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Spare to share? How does interindividual variation in metabolic rate influence food sharing in the honeybee?

Abbie J. Reade[a], Michael Dillon[b], Dhruba Naug[a,*]

[a] Department of Biology, Colorado State University, Fort Collins, USA
[b] Department of Zoology and Physiology, University of Wyoming, Laramie, USA

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ABSTRACT

A central benefit of group living is the cooperative acquisition and sharing of resources but the costs associated with these processes can set up a potential conflict between individual and group level fitness. Within a honeybee colony, the task of resource acquisition is relegated to the foragers and any interindividual differences in their metabolic rate and the consequent carbohydrate demand may pose a constraint on the amount of resources they can contribute to the colony. We investigated whether the carbohydrate demand of a forager is a function of her metabolic rate and if this impacts the amount of food she shares with the nestmates. Our results show that the sucrose consumption rates of foragers with high metabolic rates did not meet their carbohydrate demand, placing them at an energy deficit while those with lower metabolic rates had an energy surplus. Our food sharing experiments showed a trend but did not detect a significant difference among individuals with different consumption rates in terms of the amount of food they shared with their nestmates. These results suggest that honeybee foragers with different metabolic rates are likely to differ in terms of whether they have an energy surplus or deficit, but more long-term datasets may be required to detect how this may influence food sharing.

1. Introduction

A central benefit of group living is often considered to be an ability for higher resource acquisition (Krause and Ruxton, 2002) but what is often overlooked is that neither the costs nor the benefits associated with this process may be equally distributed among all group members. This inequitable distribution of efforts and rewards is most evident in the producer-scrounger framework, whereby certain individuals within a group – the producers – spend more effort locating resources while others – the scroungers – take advantage of these discoveries (Barnard and Sibly, 1981). While scroungers decrease the overall performance and fitness of the group, their presence is an inevitable consequence of group living and the relative frequencies of the two behavioral phenotypes are maintained by negative frequency dependent selection.

Unlike groups in which behavior is driven by considerations of individual fitness, eusocial groups such as honeybees are generally assumed to be guided by colony level selection, whereby all group members work toward maximizing the reproductive output of the colony. In almost all analyses of work performance in these eusocial groups, the general implicit underlying assumption is that all members are solely guided by colony demands, contributing maximally to colony performance. However, our earlier studies showing that the foraging rate of individual honeybees is significantly influenced by their own carbohydrate (energetic) demands (Mayack and Naug, 2013), and that dancers (akin to producers) are more responsive to the colony nutritional state than followers (akin to scroungers) (Katz and Naug, 2015, 2016), suggest that all colony members may not contribute equally. Since higher workloads are positively correlated with higher mortality rates in individual workers (Neukirch, 1982; Schmid-Hempel and Wolf, 1988; Wolf and Schmid-Hempel, 1989), it has been suggested that workers that adopt lower workloads can enjoy a fitness advantage at the expense of hard-working types, even in eusocial species (Schmid-Hempel, 1990). There is empirical evidence that individuals indeed differ in terms of the amount of work they contribute to the colony (Jeanne, 1988; Jeanson and Weidenmuller, 2014; Tenczar et al., 2014), a difference that is partly related to a difference in metabolic rate (Wolf et al., 1989; Feuerbacher et al., 2003).

Metabolic rate, due to its positive correlation with energy usage, is often considered to have a strong positive influence on rates of food consumption in animals (Hammond and Diamond, 1997; Biro and Stamps, 2010). Honeybee foragers, lacking any substantial fat reserves (Sacktor, 1970; Candy et al., 1997), but requiring a high metabolic rate to power their flight, are therefore subject to strong selection for managing their carbohydrate budgets. While it is well recognized that

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[*] Corresponding author.
E-mail address: dhruba.naug@colostate.edu (D. Naug).

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there is considerable interindividual variation in metabolic rate within a honeybee colony (Feuerbacher et al., 2003; Harrison et al., 1996; Harrison and Fewell, 2002), how this variation is related to individual carbohydrate demands, sucrose consumption and food sharing within the colony is not known. This is an important question in the context of the evolution of eusociality because it means that foragers with different metabolic rates may differ in terms of their own carbohydrate needs, which in turn would reduce the amount of food that they can share with the colony.

Most studies regarding honeybee nutritional demands are generally conducted at the colony level or with small groups of workers, with little focus on the interindividual variation that might be present among workers in terms of these demands (Brodschneider and Crailsheim, 2010). However, there could be substantial interindividual differences in appetitive behavior within the colony and recent evidence shows that even dance followers can differ from non-followers in this regard (Moauro et al. 2018). We have previously shown that there is considerable variation within a honeybee colony with respect to individual carbohydrate demands (Reade and Naug, 2016). Based on these findings, we wanted to test 1) if interindividual differences in metabolic rate are correlated to differences in sucrose consumption rates and 2) if individual carbohydrate demand poses a constraint and determines the amount of food an individual honeybee forager shares with the colony. These two questions are based on our hypothesis that individuals consuming an amount of energy that is less than what they burn will have an energetic deficit and are therefore less likely to share food with their nestmates while those that consume an amount of energy that is greater than what they burn will have an energetic surplus and are therefore more likely to share food.

