

Research papers

Nutrient transfer functions: the site of integration between feeding behaviour and nutritional physiology

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Summary. We describe and extend a graphical approach to quantitative nutrition that focuses on the interplay between behavioural and physiological components of nutritional regulation. The site of integration is the nutrient transfer function, which is the function describing the time course of nutrient transfer between serially connected nutritional compartments (e.g., from the gut to the blood). The relationship between the shape of the nutrient transfer function and the temporal patterns of feeding determines the values of two key quantitative parameters of nutrition: the rate (*power*) and the *efficiency* of nutrient acquisition. The approach can be extended to consider, in addition to the short-term behavioural and physiological decisions made by animals, some ecological determinants and longer-term, life history consequences of such decisions. Most importantly, this category of models can provide insights into the interplay among the various nutrients in an animal's diet. We illustrate this using hypothetical examples, and also present preliminary data for the power-efficiency relationships of protein and digestible carbohydrates in locusts. Finally, we consider existing evidence for the various means available to these and other insects for regulating such relationships.

Key words. nutritional models – nutrient budgets – feeding patterns – nutritional efficiency – digestive models – *Locusta migratoria*

Introduction

The fact that nutrition is the integrated outcome of behaviour (essentially foraging and feeding) and physiological processes (digestion, absorption and allocation) scarcely warrants re-stating. The quantitative details of such integration is, however, an interesting and yet largely unexplored topic in nutritional research. A major reason for the lack of progress in this area is its apparent complexity.

The purpose of this paper is to present an approach which we believe has the potential to reduce this com-

plexity, by focusing research questions on the relationships among a tractable number of key nutritional variables: the rate (*power*) of nutrient processing and its *efficiency*. Throughout, we refer to the approach as a 'framework' rather than a 'model', to emphasise the fact that it is a general scheme which can be used to derive specific models and associated predictions, rather than a model which itself gives rise to specific predictions.

Power and efficiency as key nutritional variables

Feeding delivers nutrients to the digestive, absorptive and post-absorptive physiological processes, which in turn allocate these to the various compartments of the animal's nutritional requirements (growth, reproduction, activities, secretions etc. – see Raubenheimer & Simpson 1994, 1995). Considered quantitatively, there are thus at least two relevant transfer functions in nutritional systems, connected in series: that between the environment and the animal's gut (nutrient intake), and that between the gut and the various post-ingestive physiological processes. Nested within these are the transfer of nutrients between the various physiological processes (digestion, absorption etc.), and in some cases between ecological compartments (e.g., environment to storage sites, storage sites to the animal). The key quantitative parameters of these sites of nutrient transfer are (i) the *rate* at which each operates, henceforth termed 'power' (Slansky & Feeny 1977; Watt 1986) and (ii) the *efficiency* with which nutrient is converted at each stage to a form in which it is offered as an input into later-stage processes.

There are, furthermore, several such serial pathways operating in parallel, one for each ingested nutrient. Nutritional decisions made by animals in the context of one nutrient – for instance, when to void the current contents of the gut and feed again – are therefore constrained by the simultaneous consequences for other nutritional pathways (Raubenheimer & Simpson 1993; Simpson & Raubenheimer 1993a).

In this perspective, nutrition is viewed as a multi-compartmental, multi-dimensional 'problem' which the animal must solve by maximising the benefits and minimising the costs of achieving certain power-efficiency combinations at the serial stages in the various nutri-

tional pathways. How do animals solve such problems? Are there patterns among animals explicable with reference to life history, ecology, or evolutionary lineage? What are the major constraints on the organisation of power-efficiency relationships? We believe that these and similar questions provide an important direction for future research into nutrition. The framework developed in the following sections provides a simple yet powerful analytical approach to investigating such questions.

The graphical representation

The basic concept underlying the power-efficiency approach was first applied to nutritional phenomena in the Marginal Value Theorem (Charnov 1976), which aims to predict the time that an animal should spend foraging in a food patch when the instantaneous rate of energy returns diminishes with progressive prey depletion. Cook & Cockrell (1978) and Sih (1980) subsequently adapted the model to predict the proportion of a single prey item that should be ingested when prey density, and hence expected search time for subsequent prey, varies (models of partial prey consumption). Sibly (1981), Cochran (1987), Hume (1989), and Reynolds (1990) have all considered this approach in the context of digestion.

