Insect. Soc. (2014) 61:281–287
DOI 10.1007/s00040-014-0353-7

Insectes Sociaux

RESEARCH ARTICLE

Laboratory fire ant colonies (*Solenopsis invicta*) fail to grow with Bhatkar diet and three other artificial diets

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Received: 13 December 2013 / Revised: 25 May 2014 / Accepted: 26 May 2014 / Published online: 27 June 2014

Abstract Various artificial diets have been used for rearing imported fire ants; however most of these diets include insect supplements. This study was designed to examine growth of red imported fire ant colonies (*Solenopsis invicta* Buren) on four artificial diets: a chemically undefined "oligidic" predator diet, two partly defined "meridic" diets utilized by Bhatkar and Whitcomb (Florida Entomol. 53: 229–232, 1970) and Dussutour and Simpson (Insect. Soc. 55: 329–333, 2008) for *Solenopsis* fire ants and *Rhytido-ponera* ants, respectively, and finally a completely chemically defined "holidic" diet utilized by Straka and Feldhaar (Insect. Soc. 54: 100–104, 2007a, Insect. Soc. 54: 202, 2007b Erratum) for carpenter ants. Crickets and sugar water were used as a standard diet. After 6 weeks, fire ant colonies fed crickets and sugar water were healthy and had grown considerably. In contrast, colonies fed the artificial diets showed little or no growth demonstrating that these diets are not suitable for rearing healthy fire ant colonies. Nevertheless, the holidic or entirely synthetic Straka diet may provide a suitable basis for further studies of fire ant dietary requirements because it resulted in modest production of all brood stages. We advise caution in using diets that mix sugar and protein into a single "all in one" diet because workers and brood have differing dietary requirements.

Electronic supplementary material The online version of this article (doi:10.1007/s00040-014-0353-7) contains supplementary material, which is available to authorized users.

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Keywords Formicidae · Diet · Meridic · Oligidic · Holidic · Mass rearing · Insect culture

Introduction

Various artificial diets have been suggested for rearing imported *Solenopsis* fire ants (Khan et al., 1967; Bhatkar and Whitcomb, 1970; Williams et al., 1980; Banks et al., 1981; Porter, 1989; Vogt, 2003). Most of these diets have insects as a main component because fire ants feed on insects and other small invertebrates and most importantly because insects promote growth of laboratory colonies and normal development (Sorensen et al., 1983; Vinson and Greenberg, 1986; Williams et al., 1987; Porter, 1989). A diet of beef liver and sugar water is also effective for rearing laboratory fire ant colonies for up to 6 months (Gavilanez-Slone and Porter, 2013).

Fire ants collect large quantities of sugary liquids (Tennant and Porter, 1991), which are the main source of energy for adult workers because they are unable to ingest solid foods (Vinson, 1968; Glancey et al., 1981). A liquid sugar food source significantly increases the size and growth rate of laboratory colonies of the red imported fire ant, *Solenopsis invicta* Buren (Williams et al., 1980; Porter, 1989; Macom and Porter, 1995). Solid food items collected by foraging workers are consumed almost exclusively by fourth instar larvae which, unlike the workers, need large amounts of protein for growth and development (Petralia and Vinson, 1978; Weeks et al., 2004).

Artificial diets used for rearing arthropods can be classified as holidic, meridic and oligidic based on their components (Dougherty, 1959; Dadd, 1970; Vanderzant, 1974). Holidic or synthetic diets are fully chemically defined, and are important in the study of nutritional requirements. Meridic diets contain a holidic base with one or more crude or poorly defined materials. Oligidic diets are not chemically defined because they are formed of complex or crude natural materials such as insects, meats, or plant materials.

Mankowski and Morrell (2004) and later Straka and Feldhaar (2007a, b Erratum), developed a holidic diet for carpenter ants based on several holidic diets for rearing aphids. Both diets were complex mixtures of amino acids, fatty acids, vitamins, lipogenic growth factors, glucose, salts, and trace minerals. Meridic diets and oligidic diets are less costly and much more easily formulated than holidic diets. Oligidic diets for ants have been described as early as (1904), when Fielde recommended foods such as sponge-cake moistened with honey or molasses, banana, apples, mashed walnuts, and parts of insects. Bhatkar diet (Bhatkar and Whitcomb, 1970) is a meridic diet which has been widely used (Hölldobler and Wilson, 1990) and is a popular diet for rearing ant colonies in the laboratory (Straka and Feldhaar, 2007a). Recently, Dussutour and Simpson (2008) developed a meridic diet containing whey protein, calcium caseinate and albumin for studies of *Rhytidoponera* ants.

