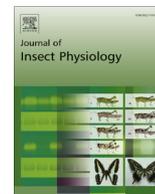




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## Modelling nutrition across organizational levels: From individuals to superorganisms

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## ABSTRACT

The Geometric Framework for nutrition has been increasingly used to describe how individual animals regulate their intake of multiple nutrients to maintain target physiological states maximizing growth and reproduction. However, only a few studies have considered the potential influences of the social context in which these nutritional decisions are made. Social insects, for instance, have evolved extreme levels of nutritional interdependence in which food collection, processing, storage and disposal are performed by different individuals with different nutritional needs. These social interactions considerably complicate nutrition and raise the question of how nutrient regulation is achieved at multiple organizational levels, by individuals and groups. Here, we explore the connections between individual- and collective-level nutrition by developing a modelling framework integrating concepts of nutritional geometry into individual-based models. Using this approach, we investigate how simple nutritional interactions between individuals can mediate a range of emergent collective-level phenomena in social arthropods (insects and spiders) and provide examples of novel and empirically testable predictions. We discuss how our approach could be expanded to a wider range of species and social systems.

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### 1. The social dimension of nutrition

Since pioneering studies on dietary self-selection in rats (Richter et al., 1938), research in nutritional ecology has made considerable advances in characterizing the nutritional strategies of animals and their physiological, behavioural and fitness consequences (Raubenheimer et al., 2009; Simpson and Raubenheimer, 2012). State-space modelling approaches such as the Geometric Framework (GF, Fig. 1) have increasingly been used to describe how individuals regulate their intake of multiple nutrients simultaneously and how this varies across taxonomic groups, developmental stages and feeding guilds (Raubenheimer et al., 2009; Simpson and Raubenheimer, 2012; Wilder et al., 2013).

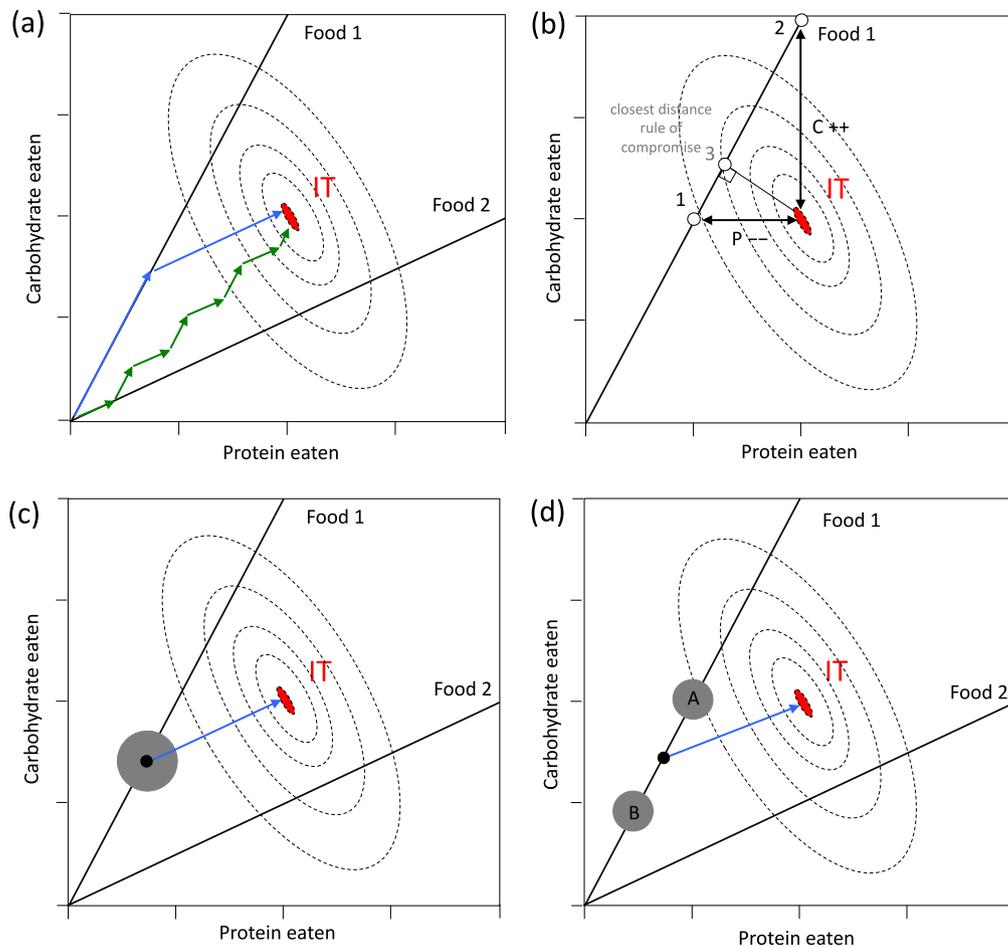
However, most of this knowledge has been deduced from studies on individual animals, thus ignoring potential influences of the social context in which nutritional decisions are made (Giraldeau and Caraco, 2000; Simpson et al., 2010). Group-living animals often signal feeding locations to each other, hunt and eat foods collectively, or collect food items for their young (Krause and Ruxton, 2002). These social interactions considerably complicate nutrition, as an individual's decision to eat a food not only depends on its own nutritional needs, but also on the needs of others. The trade-offs between optimizing individual nutrition and maintaining social cohesion may have important consequences on higher-level phenomena, such as group structures and dynamics. This raises the fundamental questions of how nutrient regulation is achieved at the individual and collective levels in animal groups and how these processes impact on each other.

Social arthropods, such as insects and spiders, offer an accessible connection between nutritional interactions at these two levels of biological organization. At the individual level, the nutritional ecology of insects (e.g. ants: Dussutour and Simpson, 2009; bees:

