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Individual energetic state can prevail over social regulation of foraging in honeybees

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Abstract The energetic state of an individual is a fundamental driver of its behavior. However, an individual in a eusocial group such as the honeybees is subject to the influence of both the individual and the colony energetic states. As these two states are normally coupled, it has led to the predominant view that behaviors, such as foraging, are dictated by the colony state acting through social regulatory mechanisms. Uncoupling the energetic state of an individual honeybee from its colony by feeding it with a non-nutritious sugar, we show that energetically stressed bees in a colony with full food stores do not consume this food to meet their energetic shortfall but instead compensate by first reducing their activity level and then by increasing their foraging rate. This suggests that foraging in eusocial groups is still partly under the regulatory control of the energetic state of the individual and supports the notion that regulatory mechanisms in solitary insects have been co-opted to drive altruistic behavior in eusocial insects. The observation that energetically stressed bees also experience higher mortality during foraging also suggests that energetic stress mediated by a variety of factors can be a common mechanism that underlies the recent observation of bees disappearing from their colonies. We also discuss how nutritional imbalance in a social insect individual can alter its behavior to influence colony life history.

Keywords Foraging regulation · Energetic state · Energetic stress · Social insects · Honeybees

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Introduction

Energy is a fundamental requirement for maintenance and growth and is therefore a primary driver of behavior in all animals. Energetic demands are highly dynamic, and animals alter their behavior in numerous ways in order to meet this constantly changing demand. For example, in order to prevent an energetic shortfall, animals may increase their overall search activity to find food (Lee and Park 2004; Mailleux et al. 2010), incur a greater risk of predation to gain access to food patches (Abrahams and Dill 1989; Croy and Hughes 1991), or prefer food patches with a higher reward variance (Caraco 1981; Stephens 1981). The analogous situation in social animals is somewhat more complex because they not only forage to meet individual energetic demands but they also share food with other group members and may even hoard food in a communal storage for inclement times. Consequently, an individual in a eusocial group such as a honeybee colony is subject to two states that can potentially dictate its foraging behavior, its own nutritional state, and the colony nutritional state given by the amount of food stores in the hive. However, due to the expected intrinsic correlation between these two states, it is difficult to evaluate the role of these two possible kinds of regulatory control on the foraging decisions of social animals (Ydenberg and Schmid-Hempel 1994).

In eusocial insects, such as the honeybees, foraging is generally considered to be regulated at the social level (Seeley 1995). While this might be largely true for pollen, which is collected by the foragers to feed the brood and is regulated by a feedback loop based on the amount of brood and stored pollen in the colony (Fewell and Winston 1992; Camazine 1993; Sagili and Pankiw 2007), the regulation of nectar foraging might be somewhat different. This is because the supplies of nectar, which serves as food for the adults, can directly affect the energetic state of the foragers, suggesting that nectar foraging can be potentially dictated

by either the individual or the colony energetic state, acting independently or together in concert (Schmid-Hempel et al. 1993; Fewell and Winston 1996). However, the discovery of various social signals that regulate foraging (von Frisch 1967; Seeley 1995) and observations such as starvation at the colony level lead to increased foraging (Howard and Tschinkel 1980; Schulz et al. 1998; Mailleux et al. 2010) have led to the general view that forager behavior is regulated at the colony level, resulting in a continuing focus on the role of social regulatory factors in social insect foraging (Jarau and Hrncir 2009).

