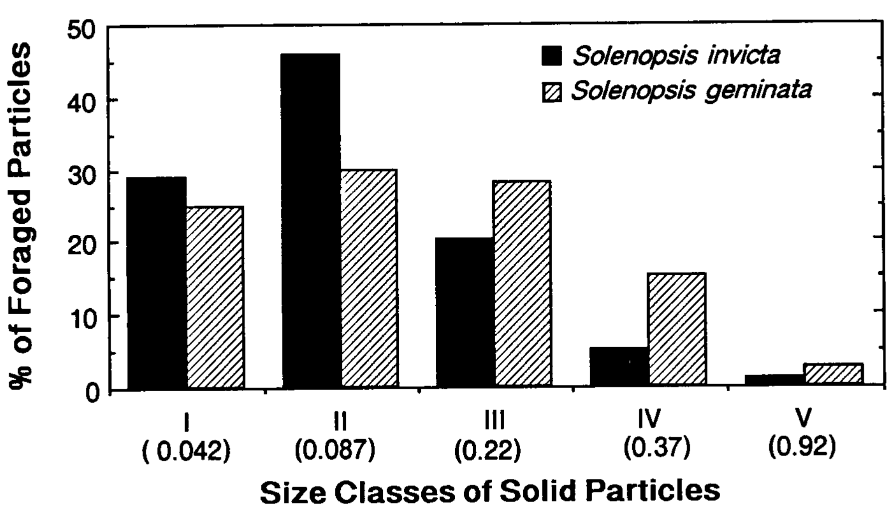

Fig. 3. Frequency distribution of particle sizes foraged by *Solenopsis invicta* and *Solenopsis geminata* workers. Mean weights (in mg) of particles in each size class are given in parentheses. Numbers of particles per size class were: *Solenopsis invicta*: I-148, II-232, III-100, IV-26, V-7; *Solenopsis geminata:* I-67, II-82, III-75, IV-41, V-7.

Table 1. Solid food particles foraged by *Solenopsis invicta* and *Solenopsis geminata* from February through April 1987.

	S. invicta		*S. geminata*	
Foraging Item	number collected	% of diet	number collected	% of diet
Plant Material				
Seeds	25	4.8	81	29.6
Plant parts	7	1.3	5	1.8
Animal Material				
Annelida	22	4.2	7	2.6
Mollusca (snail)	1	0.2	3	1.1
Arthropoda				
Aranae	17	3.3	4	1.4
Acari	3	0.6	0	-
Collembola				
Entomobryidae	52	10.0	19	7.0
Sminthuridae	7	1.4	2	0.7
Isoptera	4	0.8	2	0.7
Hemiptera nymph	4	0.8	1	0.4
Homoptera				
Cicadellidae nymph	8	1.5	2	0.7
Aphididae	7	1.3	3	1.1
Delphacidae nymph	5	1.0	0	-
Coccoidea	2	0.4	2	0.4
Psyllidae	0	-	1	0.4
adult (unidentified)	1	0.2	2	0.7
nymph (unidentified)	6	1.2	3	1.1
Coleoptera				
Carabidae larva	7	1.3	5	1.8
Carabidae	2	0.4	0	-
adult (unidentifed)	1	0.2	3	1.1
larva (unidentified)	18	3.5	4	1.4
Lepidoptera				
larva (unidentified)	16	3.1	6	2.2
pupa (unidentified)	6	1.2	0	-
Diptera				
Mycetophilidae	7	1.3	1	0.4
Tipulidae	1	0.2	0	-
Chironomidae	1	0.2	0	-
adult (unidentified)	14	2.7	5	1.8
pupa (unidentified)	8	1.5	0	-
larva (unidentified)	12	2.3	4	1.4
Hymenoptera				
Formicidae	7	1.3	4	1.4
Ichneumonoidae	0	-	1	0.4
adult (unidentified)	1	0.2	0	-
larva (unidentified)	0	-	1	0.4
Fecal Matter	1	0.2	0	-
Unidentifiable animal matter	246	47.4	103	37.7
Total	519	100.0	274	100.0

the plant material. Collembolans were important items, making up 7.7% while Coleoptera larvae accounted for 3.2% of the solid items. Other important components were annelid parts (2.6%) and Lepidoptera larvae (2.2%). Of the 274 items collected, unidentifiable particles constituted 37.2%.

