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Enikő Csata, Audrey Dussutour

► **To cite this version:**

Enikő Csata, Audrey Dussutour. Nutrient regulation in ants (Hymenoptera: Formicidae): a review. Myrmecological News, 2019, 29, pp.111-124. 10.25849/myrmecol.news_029:111 . hal-02344462

HAL Id: hal-02344462

<https://hal.science/hal-02344462>

Submitted on 4 Nov 2019

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Nutrient regulation in ants (Hymenoptera: Formicidae): a review

Enikő Csata & Audrey Dussutour

Abstract

As for all living organisms, the nutritional needs of ants change over time in response to varying environmental conditions and demands for growth, health, and reproduction. Solitary individuals regulate their nutritional intake to maintain an appropriate balance of nutrients by selectively choosing the quality and quantity of food that meet their nutritional requirements. For social organisms, such as ants, food collection for the entire colony relies on a few individuals whose nutritional requirements may be very different from those of other members of their colony. Recent studies have used an integrative framework, the “geometric framework”, to better understand how living organisms regulate macronutrient intake to defend a specific nutrient “intake target”. In this review, we first reveal how the geometric framework has been used to deepen our understanding of ant communal nutrition. Second, we describe how this framework might be used to also understand the nutritional strategies used by ants facing infection challenges. Lastly, we conclude with a brief discussion of the promising techniques that could be used in the future to improve our understanding of communal nutrition in ants.

Key words: Ants, nutrition, geometric framework, food intake, parasite, review.

Received 6 March 2019; revision received 1 July 2019; accepted 6 July 2019

Subject Editor: Heike Feldhaar

Enikő Csata (contact author), Hungarian Department of Biology and Ecology, Babeş-Bolyai University, Clinicilor 5-7, 400006, Cluj-Napoca, Romania; Centre de Recherches sur la Cognition Animale (CRCA), Centre de Biologie Intégrative (CBI), Université de Toulouse, CNRS, UPS, 31062, Toulouse, France. E-mail: csataeniko88@gmail.com

Audrey Dussutour, Centre de Recherches sur la Cognition Animale (CRCA), Centre de Biologie Intégrative (CBI), Université de Toulouse, CNRS, UPS, 31062, Toulouse, France.

Introduction

Ants, as all living organisms, face basic nutritional challenges. They must find the correct amounts and balance of nutrients to satisfy their needs in terms of growth, maintenance of body functions and reproduction (SIMPSON & RAUBENHEIMER 2012). Foods offer complex mixtures of nutrients, each nutrient having its own functional implication for the animal. For instance, the two main life history traits reproduction and lifespan often have different nutritional optima. In many insects, high-carbohydrate diets increase lifespan but reduce breeding performances, whereas high-protein diets dramatically reduce lifespan, but favour reproduction (SIMPSON & RAUBENHEIMER 2012).

To regulate its nutrition, an organism, such as an ant, needs to (i) determine the nutritional quality of available food sources; (ii) assess its current nutritional state in relation to its desired state using circulating metabolites and hormones; (iii) and integrate its nutritional requirements with food source availability to produce optimal behav-

ioral and physiological responses (LENARD & BERTHOUD 2008, SIMPSON & RAUBENHEIMER 2012). However, ants face an additional challenge: food collection is undertaken only by the foragers, which represent approximately ten to twenty percent of the colony (HÖLLEDOBLER & WILSON 1990). Thus, foragers need to collect food that meets their own nutritional requirements, but also fulfill the needs of other members of the colony such as inner-nest workers, reproductives and larvae.

The main aim of this review is to illustrate how we can use an integrative framework to deepen our understanding of ant nutrition. First, we will give a brief overview of ant nutritional ecology and ant foraging behaviour. Second, we will present the geometric framework as an integrative approach, that takes into account the interaction between food attributes and ant behaviour. Third, we will describe how this approach enables us to understand ant foraging strategies and their impact on colony performance. Fourth, we will discuss how this framework may be used to un-

