



Dancers and followers in a honeybee colony differently prioritize individual and colony nutritional needs



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The evolution of sociality is often accompanied by nutritional conflicts and the evolution of mechanisms to resolve them. The foraging behaviour of eusocial animals such as the honeybee, *Apis mellifera*, is generally considered to be largely regulated by the colony nutritional state. Previous work based on the information primacy hypothesis has however found that honeybee foragers explore (sample resources) and exploit (consume resources) in accordance with their individual nutritional state. We therefore hypothesized that individual and colony nutritional states differ in their influence on individuals of different behavioural phenotypes such as dancers and followers, who are akin to producers and scroungers, respectively. This leads to the prediction that these two behavioural groups will differ with respect to their exploration–exploitation trade-off and in terms of how they prioritize individual and colony nutritional states. We tested our predictions by creating a mismatch between individual and colony nutritional states. Our results show that dancers and followers do not differ in their levels of exploration and exploitation, but dancers are more responsive to colony nutritional state than are followers with regard to managing their exploration–exploitation trade-off. We discuss these results in the context of how these two behavioural phenotypes may differ in their sensitivity to the different nutritional pathways regulating worker behaviour in a eusocial colony and the evolution of sociality in general.

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Social groups are typically characterized by not only cooperation, but also conflict among group members. While such within-group conflict has been mostly studied in the context of reproductive allocation (Keller & Reeve, 1994; Ratnieks, Foster, & Wenseleers, 2006), the basic principle behind such conflicts also applies in the context of altruistic foraging. Members of a group may differ in terms of their nutritional requirements, and an individual's own requirements might not necessarily match those of the group as a whole. Integration of nutritional needs and metabolic complementation have been considered key prerequisites to the evolution of group living, and are regarded as critical drivers in the evolution of eukaryotes through endosymbiosis and the evolution of multicellularity (Blackstone, 2013). Mechanisms that mediate any nutritional conflicts among the lower-level components are therefore critical in order for higher-level units to evolve through cooperation.

Nutritional conflicts are likely to be especially strong when a subset of group members must obtain nutrition for the entire group. This is most obvious in the case of eusocial insects, where a subset of individuals, the foragers, meet the nutritional demands of the entire colony. It has been well established that the foraging behaviour of honeybee workers is regulated to a large part by the nutritional state of the colony (Seeley, 1995), but recent work suggests that the nutritional state of an individual also plays a strong regulatory role in determining the foraging behaviour of individual bees (Toth, Kantarovich, Meisel, & Robinson, 2005). While colony and individual nutritional states are normally tied to each other, uncoupling the two shows that fed bees in starved colonies behave more similarly to bees in fed colonies than to bees in starved colonies (Schulz, Huang, & Robinson, 1998), and that honeybee foragers at a higher nutritional state forage less often than bees at a lower nutritional state in a shared colony environment (Mayack & Naug, 2013). These studies suggest that honeybee foragers use information about both individual and colony nutritional states to make their foraging decisions.

The nutritional state of an animal has been predicted to be the primary driver of a key foraging decision: whether to explore or to exploit. Foragers must divide their time between gathering

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information about available resources (exploration) and applying that information to utilize the best available resource (exploitation; Hills, Todd, Lazer, Redish, & Couzin, 2015); these activities cannot be performed simultaneously and must trade-off with one another. The information primacy hypothesis predicts that animals will give precedence to information gathering (exploration) when they have a nutritional surplus and will prioritize food gathering (exploitation) when they are at a nutritional deficit (Inglis, Langton, Forkman, & Lazarus, 2001), thus allowing them to adaptively manage their own nutritional budget over time. A manipulation of the individual nutritional state in honeybees showed that those at a higher nutritional state explore more and exploit less compared to bees at a lower nutritional state, in support of this hypothesis (Katz & Naug, 2015). However, since the foraging decisions of honeybees are known to be subject to the nutritional state of the colony, it is important to evaluate whether colony nutrition has a similar influence on the exploration–exploitation trade-off.

Within a colony, some bees use the waggle dance to transmit foraging information to other bees that follow the dance. This allows us to divide the foragers into two behavioural phenotypes, information gatherers (the dancers) and information consumers (the followers), colony-level units of exploration and exploitation. This dancer–follower framework thus allows an evaluation of the exploration–exploitation trade-off at the group level and helps us to determine whether the colony nutritional state drives an adaptive allocation of individuals into these two behavioural phenotypes. The behaviour of dancers and followers can also be interpreted in light of the producer–scrounger framework, according to which foraging groups consist of producers, which locate new food patches, and scroungers, which take advantage of the producer's find and feed at the same patch (Barnard & Sibly, 1981). As followers forage at patches originally located by dancers, it can be argued that these followers are similar to scroungers while dancers are similar to producers.