The above studies, however, cannot rule out whether there are regulatory factors operating at the individual level that influence the foraging behavior of a social insect worker because the individual state remained coupled with the colony state in all of these studies. In certain situations, such as when an individual is parasitized, its energetic state may, however, become uncoupled from that of the colony (Mayack and Naug 2010), making it necessary for the individual to compensate for its own depleted energetic state. A few recent studies have provided some evidence regarding such a possibility. The lipid level of an individual honeybee has been shown to play an important regulatory role in dictating its ontogeny of foraging, acting independently of age, experience, and social cues (Toth and Robinson 2005; Toth et al. 2005; Ament et al. 2008). Lipid levels have also been found to be the best predictor of which individuals leave the nest to forage in ants and wasps (Blanchard et al. 2000; Daugherty et al. 2011), with a few lean foragers performing the majority of the colony foraging activity (Robinson et al. 2009, 2012). However, these experiments, using treatments at the colony level, do not uncouple the energetic state of the individuals from that of the colony and largely address how long-term nutritional stress can alter the ontogeny of foraging. In probably the only study that comes closest to uncoupling the two energetic states, Schulz et al. (1998) showed that the foraging ontogeny of fed bees in starved colonies was similar to that of bees in fed colonies, but significantly different from that of bees in starved colonies, thus suggesting that colony energetic state is not the only driver of foraging behavior in social insects.

In insects, the amount of trehalose in the hemolymph is known to be an important regulator of feeding behavior (Friedman et al. 1991; Simpson and Raubenheimer 1993), suggesting that it could serve as a constant monitor of the internal energetic state (Thompson 2003) and also play a critical role in regulating foraging. Hemolymph trehalose titer was found to be correlated with activity in ants under a starvation treatment, suggesting that it may be an important behavioral modulator in an individual responding to energetic stress (Schilman and Roces 2008). Our own recent research has shown that a lowering of trehalose levels can have a significant effect on the behavioral decisions of honeybee foragers that have been isolated from their social environment (Mayack and Naug 2011), although it is not clear from that study if a similar effect would be observed in the presence of a social context that includes competing colony level regulatory cues. The objective of this study is therefore to determine if a honeybee forager can alter its foraging behavior in response to energetic stress at the individual level even when the colony as a whole is in a positive energetic state. By lowering the trehalose levels of experimental bees by feeding them with a sucrose solution containing the non-nutritious sugar sorbose, we experimentally uncoupled the energetic state of the individual from that of the colony to address whether individual energetic state can independently drive foraging behavior in social insects.

Methods

Observation hive setup

We set up a three-frame observation hive consisting of two brood frames, a full honey frame, a laying queen, and about 7,000 bees. The hive was located in a dark room with diffuse light, maintained at approximately 25 °C, and was connected to the natural environment outside through a tube. Blocks were placed inside the hive such that bees could enter and exit the colony from only one side, the one facing the observer. The front glass pane of the observation hive was marked with a 5×5-cm grid to assist behavioral and spatial sampling of the experimental bees. In order to ensure that the colony energetic state remained the same throughout the experiment, we made sure that there was a full honey frame at the start of each experimental trial. We performed four trials of the experiment in four consecutive weeks to control for any changes in the environmental conditions.

Energetic stress treatment

We created an energetic stress in individual bees by feeding them ad libitum, once daily for 3 days with a 30 % sucrose solution containing 2 % sorbose (2 g of sorbose in 100 mL of 30 % sucrose solution). Sorbose is a non-nutritious sugar that reduces trehalose levels in the hemolymph, probably by reducing the synthesis of trehalose from glucose, and is known to affect only the level of trehalose but not that of any other sugars in the hemolymph (Blatt and Roces 2002). It is also not known to be toxic or have any other detrimental effects in honeybees (Crailsheim 1988; Roces and Blatt 1999). In preliminary studies, we found that bees fed once daily with ad libitum amounts of 30 % sucrose solution

containing 1 % sorbose lowered their trehalose levels without compromising their immediate survival (Supplementary Material, Fig. S1). The difference in trehalose levels between the sorbose treated and control bees was also significantly correlated with the difference in their survival (Supplementary Material, Fig. S2), suggesting that energetic stress in treated bees is primarily responsible for this lowered survival. However, since the energetic stress in treated bees was observed to be lower in bees in the observation hive as compared to harnessed bees, it led us to use a 2 % dosage to create energetically stressed bees in the main experiment.