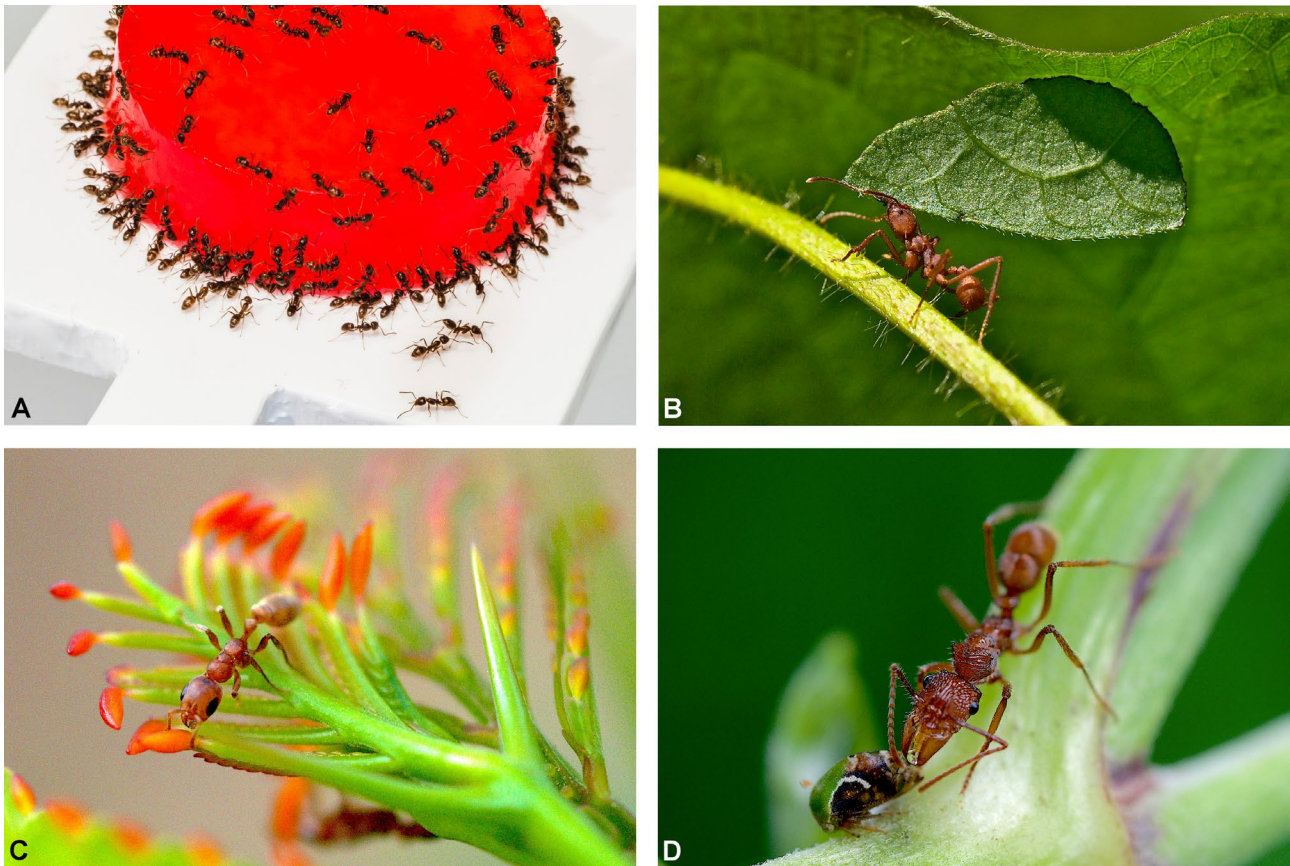


Fig. 1: Ants feeding on different food source (A) The Argentine ants *Linepithema humile* feeding on artificial food, (B) *Atta cephalotes* medium worker carrying a leaf fragment back to the nest to feed their symbiotic fungus, (C) *Pseudomyrmex ferruginea* collecting Beltian bodies, (D) *Ectatomma tuberculatum* collecting honeydew from a membracid adult. (Photograph A by David Villa, B - D by Jean Paul Lachaud).

derstand foraging strategies used by ants facing not only nutritional but infection challenges. Lastly, we will present promising techniques that can be used in the future to improve our understanding of communal nutrition in ants.

Ant nutritional ecology

Two recent papers have extensively reviewed ant nutritional ecology. The first one concentrated on nutritional niche plasticity and its influences on ant communities (FELDHAAR 2014). The second one focused on how resources affect ant nutritional ecology, describing ants trophic position, ants natural food sources and ants digestive physiology (BLÜTHGEN & FELDHAAR 2009). Hence, ant nutritional ecology will only be discussed briefly in this review.

Ants have extremely diversified lifestyles, ecological characteristics, social organisations and habitat requirements. They are present in all kinds of terrestrial environment, even when those seem inhospitable. They are often classified as ecosystem engineers, since they shape in large part the structure and diversity of their habitats (FOLGARAIT 1998). Most ants are considered to be omnivores (HUNTER 2009) utilizing a large variety of nutritional

resources and feeding on more than one trophic level. Yet, a few ant species are specialized on specific food, some being herbivores (direct consumers of plant resources) or indirect herbivores (collectors of hemipteran honeydew) predators, pollenivores, nectarivores, fungivores or granivores (Fig. 1, Fig. 2; BEATTIE 1985, HÖLLDOBLER & WILSON 1990). Numerous field studies have shown, using stable isotopes, that within ant communities, species forage in different nutritional niches, for example, formicines forage on lower trophic levels in comparison to myrmicines or ponerines (BLÜTHGEN & al. 2003, DAVIDSON & al. 2003, FIEDLER & al. 2007, O'GRADY & al. 2010). Yet, ant nutritional niches can vary depending on environmental conditions. For instance, studies have shown that in the presence of a superior competitor, some ant species are excluded from their favourite food to feed on less preferred ones (BLÜTHGEN & FIEDLER 2004a, b). Likewise, ants cease to feed on certain food depending on food availability (KAY 2004, PETRY & al. 2012). For example, *Formica podzolica* foragers supplemented with carbohydrates stop collecting honeydew and floral nectar (PETRY & al. 2012). Both in the field and in the lab, when studying ant nutritional ecology and in particular food selection, researchers have focused their attention on forager behaviour.



Fig. 2: Ants feeding on different food source (A) *Ectatomma ruidum* workers carrying a prey back to their nest, (B) *Pseudomyrmex gracilis* worker carrying a female parasitoid wasp, (C) *Odontomachus hastatus* carrying a *Lucilia sericata* larva, (D) *Messor barbarus* transporting a seed back to the nest. (Photographs A, B by Jean Paul Lachaud, C, D by Iago Sanmartín-Villar).

Foraging behaviour

Ant foraging activity is influenced by 1) the distribution of food resources in time and space, 2) the quality of the food, and 3) the competition level, and 4) the risk of predation or parasitization. The behaviour of a forager mostly depends on the activities of other foragers and the nutritional state of the colony as a whole (TRANIELLO 1989). Both experimental and theoretical works investigating foraging strategies in ants have emphasized the importance of social information as a mechanism for selecting the highest quality food source in the environment (reviewed in JEANSON & al. 2012). For instance, in many species of ants, when a forager finds a food source, it lays an odour trail (pheromone trail) on its way back to the nest to recruit its nestmates to its discovery. Recruited ants use the trail to reach the food source and reinforce it on their return journey (HÖLLDOBLER & WILSON 2009).

Numerous lab studies have shown that once a forager encounters a food source the decision to lay a trail depends on various parameters: 1) food quality: *Linepithema humile* (see ARGANDA & al. 2014), *Lasius niger* (see PORTHA & al. 2002, DUSSUTOUR & SIMPSON 2012), *Solenopsis invicta* (see CASSIL & TSCHINKEL 1999), *Solenopsis geminata*