Liquid Food. Comparison of the mass of incoming and outgoing *S. invicta* foragers revealed that the incoming foragers with liquid were carrying an average of 35% of their body mass as liquid (Fig. 4). This percentage remained constant across the full range of worker sizes. Wet mass of liquid load carried by the average minor worker was approximately 0.20 ± 0.06 mg while average dry mass was 0.05 ± 0.02 mg. Thus, the liquid contained approximately 25% solute. *S. geminata* workers carried larger loads of liquid in the crop compared to *S. invicta* (Fig. 4) but the amount of this liquid load as a percentage of body weight was similar to that of *S. invicta.*

Analysis of Liquids. Sugar analyses of the liquid collected by *S. invicta* foragers in the field revealed that it was composed primarily of fructose and glucose. No sucrose was detected in this liquid. Analyses of the crop contents of ants fed sucrose also revealed a composition primarily of fructose and glucose. Faint traces of sucrose were seen in two of the six samples. In these cases, and

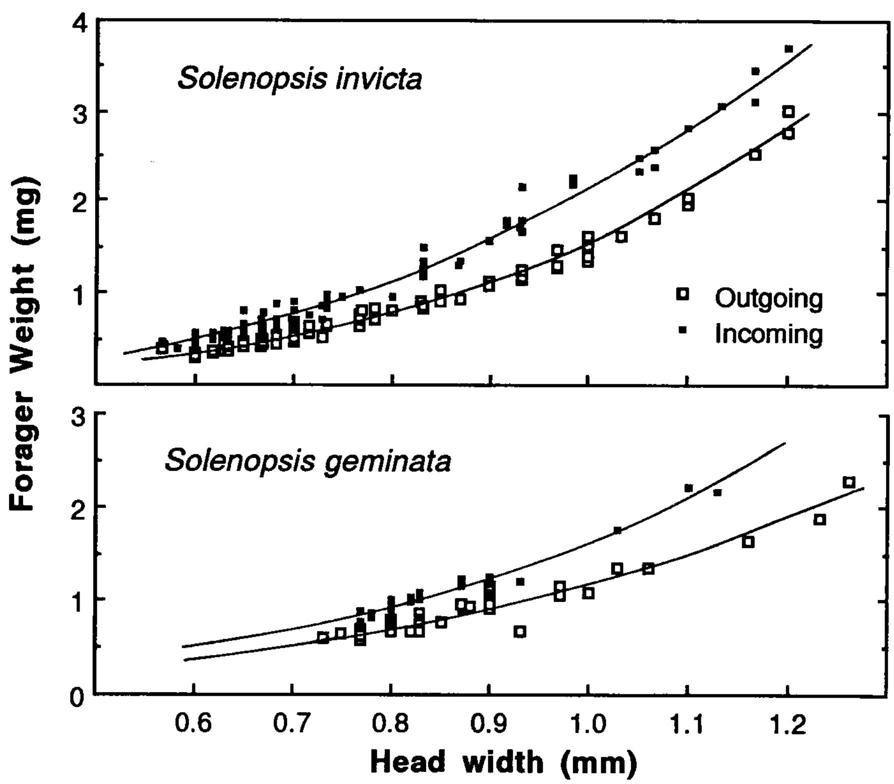

Fig. 4. Weights of incoming and outgoing foragers from three *Solenopsis invicta* and two *Solenopsis geminata* colonies as a function of body size (head width). Weight of the liquid load was computed by taking the difference between the two lines.

probably in the case of field samples as well, sucrose was broken down into fructose and glucose in the crop. By comparing intensities of spots of liquid collected from foragers to those of known concentrations of standard fructose, glucose, and sucrose solutions, we could infer the relative concentrations of sugars in the foraged liquid. The nine field samples of small workers and four field samples of large workers did not differ in the types or concentrations of sugars collected. None of the field samples corresponded to known 1 M fructose or glucose concentrations while all appeared to be in the range of 0.25 - 0.5 M.