2. Methods

2.1. Experiment 1: the influence of metabolic rate on sucrose consumption rate

Returning foragers were collected from a honeybee colony (*Apis mellifera*), transported back to the lab in a flight cage, chilled on ice until immobile and harnessed into a plastic straw using a thin piece of wire around their petiole. Bees were fed to satiation with 30% sucrose solution to equalize their energetic states and placed in an incubator at 25° C and 60% RH for 18 h.

After 18 h, each harnessed bee was placed in a cylindrical glass respirometry chamber (47 mm length × 17 mm diameter) within a dark box and allowed to acclimate for 5 min before its metabolic rate was estimated by carbon dioxide respirometry for 10 min at room temperature (25 °C). Room air was drawn through a 25-liter carboy, scrubbed with two anhydrous $CaSO_4$ columns and then pushed through the chamber at a flow rate of 150 ml/minute. The CO_2 content in the excurrent air was measured with a Licor LI-7000 CO_2 analyzer (Lincoln, NE, USA), interfaced with Sable Systems hardware and software (Las Vegas, NV, USA). Baseline CO_2 data were collected immediately before and after each recording from an identical but empty chamber to correct for any CO_2 drift and lags.

Immediately following the respirometry measurement, each bee was weighed (the weight used as its body weight for all corrections), fed to satiation with a 30% sucrose solution and then weighed once again to calculate the amount of sucrose it consumed. This amount was divided by the number of hours the bee was starved since it was satiated the previous day and this was used to calculate its sucrose consumption rate (mg sucrose/hr).

2.2. Experiment 2: The influence of individual carbohydrate demand on food sharing

A three-frame observation hive, with approximately 3500 bees, was set up and foragers were trained to a metered pump feeder, containing a 40% w/w sucrose solution, located 50 m away. Bees at the feeder were individually marked using a small dot of Testor's paint on their abdomen and the duration for which an individual collected sucrose solution at the feeder during a foraging bout was recorded for a total of three trips. The end of each food collection bout was communicated to an observer seated by the observation hive and the total time spent by a marked forager engaging in trophallaxis with hive bees following her return was recorded, until the forager departed the hive on its next foraging bout.

Each marked forager was captured on her fourth visit to the feeder and was transported to the lab, chilled on ice, harnessed into a straw, fed to satiation with a 30% sucrose solution to equalize their energy levels, and placed in an incubator maintained at 25° C and 60% RH. After 16 h each bee was weighed, fed to satiation, freed from its harness and placed into a feeding chamber equipped with two feeding capillaries (a CAFE assay), and its sucrose consumption was measured over a duration of 12 h to measure its carbohydrate demand (for details see Reade and Naug, 2016; Reade et al. 2016).

2.3. Data analysis

We estimated the resting metabolic rate of each bee as the average of two minutes of data with the lowest CO_2 emission. Assuming a respiratory quotient of 1.0 (Rothe and Nachtigall, 1989; Feuerbacher et al., 2003), we converted the CO_2 emission rates to metabolic rates (in Joules/hr), assuming 21.4 J per ml CO_2 (Gordon, 1982; Feuerbacher et al., 2003). We excluded two bees, which were calculated to have a metabolic rate more than three times the average metabolic rate of the other bees, from our analysis to ensure that only resting bees were included in the data. We then calculated the carbohydrate demand (in Joules/hr) of each bee from its sucrose consumption rate (mg/hr), assuming 16.7 J per mg of sugar. Both metabolic rate and sucrose consumption rate of each bee were divided by its body weight to convert them into weight specific values for all analyses.

In the food sharing experiment, the total time spent by a forager at the feeder was multiplied by the flow rate at the feeder to calculate the amount of sucrose she collected in each foraging bout. Making the assumption that the rates of regurgitation were equal to the rates of collection, we converted the time the forager engaged in trophallaxis on her return from a foraging trip to the amounts of sucrose shared by her, which were translated into energetic equivalents (in Joules). While the two rates may not be equal, the important point is that any difference between the two rates should be systematically uniform across all bees and all interactions given that all the focal bees were collecting food at the same source. Both the collected and the shared amounts were corrected for the body weight of the forager. The carbohydrate demand (in Joules) of each forager was then calculated from the hourly rate of sucrose consumption in the CAFÉ assay and corrected for its body weight as described above.