(see HANGARTNER 1969), *Lasius niger* (see BECKERS & al. 1992), *Monomorium* and *Tapinoma* (see SZLEP & JACOBI 1967), *Tetramorium impurum* (see VERHAEGHE & DENEUBOURG 1983), *Tetramorium caespitum* (see COLLIGNON & DETRAIN 2009), *Myrmica sabuleti* (see De BISEAU & al. 1991), *Monomorium pharaonis* (see SUMPTER & BEEKMAN 2003), *Rhytidoponera* sp. (see DUSSUTOUR & NICOLIS 2013), *Linepithema humile* (see REID & al. 2012); 2) food quantity: *Lasius niger* (see MAILLEUX & al. 2003); 3) food handling time: *Pheidole pallidula* (see DETRAIN & DENEUBOURG 1997); 4) level of colony starvation: *Lasius niger* (see MAILLEUX & al. 2006); and 5) foraging risk: *Lasius pallitartis* (see NONACS 1990). Overall, depending on the species, foragers recruit more intensively 1) to carbohydrate than to protein (*Lasius niger*, see PORTHA & al. 2002); 2) to highly concentrated foods than to diluted ones (*Monomorium pharaonis*, see SUMPTER & BEEKMAN 2003); 3) when they are starved than when they are satiated (*Lasius niger*, see MAILLEUX & al. 2006); 4) for big prey items than for small ones (*Pheidole pallidula*, see DETRAIN & DENEUBOURG 1997); and 5) for safe location than for risky ones (NONACS 1990). The modulation of this trail laying behaviour often leads to the selection of the best food option, when two food sources varying in characteristics are offered (FRANKS 1985, see review TRANIELLO

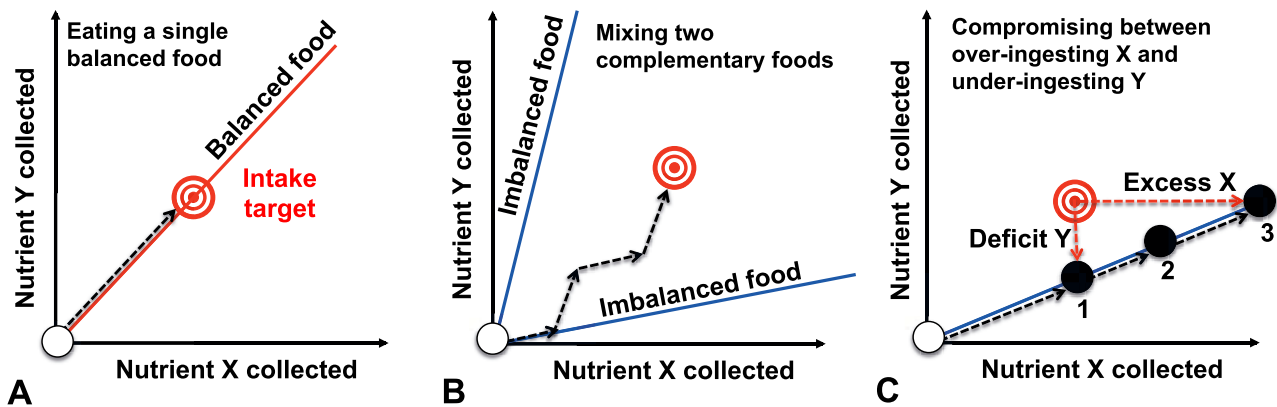


Fig. 3: Nutritional geometry (A) The ant individual can reach its intake target, IT (red target), by eating a balanced diet (the food contains the same X:Y ratio as the IT). (B) The ant individual can reach its IT by eating two imbalanced but complementary foods. (C) The ant individual is confined to an imbalanced food and has three options: 1) under-eat the food to regulate nutrient X and suffer a lack of Y, 2) make a compromise by reaching the closest distance to the IT, or 3) over-eat the food to regulate nutrient Y and ingest an excess of nutrient X. The white dot represents the ant individual's nutritional state and the nutritional rails (lines) represent the X:Y ratio of the diet. (Adapted from SIMPSON & RAUBENHEIMER 2012).

1989, DETRAIN & al. 1999, HÖLLDOBLER & WILSON 2009, JEANSON & al. 2012).

Studies investigating collective decisions in a foraging context have brought significant understanding of ant nutrition. Yet, even though all naturally available food items encountered by ants in the field contained multiple nutrients, most studies used carbohydrates as a food source or often investigate the effects of protein and carbohydrate in isolation from one another (PORTHA & al. 2002, 2004). In addition, these studies were often conducted on a short-term basis i.e., the experiments never exceeded few hours (JEANSON & al. 2012), while both the nutritional state and the nutritional optima of the colony might change in time according to seasons (COOK & al. 2011), colony growth (DUSSUTOUR & SIMPSON 2008), and colony composition (DUSSUTOUR & SIMPSON 2009). Thus, understanding how ants maintain nutrient supply at both a collective and an individual level in response to changes in the nutritional composition of available foods and colony characteristics would provide an important extension to models of collective foraging behaviour. Such important questions about ant nutrition can only be answered using an integrative approach.

An integrative approach: geometric framework

In a seminal paper, RAUBENHEIMER & SIMPSON (1993) presented for the first time an integrative approach, named geometric framework (GF) to model animal nutrition that takes into account the regulation of different nutrients simultaneously. The GF is a state-space modelling approach that presents how an animal solves the problem of balancing nutrient demands in an ever-changing environment (RAUBENHEIMER & SIMPSON 1993, SIMPSON & al. 2003, SIMPSON & RAUBENHEIMER 2005). The GF uses a nutrient space which is a geometric space built of multiple axes, where each axis represents a particular nutrient. The

nutritional state of the animal is represented as a point in this nutrient space, which moves over time with nutrient intake, metabolism, growth, reproduction and excretion (Fig. 3). The amount of nutrients that an animal needs to ingest to maximize its fitness is represented as a point in the nutrient space, called the intake target (SIMPSON & RAUBENHEIMER 2012).

Foods are modelled in this nutrient space as vectors with a slope indicating the balance of nutrients they contain (nutritional rails). By eating, the animal changes its nutritional state along the vector of the chosen food rail. A nutritionally balanced food enables the animal to reach its intake target (Fig. 3A), whereas an imbalanced diet forces the individual into a compromise between over-ingesting some nutrients while under-ingesting others. If two or more foods are available and encompass the intake target, they are called complementary, as the animal can achieve its intake target by eating from both foods (Fig. 3B, Fig. 3C) (SIMPSON & RAUBENHEIMER 2012).

