Food and Energy Requirements of Laboratory Fire Ant Colonies (Hymenoptera: Formicidae)

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ABSTRACT   This study was designed to determine how much food is needed to sustain colonies of the fire ant *Solenopsis invicta* Buren. Thirty laboratory colonies were fed 1, 2, or 4 crickets per day. Half were given access to unlimited sugar water. Colony biomass, cricket collection, and sugar collection were monitored weekly until each colony stopped growing. Caloric intake was strongly correlated with and directly proportional to colony biomass (live weight) over an 8-fold range (2–16 g). Colonies needed ≈1.14 ± 0.29 (Standard deviation) Kcal of food per gram of colony per week to sustain themselves. The presence of sugar decreased the amount of cricket biomass collected (dry weight) from 0.186 g/g of colony per week for colonies receiving crickets to 0.106 g/g of colony per week for colonies receiving both sugar water and crickets. Colonies fed only crickets approximately doubled their final size with the doubling of cricket availability; whereas, colonies receiving both crickets and sugar increased to a lesser extent. The laboratory food collection rates in this study suggest that a field population of fire ants with 90 mature mounds per hectare would require ≈21,000 Kcal or 16.0 kg of insects and sugar (combined wet weight) per week in the summer.

KEY WORDS   collection, growth, bioenergetics

THE STUDY OF food utilization of organisms is vital in understanding their effects on the environment and other organisms (Davis & Solomon 1986). The diet of the fire ant *Solenopsis invicta* Buren has been of particular interest to researchers since their introduction into the United States some 60 yr ago (Lofgren 1986). Fire ants, like most ants, are omnivorous feeding primarily on sugar solutions and arthropods (Tennant & Porter 1991). Early studies on the diet of the fire ant centered on food preference (Glunn et al. 1981) and food distribution within the colony (Howard & Tschinkel 1981, Sorensen & Vinson 1981). Very little, however, is known about the quantity of food required by colonies for growth and maintenance.

Ayre (1966), Dlussky and Kupianskaya (1972), and Brian (1973) conducted colony size and food consumption tests for several species of *Myrmica* and *Formica*. They found that the more protein or insect material colonies were fed the larger they became. They did not, however, assess food intake as a function of colony biomass. Several other authors have estimated food collection and consumption rates for field colonies but this was done on a yearly basis over a wide range of temperatures (Nielsen 1972, Jensen 1978, Mackay 1985). Our primary objective was to determine the amount of food collected by S. *invicta* colonies as a function

of their size. This information should be useful in estimating the importance of fire ants in their ecosystem. We were also interested in determining if larger colonies collected disproportionately more or less food per gram of colony. This question is of interest because food intake in fire ant colonies might decrease because of lower metabolic rates associated with larger organisms (Hoar 1975), or it might increase because of lower efficiency associated with larger colonies or social groups (Michner 1964).

Materials and Methods

Twelve polygyne S. *invicta* colonies were collected south of Gainesville, FL (November 1992). These colonies were brought back to the laboratory and separated from the remains of their mounds. Colonies were then mixed to produce a large composite colony; this was possible because polygyne colonies readily accept other polygyne workers and queens (Porter 1989). The composite colony was then divided into 30 uniform test colonies, each containing six queens, 1.0 g of workers and 1.0 g of brood. Colonies were given 2 wk to recover from the initial setup before beginning the experiment. Almost all of the queens in the experiment were inseminated as determined by their dissection after the experiment.

The colonies were assigned to one of six diets, consisting of one, two, or four crickets per day or

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one, two, or four crickets per day with access to unlimited amounts of sugar water. All colonies received unlimited water and excess nest space, and they were kept under constant light at 29 ± 1°C. The experiment was repeated (June 1993) for colonies (n = 12) receiving both crickets and sugar, because the colonies with more crickets did not grow as large as we expected.

