

UNRAVELLING THE TANGLE OF NUTRITIONAL COMPLEXITY
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I. Introduction

At face value, the challenge of eating sensibly is relatively straightforward: simply get enough of the right foods and you've done the job. But scratch the surface, even slightly, and you will unearth a staggeringly complicated tangle of interrelated questions. What, for example, *are* the right foods, and why these and not others? How does this differ in different life stages of a species of animal and indeed between different species? How did the between-species differences come about? What, in a given circumstance, *is* enough of a food? How does this change with the recent feeding experiences and other circumstances of an animal? What are the consequences for the animal of eating too little, or too much, of the right foods? And what are the consequences of eating more or less of the *wrong* foods?

That such problems are solved on a daily basis by animals as simple as insects and as complex as chimpanzees provides little succour to nutritional scientists. Instead, it gives rise to further questions: *how* do insects with a brain no larger than a pinhead solve such complex tasks? Why do chimpanzees with their large and complex brains not do appreciably better? Perhaps most intriguing of all is the question why humans, with our state-of-the-art brains, are prone to do substantially *worse* at diet selection than even the humble insect? And why have nutrition-related diseases such as diabetes, heart disease and various cancers *increased* rather than decreased over the past few decades despite scientific and technological advances that have empowered us to identify, produce and distribute the nutritionally optimal diet at will?

Our aim in this and the following article is to provide an overview of a research program that we have built over the past 15 years into the nutritional biology of animals (reviewed by Raubenheimer and Simpson 1997; Simpson and Raubenheimer 2000) and, more recently,

humans (Simpson, et al. 2003). Central to this programme has been the development of a geometrical approach for unravelling the kinds of complexities that underlie the nutritional decisions that are taken on a daily basis by members of our own and other species.

In the first article, we begin by outlining in general terms some of the reasons that nutrition is a particularly complex biological challenge. We then present an outline of our geometrical models, showing how they incorporate the basic components of nutritional decision-making – foods, food constituents, an animal's current nutritional state, its nutritional needs and so forth. In the last two sections, we show how this approach can be used to explore questions about the evolution of nutritional decision-making. Throughout this article, we use examples from a group of animals that has played a leading role in our work, the insects. In the second article, we extend the approach to a species at the other end of the complexity spectrum, humans.

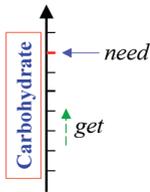
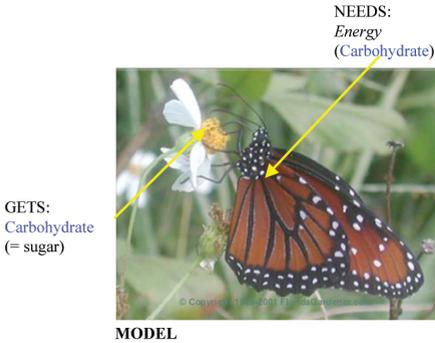
II. The Complexities of Nutrition

For some animals, the challenges of feeding are less extreme than for others. Many species of butterflies, for example, acquire and store during the juvenile (caterpillar) stages most of the nutrients they will need as adults. Usually, the adult nonetheless needs to do *some* foraging for itself, principally to meet the substantial energetic demands of flight. The target food is nectar, which consists largely of energy-rich simple carbohydrates (sugars) and water. For these animals, nutrition can be modelled as a simple process of matching carbohydrate acquisition to carbohydrate requirements (Fig. 1 a).

Even here, though, the complexity of nutrition is not avoided, but merely transferred to a different stage in the life cycle. Caterpillars need to obtain carbohydrates as a source of energy (unlike mammals, herbivorous insects cannot extract energy from dietary fats) as well as proteins (for growth and to meet their future needs as adults) and several micronutrients including sterols, minerals, etc. Not surprisingly, then, caterpillars select foods, such as leaves, which contain a wider range of nutrients than does nectar and so can better satisfy their more complex nutrient requirements.

However, selecting leaves rather than nectar provides only a very crude solution to the nutritional challenges facing caterpillars. Firstly, nutrient requirements are not fixed, but change as an animal grows, with different levels of activity, and so forth. For this reason, it is unlikely that any one kind of leaf will be ideal throughout the life of a caterpillar. To further complicate issues, the nutrient content of leaves also changes in time, for example

(a) Simple case - butterfly



(b) More complex - caterpillar

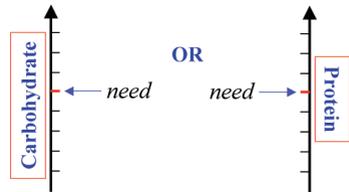
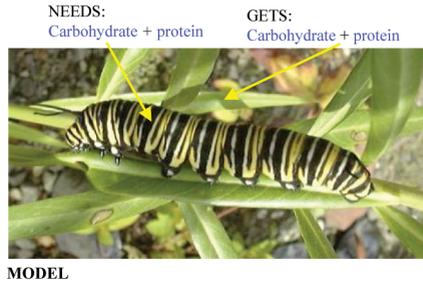