The GF has enabled to understand some of the most fundamental principles of animal nutrient regulation strategies and how they vary across a wide range of taxa, ecological contexts and feeding guilds (see review SIMPSON & RAUBENHEIMER 2012). This framework was first developed to study insects, especially grasshoppers, locusts and caterpillars (ZANOTTO & al. 1997, BEHMER & al. 2001, LEE & al. 2002, BEHMER & al. 2005, LEE & al. 2006, BEHMER 2009, DEANS & al. 2015, TESSNOW & al. 2017). In the last decades, the GF has been applied successfully to various species, including slime molds (DUSSUTOUR & al. 2010), social insects (ants: DUSSUTOUR & SIMPSON 2008, DUSSUTOUR & SIMPSON 2009, COOK & al. 2010, SHIK & al. 2016; bees: ALTAYE & al. 2010, PAOLI & al. 2014, VAUDO & al. 2016a, 2016b), fish (RUOHONEN & al. 2007), rats (SIMPSON & RAUBENHEIMER 1997), mice (SORENSEN & al. 2008, SOLON-BIET & al. 2014, 2016), birds (KÖHLER & al.

2012), domestic mammals (HEWSON-HUGHES & al. 2011), and humans (SIMPSON & al. 2003, SIMPSON & RAUBENHEIMER 2005, 2012, RAUBENHEIMER & SIMPSON 2016). A major advantage of this framework is that it can be used for generating new empirically testable predictions about what animals should eat, how much and when.

However, until recently, most researchers have viewed the world of nutrition from the perspective of individual animals. As a result, we have an extensive knowledge about nutritional regulation in solitary insects (SIMPSON & al. 1988, ZANOTTO & al. 1997, BEHMER & al. 2001, LEE & al. 2002, BEHMER & al. 2005, LEE & al. 2006, see review BEHMER 2009, SIMPSON & RAUBENHEIMER 2012). Solitary insects require about 30 nutrients to fuel life processes, like amino acids, sugars, fatty acids, vitamins, sterols, salts, and the nutrient amount, and balance required are species specific (see review BEHMER 2009). Moreover, solitary insects possess separate appetites for particular nutrients and are able to compensate for changes in food composition. They are also capable of selecting among nutritionally complementary foods to achieve a nutritional “intake target”.

In social insects, regulation of nutrient intake is far more complex than in solitary ones. First, in social insects, such as ants, only a small proportion of individuals forage while their congeners remain in the nest. Thus, the foragers need to relate their own nutritional needs to the ones of the colony. Second, ant individuals within the colony might differ in their nutritional needs (SORENSEN & al. 1985, DUSSUTOUR & SIMPSON 2009, see review by FELDHAAR 2014).

Different nutritional requirements within a colony

Different nutritional requirements across members of the colony: Ants within the colony have their own nutritional needs, which might vary depending on their growth stage, their age and / or their role in the colony (SORENSEN & al. 1985, DUSSUTOUR & SIMPSON 2009, COOK & al. 2010, see review by FELDHAAR 2014). Adults such as foragers and nurses mostly need carbohydrates as a source of energy (WILSON & EISNER 1957, MARKIN 1970), whereas larvae and reproductive adults rely also heavily on proteins for growth and egg production respectively (MARKIN 1970, HOWARD & TSCHINKEL 1981, SORENSEN & VINSON 1981, CASSILL & TSCHINKEL 1999, HÖLLDOBLER & WILSON 2009). These differences in nutritional needs are reflected by the proportion of nitrogen (N) in the dry body mass, which increases from the stage of larvae through pupae to adult workers (KAY & al. 2006). These differential needs within a colony are evident in honeybees, another social insect, where larval bees feed on different diet to adults. Adults primarily feed on nectar, which is rich in carbohydrate while larvae feed almost exclusively on pollen, a protein rich food (see review by BRODSCHNEIDER & CRAILSHEIM 2010).

Therefore, the colony as a whole, needs to adjust its nutritional regulatory strategies to satisfy the nutritional needs of all the individuals. As foragers are the only work-

ers that venture outside the nest to collect food, if they would respond only to their own nutritional needs, they would collect only carbohydrates for fuelling their activity, since they are already fully-grown while the brood, queen, nurse ants and other inner-nest workers would soon starve to death. However, it was shown that the number of workers and the presence of larvae influences the mobilization of foragers and increases the total amount of food collected by workers in *Pheidole megacephala*, *Ochetellus glaber*, *Lasius niger* and the amount of protein in *Rhytidoponera* sp. (CORNELIUS & GRACE 1997, PORTHA & al. 2002, 2004, DUSSUTOUR & SIMPSON 2008, 2009), demonstrating that foragers respond to colony demography and the presence of larvae. A key question, therefore is how foragers maintain the supply of an appropriate balance of nutrients for the colony as a whole?

The question was answered by DUSSUTOUR & SIMPSON (2009) using the GF, where they showed that, when offered a choice between two imbalanced but complementary foods, green headed ants (*Rhytidoponera* sp.) are able to meet the nutritional requirements of all the members of the colony to optimize its growth and its survival. They demonstrated that (i) colonies with larvae maintain a higher nutrient intake than colonies without larvae; (ii) proteins comprise a higher proportion of the macronutrients collected when larvae are present in the nest; and (iii) foragers maintain nutrient intake constantly across a range of nutrient dilutions only when larvae are present within the colony. Hence, the presence of larvae changes the nutritional requirements (i.e., intake target) of the colony, but also contributes to the effectiveness of nutritional regulation.

How do foragers “know” that they need to collect more food and especially more proteins when larvae are present in the nest? In ants, nutrition is a decentralized homeostatic process where the food is exchanged from individual to individual in a chain-of-demand in which recipients solicit food from donors (CASSILL & TSCHINKEL 1999). In the colony, the chain of demand starts with larvae emitting signs of hunger to nurses. Then, inner nest workers transfer this information to foragers, which leave the nest to collect food (SORENSEN & al. 1981, 1985, CASSILL & TSCHINKEL 1999).

To explain how green-headed ants adjust food collection depending on colony composition, we suggest the following scenario that could be extended to other species: A forager collects a piece of high-protein / low-carbohydrate food and returns to the nest. An inner nest worker takes this piece of food and feeds it to the larvae. Having had its food piece taken, the forager heads back outside to collect some more. If, in contrast, a forager goes back to the nest with a piece of low-protein / high-carbohydrate food piece and has difficulty off-loading its load because inner nest workers are carbohydrate replete and larvae refuse to consume it, then the forager would be less likely to return to the same food source (GREENWALD & al. 2018). Hence, fewer foragers would be recruited to a low-protein / high-carbohydrate food source than to

a high-protein / high-carbohydrate diet. Following this scenario, foragers responding to cues from their congeners would be able to answer colony needs by making intricate adjustments to their foraging behaviour acting both as a collective mouth and gut. Similar scenario has been demonstrated in bees, where foragers adjust their recruitment behaviour to their unloading time i.e., foragers stop foraging if they experienced long waiting time before unloading their nectar (SEELEY 1989).

