



Inter-individual variation in nutrient balancing in the honeybee (*Apis mellifera*)



Abbie J. Reade, Dhruva Naug*

Department of Biology, Colorado State University, Fort Collins, CO 80523, USA

ARTICLE INFO

Article history:

Received 22 April 2016

Received in revised form 1 September 2016

Accepted 2 September 2016

Available online 8 September 2016

Keywords:

Nutritional geometry

Feeding behavior

Social behavior

Inter-individual variation

Eusociality

Honeybee

ABSTRACT

The Geometric Framework approach in nutritional ecology postulates that animals attempt to balance the consumption of different nutrients rather than simply maximizing energetic gain. The intake target with respect to each nutrient maximizes fitness in a specific dimension and any difference between individuals in intake target therefore represents alternative behavioral and fitness maximization strategies. Nutritional interactions are a central component of all social groups and any inter-individual variation in intake target should therefore have a significant influence on social dynamics. Using the honeybee colony as an experimental model, we quantified differences in the carbohydrate intake target of individual foragers using a capillary feeder (CAFE) assay. Our results show that the bees did not simply maximize their net energetic gain, but combined sugar and water in their diet in a way that brought them to an intake target equivalent to a 33% sucrose solution. Although the mean intake target with respect to the nutrients sucrose and water was the same under different food choice regimens, there was significant inter-individual variation in intake target and the manner in which individuals reached this target, a variation which suggests different levels of tolerance to nutrient imbalance. We discuss our results in the context of how colony performance may be influenced by the different nutrient balancing strategies of individual members and how such nutritional constraints could have contributed to the evolution of sociality.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

All animals must obtain a specific combination of different nutrients to optimize different life history traits. For instance, an animal that is maximizing growth or reproduction may require a larger proportion of protein in its diet, while an animal that is more concerned about survival is likely to maximize the intake of carbohydrates as a quickly available fuel source. This is in contrast to what is predicted by optimal foraging theory (Charnov, 1976), which has traditionally considered energetic gain as the primary currency driving the foraging decisions of animals. Nutritional geometry, a bottom-up, state-space modeling approach specifically developed to address this issue, explains foraging behavior in terms of satisfying a ratio among different nutrients that maximizes fitness (Simpson and Raubenheimer, 1993, 2012). The level of a nutrient that provides the maximum contribution to a given life history trait is defined as the intake target for that nutrient, thus requiring an animal to satisfy a multidimensional intake target. Faced with different food items that vary in their nutritional

compositions, an animal is therefore confronted with the complex problem of how to reach or approach this multidimensional target in a way that achieves a nutritional balance for maximum fitness.

Nutritional geometry has been shown to be a robust model for explaining how animals regulate their foraging to balance the intake of different nutrients. While the Geometric Framework has been used to explain nutrient balancing with respect to different fitness parameters in a variety of species (Simpson and Raubenheimer, 2012), whether such nutritional regulation plays any role in social dynamics is only beginning to be considered (Behmer, 2009; Cook et al., 2010; Lihoreau et al., 2014). Social insect colonies of honeybees and ants have been shown to behave in a manner consistent with the Geometric Framework of nutrient balancing, regulating their nutrient intake at a collective level (Dussutour and Simpson, 2008, 2009; Hendriksma and Shafir, 2016). In an interesting contrast to what might be expected from optimal foraging theory, ant colonies were found to switch from consuming a concentrated sugar solution to a more dilute solution with time, which suggests that they were balancing their diet with respect to the nutrients sugar and water, rather than simply maximizing their energetic intake (Dussutour and Simpson, 2008).

Within any group such as a social insect colony, one can expect a substantial amount of inter-individual variability in intake

* Corresponding author.

E-mail addresses: abbie.ream@colostate.edu (A.J. Reade), dhruva.naug@colostate.edu (D. Naug).

targets not only between members of different behavioral groups (Paoli et al., 2014), but also within a behavioral group with each individual possessing different physiological dispositions. For example, it has been shown that pollen foragers have higher metabolic rates than non-pollen foragers (Feuerbacher et al., 2003) and these foragers with higher metabolic demands could exhibit a higher carbohydrate intake target than other foragers. Individuals varying in their overall foraging efforts might also be driven in part by how closely they monitor their own intake target, which has been referred to as an individual's 'nutritional latitude' (Senior et al., 2015). It is therefore important to understand the nature of such variation within a colony and how it might impact the nutritional intake at the colony level, which in turn might have played a role in the evolution of social behavior itself.

The capillary feeder (CAFE) assay, originally developed to examine the prandiology of the fruit fly, *Drosophila melanogaster* (Ja et al., 2007), is a technique that allows precise measurement of liquid food consumption by individual animals and can be applied to both short- and long-term feeding experiments (Deshpande et al., 2014). Because the diet of adult workers in social insect colonies consists primarily of carbohydrates (Altaye et al., 2010; Ihle et al., 2014; Paoli et al., 2014), we used a modified CAFE assay to investigate the variation in carbohydrate intake target and nutrient balancing strategy with respect to sucrose and water among individual honeybee foragers. In the absence of any substantial fat reserves, these foragers critically rely on their nectar based carbohydrate diet, consisting mainly of water and sucrose, to meet their large energetic requirement for flight and foraging performance (Sacktor, 1970; Candy et al., 1997), subjecting them to strong selection for managing their carbohydrate budgets. By removing a forager from the colony and allowing her to choose between two different concentrations of sucrose solutions, we were able to examine the variation in how an individual bee regulates her nutritional requirements, independent of the nutritional state of the colony.