We extend the approach in several respects. First, although we deal in this paper specifically with the transfer of nutrient from the gut to the blood of animals (absorption), we emphasise that the approach is in theory relevant to any transfer of nutrient among compartments within or between nutrient budgets (Raubenheimer & Simpson 1995). Second, the approach is extended to include periods beyond individual foraging/feeding events, and in this way provides a means of linking behaviour and nutritional physiology with longer-term phenomena, such as life history decisions. Third and most importantly, application of the power-efficiency framework to consider simultaneously several nutrients (parallel nutritional pathways) gives rise to insights which are overlooked in the single-currency approach (Raubenheimer & Simpson 1996). To illustrate, we present data for the power-efficiency relationships in the transfer of protein and carbohydrates from the gut to the blood of locusts. Finally, we consider the various ways that animals could potentially regulate homeostatically the relationships among power and efficiency, and evaluate the scattered evidence for this in one of the best understood nutritional systems, the locust.

In accordance with our desire to apply the approach to empirical as well as theoretical studies, we consider throughout the gross rather than the net transfer of nutrients, since the latter is considerably more difficult to measure. However, where the nutrient-specific costs of acquiring and processing nutrients can be measured, net gains can be dealt with in a manner identical to gross gains. We also restrict our consideration to animals that feed in discrete meals, since

continuous feeders (*e.g.*, filter feeders) have been dealt with elsewhere (Penry & Jumars 1986). We stress, however, that both groups can be modelled using a similar approach, although it is considerably more complex to model graphically net nutrient transfer in continuous feeders than gross nutrient transfer.

The basic concept is illustrated in Figure 1. Here the time for which a quantity of nutrient is processed by stage S in a serial nutritional pathway is plotted against the cumulative release of the nutrient to the following stage (S + 1). Stage S might be foraging (as in the Marginal Value Theorem), ingestion (as in the models of partial prey consumption), digestion (as in the digestive models), or even specific components of ingestion (*e.g.*, chewing) or reactions within the digestive process (*e.g.*, proteinases, polypeptidases etc.).

The dashed horizontal line depicts the total amount of nutrient available for processing by stage S. This can be replenished by transfer from stage S - 1, which in turn is supplied by S - 2, all stages ultimately relying on ingestion. The transfer function (cumulative nutrient release from S to S + 1 as a function of time) in this hypothetical example is sigmoidal, as observed in the transfer of nutrient from the gut to the blood of locusts (see below, and Fig. 5). Although a sigmoidal curve is in general to be expected for processes which are limited by enzymatic reactions in which there is substrate depletion or product inhibition (see also Sibly 1981), the general approach is valid whatever the shape of the transfer curve (further discussed below).

The rate of nutrient transfer to S + 1 at a given time (*t*) can be read off as the slope of the line which passes through the origin and intercepts the curve at *t* (we refer to this rate as 'power' to distinguish it from the *instantaneous rate* of transfer, which is given by the tangent to the curve at *t*). Thus, in the figure, the slope of line P depicts the greatest rate at which nutrient can be transferred from S (=the greatest power). This rate

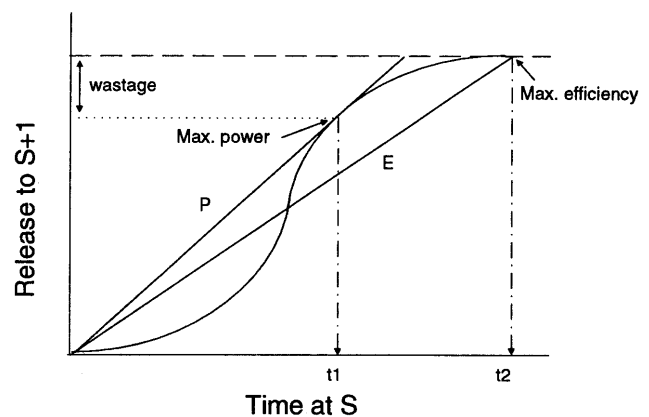


Fig. 1 Cumulative release of a nutrient from stage S in a hypothetical serial nutritional pathway plotted as a function of time. The horizontal dashed line represents the amount of nutrient available for transfer. The slope of line P gives the maximum rate of transfer (power) to S + 1, which is achieved by allowing unprocessed nutrient to bypass S at time t_1 and beginning to process a new batch. Maximum efficiency is achieved by accepting a new batch of substrate at t_2 , but at the cost of reduced power (slope of line E)