Different nutritional requirements across partners: Some ant species, like fungus-growing ants rear other organisms such as basidiomycete fungi that turn nutrients into digestible food for the colony. The intake target of these ants seldom matches the one of their “partner” and therefore face an additional nutritional challenge. For instance, the leaf-cutting ants *Mycocepurus smithii* farm a fungal cultivar as their primary nutrient source. This fungus grows on fresh plant material (grass or leaves) carried to the nests by the foragers. Using the GF approach, SHIK & al. (2016, 2018) showed that the intake target of these leaf-cutting ants is different from the one of the fungal cultivar. The authors designed 36 experimentally defined artificial media varying in total amounts and relative amounts of protein and carbohydrates to grow the cultivar. They demonstrated that the fungal cultivar grows differently according to the protein to carbohydrate ratio of the diet. They revealed that the growth of edible somatic tissues is maximised on high-carbohydrate / low-protein diet, while this diet suppresses the production of reproductive tissues. Interestingly, ants offered a choice between two complementary artificial diets, collect protein and carbohydrates in amount and ratio that maximize growth of fungal somatic tissues but inhibit independent reproduction of the fungal cultivar (SHIK & al. 2016). How do the ants know what to collect? As for larvae, there is a feedback mechanism that operates in leaf-cutting ant colonies, with the fungus signaling its condition to the ants using chemical cues (reviewed in GREEN & KOOLJ 2018). However, the exact chemical compounds involved in this signalling are not known yet.

Nutritional requirements depend on species ecology: Several studies have now applied the GF to study ant nutrition and show that the intake target of a species depends on its ecology and trophic niche. For instance, predatory ants favoured more protein biased diets whereas ants feeding on plant-based resources prefer carbohydrate biased diets (*Rhytidoponera* sp: see DUSSUTOUR & SIMPSON 2009, *Solenopsis invicta*: see COOK & al. 2010, *Iridomyrmex suchieri*: see CHRISTENSEN & al. 2010, *Nylanderia* sp. nr. *pubens*: see COOK & al. 2012, *Lasius niger*: see DUSSUTOUR & SIMPSON 2012, *Mycocepurus smithii*: see SHIK & al. 2016). These studies suggest that one of the tenets of ecological theory is that coexisting species use different resources, a process that could have driven niche differentiation and local development of biodiversity as observed in grasshoppers (BEHMER & JOERN 2008).

Newly arrived ants in novel habitats such as invasive ants consume food items that can be different from foods

usually encountered in their native habitats. Invaders are believed to be more flexible and able to collect a wide range of foods while exploiting different habitats. Indeed, Argentine ants, which have successfully invaded all continents apart from Antarctica, have a larger trophic niche and a larger tolerance to diet imbalance (ARGANDA & al. 2017) than co-occurring native species such as *Lasius niger* (see DUSSUTOUR & SIMPSON 2012). MACHOVSKY-CAPUSKA & al. (2016) proposed that invasive species might be able to combine highly disparate food sources in their macronutrient composition to reach their intake target and as a result might be more tolerant to nutrient imbalance. The GF might be an appropriate tool to test this hypothesis and to investigate how diet breadth and diet plasticity interact to favour invaders.

Solving nutritional challenges

Having different nutritional requirements to meet is not the single challenge that an ant colony is facing. Nutrient availability is another issue that the colony needs to tackle on a regular basis. Sometimes, ants have neither access to a balanced food nor to nutritionally complementary but only to imbalanced food sources. For instance, if ants are confined to a high-protein / low-carbohydrate diet, they can either decide to eat a small quantity of food to satisfy their requirement in protein but in doing so they will suffer a carbohydrate shortage. Alternatively, they can eat large quantity of food to satisfy their carbohydrate requirements but in doing so they will overeat protein. Lastly, they can feed to some point intermediate between these extremes (Fig. 4). In GF models, the strategy adopted is known as a rule of compromise, because it represents the compromise between over-eating some nutrient and under-eating others.

A comprehensive description of the rule of compromise followed by ant colonies has been investigated in some species: *Lasius niger* (see DUSSUTOUR & SIMPSON 2012), *Ectatomma ruidum* (see COOK & BEHMER 2010), *Iridomyrmex mayri* (see POHL & al. 2016), *Iridomyrmex suchieri* (see CHRISTENSEN & al. 2010), *Linepithema humile* (see ARGANDA & al. 2017), *Odontomachus hastatus* (see BAZAZI & al. 2016), *Rhytidoponera metallica* (see DUSSUTOUR & SIMPSON 2008), *Solenopsis invicta* (see SORENSEN & al. 1985, COOK & al. 2010, WILDER & EUBANKS 2010). In these species, when ant colonies are confined to a diet containing a fixed ratio of protein to carbohydrate for a long period of time (from days to weeks), individuals adjust both their recruitment and food consumption to the diet composition. On a high-protein / low-carbohydrate diet, ants collect more food and recruit in larger numbers than colonies given a low-protein / high-carbohydrate diet. This suggests that ants are prioritizing carbohydrates and maintain the supply of carbohydrates to the colony at a target level (Fig. 4). This compensatory feeding to gain carbohydrates, results in overconsumption of protein. Yet, such regulation was not observed on extremely unbalanced diets (DUSSUTOUR & SIMPSON 2012, COOK & al. 2010).