On the morning of day 1 of a trial, around 9:00 a.m., just when the bees are starting to forage, after temporarily blocking the entrance of the observation hive, we captured returning nectar foragers individually, five at a time, and chilled them on ice until they were immobile. Using tags of two different colors (randomly assigned across trials) to divide the bees into two groups, we then put a unique number tag on each bee and fed them ad libitum (control: 17–70 μL, sorbose: 10–80 μL) using a micropipette, terminating feeding when the bee no longer extended her proboscis to feed. We fed the bees in the control group with 30 % sucrose solution and fed the ones in the treatment group with 30 % sucrose solution containing 2 % sorbose and placed each group of bees in a separate flight cage. We repeated the entire procedure until there were 25 foragers for each group, and 30 min after the last bee was fed (to allow for crop emptying and reduce the chances of these bees engaging in trophallaxis with others in the colony), we released all the bees outside the entrance to the observation hive and observed all the tagged individuals flying back into the colony.

On the mornings of day 2 and 3 of a trial, before foraging started for the day, all tagged foragers found in the hive were individually re-captured, chilled, fed, and released in the same way as the first day. At the end of the third day, all the remaining tagged bees were captured, euthanized by freezing, and their hemolymph was extracted and assayed for trehalose and glucose titers (for details see Mayack and Naug 2010). Briefly, this consisted of bleeding the bees through their antennae and using a colorimetric o-toluidine assay to quantify the amount of glucose in two subsamples, one with and one without trehalase that breaks down the trehalose into glucose.

Behavioral observations

On each of the 3 days of a trial, starting 30 min after the two groups of foragers were released and allowed to go back into the colony, we conducted behavioral observations consisting of one 3–4-h session of focal animal sampling and an equally long session of focal behavior sampling, from about 12–7 p.m., alternating the order in which the two kinds of sampling was done across the different days of a trial. This resulted in a total of 72 h of behavioral observations across all the trials. The focal animal sampling quantified the proportion of time spent by tagged bees in specific in-hive behaviors (standing, walking, head inside nectar cell, and trophallaxis), while focal behavior sampling on the hive entrance quantified their foraging frequency. For focal animal observations, we selected a specific grid square using a random number, and if a single tagged bee was present within this square, we recorded her behavior with an instantaneous scan every 15 s for 10 min. If no bee or multiple bees were present in the selected square, another square was randomly chosen. In order to ensure equal representation of the two groups in the behavioral sample, bees from each group were chosen alternately in successive focal animal sessions. Observations were terminated for a bee before the 10-min period if she left for foraging or went to the other side of the observation hive. From these data, the proportion of time spent in each behavior by a bee was calculated by dividing the total number of times a behavior was observed by the total number of scans obtained for that bee within the 10 min. The locomotory rate of a bee was determined by calculating the sum of the shortest distance between the squares it was located at during successive scan intervals of 15 s and dividing it by the total time the bee was observed.

Focal behavior sampling consisted of observing the entrance tube of the observation hive and recording the time a tagged bee left or entered the hive. From these data, the foraging frequency of each bee was calculated by dividing the number of trips she made by the total length of the observation period. The time spent in a foraging trip as well as the time spent inside the hive between two trips by each bee was also calculated by using the successive departure and arrival times. At the end of each day, we performed a census of the tagged bees present in the colony, and from these data, we calculated the number of foragers lost from each of the two experimental groups.

Statistical analysis

A two-way ANOVA with treatment as fixed effect and trial as random effect was used to compare the hemolymph sugar levels of the two groups measured on the final day of the trials. We used a general linear mixed model with treatment as fixed effect, trial and days nested within trials as random effects, and subject bees across days as a repeated measure, to compare the two groups in terms of the proportion of time spent in each in-hive behavior, their locomotory rates, the time spent in foraging trips, and time spent in the hive between two successive trips. We found that there were no significant effects of trials and days within trials for any of

these measures (see Supplementary Material, Table S1 for details), and so the data presented for each of these variables are pooled across days and trials. A Pearson's correlation analysis was used to assess the relationship between the proportion of time spent standing by a bee in the hive and its trehalose level. Due to the ordinal nature of the data, the foraging frequencies of the two groups were analyzed using a Kruskal–Wallis test with a Scheirer–Ray–Hare extension that tests for an interaction effect (Sokal and Rohlf 1995). In addition, a Spearman's rank correlation was used to assess the relationship between foraging frequency and the trehalose level of a bee.