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**Fig. 1.** Examples of GF models for hypothetical animals featuring two food types (1 and 2) varying in their relative amounts of protein (P) and carbohydrates (C). In these graphical illustrations, the nutritional rails (thick black lines) represent the ratio of the two nutrients in each food. The intake target (IT, red surface) is the optimal amount and balance of the nutrients required by the individual. Fitness contours (dashed lines) are maximal at the IT and decrease non-linearly with increasing distance from it. (a) Model for an individual in the presence of two foods that are individually imbalanced (do not contain the same balance as the IT) but nutritionally complementary (fall on opposite sides of the IT). Sequences of arrows (blue and green) show two alternative routes that the individual could use to reach its IT by combining its intake from the two foods. (b) Model for an individual restricted to one nutritionally imbalanced food that must compromise between over-ingesting one nutrient and under-ingesting the other. Three options are described: at point 1, the individual satisfies its carbohydrate needs but suffers a shortfall of protein (P--); at point 2, it satisfies its protein needs but over-ingests carbohydrates (C++); and at point 3 it suffers both a moderate shortage of protein and a moderate excess of carbohydrate by minimizing the Euclidean distance between its nutritional state and its IT (closest distance rule of compromise). (c) Model for a group of gregarious individuals with similar nutritional needs. All individuals have the same IT. However, their physiological states vary as shown by the average (black circle) and the distribution (grey ellipse) of nutritional states. In this example where the nutritional states are unimodally distributed around the mean, the average nutritional state for all individuals could help predict the onset and direction of a collective movement between the two food types. The average nutritional state falls on the rail of food 1 at a critical switching point to reach the IT; most individuals require changing from eating food 1 to food 2 to avoid over-eating carbohydrates. (d) Model for a group of gregarious individuals with different nutritional needs. All individuals have the same IT but the distribution of their nutritional states is bimodal, thus forming two physiological subgroups (A and B). In this example, the shape of the variance in nutritional states could help predict the onset of the collective movement between foods, its direction and the roles of the different individuals. Individuals having ingested the highest amount of carbohydrates (subgroup A) have the greatest need for food 2. These individuals would be more likely to initiate the collective movement to food 2 by effectively acting as leaders motivated by their nutritional state. Individuals having ingested the lowest amount of carbohydrates (subgroup B) will be more likely to act as gregarious followers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Altaye et al., 2010; cockroaches: Raubenheimer and Jones, 2006; locusts: Raubenheimer and Simpson, 1993) and spiders (e.g. Mayntz et al., 2005) has been intensely studied. Most species require the same suite of nutrients (amino acids, sugars, fatty acids, minerals, vitamins and sterols) in amounts and ratios that differ among and within species, depending on developmental or reproductive status (Behmer, 2009a). At the collective level, there is a long tradition of envisioning arthropod societies as complex systems, in which self-organized behaviour and structures emerge from simple interactions among individuals (Camazine et al., 2001; Deneubourg and Goss, 1989; Sumpter, 2010). Many of these interactions are related to nutrient acquisition. In the simplest cases, individuals form temporary feeding aggregations that rapidly develop and erode as they become satiated (Lihoreau et al., 2010). In the most advanced societies, nutrient collection and processing

involve the coordinated activities of up to hundreds of thousands of individuals working together as a functional “superorganism” (Hölldobler and Wilson, 2009; Wheeler, 1911). Nutritional balance is achieved socially via a dual contribution of individuals to their own (individual) level state regulation, as well as higher (collective) level state, partly mediated through the same behaviours (foraging and feeding).

Here we argue that considerable insight about the nutritional strategies of social arthropods can be gained by studying individual- and collective-level nutrition in a common conceptual framework. To test this idea, we develop an individual-based model implementing the concepts of the GF. We then use variations of this model to illustrate how some classical examples of collective behaviour in insects and spiders can emerge from specific nutritional interactions between individuals.

## 2. Modelling individuals and groups in the Geometric Framework

### 2.1. The Geometric Framework

The GF employs a state-space modelling approach to explore how animals solve the problem of balancing multiple and changing nutrient needs in a multidimensional and variable nutritional environment (reviewed in [Simpson and Raubenheimer \(2012\)](#)). In GF models, individuals, foods and their interactions are represented in a geometric space (nutrient space) defined by two or more food components (often the macronutrients protein and carbohydrate) in a Cartesian coordinate system. Foods are vectors at angles from the origin determined by the ratio of the component nutrients they contain (nutritional rails), and the animal's nutritional state is a point that changes over time (see examples in [Fig. 1a](#) and [b](#)). As the animal eats a food item, its nutritional state changes along the nutritional rail for the chosen food. The functional aim for the animal is to select different foods and eat them in appropriate amounts to reach a nutritional state that maximizes its fitness (the intake target) ([Fig. 1a](#)). When the animal is unable to reach its intake target, for instance if neither a single balanced food nor several complementary foods are available, the animal can employ a rule of compromise to minimize the costs of over-eating one nutrient while under-eating another ([Fig. 1b](#)). A major advantage of this approach is that it combines principles of physiology (homeostasis), behaviour (feeding) and evolution (fitness consequences), thus enabling the derivation and testing of predictions about behaviour based on the nutritional state in relation to the nutritional opportunities of animals ([Raubenheimer et al., 2012](#)).

Although GF models have initially been developed to explore nutrient regulation in individual animals ([Raubenheimer and Simpson, 1993](#); [Simpson and Raubenheimer, 1993](#)), they also provide a modelling platform for characterising individual- and collective-level nutritional phenotypes in the same conceptual framework. Just as an individual is represented by the position of its nutritional state relative to its intake target in a nutrient space, a group can be viewed as a collection of individuals, each attempting to defend their own target while interacting with one another (see examples in [Fig. 1c](#) and [d](#)). In this approach, two nutritional factors are expected to influence interactions among individuals, both of which can be accounted for and modelled by the GF.

The first factor is the average nutritional state of all individuals, relative to their intake targets and the availability of nutrients in foods. This value reflects the nutritional needs at the collective level. In relatively simple groups, such as a cohort of gregarious animals, individuals are expected to eat similar foods (unimodal distribution of their nutritional states) and have similar nutritional needs (similar intake targets). In this case, the average nutritional state reflects the needs of the majority of the individuals and it should have a strong influence on the outcome of collective-level behaviours, as for instance the decision to leave a food source for another ([Fig. 1c](#)). However, the predictive power of the average nutritional state is much reduced in more complex groups, for instance family groups when adults and juveniles eat different foods (multimodal distribution of their nutritional states) and have different nutritional needs (different intake targets). Even if all group members have the same intake target, there can be some degree of variance in the extent to which they reach it depending on the availability of nutrients in the environment, the foraging performance of each individual, and the strength of competition ([Simpson and Raubenheimer, 2012](#)). Therefore, a second important factor to take into account is the variance in the distribution of nutritional states and intake targets among individuals. The shape and amplitude of this variance in the nutrient space reflects the

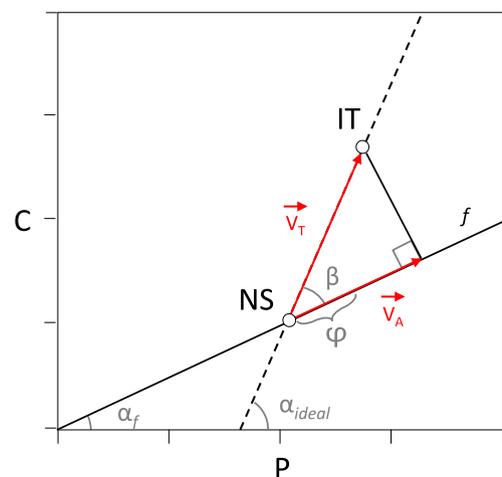
strength and direction of the influence of individuals' nutrition on collective-level behaviour ([Fig. 1d](#)). In moving groups, for instance, small fluctuations in the dynamics of nutrient acquisition among individuals can trigger the emergence of temporary behavioural roles, where the most nutritionally deficient individuals tend to initiate movement and lead groups, whereas satiated individuals follow behind ([McClure et al., 2011](#)). In groups with a division of labour, such as colonies of eusocial insects, the nutritional decisions of foragers are influenced by the nutritional states and intake targets of all other group members ([Dussutour and Simpson, 2009](#)).

