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Responses to nutritional challenges in ant colonies

Sepideh Bazazi [a, b], Sara Arganda [a, b], Mathieu Moreau [a, b], Raphael Jeanson [a, b], Audrey Dussutour [a, b, *]

[a] Centre de Recherches sur la Cognition Animale (CRCA), Université Toulouse III, Toulouse, France
[b] Centre de Recherches sur la Cognition Animale (CRCA), CNRS, Toulouse, France

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In social insects, food collection for the entire colony relies on a minority of its workers. How can the colony choose between resources, determine the task allocation of workers and exhibit a flexible food storage strategy from the foraging decisions taken only by a minority? We addressed this question by posing nutritional challenges to trap-jaw ants, *Odontomachus hastatus*, and explored their response in terms of survival, foraging behaviour and energy storage. In the first challenge, ants alternated between long periods of confinement to a high-protein diet and short periods of confinement to a high-carbohydrate diet. In the second challenge, ants alternated between long periods of confinement to a high-carbohydrate diet and short periods of confinement to a high-protein diet. In the third challenge, ants were given simultaneously a high protein and high-carbohydrate diet. First, we showed that (1) mortality increased with protein consumption, (2) a brief exposure to a high-carbohydrate diet lessened the negative consequence of high protein consumption and (3) ants given a choice of complementary diets regulated intake and minimized mortality. We also demonstrated that ants used an energy-saving strategy to overcome challenging nutritional environments. In addition we showed that the ants had an extraordinary capacity to regulate the amounts of food entering the nest both at the collective level by allocating more workers to foraging on a high-protein diet and at the individual level by collecting more food on a high-carbohydrate diet. Our study provides new insights into the strategies used by ants facing nutritional challenges and deepens our understanding of the nutritional ecology of ants and, thereby, their vast ecological success.

Animals live in a heterogeneous environment and their nutritional needs are likely to change over time, given the different demands for growth and reproduction. Thus maintaining an appropriate balance of nutrients is a major challenge for all animals. Individuals living alone regulate their nutritional intake by selectively choosing the quality and quantity of food that meet their needs (Behmer, 2008; Simpson & Raubenheimer, 2012). The complication for animals living in groups, such as social insects, is that a minority of workers collects the food for the entire colony, and these individuals may have very different nutritional requirements to other members of their colony (Brian & Abbott, 1977; Cassill & Tschinkel, 1999; Hölldobler and Wilson, 1990; Sorensen, Busch, & Vinson, 1985; reviewed in Feldhaar, 2014). For example, the egg-laying queen and the larvae have a much higher need for protein than workers. Consequently, social insects exhibit a striking division of labour in which nutritional feedbacks emanating from brood and workers exist and must be integrated by foragers during food harvesting (Dussutour & Simpson, 2008a, 2009). Therefore, it is essential to understand how individuals modulate their behaviour in order to obtain the nutrients necessary for the survival, development and reproduction of not only themselves but all members of the group.

Important questions about animal nutrition can only be answered using an integrative approach, which takes into account several attributes of the environment (for example protein and carbohydrate content of the food) and of the animal (physiology, behaviour, etc.), and enables the interactions among these components to be studied. The geometric framework (GF), a state-space modelling approach, has been specifically designed to address such questions (Simpson & Raubenheimer, 2012). This framework enables the distinct and interactive roles of protein and carbohydrate in animal physiology and behaviour to be elucidated.

* Correspondence: A. Dussutour, Centre de Recherches sur la Cognition Animale, UMR 5169 CNRS, Batiment 4R3, Porte 220, Université Toulouse III, 118 route de Narbonne, 31062 Toulouse, France.
E-mail address: dussutou@gmail.com (A. Dussutour).

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Its application to the study of nutrition in a wide range of animals, from slime moulds to humans (Simpson & Raubenheimer, 2012), has helped answer important questions in nutritional ecology and biology, from the distribution of animal communities to the vulnerability of humans to obesity (Simpson & Raubenheimer, 2012).

Using the GF, recent studies have shown that, as with other nonsocial organisms, ant colonies regulate separately their intake of both protein and carbohydrate when nutritionally imbalanced but complementary diets are available (Cook & Behmer, 2010; Cook, Eubanks, Gold, & Behmer, 2010; Dussutour & Simpson, 2008a, 2009). When restricted to a single nutritionally imbalanced diet, food intake is driven essentially by carbohydrate, increasing as the percentage of carbohydrate in the diet decreases (Dussutour & Simpson, 2009). Therefore, when ants are on a high-protein–low-carbohydrate diet, they compensate for the shortage of carbohydrate by drastically increasing their food intake to meet their carbohydrate requirements (Dussutour & Simpson, 2009, 2012). However, this compensation comes at a cost: when ants consume a higher proportion of protein than required, mortality is higher, as observed in many other insects (Hamilton, Cooper, & Schal, 1990; Lee et al., 2008; Maklakov et al., 2008; Pirk, Boodhoo, Human, & Nicolson, 2010).