The biomass of each colony was monitored weekly by removing the colony from its nest and quickly weighing it in a small cup. We used the average colony weekly weight, calculated from its weight at the beginning and end of the week, to correlate food intake with colony biomass. We would like to note here that the term intake in this article refers to food the fire ants collected and brought into their nest and not the amount of food ingested. The maximum sustained biomass was determined when a colony collected all the crickets it was given and reached zero or near zero growth for at least 2 wk. A final brood and worker weight was taken for each colony in the first experiment.

Cricket intake was estimated by subtracting the dry weight of the cricket remains from the estimated dry weight of the crickets presented to the colony during each week. Crickets used in the study consisted of male *Acheta domestica* L. with their legs removed to reduce size and weight variability. Variability in cricket biomass presented to each colony was ≈1–4% each week, depending on the number of crickets in the respective treatments. Average cricket dry weight was 0.075 ± 0.013 g (standard deviation) in the first run and 0.069 ± 0.011 g in the second run.

Sugar wads were prepared by soaking lab tissues in a 1.0-M solution of sucrose, then placing them into a drying oven at 60°C for at least 3 d. The sugar wads were presented to the colonies in special cups that had fluon placed around the outside top and holes melted half way up the side. These holes usually prevented the ants from using the cups to pile debris. The plastic cups and dry sugar wads were weighed before being placed in the test colonies. The sugar wads were then carefully moistened daily with water. After 1 wk, the sugar wads and cups were removed, dried for 3 d in a drying oven and weighed. Weekly sugar intake was determined by subtracting the dry weight of sugar wads before and after their presentation to the test colonies. Plastic cups that contained debris were eliminated from the study (n = 8).

Caloric intake was determined by multiplying the caloric value of the crickets (5.9 Kcal/g dry weight; Cummins & Wuycheck 1971) and sugar (4.0 Kcal/g dry weight) by the amount of dry weight collected.

For colony size analyses, colony biomass was log-transformed to equalize the variance and normalize the distribution. Colony biomass was not significantly different between the first and second trials that received both crickets and sugar (two-way analysis of variance [ANOVA] F = 1.11; df =
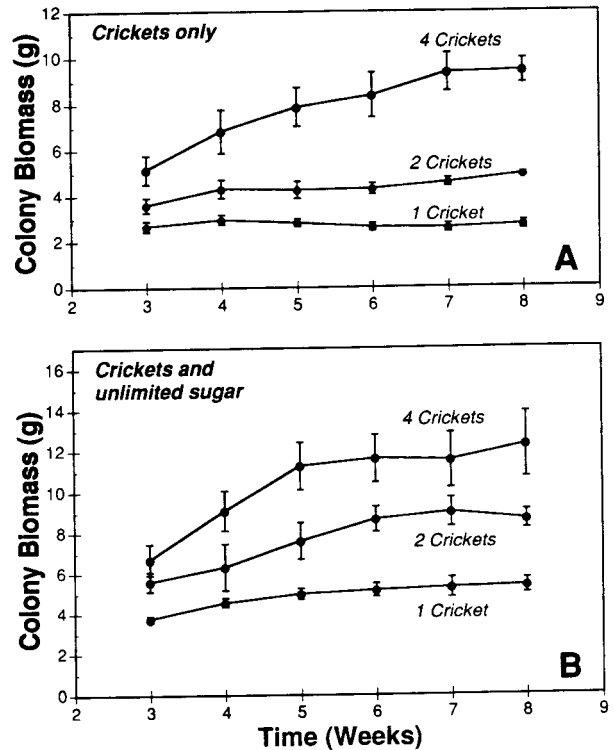

Fig. 1. Mean biomass of colonies (live weight) receiving only crickets plotted against time. (B) Mean biomass of colonies receiving crickets and sugar plotted against time. Error bars show standard errors of the means.