Effective standardized diets are essential for many research projects involving laboratory reared arthropods (Lapointe et al., 2008). Artificial diets for rearing fire ants have the advantages of being reliably disease free, less costly, and potentially more nutritionally consistent than insect prey. However, despite these potential advantages, the effectiveness of artificial diets, especially Bhatkar diet, have not yet been properly confirmed with *Solenopsis* fire ant colonies. This study was designed to compare the growth of *S. invicta* fire ant colonies fed a standard diet of crickets and sugar water against four artificial diets: Bhatkar diet, Dussutour diet, Straka diet, and an experimental predator diet. We also retested the Bhatkar diet using the original vitamin-mineral formulation because the McKesson Bexel capsule is no longer available.

Materials and methods

All experimental colonies, except where noted, were reared from founding queens collected in Gainesville, FL in June 2011. Colonies were maintained in a rearing room at 28 ± 1 °C (SD) in nest trays [for rearing details see supplementary material, Gavilanez-Slone and Porter (2013), Valles and Porter (2013)].

The agar-based test diets were prepared monthly, refrigerated for 1–2 days, then cut into small cubes of 1.5 ± 0.4 g (SD) and kept frozen at −20 °C to allow longer shelf life. Test colonies were fed whole frozen adult house crickets, *Acheta domesticus* (L.) (Ghann's Cricket Farm Inc., Augusta, GA), the control standard diet. All diets and sugar water were presented ad libitum (M-W-F) unless otherwise specified.

At the end of each experiment, brood and workers were separated using sorting sheets (Porter and Tschinkel, 1985) and weighed. Final colony weights were log-transformed to normalize variance. Either a one- or two-way general linear model analysis of variance (GLM ANOVA) was used to evaluate final colony weight and the brood to worker ratios. Tukey–Kramer multiple-comparison tests ($\alpha = 0.05$) were performed to compare means (Hintze, 2001; NCSS, 2001).

Dussutour and predator diet experiment

Eleven established colonies were used to evaluate: (1) a modified meridic Dussutour diet ($n = 4$ colonies), (2) an experimental oligidic predator diet ($n = 4$), and (3) the standard cricket and sugar water diet ($n = 3$). The Dussutour diet (Dussutour and Simpson, 2008) consisted of whey protein, calcium caseinate and albumin (see supplementary material for details about preparation and ingredients). The predator diet contained whey protein, pollen substitute, Brewer's yeast, and sugar in an agar matrix (see supplement for details). Colonies were reduced to 2 g of brood and 1 g of workers and fed three house crickets per week, and provided sugar water ad libitum for 2.5 weeks before starting the experiment. Colonies weighed 4–5 g at the start of the test. This experiment was conducted from 18 February to 30 March 2012.

First Bhatkar diet experiment

Fourteen colonies were used to evaluate the Bhatkar diet with a sugar water supplement against the standard house cricket and sugar water diet. The Bhatkar diet consisted of raw eggs, honey, and a vitamin supplement blended in an agar matrix. We modified the original recipe by reducing the water by half and substituting a Mature Complete Multivitamin tablet (Equate, Wal-Mart) for a McKesson Bexel capsule which is no longer available (see Bhatkar and Whitcomb 1970 and supplementary material for details). Six small colonies (1 g brood, 0.5 g workers) and another eight larger colonies (2 g brood, 1 g workers) were used. Three small and four large experimental colonies were randomly selected for each of the two treatments. Colonies were reared for 6 weeks (19 Dec 2011–31 Jan 2012).