Amino acid analyses revealed a wide range of total amino acid concentrations in liquid collected from field ants (Fig. 5, Table 2). Only the most common 14 amino acids were used to calculate total amino acid content in order to facilitate comparisons with published reports of the amino acid contents of possible liquid sources. These amino acids were: aspartic acid, threonine, serine, asparagine, glutamic acid, glutamine, proline, glycine, alanine, valine, cystine, isoleucine/leucine, tyrosine and phenylalanine. Hereafter, reference to total amino acid concentrations from this study will include only these amino acids. Figure 5 shows that small amounts of amino acids were detected in liquid from sucrose fed ants. These amino acids must have originated in the crops of the fire ants, since there were no amino acids in the pure sucrose solution.

Root homopterans were found on 36 of 90 (40%) plants surveyed while ants were found on 25 of 90 (28%). Only 10 of 90 plants had both homopterans and ants. A Chi-square analysis revealed that there was no association between the presence of root homopterans and ants ($\chi^2 = 0.473$, $p > 0.05$). It was often difficult to assess whether ants were actually on the roots since the area was so heavily infested with fire ants. We often knocked ants off the plants during the digging process.

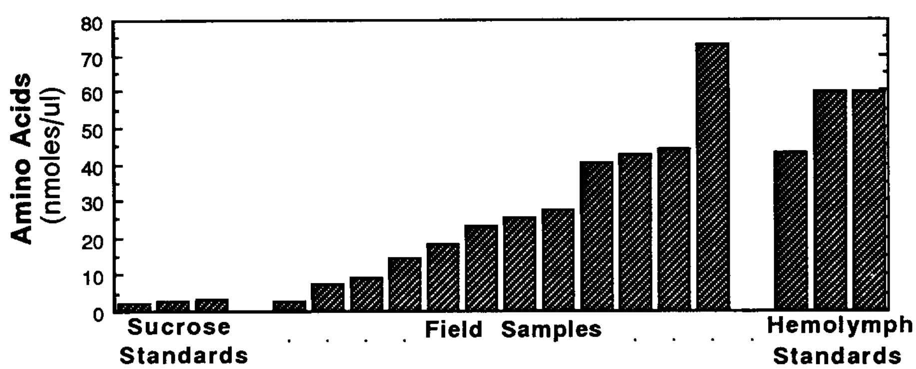

Fig. 5. Concentrations of the 14 most common amino acids (nmoles/μl) in liquid from crops of *Solenopsis invicta* foragers. Field samples are compared to concentrations in laboratory ants fed 1 M sucrose solution (sucrose standards) and body fluid standards of crickets and an earthworm.

Table 2. Comparison of sucrose, glucose, and fructose concentrations, and concentrations of 14 selected amino acids in the solutes of the liquid collected from the crops of fire ants in the field, and in a sample of possible sources.

Source	sucrose (M)	glucose (M)	fructose (M)	amino acids (nmoles/µl)	Reference
Fire Ant Crops					
	0.25 - 0.50*	0.25 - 0.50	0.25 - 0.50	2.66 - 72.8	present study
Insect Hemolymph					
	-	0.001 - 0.02	low	high	Buck 1953, Wyatt 1961
	-	-	-	42.80 - 59.84	present study
Plant Sap					
	-	0	0	-	Devlin 1975
	-	0	0	0.70 - 129.20	Ziegler 1975
	0.14 - 0.45	-	-	-	Noggle and Fritz 1976
Plant Nectars					
	1.00 - 5.00	0.52 - 2.45	0.52 - 2.45	4.72 - 95.39	Lanza (pers comm.)
	5.72	1.65	1.77	3.58 - 57.80	Smith et al. 1990
Homopteran Honeydew					
	0.01 - 0.79	some	some	27.20 - 92.60	Auclair 1963

* before breakdown to glucose and fructose.