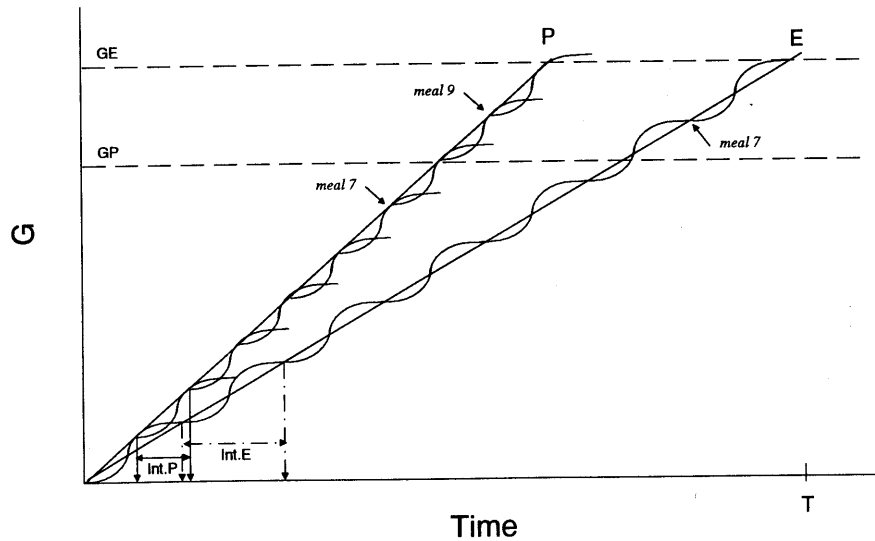


Fig. 2 Accumulation of identical curves representing the transfer of ingested nutrient to utilisation sinks (G) across consecutive meals. Maximal rate of transfer (line P) is achieved by voiding the gut and feeding again at intervals of *Int.P*, a strategy which wastes unprocessed nutrient. Maximal efficiency is achieved by feeding at intervals of *Int.E*, but at the cost of reduced transfer rate (line E). Line GE shows the amount of nutrient gained after processing 9 meals if power is maximised, or 7 meals if efficiency is maximised; for comparison, line GP shows the gains from 7 meals if power is maximised

is achieved by allowing unprocessed nutrient to bypass S, hence not becoming available to S + 1, at time *t1* and beginning to process the more recent product of S - 1 - in models of absorption, for example, the current gut contents would be voided and a fresh meal ingested. However, while feeding at *t1* maximises power, it involves wasting ingested nutrient which remains as yet unabsorbed (denoted *wastage* in the figure) and so decreases nutritional efficiency. Maximal efficiency would be achieved by voiding the gut at *t2*, by which time all of the ingested nutrient is absorbed, but at the cost of reduced power (line E).

Such relationships between power and efficiency are a central feature in the design of nutritional systems and have been discussed, qualitatively at least, in the context of organisms ranging from insects (Scriber & Slansky 1981; Reynolds *et al.* 1985; Lawton 1970) to molluscs (Boucher-Rodoni & Mangold 1977; Calow 1975), reptiles (Krebs & Harvey 1986; Karasov *et al.* 1986; Bjorndal 1989), fish (Nicieza *et al.* 1994), birds (Diamond & Obst 1988; Jackson & Place 1990) and mammals (Milton 1981; Karasov *et al.* 1986; Karasov & Diamond 1987).

The longer-term

While the above discussion considers a single nutritional event (*e.g.*, a meal), the framework can readily be extended to longer periods in the life-cycle of an animal (Raubenheimer & Simpson 1996). In what follows we will consider S to be the absorption of nutrient from the gut, and S - 1 to be ingestion. S + 1 is the end-point of nutrient processing, the gain of nutrient (G) in a form suitable for investment in fitness-enhancing functions [*i.e.*, for transfer to the term U in the nutritional budgets of Raubenheimer & Simpson (1995)]. We still consider a single currency, nutrient A.

The effects of individual nutritional events, such as meals, on an organism are cumulative. Thus, the

amount of nutrient delivered to the gut over time T (say a stadium in the life cycle of an insect) can be calculated as:

$$\text{Ingestion rate} = I_A/T = (I_1 + I_2 + I_3 \dots I_n)_A/T$$

where *I1*, *I2* etc. are the amount of A ingested in individual meals.

Likewise, the efficiency at which nutrient A is gained can be computed as:

$$\text{Efficiency} = (G/I)_A = [(G_1 + G_2 + G_3 \dots G_n) / (I_1 + I_2 + I_3 \dots I_n)]_A$$

where G represents the total utilisable gains of A in time T, and *G1*, *G2* etc. are the gains from individual meals. Finally, the rate at which utilisable gains in A are accrued is calculated as:

$$\text{Rate of gain} = (G/T)_A = [(I/T) \times (G/I)]_A$$

From this it follows that the nutritional processes involving A in time T can be modelled as an accumulation of power-efficiency relationships, as depicted in Figure 2.