### 2.2. The individual-based model

To illustrate how the integration of individual- and collective-level nutritional phenotypes can be used to generate predictions about the nutritional ecology of social animals, we developed an individual-based model implementing the main concepts of the GF. In this general model, individuals are represented by points corresponding to their current nutritional state (NS) and their intake target (IT) in a  $n$  dimensional Cartesian coordinate system ([Fig. 2](#)). Here we restrict ourselves to a two dimensional space where the  $x$ -axis corresponds to protein and the  $y$ -axis to carbohydrate. Food nutritional rails are represented by straight lines extending outwards (from the origin or the individual's NS) with a slope corresponding to the ratio of carbohydrate to protein (C/P). The quantity of a food an individual ingests is determined by its appetite  $A_i$ . Calculation of the appetite is based on the "closest distance rule of compromise" ([Simpson and Raubenheimer, 2012](#)) in which the individual attempts to get its NS to the nearest point (by Euclidian distance) to its IT along the selected food rail ([Fig. 1b](#)), as follows:

$$A_i = \|V_T\| \cos \beta, \quad A_i = \varphi \text{ if } A_i > \varphi$$

where  $\beta$  is the angle between two vectors; the first,  $\vec{V}_A$ , joining the NS of individual  $i$  to the point of compromise (the nearest point to the IT) along the selected food rail; the second,  $\vec{V}_T$ , joining the NS to



**Fig. 2.** Illustration of the variables influencing the nutritional decisions of animals in the individual-based model. Each individual is represented by its current nutritional state (NS) and its intake target (IT) in a two dimensional space defined by protein (P) and carbohydrates (C). The individual's decision to eat a food is determined by the angle  $\alpha_{ideal}$  associated with the vector  $\vec{V}_A$ , linking the NS to the IT, and the angle  $\alpha_f$  associated with the vector  $\vec{V}_T$ , linking the NS to the nearest point to the IT along the selected food rail  $f$  (closest distance rule of compromise; [Fig. 1b](#)).  $\beta$  is the angular difference between  $\alpha_{ideal}$  and  $\alpha_f$ .  $\varphi$  is the maximal amount of food that the individual can eat during one time step.

the IT (Fig. 2). If the quantity of food required to reach this point is more than the quantity that the individual can eat in one step ( $\varphi$ ), the NS is updated by moving along the food rail by a distance of  $\varphi$ . Given that an individual's IT represents the point where its maximal fitness can be achieved, we measured the fitness of an individual using the Euclidian distance,  $D_N$ , between its NS and its IT as follows:

$$\text{fitness} = e^{-c \cdot D_N}$$

where  $c$  is a constant ( $c = 2$  in all our simulations). In the simulation runs, we set the IT position along a chosen rail (for details see examples below) at a distance of  $D_{IT} = 1$  and the initial NS of each individual is set at a distance  $D_{NS} = F \cdot D_{IT}$  along the same rail, with  $F = 1/500$  in the simulations described in Sections 3.2 and 5.2, and  $F = 1/100$  for those described in Section 4.2.

In the following sections, we present examples of how this general modelling approach can be used and expanded to explore some nutritional strategies observed in arthropod groups and societies. The main differences between the model variations that we used in each case relate to how individuals select or leave foods based on their own requirements (individual influence) and their interactions with other individuals (social influence). In each example, we restricted ourselves to simple model structures in order to illustrate the utility of our approach instead of providing an in-depth exploration of the nutritional mechanisms involved. Simulations of the model were run in MATLAB 7.12 (MathWorks, MA).

### 3. Collective foraging decisions

#### 3.1. Empirical observations

Group-living arthropods often make collective foraging decisions, whereby all or the majority of the group makes a choice to feed on one food source among several alternatives (Jeanson et al., 2012). These collective decisions emerge from social amplification (positive and negative feedbacks) by which each individual's probability of joining and leaving a particular food source varies non-linearly with the number of individuals already present on it. Groups operate as information gathering and processing systems, allowing individuals to make faster and more accurate decisions collectively than that they would do independently (Couzins, 2009). For instance, ant and bee colonies can rapidly select a food source with an optimal concentration of sugar (Beckers et al., 1990; Seeley et al., 1991). However, in many natural conditions, animals do not have access to optimal (nutritionally balanced) foods. Rather they must exploit multiple nutritionally complementary foods to reach a balanced diet (Simpson and Raubenheimer, 2012). Efficient collective foraging strategies thus imply that groups alternate between exploiting different food sources to satisfy the requirement of all their members.

Studies on gregarious arthropods suggest that collective foraging decisions have important consequences on the nutrient balancing efficiencies of individuals. German cockroaches (*Blattella germanica*), for instance, are robust to enforced periods of nutritional imbalance and spectacularly capable of correcting accrued nutritional imbalances through extended periods of complementary food selection when foraging individually (Raubenheimer and Jones, 2006). However, under high population densities, cockroaches form large aggregations on foods as a result of a social facilitation for feeding mediated via contact cues (Lihoreau et al., 2010). The probability of a cockroach to join and stay on a food thus increases sharply with the number of cockroaches on that food (Lihoreau and Rivaut, 2011), which may ultimately influence

the ability of individuals to regulate their nutrient intake. In another gregarious insect, the forest tent caterpillar (*Malacosoma disstria*), strong social cohesion leads to suboptimal nutritional decisions (Dussutour et al., 2007). While individual caterpillars show a preference for nutritionally balanced diets over diets deficient in protein or carbohydrate (Despland and Noseworthy, 2006), groups tend to make random choices by settling on the first food discovered (Dussutour et al., 2007). Presumably, the excessively strong and rapid amplification, due to the silk loaded with pheromone laid down by caterpillars during foraging, constrains the flexibility of the collective decision and thus impairs the nutritional strategies of individuals. These observations suggest that in gregarious species where group members do not actively signal the quality of food sources to each other, individuals can balance their diet collectively providing that social cohesion is neither too loose nor too strong within a given environmental context.