It remains unclear how being confined to a high-protein diet increases mortality rates. First, such a decrease in longevity could result from a deficit in energy reserves. In insects, lipid storage reserves tend to decrease as they feed on a high-protein diet and tend to increase as they feed on a high-carbohydrate diet (Behmer, Simpson, & Raubenheimer, 2002). In most insects, carbohydrates are converted to lipids by lipogenesis and stored in the fat body (Canavoso, Jouni, Karnas, Pennington, & Wells, 2001). Cook et al. (2010) suggested that generating energy stores from protein via gluconeogenesis is possible in ants but might incur a cost at the physiological level and ultimately affect colony survival. Second, increased effort spent on foraging activities when on a high-protein diet may weaken ants and explain the decrease in survival probability (Houston & McNamara, 2014; Straka, Černá, Macháčková, Zemenová, & Keil, 2014). It has been shown in previous studies that ants fed a high-protein diet significantly increase their foraging activity to collect more food in order to compensate for the lack of carbohydrate (Cook et al. 2010; Dussutour & Simpson, 2012). Therefore, a key step in building links between a high-protein diet and life span is to clarify how nutritional challenges such as carbohydrate scarcity or/and protein excess affect physiological (energy stores) and behavioural (foraging activity) traits and relate these to survival. However, until now, foraging behaviour (Cook et al., 2010; Dussutour & Simpson, 2012) and energy storage (Cook et al., 2010) have only been measured at the colony level, unlike measures of survival. However, as insect colonies can consist of individuals radically different in form and function (Jeanson and Weidenmüller, 2014; Oster & Wilson, 1978), it is essential to determine what happens at the individual level in order to better understand the strategies observed at the colony level.

In this study, we exposed ant colonies to nutritional challenges such as carbohydrate scarcity and/or protein excess and explored their response at both the individual and collective level in terms of survival, foraging behaviour and energy storage. The experiments were conducted with colonies of the arboreal trap-jaw ant, *Odontomachus hastatus* (Hymenoptera: Formicidae), a predatory ant species originally from French Guiana. In this species, workers are relatively large, which allows us to equip ants with passive microtransponders and automatically record their foraging activity (Jeanson, 2012; Moreau, Arrufat, Latil, & Jeanson, 2011). In addition, their large sizes make them ideal to measure fat storage at an individual level.

METHODS

Study Species and Rearing Conditions

Odontomachus hastatus ants measure approximately 13 mm long and are monomorphic. They live in the tropical forests of Central and South America and nest in the roots of epiphytic plants or in leaf litter accumulated at the base of palm trees. In this species, colony size varies from 20 to 500 individuals (R. Jeanson, personal observation). Their diet is composed mainly of arboreal arthropods (Camargo & Oliveira, 2012). We collected 12 colonies in French Guiana (GPS: 4°05′N, 52°41′W) in January 2012. In French Guiana colonies of *O. hastatus* have one reproducing queen (i.e. are monogynous; Jeanson, 2012). We housed each colony in a plastic box inside which we placed several test tubes acting as nests. The tubes contained a reservoir of water held with a cotton plug and were surrounded by black paper, thereby recreating the dark, humid conditions found in nature. Before starting the experiments, we supplied colonies ad libitum with water and a mixed diet of vitamin-enriched food containing a 1:3 ratio of total proteins to digestible carbohydrates. (Dussutour & Simpson, 2008b), replenished every 2 days.

Before starting the experiments, we subdivided the 12 colonies into experimental queenless subcolonies. We placed the ants in an experimental nest that was connected to a foraging arena with plastic tubes. The nest consisted of a square petri dish (10 × 10 cm and 1 cm deep) with a 5 mm layer of moist cotton, which we remoistened every 2 days to keep the nest chamber humidity levels high. We covered the nest compartment with a cardboard cover. The foraging arena consisted of a similar petri dish divided into two compartments (10 × 5 cm each) using wire mesh (10 × 1 cm) preventing displacements between compartments. A plastic tube (7 mm diameter) connected each foraging compartment to the nest (see Fig. A1). We placed the ants in experimental nests 3 days before the start of experiments to allow them time to habituate to the set-up. We carried out the experiments under red light with the nest cardboard cover removed, as foraging activity in this species is concentrated at night (Camargo & Oliveira, 2012). We maintained all the colonies under a 12:12 h light/dark photoperiod at ambient humidity and temperature.

Synthetic Foods

We used two artificial diets varying in the ratio of protein and carbohydrate with a fixed total macronutrient of 200 g/litre: a high-protein diet, P, with a protein to carbohydrate ratio of 5:1, and a high-carbohydrate diet, C, with a protein to carbohydrate ratio of 1:5 (Dussutour & Simpson, 2012). We used casein (Nutrimuscle), whey protein (Nutrimuscle) and whole egg as sources of protein and glucose as a source of carbohydrate. The quantity of whole egg was identical in each diet to keep the same concentration of fat and minerals. The diets contained 0.5% vitamins (Vanderzant vitamin mixture for insects; Sigma). We offered the nutrients in a 1% agar gel. Each diet had total P + C of 200 g/litre (for further preparation details see Dussutour & Simpson, 2008b, 2012).

Experiment 1

In the first experiment, we investigated the effect of various nutritional challenges on the ants' longevity, lipid stores and foraging activity.

We confined 24 experimental colonies consisting of 30 ants and eight larvae originating from eight colonies to one of three diet treatments (eight experimental colonies per treatment). In the first (treatment P), we explored the responses of colonies when