For simplicity the figure assumes that the transfer function is identical for all meals, but this need not be the case, as discussed below. The horizontal line GE depicts the total amount of A ingested in time T, hence that which would be transferred to G if the animal was operating at 100% efficiency (*i.e.*, $GE = I_A$). It could achieve this level of efficiency by feeding at the relatively long interval of *Int. E*. (equivalent to processing each meal to time *t2* in Figure 1), but at the cost of reduced power (as can be seen in the shallower slope of line E compared with P). To maximise power, the animal should feed at the shorter interval of *Int. P* (equivalent to feeding at *t1* in Figure 1), a strategy which would entail reduced efficiency ($GP/I_A < GE/I_A$).

This example demonstrates that by regulating only the interval between meals, an animal can maximise either power or efficiency, or can achieve any intermediate between these extremes. Under which conditions should animals opt for high power and under which for high efficiency? All else being equal it might be expected that there is a selective premium on achieving a given nutritional outcome in a shorter time, so the high power option should be favoured. There are, however, at least three circumstances in which increased efficiency (reduced power) might be favoured. Firstly, where a nutrient is scarce (Ydenberg *et al.* 1995) animals should maximise the gains from a given number of meals. In Figure 2, for example, the hypothetical animal maximising efficiency by feeding at intervals of Int. E would gain GE units of nutrient A after processing 7 meals, whereas the animal operating at maximal power would gain only GP in the same number of meals. Secondly, when there are high costs to feeding (time costs, risk etc.) animals should satisfy their nutrient requirements in as few meals as possible. For instance, if line GE in Figure 2 represents the optimal requirements for A, it can be seen that this is achieved in 7 meals by maximising efficiency while 9 meals are required if power is maximised. Thirdly, an animal might reduce the rate at which nutrient A is accumulated when it is present in the food in excess relative to some other limiting nutrient, B. Whether or not this should occur depends on the relative shapes of the transfer functions for A and B, a subject which forms the main topic of the rest of this paper.

Multiple nutrients

Above, we have considered the behavioural decisions (how frequently to feed) made by an animal attempting to optimise its gains of a single nutrient under various circumstances. In reality, such decisions might be complicated by the need to balance the often conflicting demands of separate nutrient systems (Raubenheimer 1992; Raubenheimer & Simpson 1993; Simpson & Raubenheimer 1993a). Nutritional decisions are then best understood by considering the interplay among the transfer functions for several nutrients. In what follows we illustrate this point, and discuss in these terms some of the behavioural and physiological ways that animals regulate their nutrition in the face of the conflicting demands of multiple nutrient systems.

Regulating intermeal intervals: Our first example involving more than one nutrient demonstrates the potential importance of regulating intermeal intervals in animals that eat foods which differ in content from the nutritional requirements of their tissues (*e.g.*, herbivores). Figure 3 shows the hypothetical transfer functions for two nutrients in an animal feeding on a single food type. The nutrients are present at 2 parts of A to 1 part B (hence $I_A = 2I_B$), while the animal's tissues require the nutrients in a 1:2 ratio. There is, however, a point on the x-axis (t_3) at which the gain of B (G_B) is twice that of A (G_A). The animal can therefore obtain

a balanced diet despite the discrepancy between its requirements and the food's composition, by voiding the contents of the gut and feeding again at t_3 .

Note that in this case the animal's behaviour cannot be understood with reference to the maximisation of either power or efficiency. Feeding at t_1 would enable it to achieve a greater rate of gain of the scarce nutrient B, but at the cost of gaining too little A, while feeding at t_2 would maximise the efficiency with which B is obtained but result in an excess being gained of A. Rather, by feeding at t_3 the animal optimises a third variable, nutrient balance.

Such interactions between nutrients can be considered in the longer-term, as outlined for a single nutrient above. We will use the converse of the above example to illustrate this; namely where a food containing the same proportion of two nutrients as are required by an animal's tissues is nutritionally imbalanced as a result of the shapes of the transfer functions. The hypothetical animal in the previous example, which requires a 1:2 ratio of nutrients A and B, would thus perform sub-optimally on a food containing the same balance of the nutrients.

In Figure 4a are presented the transfer curves for the two nutrients when the animal feeds on the food in question. Intermeal intervals of duration shorter than t_1 would result in the nutrients being gained in proportions which are reversed relative to requirements (*i.e.*, $G_A > G_B$). At t_1 they are obtained in equal amounts, and thereafter in proportions where the amount of B is increasingly greater than A. The animal could obtain the two nutrients in a 1:2 proportion as required, but only by delaying feeding until time t_2 , at which point all of A has long-since been processed. The rates of acquisition of the two nutrients if the animal feeds at t_2 are presented as lines P_A and P_B .

