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Technical article

Description of a simple synthetic diet for studying nutritional responses in ants

A. Dussutour and S.J. Simpson

School of Biological Sciences, The University of Sydney, NSW 2006, Australia, e-mail: adussutour@usyd.edu.au

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Abstract. A chemically defined diet is a powerful tool for the study of nutritional physiology. We have developed a simple, standardized diet for *Rhytidoponera* ants to facilitate experiments on nutrititional regulation and nutrient balancing in these ants. Colonies of *Rhytidoponera metallica* were fed with a standardized diet, containing a 1:2 ratio of total proteins to digestible carbohydrates. After 8 weeks, colony performance (number of brood raised, the mass of pupae, and the mortality of workers) was superior to that of colonies fed with Bhatkar-Whitcomb diet and similar to colonies fed with *Drosophila* and honey-water.

Keywords: Artificial diet, nutrition, colony growth, green headed ant.

Introduction

A major challenge for any animal is to meet the demands of growth, development and reproduction in a nutritionally heterogeneous environment. Extensive studies have elucidated the nutritional regulatory strategies and mechanisms employed by a range of non-social insects and other animals (e.g. Raubenheimer and Simpson, 1999; Simpson and Raubenheimer, 2000; Simpson et al., 2004; Raubenheimer and Jones, 2006, Raubenheimer et al., 2007). Herbivorous, omnivorous and predatory insects have been shown to possess separate appetites for protein and either carbohydrate or fat, which underlie an ability to compensate for changes in nutrient density in foods and to select among nutritionally complementary foods to achieve a nutritional 'intake target'. How social insects such as ants maintain nutrient supply at both a collective and an individual level in response to changes in the nutritional composition of available foods, colony demography and larval growth is not known (but see Kay, 2004) Such an understanding would provide an important extension to models of collective behaviour and to the study of nutritional ecology.

Ants and all social insects are faced with a nutritional challenge. Colonies need to adjust their harvesting strategy to the internal demands for nutrients within the nest, where larvae and workers have different needs. Worker ants need carbohydrates as a source of energy (Markin, 1970; Schneider, 1972; Wilson and Eisner, 1957), whereas larval growth relies more heavily on proteins (Cassill and Tschinkel, 1999; Markin, 1970; Sorensen and Vinson, 1981). Hence, numerous authors have shown that the distribution of food among the different individuals of the colony indeed depends upon the type of food collected (Abbott, 1978; Howard and Tschinkel, 1980, 1981a,b; Sorensen and Vinson, 1981; Sorensen et al., 1981, 1985; Sudd, 1967; Wilson, 1971).

To investigate the nutritional responses of ants – specifically the green headed ant, *Rhytidoponera metallica* – we wished first to develop a standardized artificial diet which will support colony growth and provide the opportunity to allow experimental control over nutritional manipulations.

The most commonly used artificial diet for ant breeding is the chemically undefined Bhatkar and Whitcomb diet (Bhatkar and Whitcomb, 1970). This diet comprises whole raw egg, honey and the contents of vitamin-mineral capsules set in agar (Bhatkar and Whitcomb, 1970). When kept on Bhatkar-Whitcomb diet alone, several ant species cannibalised more larvae (Buschinger and Pfeifer, 1988) or raised fewer pupae than did colonies supplied with dead insects and sugar water or diluted honey (Porter, 1989; Alloway et al., 1991), which is why numerous studies have supplemented this diet with added protein in the form of insect pieces (e.g Banks et al., 1981; Porter, 1989; Vogt, 2003), raw eggs (Bhatkar and Whitcomb, 1970), or steak

Table 1. Quantity of protein and carbohydrates in each of the five foods used in the first experiment. The numbers in bracket represent the actual quantity of protein.