Results

Energetic stress treatment

The trehalose levels of the sorbose-treated bees were significantly lower than the control bees at the end of the third day ($F_{1,64}$=6.00, P=0.01) although there was no difference between the two groups in terms of their glucose levels ($F_{1,64}$=0.21, P=0.64; Fig. 1).

In-hive behaviors

Sorbose-treated, energetically stressed bees spent a significantly higher proportion of time standing (t=3.04, P=0.003) and correspondingly a significantly lower proportion of time walking (t=2.10, P=0.03, Fig. 2a) compared to control bees. However, there was no significant difference between the two groups in terms of the proportion of time engaging in trophallaxis (t=1.40, P=0.16), and time with their head inside nectar cells (t=0.69, P=0.48). There was also no significant difference between the two groups in terms of their locomotory rate

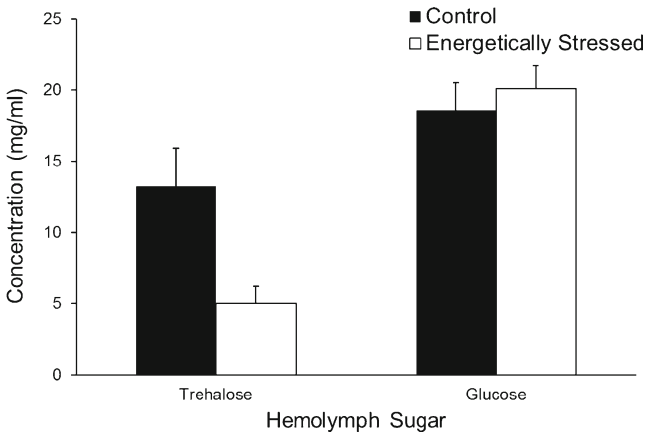

Fig. 1 Energetic states of control (N=39) and energetically stressed (N=30) bees in terms of hemolymph trehalose and glucose levels on the third day, at the end of each trial. In each case, data represent means with standard error bars

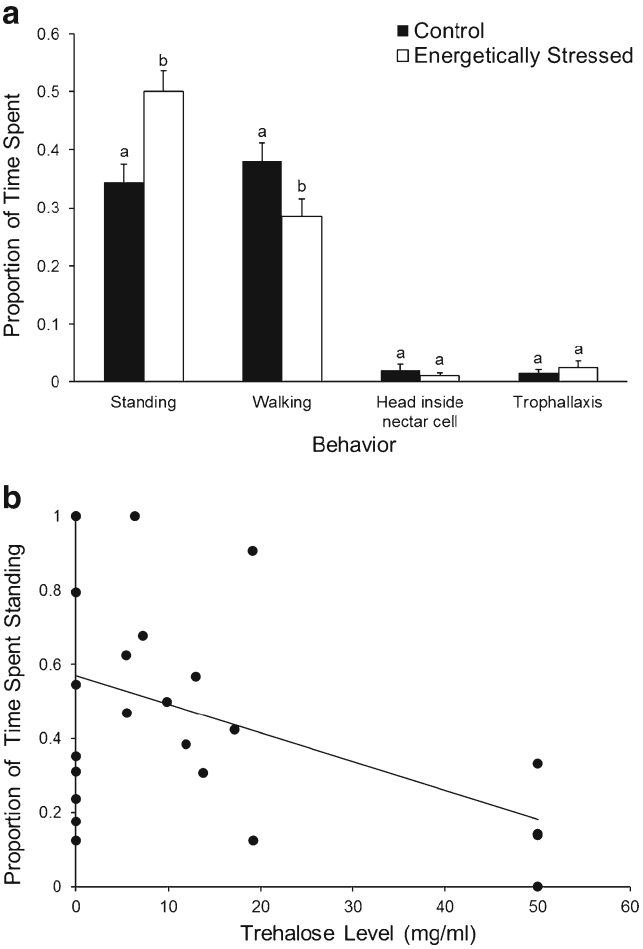

Fig. 2 Proportion of time spent in **a** various in-hive behaviors performed by bees in the control (N=59) and energetically stressed group (N=62) with data representing means ± standard errors, and the *letter* above each bar representing significant differences between the two groups at α=0.05 and **b** standing plotted against hemolymph trehalose levels for both treated and control bees on the third day of the trial, with data points (N=23) representing individual bees