Fig. 1. Modelling nutrition using the single-nutrient approach. In (a), a butterfly feeds only on nectar, which consists almost entirely of sugar solution, so its nutritional needs and gains can be modelled on a single carbohydrate axis. A caterpillar, by contrast, needs not only sugar, but also protein and other nutrients (b). In the single-nutrient approach, the potential complexity of this situation is avoided by modelling the interaction in terms of one or the other of the nutrients.

as plants develop or their growth conditions (such as soil water, nutrients and exposure to sunlight) change. Since there is no incentive for leaves to oblige the nutrient requirements of their predators, these changes are either independent of, or even systematically hostile to, the needs of herbivorous animals. Further, many plants produce noxious chemicals precisely to deter the advances of predators, and these toxins are usually produced to the greatest extent when leaves are nutritionally more attractive (e.g. in young succulent leaves). So what all this amounts to is that animals often face the problem of matching uncertain, changing and hostile nutrient availability to changing and sometimes uncertain nutrient requirements.

How do we model this more complex – and more typical – association between an animal that has multiple nutrient needs and foods with multiple components? A common approach has been to avoid the complexity, by focusing on one *or* the other nutrient (Fig. 1 b).

The chosen nutrient is then treated as the sole *currency* in the model, which takes on a structure much like that developed for butterflies feeding on nectar in Fig. 1 a.

Although in some cases this simplification might be useful, our interest in the complexities of animal nutrition has led us to devise an alternative approach. The aim is to integrate in a single model the key components of an animal's nutritional universe, such as the animal's nutritional state at a given time, the optimal state it could achieve, the foods that it should and should not eat in order to achieve that state, and the consequences of eating various foods available to it. Most important, these questions are addressed for two or more food components simultaneously within a single model. This enables us to explore not only the way the animal responds to various food components, but also how these components *interact* in their influence on the nutritional biology of animals.

III. Model Basics

A. The Nutrient Space

Our modelling procedure differs from the single-currency approach in two fundamental respects. Firstly, we consider more than one nutrient simultaneously, each represented by its own axis (Fig. 2 a). Secondly, and most important, we focus on the *interactions* among the various nutrients. We do this by combining the various axes into a single *nutrient space*, which has as many dimensions as there are food components in the model (Fig. 2 b).

To begin with, we will consider only two dimensions, the macronutrients protein and carbohydrate, but in principle any number of food components could be included in a model, whether they be nutrients or non-nutritional food components such as plant toxins (Simpson and Raubenheimer 2001; Behmer, et al. 2002) or indigestible bulk (Lee, et al. 2003). Our decision to focus on two nutrients for the time being is not only useful for illustrative purposes, but also has good biological justification: protein, carbohydrates and their interactions explain by far the major component of the variance in food choice and feeding behaviour in the insects we've studied. (In Section III H we present data which illustrate this, from an experiment in which mineral salts as well as protein and carbohydrate were varied in the diets of locusts.) In other cases, more than two nutrients might exert a significant influence on feeding behaviour – mammals, for example, can use dietary lipids as well as carbohydrates as energy sources and also need to eat protein. In such cases it might be preferable to use higher-dimensional models. Alternatively, there might be specific

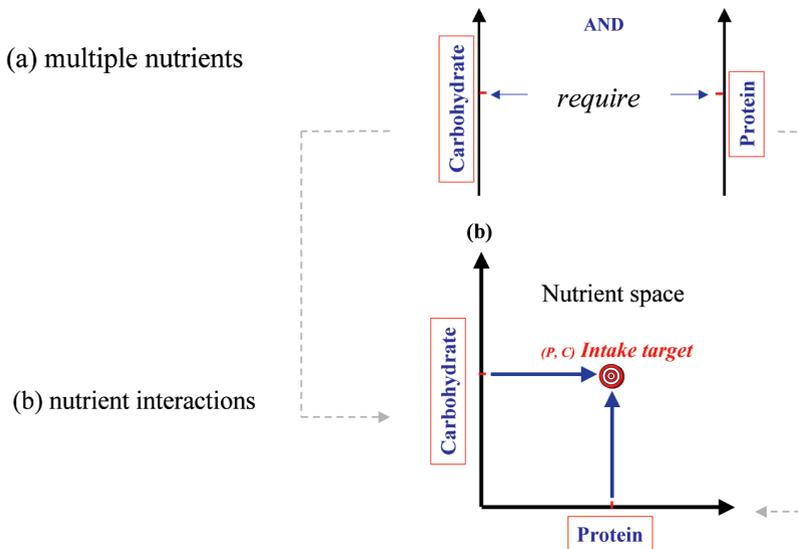


Fig. 2. Geometrical models include two or more nutrient axes (a), which are combined into a nutrient space (b). This defines a single point which represents the integrated requirements of the animal for several nutrients, the intake target.

circumstances which warrant combining two or more of the components on a single *compound axis*. In Section III H we provide an example of this, where protein and carbohydrate are combined in a single axis and plotted against mineral salts. Another case is discussed in the companion article in which carbohydrates and fats in the diets of humans can for some purposes be combined into a single axis.

Whatever the number of dimensions, constructing a nutrient space has the same principle advantage: it enables the critical nutritional factors to be described as a composite of several components simultaneously, and from this flows insights that otherwise would not be available.