3. Results

3.1. Experiment 1

If a bee consumes energy (sucrose) at the same rate as she burns it, she would display a positive relationship between her sucrose consumption and metabolic rate with a slope of 1 and would be defined as being in mass balance (Fig. 1). Individuals falling above this line can therefore be considered to have an energy surplus while those falling below it to have an energy deficit. There was significant interindividual variation regarding this relationship among the bees. Out of 41 bees only 4 were approximately in mass balance while 15 showed a surplus and 22 showed a deficit. There was a significant negative correlation between the metabolic rate and the sucrose consumption rate of an individual ($r = -0.32$, $N = 41$, $P = 0.03$), showing that bees with higher metabolic rates are more likely to be in energy deficit.

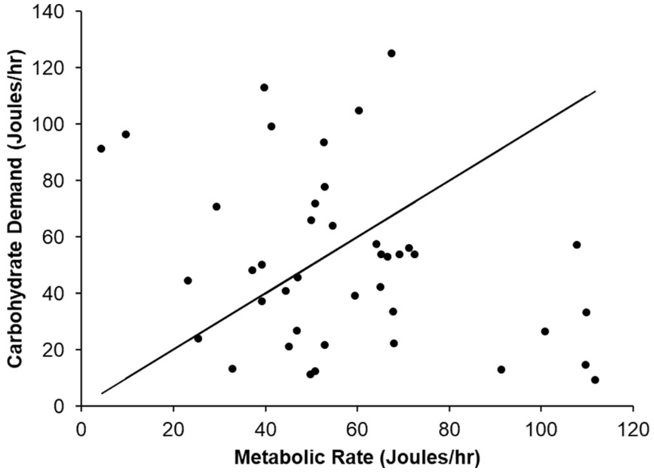

Fig. 1. Inter-individual variation in mass balance in a sample of honeybees (N = 41). The solid line depicts the theoretical 1:1 relationship between metabolic rate and carbohydrate demand such that individuals falling on it are in mass balance. Each dot represents a single bee, with those falling above the line showing an energy surplus while those below it showing an energy deficit.

3.2. Experiment 2

The amount of food shared by a forager was significantly influenced by the amount it collected, but sharing was not significantly influenced by the individual carbohydrate demand of the forager, although there was a positive trend in this relationship (One-way Anova, Main effects: Carbohydrate Demand: $F_{1,\ 31} = 3.95$, $P = 0.05$; Amount Collected: $F_{1,\ 31} = 4.80$, $P = 0.03$; Interaction effect: Demand × Collected: $F_{1,\ 31} = 3.57$, $P = 0.06$; Fig. 2). The carbohydrate demands are higher in this experiment compared to the previous one because these bees were free moving while they were harnessed in the first experiment.

4. Discussion

Our results demonstrate that there is interindividual variation within a honeybee colony in terms of both metabolic rate and carbohydrate demand. Our results show that foragers with higher metabolic rates are more likely to be at an energy deficit while those with lower metabolic rates are likely to have an energy surplus. This also predicts that everything else being equal, the latter types of bees are more likely to share food with their nestmates. Contrary to our expectations, individual carbohydrate demand, however, did not translate to significant differences in the amount of food an individual forager shared with its nestmates. Our premise that bees in positive mass balance are more likely to have spare to share while those that need to metabolize an amount equal to all the carbohydrate that they have gathered in order to maintain mass balance are less likely to share food was not fully supported. However, bees that shared more tended to be those with a higher carbohydrate demand and therefore those that were likely to be in positive mass balance. Since consumption rates are likely to be constrained by a variety of factors such as gut size, assimilation efficiency, etc., one may need longer and more continuous estimates of carbohydrate demand and food sharing to fully explore this question. In the absence of a definitive evidence of the metabolic rate of an individual influencing its extent of food sharing, the positive correlation between food sharing and the amount of food collected by a forager could also be a reflection of other factors such as colony demand. Moreover, even though the range of our estimated resting metabolic rates are comparable to those obtained in other studies (Rothe and Nachtigall, 1989; Stabentheiner et al., 2003; Kovac et al., 2007), these studies point out the difficulty of measuring resting metabolic rate and the wide variation in these estimates, suggesting that a future study along these lines may profit from more careful and long term respirometry data (Tomlinson et al., 2017).