2. Methods

2.1. Gustatory responsiveness assay

We collected returning honeybee (*Apis mellifera*) foragers from five different colonies, noting whether or not they were carrying pollen, and chilled them on ice just enough to allow them to be harnessed into plastic straws. The gustatory sucrose sensitivity of each bee was assessed by stimulating its antennae first with water and then with an ascending series of sucrose concentrations up to 60% (0, 0.1, 0.3, 1, 3, 10, 30, 45 and 60%) and testing for the extension of its proboscis, the Proboscis Extension Response (PER). All bees were stimulated with water between the presentations of two successive sucrose concentrations in order to reduce the effects of any potential sensitization to sucrose. The concentrations of all sucrose solutions in this study were prepared and reported as w/w sucrose solution: weight (g) sucrose/(weight (g) sucrose + (g) water). A Gustatory Responsiveness Score (GRS) was calculated for each bee as the sum of the PERs elicited to the initial presentation of water and the eight sucrose concentrations (Scheiner et al., 2001). The GRS scores in this experiment therefore has a range of 0–9, a score of 0 indicating that the bee did not respond to any of the stimuli, including the first presentation of water, while a score of 9 indicates that the bee responded to the initial water presentation and all the sucrose concentrations.

2.2. CAFE assay

Immediately following the GRS assay, each bee was fed until satiation with a 30% sucrose solution (to equalize their energetic

states) and subjected to a 16-h CAFE assay to determine its individual intake target with respect to sucrose and water. Each bee was placed in a clear acrylic chamber (3 cm ID and 3 cm tall) with ventilation holes and two glass capillary feeding tubes (152 mm long, 1.12 mm ID; World Precision Instruments, item number: TW150-6), each filled with 110 μ l of sucrose solution of a different concentration, representing two alternative food choices. The two solutions were enhanced with either blue or yellow food coloring to enable their discrimination during analysis and the two colors were alternated between the two concentrations and the two sides of the chamber in different replicates to correct for any potential color or side bias. The chambers were placed in an incubator set at 25 °C and 60% Relative Humidity (RH) and a camera with an automatic timer was used to record the level of the solution in each capillary at hourly intervals. We conducted two series of CAFE assays, one in which the two sucrose solutions provided were 45% and 5%, and another in which the two solutions were 45% and 1%. Each replicate of the assay also included a control chamber identical to the others, but without a bee in it, to account for any evaporative loss of the solutions.

2.3. Statistical analysis

The hourly consumption of each solution by each bee was calculated after subtracting the average hourly rate of evaporation from the control chambers, and from this the total amounts of sucrose and water consumed were used to calculate the hourly intake and the final intake target for each bee, expressed as sucrose concentrations. A one-sample *t*-test was used to compare the average final intake target across all bees to an intake target equivalent to the mean concentration of the two solutions. A two-sample *t*-test was used to compare the intake targets in the two treatments. An *F*-test of variance was used to compare the variation in the amount of water consumed to the variation in the amount of sucrose consumed. The nutritional latitude of a bee was calculated as the mean absolute difference between its final intake target and its intake target at each hour, given by $(\sum |IT_{final} - IT_{hour}|) / n$, where *n* is the number of hourly observations for the bee. Kolmogorov-Smirnov goodness of fit tests were used to compare the distributions of individual intake targets and nutritional latitudes with expected normal distributions. Pearson's correlations were used to investigate the relationships between gustatory responsiveness, forager type, and the final intake target of each bee. All statistical analyses were conducted using R (version 3.1.1).

3. Results

3.1. Intake target

A total of 200 bees, which completed the CAFE assay without exhausting either of the sucrose solutions, were used in the analysis to ensure that all of them had a choice between the two foods during the entire assay. At the end of the 16-h assay, the bees in the two CAFE assays, consisting of different pairs of sucrose concentrations, converged on the same, statistically indistinguishable intake target (Welch Two-sample *t*-test: $t_{188} = 0.15$, $p = 0.88$, Fig. 1A). The intake target for the experiment in which the bees had a choice between 1% and 45% solutions was 0.33 ± 0.009 and the intake target observed in the experiment with 5% and 45% solutions was 0.33 ± 0.01 , both equivalent to a 33% sucrose solution. The two intake targets were significantly different from the mean of the two concentrations in both treatments (1% vs. 45%: $t_{109} = 2485.51$, $p < 0.0001$; 5% vs. 45%: $t_{89} = 2351.48$, $p < 0.0001$), demonstrating that the bees were not simply feeding randomly. In both treatments, the pattern of hourly intake indicates an initial

Download English Version:

<https://daneshyari.com/en/article/2840250>

Download Persian Version:

<https://daneshyari.com/article/2840250>

[Daneshyari.com](https://daneshyari.com)