Discussion

Success rates. Liquid food was collected more frequently than was solid food by both ant species, indicating that liquid food is a more substantial component of the fire ant diet than previously suggested. Although these two species have long been known to feed on liquids (Wheeler 1910; Wilson and Eisner 1957; Hays and Hays 1959; Agnew et al. 1982), they are usually described simply as scavengers of arthropods (Wilson and Oliver 1969; also see reviews by Vinson and Greenberg 1986; Lofgren et al. 1975). Liquid collection was consistently higher than solid food collection and did not vary with seasonal rates of colony brood production. Even the June 1989 *S. invicta* colonies, which contained large amounts of brood, exhibited higher rates of liquid than solid food collection. Liquid is also a large component of the diets of several other ant species. For example, liquid always forms greater than 50% of the total colony diet of *Formica rufa* (Skinner 1980), and liquid was collected 60 - 110 times more frequently than solid food items by *Wasmannia auropunctata* foragers on Santa Cruz Island, Galapagos (Clark et al. 1982).

S. invicta displayed a significantly higher rate of liquid retrieval (40%) than did *S. geminata* (28%). This difference in foraging efficiency may be an important factor in *S. invicta's* displacement of *S. geminata* at the Brackenridge Field Laboratory; however, the statistical significance of this difference was marginal and should also be investigated in other habitats.

Approximately 50 - 70% of foragers of both species returned to the mound without observable food. Similar low rates have been reported for other ants (e.g. Rogers 1974; Jorgensen and Porter 1982). Presumably some foragers were engaged in other activities such as the maintenance and construction of foraging trails or defense. The remaining workers were either unsuccessful or carried loads too small to be detectable.

Solid Food. Solid food items collected by *S. invicta* were very similar to those found in previous studies (Hays and Hays 1959; Wilson and Oliver 1969). Collembola was the most abundant identifiable prey item collected in pasture areas and Annelids were second. Seeds constituted 3.9% of the diet of *S. invicta*, which is somewhat greater than the 1.5% reported by Wilson and Oliver (1969). Seeds constitute a minor part of the diet of *S. invicta* (see review in Wilson 1978).

Results of this study confirm that seeds are an important component (30%) of the diet of *S. geminata.* While this information is well known (Wheeler 1910; Wilson 1978) it has been rarely quantified (Carroll and Risch 1984). *S. geminata* is not, however, strictly a seed specialist but is omnivorous and preys on the same arthropods as does *S. invicta. S. geminata* in eastern Mexico is similarly an important predator of many crop pests, including Coleoptera larvae and Aphididae, as well as a collector of seeds (Risch and Carroll 1982).

Neither species specializes exclusively on any one food item but captures whatever is available in the area. Both species most often collect the easily accessible larval forms and ground dwelling arthropods. Although *S. geminata* does feed on more seeds than does *S. invicta,* the arthropod composition of their diets are comparable.

Omitting the unidentifiable solid animal matter, 20 of 25 (80%) forage item categories collected by *S. geminata* were also collected by *S. invicta* (Table 1). Similarly, 20 of 32 (63%) forage item categories collected by *S. invicta* were also collected by *S. geminata.* Overlap for solid food items was calculated at 59% (after Pianka 1983), a relatively high food niche overlap between two sympatric congeners. This high overlap indicates that there is substantial direct competition between the two species for food resources and may be one explanation as to why the two species are unable to coexist. The larger seed portion of the diet and the slightly greater head sizes of *S. geminata* foragers compared to *S. invicta* may provide a partial dietary refuge for *S. geminata.* However, there is not a distinct differentiation in food items or sizes between the two species that would foster coexistence as has been found for other ant species. Dietary overlap between *S. invicta* and *S. geminata* is further intensified by the fact that both species collect mostly liquid food, probably from the same sources.

