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Nutritional ecology and foraging theory

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Historically, two fields of research have developed theory around foraging and feeding that have influenced biology more broadly, optimal foraging theory and nutritional ecology. While these fields have developed largely in parallel, they are complementary with each offering particular strengths. Here we show how an approach developed in the study of insect nutrition, called nutritional geometry, has provided a framework for incorporating key aspects of optimal foraging theory into nutritional ecology. This synthesis provides a basis for integrating with foraging and feeding the many facets of biology that are linked to nutrition and is now influencing diverse areas of the biological and biomedical sciences.

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Introduction: historical perspective

Foraging and feeding are fundamental to many areas of biology. Historically, two fields of research have developed theory around these behaviors that has influence biology more broadly: optimal foraging theory (OFT) [1], and nutritional ecology [2]. While these fields have developed largely in parallel, more recently the study of insect nutritional ecology has led an integration of the optimal foraging and nutritional ecology approaches, which is now influencing many areas of biology and biomedical science [3••,4•].

The parent discipline of OFT, behavioral ecology, formed around the broad question of how animals solve the challenges presented by the environment in a way that increases their fitness [5]. The influential contribution of OFT was to draw a parallel between foraging and economic decision-making, and introduce economic-inspired mathematical approaches for modeling the foraging decisions of animals [6]. This approach requires that a variable which correlates with fitness is nominated as a 'currency' to represent the proximal goal of foraging, that is, that which an optimal forager should maximize or minimize. The amount of energy gained (to be maximized), time spent on gaining energy (to be minimized), or their interaction (rate of energy gain) were early adopted as general foraging currencies, assumed to apply across diverse circumstances and taxa [1,7].

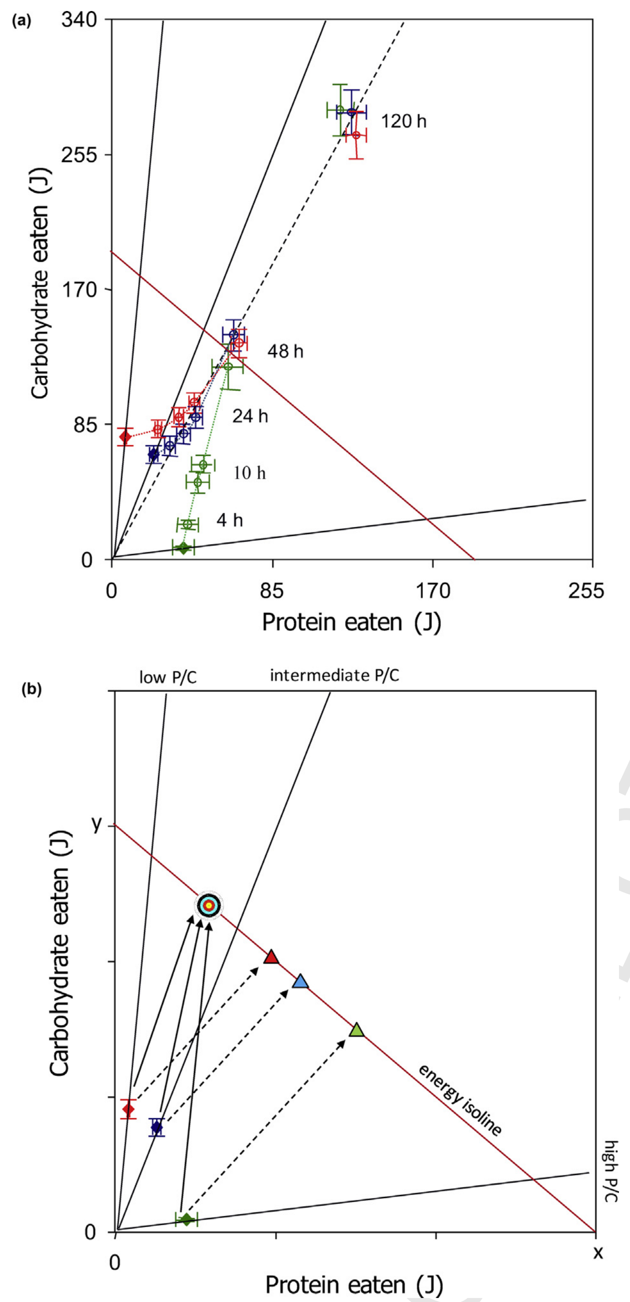
The study of insect feeding and foraging followed a different route. Rather than assume a simple, universal currency as a strategy for understanding the evolution of foraging, insect studies were concerned with elucidating what the foraging currencies actually were, how they influenced performance (survival, growth and reproduction), and the proximal mechanisms through which diet influenced behavior and performance. Initially, some workers emphasized nutrients as the foraging currency (e.g. [8]), while others emphasized the role of plant secondary metabolites (e.g. [9]). However, the field was early to converge on the view that there is no simple answer: nutrients, secondary metabolites and their respective subcategories can all influence the foraging decisions and performance of insects, often through complex interactions [10,11]. The field that studied these influences came to be known as nutritional ecology (NE) [12,13].