#### 3.2. Theoretical exploration

We explored how groups of individuals with various levels of gregariousness can regulate their diet collectively by combining their intake of two nutritionally complementary food sources. In this variant of our general model, an individual can choose to visit a randomly selected food source (each food rail is a food source) and consume an amount of it. At the end of each step during which the individual consumed food, it can choose to stay on the food or leave it according to two influences. The individual influence ( $P_{ind}$ ) is determined by the angular difference between the selected food rail and the ideal rail that would point directly to the individual's IT (Fig. 2). The social influence ( $P_{soc}$ ) is determined by the number of individuals currently present on that food. The probability for an individual to leave the food source is calculated as follows:

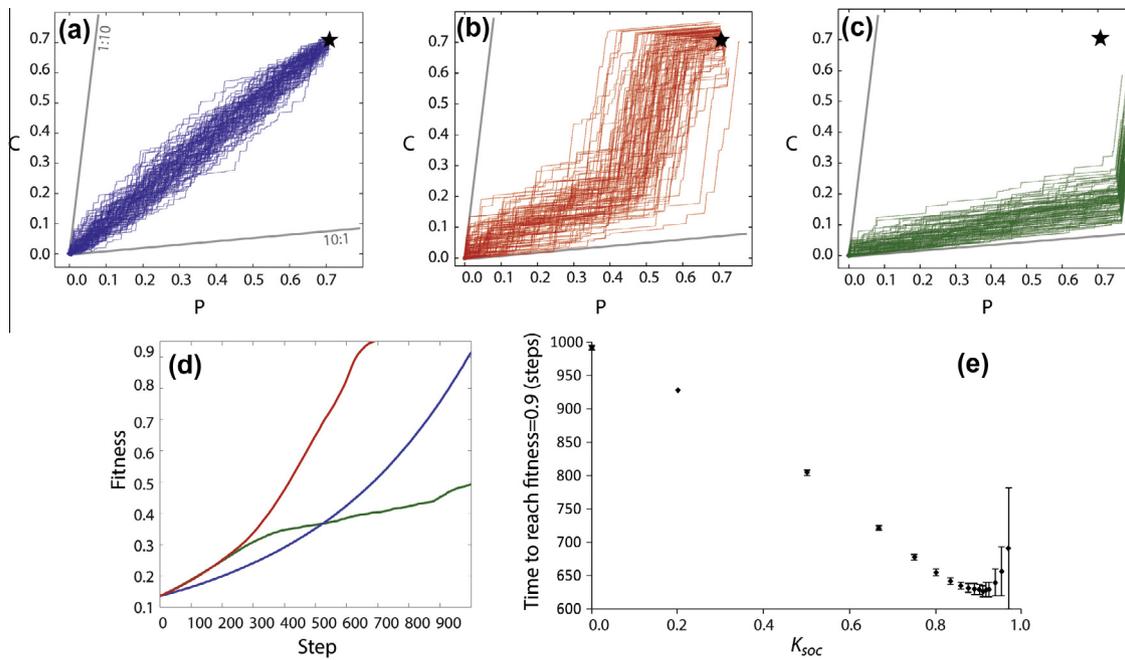
$$P_{ind} = \frac{|\alpha_{ideal} - \alpha_f|}{\pi/2}, \quad P_{soc} = e^{-\lambda \cdot N_f/N}$$

and

$$P_{leave} = [(1 - K_{soc}) \cdot P_{ind}] + (K_{soc}) \cdot P_{soc}$$

where  $\alpha_{ideal}$  and  $\alpha_f$  are the angles (measured in radians) associated with the ideal rail joining the NS and the IT of the individual and with the food rail  $f$  respectively (Fig. 2).  $\lambda$  is a constant ( $\lambda = 7$  in all our simulations),  $N_f$  the number of individuals on the food source  $f$  and  $N$  the total number of individuals in the simulation.  $K_{soc}$  is a constant controlling the strength of the social influence relative to the individual influence. When an individual leaves a food, it must wait for a time  $T_t$  (simulating the time required to travel and find a new food source) before being able to select a new food ( $T_t = 2$  in all our simulations).

Fig. 3 shows an example of the progression of the NS of 100 individuals with the same IT (P:C 1:1) given a choice between two complementary food sources (P:C 1:10 and P:C 10:1). In groups with no social influence ( $K_{soc} = 0$ , Fig. 3a), individuals frequently shift from one food to another, thereby distributing themselves uniformly between the two food sources and moving their NS along the optimal P:C 1:1 rail. Introducing a social component in the probability of leaving foods ( $K_{soc} > 0$ ) can lead to collective decisions whereby most individuals simultaneously eat from same food (average proportion of individuals on the same food during the last 250 steps:  $77.2 \pm 12\%$  (standard deviation) for  $K_{soc} = 0.83$ ,  $83.6 \pm 9\%$  for  $K_{soc} = 0.98$ ). At intermediate values of  $K_{soc}$  ( $K_{soc} = 0.83$ , Fig. 3b), the group rapidly shifts between the two food sources in order to track and reach the individuals' IT. However, for higher values of social influence ( $K_{soc} = 0.98$ , Fig. 3c), the group is trapped



**Fig. 3.** Example of simulations of collective foraging decisions (for details see Section 3.2). The figure shows three different simulation runs for groups of 100 individuals exploiting two food sources characterized by different protein (P) to carbohydrate (C) ratios (P:C 1:10, 10:1, shown as grey lines). All individuals have the same intake target located on the rail P:C 1:1 (black star). Panels a–c show the trajectories of each individual's nutritional state (coloured dots) in the nutrient space during a simulation run (1000 steps shown). (a) Example of a simulation run where the probability for an individual to leave a food source is not influenced by other individuals ( $K_{soc} = 0$ ). (b, c) Two examples of simulation runs where the probability of an individual to leave a food source is based on a combination of individual and social influences, whereby the more individuals are present at a source, the more likely the individual is to stay. When the strength of social influence is intermediate (panel b:  $K_{soc} = 0.83$ ), individuals collectively choose and alternate between the two food sources until they reach their intake target. When the social influence becomes stronger (panel c:  $K_{soc} = 0.98$ ), all individuals gather on one food source but the group stays on it for too long and the individuals' nutritional states end up deviating far from their intake target. (d) Fitness dynamics for the three examples shown in (a–c). Each curve represents the average fitness measured in a–c with the matching colour. (e) Average time required to reach a fitness of 0.9 as a function of  $K_{soc}$  ( $N = 50$  replicates per parameter value, bars indicate standard deviation). For the two highest values of  $K_{soc}$  (0.952 and 0.968) some simulation runs (24% and 80% respectively) never reached the target of a fitness equal or higher than 0.9 after 5000 steps.

on one food source, so that all individuals deviate from their IT without being able to reach it within the duration of the simulations. While individuals can track their IT with a great accuracy in absence of social influence (Fig. 3a), changing food sources can be costly if the time required to find a new food source is high. With a moderate level of social influence ( $K_{soc} = 0.83$ ), individuals remain on the same food for long periods of time, thus enabling them to track their IT faster than individuals foraging independently from each other ( $K_{soc} = 0$ ) as shown by the fitness curves (Fig. 3d). Our model predicts a range of values of  $K_{soc}$  optimizing this nutritional benefit of collective decisions (Fig. 3e). In more complex scenarios,  $K_{soc}$  would also provide additional indirect costs and benefits associated with group formation, such as competition and predator protection (Krause and Ruxton, 2002).

