Flow of Carbohydrates, Lipids, and Protein Among Colonies of Polygyne Red Imported Fire Ants, *Solenopsis invicta* (Hymenoptera: Formicidae)

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ABSTRACT This research quantified food collection of three nutritionally important foods (carbohydrates, protein, and lipids) by several neighboring polygyne red imported fire ant, *Solenopsis invicta* Buren, colonies. Six rare earth elements (samarium, rubidium, ytterbium, europium, neodymium, and lanthanum) were mixed with protein (tuna packed in water), carbohydrate (60% solution of glucose, sucrose, fructose, and water), and lipid baits (peanut oil) to track food collection by colonies. Food collection among six neighboring colonies was quantified in each of 14 plots for a total of 84 colonies. A uniquely labeled food type (1.5 g) was placed within 20 cm of each colony. Two replicates of each food type were used in each plot. Neutron activation analysis (NAA) was used to quantify the type and amount (μg) of rare earth elements found in samples of both workers and larvae from colonies 12 h after foraging on baits. Multiple regression results showed that distance to food sources was the most significant independent variable in determining the distribution of food resources among colonies. Food type interacted significantly with life stage (worker or larvae) and the distance colonies harvested food baits. Significantly more protein was detected in larvae compared with lipids and carbohydrates and at farther distances from baits. In contrast, workers collected significantly more carbohydrates from farther distances than lipids and protein. Results indicate that patterns of food flow among neighboring polygyne red imported fire ant colonies are largely determined by the distance between colonies, food resources, and the type of food being collected.

KEY WORDS rare earth elements, food flow, polygyne fire ants, foraging behavior

FOOD USE BY INVASIVE species is important in understanding their ability to become pest species (Sakai et al. 2001). Several economically important pest ant species including *Solenopsis invicta* are polygynous and have colonies that are referred to as polydomus (single colony occupying several nests), "unicolonial," or "supercolonial" (e.g., the argentine ant *Linepithema humile* [Chen and Nonacs 2000, Tsutsui et al. 2000, Giraud et al. 2002] and *Monomorium pharaonis* L. [Thompson 1990]). Food availability and use among neighboring colonies have direct impacts on colony growth, reproduction, and mound densities within fields. Foraging behavior of monogyne red imported fire ants, *S. invicta*, has been well described (Hölldobler and Wilson 1990, Vinson 1997, Tschinkel 1998). However, comparatively little is known about foraging patterns, habitat partitioning, resource acquisition, or allocation among polygyne *S. invicta* colonies (Bhatkar 1987, Bhatkar and Vinson 1987a). Traditionally, polygynous *S. invicta* populations have been referred to as "supercolonies" with "free exchange of workers" and food between nests (Bhatkar and Vinson 1989, Macom and Porter 1996, Vander Meer and Porter 2001). Because of reduced nestmate recognition ability, populations of polygyne fire ants may be two times larger, on average, than monogyne field populations (Balas and Adams 1996, Macom and Porter 1996). Long-term data indicates that both monogyne and polygyne populations may coexist and remain stable over time without displacing each other (Greenberg et al. 1992). However, both social forms use the environment very differently (Bhatkar and Vinson 1987a, Vinson 1997). Monogyne *S. invicta* aggressively defend food resources against conspecifics (Tschinkel 1998). Density-dependent factors resulting from territoriality have been shown to limit monogyne populations (Adams and Tschinkel 1995, Balas and Adams 1996).

Previous studies have established that there is movement of food (e.g., toxic bait, radioactive elements) among workers and polygyne fire ant colonies (Bhatkar and Vinson 1989, Vargo and Porter 1989, Drees et al. 1992). Drees et al. (1992) examined the toxic effects of an insect growth regulator (IGR) ap-

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plied to individual mounds on nontarget colonies. Mound applications consisted of 20.78 g of Logic Fire Ant Bait (active ingredient; fenoxycarb). They sampled all mounds in a 9.14-m radius to estimate the total number of mounds affected by the single mound application of insecticide. After all applications, significant negative correlation was found between the percentage of affected mounds and the mean distance interval from the mound treated. The average distance from mound application to a distance at which 50% of the mounds were affected by the treatment was 2.8 m, and the maximum distance from treatment location to affected mound was 7.0 m.