In this study, we manipulated colony nutritional state to study how it dictates the colony-level distribution of behavioural phenotypes and their behaviour, as per the information primacy hypothesis. Our first prediction was that colonies at a higher nutritional state would have a higher proportion of dancers than colonies at a lower nutritional state and that dancers would show an overall higher level of exploratory behaviour. By creating either a match or a mismatch between individual and colony nutritional states, we also examined how dancers and followers prioritize individual and colony needs with respect to their exploration and exploitation behaviour. Our second prediction was that when colony and individual nutritional states are similar and therefore 'matched', all bees would respond to an overall high nutritional state by exploring more and respond to an overall low nutritional state by exploiting more. However, when the two states are 'mismatched' and the individual state differs from that of the colony, it presents a nutritional conflict to the bees. Our third prediction was that under such a mismatch, dancers would be more sensitive to colony nutritional state, as per the producer–scrounger framework. The test of these three predictions addresses whether the two behavioural phenotypes, dancers and followers, differ in their predispositions to show exploration and exploitation behaviours and differ in their response to nutritional conflict, and whether the information primacy hypothesis scales to the colony level.

METHODS

Observation of In-hive Behaviour

We set up two observation hives, each with one brood frame and about 3000 bees, and created two nutritional treatments at the

colony level. A colony with higher nutrition ('full colony') was created by providing it with a frame that had at least 75% honey and a colony with lower nutrition ('empty colony') was created by providing it with a frame that contained no more than 10% honey. These two nutritional treatments were rotated between the two colonies on a weekly basis to control for any confounding effects of colony identity for a total of 9 weeks of data collection. About 500 individually tagged newly emerged bees were added to each colony after the nutritional rotation each week. Allowing 2.5 days for the nutritional treatment to have an effect, we then observed the dance floor of each colony for 2 h each week, using scan sampling to identify the bees performing a waggle dance or following a waggle dance. The scan sampling consisted of dividing the dance floor into squares that were 1/6th of the entire frame in size, sampling these squares sequentially for a duration of 1 min each and recording the identities of all tagged bees found performing a waggle dance or following a waggle dance within the square during this period. Based on which of these two activities a bee was observed to perform during this entire observation period, we categorized each bee as either a 'dancer' or a 'follower', ignoring bees observed both dancing and following (3.5% of observed bees).

Two-alternative Proboscis Extension Response Assay

We captured a subset of these dancers and followers and harnessed them in plastic straws. The bees were starved for 3 h inside a dark incubator maintained at 25 °C and 60% relative humidity to increase their motivation for learning an appetitive stimulus. We trained these bees to associate an odour with a sucrose reward using an appetitive-conditioning procedure involving the proboscis extension response (PER) assay (Bitterman, Menzel, Fietz, & Schäfer, 1983). Sucrose placed on the antenna (the unconditioned stimulus, US) was paired with an odour (eugenol or 1-octanol; the conditioned stimulus, CS) to elicit a proboscis extension (a conditioned response, CR) in six conditioning trials. Each trial consisted of presenting the odour for 6 s with the final 2 s of the odour pulse coinciding with the presentation of the sucrose reward, with an 11 min intertrial interval (ITI).

Subsequent to the conditioning procedure, we created a high and a low nutritional treatment at the individual level, by feeding half the bees with 30 µl of 30% sucrose solution ('fed bees') and not feeding the other half ('starved bees'), thus giving us a 2 × 2 nutritional treatment consisting of fed and starved bees from full and empty colonies. We kept these bees in an incubator, under the same conditions as described above, for 3 h to allow the individual nutritional treatment to have an effect before subjecting them to a two-alternative assay (Shafir, Wiegmann, Smith, & Real, 1999) designed to test for exploration and exploitation behaviour (Katz & Naug, 2015). The assay consisted of presenting each bee with the odour they were previously conditioned to and a novel odour on opposite sides of her head. Each odour was presented twice for 0.8 s with 0.2 s of odourless air in between successive odour pulses in the pattern ABAB. The number of head turns made by a bee as she sampled the two odours was interpreted as a measure of exploration and the duration of its proboscis extension was interpreted as a measure of exploitation (Katz & Naug, 2015).

Statistical Analysis

All data were analysed using ANOVAs chosen through stepwise Akaike's information criterion (AIC) model selection. AIC selection for predicting the colony's proportion of dancers started from a model including a three-way interaction between colony nutrition, day of observation and colony identity. AIC selection for predicting individual behaviour started from a model including the three-way

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