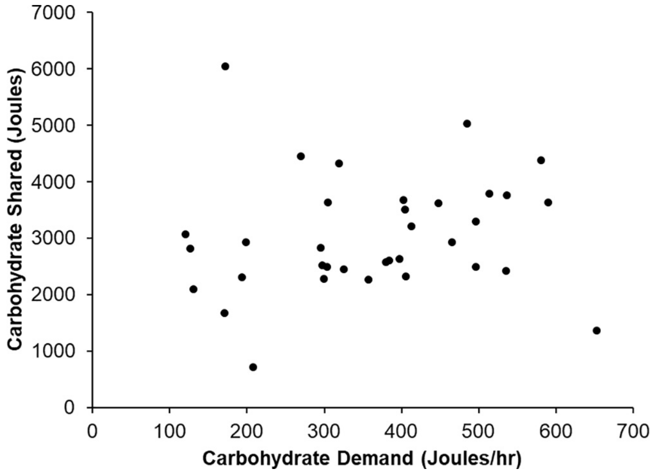

Fig. 2. Magnitude of food sharing by an individual honeybee forager as a function of her own individual carbohydrate demand, with each dot representing a single bee (N = 35).

Our results nonetheless show that honeybee foragers with different metabolic rates may have different maintenance costs that they impose on the colony. It is well known that there is substantial interindividual variation with respect to flight metabolic rate within a honeybee colony, a variation which has been proposed to have colony-level energetic consequences (Harrison and Fewell, 2002). While it is not known whether there is a correlation between an individual's resting and active metabolic rates, if foragers with higher metabolic rates have an overall higher maintenance cost, it would require them to either draw a larger quantity of carbohydrates from colony food stores or share a lower fraction of the food they bring back to the colony. Studies show that honeybee foragers either self-feed or are fed by other colony members with a supply of carbohydrate nectar (Harano and Nakamura, 2016), but it is not known whether foragers with higher metabolic rates need to feed more.

Metabolic rate, the biological rate of energy processing, has been considered to be the fundamental driver of performance at all levels of biological organization (Brown et al., 2004). It therefore follows that any intraspecific variation in metabolic rate, by creating differences in rates of energy acquisition and expenditure, should translate to differences in performance (Burton et al., 2011; Careau et al., 2008). It has been pointed out that although a higher metabolic rate, by allowing a higher level of activity, may lead to higher rates of energy acquisition, the maintenance of a high metabolic rate also requires higher rates of carbohydrate expenditure (Biro and Stamps, 2010). It is therefore not entirely clear how intraspecific differences in metabolic rate may translate to differences in net performance, although it has been shown that individuals with high metabolic rates might have an advantage only in environments with high resource abundance (Auer et al., 2015). This means that the composition of a honeybee colony in terms of the interindividual variation in metabolic rate is likely to have a significant impact on the rates of energy acquisition and expenditure at the colony level, which in turn will have a significant influence on life history parameters such as colony survival and growth.

Differences in metabolic rate are also predicted to underlie differences in behavioral phenotype or personality (Careau et al., 2008; Biro and Stamps, 2010) and individuals with a higher metabolic rate are often bolder, more risk prone, more exploratory and more active in general (Mathot et al., 2015). In a honeybee colony, such differences are similar to the behavioral differences that can be expected between scouts and recruits. Our earlier work has shown that the differences between foragers in terms of their relative levels of exploration and exploitation, their sensitivity to colony carbohydrate (energetic) demand and their individual foraging rates are all strongly influenced by an individual's own carbohydrate (energetic) demand (Mayack and Naug, 2013; Katz and Naug, 2015, 2016). It therefore suggests that individuals with different metabolic rates within the colony may qualitatively and quantitatively differ in terms of their contribution to the colony phenotype. Individuals with higher metabolic rates may act as scouts, specializing on exploration and the collection and sharing of information, allowing a colony to more effectively respond to periods of resource abundance, while those with lower metabolic rates may allow the colony to reduce its overall maintenance costs during times of resource scarcity. While resource abundance in the environment is known to adaptively modulate physiological parameters such as sucrose sensitivity in honeybees through developmental mechanisms (Pankiw et al., 2004), it would be interesting to ask if it can similarly regulate the metabolic (rate) composition of the colony. It has been recently shown that larval starvation improves the metabolic responses of adult bees without affecting metabolic rate (Wang et al. 2016), and this is an interesting avenue for further research.

Behavioral diversity and individual specialization have been considered as assets to all group living animals (Bolnick et al., 2003) and this is particularly true for eusocial insect colonies (Jeanson and Weidenmuller, 2014). A number of studies have shown the positive contributions of such behavioral diversity in honeybee colonies (Jones et al., 2004; Mattila and Seeley, 2007; Page et al., 1995). However, whether physiological diversity in terms of metabolic rates can benefit a social group is an idea that needs to be tested, given that metabolic rate and energy processing are the fundamental drivers of life history traits that set the pace of life (Réale et al., 2010). Studies have shown that individuals of different metabolic rates are suited to different environmental conditions and flexibility in metabolic capacity can provide advantages under changing conditions (Auer et al. 2015). A eusocial group such as the honeybee colony, by maintaining a population of individuals with different metabolic rates, can display a distributed metabolic capacity which imparts flexibility to respond to a variety of environmental challenges.

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