Food dye, radioactive labels, and rare earth elements have all been used as internal markers to follow the flow of food within single colonies and food transmission between individual ants (Wilson and Eisner 1957, Eisner and Wilson 1958, Summerlin et al. 1975, Bhatkar and Kloft 1977, Bhatkar 1979a, b, Showler et al. 1989). Internal markers have been used to determine the extent of foraging territories in monogyne colonies (Markin and Dillier 1971). Showler et al. (1989) used samarium, a single nonradioactive, stable tracer element to examine the foraging territories of monogyne imported fire ants in sugarcane habitats. They showed that fire ants foraged more in weedy areas compared with weed free areas. Studies that use internal markers to follow dispersion patterns of ants and/or food show that these materials are often dispersed outside of target colonies. Dispersal occurs either directly through the foraging activities of workers from neighboring colonies or through trophallaxis, the exchange of alimentary liquids between colony workers (Bhatkar 1979b, Drees et al. 1992). The social movement of food through trophallaxis may overestimate the extent of polydomy in polygyne populations, where appeasement food sharing may occur between two different colonies.

The objective of this research was to quantify the distribution of three nutritionally important food types, protein, lipids, and carbohydrates, within and among field colonies using six rare earth elements to individually label food items. Many food-tracking techniques have relied on the presence or absence of a marked food item to infer foraging behavior and food flow (Summerlin et al. 1975, Sorensen and Vinson 1981). To our knowledge, the flow of different food types among polygyne field colonies has not been quantified or previously characterized. By quantifying patterns of food collection among polygyne colonies, food distribution models can be developed to better estimate foraging areas and levels of social interactions in polygyne situations. Field application and instrumental neutron activation analysis (NAA) of rare earth elements is an environmentally conscientious alternative to placing radioactive isotopes in the environment. These rare earth elements can be detected at low levels (<1 μg) and quantified in the laboratory by measuring the gamma ray emissions from neutron-induced (i.e., activated) radioactive elements in a sample (Showler et al. 1989).

Materials and Methods

Field Sites. This research was conducted in five domestic cattle grazing pastures in College Station, TX, that have had known polygyne populations for several years. Pastures were separated by $\geq$1 km in well-drained areas. Six neighboring polygyne colonies in 14 sites were used as treatment colonies (84 colonies total). Ants from six neighboring colonies were collected at each site after feeding on food baits labeled with rare earth elements. Sampling occurred from 15 May 2001 through 30 August 2001.

Social Status of Ants. Determination of the social form of *S. invicta* (monogyne versus polygyne) was accomplished by evaluating colonies as being aggressive (fighting and biting = monogyne) or not aggressive (polygyne) based on an aggression behavioral bioassay (after the design of Obin et al. 1993). Five ants from each treatment colony were placed into a plastic nest box (19.5 cm length by 14 cm width by 9.5 cm height) lined with Fluon and observed for ant interactions for 5 min. Ants from two colonies from each sampling site were paired in plastic trays at a time until all colonies within a site were evaluated against each other for aggressive encounters. No fighting or biting was observed among workers from any of the colonies examined in this study.

Rare Earth Elements. Three food types were used at each site, protein (tuna fish packed in spring water), lipids (peanut oil), and carbohydrates (60% sugar/H_2O solution = 20% sucrose + 20% glucose + 20% fructose + 40% de-ionized H_2O). To quantify the amount of food collected by a colony, six nonradioactive rare earth elements (i.e., samarium, europium, lanthanum, neodymium, ytterbium, and rubidium) were used to individually label each food type. Colonies were examined in sets of six, corresponding to the six rare elements, so that food collection among six neighboring colonies could be quantified by following two uniquely marked protein, lipid, and carbohydrate baits for each set of colonies. To quantify the background levels of the six rare earths in ants, four samples of ants (100–200 mg) were collected from each field site before any rare earth elements were placed in field sites.