PC	Whey Protein Concentrate (g)	Calcium caseinate (g)	Whole Egg Powder (g)	Sucrose (g)	Water (mL)	Agar (g)
3:1	22.3 (18.6)	20.4 (18.6)	16 (7.8)	15	300	4
2:1	19.3 (16.1)	17.7 (16.1)	16 (7.8)	20	300	4
1:1	13.3 (11.1)	12.2 (11.1)	16 (7.8)	30	300	4
1:2	7.3 (6.1)	6.7 (6.1)	16 (7.8)	40	300	4
1:3	4.3 (3.6)	4 (3.6)	16 (7.8)	45	300	4

(Keller et al., 1989). At the other extreme of chemical definition, the completely chemically defined (holidic) diet recently published by Straka and Feldhaar (2007) was sufficient to guarantee a high brood production and normal growth rate of larvae in carpenter ants, *Camponotus floridanus*. However, because it comprises all amino acids in free form, the diet is somewhat expensive and time-consuming to prepare.

Our aim was to derive a diet which would support good development of ant colonies and would be straightforward to prepare, yet be chemically standardized. In order to reach this compromise we decided to use protein powders rather than a mixture of free amino acids. Protein powders have been used in many other insect diets (Singh, 1977; Cohen, 2004). Casein, the most commonly used protein powder, does not provide a good balance of amino acids, in particular being deficient in methionine/cysteine. Hence we chose to use a mix of three different protein powders. The most successful mix we tried combined whey protein, calcium caseinate and albumin. Interestingly, ants would not accept the protein mix used in the diet that has been used in many nutritional studies on locusts and caterpillars, comprising a 3:1:1 mixture of casein, albumin and peptone (stemming from Simpson and Abisgold, 1985 after Dadd, 1961).

It is well known that the ratio of protein to carbohydrate (P:C) in the diet is critical to performance in a range of insect species (Raubenheimer and Simpson, 1999; Simpson et al., 2004; Lee et al., 2008). In ants, the artificial diets used so far contain a low P:C (Bhatkar and Whitcomb diet: protein concentration 1.4%, P:C, 1:12; Straka and Feldhaar diet: 2.1%; P:C, 1:9.5). To establish which P:C was most effective for rearing ant colonies we needed to conduct a preliminary experiment in which ant colonies were given one of several foods differing in P:C. Performance was assessed by measuring the number of dead ants and the number of brood produced. The ratio that gave the best performance was then chosen for detailed testing against the Bhatkar and Whitcomb diet and a more natural diet (honey and adult *Drosophila*).To assess the suitability of our diet we counted for each colony the number of larvae produced, the number and weight of pupae raised and the number of dead ants after eight weeks.

Methods

Species and rearing conditions

The ponerine ant genus *Rhytidoponera*, commonly called green headed ants, is distributed throughout Australia and its neighboring islands. Colonies of *R. metallica* are found under rocks, in decaying logs, or in leaf-litter and superficial layers of soil (Haskins and Haskins, 1979; Ward, 1986). In *R. metallica*, nest founding occurs mainly by budding (Haskins and Haskins, 1979) and is associated with the presence of multiple fertilised egg-laying workers (gamergates) in the colony (Ward, 1986). Haskins and Haskins (1983) mentioned that from 5 to 15% of the females become gamergates in *R. metallica.* As with most ponerines, workers are monomorphic (Haskins and Haskins, 1979).

First experiment

Six colonies of almost 1500 ants were collected in October 2006 in Sydney, Australia. We collected five groups of 250 workers from each colony, yielding a total of five groups of six experimental colonies. These experimental colonies were housed in plastic boxes (20*20*6 cm), the bottoms of which were covered by a layer of cardboard moistened by a cotton plug soaked from a water reservoir underneath. Each box was connected to a foraging arena (20*20*10 cm) by a transparent tube. We allowed the experimental colonies to settle for two weeks before doing the experiment. During this period we made sure that each colony produced fertilized eggs indicating the presence of gamergates. We removed these eggs when we started the experiment.

In total, five foods differing in their content of protein (P) and digestible carbohydrates (C) were prepared: 3:1, 2:1, 1:1, 1:2 and 1:3. The protein content of all the foods consisted of a mix of calcium caseinate (Myopure), whey protein (Myopure) and whole egg powder (Myopure), while sucrose was the digestible carbohydrate. The quantity of whole egg powder was kept constant in each diet in order to keep the quantity of fat identical (Table 1). We added 2 g of Vanderzant vitamin mixture for insects (Sigma) and 1 g of Methyl 4-hydroxybenzoate (Sigma) in each diet. No mineral supplement was necessary, as levels in protein powders were sufficient (Table 1). The food was presented to the insects in a 1.3% agar solution at a 5:1 ratio of agar solution to dry mass of ingredients. Further preparation details are given below.