(control: 0.12 cm/s±0.012 SE; energetically stressed: 0.11 cm/s±0.014 SE; t=0.70, P=0.48). There was a strong negative correlation (Pearson's r=−0.40, N=24, P=0.05; Fig. 2b) between the trehalose level of a bee and the proportion of time it spent standing on the third and final day of a trial.

Foraging behavior

There was a significant change in the foraging frequency with time in the two groups (Kruskal–Wallis test: $H_{2,138}$=11.31, P=0.004), with a significant interaction between time and treatment (Scheirer–Ray–Hare extension: $H_{2,138}$=21.69, P<0.0001, Fig. 3a), which shows a lower foraging frequency by energetically stressed bees at first that then increases to exceed the level displayed by control bees. There was a significant negative correlation (Spearman's r=−0.55, N=21, P=0.01, Fig. 3b) between the trehalose level of an individual and its foraging

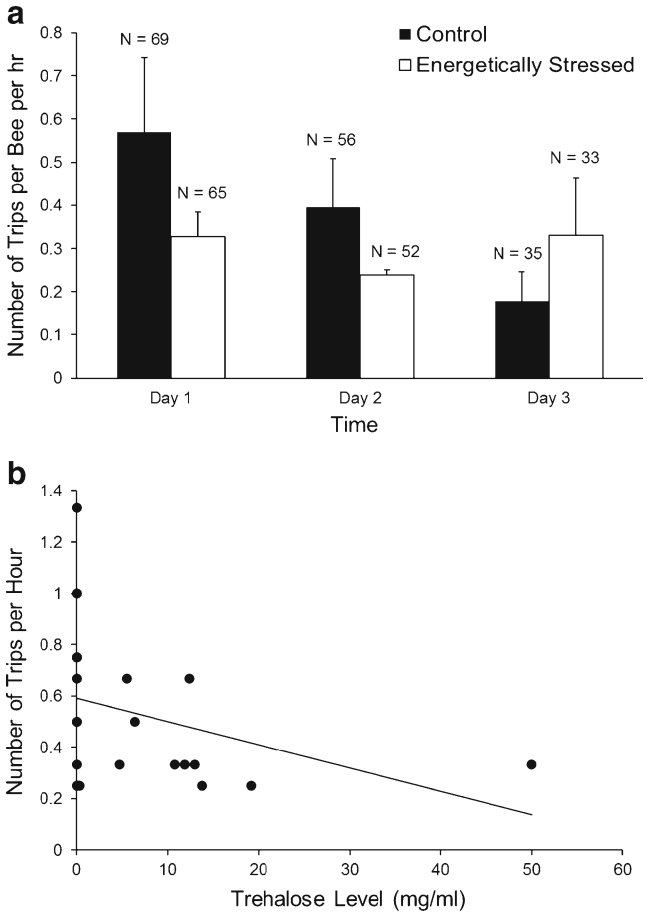

Fig. 3 Foraging behavior of control and energetically stressed bees across the 3 days of experimentation in terms of **a** foraging frequency of the two groups with data representing means across the four trials with corresponding standard error bars and **b** foraging frequency as a function of hemolymph trehalose levels for both treated and control bees on the third day of the trial, with data points (N=21) representing individual bees