The rare earth elements used in this study were powder or crystalline in form. A set of serial dilutions using 1.0 g of each element was prepared. For the initial dilution series, 1.0 g of each labeled material was dissolved in 25 ml of de-ionized water. For the second dilution series, 1 ml of the first dilution series was added to 9 ml of de-ionized water.

Protein baits consisted of 1.5 g of drained and pressed-dry tuna fish (generic brand packed in water). Each of the 1.5 g tuna baits was mixed with 1 ml of each 1:9 stock solution and ground with a mortar and pestle to mix and homogenize the protein bait. Protein baits were placed in small plastic weigh boats for easy access by ants in the field.

Carbohydrate baits were a mixture of 1.5 ml of a 60% sugar/H_2O solution (1.8 g sucrose + 1.8 g glucose + 1.8 g fructose + 30 ml de-ionized water) and 1 ml of

each 1:9 stock solution. Small (11 by 21 cm) crumpled sheets of tissue paper (Kimwipes, Kimberly-Clark Corp., Roswell, GA) were placed in small plastic dishes and used to soak up labeled carbohydrate solutions. This created more surface area for ants to forage on and prevented ants from drowning in the aqueous solution.

For lipid baits, 1.5 ml of peanut oil was mixed with 1 ml of each 1:9 stock solution. To mix oil and water for the final lipid bait, it was necessary to add a small drop of ethyl alcohol (0.05 ml) to emulsify the 1 ml stock solution of element and water with the 1.5 ml lipid bait. After 30–45 s of vigorous mixing, the emulsified lipid solution was applied to crumpled tissue paper (Kimwipes) in small plastic dishes similar to carbohydrates above. Kimwipes provided a permeable surface for the lipid solution to remain emulsified longer.

Food baits were mixed fresh each morning before each field trial. To remove any potential rare earth element and food type interactions that may have biased the results, rare earth elements were randomly assigned to food baits; therefore, each element was assigned to each food type at least once. Six food baits were randomly assigned to six neighboring colonies in each site and placed ≈20 cm from each colony.

Ant Sampling. Twelve hours after labeled food baits were introduced near field colonies, the six treatment colonies in each site were excavated into 18,900-ml plastic buckets lined with baby powder. Ants were "dripped" out of the soil by placing buckets on a lab bench and slowly dripping water into the center of the bucket. *S. invicta* is a flood-plain adapted species, which builds living rafts of ants that can float on top of water (Hölldobler and Wilson 1990), making them easy to collect using this method. After soil extraction, ants and brood floated from colonies were anesthetized with CO_2 and weighed. Four (≈100–200 mg) samples of brood (larvae, eggs, and pupae) and four samples of workers were collected from each colony for NAA of the rare earth elements present in ants. A total of 672 samples of ants were collected from the 84 colonies examined.

NAA. Ant samples were analyzed for the amount (μg) of each rare earth element in each milligram sample of ants. Irradiations for NAA were conducted at the Texas A&M Nuclear Science Center, and quantification of the specific gamma ray emissions from each of the activated rare earth elements in ants was conducted at the Center for Chemical Characterization and Analysis (CCCA). NAA consists of neutron irradiation of each sample in a calibrated flux of $\approx 1 \times 10^{13}$ thermal neutrons/cm^2/s for 14 h in a TRIGA research nuclear reactor. After irradiation, ant samples were transported to the CCCA, and activated rare earth elements were counted on a lithium-drifted germanium crystal detector connected to a multi-channel analyzer. For example, samarium can be detected by measuring the intensity of the 0.103 MeV gamma ray of the 46.7 h Sm-153 isotope produced from the stable Sm-152 (Showler et al. 1989).