Every two days experimental colonies received a 2 cm^3 block of food of the five foods differing in their protein to carbohydrate ratio for 6 weeks. The first group of 6 experimental colonies received 3:1, the second group 2:1 and so on. The remains of the previous block of food were removed before giving a new one. All experimental colonies were provided with distilled water ad libitum.

To assess colony performance the number of larvae and the number of dead ants within each experimental colony was evaluated after 6 weeks.

Second experiment

Ten colonies of *R. metallica* were collected in January 2007 in Sydney, Australia. All colonies were considered mature because males were present, signifying colony reproduction. The soil was soft in the collecting site, making it easy to excavate the nests and collect almost all colony members.

We collected three groups of 250 workers (including gamergates, see above) from each colony, yielding a total of three groups of ten experimental colonies. These experimental colonies were housed in similar nest that the ones describe above. None of these experimental colonies had brood when we started the experiment.

The first group of 10 experimental colonies was supplied with Bhatkar and Withcomb diet (1970). The second group of ten colonies received honey (15% w/v) as well as 100–200 adult *Drosophila melanogaster.* The third group of ten colonies received our standardized diet with a protein to carbohydrate ratio 1:2. All the experimental colonies were fed twice a week (Monday and Thursday) for 8 weeks. Every experimental colony fed with artificial diet received a 2 cm^3 cube of diet. The remains of the previous block food were removed before giving a new one. All experimental colonies were provided with distilled water ad libitum.

Bhatkar-Whitcomb diet was modified using Vanderzant vitamin mixture for insects instead of the vitamin-mineral capsule (McKesson Bexel). The diet was prepared as follows: 500 ml distilled water were boiled with 10 g Agar-Agar (Sigma). Two raw eggs, 2 g of Vanderzant vitamin mixture for insects (Sigma) and 170 g honey were stirred into another 500 ml of water and mixed with the cooled agar solution. The mixture was poured into Petri dishes dish and stored at 4°C (modified after Bhatkar and Whitcomb, 1970).

The standardized diet was prepared as follows: 500 ml distilled water was boiled with 10 g Agar-Agar (Sigma). Into another volume of 250 ml was stirred 35 g whole egg powder (Myopure), 35 g whey protein (Myopure), 35 g calcium caseinate (Myopure), 2 g of Vanderzant vitamin mixture for insects (Sigma), 1 g of Methyl 4-hydroxybenzoate (Sigma) and 165 g sucrose (Sigma) and mixed with the agar solution. The mixture was poured into Petri dishes dish and stored at 4°C. The detailed nutritional composition of the diet is presented in Table 2.

To assess field colony performance, soon after collection, the number of workers, larvae and pupae within each colony was counted and 30 pupae per colony were weighed. For the experimental colonies, we counted the number of ants, pupae and larvae in each colony at the end of the experiment (after 8 weeks). We then weighed each pupa to evaluate colony performance (scale: XS105 Dual Range, Mettler Toledo, d=0.01 mg). To asses mortality in the experimental colonies we counted the number of dead ants in each nest.

Table 2. Nutrient composition of the standardized artificial diet diluted in 1L water, based upon data provided by manufacturers of the ingredients.