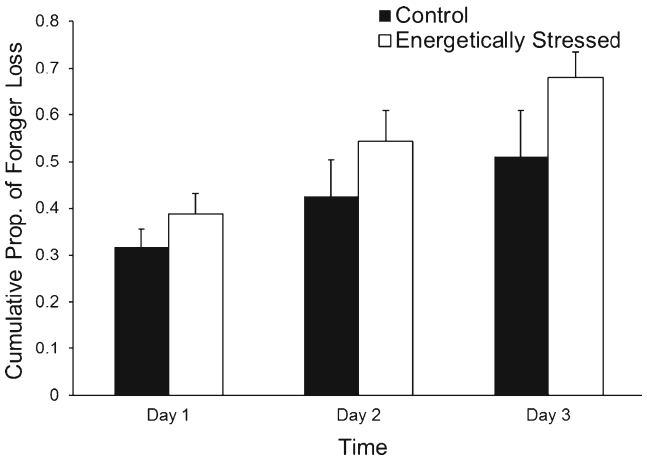

Fig. 4 Cumulative proportion of forager loss across the 3 days of each trial with data representing means across the four trials with corresponding standard error bars

frequency on the final day of trial. However, the times spent by bees from the two groups in a foraging trip (control: 47 min ±9.72 SE; energetically stressed: 41 min±9.21 SE; t=0.23, P=0.81) or in the hive between two trips (control: 50 min±11. 38 SE; energetically stressed: 62 min±13.65 SE; t=1.69, P=0.09) were not significantly different. There was also a significantly higher proportion of cumulative forager loss across the 3 days in the energetically stressed group (Wilcoxon signed rank test: Z=1.96, N=12, P=0.05; Fig. 4).

Discussion

These results confirm our earlier findings that the energetic state of an individual in a eusocial group can indeed be uncoupled from that of the colony and can dictate its behavior independently of the colony energetic state (Mayack and Naug 2010, 2011). Although the four trials pertain to a single colony, this study, to the best of our knowledge, is the first one to successfully implement an energetic stress at the level of the individual in a eusocial group without altering the colony energetic state. The sorbose treatment significantly lowered the level of only trehalose, the primary regulatory sugar found in the insect hemolymph, which in turn was significantly correlated with changes in both in-hive activity patterns and foraging behavior of an individual. This supports the notion that trehalose is the hemolymph sugar than gives a good approximation of the energetic state of a bee (Blatt and Roces 2001) and therefore dictates its behavior.

Our behavioral observations suggest that energetically stressed foragers did not compensate by feeding from the colony food stores or acquiring food from nestmates via trophallaxis as what has been documented when starvation is imposed at the colony level (Howard and Tschinkel 1980, 1981; Schulz et al. 2002). Instead, energetically stressed foragers were seen here to reduce their activity level within the colony, which included more standing and less walking, presumably to conserve energy. A similar reduction in activity levels was found to be an effective strategy in ants for conserving energy, where individuals that did not move at all had enough energy to survive for an additional 22 h compared to others in the colony (Schilman and Roces 2008). Although the observed inactivity might be counterproductive to colony ergonomics, it may be an effective short-term strategy at the individual level to meet an energetic shortfall. Given that the observed frequency of the various behaviors in the control bees is similar to what has been previously recorded (Kolmes 1985; Seeley 1995; Arathi et al. 2000) and that the activity level of a bee was correlated with its trehalose level, the observed inactivity in the sorbose fed bees can be attributed to an effect of energetic stress. While solitary insects are also known to use hyperactivity in response to hunger, probably to increase the search area for food (Lee and Park 2004), it is

known to occur in a fairly short burst and can be difficult to observe (Renault et al. 2003).

It seems that the energetically stressed bees initially try to compensate for their reduced energetic state by reducing their activity level and only resort to foraging when their energetic state continues to remain at a sustained low level. This could be a reason why bees starved at the colony level show a delayed response in starting to forage (Schulz et al. 2002). On the other hand, control bees with their trehalose maintained at a constant high level from being fed until satiation with sucrose every day, reduced their foraging activity. The role of individual energetic state in driving the foraging behavior in honeybees is also supported by the observed negative correlation between the trehalose level of a forager and its foraging frequency. While one could hypothesize that energetically stressed foragers may also take shorter trips to save energy (Schilman and Roces 2006), in our study, the time spent in a foraging trip did not significantly differ between bees from the two groups. Foraging trip time, however, is a function of both the distance a forager flies and the speed at which she flies, and it is possible that the negative influence of energetic stress on both these variables might result in a net lack of effect on trip time in comparison to control bees, but further investigations would be necessary to resolve these effects.