Data Analyses. NAA determined the μg of each element detected in each sample of ants (e.g., μg element/mg ants). NAA results were "corrected" to identify NAA readings above background readings from ants collected in the field. Average background readings in ants for each element were calculated from four samples of ants randomly selected from field sites before "spiked" foods were introduced. To "correct" NAA readings, the average background reading for each element was subtracted from the NAA readings for that element in each sample. The average background values for each element were samarium = 0.062 μg/g sample, ytterbium = 0.036 μg/g sample, rubidium = 2.12 μg/g sample, lanthanum = 0.28 μg/g sample, and europium = 0.006 μg/g sample. The background level for neodymium was below detectable levels. The proportion of each rare earth element (i.e., food) collected by workers, including food passed to larvae, in individual colonies was determined by multiplying the "corrected" concentration (μg/mg) of element detected in each sample by the total estimated biomass of workers and brood in the colony for that sample. The mean proportions of the total available μg element in each bait that was detected in both worker and brood samples were used as dependent variables for statistical analyses. Mean proportion of rare element detected was calculated using four samples of workers and four samples of larvae for each colony. There were 4,032 total possible NAA measurements (84 colonies × 8 samples per colony [4 worker and 4 larvae] × 6 rare earth elements per sample). Of these, 2,355 observations did not exceed average background levels and were excluded from the analyses. Some samples were lost during irradiation because of heat build-up that caused melting of the vials (120 larvae and 95 workers). Therefore, the total number of usable NAA values for statistical data analyses was 1,462, resulting in 475 of a possible 1,008 mean proportions (1,008 possible means = 84 colonies × 6 rare earth elements × 2 life stages). Of the 475 mean proportions estimated, only 7 (1.4%) had values >1, implying that these colonies collected more food than was available. These overestimates indicate some unaccounted for variation in the estimates. Variation may come from uncertainty in the standards used in the NAA, differences in sample positions relative to the reactor core, or from error in the estimates of colony size. Exploratory analyses indicated that exclusion of these mean values did not change the significance of the main effects or interaction terms in the regression analyses.

JMP software (SAS Institute 2000) was used to perform step-wise multiple regression to fit a response surface describing the effects of distance to food sources, food type, life stage, colony size, and major interactions on the mean proportion of food collected by each colony. Food type (carbohydrates, lipids, protein) and life stage (worker, larvae) are qualitative variables that were recoded into quantitative dummy variables (food type = 1, 2, 3; life stage = 1, 2) for multiple regression analyses. To satisfy tests for homogeneity of variance, the dependent variable mean proportion of food collected was transformed to

Table 1. Results of a step-wise multiple regression to fit a response surface describing the effects of distance to food sources, food type, life stage, colony size, and major interactions on the mean proportion of food collected by each colony

Source	df	Sum of squares	Mean square	*F* ratio	$P > F$	R^2
Model	11	1,234.68	112.24	34.44	<0.001	0.44
Error	464	1,512.36	3.26			
Total	475	2,747.03				

The dependent variable was the mean proportion of rare earth element (μg) found in colonies of the total that was placed in 1.5 g of bait. Independent variables included colony size, distance to food resources, food type (carbohydrates, lipids, and proteins), and life stage (workers vs. larvae). Food type (carbohydrates, lipids, protein) and life stage (worker, larvae) are qualitative variables that were re-coded into quantitative dummy variables (food type = 1, 2, 3; life stage = 1, 2) for multiple regression analyses.

$\log_e$ (mean food collected). All tests of significance were evaluated at $P = 0.05$.