While studies on collective foraging decisions in arthropods have typically involved choices between two identical foods or between one optimal and one or several poor quality foods (Jeanson et al., 2012), we investigated a situation where groups were given a choice between imbalanced foods. Our results suggest that taking into account the nutritional composition of foods is critical to interpret the collective dynamics observed. Specifically, we identified potential costs and benefits of collective foraging decisions depending on the strength of social cohesion among foragers. An empirical test of this prediction would involve comparing the ability of individuals to defend their IT when feeding from nutritionally complementary foods in groups with varying levels of social cohesion, for instance in cockroaches, whose aggregation tendencies have been characterized and vary both within species across developmental stages (Jeanson and Deneubourg, 2007) and between species (Lihoreau and Rivault, 2008).

## 4. Colony provisioning

### 4.1. Empirical observations

In more advanced societies characterised by a division of labour, collective nutrient balancing strategies are more complex as individuals are nutritionally dependent on each other. In eusocial insects (ants, bees, wasps and termites), the assessment and collection of food is undertaken by the coordinated action of a minority of individuals (the foragers) on behalf of the entire colony. Food entering the nest is transferred and processed through a cascade of interactions between nest-bound workers (nurses), the queen(s) and the larvae (Hölldobler and Wilson, 1990; Seeley, 2010). While workers primarily consume carbohydrates as a source of energy, larvae and queens require protein-rich diets for growth and reproduction (Cassil and Tschinkel, 1999; Sorensen and Vison, 1981). The challenge for a forager is to find appropriate food items and recruit its nestmates towards them in order to address its own nutritional requirements as well as those of all other colony members.

In ants, foragers balance their collection of carbohydrate and protein to maintain colony-level targets optimizing colony growth and survival (Christensen et al., 2010; Cook and Behmer, 2010; Cook et al., 2010; Dussutour and Simpson, 2012, 2009). These mechanisms are best understood in the green-headed ant (*Rhytidoponera metallica*), an omnivorous species which feeds on dead insects, seeds and honeydew (Dussutour and Simpson, 2009). When given a choice of two complementary foods, foragers adjust their balance of nutrient collection in response to the presence or absence of larvae in the nest. If constrained to an imbalanced food

rich in protein, ants do not consume all the food collected. Rather workers (foragers and nurses) extract the limiting carbohydrate and deposit the excess protein outside the nest as pelleted discard (Dussutour and Simpson, 2009). These experiments suggest the following sequence of nutritional interactions within colonies (Behmer, 2009b). First, foragers select foods in response to the colony needs and extract carbohydrates to satisfy their individual nutritional requirements. When food enters the nest, nurses may also eat before passing the food to the brood. Larvae then digest the protein required for growth before residual excess of protein is removed from the colony and dumped by the foragers. Acceptance or rejection of food returned to the colony may heavily influence a forager's decision to return to a similar food type at its next foraging bout, presumably acting as a nutritional feedback (Cassil and Tschinkel, 1999; Dussutour and Simpson, 2009). Therefore, the ant colony is not only a nutrient balancing superorganism at the level of food collection, but also a collective nutrient processing, storage and waste disposal device.

#### 4.2. Theoretical exploration

We explored how efficient collective nutrient regulation can emerge in groups with a division of labour between forager and non-forager individuals based on a system of nutritional feedbacks, as suggested by ant studies (Cassil and Tschinkel, 1999; Dussutour and Simpson, 2009). In this variant of the model, 100 foragers collect food from 8 food types evenly distributed across the nutrient space (P:C 1:16, 1:3.9, 1:1.94, 1:1.23, 1.23:1, 1.94:1, 3.9:1, 16:1). The aim for the foragers is to reach their individual intake target (IT<sub>F</sub>, P:C = 1:1.2) as well as to nourish 500 non-foraging larvae with a different intake target (IT<sub>L</sub>, P:C = 2:1). We chose the values of IT<sub>F</sub> and IT<sub>L</sub> based on Dussutour and Simpson (2009). On each time step, a forager brings back a fixed quantity of a selected food to the nest and keeps a constant proportion for itself. The remaining fraction of food ( $f_p$ ) is passed to a randomly selected larva. To keep the model simple, the forager cannot selectively extract carbohydrates or protein, but consumes a fraction of the entire food

defined by its appetite. The larva, however, can manipulate food and reject any amount of protein in the form of waste pellets in order to eat a ratio of nutrients pointing towards its IT<sub>L</sub>. If the rail of the food received has a shallower slope than the vector joining its NS<sub>L</sub> to its IT<sub>L</sub>, the larva can adjust its food consumption to follow a rail pointing directly towards its IT<sub>L</sub>. However, if the food received has a steeper slope than the vector joining its NS<sub>L</sub> to its IT<sub>L</sub>, the larva cannot adjust its food consumption to follow a rail pointing directly towards its IT<sub>L</sub>. In this case, the larva emits a “begging” nutritional feedback towards the forager.

At the end of its step, the forager selects a food type based on two influences. The individual influence ( $W_F$ ) depends on the angular difference between the rail the forager selected and a rail pointing directly towards its IT<sub>F</sub>. The social influence ( $W_L$ ) is determined by the proportion of begging larvae. The forager's probability of selecting food purely for itself is defined as follows:

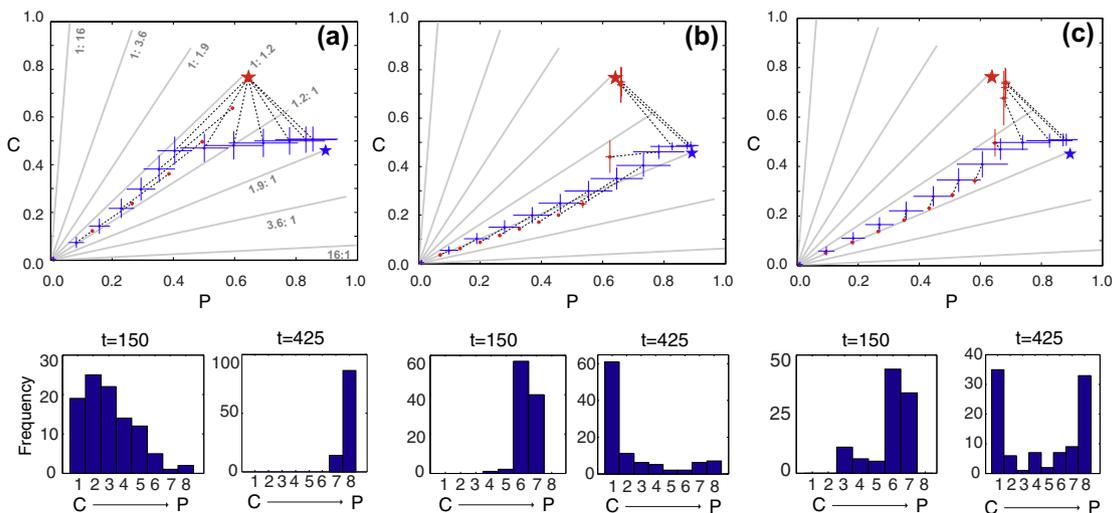
$$W_F = K_F \cdot \frac{|\alpha_{\text{ideal}} - \alpha_f|}{\pi/2} \quad W_L = (1 - K_F) \cdot b/N_L$$