Liquid Food Sources. The source of the liquid collected by the two fire ant species is difficult to pinpoint due to the tremendous variation in sugar and amino acid concentrations and components in both the liquid analyzed and in the possible sources (Table 2). Sugar analyses of the crop contents of foragers revealed fairly high concentrations of fructose and glucose. However, our analyses suggest that the sugar in the source liquid may have been sucrose which was broken down into fructose and glucose in the crop. This occurs by way of the enzyme invertase which has been found in the crop of fire ants (Ricks and Vinson 1972b). Total amino acid concentrations and compositions in samples of the liquid collected by fire ants in the field span the range between sucrose-fed an insect-fed ants. No indicative amino acids were found that clearly indicate origin of the field liquid. While fire ant foragers collect liquid from a variety of sources, we attempted to identify the main source of this liquid food. Possible sources of the liquid which will now be considered are: insect hemolymph, plant saps, plant nectars, and homopteran honeydew.

Insect hemolymph is a potential but not very probable primary source because it contains lower concentrations of sugars and slightly higher concentrations of amino acids than did most of our field samples (Table 2). Trehalose, a glucose-glucose disaccharide, is the most common blood sugar in insects (Wyatt and Kalf 1957; Wigglesworth 1972). Consequently, sugar analyses of liquids derived from insect hemolymph should reveal relatively little fructose or low fructose to glucose ratios, which we did not find. Further, trehalose concentrations in insects can range between 0.007 - 0.06 M, much lower than our values (Wyatt 1961). Insect hemolymph contains high concentrations of free amino acids which differ greatly between species and between different developmental stages of an insect (Wyatt 1961; Chen 1971; Wigglesworth 1972). Published reports of amino acid concentrations of insect hemolymph in units directly comparable to our results were not found, but total amino acid concentrations of our field samples were on the average lower than both the cricket-fed and annelid-fed samples from our study (Table 2). The composition of amino acids in insect hemolymph is often similar to that of some of our field samples (Buck 1953; Chen 1971; Wigglesworth 1972); however, the amount of liquid collected by foragers (70 - 80% of the diet) seems too great to be provided solely from randomly encountered insects.

Plant sap (phloem) is composed of sugar and amino acid concentrations similar to the liquid recovered from ants in the field. Concentrations of amino acids differ for an individual plant during different life stages (Devlin 1975). Plant saps contain primarily sucrose and no or little fructose or glucose (Noggle and Fritz 1976). This might also have been the case in our field samples before sucrose breakdown in the fire ant crop.

The large amounts of liquid involved suggest that the ants may be obtaining some of the liquid by tapping into plant saps directly (Smittle et al. 1983). Several studies have reported imported fire ant feeding on the seeds, roots, stems, and leaves of corn (Lyle and Fortune 1948; Eden and Arant 1949) and soybean plants (Adams et al. 1983; Apperson and Powell 1983). Smittle et al. (1983) used radioactive tracers to detect imported fire ant feeding on the roots of corn, okra, and soybean plants. Adams (1986) reported *S. invicta* feeding on the fruit, sap, flowers, and new growth of citrus trees. Adams (1986) suggested that "the plant-feeding aspect of imported fire ant behavior has been neglected since the early report of Wilson and Eads (1949)." *S. geminata* has also been reported feeding directly on plants. (Travis 1941).