Results

The average colony size for the 84 colonies was 15,578 mg (range, 1,340–61,040 mg). The average distance between the 84 colonies was 235 cm (range, 23–920 cm). Step-wise multiple regression analysis provided a significant response surface model (Eq. 1, Table 1). The model describes the effects of distance to food sources, food type, life stage, colony size, and major interactions on the mean proportion of food collected by each colony. The independent variables of life stage, colony biomass, and distance were significant terms in the response surface model (Table 2). Food was not significant as a main effect but was significant as an interaction term with distance to food sources and life stage (Table 2). The final form of the model ($R^2 = 0.44$; $P < 0.001$; df = 11, 464; $F = 34.44$) was:

$$\log_e(\textit{mean proportion of element } (\mu g) \textit{ detected in a colony/ total } \mu g \textit{ element in bait}) =$$
$$-4.28990 + (-0.5104*x_1) + (0.0001*x_2) + (0.0280*x_3) + (-0.0054*x_4)$$
$$+ [(x_2-15549.9580)*(x_2-15549.9580)*-2.6198e-9] + [(x_3-1.9517)*(x_1-1.542)*0.5082] + [(x_3-1.9517)*(x_2-15549.958)*0.1298e-4] + [(x_3-1.9517)*(x_3-1.9517)*0.6625] + [(x_4-294.3836)*(x_2-15549.958)*5.5274e-8] + [(x_4-294.3836)*(x_3-1.9517)*0.1677e-2] + [(x_4-294.3836)*(x_4-294.3836)*0.7315e-5] \quad [1]$$

where x_1 = life stage (dummy variable), x_2 = colony biomass (mg), x_3 = food type (dummy variable), and x_4 = interval distance between colonies and food baits.

Table 2. Results for the main effects and interactions terms of stepwise multiple regression analysis of the mean proportion of rare earth elements (μg) detected in colonies out of total that was placed in 1.5 g of bait in field sites

Source	Sum of squares	*F* ratio	$P > F$
Life stage	30.50	9.35	<0.0023
Colony biomass	396.52	121.66	<0.0001
Food type	0.25	0.08	0.7812
Distance	701.04	215.08	<0.0001
Colony biomass × colony biomass	168.10	51.57	<0.0001
Food type × life stage	21.31	6.54	0.0109
Food type × colony biomass	9.11	2.79	0.0953
Food type × food type	42.74	13.11	0.0003
Distance × colony biomass	11.62	3.56	0.0596
Distance × food type	59.96	18.40	<0.0001
Distance × distance	117.09	35.92	<0.0001

Food type (carbohydrates, lipids, protein) and life stage (worker, larvae) are qualitative variables that were re-coded into quantitative dummy variables (food type = 1, 2, 3; life stage = 1, 2) for multiple regression analyses. Degrees of freedom = 1 for all effects.

The highest proportion of variation was explained by distance of the bait from a colony (*F* ratio 215; $P < 0.0001$; Table 2). As the distance between colonies and food sources increased the mean proportion of food collected by colonies declined. There was a significant interaction effect between food type and distance to baits (Table 2). More carbohydrates were detected in workers from greater distances than either proteins or lipids (Fig. 1a). In contrast, proteins were detected in higher proportions in larvae, at distances >100 cm from baits than lipids or carbohydrates (Fig. 1b). Food type and life stage interacted significantly (Table 2). Mean separation tests show that significantly more protein was detected in larvae than carbohydrates or lipids (Fig. 2). In contrast, carbohydrates and lipids were detected significantly more than protein in workers (Fig. 2). Also, more protein was detected in larvae than in workers.