Figure 4b shows the longer-term consequences of delaying feeding until t_2 (*i.e.*, the consequences accumu-

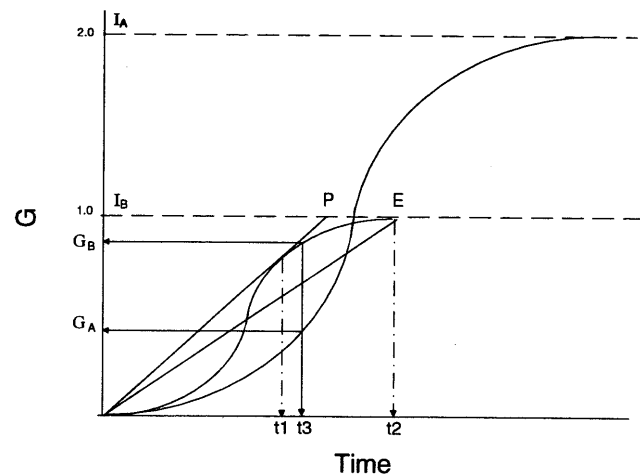


Fig. 3 Transfer functions for two nutrients, A and B, in a hypothetical food. The food contains nutrients A and B in a 2:1 proportion, and therefore twice the amount of A is ingested (I_A) than B (I_B). An animal can nonetheless obtain the nutrients in a 1:2 proportion by voiding the gut and feeding again at t_3 , since at this point the rate of gain of B (G_B) is twice that of A (G_A).

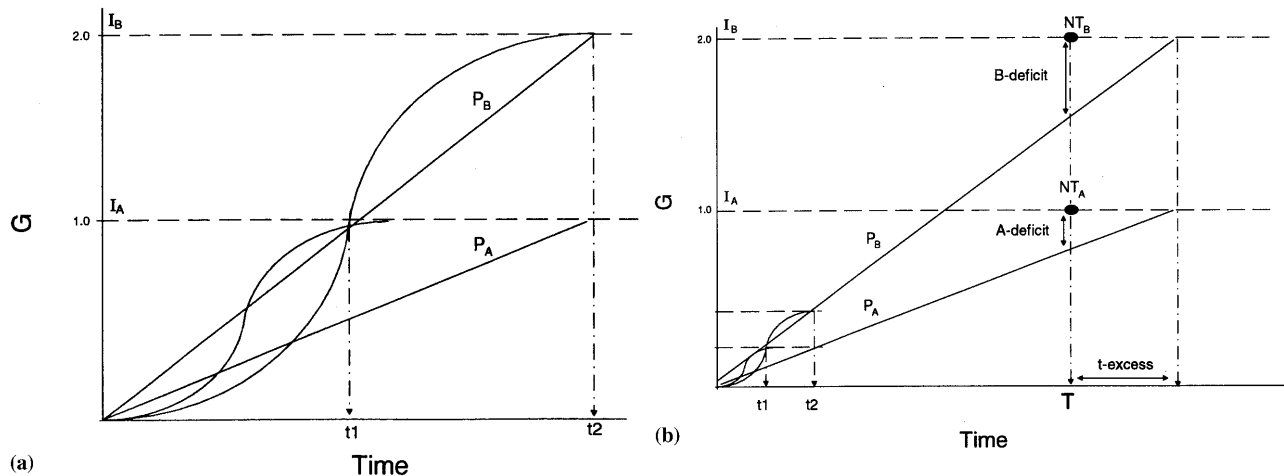


Fig. 4 (a) Transfer functions for nutrients A and B in a hypothetical animal eating a food containing the nutrients in a 1:2 proportion. Even though the nutrients are ingested in a 1:2 proportion, they become available for use by the animal in this proportion only if it delays feeding until time t_2 , by which time all of A has long-since been processed. The consequences of this extended intermeal interval over a stadium (T) in the life-cycle of a hypothetical insect are presented in (b). NT_A and NT_B represent its optimal requirements for nutrients A and B over T , and P_A and P_B represent, as in (a), the rates of gain of the nutrients when feeding at intervals of t_2 . Despite the insect having gained the correct balance of nutrients over T , the slow rates of acquisition mean that it must either moult into the following stadium with shortfalls of *A-deficit* and *B-deficit*, or it must extend the stadium by *t-excess* time units

lated over several meals as in Figure 2). For simplicity, the transfer functions for all but the first meal have been omitted from the figure. Optimal requirements for the nutrients A and B over time T (say a stadium in the life cycle of an insect) are depicted as NT_A and NT_B [that is, the A and B co-ordinates of the nutrient target *sensu* Raubenheimer & Simpson (1993)]. The rates of acquisition of the nutrients if the animal feeds at t_2 (lines P_B and P_A from Figure 4a) are also presented.

