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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.

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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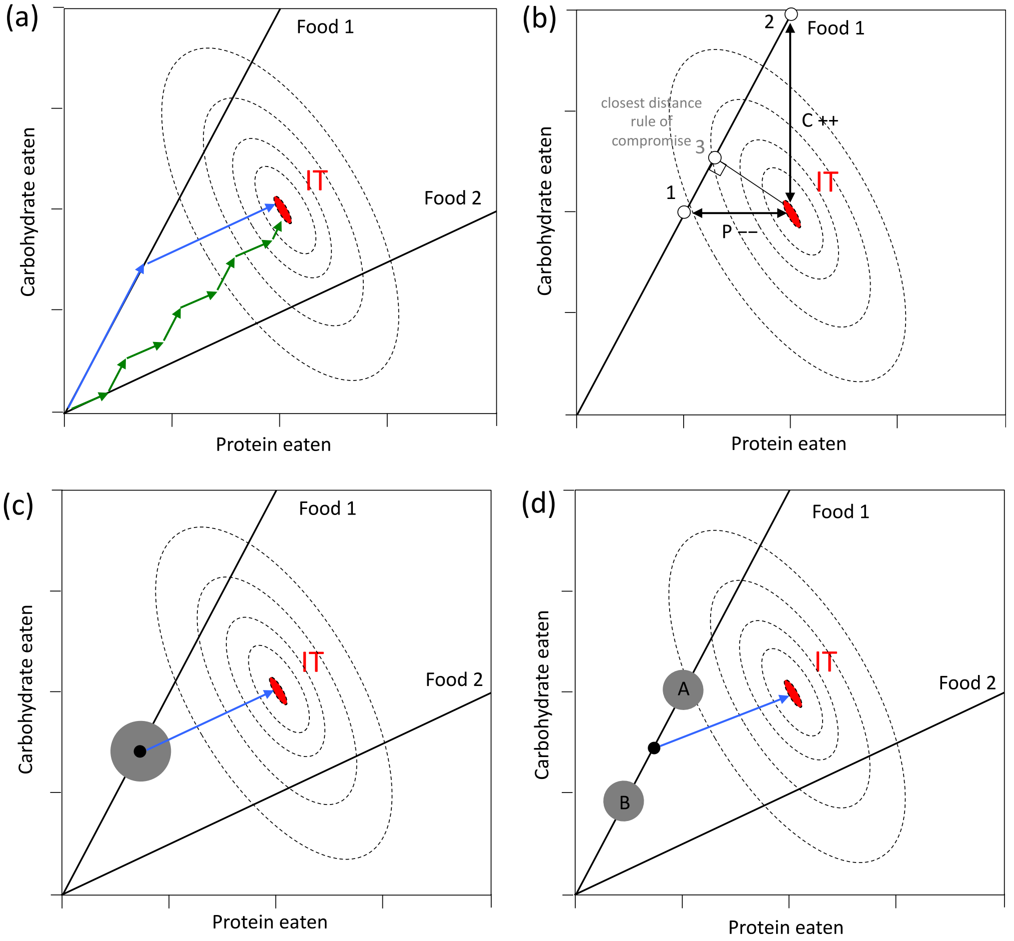

Fig. 1. Examples of GF models for hypothetical animals featuring two food types (1 and 2) varying in their relative amounts of protein (P) and carbohydrates (C). In these graphical illustrations, the nutritional rails (thick black lines) represent the ratio of the two nutrients in each food. The intake 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 best 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.