Discussion

This research provides quantitative data on resource collection among polygyne imported fire ant colonies that focus on the distance of food resources from colonies, colony size, and food type. Some food flow occurs between polygyne colonies, either indirectly or directly through trophallaxis (Wilson and Eisner 1957) or through foraging overlap on baits and/or turnover on baits by different colonies. A quantitative analysis of food flow shows that foods are not shared equally among colonies nor are they shared equally among colony life stages. Labeled proteins were found distributed among larvae in colonies in higher proportions than lipids or carbohydrates. The proportion of food collected was a positive function of

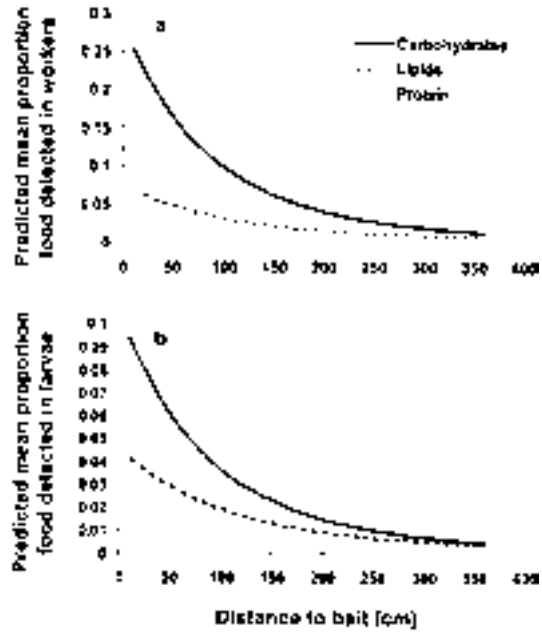

Fig. 1. Graph of stepwise nonlinear regression of predictions of the mean proportion of each food type collected/detected in (a) workers and (b) larvae as a function of average colony size 15, 578 mg and increasing distances from colonies to food baits. Note scale differences between worker (a) and larvae (b) graphs.

colony size. Studies have shown that proteins are preferentially directed toward developing larvae within the colony (Howard and Tschinkel 1981, Sorensen and Vinson 1981). Sorensen and Vinson (1981) quantified the distribution of several food types within a laboratory colony of monogyne fire ants. They found that the form of the protein, solid versus liquid, determined the final distribution of the radioactive label they used. Solid food was given to larvae for digestion, while liquid protein was split equally among workers and larvae. This was a similar pattern both within and among field colonies. In *S. invicta*, the fourth-instar larvae are responsible for most of the protein digestion for the colony. Therefore, this stage is the limiting factor in protein collection and assimilation for the colony (Howard and Tschinkel 1981, Sorensen and Vinson 1981). A colony's ability to store and assimilate different food types is a function of both worker and larval biomass and has a direct impact the amount of food harvested by colonies.

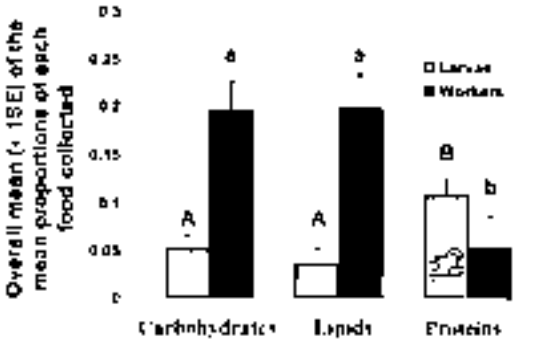

Fig. 2. Histogram of the overall mean ± SEM of the mean proportions estimated. Mean proportions were calculated from colonies as a function of distance to food baits, food type, and colony size. Means for larvae with different capital letters were significantly different at $P = 0.05$ using Tukey's honestly significant difference (HSD). Means for workers with different lower case letters were significantly different at $P = 0.05$ using Tukey's HSD.

In the current research, proteins were distributed to larvae more than liquid lipid or carbohydrate food sources at distances >1 m. This may be a result of colonies closest to food sources reaching their limit in protein intake and handling ability and consequently reducing their recruitment signal to that food source. In contrast, carbohydrates and lipids can be stored in workers, which represent a larger part of the colony's social stomach than do larvae. Some colony members in *S. invicta* colonies may act as storage units (i.e., repletes) for storage of liquid resources in their crops (Glancey et al. 1973). However, the storage of proteins has not been shown. This suggests that the capacity to store food resources may be responsible for the observed patterns of food distribution.