B. Nutrient Requirements

Take, for example, the nutrient requirements of an animal. In the single-currency approach, an animal's nutrient requirements are represented as separate points on the

relevant axes – one on the carbohydrate axis, another on the protein axis and so forth (Fig. 1 a and b). Bringing the axes together into a nutrient space merges these, creating a *single point* which represents the needs of the animal for the various nutrients (Fig. 2 b). Since, by definition, this is the point of intake of the various nutrients that would benefit the animal most if it could get there, it is the point that we would expect a well-adapted animal to try to achieve. For this reason, we have called it the *intake target*.

Before showing how nutrient spaces deal with other important aspects of an animal's nutritional universe, such as foods and feeding, it is worth emphasising an important point and re-emphasising another. The first is that our use of the word "target" implies nothing about conscious striving (if it did, we would have some difficulty justifying its use in the context of insects). Rather, the intake target is a target towards which the regulatory mechanisms of a well-adapted animal should aim, in the same sense that an enemy aeroplane might be considered the target towards which a well-designed heat-seeking missile should aim. Neither does it categorically exclude consciousness; it might well be, in our species at least (and possibly in others), that conscious intent is one component of the mechanisms involved in nutritional regulation. Our use of the term "target" is thus purely mechanistic – for those familiar with philosophy of biology, it is teleonomic and not teleological.

The point we wish to re-emphasise is that nutrient requirements (i.e., intake targets) are not static, but change with time. Therefore, although an intake target can be treated as a fixed point when integrated over a stipulated time period (e.g. the first 10 days of the life of a caterpillar), in reality it traces a trajectory through nutrient space. For example, when our caterpillar develops into a butterfly the intake target shifts from comprising appreciable proportions of both carbohydrates and proteins to a composition almost devoid of protein. Likewise, some species of fish start life as carnivores and at some point switch to eating only seaweeds – in them, the intake target moves from a very high to an intermediate proportion of protein. As we will show in Section IV A, intake targets shift not only with development, but also over longer, evolutionary, timescales.

C. Foods and Feeding

Foods can be represented in a nutrient space in two ways. A food item, such as a leaf, can be depicted as a point whose position is determined by the *amounts* of the various nutrients it contains, in the same way that an intake target describes the amounts of the various nutrients that the animal needs. This allows us at a glance to compare the animal's nutrient

needs with the nutrients available in a particular food item and so to determine the suitability of the food item for the animal. Leaf 1 in Fig. 3 a, for example, contains more of both protein and carbohydrate than the animal needs, and thus seems a good choice of food for the animal.

The other aspect of Leaf 1 that is important from the animal’s point of view – possibly even more important than the amounts of the nutrients that it contains – is the *proportions* of the various nutrients. This is represented by a line that passes from the origin of the nutrient space (the point 0,0) through the nutrient coordinates for the food (Fig. 3 b). We refer to these lines representing the balance of nutrients in foods as *nutritional rails*.

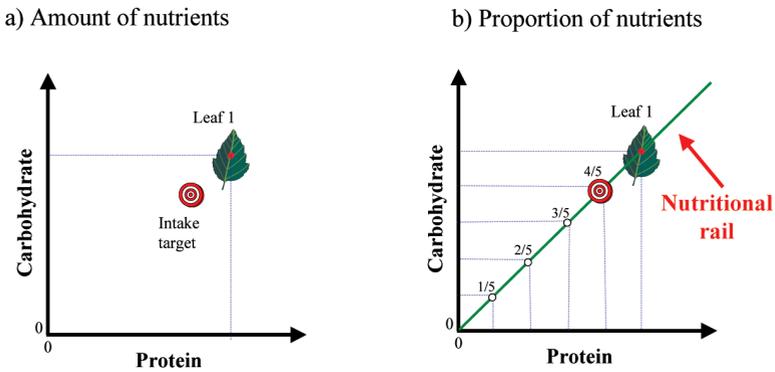


Fig. 3. Foods are represented by a point describing the amounts of nutrients they contain (a), or by the slope of a line (called a nutritional rail) describing the proportion of nutrients they contain (b). See text for further details.

The reason that the proportion of nutrients in a food can be represented as a line and the reason that we call these lines “nutritional rails” is illustrated in the following example (Fig. 3 b). Imagine an animal that has encountered but not eaten any of Leaf 1. Since it has gained none of the protein or carbohydrate that the leaf contains, the animal could initially be represented as a point with values 0 for protein, and 0 for carbohydrate (i.e., its state coincides with the origin of the plot). It now eats a meal of the food, which amounts to $\frac{1}{5}$ of the total amount of the leaf, and so moves $\frac{1}{5}$ of the distance on the x-axis towards the value of the protein coordinate of the leaf, and $\frac{1}{5}$ of the distance towards the value of the carbohydrate component. Its post-meal status is then defined by point $\frac{1}{5}$. After taking a

second meal of similar size, it would have moved to point $\frac{2}{5}$, after the third meal it would be at point $\frac{3}{5}$ and so on. Therefore, as the animal eats a food, it effectively “moves” – like a train on a railway line – along a linear trajectory with a slope which is determined by the balance of nutrients in the food.