1, 33; P = 0.82); therefore, the results were combined and trial was dropped as a factor in subsequent analyses. A two-way ANOVA was used to examine differences in colony size resulting from the cricket and sugar treatments. Regressions were used to examine the relationship of cricket intake, sugar intake and caloric intake to colony biomass. A t-test was used to compare per gram caloric intake for colonies that received only crickets and those that received both crickets and sugar. Nine colonies were eliminated from analyses of colony growth because they did not reach the point of food limitation (n = 5) or they were small and sickly (n = 4). All colonies except those appearing sick were included in analyses of colony food intake. Subsequent means are shown plus or minus one standard deviation unless otherwise indicated.

Results

Doubling the cricket biomass caused an approximate doubling in colony biomass for the colonies receiving only crickets (Fig. 1A). However, colonies receiving sugar and crickets grew only 65 and 40% larger with the doubling of crickets from one to two and two to four, respectively (Fig. 1B). Not surprisingly, the two-way ANOVA of these data was significant both for the main effect of cricket number (F = 80.34; df = 2, 28; P < 0.0001) and for the interaction between crickets and sugar
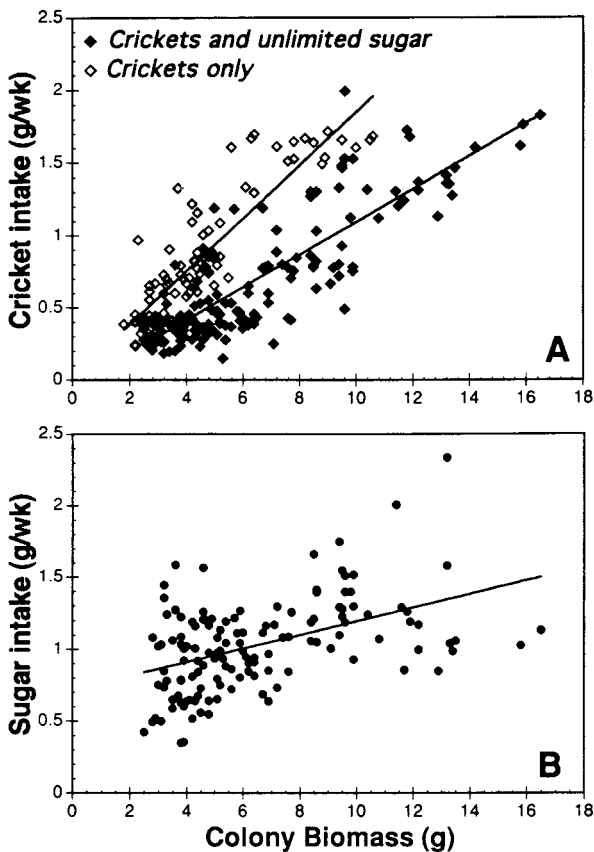
Fig. 2. (A) Weekly cricket intake (dry weight) as a function of colony biomass (live weight). Crickets only: $y = 0.183x + 0.017$, ($R^2 = 0.81$, $P < 0.0001$); Crickets and sugar: $y = 0.114x -0.044$, ($R^2 = 0.78$, $P < 0.0001$). (B) Weekly sugar intake (dry weight) for of colonies receiving both crickets and sugar regressed over colony biomass ($y = 0.047x + 0.72$, $R^2 = 0.22$, $P < 0.0001$).

Fig. 3. (A) Weekly total caloric intake of colonies regressed over colony biomass (live weight). Crickets only: $y = 1.054x + 0.76$, ($R^2 = 0.78$, $P < 0.0001$); crickets and sugar: $y = 1.12x + 0.33$, ($R^2 = 0.83$, $P < 0.0001$). (B) Weekly total caloric intake per gram of colony. In both diet treatments, caloric intake per gram of colony was independent of colony biomass over the 8-fold range examined in the experiment ($P > 0.05$).

($F = 4.93$; df $= 2$, 28; $P < 0.05$). The main effect of sugar was also significant (Fig. 1; $F = 69.12$; df $=1$, 28; $P < 0.0001$); colonies receiving sugar with crickets grew significantly larger than those that only received crickets. Colonies receiving one, two, or four crickets per day and unlimited sugar were 2.2-, 1.8-, and 1.3-fold larger than corresponding treatments that did not receive sugar water.