Straka diet and second Bhatkar diet experiment

Twenty-four colonies were used to evaluate the holidic Straka diet and the second Bhatkar diet against the standard cricket and sugar water diet (see supplementary material for formulation details). The Straka diet was prepared as described by Straka and Feldhaar (2007a, b Erratum). The second Bhatkar diet used in this experiment was prepared as in the first Bhatkar experiment, but instead of a multivitamin tablet, we used the individual chemicals as contained in the original McKesson Bexel capsule (see supplementary material). Half of these colonies were from founding queens collected in the Savannah River Site, a National Environmental Research Park in South Carolina and the other half were from queens collected in the Gainesville, FL area both in May 2012. Test colonies were reduced to an average of 1.30 ± 0.11 (SD) g of brood and 1.28 ± 0.10 g of workers. The experimental colonies were reared in 17 × 12 × 6 cm boxes (R750B, Sterling King Products) with clear lids containing 16 × 125 mm nest tubes. Nest tubes were added as colonies grew. Colonies receiving the Straka and Bhatkar diets were fed ad libitum three times a week (M-W-F), but growth of the cricket and sugar water standards were probably limited by the use of the banded cricket (*Gryllodes sigillatus* F. Walker) in place of the house cricket (*A. domesticus*) which was used in the previous tests (Gavilanez-Slone and Porter, 2013).

The cricket colonies received ad libitum 1.5 M (513 g/L) sugar water presented in 10 × 75 mm test tubes plugged with a short piece of cotton wick. Neither the Straka colonies nor the Bhatkar colonies received supplemental sugar water to ensure nutrient intake in these test diets was not reduced by consumption of an alternate food source. This experiment ran from 11 Feb to 25 Mar 2013.

At the end of the experiment, we added 1.5 M sugar water tubes to all eight of the Straka colonies and continued feeding them the Straka diet for an additional 4 weeks as a pilot test. Three of these colonies were also supplemented with canola oil and three colonies were supplemented with a soft paste of 100 % whey protein concentrate to test for improved growth.

Results

Workers in the following tests readily approached, collected, and ingested the treatment and standard diets. Collection of each test diet was determined by observing the workers carrying off the diet and bringing it to or pilling it by their nests. Ingestion of each of the diets was confirmed by adding blue food coloring (0.1 % by weight, royal blue concentrate paste, Icing Colors, Wilton Industries, Inc.) to the diets in 2–3 newly established colonies per diet. Then we observed the presence of the ingested blue coloring in both workers and brood 24, 72, 96, and 168 h after being given access to test diets containing the food coloring.

Dussutour diet and predator diet experiment

While the house crickets and sugar water diet produced rapidly growing colonies; the Dussutour and predator diets with their sugar water supplements both failed to produce rapid growth normally seen in healthy colonies (Fig. 1A; GLM ANOVA, $F_{2,10} = 52.7$, $P < 0.0001$). By the end of the 6-week test, the brood to worker ratios for the cricket, predator and Dussutour diets were 1.2, 0.20, and 0.14 respectively (Fig. 1A; GLM ANOVA, $F_{2,10} = 28.6$, $P = 0.0002$). Colonies receiving the two artificial diets contained some larvae but very few pupae, indicating a developmental problem.

First Bhatkar diet experiment

Workers readily approached, collected, and ingested the Bhatkar diet. However, after 6 weeks, the total final weight of *S. invicta* (workers + brood) in the diet treatments differed substantially (Fig. 1B; GLM 2-WAY ANOVA, $F_{1,14} = 838.6$, $P < 0.0001$). The total final weight of colonies fed Bhatkar diet declined 23 % (13 and 28 % for the small and large colonies, respectively). Colonies fed Bhatkar diet contained no pupae and showed an overall 84 % decline in the total final weight of brood (80 and 86 % for the small and large colonies, respectively). A small amount of larvae were present in each colony, but they were apparently incapable of pupating because no pupae were present. Colonies receiving Bhatkar diet were clearly not healthy and not growing. Worker weight increased slightly,