D. Nutrient Balance

The above example also illustrates another very important point. The nutritional rail for Leaf 1 passes through the animal’s intake target, and as a consequence the target can be reached by eating this food – in the figure, the animal would do so by taking a fourth meal on the leaf. Foods which contain the same proportion of nutrients as are required by an animal are called *nutritionally balanced* foods.

But now consider Leaf 2 in Fig. 4 a. This has a greater proportion of carbohydrate to protein than Leaf 1, and as a consequence its nutritional rail is steeper than that for Leaf 1. Since the steeper rail does not pass through the intake target, the target cannot be reached by eating this food – in other words, this food will not optimally satisfy the animal’s nutrient requirements. Foods whose nutritional rail does not pass through the animal’s intake target are *nutritionally imbalanced* foods.

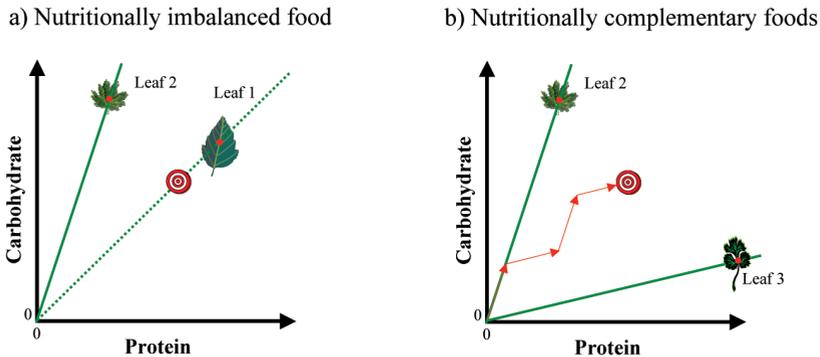


Fig. 4. a) The rail representing a food that is nutritionally balanced with respect to the nutrient requirements of an animal passes through the intake target for that animal (e.g. Leaf 1). In contrast, rails of nutritionally imbalanced foods do not pass through the intake target (Leaf 2). b) The animal can nonetheless reach its intake target by mixing its intake from two imbalanced foods which are nutritionally complementary (Leaves 2 and 3).

E. Nutritionally Complementary Foods

But a nutritionally imbalanced food can, nonetheless, *help* an animal satisfy its optimal nutrient requirements, if properly paired with other nutritionally imbalanced foods. Recall that Leaf 2 in Fig. 4 a is nutritionally imbalanced and so would confine the animal to a trajectory that is off-course from the target. But if the animal switched between eating this food and a second food with a different balance of nutrients (e.g. Leaf 3 in Fig. 4 b), then it would not be confined to a single trajectory but could alternate between the trajectories of the rails for the two foods. In this way it could “move” over wider areas in the nutrient space – in fact, it could zigzag its way to any point within the cone enclosed by the rails for the two foods. If, as in the figure, the cone encloses the intake target (i.e., if the rails for the foods fall on opposite sides of the target), then this combination of nutritionally imbalanced foods enables the animal to satisfy its nutrient requirements. Such pairs of nutritionally imbalanced foods which jointly enable an animal to reach its intake target are known as nutritionally *complementary* foods.

F. Measuring Intake Targets

That intake targets can be reached by composing a diet from two or more nutritionally imbalanced foods is undoubtedly useful for animals. It is also useful for researchers, because it provides a means of measuring the position of the intake target of an animal. The reason for this is that if you give a well-adapted animal a suitable pair of nutritionally complementary foods, then it should mix its diet in such a way as to reach the intake target, thus revealing the position in nutrient space of this target.

But an important precaution needs to be taken in interpreting the outcome of such an experiment: it must be demonstrated that the point in nutrient space selected by the animal is in fact *actively* selected and not arrived at by some other means, such as indiscriminately feeding on the available foods. The way to do this is to challenge the animal by altering the nutrient composition of one or both foods and to see whether it compensates by altering its intake of the two foods in such a way as to maintain the original point of nutrient intake. If the animal does not compensate for the changed composition of the foods, then it will arrive at a different point in nutrient space, providing no evidence that the original point is of any importance to it. If, on the other hand, it alters its behaviour so as to reach the same point of nutrient intake despite the altered composition of the foods, this demon-

strates that the point is actively selected; the animal is *defending* a point of nutrient intake, which is in all likelihood the intake target.

Fig. 5 shows an example of such an experiment, performed using larvae of the African migratory locust, *Locusta migratoria*. In this case, synthetic foods were used, in which one food in the pair contained a 1:2 ratio of protein to carbohydrate and the other contained a 2:1 ratio. To demonstrate target defence, there were four treatments in which one, the other, both or neither of the two foods were diluted by 50% using indigestible bulk (cellulose). One treatment comprised foods (% protein:% carbohydrate) 14:28 and 28:14, another 14:7 + 28:14, a third 14:28 + 14:7 and a fourth 7:14 + 14:17. Rather than testing the same animal on all four of the food combinations, a group of 10 different locusts was confined to each of the four pairings. Since these groups were indistinguishable at the start of the experiment, we were able to assume that the response of each group of animals to its particular treatment represented the response of any animal in the experiment, had it been exposed to that treatment.