Using individual energetic state as a reference for the overall colony energetic state and for making decisions about whether to forage has some advantages because the two states are generally coupled in a normal colony and could cut down on the cost of using social information for such decisions (Dechaume-Moncharmont et al. 2005). A decision mechanism based on the individual state also allows one to adaptively adjust its foraging behavior in the event of an uncoupling of the individual from the colony energetic state, as what might occur due to poor nutrition (Abou-Seif et al. 1993), parasites (Mayack and Naug 2009, 2010) or exposure to pesticides (Alaux et al. 2010). Our results thus suggest that foragers experiencing an energetic stress via any of these means might be driven to leave the colony to forage at an increased frequency, which by itself would lower their survival (Schmid-Hempel and Wolf 1988). In addition, given that such energetically stressed foragers are also likely to demonstrate poor thermoregulatory ability (Campbell et al. 2010), cognitive impairments (unpublished data), and risk-prone behavior (Mayack and Naug 2011), each of these factors by itself as well as acting synergistically can increase their mortality rate outside the colony. Such mortality could be further compounded by the fact that recent reductions in suitable habitat might be forcing bees to fly longer distances from the hive to find forage (Naug 2009). We, therefore, speculate that energetic stress could be an underlying mechanism that plays a major role in the recently observed depopulation and weakening of honeybee colonies known as colony collapse. How the nutritional physiology of an animal can interact with its ecology to alter its behavior and life history in unexpected ways, which can sometimes even lead to a depopulation event, has been recently demonstrated in ants (Dussutour and Simpson 2012).

However, one question that arises here is what makes an energetically stressed individual in a colony full of food stores go foraging when there are sufficient nectar reserves within the colony to meet its energetic demand? Previous research suggests that different neural pathways are involved in gaining satiation through individual food acquisition and through receiving food from nestmates (Wada-Katsumata et al. 2011). Our findings suggest that trehalose levels probably play a more important role in modulating the regulatory pathway that controls individual food acquisition. The fact that these two pathways can function independently of one another possibly explains how a bee might be able to make a decision to seek satiation by foraging instead of staying in the colony and seeking food from its nestmates. The observed link between energetic depletion and the expression of individual level strategies is consistent with studies showing that being social is energetically costly as it requires complex neural processing (Gailliot and Baumeister 2007; DeWall et al. 2008, 2011). Energetic expenditure or metabolic rate has also been suggested to be positively correlated with impulsivity (Tobin and Logue 1994), which might also explain why energetically stressed bees took to foraging even though honeybees are normally known to resist impulsivity presumably due to their eusocial nature (Cheng et al. 2002).

In summary, in a social insect colony, while the individual energetic state is typically co-opted with the colony state and they work together in concert to maximize colony fitness, our study shows that the individual state can regulate behavioral decisions independently of the colony state when the two are uncoupled. Lipid levels of social insect individuals have earlier been shown to play an important role in shaping their ontogeny of division of labor (Toth and Robinson 2005; Toth et al. 2005), in this study we take a step further and show how the energetic state of an individual given by its trehalose level can affect division of labor in a shorter, more dynamic, time scale. These results can probably be generalized to other social insects as pathways for nutritional regulation of foraging, such as the insulin signaling pathway, are highly conserved (Ament et al. 2008; Daugherty et al. 2011) and selection is known to have shaped social behavior by a tinkering of already existing genetic pathways found in solitary insects (Toth and Robinson 2007). Most importantly, our study suggests that a nutritional imbalance at the individual level due to a range of factors can force it to make physiological and behavioral adjustments that are likely to have a significant impact not only on its own but also on the colony life history.

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