Cricket and sugar intake were closely correlated to colony biomass (Fig. 2). Cricket intake per gram of colony was greater in colonies receiving only crickets than in colonies receiving both sugar and crickets (0.186 ± 0.037 versus 0.106 ± 0.050 g cricket dry weight per gram of colony live weight per week; t-test, $t = 14.56$, df $= 249$, $P < 0.0001$). Sugar intake was also correlated to colony biomass (Fig. 2B; $R^2 = 0.22$, $P < 0.0001$).

Weekly food intake was transformed into caloric intake and a linear regression was performed to determine its relation to colony biomass. A plot of this relationship (Fig. 3A) shows that the caloric requirements of colonies with and without sugar were similar. The average caloric intake was 1.14
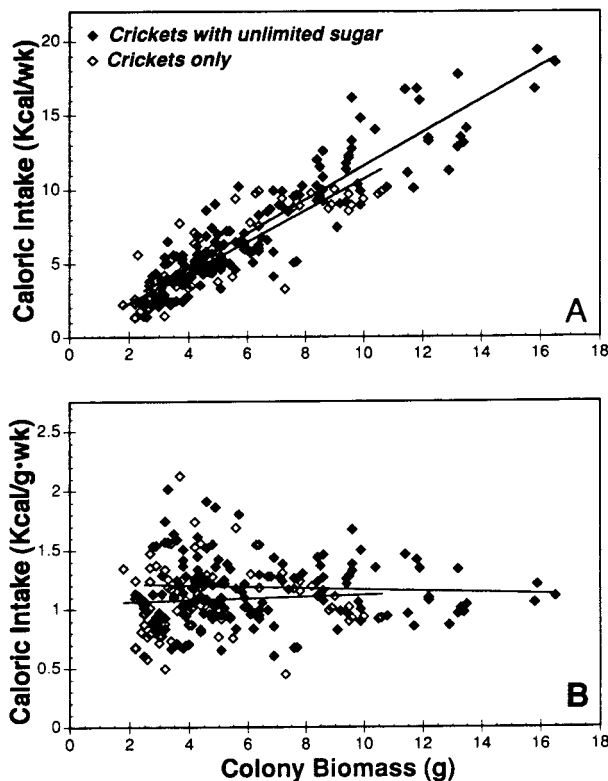
$\pm$ 0.29 Kcal/g live weight per week (Fig. 3B) or 3.46 $\pm$ 0.17 Kcal of food per gram dry weight per week. This constant was independent of colony biomass. However, sugar availability appeared to increase the average caloric intake of colonies by 8% (1.18 ± 0.27 versus 1.09 ± 0.29 Kcal of food per gram per week; $t = -2.53$, df $= 246$, $P = 0.012$). Variability in energy requirements resulting from colony composition was apparently too small to be detected. We also checked to see if rapidly growing colonies had higher rates of food collection than slower growing colonies, but variability was again too high to see any patterns.

At the end of the experiment, all the colonies were separated into worker biomass and brood biomass to determine their relationship to sugar and cricket intake for the last week. Worker biomass was correlated to sugar intake ($R^2 = 0.72$, $P < 0.0001$) and cricket intake ($R^2 = 0.76$, $P < 0.0001$). Brood biomass was moderately correlated to sugar intake ($R^2 = 0.58$, $P = 0.002$), but surprisingly it was not correlated to cricket intake ($R^2 = 0.13$, $P = 0.13$). The reason for the low correlation between larval biomass and cricket intake is

unclear. Time-lagging the relationship did not improve the correlation.