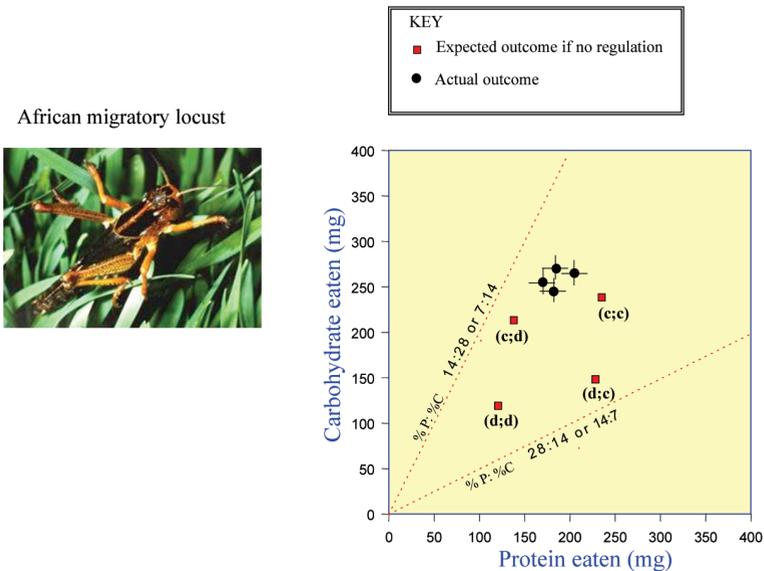


Fig. 5. Defence of an intake target by 5th-stadium nymphs of the African migratory locust. See text for details.

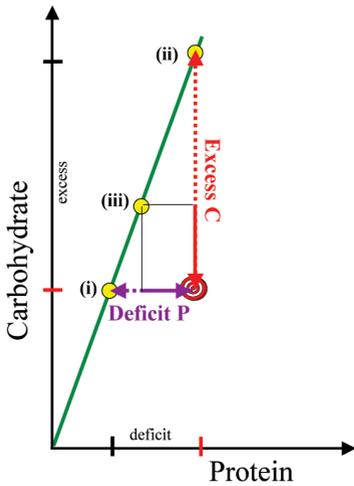
The square symbols in the figure represent the expected outcome for the four groups if each fed indiscriminately from its respective food pairing – i.e., in the absence of target defence. The round symbols show that, on the contrary, all four groups of animals ended up at a point that was statistically indistinguishable from the points achieved by the other three groups. To do so, the four groups had to eat very different proportions of the two foods, thus demonstrating that the observed outcome is actively defended against differences in the food pairings; it is, in all likelihood, an intake target.

G. Rules of Compromise

A foraging animal that encounters a nutritionally imbalanced food faces some serious nutritional decision-making. It could, on the one hand, reject the food and continue to search for a balanced one. But if it could not be sure that this was attainable, then it might be better off eating the imbalanced food in the hope it might subsequently find a complementary one. Even if there is little prospect of encountering a complementary food, the animal might still be better off eating the imbalanced food than foregoing feeding altogether. But having opted to settle for the imbalanced food, its nutritional decision-making is not over; depending on how much of the food it ate, the nutritional outcomes – and associated costs and benefits – would be very different. The nutrient-space approach allows these various outcomes to be clearly defined and measured.

The problem with nutritionally imbalanced foods is that they place an animal in a predicament in which it is forced to accept too little of some nutrients and/or too much of others. For example, a caterpillar confined to the nutritionally imbalanced food in Fig. 6 has three basic options. It could, firstly, eat until it reached position (i) on the rail. At this point it would have satisfied its requirement for carbohydrate, but would suffer a shortfall of protein. At the other extreme, it could eat until it reached point (ii) where it would have gained exactly the required amount of protein, but only by eating an excess of carbohydrate. It could, thirdly, feed to an intermediate point, where it suffers both a shortage of protein and an excess of carbohydrate, but neither of which are as large as at the extremes [e.g. point (iii)]. To the extent that nutritionally imbalanced foods are an important component of the daily lives of animals – and for many there is good evidence that this is so – one would expect that mechanisms would have evolved to enable animals to arrive at the compromise between overeating some nutrients and undereating others which minimised

a) Nutritional errors



b) Rule of compromise

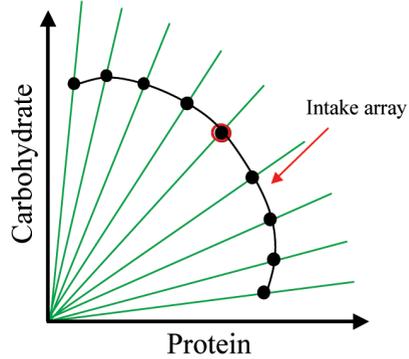


Fig. 6. a) Animals eating a nutritionally imbalanced food are forced into a trade-off between eating too much of some nutrients and/or too little of others. In the hypothetical example, if the animal fed to point (i) it would gain the required (target) amount of carbohydrate, but suffer a shortfall of protein; at point (ii) it would get enough protein, but too much carbohydrate, and at point (iii) it would have both a deficit of protein and an excess of carbohydrate. b) An array of intake points, whose shape provides information about the rule of compromise for balancing the excesses and deficits of nutrients ingested from imbalanced foods.

the costs of that predicament. This trade-off which animals must settle on when eating nutritionally imbalanced foods is known as a *rule of compromise*.