and

$$P_F = \frac{W_F}{W_F + W_L}$$

where  $\alpha_{\text{ideal}}$  and  $\alpha_f$  are the angles associated with the ideal rail joining the NS<sub>F</sub> and the IT<sub>F</sub> and with the selected food rail  $f$  respectively (Fig. 2),  $b$  is the number of larvae begging and  $N_L$  the total number of larvae.  $K_F$  is a constant controlling the strength of the forager's individual influence on its next foraging decision. When the forager collects food for itself, it chooses the food rail which is the closest to the rail pointing towards its IT<sub>F</sub>. When the forager responds to the larvae's nutritional feedback, it proceeds as follows: if the selected larva rejected proteins, the forager shifts to the next food with a higher carbohydrate content; if the larva begged, the forager shifts to the next food with a higher protein content.

Fig. 4 shows examples of simulation runs where variations in the fraction of food passed to the larvae ( $f_p$ ) and in the weight of individual influence in food selection ( $K_F$ ) produce dramatically



**Fig. 4.** Example of simulations of colony provisioning (for details see Section 4.2). The figure shows three different simulation runs using a varying fraction of food passed from a forager to a larva ( $f_p$ ) and the relative weight of the forager nutritional requirements ( $K_F$ ). The higher  $K_F$ , the more likely a forager will seek to collect a food addressing its own nutritional requirements and ignore the larvae's feedback. On the upper part of each panel, the figure shows the nutritional state of foragers (red dots) and the one of larvae (blue dots) every 50 steps during a simulation of 600 time steps (bars indicate standard deviation) and their respective intake targets (stars). Each pair of foragers' and larvae's nutritional states for a given time step are linked by a dotted line. The 8 food rails (grey lines) are characterized by different protein (P) to carbohydrate (C) ratios. In the lower part of each panel, two histograms show the distribution of foragers on each food at two different times of the simulation, with the food rails numbered from 1 to 8 starting with the lowest P:C ratio (food 1 = P:C 1:16). (a) Example of simulation when foragers only pass 75% of their food and have a high tendency to follow their own nutritional requirements ( $K_F = 0.6$ ). (b) Example of simulation when foragers pass 90% of their food and have a low tendency to follow their own nutritional requirements ( $K_F = 0.05$ ). (c) Example of simulations with intermediate values of  $f_p = 0.86$  and  $K_F = 0.2$ . (For interpretation of the references of colour in this figure legend, the reader is referred to the web version of this article.)

different collective dynamics by the foragers. In the first example (Fig. 4a), when foragers only pass 75% of the food collected and have a higher tendency to follow their own nutritional requirements ( $K_F = 0.6$ ), they start collecting foods rich in carbohydrate (see histogram at  $t = 150$ ) and both  $NS_F$  and  $NS_L$  initially move directly towards the  $IT_F$ . However, once the foragers reach their  $IT_F$ , they suddenly shift towards collecting foods rich in proteins (see histogram at  $t = 425$ ) based on the nutritional feedback from the larvae (begging) to reach the  $IT_L$ . In the second example (Fig. 4b), foragers pass 90% of the food collected and have a much lower tendency to follow their individual nutritional requirements than previously ( $K_F = 0.05$ ). Even though the foragers have no explicit knowledge of the larvae's  $IT_L$ , they quickly select a food rich in protein satisfying the larvae (see histogram at  $t = 150$ ). It is then only after the larvae have reached their  $IT_L$  that the foragers start collecting foods rich in carbohydrates, enabling them to redress their  $NS_F$  towards the  $IT_F$  (see histogram at  $t = 425$ ). In the third example with intermediate values for  $f_p$  and  $K_F$  (Fig. 4c), despite the foragers' initial tendency to prioritise the larvae's nutritional requirements (see histogram for  $t = 150$ ), there is a wider spread in the foods selected. As both the  $NS$  of foragers and larvae move together in the nutrient space, the angle pointing towards their respective  $IT$  increases to a point where the distribution of foragers on foods becomes U-shaped, with the majority of them collecting foods at both extreme ends of the available food rails (see histogram at  $t = 425$ ) until both larvae and foragers simultaneously reach their  $IT$ .

As shown by the simulations, efficient nutrient regulation can be achieved in groups where food collection is made by a minority of individuals and group members have different intake targets, provided that there is a nutritional feedback from non-foragers to foragers. In our simple model individuals have no or a limited ability to manipulate the nutrient composition of the food. Consequently, foragers distribute themselves mostly around the two food rails matching their  $IT$  or that of the larvae, either by sequentially selecting one then shifting to the other, or by selecting both at the same time and forming a U-shaped distribution of selected food. If foragers were able to differentially extract carbohydrates first, as suggested by recent studies (Cook et al., 2010; Dussutour and Simpson, 2009), we would expect them to select a food with an intermediate rail between the one satisfying the  $IT_F$  and  $IT_L$ . These predictions can be experimentally tested by tracking the distribution dynamics and food collection rates of foragers in ant colonies exploiting multiple complementary foods.

## 5. Reproductive division of labour

### 5.1. Empirical observations

The amount and blend of nutrients that animals eat can have direct consequences on their fecundity (e.g. Lee et al., 2008; Maklakov et al., 2008). In a social context, variations in the nutrient state among individuals can lead to reproductive skews that characterize most advanced stages of sociality. In eusocial insects, differential nourishment of the larvae by the nurses is a proximate mechanism for reproductive division of labour (Hölldobler and Wilson, 2009). Larval nutrition is most influential in honeybees (*Apis mellifera*) where individuals fed large amounts of royal jelly develop into fertile queens whereas individuals only receiving small amounts develop into sterile workers (Kamakura, 2011). Studies on cooperative breeding arthropods suggest that differential nutrition is also an important mechanism regulating reproductive skews, where a subset of individuals only reproduces (breeders) while others perform alloparental care (helpers). The best evidence comes from studies on spiders of the genus *Stegodyphus* that form

colonies of several hundreds of individuals in which less than half of the females reproduce (Lubin and Bilde, 2007). These spiders share large webs on which many females feed on the same prey items, thus setting the stage for intense competition over food acquisition. Colonies are typically composed of individuals with a wide range of body sizes and the largest females tend to exclude smaller ones from foods (Rypstra, 1993; Whitehouse and Lubin, 1999). Contest competition increases body size asymmetries, thus enabling large dominant females to monopolize limited nutritional resources required for reproduction (Lubin, 1995; Ulbrich and Henschel, 1999). Experimental manipulation of prey nutritional composition in these species shows that the amount of lipids available to colonies is positively correlated with the number of reproductive females, thus indicating a direct effect of nutrition on reproductive skews (Salomon et al., 2008). A similar mechanism has been described in burying beetles (*Nicrophorus vespilloides*), where dominant and subordinate females form breeding associations in which they feed and defend their larvae on shared buried carcasses (Eggert et al., 2008). In this species, reduced reproduction of subordinates arises from a limited access to protein due to aggressive interactions with dominants on the carcasses.