AMINO ACIDS (g)		**VITAMINS (mg)**	
Isoleucine	4.37	Vitamin E	2.93
Leucine	8.57	Vitamin D	0.01
Valine	5.03	Vitamin A	0.01
Lysine	6.80	Vitamin C	0.54
Methionine	2.20	Thiamin (B1)	0.14
Phenylalanine	3.87	Riboflavin (B2)	0.61
Threonine	4.20	Niacin	4.72
Tryptophan	1.67	Pantothentic Acid	2.82
Alanine	3.50	Vitamin B6	0.09
Arginine	3.43	Folate	0.07
Aspartate	7.53	Vitamin B12	0.00
Cystine	1.13	Biotin	0.09
Glutamate	14.77	Retinol	0.29
Glycine	1.80	Alpha Tocopherol	2.73
Histidine	2.07	Alpha Tocotrienol	0.13
Proline	5.67	Beta Tocopherol	0.13
Serine	4.90	Gamma Tocopherol	0.26
Tyrosine	3.70	Choline chloride	0.10
		Myo-inositol	0.04
CARBOHYDRATES (g)			
Sucrose	152.89	**MINERALS (mg)**	
Lactose	1.73	Calcium	466.67
		Sodium	154.90
LIPIDS (g)		Copper	0.10
Saturated fatty acids	6.47	Iron	2.73
Mounounsaturated fatty acids	6.44	Magnesium	13.07
Polyunsaturated Fatty Acids	3.06	Manganese	0.07
Cholesterol	0.69	Phosphorus	266.57
		Potassium	146.33
ANTIMICROBIAL AGENT (g)		Selenium	0.03
Methyl 4-hydroxybenzoate	1.00	Iodine	0.03
		Zinc	0.03

Results

First experiment

After 6 weeks of feeding, ant mortality did differ significantly among experimental treatments (Table 3; MANOVA, P:C ratio effect on the number of dead ants $F_{4,30}$=8.05; P<0.001). The highest mortality was observed with the P:C ratio 3:1 (Post hoc test Bonferroni, P= 0.284, P=0.003, P=0.001 and P=0.001, for 3:1 *vs* 2:1, 3:1 *vs* 1:1, 3:1 *vs* 2:1 and 3:1 *vs* 1:3 respectively). The ratio 1:2 allowed the experimental colonies to raise considerable numbers of larvae (Table 3; MANOVA, P:C ratio effect on the number of larvae $F_{4,30}$=17.17; P<0.001). The colonies fed with the others food were less successful, especially the ones that were fed with 3:1 in which no colony raised more than 30 larvae (Post hoc test Bonferroni, P = 0.002, P = 0.002, P < 0.001 and P = 0.043, for 1:2 *vs* 3:1, 1:2 *vs* 2:1, 1:2 *vs* 1:1 and 1:2 *vs* 1:3 respectively).

Second experiment

After 8 weeks of feeding, all experimental colonies had raised considerable numbers of larvae and pupae (see Table 4). In the experimental colonies fed with the standardized artificial diet, the number of larvae and pupae did not differ significantly from the experimental colonies fed with *Drosophila* and honey water (Post-hoc Test Bonferroni P=0.462 and P=0.345 for the number of larvae and pupae respectively) but differed significantly

Table 3. Number of larvae per experimental colony and worker mortality of the colonies of *R. metallica* after 6 weeks of being restricted to one of five foods differing in their P:C ratios. The mean and the standard deviation per treatment are shown.

PC	Initial number of ants	Number of dead ants	Number of larvae
3:1	250	111±65	10±14.8
2:1	150	63±39	13±22.3
1:1	250	24±20	32±23.7
1:2	250	14±7	117±33.7
1:3	250	16±9	68.8±33.5

from the experimental colonies fed with Bhatkar-Whitcomb diet (MANOVA, diet effect on the number of larvae and pupae: $F_{2,30}$=20.38 P<0.001 and $F_{2,30}$=8.6 P=0.001; Post-hoc P<0.001 and P=0.001 for the number of larvae and pupae respectively). The mass of pupae differed significantly between the feeding treatments (nested two-ways ANOVA, diet effect on pupal mass $F_{30,823}$=17.56 P<0.0001, colony effect (diet) $F_{9,823}$=0.736 P=0.676). In the experimental colonies fed with the standardized artificial diet, the pupae did not differ significantly from the experimental colonies fed with *Drosophila* and honey (Post-hoc Test Bonferroni P=0.065) but were significantly bigger than the pupae of the experimental colonies fed with Bhatkar-Whitcomb diet (Post-hoc Test Bonferroni P<0.001) and smaller than the pupae collected in the field (Post-hoc Test Bonferroni P<0.001).