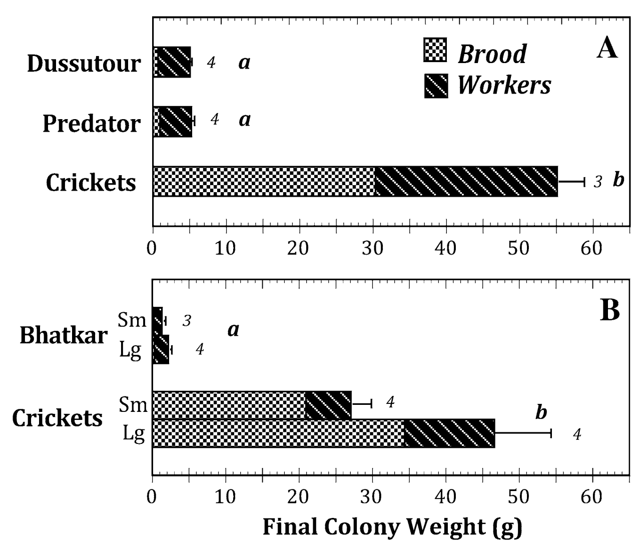

Fig. 1 Mean final colony weight (brood plus worker live weight ± SE) of *Solenopsis invicta* fire ant colonies in the Dussutour and predator diet experiment (**A**), and the first Bhatkar diet experiment (**B**) both after six weeks. Only large (Lg) colonies were used in the top experiment (**A**) while both large and small colonies were used in the lower experiment (**B**). Mean final weights for both workers and worker brood are shown for each treatment. The number of replicate colonies is shown by *each bar*. *Different letters* indicate significant differences among diet treatments (Tukey–Kramer multiple-comparison tests, $P < 0.05$)

but probably only because pupae at the start of the experiment completed development into workers. The colonies that received the standard house cricket and sugar water diet were healthy, and the final average weight was 22 times heavier than the initial biomass (Fig. 1B). Colony size (large versus small) was also significant as a factor (GLM 2-WAY ANOVA, $F_{1,14} = 24.3, P < 0.0005$); however, the interaction between colony size and diet was not significant ($P > 0.05$). Separate analyses of the final weight of brood and workers revealed similar results. Brood to worker ratios among both diet treatments were significantly different, but not between colony sizes nor their interaction with diet type (Fig. 1B; GLM 2-WAY ANOVA, $F_{1,14} = 169.5$, $P < 0.0001$; $F_{1,14} = 2.15$, $P = 0.171$; and $F_{1,14} = 1.73$, $P = 0.215$, respectively).

Straka diet and second Bhatkar diet experiment

Colonies that received the banded cricket (*G. sigillatus*) and sugar water diet were substantially heavier than the second Bhatkar and Straka diets (Fig. 2; GLM 2-WAY ANOVA, $F_{2,23} = 86.6$, $P < 0.0001$). Queen source (FL and SC) and its interaction with diet type were not significant ($F_{1,23} = 0.07$, $P = 0.79$ and $F_{2,23} = 0.58$, $P = 0.57$, respectively). Total final weights of colonies fed Straka and Bhatkar diets were not significantly different ($P > 0.05$, Tukey–Kramer test). Results for the second Bhatkar diet were similar to the first Bhatkar diet experiment above, in that colonies produced a small number of larvae but no pupae (Figs. 1B, 2). However, unlike the Bhatkar diet, colonies fed the Straka diet contained all brood stages (eggs, larvae, and pupae) and about 35 % of brood were pupae. The percent declines in the amount of brood for Bhatkar and Straka diets at the conclusion of the test were 96 and 67 %, respectively (Fig. 2). Brood to worker ratios among these diet treatments were statistically different (GLM ANOVA, $F_{2,23} = 49.7$, $P < 0.0001$; $\log(x + 0.01)$ transformation). Colonies fed crickets, Straka, and Bhatkar diets had an average brood to worker ratio that all differed significantly from each other (0.90, 0.22, and 0.03, respectively; Tukey–Kramer test).

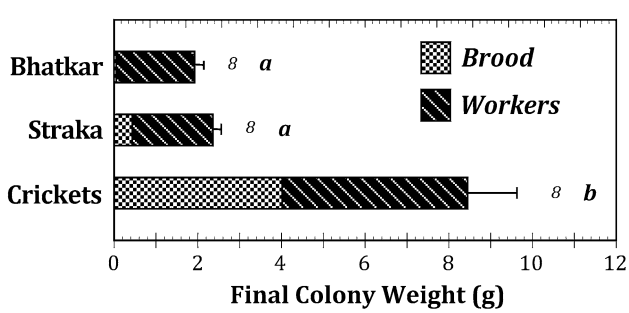

Fig. 2 Mean final weight (brood plus worker live weights ± SE) of experimental *Solenopsis invicta* fire ant colonies in the Straka and second Bhatkar diet experiment after 6 weeks. Mean weight of both workers and worker brood is shown for each treatment. The number of replicate colonies is shown by *each bar*. *Different letters* indicate significant differences among diet treatments (Tukey–Kramer multiple-comparison tests, $P < 0.05$)