As long as feeding takes place at an interval of t_2 time units, the rates of acquisition of A and B will be 1:2 as required (this intermeal interval effectively enabling the animal to 'move' along lines P_A and P_B in the figure). However, while the required *balance* of the nutrients may be obtained in this way, the relatively long intermeal interval of t_2 means that the overall *rates* at which they are acquired are low, preventing the animal from satisfying its requirements for either A or B within the optimal time T . Either it must moult into the following stadium in a nutritionally sub-optimal state (deficient by '*A-deficit*' and '*B-deficit*' units), or extend the instar by '*t-excess*' units of time in order to achieve the required levels of the nutrients.

Regulating meal size: The animal in the previous example was restricted to an intermeal interval of t_2 time units in order to obtain the correct balance of nutrients, but nonetheless suffered life-history consequences due to a lower-than-optimal ingestion rate. It might, however, ameliorate these consequences by altering the other major quantitative component of the pattern of feeding, meal size (Simpson 1990). This would have the effect of raising lines I_A and I_B in Figure 4a, thus increasing the slopes of P_A and P_B and hence the rate of gain of nutrients A and B. The long-term result would be a reduction in the magnitude of *A-deficit* and *B-deficit* and/or in *t-excess* (Fig. 4b). Increased meal size might, however, have complex ef-

fects on parameters of the curves other than height (an empirical question), which could result in an optimal intermeal interval other than t_2 .

Food choice: An important behavioural means of regulating nutrient transfer functions is through food selection (Simpson & Simpson 1990; Waldbauer & Friedman 1991; Chambers *et al.* 1995). This can have the effect of changing the positions of the lines I_A and I_B (Fig. 4), and hence the slopes of P_A and P_B (as mentioned above in the context of regulating meal size, other parameters of the curves might also be changed). Food selection is therefore a means of varying independently the shapes of the transfer functions for two or more nutrients which in a single food might be fixed in relation to each other.

Nutrient transfer functions in locusts: We have to this point presented various hypothetical scenarios to illustrate the potential utility of focusing quantitative nutritional studies on nutrient transfer functions. We now present preliminary data for nutrient transfer functions in locusts, and in the section which follows we consider the scattered evidence for the physiological regulation of the shapes of nutrient transfer curves in these and other insects.

Figure 5 shows the transfer curves of protein and carbohydrate from the gut to the blood of 24-h old fifth instar *Locusta migratoria*. The insects were allowed to feed on synthetic foods (Simpson & Abisgold 1985) containing 21% each of protein and digestible carbohydrate for the duration of an average meal (6 min), then dissected at 4 min intervals through the following 20 min (average intermeal interval on these foods). The durations of meals and intermeal intervals were determined in observations of a separate sample of locusts feeding *ad-libitum*. The proportions of protein and digestible carbohydrate in the gut contents were measured, and from this the proportions absorbed could be