Interestingly, the ratio of brood items (larvae+pupae) per ant did not differ between field and standardized diet (Post-hoc Test Bonferroni P=1, after ANOVA on arcsin-transformed data, with diet effect on the ratio of brood per ant $F_{3,43}$=28.96, P<0.001;) but were significantly different from colonies fed with Bhatkar-Whitcomb diet (Post hoc Test Bonferroni P=0.04)

Ant mortality did not differ significantly among experimental treatments (MANOVA, diet effect on the number of dead ants $F_{2,30}$=1.95; P=0.161). In the experimental colonies fed with standardized diet the number of ants in the experimental colonies after 8 weeks did not differ significantly from the experimental colonies fed with *Drosophila* and honey water (Post-hoc Test Bonferroni P=0.957) but was marginally higher than the number of ants in the experimental colonies fed with Bhatkar-Whitcomb diet (Post-hoc Test Bonferroni P=0.014, after MANOVA, with diet effect on the number of ants $F_{2,30}$=5.35; P=0.045).

Discussion

Number and weight of pupae raised did not differ significantly between the experimental colonies fed the standardized diet and those fed with *Drosophila* and honey-water. Thus, our diet is sufficient to guarantee normal brood production and growth rate of larvae for at least a period of two months. The question arises as to whether the same diet would also support good performance in other ant species and would work for longer period (Williams et al., 1987). We ran a trial with *Pheidole megacephala,* which succeeded in maturing sexual forms when fed only on this diet (Dussutour, unpubl. data). We suggest that by modifying the ratio of protein to carbohydrate and monitoring worker survival, breeding success and larval growth rate the same diet may well be used for many ant species. The optimal P:C ratio was 1:2 in the case of *R. metallica*, and is likely to vary between ant species according to their feeding guild and diet breadth, as has been found in other insects (Simpson and Raubenheimer, 1993; Raubenheimer and Simpson, 2004). Some species of ants are predominantly insectivorous, some granivorous, some fungivorous and that many others feed to a considerable extent on the sugary excreta of Homoptera (review in Wheeler and Bailey,1920; Stradling, 1978; Cook and Davidson, 2006). Certain ants have such specialized appetites that they confine themselves to one or a very few food-substances. Thus some feed mainly or exclusively on termites, others on terrestrial isopods, others, like the leaf cutting ants on particular species of fungi, while still others, intimately associated with some of the higher plants (neotropical acacias), have long been supposed to eat only particular plant structures called food bodies (Heil et al., 1998). Hopefully our diet would be suited to evaluating the optimal ratio of protein and carbohydrates for different species in relation to their feeding habit.

The diet will enable a range of questions to be addressed in ant nutrition. For example, to what extent are ants able to regulate their intake of macronutrients at the individual and colony level? And how do nutritional

Table 4. Number of larvae and pupae raised per experimental colony, pupal weight and worker mortality of the worker colonies of *R. metallica* after 8 weeks of feeding with Bhatkar-Whitcomb diet, diluted honey and *Drosophila*, or our standardized diet. The mean and the standard deviation per treatment are shown.

	Initial number of ants	Final number of ants	Numer of dead ants	Number of larvae	Number of pupae	Pupae weight (mg)
Bhatkar-Whitcomb diet	250	243.8±5	7±4.9	57±16	12±4.9	4.9±0.86
Honey and Drosophila	250	261.5±14	8.3±3.8	108±25	22±6.8	6.6±0.74
Standardized Diet	250	258±13	11.4±5.6	125±27	28±12	6.3±0.65
Field	1112±279	–	–	405±159	303±95	7.4±0.63

requirements change both quantitatively and qualitatively in relation to colony size and composition, to reflect the fact that worker ants need carbohydrates as a source of energy (Markin, 1970; Schneider, 1972; Wilson and Eisner, 1957), whereas larval growth relies more heavily on proteins (Cassill and Tschinkel, 1999; Markin, 1970; Sorensen and Vinson, 1981)?

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