Supplementing the Straka test colonies with (1) sugar water alone, (2) canola oil and sugar water, or (3) whey protein and sugar water for an additional 4 weeks did not improve the effectiveness of this diet. In this pilot test, colonies in all three treatments declined in weight [−24 ± 7 % (SE), −18 ± 6 %, −5 ± 6 %, respectively; $P > 0.05$, GLM ANOVA] compared to their weight at the end of the original test above (see Fig. 2).

Discussion

Tests of the Bhatkar, Dussutour, and predator diets were disappointing (Figs. 1, 2). Colonies fed these diets gradually reduced brood production and almost ceased growing. Porter (1989) reported that a Bhatkar diet supplemented with cooked eggs and a vegetable purée produced no colony growth. The main issue with the artificial diets is likely nutritional (Mankowski, 2002; Lapointe et al., 2008) instead of gustatory given that colonies actively gathered, ingested, and stored large quantities of these artificial diets.

We found Bhatkar diet entirely unsuitable for rearing fire ants because colonies did not grow (Figs. 1, 2) and were not able to produce pupae. Other studies have also reported or provide data which indicate that Bhatkar diet is unsuitable for rearing fire ants and other ants when used without insect supplements (see Williams et al., 1980; Buschinger and Pfeifer, 1988; Keller et al., 1989; Porter, 1989; Alloway et al., 1991; Straka and Feldhaar, 2007a; Dussutour and Simpson, 2008; Sorvari and Haatanen, 2012). Bhatkar and Whitcomb (1970) claimed that their diet was good for rearing several species of ants, but they did not report any observations of colony brood production or growth to support this claim. The use of a different multi-vitamin than that used by Bhatkar and Whitcomb (1970) is probably not an explanation for the failure of this diet in our first experiment (Fig. 1B). We recreated the McKesson multivitamin from scratch and the results in the second Bhatkar diet experiment were similar to the first experiment (Fig. 2), ending with few larvae and no pupae. The elimination of the sugar water supplement from the second test demonstrates that the problem was not a consequence of poor nutrition from consuming too much sugar water in place of the Bhatkar diet.

Despite the total absence of evidence for the efficacy of Bhatkar diet, a recent inspection of the Web of Science Citation Report (Nov 2013) shows that the Bhatkar diet has been cited in 215 published articles since 1973 with the yearly citation rate gradually increasing up to an average of about 15 times per year in the last 5 years. In short, we agree with Buschinger and Pfeifer (1988) and Keller et al. (1989) that Bhatkar diet should not be used alone for rearing ants. We also recommend against its use as a dietary supplement because no evidence is currently available to show net benefits of preparing and using this diet.

According to Dussutour and Simpson (2008), their standardized diet was superior for rearing colonies of *Rhytidoponera* ants when compared to a Bhatkar diet and similar to a diet of *Drosophila* and honey-water. We, however, found Dussutour diet unsuitable for rearing *S. invicta* fire ants (Fig. 1A). Fire ant workers were attracted to it and they fed on it, but they did not thrive and brood production essentially stopped. Modified Dussutour diets fed to fire ant colonies in a recent study of protein and carbohydrate ratios showed substantial declines in food consumption over a 7-week period indicating that test colony size and/or health also declined considerably (Cook et al., 2010). We suspect that Dussutour diet may not allow much colony growth for *Rhytidoponera* ants either, because pupa to worker ratios were 60–80 % lower than those from field colonies (Pamilo et al., 1985; Dussutour and Simpson, 2008; Lubertazzi et al., 2010). Suboptimal temperatures might explain why growth was similar for colonies fed the Dussutour and fly diets (Dussutour and Simpson, 2008), if rearing temperatures were at or near the lower limit for brood production (Porter, 1988).