Discussion

Effects of Diet on Colony Biomass. Fire ant colonies grew larger and maintained a larger biomass with increasing cricket availability (Fig. 1). These results were similar to those Ayre (1966) Brian (1973), and Dlussky and Kupianskaya (1972) reported for *Myrmica* and *Formica* in their studies on feeding and colony growth. Brood production and maintenance require protein, and crickets were the only source. Doubling cricket availability should have allowed colonies to double in size. Colonies fed only crickets followed this pattern, approximately doubling colony biomass with a 2-fold increase in food availability. In contrast, colonies receiving unlimited sugar and crickets did not follow this pattern. They grew only 40–65% larger with the doubling of crickets. The reason for this difference is unclear, but it may be a real effect because the second trial produced results that were similar to the first. Colonies receiving crickets and unlimited sugar grew significantly larger than colonies receiving only crickets. This result was expected because of the increase in available food energy for the colonies.

Food Collection and Caloric Intake. Sugar solutions and arthropod prey are both important components of fire ant diets (Porter 1989). Studies on food flow in the fire ant showed that protein-rich foods are channeled primarily to the larvae (Howard & Tschinkel 1981, Sorensen & Vinson 1981). The absence of protein from fire ants diets, causes the colonies to cease brood production within a week or so (Porter 1989). Cricket intake was highly correlated with biomass in all of the colonies (Fig. 2). What was unexpected was the poor correlation between brood biomass and cricket intake because arthropod prey is essential for the production of brood.

Fire ant workers and workers of many other ant species rely on sugars as a fuel source to power worker activities, whereas protein stores are used for brood production (Brian 1973, 1983; Porter 1989). In the current study, sugar made up ≈55% of the total diet (dry weight) in colonies receiving both sugar and crickets, which comes to ≈45% of colony energy intake. The presence of sugar reduced the amount of crickets needed per gram of colony per week by 44% from 0.186 to 0.106 g (Fig. 2). These results should reflect the maximum and minimum range of cricket or protein collection of fire ant colonies in relation to sugar availability.

The most interesting results occurred when cricket and sugar intake were converted into caloric energy. Caloric intake was similar for all treatments (Fig. 3A; ≈1.14 ± 0.27 Kcal/g of colony per week); however, the per gram caloric intake for the colonies with sugar and crickets was 8% higher than the intake for colonies with only crickets. It

is unclear whether this difference was caused by lower usability of energy in the cricket tissue compared with sugar, a cricket tissue to Kcal conversion that was slightly high for the crickets we used, or increased metabolic rates associated with less conservative energy use in colonies with sugar caused by the presence of an unlimited food source.

It should be pointed out that the caloric values reported above are probably temperature dependent. Porter & Tschinkel (1993) reported that fire ant colonies with a limited food supply grew ≈30% less at 30°C than they did at 25°C. This difference approximated the 36% increase in metabolism that Calabi & Porter (1989) reported for the same temperature range. We would expect that temperature would affect rates of colony food collection in the same manner as it affects colony growth and metabolic costs.

The adjusted per gram caloric intake was independent of colony size over the 8-fold range tested in this experiment (Fig. 3B). Wheeler (1911) proposed "that colonies of social insects act like a single organism." If this is true we would hypothesize that food requirements in large fire ant colonies might decrease per gram of colony because of lower metabolic rates associated with larger organisms (Hoar 1975). If a colony is acting like a superorganism, then total food intake should increase as colony biomass increases, but it should decrease per unit weight of colony. However, one can look at a colony of fire ants as a group of individuals working together. The larger the colony becomes the less efficient it should become (Michner 1964), because of higher costs for transportation, communication, and food distribution associated with maintaining larger colonies. However, neither of these hypotheses were supported by the results of this experiment. Possibly, the size range of the colonies tested (1–18 g) was too small (mature colonies are often 200 g).

The findings of this study can be used to estimate the amount of food flowing into fire ant colonies. For example, a single mature colony weighing 200 g (Porter & Tschinkel 1987) would require about 230 Kcal to sustain it for 1 wk in the summer with temperatures averaging around 29°C (Markin et al. 1974). Thus, a field population containing 90 mature colonies per hectare would require ≈21,000 Kcal of food per week. This translates into a total dry weight of ≈4.0 kg of sugar and insects per week. On a wet weight basis, this would be ≈3.1 kg of insects and 12.9 liters of sugar solution per week, assuming an average molarity of 0.5 M, (Tennant & Porter 1991).