Polygyne ants do not aggressively defend foraging territories but instead use foraging strategies that rely on fast recruitment and high numbers of ants to secure baits within their reach. Previous research has shown that polygyne colonies can monopolize food baits by recruiting high numbers of foragers to individual baits (unpublished data). Competitive interactions among polygyne *S. invicta* colonies represents an alternative view of polygyne ant foraging than previous views associated with the term "supercolony" (Bhatkar and Vinson 1987a, Macom and Porter 1996, Vander Meer and Porter 2001). Foraging as a function of colony demand, satiation, and recruitment ability provides a simple, ecologically based, process for explanations of food flow, and nontarget effects of pesticides (Drees et al. 1992) among polygyne colonies. Food flow among colonies may occur through limited overlap among colonies on individual baits and through multiple colony turn-over on baits after individual colonies reach satiation.

Most of the toxic baits that are used to control ants are oil based (Kidd et al. 1985). However, based on these results, in some situations, protein baits may be used as carriers for insecticides to impact more colonies in an area. Protein baits applied during reproductive periods (spring) may be more useful in spreading pathogens or ant toxicants to the developing larvae than lipid based baits.

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References Cited

Adams, E. S., and W. R. Tschinkel. 1995. Density-dependent competition in fire ants: effects on colony survivorship and size variation. J. Anim. Ecol. 64: 315–324.

Balas, M. T., and E. S. Adams. 1996. Nestmate discrimination and competition in incipient colonies of fire ants. Anim. Behav. 51: 49–59.

Bhatkar, A. P. 1979a. Evidence of intercolonial food exchange in fire ants and other Myrmicinae using radioactive phosphorus. Experientia. 35: 1172–1173.

Bhatkar, A. P. 1979b. Trophallactic appeasement in ants from distant colonies. Folia Entomol. Mex. 41: 135–143.

Bhatkar, A. P. 1987. Foraging strategies of fire ants, pp. 525–526. *In* J. Eder, and H. Rembold (eds.), Chemistry and biology of social insects. Verlag J. Peperny, Munich, Germany.

Bhatkar, A. P., and W. J. Kloft. 1977. Evidence, using radioactive phosphorus, of interspecific food exchange in ants. Nature (Lond.). 265: 140–142.

Bhatkar, A. P., and S. B. Vinson. 1987a. Foraging in mono- and polydomous *Solenopsis invicta* Buren colonies, pp. 545–546. *In* J. Eder, and H. Rembold (eds.), Chemistry and biology of social insects. Verlag J. Peperny, Munich, Germany.

Bhatkar, A. P., and S. B. Vinson. 1987b. Colony limits in *Solenopsis invicta* Buren, pp. 599–600. *In* J. Eder, and H. Rembold (eds.), Chemistry and biology of social insects. Verlag J. Peperny, Munich, Germany.

Bhatkar, A. P., and S. B. Vinson. 1989. Monodomy, polydomy, and patterns of nest dispersion in *Solenopsis invicta* Buren (Hymenoptera: Formicidae). Soc. Mex. Entomol. Mem. 1: 83–99.

Chen, S. C., and P. Nonacs. 2000. Nestmate recognition and intraspecific aggression based on environmental cues in Argentine ants (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 93: 1333–1337.

Drees, B. M., C. L. Barr, and S. B. Vinson. 1992. Effects of spot treatments of logic fenoxycarb on polygynous red imported fire ants: an indication of resource sharing? Southwest. Entomol. 17: 313–317.

Eisner, T., and E. O. Wilson. 1958. Radioactive tracer studies of food transmission in ants. Proc. 10th Int. Congr. Entomol. 2: 509–513.