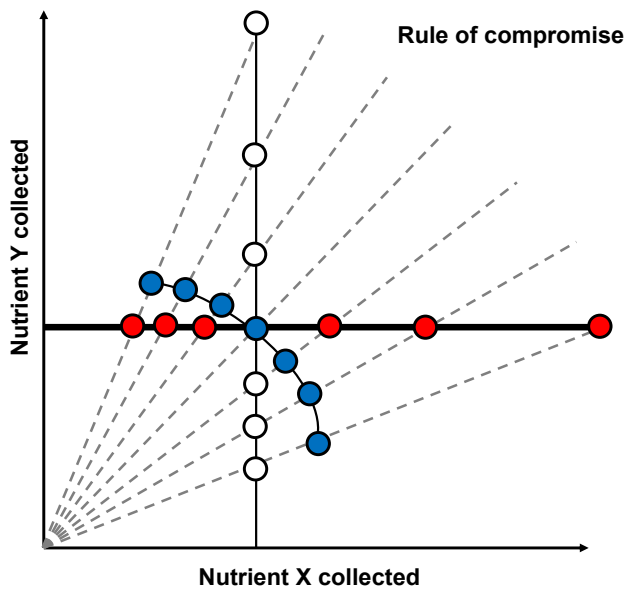


Fig. 4: Rule of compromise. When an animal is confined to one of six imbalanced diets (black line), it has three options : 1) satisfy its requirement of Y no matter the lack or the excess of X it will suffer (red dots – non interaction rule) 2) satisfy its requirement of X no matter the lack or the excess of Y it will suffer (white dots – non-interaction rule) 3) suffer both an excess of Y (X) and a lack of X (Y) but not as large as the extreme (blue dots: closest distance rule). The chosen strategy, also called the rule of compromise, usually reflect the cost of over-ingesting Y (X) and under-ingesting X (Y). (Adapted from SIMPSON & RAUBENHEIMER 2012).

DUSSUTOUR & SIMPSON (2009) and COOK & al. (2010) showed that ants are able to restore a certain degree of nutritional balance by retaining carbohydrates and getting rid of proteins post-ingestively. For instance, green headed ants confined to high-protein /low-carbohydrate diet chew the food to extract the limiting carbohydrates and reject the excess protein as pellets. When larvae are present within the nest, green headed ants are more effective at getting rid of excess protein than when they are absent. Thus, not only do larvae offer nutritional feedbacks that improve nutrient regulation, they also enhance nutrient extraction (DUSSUTOUR & SIMPSON 2009). Larvae are not the only ones that can help the workers solving nutritional challenges. Intracellular bacteria from the genus *Blochmannia* provide the hosts with the resources required for successful development (RUSSELL & al. 2017). FELDHAAR & al. (2007) showed that endosymbiotic *Blochmannia floridanus* nutritionally upgrade the diet of the ants (*Camponotus floridanus*) to provide essential amino acids and enhance its competitive ability toward other ant species lacking such an endosymbiont.

Cost of nutritional regulation

In most living organisms, a determinant of the relationship between diet and longevity is the balance of protein to carbohydrate and social insects are no exception (SIMPSON

& RAUBENHEIMER 2012). In all species tested so far, ants die sooner on high-protein /low-carbohydrate diets than on low-protein /high-carbohydrate diets (*Lasius niger*, see DUSSUTOUR & SIMPSON 2012; *Linepithema humile*, see ARGANDA & al. 2017; *Odontomachus hastatus*, see BAZAZI & al. 2016; *Rhytidoponera metallica*, see DUSSUTOUR & SIMPSON 2008; *Solenopsis invicta*, see COOK & al. 2010). Hence; eating excess of proteins to reach a carbohydrate target comes at a cost. Interestingly, in green headed ants the presence of larvae helped offset the costs of over ingesting proteins (DUSSUTOUR & SIMPSON 2009) highlighting their importance as the “digestive caste” of the colony (MARKIN 1970, SORESENSEN & al. 1983, CASSILL & TSCHINKEL 1999, ERTHAL & al. 2007).

Unlike larvae, most adult workers are restricted to take up solid food particles, due to their proventriculus (CASSILL & al. 2005), thus the larger food fragments are usually given to the larvae (SORESENSEN & al. 1983, CASSILL & al. 2005). Moreover, ants produce only very small amounts of proteases in comparison to larvae (RICKS & VINSON 1972, ABBOTT 1978, PETRALIA & al. 1980, SORESENSEN & al. 1983, WHITWORTH & al. 1998). Therefore, DUSSUTOUR & SIMPSON (2009) suggested that green headed ants overcome some of the deleterious effects of excess protein by transferring the food directly to the larvae which in turn digest and redistribute it as liquid pre-processed food to the workers.

However, it remains unclear how high-protein /low-carbohydrate diets shorten lifespan in ants. ARGANDA & al. (2017) started to answer this question in a recent study. They showed that high-protein diets shorten lifespan in Argentine ants *Linepithema humile*, because the final products of the protein digestion i.e., the amino acids are harmful, especially: methionine, serine, threonine and phenylalanine. They showed that these amino acids shortened lifespan even more than crude proteins. The hypothesis is that an excess in amino acids increases potentially toxic nitrogen waste products (WRIGHT 1995) and over-stimulates nutrient-sensing pathways that regulate lifespan such as the TOR pathway, a genetic pathway functionally conserved throughout evolution (PANKAJ & BRIAN 2004, SIMPSON & RAUBENHEIMER 2009).

Nevertheless, if an excess of protein decreases individuals’ lifespan, it can increase the reproduction and the growth of the colony. For instance, when *Camponotus floridanus* colonies are fed with a surplus protein the egg production by queens increases (NONACS 1991). Some studies have also shown that colonies supplemented with protein produced more sexuals (male and /or female), more larvae and larger individuals (BACKUS & HERBERS 1992, ARON & al. 2001). A recent study (BERNADOU & al. 2018) unveiled that reproductive division of labour is also influenced by food quality. Genetically identical individuals that experience poor nutritional conditions are less likely to become reproductive than well-fed clonemates (*Platythyrea punctata*).

Nutritional imbalance does not solely influence survival and reproduction, but can also elicit distinct activity

rates and behavioural responses, such as aggressiveness, in numerous ant species. For example, when fed with a high-carbohydrate diet, the metabolic rates of ants accelerate, and they display behaviours that further enhance their abilities to secure resources (*Linepithema humile*, see HOLWAY 1999; *Ectatomma ruidum*, see KAY & al. 2012; Neotropical litter ant community, see KASPARI & al. 2012; *Linepithema humile*, see SHIK & SILVERMAN 2013). Alternatively, carbohydrate scarcity limits both aggression and activity and tune-down foraging activity rates (*Lasius niger*, see DUSSUTOUR & al. 2016; *Linepithema humile*, see GROVER & al. 2007).