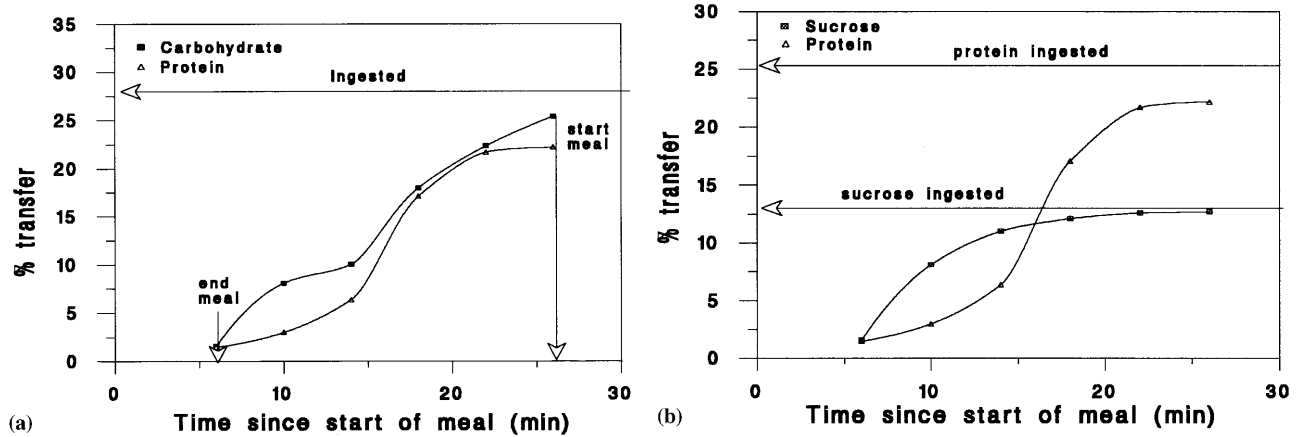


Fig. 5 (a) Measured cumulative transfer of protein and digestible carbohydrates (combined starch and sucrose) from the gut to the blood of locusts fed a synthetic food containing 21% of each of the two nutrient groups. In (b) is plotted the transfer curve for protein, together with an estimated curve for sucrose. This approximates the situation for locusts fed a food containing 21% of protein and 10.5% of sucrose. Percentage transfer of, for example, protein (P) at time t is calculated as the difference between % P in the food (represented by the horizontal line labelled 'Ingested') and % P in the gut at time t . These percentages are calculated relative to the indigestible bulking agent in the food, cellulose [e.g., % $P = (P/P + \text{Cellulose}) \times 100$], and are thus independent of changes in the concentration of other nutrients in the gut. See text for further details

calculated as the difference between that present in the food when ingested and that currently present in the gut.

The transfer curve for protein was sigmoidal as predicted (see above) (Fig. 5a). For carbohydrates, there was an initial high rate of transfer during the first 4 min following the meal, and thereafter the curve resembled the decelerating phase of a sigmoidal curve. The digestible carbohydrate in the foods was comprised of equal quantities of sucrose and starch, and most likely the initial steep phase of the carbohydrate curve was due to the transfer to the blood of the more readily absorbed sugar. The decelerating stages of the curves for the two nutrient groups were similar, but by the expected time of meal initiation (minute 26 in the figure) more carbohydrate had been absorbed than protein (carbohydrate:protein ratio = 1.14). This ratio is, interestingly, very similar to the ratio of carbohydrate:protein selected for ingestion by locusts feeding *ad-libitum* in choice assays (=1.22; Chambers *et al.* 1995).

In Figure 5b is depicted our approximation, based on the data in Figure 5a, of the transfer curves for locusts fed foods containing 21% protein and 10.5% sucrose. The figure suggests that locusts fed such a food could regulate over a wide range the balance of nutrients absorbed by altering the interval of feeding. By feeding again at approximately 16 min after the initiation of the previous meal, equal proportions of protein and carbohydrate would be extracted. At shorter intervals, a greater amount of carbohydrate than protein would be extracted and at intervals exceeding 16 min the converse would be the case. This is very similar to the hypothetical example in Figure 3. We are currently performing a detailed study of the transfer functions for protein and carbohydrates in locusts and cockroaches fed foods differing systematically in the balance and levels of these nutrient groups.

Physiological regulation of nutrient transfer functions: To this point we have assumed that the transfer function for each nutrient in a food is fixed by natural selection, so the only way an animal has to regulate power-efficiency relationships is behaviourally, through food selection or altering the spacing and size of meals. Under circumstances where the genotype can predict accurately the composition and availability of foods (e.g., suckling infants, specialist feeders, endoparasites etc.), this assumption might be representative. For most organisms, however, there is uncertainty in the nutritional environment and additional flexibility in the shape of nutrient transfer functions would enable animals to compensate for this. Physiological regulation might be at the levels of digestion, absorption, various post-absorptive processes, excretion or selective re-absorption.

The major means of regulating digestion is through the control of the production of digestive enzymes. However, where such regulation has been observed in insects, it is in the form of a positive feedback such that enzyme secretion increases with the amount of substrate ingested (secretagogue mechanism; see references in Simpson *et al.* 1995). This is counter-homeostatic, and thus seems unlikely on its own to constitute a means of nutrient balancing (but see below). Similarly, observed instances of altered absorption capacity correlate positively with substrate availability (Yang & Joern 1994), rather than negatively as would be expected of a homeostatic system. Similar results have been obtained for vertebrates (Karasov & Diamond 1987).

Available evidence for locusts suggests that the major site of regulation is post-absorptive. Zanotto *et al.* (1993) found that locusts fed nutritionally imbalanced synthetic foods digested, absorbed and de-aminated excess proteins before excreting the nitrogenous residues as uric acid. Excess carbohydrates, on the other hand, were metabolised and the carbon skeletons removed as carbon dioxide via increased respiration (Zanotto *et al.* 1997).