The original predator diet has been successfully used for rearing several species of chrysopids (*Chrysoperla externa*, *C. rufilabris*, and *C. carnea*) and a species of lady beetle (*Cryptolaemus montrouzeri*, unpubl. obs.). However, the predator diet clearly lacked something fire ants need in order to thrive (Fig. 1A).

While the holidic Straka diet was not suitable for rearing growing fire ant colonies, modest numbers of fire ant brood were capable of completing development with this diet (Fig. 2). Consequently, the Straka diet may be an acceptable starting point for detailed studies of fire ant nutrition. The Straka diet has been successfully used to investigate nutritional contributions of microbial symbionts in *Camponotus* carpenter ant colonies (Blüthgen and Feldhaar, 2009) and similar studies of microbial symbionts could be attempted with fire ants. Further studies with a holidic diet might also provide insights into why the artificial diets in this paper failed to produce healthy growth and how these diets could be improved. Recent studies have provided evidence that inland ant populations are sodium limited (Kaspari et al., 2008; Resasco, 2013). An effective holidic diet would be useful in assessing the impacts of sodium limitation on laboratory fire ant colonies.

All of the artificial diets tested in this paper (Bhatkar, Dussutour, Straka and the predator diet), are examples of "all-in-one" diets that combine both proteins and sugars into a single diet. We are skeptical that "all-in-one" diets are appropriate for rearing fire ants and perhaps most other ant species because solid protein-rich foods are entirely processed, and consumed by ant larvae (Howard and Tschinkel, 1981; Sorensen and Vinson, 1981; Cassill and Tschinkel, 1999). Worker ants possess a buccal tube filter in their head which filters out all solids down to bacterial sizes (Petti, 1998; Oi, 2006). Adult workers, on the other hand, need sugars to power their activities, but they need very little protein because they are not growing. Not surprisingly, laboratory fire ant colonies without larvae ignore insect prey, while sugary liquids remain attractive (Porter, 1989). Furthermore, field studies with fire ants indicate that protein and carbohydrate food sources are usually collected separately; that is, foragers return with either protein-rich arthropod prey in their mandibles or carbohydrate-rich liquids in their crop (Tennant and Porter, 1991). In short, mixing solid proteins and liquid carbohydrates into a single diet is probably acceptable for larvae, but mixtures may make it hard for fire ant workers and workers of other ant species to ingest the liquid sugars that they need. Indeed, studies forcing workers of *Rhytidoponera* (Dussutour and Simpson, 2009) and *Solenopsis* (Cook et al., 2010) to consume diets low in sugar and high in protein considerably increased rates of worker mortality. Dussutour and Simpson (2012) reported that *Lasius* workers did better when they had a choice of separate protein and carbohydrate diets.

Honey bees (*Apis mellifera* L.) and fire ants have a similar divided food flow. In honey bees, nurse workers use pollen as the main source of protein to produce glandular secretions like royal jelly and also to feed larvae and young adult bees; while honey, the main carbohydrate source, is consumed mostly by foraging workers (Winston, 1991). Unlike many ants (Eisner and Happ, 1962), honey bees do not have an infrabuccal filter so they are able to ingest and digest solid particles like pollen (Bailey, 1952).

In conclusion, more work needs to be done regarding how specific nutrients and nutrient ratios influence the development of fire ant larvae and the growth of fire ant colonies. Even though several artificial diets have been proposed, none has yet proven to be suitable for maintaining healthy growing fire ant colonies (Figs. 1, 2) without insect or liver supplements (Gavilanez-Slone and Porter, 2013).

Acknowledgments The authors appreciate the assistance provided by Darrell Hall (CMAVE, Gainesville, Florida) in helping with processing samples and feeding the colonies. We thank Ulrich Bernier, Alisa Huffaker, Rodney Nagoshi, Peter Teal, Steven Valles, Robert Vander Meer (all CMAVE), and Aaron Hirko (SFC, Gainesville) for sharing chemicals needed for the diets. We thank Robert Vander Meer (CMAVE), Deby Cassill (USF, Tampa, Florida), Andrea Dussutour (CNRS, Toulouse, France) and an anonymous reviewer for helpful comments. Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and

does not imply recommendation or endorsement by the U.S. Department of Agriculture.

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