Beyond proteins and carbohydrates

Until now, all experiments that used the GF to understand ant nutrition have focused their investigations on macronutrients – protein and carbohydrates. As the literature shows in other animals such as locusts, caterpillars, mice, etc. (SIMPSON & RAUBENHEIMER 2012), these two macronutrients can explain a large proportion of the variation in the behavioural, physiological and performance responses. These two macronutrients are, however, clearly not the only functionally important nutritional components of foods.

In ants, beyond protein and carbohydrates, little is known about other dietary requirements. Lipids, the third macronutrient, are essential for larvae growth, egg production and ovary development (BLÜTHGEN & FELDHAAR 2009) but their regulation and their interactions with protein and carbohydrate have yet to be studied. Lipids are abundant in prey (HUGHES & al. 1994), in seeds (BREW & al. 1989), and are also important components of extrafloral nectar and honeydew (FORREST & KNIGHTS 1972, BEATTIE 1985). Lipids are very attractive in some species of ants as illustrated by their extensive use in baits design (see review STANLEY 2004). Lipids are also attractive in natural food sources, for instance myrmecochorous seeds and some tropical plants offer lipid-rich food rewards (elaiosome and food bodies respectively) which are very attractive to foragers (BLÜTHGEN & FELDHAAR 2009). In a field study, PIZO & OLIVEIRA (2001) showed that recruitment rate and ant attendance (23 ant species, Atlantic forest of South-east Brazil) were higher for lipid-rich diaspores than for lipid-poor ones. Lipids are also essential to colony growth and survival, for instance sterols are required as hormone precursors and as a component of cell membranes and cannot be synthesized by insects and, thus need to be obtained from food consumption or symbionts (HERBERT & al. 1980, HAGEN & al. 1984, BEHMER & al. 1999, NATION 2002). GAMMANS & al. (2005) showed that providing the ant *Myrmica ruginodis* with four essential fatty acids and four essential sterols through the addition of elaiosomes (*Ulex*) in the diet increases larvae production and larvae weight.

Vitamins and minerals are also essential to health and also play a critical role in animal nutritional strategies. For instance, sodium is vital for the physiological functioning of all animals including ants (homeostasis,

muscle activity, and nervous system function) (FRAUSTO DA SILVA & WILLIAMS 2001), but is often rare in the environment (KASPARI & al. 2008, 2009). Numerous field studies showed that ants are able to track sodium availability in the environment (KASPARI & al. 2008: 17 ant communities, CHAVARRIA PIZARRO & al. 2012: leafcutter ants *Atta cephalotes*, HERNÁNDEZ & al. 2012: *Camponotus mirabilis*, VIEIRA & VASCONCELOS 2015: neotropical ants). It has also been shown that ants recruit more workers on diets offering folic acid, B12, inositol and biotin (RICKS & VINSON 1970: imported fire ants *Solenopsis saevissima richteri* and *Solenopsis saevissima saevissima*, POISSONNIER & al. 2014: black garden ants *Lasius niger*). Moreover, POISSONNIER & al. (2014) showed that vitamins deficiency, as macronutrient deficiency, affects health, performance, and behaviour in ants.

A future avenue: influence of nutrition in parasite-host relationship

Besides longevity and reproduction, food intake can also affect animal health. In most animals, infections have adverse effects on nutritional status whereas nutrient deficiency impairs resistance to infection. For instance, AYRES & SCHNEIDER (2009) showed that reduced food intake in flies (*Drosophila melanogaster*) limits their ability to fight a *Listeria monocytogenes* infection and as a consequence increases their mortality rate. In addition, the quantity and quality of food resources influence the abundance and development of parasites (VALE & al. 2013, HALL & al. 2009), and directly shape virulent effects of parasitic infections (TSENG 2006). Parasites, pathogens are fundamental actors in ant nutrition and they are often forgotten when studying nutritional regulatory strategies. Parasites may modify the intake target of the ants to satisfy their nutritional needs, ultimately influencing the foraging decisions of the colony and the level of infection. Alternatively, ants may modify their nutritional state to enhance their ability to fight the infection.

So far, studies in invertebrates have focused on how nutrient deprivation or starvation influences immune functions or parasite resistance (MORET & SCHMID-HEMPEL 2000, TRIGGS & KNELL 2012). In caterpillars, resistance to parasites depends on the relative amounts of protein and carbohydrate (LEE & al. 2006, POVEY & al. 2009). When caterpillars are allowed to self-select their diet, virus challenged insects temporarily increase the relative protein content of their diet to better fight the viral infection (POVEY & al. 2013). This result suggests a form of macronutrient self-medication in bacteria or virus-challenged caterpillars (LEE & al. 2006, POVEY & al. 2009, 2013).

Can parasite infection influence macronutrient balancing in ants? In social insects, the effect of parasites and macronutrient intake are often studied at the level of the individual (MORET & SCHMID-HEMPEL 2000, TRIGGS & KNELL 2012), while responses at the colony level, are usually neglected. Ant societies are attractive targets to parasites and pathogens (bacteria, fungi, mites, fluke worms, nematodes, beetles, butterflies) as they provide

them with a rich hunting ground and a promising nutrient source (LACHAUD & al. 1998, SCHMID-HEMPEL 1998, CSÓSZ & MAJOROS 2009, ESPADALER & SANTAMARIA 2012, CSATA & al. 2013, WITEK & al. 2014, TRAGUST & al. 2016, CSATA & al. 2017a, b, ARAÚJO & al. 2018, DE BEKKER & al. 2018).

Ants have evolved a variety of adaptations to fight parasites, including behavioral, biochemical and immunological responses (external: antimicrobial secretions) to both reduce virulence and transmission of entomopathogen agents (NUNN & ALTIZER 2006, TRAGUST & al. 2013, CSATA & al. 2014, TRAGUST 2016). In addition to individual strategies, ants have evolved a collective defence also known as “social immunity”, that is, individuals living in groups or societies cooperate to fight against the transmission of parasites and pathogens (CREMER & al. 2007). The means to socially fight parasites are various and range from social exclusion to application of antimicrobial secretions to congeners (review CREMER & al. 2007).