H. Measuring Rules of Compromise

How do we measure such rules of compromise? Since they involve the balance between excesses and deficits of nutrients *relative to the optimal requirements*, a first step is to determine the position of the intake target. This can be done using complementary foods, as described in Section III F). We can then allow the animal to move its chosen distance along the rail representing an imbalanced food – for example, to points (i), (ii) or (iii) in Fig. 6 a – and measure the *nutritional errors* (excesses and deficits of the two nutrients) it has settled

on. The relationship between these excesses and deficits is what we are looking for: the rule of compromise.

The problem is, this procedure will tell us about the rule of compromise for one food only; it will tell us nothing about how the animal would respond to foods which are imbalanced to a greater extent or in the opposite direction. To get a broader picture, we would have to perform an experiment involving several groups of animals, each confined to one of a range of foods with different nutrient proportions. Such an experiment would generate a nutrient space traversed by several nutritional rails, and an intake point associated with each. Jointly, these intake points would constitute an *intake array*, whose shape and position in relation to the target would contain the information we are seeking (Fig. 6 b).

A real example of such an intake array is presented in Fig. 7. Here, African migratory locusts were made to trade off their intake of mineral salts against a balanced complement of the macronutrients protein and carbohydrate. The figure shows the selected intake point for groups of animals allowed to compose a diet from nutritionally complementary foods (i.e., the intake target), as well as the array for four treatment groups each fed a food with a different proportion of the two nutrient groups. The resulting straight and vertical array is easy to interpret: it shows that these animals regulated so as to achieve their target intake of macronutrients, irrespective of the excess or deficit of ingested salts that this would

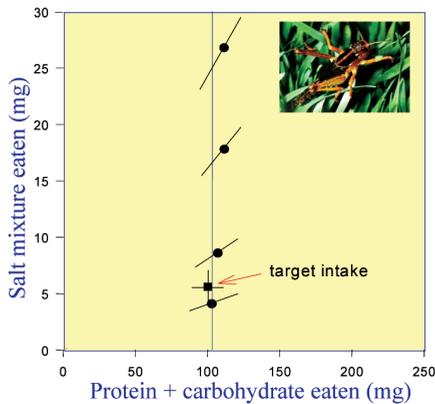


Fig. 7. Intake array for African migratory locusts forced to trade off a balanced complement of macronutrients (protein and carbohydrate) against mineral salts.

entail. Therefore, while they balanced their intake of macronutrients and salts when they had the luxury of switching between complementary foods, when confined to a single imbalanced food the animals prioritised the mixture of protein and carbohydrate, while abandoning regulation of salts. This suggests that, at least over the timescale of this experiment, they value the macronutrients as a resource more highly than they do mineral salts. In the following section, we present more examples of rules of compromise in animals.

Before doing so it is worth commenting on a particular aspect of Fig. 7, the reason that we combined protein and carbohydrate into a single axis rather than using a separate axis for each. Our justification for doing so is that the macronutrients were present in all foods in fixed and balanced proportions relative to each other – i.e., in the target proportion. In this circumstance, from the animal’s point of view, they effectively *are* a single resource, since once it has eaten enough of one of the nutrients it has eaten enough of both of them.

IV. Applying the Models: Evolution of Nutritional Strategies

Up to this point, we have presented the nutrient-space approach largely as a descriptive tool for quantifying key aspects of animal nutrition. Our main interest in developing these models, however, is to apply them to real biological questions, concerning such factors as the ecology, physiology and evolution of nutritional strategies. In this section, we provide two illustrations of how this approach can be used to test specific nutritional hypotheses, both concerning the ecology and evolution of nutritional responses in insects. Examples concerning the mechanisms of nutritional regulation can be found elsewhere (e.g. Simpson and Raubenheimer 1993 a, 1996; Raubenheimer and Simpson 1998).

A. The Position of the Intake Target

In Section III A, we mentioned that intake targets move over evolutionary timescales, as animals adapt to their nutritional environments. At one level this is obvious – carnivores have evolved to eat foods with a higher protein/carbohydrate ratio than do most herbivores, which in turn eat more protein relative to carbohydrate than do animals that feed on plant sap or other sugar-rich foods. There are, nonetheless, many subtler questions to ask about the evolutionary influences of an animal’s environment and lifestyle on its patterns of nutritional regulation.

For example, some insects have evolved an interesting association with a group of microbes known as mycetocyte bacteria. These bacteria exist only in specialised cells within the fat body (the insect equivalent of the liver) of their hosts, cells which appear to have evolved specifically for the purpose of housing the microbes. This provides a clue to the nature of the association: the bacteria are most likely paying guests, or symbionts, rather than parasites or pathogens which inflict a cost on the host. Further evidence that this relationship is an amicable one comes from experiments showing that when these bacteria are removed (using antibiotics) the health of the cockroaches is impaired – they grow more slowly and reach a smaller size as adults. The relationship is therefore almost certainly based on mutual benefit, rather than exploitation of one party by the other.