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References Cited

Ayre, G. L. 1966. Colony size and food consumption of three species of *Formica*. Entomol. Exp. Appl. 9: 461–467.

Brian, M. V. 1973. Feeding and growth in the ant *Myrmica*. J. Anim. Ecol. 42: 37–53.

1983. Social insects, ecology and behavioral biology. Chapman & Hall, London.

Calabi, P. & S. D. Porter. 1989. Worker longevity in the fire ant *Solenopsis invicta*: ergonomic considerations of correlations between temperature, size and metabolic rates. J. Insect Physiol. 35: 643–649.

Cummins, K. W. & J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Int. Ver. Theor. Angew. Limnol. 15: 1–158.

Davis, P. W. & E. P. Solomon. 1986. Processing food, pp. 559–573. *In* P. W. Davis & E. P. Solomon [eds.], The world of biology, 3rd ed. Saunders, Philadelphia.

Dlussky, G. M. & A. N. Kupianskaya. 1972. Consumption of protein food and growth of *Myrmica* colonies. Ekol. Pol. 20:73–82

Glancey, B. M., R. K. Vander Meer, A. Glover, C. S. Lofgren & S. B. Vinson. 1981. Filtration of microparticles from liquids ingested by the imported fire ant, *Solenopsis invicta* Buren. Insectes Soc. 28: 395–401.

Glunn, F. J., D. F. Howard & W. R. Tschinkel. 1981. Food preference in colonies of the fire ant, *Solenopsis invicta*. Insectes Soc. 28: 217–222.

Hoar, W. S. 1975. General and comparative physiology, 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.

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

Jensen, T. F. 1978. An energy budget for a field population of *Formica pratensis* Retz. (Hymenoptera: Formicidae). Natura Jutlandica. 20: 203–226.

Lofgren, C. S. 1986. History of imported fire ants in the United States, pp. 36–47. *In* C. S. Lofgren & R.

K. Vander Meer [eds.], Fire ants and leaf-cutting ants: biology and management. Westview, Boulder, CO.

Mackay, W. P. 1985. A comparison of the energy budgets of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). Oecologia (Berl.) 66: 484–494.

Markin, G. P., J. O'Neal, J. H. Dillier & H. L. Collins. 1974. Regional variation in the seasonal activity of the imported fire ant, *Solenopsis saevissima richteri*. Environ. Entomol. 3: 446–452.

Michner, C. D. 1964. Reproductive efficiency in relation to colony size in hymenopterous societes. Insectes Soc. 11: 317–341.

Nielsen, M. G. 1972. An attempt to estimate energy flow through a population of workers of *Lasius alienus* (Först) (Hymenoptera: Formicidae). Natura Jutlandica. 16: 99–107.

Petralia, R. S. & S. B. Vinson. 1978. Feeding in the larvae of the imported fire ant, *Solenopsis invicta*: behavior and morpholoical adaptations. Ann. Entomol. Soc. Am. 71: 643–648.

Porter, S. D. 1989. Effects of diet on the growth of laboratory fire ant colonies (Hymenoptera: Formicidae). J. Kans. Entomol. Soc. 62: 288–291.

Porter, S. D. & W. R. Tschinkel. 1987. Foraging in *Solenopsis invicta* (Hymenoptera: Formicidae) effects of weather and season. Environ. Entomol. 16: 802–808.

1993. Fire ant thermal preferences: behavioral control of growth and metabolism. Behav. Ecol. Sociobiol. 32: 321–329.

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

Tennant, L. E. & S. D. Porter. 1991. Comparison of diets of two fire ant species (Hymenoptera: Formicidae): solid and liquid components. J. Entomol. Sci. 26: 450–465.

Wheeler, W. M. 1911. The ant-colony as an organism. J. Morphol. 22: 307–325.

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