### 5.2. Theoretical exploration

We explored whether random differences in access to limited nutrients among members of a group can lead to dominance hierarchies. Pronounced differences in the nutritional states between dominants and subordinates is the basis for reproductive division of labour to emerge, as indicated by studies on spiders (Salomon et al., 2008) and beetles (Eggert et al., 2008). The idea that a group structure can emerge from an initially homogeneous population as a result of the cumulative effect of contest competition has previously been studied in the context of the dominance hierarchy in paper wasps (Bonabeau et al., 1996; Camazine et al., 2001). In the original model, individual wasps engage in a series of contests where the probability of each competitor winning depends on the difference between its force  $f_i$  and the force of its opponent  $f_j$ . By winning, an individual increases its force by a set amount, therefore improving its chances to win future contests. Ultimately, the cumulative effect of contest competition generates a stable dominance order (Bonabeau et al., 1996; Camazine et al., 2001). Here, we extended this model and embedded it in the GF by replacing the force, an abstract quantity, by the success of individuals at tracking their nutritional requirements, namely fitness as we defined it earlier. Therefore, during a competition between individual  $i$  and individual  $j$ , the former will win the contest with a probability given by:

$$Q_{ij} = \frac{1}{1 + e^{-\eta(f_i - f_j)}}$$

where  $f_i$  and  $f_j$  represent the fitness of individual  $i$  and  $j$  respectively, and  $\eta$  is a constant ( $\eta = 25$  in all our simulations). We simulated a situation where food could be limited, with individuals having to compete and displace others to acquire it. In our example, all individuals have the same  $IT$  (P:C 1:1) and have access to 3 food types (P:C 16:1, 1:1, 1:16). The global capacity  $c$  defines the number of food items per individual available at each time step. Food access is distributed evenly across the 3 different food rails, and therefore there are only  $c/3$  food items per individual available on a given rail at any time (e.g. if  $c = 1$ , only a third of the individuals can feed on a given rail). On each step, an individual attempts to feed on a randomly selected food rail, but if there are already other individuals present in a number equal to the capacity of this food rail, they engage in a contest determined by  $Q_{ij}$ . If the newcomer wins, it can eat the food. The resident is evicted and will have to search for another food rail on its next step. If the newcomer loses, it will

attempt to find a new food rail on the next step. After eating, the probability  $P_{\text{leave}}$  that an individual spontaneously leaves the food depends on the quantity it consumed and on the angular difference between the food rail and the ideal rail that points directly to its IT, calculated as follows:

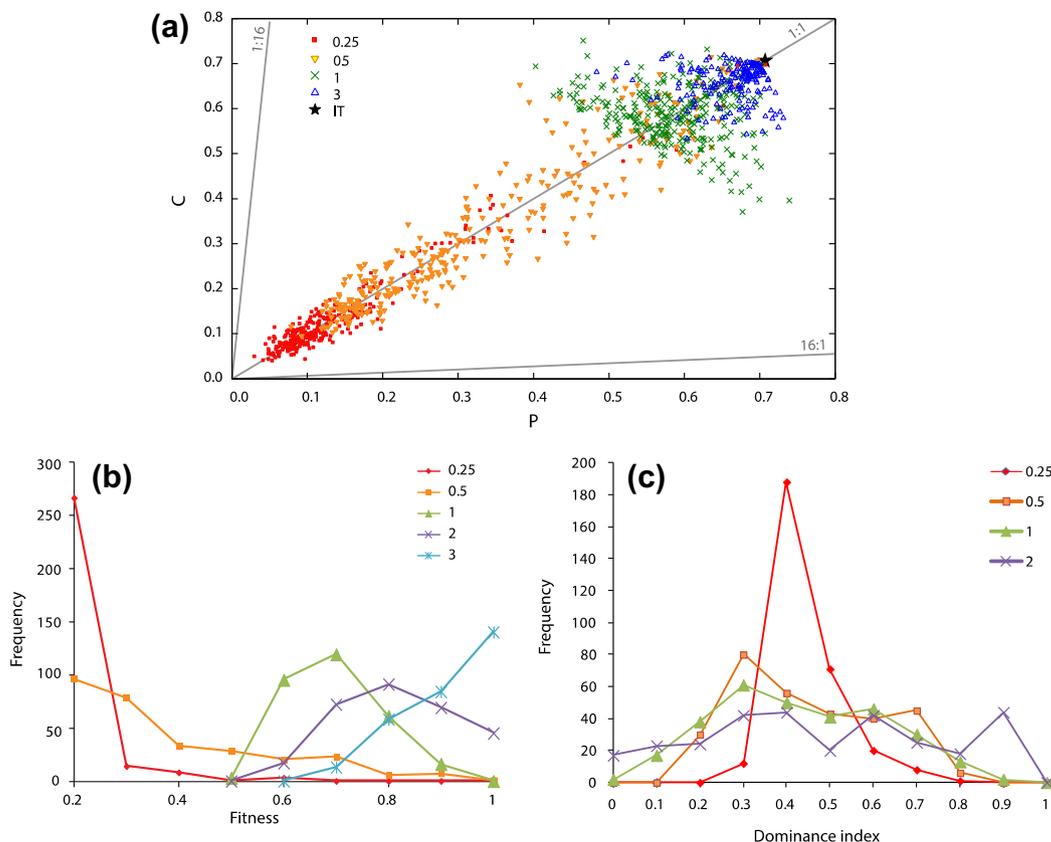
$$P_{\text{leave}} = K \cdot \frac{|\alpha_{\text{ideal}} - \alpha_f|}{\pi/2} + (1 - K) \cdot \frac{\varphi - A_i}{\varphi}$$

where  $\alpha_{\text{ideal}}$  and  $\alpha_f$  are the angles associated with the ideal rail joining the NS and the IT of the individual and with the food rail  $f$  respectively (Fig. 2).  $K$  is a constant representing the relative importance of the two terms ( $K = 0.2$  in all our simulations). With these rules, individuals can improve their fitness by acquiring the appropriate food and tracking their IT. The faster individuals increase their fitness relative to their competitors, the better their chances to win contests and monopolize the required foods.