In 1993 a graphical approach, the nutritional geometry framework (NGF), was introduced for modeling the complex multi-dimensional effects of foods and diets on animals [14,15]. The framework is integrative in the sense that it models the interactions of diet components and their effects across multiple levels including physiology, behavior, development, performance and ecology [16,17]. Here we show how recent developments in NGF have enabled the integration of the detailed perspectives of insect nutritional ecology with the adaptive approach of OFT to generate new perspectives on foraging and feeding.

Nutritional geometry framework in a nutshell

The logic, structure and breadth of application of NGF have been the subject of several reviews in recent years [2,18,19]. We therefore restrict our coverage to the core aspects that are most relevant for the present context, foraging theory. We begin by illustrating with examples how the core components of nutritional ecology — intake regulation and its consequences — are represented in NGF models.

Figure 1



Experimental test to distinguish macronutrient balancing from energy prioritization. Lines radiating from the origin are nutritional rails, which represent the protein:carbohydrate ratio (P/C) of three experimental foods (high P/C, intermediate P/C and low P/C). Solid diamonds are data symbols (mean ± SE) showing intakes of experimental groups of cockroaches (*Blatella germanica*) following a 48 hours pre-treatment during which they were confined to either the low, intermediate or high P/C diet. The negative diagonal is an energy isoline, representing the equation $x + y$ = constant (P J + C J = constant J), such that all intakes falling on that line are iso-energetic. **(a)** Geometric model predicting the intakes of cockroaches under the nutrient balancing versus energy prioritization hypotheses if after the 48 hours of restriction to low, intermediate or high P/C foods the insects were allowed to freely compose a diet from all three. Under energy prioritization, all three groups would be predicted to take the shortest trajectory to the energy isoline. They would thus head in parallel directions and end up with equal energy intake (on the energy isoline) but different macronutrient ratios (spread across the isoline), as shown by the triangles. Under nutrient balancing, the three groups would take different trajectories to converge on an intake target (represented by the target symbol). **(b)** Experimental data showing cumulative intakes of the cockroaches over 120 hours of self-selecting a diet from all three foods. Results showed that the animals took different trajectories to converge on an intake target by 48 hours, and thereafter took the same trajectory to maintain the target dietary balance.
Data from Raubenheimer and Jones [22].

Homeostatic targets

A fundamental component of NGF is the concept of homeostasis, which is critically important in directing the animal's responses to its nutritional environment and in this way revealing to researchers what the animal has evolved to prioritize [20]. Borrowing from control theory [21], in NGF the nutritional goals of animals are expressed as points or small regions in a 'nutrient space', called 'targets'. Thus, the 'intake target' (IT) is a geometric representation of the nutrient mixture that the regulatory systems target through foraging and feeding. ITs have been measured empirically in laboratory studies of many insects species, an example of which is given in Figure 1 [22]. Further examples are reviewed by Simpson and Raubenheimer [19], with more recent studies including Jonas and Joern [23], Paoli *et al.* [24], Stabler *et al.* [25], Reade and Naug [26], Vaudo *et al.* [27], Srygley [28], VanOverbeke *et al.* [29], de Carvalho *et al.* [30] and others. An interesting question is how ITs of insects adapt to their ecological circumstances (see [15] for a comparative analysis that addresses this issue).

Making good of bad: response to nutritional constraint

In many ecological circumstances, constraints on the quantity and quality of available foods prevent animals from ingesting a balanced diet. The animal is then forced to over-ingest some nutrients and under-ingest others, relative to the intake target, and its dietary challenge is to settle on the combination of deficits and surpluses that minimizes the cost of this predicament [16,31].

The regulatory responses to such constraint, called the 'rule of compromise' (ROC), have been measured in many insects (e.g. [17–19,29,32–35]), but as yet little is understood about the ecological circumstances that drive the diversity of these responses. An exception is diet breadth in insect herbivores. Theory predicts that generalist feeders should have evolved flexible nutritional physiology that enables them to tolerate ingested nutrient surpluses to a greater extent than specialists [36,37]. Several studies have provided support for this, including contrasts between closely related generalists and specialists and between generalist and specialist phenotypes that develop from the same genotype (reviewed by Simpson and Raubenheimer [19]).

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