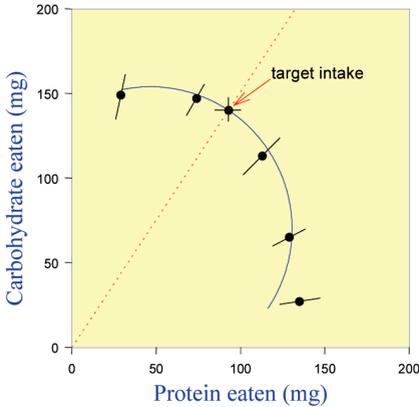
The advantages to the bacteria are clear: they thrive in custom-built accommodation, where they are protected in a stable, physiologically regulated environment from the hostile outside world and constantly bathed in a nutrient-rich medium. But what do the insect hosts get out of the association? We set about exploring the hypothesis that they benefit nutritionally, through the ability of mycetocyte bacteria to convert uric acid (a nitrogen-based waste product which is usually excreted by insects) into usable amino acids (the building blocks of protein). This would, effectively, amount to recycling waste nitrogen and so conserving this precious resource for the insects' use (Simpson and Raubenheimer 1993 b).

If our hypothesis is correct, then animals with mycetocyte bacteria would be more efficient at using the nitrogen they eat, and so, on average, would need less of this precious nutrient in their diet than do animals that lacked such an on-board recycling plant. To test this, we compared the position of the intake target rail of a large number of insect species that either do or do not harbour mycetocyte bacteria. As predicted, the target position of those species with symbionts had a significantly lower proportion of protein compared to those without.

B. The Evolution of Rules of Compromise

Above we showed that African migratory locusts abandon salt regulation and prioritise macronutrient intake when forced to reach a trade-off in the ingestion of these nutrient groups (Section III H). In a separate experiment in which the same species was made to trade-off protein and carbohydrate against *each other*, the outcome was very different: rather than the vertical line expected if one of the nutrients was prioritised, the intake array

a) African migratory locust:
a grass-feeding specialist



b) Desert locust:
a generalist feeder

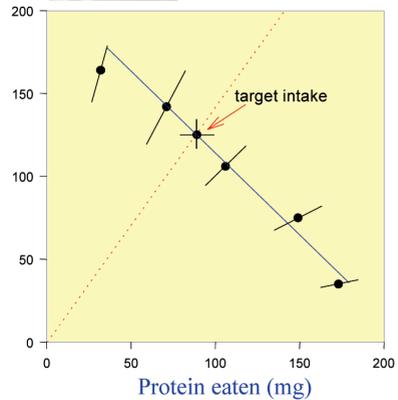


Fig. 8. Intake arrays for the specialist-feeding African migratory locust (a) and the generalist-feeding desert locust (b) fed a range of foods imbalanced in the relative proportions of protein and carbohydrate.

was arc-shaped (Fig. 8 a). This shows that the locusts ingested *both* an excess of one of the nutrients and a deficit of the other – they settled for a compromise, or trade-off, in the regulation of the two nutrients. But exactly what is the nature of this trade-off? While we will not go into the mathematical details here, it can be demonstrated that this arc-shaped configuration arises when the animals on each of the imbalanced foods feed to the point on their respective rails that is as close as they can get to the intake target. They are, in other words, minimising the sum of the nutritional errors (excesses and deficits) they suffer when eating the imbalanced food.

Minimising nutritional errors seems, intuitively, to be a reasonable way of coping when confined to nutritionally imbalanced foods. It seems even more reasonable considering that African migratory locusts are specialist feeders, which in nature eat only grasses, and so likely encounter a relatively narrow range of food compositions. Such animals might be expected to lack specific physiological adaptations for dealing with large nutritional excesses and deficits and hence to avoid subjecting their physiology to these nutritional errors.

If this idea is right, we would anticipate that generalist feeders – animals which are evolutionarily accustomed to eating foods with a wide range of nutrient compositions – would better cope with larger nutritional errors and possibly even benefit from them. As a first test of this, we also measured the rule of compromise in the generalist-feeding desert locust (*Schistocerca gregaria*). As shown in Fig. 8 b, the desert locust did not produce an arc-shaped array indicating minimisation of nutritional errors, but rather a linear array with negative slope. This array shows that the desert locust ingested larger surpluses of the excessive nutrient in the food than did their specialist-feeding cousins (Raubenheimer and Simpson 1997), providing support for our hypothesis. We have since shown a similar correspondence between dietary breadth and rules of compromise in a range of other generalist/specialist comparisons (Raubenheimer and Simpson 2003).