Using the GF approach, KAY & al. (2014) investigated for the first time how diet macronutrient composition affects immunity of ants at both an individual and collective level. They challenged the ants *Ectatomma ruidum* with a pathogenic fungus (*Metarhizium anisopliae*) and showed that workers reared in groups survived longer, when fed a high-carbohydrate diet than workers confined to a high-protein diet. Interestingly, this effect of macronutrient composition was not observed on workers reared alone (Fig. 5). Interestingly though, they showed that when larvae were removed from the colony, the beneficial effect of a high-carbohydrate diet disappears suggesting that larvae improve worker immunity as they improve nutritional regulation (DUSSUTOUR & SIMPSON 2009). Further researches are needed to clarify how macronutrient composition affects social immunity. KAY & al. (2014) suggest that carbohydrate exploitation by social insects may provide an evolutionary advantage. In another study, KONRAD & al. (2015) showed that the negative impact of the fungus *Laboulbenia formicarum* on the survival of the host ant *Lasius neglectus* is enhanced under nutritional stress (starvation).

An intriguing question is whether infection with parasites/pathogens can induce a change in diet selection to fight the infection (self-medication) or to sustain parasites/pathogens growth (manipulation)? Self-medication is considered to be prophylactic if both infected and uninfected individuals consume harmful substances that promote parasites resistance, but therapeutic if the harmful substance is consumed only after an infection (ABBOTT 2014). BOS & al. (2015) revealed that infected ants (*Formica fusca*) readily consume reactive oxygen, an harmful substance that promotes fungal resistance and survival, after being exposed to a fungal pathogen (*Beauveria bassiana*), while uninfected ants avoid it. This result could well be considered as the first evidence for self-medication in ants.

Whether foragers adjust their nutrient intake to the infection states of their nestmates is virtually unexplored

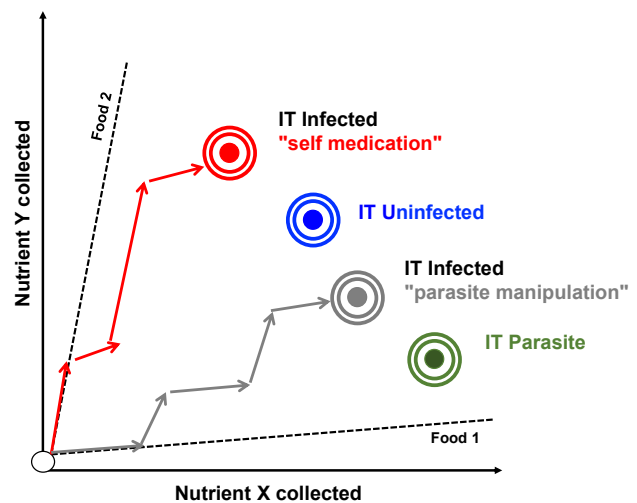


Fig. 5: Hypothetic intake regulation strategies in a colony of ants infected by a parasite. We first determine the intake target of the uninfected host and the parasite. Then an infected host is offered two foods, offering varying amount of protein and carbohydrate. Foods 1 and 2 are imbalanced but complementary (fall on opposite sides of both the intake target, IT, of the parasite and the IT of the uninfected host). The infected individual can either choose to eat more from Food 1 to reach an intake that maximize resistance to the parasite (self-medication) or eat more from Food 2 and satisfies the requirement of the parasites (manipulation).

and should be investigated in the future. To study how parasites/pathogens, affect ant nutrition using the GF approach we need to follow a 3-steps plan. In a first step, we have to define independently the intake target of the parasite, the uninfected host and then the infected host. This requires to be able to rear the parasites separately from their host. In a second step, we must study how infected and uninfected hosts perform when confined to diets offering varying amount of protein and carbohydrate. By doing so, we shall identify a diet that promotes infection or lessens infection. In a third step, we need to offer both, infected colonies and uninfected ones a choice between various diets to decipher if parasites are manipulating the host foraging strategies to promote their own growth or if the host is fighting the parasite to survive (Fig. 5).

Conclusions

What does the future hold for the study of nutrient regulation in ants? In ants, the nutritional decisions of a forager not only depend on its own nutritional needs but also critically on the nutritional requirements of its congeners. As food is shared through multiple interactions between ants, tracking food distribution is challenging. Until now, authors have used stable isotopes (FELDHAAR & al. 2010) or radiolabeled nutritive solutions (BUFFIN & al. 2012) to track food flow within colonies. Mass spectroscopy and RNA sequencing has also been used to identify the molecules present in the ant crop and quantify what is shared via trophallaxis (LEBOEUF & al. 2016). However,

while these techniques bring us a large range of insights into ant nutritional ecology, they lack temporal and/or spatial resolution. Fortunately, a new technological advance is now available to complement these approaches (GREENWALD & al. 2015, 2018). GREENWALD & al. (2015) combining individual tracking using QR codes and food labelling using fluorescent dye were able to successfully track carbohydrate distribution within an ant colony. This new method has a high spatial and temporal resolution allowing a precise quantification of ant trophallactic networks and food dissemination dynamic. The next step would be to combine this approach with the GF and track multiple nutrients simultaneously to see how they interact with each other and how they are shared, distributed and stored among individuals within the nest. This will help us better understand communal nutrition in ants.

The geometric framework (GF) approach has greatly advanced our understanding of ant nutrition. In the future, it would be interesting to expand the researches to three or more nutrient dimensions to better understand ant foraging behaviour. Fortunately, the GF offers ways to deal with such dimensionality which will enable a better understanding of how nutritional interactions shape the behaviour of the colony. Until now, studies have been restricted to a few species and are mainly conducted under laboratory conditions. It is now necessary to characterize the nutritional niche of a broader range of species, from generalist to specialist, from invasive to native ant species. The GF offers ways to study networks of interactions within and among ant communities and might help us to predict how these communities will respond to changing environmental conditions.

Acknowledgements

The authors are grateful for helpful feedback from reviewers. We thank Subject Editor Heike Feldhaar for providing constructive comments on the manuscript. We thank Jean Paul Lachaud, Iago Sanmartín-Villar, and David Villa for providing photographs. E.Cs. was supported by the Fyssen Foundation Grant and A.D was supported by the CNRS.

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