Plant nectars also contain similar sugar composition and amino acid concentrations to our field samples (Table 2). Sugars, including fructose, glucose, sucrose, and saccharose in a wide range of concentrations, are the most abundant solutes in nectars (Baker and Baker 1975; Gottsberger et al. 1984; Lanza [pers. comm.]). All analyses of floral and extrafloral nectars report great variability in amino acid composition and concentration between plant species (Baker and Baker 1975, 1977; Gottsberger et al. 1984; Baker and Baker 1986). Furthermore, floral and extrafloral nectars on a single plant may vary in both amino acid composition and concentration (Baker and Baker 1986). Studies have shown that fire ants are attracted to extrafloral nectar both in the field and in the laboratory (Agnew et al. 1982; Lanza 1988; Lanza 1990). However, few extrafloral nectaries were seen in the area and fire ants were not observed in great numbers on flowers or vegetation.

Homopteran honeydew is also similar to our field samples in sugar and amino concentrations (Table 2) but can contain a wide variety of sugars (including sucrose, glucose, and fructose) found in the host plant plus modified versions of these sugars such as melezitose (Auclair 1963; Way 1963; Hussain et al. 1974). Sucrose usually predominates. The wide range of sugar concentrations found in honeydews varies according to the species and age of the host plant, the part of the plant on which the insect feeds and the length of time it feeds (Way 1963). Total dry mass of honeydew may vary between 6.5 - 11% (Mittler 1958; Auclair 1963) compared to about 25% solute in our field samples. Fire ants have been observed collecting liquid from aphids and other homopterans such as root coccids (Wheeler 1910; Van Pelt 1958; Hays and Hays 1959). Considering that 35% of the plants sampled around the mounds had root homopterans, it is quite possible that these insects are a major source of liquid food.

Conclusions

Liquids are a major component of fire ant diets. Our results indicate that most of these liquids are of plant origin; however, the exact sources of liquid foods and their relative frequencies is a subject for future research. A comprehensive analysis of carbohydrates, amino acids, proteins, and lipids in liquid food will also be needed to fully quantify the diet of field colonies.

The answer to why fire ants collect so much liquid food probably lies in colony energetics and dietary requirements. Fire ant colonies must have a liquid energy source to fuel their worker population because worker respiration requires roughly one-half to two-thirds of a colony's total energy budget (Porter and Tschinkel 1985). *S. invicta* workers are not capable of passing solid particles greater than one micron to the crop (Glancey et al. 1981) and often obtain their protein from larval secretions (Sorensen et al. 1983). This explains, to a large extent, why sugar solutions are primarily distributed among the workers while proteins are directed toward the larvae and queen (Howard and Tschinkel 1981; Sorensen and Vinson 1981; Vinson 1968). Fire ant larvae are capable of converting solid food into useable liquids which could then be transferred to the workers; however, larvae are not always sufficiently abundant in a colony, especially in the winter months, and insects alone are a poor diet for healthy *S. invicta* colonies (Williams et al. 1980). Laboratory colonies fed only insects (crickets) grow 50% slower than those with access to sugar solution (Porter 1989).

The averge dry weight of dissolved material in liquid retrieved by *S. invicta* foragers (0.05 ± 0.02 mg) was less than the average dry weight per solid particle retrieved (0.12 mg) (similar results were found for *S. geminata*); however, a portion of solid food is undigestible cuticle, making the digestible portion of solid particles somewhat less than 0.12 mg, perhaps even as low as 0.05 mg. Since 70 - 80% of successful foragers collected liquid, five times as much as solid food (Fig. 1), the total dry weight of material collected in liquid may be as much as two to five times greater than the amount collected as solids. Thus assuming that most of the solutes are digestible, liquid consituted a greater portion of the useable food supply than did solid food.

With such a large proportion of their diet apparently made up of plant liquids, fire ants are probbly not simply scavengers — to a large extent they may be functioning as primary consumers. The exploitation of liquids from plant sources may partially explain how fire ants are able to exist in such dense populations as those found in Texas (Porter et al. 1991) and other parts of the southeastern United States.

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