Giraud, T., J. S. Pedersen, and L. Keller. 2002. Evolution of supercolonies: The Argentine ants of southern Europe. Proc. Natl. Acad. Sci. USA. 99: 6075–6079.

Glancey, B. M., C. E. Stringer, Jr., C. H. Craig, P. M. Bishop, and B. B. Martin. 1973. Evidence of a replete caste in the fire ant *Solenopsis invicta.* Ann. Entomol. Soc. Am. 66: 233–234.

Greenberg, L., S. B. Vinson, and S. Ellison. 1992. Nine-year study of a field containing both monogyne and polygyne red imported fire ants (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 85: 686–695.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard University Press, Cambridge, MA.

Howard, D. F., and W. R. Tschinkel. 1981. The flow of food in colonies of the fire ant, *Solenopsis invicta:* a multifactorial study. Physiol. Entomol. 6: 297–306.

Kidd, K. A., C. S. Apperson, and L. A. Nelson. 1985. Recruitment of the red imported fire ant, *Solenopsis invicta,* to soybean oil baits. Fla. Entomol. 68: 253–261.

Macom, T. E., and S. D. Porter. 1996. Comparison of polygyne and monogyne red imported fire ant (Hymenoptera: Formicidae) population densities. Ann. Entomol. Soc. Am. 89: 535–543.

Markin, G. P., and J. H. Dillier. 1971. The seasonal life cycle of the imported fire ant, *Solenopsis saevissima richteri,* on the Gulf coast of Mississippi. Ann. Entomol. Soc. Am. 64: 562–565.

Obin, M. S., L. Morel, and R. K. Vander Meer. 1993. Unexpected, well-developed nestmate recognition in laboratory colonies of polygyne imported fire ants (Hymenoptera: Formicidae). J. Insect Behav. 6: 579–589.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annu. Rev. Ecol. Syst. 32: 305–332.

SAS Institute. 1995. JMP statistics and graphics. SAS Institute Cary, NC.

Showler, A. T., R. M. Knaus, and T. E. Reagan. 1989. Foraging territoriality of the imported fire ant, *Solenopsis invicta* Buren, in sugarcane as determined by neutron activation analysis. Insect. Soc. 36: 235–239.

Sorensen, A. A., and S. B. Vinson. 1981. Quantitative food distribution studies within laboratory colonies of the imported fire ant, *Solenopsis invicta* Buren. Insect Soc. 28: 129–160.

Summerlin, J. W., W. A. Banks, and K. H. Schroeder. 1975. Food exchange between mounds of the red imported fire ant. Ann. Entomol. Soc. Am. 68: 863–866.

Thompson, C. R. 1990. Reproductive strategies of the fire ant, pp. 51–67. *In* R. K. Vander Meer, K. Jaffe, and A. Cedeno (eds.), Applied myrmecology, a world perspective. Westview Press, Boulder, CO.

Tschinkel, W. R. 1998. The reproductive biology of fire ant societies. BioScience. 48: 593–605.

Tsutsui, N. D., A. V. Suarez, D. A. Holway, and T. J. Case. 2000. Reduced genetic variation in the success of an invasive species. Proc. Nat. Acad. Sci. USA. 97: 5948–5953.

Vander Meer, R. K., and S. D. Porter. 2001. Fate of newly mated queens introduced into monogyne and polygyne *Solenopsis invicta* (Hymenoptera: Formicidae) colonies. Ann. Entomol. Soc. Am. 94: 289–297.

Vargo, E. L., and S. D. Porter. 1989. Colony reproduction by budding in the polygyne form of *Solenopsis invicta* (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 82: 307–313.

Vinson, S. B. 1997. Invasion of the red imported fire ant (Hymenoptera: Formicidae) spread, biology, and impact. Am. Entomol. 43: 23–39.

Wilson, E. O., and T. Eisner. 1957. Quantitative studies of liquid food transmission in ants. Insect Soc. 4: 157–166.

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