Fig. 5 shows examples of simulations runs where increasing competition (decreasing global capacity  $c$ ) leads to dramatic changes in the distribution of the resulting NS for a population of 300 individuals with the same IT (P:C 1:1). In the absence of competition ( $c = 3$ ) most individuals reach their IT. However, with increasing levels of competition, the distribution of IT within the population becomes more and more skewed. Under extreme competition ( $c = 0.25$ ), for instance, only one individual reaches its IT. Skewed fitness distributions obtained in the simulations (Fig. 5b) are reminiscent of the distributions observed for dominance traits

such as body size mediating reproductive differences in spiders (Rypstra, 1993; Ulbrich and Henschel, 1999). Furthermore, calculating dominance indices for each individual (the proportion of contests won (Bonabeau et al., 1996)) reveals that increasing levels of competition leads to the emergence of stable dominance hierarchies (Fig. 5c). As in paper wasps, most individuals lose more often than they win, while a small minority of individuals win most of the contests (Bonabeau et al., 1996).

Our model shows that non-uniform distributions of NS can emerge in groups of individuals competing over the acquisition of specific nutrients. If these differences in NS translate to differences in the reproductive capacity of individuals, then the model provides a mechanism for reproductive division of labour. Such a model can be used to predict which individuals would grow bigger and become dominant after experimental removal of dominant individuals and/or restriction of the group to a single food rail advantaging individuals whose NS occupy a particular region of the nutrient space (e.g. by making them the only ones capable of reaching their IT). While we have limited ourselves to the simple assumption that fitness outcomes are symmetrical in the nutrient space (determined by the Euclidian distance to a single point, the IT), empirical evidence show that that fitness responses often vary with the life history traits measured (e.g. lifespan, egg production) and form asymmetric patterns, where overeating one nutrient can have different consequences than overeating another one (e.g. fruit flies: Lee et al., 2008; field crickets: Maklakov et al., 2008).



**Fig. 5.** Example of simulations of the emergence of reproductive division of labour (for details see Section 5.2). All individuals have access to 3 foods (P:C 1:16, 1:1, 16:1, shown as grey lines) characterized by different protein (P) to carbohydrate (C) ratios, and have the same intake target (P:C 1:1). At each step, there was only a limited amount of food items available, which we spread equally between the 3 food rails. The global capacity  $c$  is the total number of food items available per individual at any time. On their turn, individuals have a chance to join a food at random, but if its capacity is exceeded, a newcomer must displace a randomly chosen resident. The probability that the newcomer displaces the resident is a function of the difference between the fitness of the two individuals. (a) Examples of the distribution of nutritional states of 300 individuals at the end of a simulation run (stopped when one individual reaches fitness = 0.975, which always occurred within 1000 steps). The star indicates the position of the intake target common to all individuals. Each colour represents a simulation run for different level of competition (global capacity) from none (blue triangles, high capacity:  $c = 3$ ) to high (red squares, low capacity:  $c = 0.25$ ). (b) Distribution of fitness and (c) distribution of dominance index (proportion of contests won per individual) at the end of simulation runs for varying levels of capacity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Incorporating empirically determined fitness landscapes within the model should further improve the predictions.

## 6. Future directions

Nutrition impinges on all levels of biological organization. Yet very few studies have considered how nutritional processes at different levels interact and impact on each other (Simpson et al., 2010). Here, we have presented and tested a modelling platform linking individual- and collective-level nutritional phenotypes in animal groups and societies. Our approach integrates concepts of nutritional ecology and collective animal behaviour within a common theoretical framework to explore how complex collective behaviour and social structures can emerge from simple nutritional interactions among individuals.

Our preliminary exploration of this approach in insects and spiders shows that nutrient regulation can be achieved simultaneously by individuals and by groups based on simple decision rules, even if group members have different nutritional needs and foraging abilities. While we are still far from fully understanding how nutritional homeostasis is maintained in colonies of eusocial insects via the coordinated actions of different castes of workers, the queens and the brood, our models provide a first entry point into these complex “nutritional” systems. The theoretical exploration of some classical examples of collective behaviour in insects and spiders has generated novel qualitative and quantitative predictions about the role of nutrition in driving these behaviours. Importantly, these predictions can be empirically tested by characterising the nutritional strategies of individuals and groups in controlled conditions in experiments involving animals with known nutritional states fed with chemically defined artificial diets. Combining computer simulations and experiments to investigate the nutritional ecology of social arthropods and to compare them across species with various levels of social complexities will be an important step forward to clarify how animals trade-off individual and social influences when making nutritional decisions.

In addition to bringing insight into the nutritional underpinnings of social interactions, the mechanistic approach we propose may also help identify evolutionary pathways through which nutrition may drive the series of steps that lead to groups with increasing organizational complexities. Several authors argue that nutritional constraints, such as limited access to food (or specific nutrients) at different stage of the developmental cycle, have been critical factors for the evolution insect eusociality (Amdam and Page, 2010; Hunt and Nalepa, 1994; Hunt, 2007; Tibbetts et al., 2013; West-Eberhard, 2003). However, empirical evidence for this hypothesis is still scarce. GF models already incorporate fitness outcomes of nutrition in the form of performance consequences of excesses and deficits of multiple nutrients on key life history traits such as longevity and reproductive success (Simpson and Raubenheimer, 2012). Future developments of these models to include evolutionary algorithms (Ashlock, 2006) will enable the testing of specific scenarios about the role of nutrition in the evolution of social behaviour. In the context of arthropod sociality, a fundamental question is how nutritional factors influence the major forces of multilevel selection (individual direct selection, kin selection and between group selection) and their different targets (organism and superorganism) to drive the evolution of cooperation and functional interdependence (Hölldobler and Wilson, 2009). Comparing these effects across nutritional environments and social systems will significantly broaden the focus of research on social evolution in this group (Costa, 2006).

Although we have primarily focused on social arthropods, our approach is applicable to virtually all socially interacting animals. Regulatory strategies of nutrient intake and allocation have been

described across the animal kingdom, including in humans (Simpson and Raubenheimer, 2012) and many of the collective activities observed in arthropods are also commonly encountered in vertebrates (Couzin and Krause, 2003). Collective decisions, for instance, are an important component of the foraging behaviour of schooling fish, flocking birds and herding mammals (reviewed in Sumpter, 2010). Many birds and mammals provision their altricial young for extended periods of time (Royle et al., 2012). It is therefore likely that adequate nutritional decisions by adults involve similar nutritional feedbacks as those ruling colony-level nutrient balancing in ant colonies. Expanding our models to a wider range of animals is easily conceivable and holds considerable promise to delineate general principles about the nutritional ecology of social animals. Ultimately, the same approach could be used to integrate additional organisational levels and explore the complete cascade of interactions between nutritional processes from cells to ecosystems.

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