V. Measuring the Consequences of Nutritional Decisions

In the previous section, we provided examples of how nutritional strategies adapt over long, evolutionary timescales to various circumstances of a species' existence. In Darwin's theory of natural selection, this means that those variants of the species that showed the strategies in question – for example, reduced protein intake when harbouring mycetocyte symbionts, or minimising nutritional errors if a specialist feeder – derived some benefit compared with those that did not. In studying such evolutionary adaptations, it is often important to measure what these benefits might actually be. In this, the final section of the paper, we provide a brief illustration of how this can be done within our framework. The example we present is chosen for its simplicity; a mathematically more sophisticated approach can be found in Simpson, et al. (2003).

Our work has shown that African migratory locusts select and defend a specific point of intake in protein-carbohydrate nutrient space (Fig. 5). Since in that experiment they could, as explained in Section III E, have reached any point in the conical area between the rails representing the choice foods, the question arises *why* they selected the particular point that they did, rather than one of the other numerous points to which they had access? In evolutionary terms, such “why” questions boil down to this: what are the benefits that the animals derive from behaving as they do?

A straightforward way of examining this is to use experimental means to force some animals to select other points in nutrient space and then to compare their performance with that of animals free to select the preferred nutrient intake. The experiment presented in

Fig. 8 a takes us halfway towards that goal: by giving some groups of locusts nutritionally imbalanced foods, they were prevented from reaching the intake target, so forced to occupy other places within the nutrient space. For the cost-benefit analyses, we simply measure various consequences for the animals of occupying the different positions within the nutrient space.

Three such consequences are presented in Fig. 9. Here the x-axis represents the food rail (balance of nutrients), with high-protein foods on the left and high-carbohydrate foods on the right, and the vertical line labelled T gives the composition of the balanced (target) diet. The bottom panel shows the effects of rearing diet on the resistance to starvation in adult locusts (i.e., the duration the insects survived when they were reared on one of the diets then deprived of food altogether as they moulted into adults). The figure shows that locusts reared on high-protein foods were most vulnerable to starvation, with resistance improving as the proportion of carbohydrate in the diet increased.

The second panel shows why this is. Stores of fat in the body were proportional to the carbohydrate content of the diet, so that those locusts fed foods with low carbohydrate content had limited energy reserves on which to survive when deprived of food. This is, incidentally, an ecologically relevant scenario for locusts, since their food supply can be unpredictable, so that there is a good probability of starving to death in a natural situation.

From this it seems that a high carbohydrate intake is a good thing, giving rise to the question why locusts don't select a target even richer in this nutrient than they do. The top panel provides an answer. It shows that spontaneous deaths during development were high for locusts fed high-protein foods, decreased towards a minimum for the target food, and then increased steeply on foods containing excess carbohydrate. This shows that, although increased starvation resistance could be achieved by selecting a diet rich in carbohydrate, it would come at the cost of greatly decreased probability of surviving development to reproductive age.

There is an interesting *déjà vu* in these results – they resemble important aspects of the nutritional biology of our own species. In locusts, as in humans, the ability to accumulate fat stores is a very useful mechanism that has evolved to buffer against nutritionally lean periods. But there are also parallels of a less rosy nature: locusts fed carbohydrate rich foods developed excessive fat stores – they became obese – and suffered serious health problems. We have, it appears, uncovered an insect equivalent of what is probably *the* major nutrition-related health issue in the modern world, a topic to which we turn in our second article.

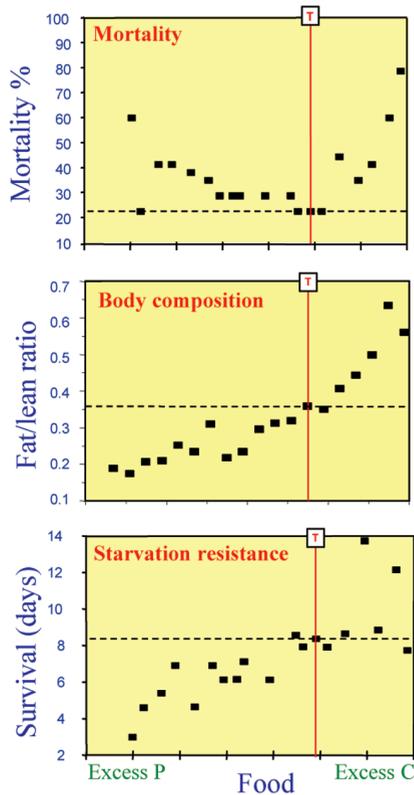


Fig. 9. Three consequences for African migratory locusts eating foods imbalanced in the relative proportions of protein to carbohydrate: spontaneous mortality during development, body fat content and resistance to starvation if raised on one of the foods then deprived of food altogether. The vertical line labelled T indicates the position of the nutritionally balanced food on the x-axis, to the left of which are foods containing excess protein and to the right foods containing excess carbohydrate.

VI. Conclusions

We have attempted in this article to show how a slight shift in focus from one to even two nutrients can go some way towards restoring order in the complex tangle of interactions that underlies the nutritional decisions of insects. In particular, it provides a set of concepts

– such as intake targets, nutritional rails, and rules of compromise – which help clarify how natural selection has shaped the nutritional biology of animals. An ultimate test is whether these concepts can contribute to the understanding of a much more complex species of animals, humans. In the following article, we put our approach to this test.

VII. References

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