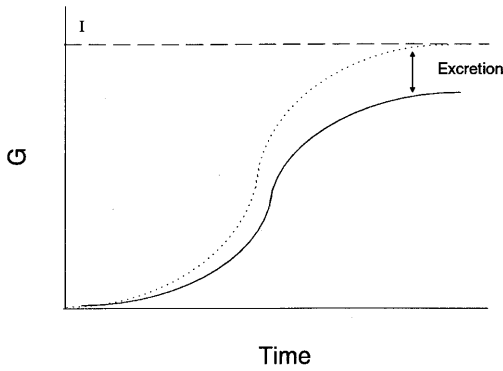


Fig. 6 Modulation of a nutrient transfer function through excretion. The dotted curve represents total uptake of the nutrient from the gut, and the solid curve represents net gains following excretion

Amounts of carbohydrates and proteins recovered in the faeces were minimal, suggesting that digestion and absorption were operating at high efficiency – an inference which is confirmed by the data in Figure 5.

It thus appears that the nutritional strategy of locusts is to extract the maximum amount of nutrient from the gut, and subsequently to alter the overall nutrient transfer curve via excretion (Fig. 6). This is consistent with the positive feedback mechanisms mentioned above in connection with digestion and absorption by insects, since the locusts' strategy would require that any excess nutrient ingested is passed from the gut to the blood rapidly so that corrective measures can be set in place. An interesting, and possibly selectively important implication of this strategy, is that the magnitude of the tradeoff between maximum power and maximum efficiency decreases as the rate of nutrient uptake increases; in the extreme case of a step function (instantaneous uptake) the tradeoff is eliminated altogether (Fig. 7).

Why should an animal take the effort to digest and absorb excess nutrients rather than eliminate it directly in the faeces? As discussed by Simpson & Raubenheimer (1993b), this has advantages in terms of inte-

grating the information required for effective nutritional decision making. Such decisions should reflect, firstly, the current state of the animal, which in insects is well represented by the nutrient content of the blood. They should, secondly, reflect the nutrient content of the food, and this can only be reliably measured once larger molecules have been broken down into the fundamental nutritional units, such as amino acids and monosaccharides.

Conclusions

We believe that the approach presented in this paper provides a powerful means of structuring both theoretical and experimental investigations into nutritional processes. Three major categories of questions arise from the power-efficiency approach. The first is the comparison of the evolved shapes of nutrient transfer functions both for different nutrient groups within an organism and between different organisms or groups of organisms. The second is the question of the homeostatic regulation of the shapes of nutrient transfer curves. For locusts we have found that regulation takes place primarily through near-complete absorption followed by selective excretion. We have ascribed this to the need for precision of regulation, but such high efficiency of absorption comes at the cost of reduced nutritional rates. It would be interesting to see whether the same is true in animals subject to extreme time constraints, such as temperate butterflies (*e.g.*, Nylin *et al.* 1989). This comparison suggests the third category of interesting questions, those involving the co-ordination of the timing of feeding with the shapes (regulated or otherwise) of nutrient transfer functions. It is our hope that with time sufficient relevant information will become available to enable comparative analyses of these and related questions, in the same way as we have used the comparative method to investigate ecological correlates of nutrient selection in insects (Simpson & Raubenheimer 1993a).

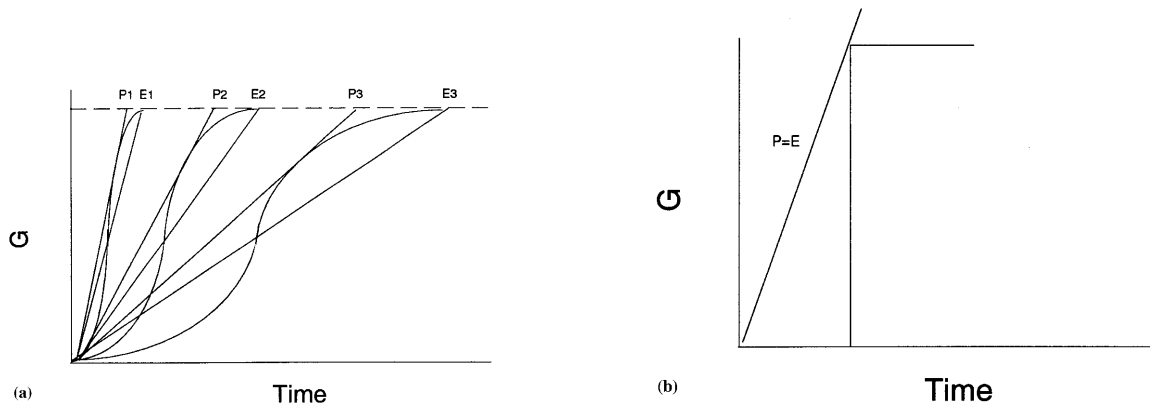


Fig. 7 (a) The discrepancy between the maximum rate of nutrient gain (P3 to P1) and the rate when operating at maximum efficiency (E3 to E1) diminishes as the transfer function becomes steeper. For a step-function, P and E are identical **(b)**

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