



Optimal foraging when regulating intake of multiple nutrients

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There is growing evidence that, rather than maximizing energy intake subject to constraints, many animals attempt to regulate intake of multiple nutrients independently. In the complex diets of animals such as herbivores, the consumption of nutritionally imbalanced foods is sometimes inevitable, forcing trade-offs between eating too much of nutrients present in the foods in relative excess against too little of those in deficit. Such situations are not adequately represented in existing formulations of foraging theory. Here we provide the necessary theory to fit this case, using an approach that combines state-space models of nutrition with Tilman's models of resource exploitation (Tilman 1982, *Resource Competition and Community Structure*, Princeton: Princeton University Press). Our approach was to construct a smooth fitness landscape over nutrient space, centred on a 'target' intake at which no fitness cost is incurred, and this leads to a natural classification of the simple possible fitness landscapes based on Taylor series approximations of landscape shape. We next examined how needs for multiple nutrients can be assessed experimentally using direct measures of animal performance as the common currency, so that the nutritional strategies of animals can be mapped on to the performance surface, including the position of regulated points of intake and points of nutrient balance when fed suboptimal foods. We surveyed published data and conducted an experiment to map out the performance landscape of a generalist leaf-feeding caterpillar, *Spodoptera littoralis*.

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The ultimate reason why animals feed is to provision themselves with nutrients that will maximize Darwinian fitness, subject to the physical, physiological and ecological constraints associated with finding, ingesting and processing foods (Schoener 1971; Stephens & Krebs 1986; Houston & McNamara 1999). Although energy/nutrient intake has often been used as a surrogate for fitness in optimal foraging theory, it is clearly a special case, since fitness maximization and energy intake maximization subject to constraints are in general not equivalent (reviewed by Illius et al. 2002). This applies

a fortiori when maximization of fitness requires the ingestion of multiple nutrients.

There is growing evidence that at least some animals regulate intake of multiple nutrients independently and, instead of maximizing intake, avoid ingesting surpluses and deficits relative to regulated points (e.g. Kyriazakis et al. 1991; Raubenheimer & Simpson 1997; Berthoud & Seeley 2000; Simpson & Raubenheimer 2001a). Some of the best-documented examples come from work on locusts, animals that, ironically, have a reputation for insatiability. A locust nymph provided with nothing to do other than eat high-quality food and rest spends only about 10–15% of its time feeding (Simpson & Raubenheimer 2000), but if the food is serially diluted up to fivefold with indigestible bulk, it increases its food consumption in direct proportion, and as a result maintains a constant nutrient intake (Raubenheimer & Simpson 1993). Such compensatory responses demonstrate that even if the insects were 'hardwired' to leave time for other activities and to minimize time spent feeding so as to avoid

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predation, and accepting that time is required for the efficient digestion of food, the locusts were clearly regulating intake rather than maximizing consumption. Further evidence that nutrient regulation, not maximization, is the central principle comes from the fact that locusts will mix nutritionally complementary foods to maintain their intake of protein, carbohydrate and salt at a multidimensional 'intake target' (Trumper & Simpson 1993; Chambers et al. 1995). In addition, if fed foods containing either protein or carbohydrate, but not both, and so made selectively deficient in one of these nutrients, when subsequently offered a range of foods locusts distribute their feeding so as to redress the accumulated nutrient imbalance (Simpson et al. 1988; Simpson & White 1990; Raubenheimer & Tucker 1997). They will also keep protein and carbohydrate intake constant by responding to changes in the relative frequency of occurrence of two nutritionally complementary foods in their environment (Behmer et al. 2001), and to changing the spacing between complementary foods (Behmer et al. 2003).

Maintaining nutrient intake requires upregulation when nutrients are in deficit in the food, and downregulation when they are in excess. When intake of more than one nutrient is regulated there is also the need to trade off ingesting surpluses of some nutrients against deficits of others when restricted to imbalanced diets (Raubenheimer & Simpson 1993; Simpson & Raubenheimer 1993). The physiological mechanisms underlying such responses are well understood for insects, and increasingly so for other organisms (Berthoud & Seeley 2000; Simpson & Raubenheimer 2000). The existence of these mechanisms, as well as the robustness of the behavioural outcomes, implies that selection has operated on these animals to avoid both nutrient surpluses and deficits. Fitness is thus expected to be maximal at the intake target and to fall away from this with ingested surpluses and deficits.

It follows that for functional models of foraging to be generally applicable, they should include terms for fitness costs associated with both excesses and deficits, and be able to deal with multiple nutrient dimensions. The most widely applied models in optimal foraging theory do not include terms for costs of nutrient surpluses, which is surprising, since the numerous intrinsic and extrinsic (ecological) costs of food intake are well documented (Illius et al. 2002; Yearsley et al. 2002). Nor do they capture the multidimensionality of nutrition, tending rather to focus on a single currency, typically energy. It is widely considered that this is sufficient to represent the diets of granivores, nectarivores, scavengers, deposit feeders and predators, but it does not adequately represent the complex diets of many omnivores and herbivores (e.g. Stephens & Krebs 1986; Simpson & Raubenheimer 1993; Bowen et al. 1995; Diaz 1995; Hanley 1997; Raubenheimer & Simpson 1999; Illius et al. 2002). In some optimal foraging theory models, other nutrients have been included as linear constraints on energy intake (e.g. Pulliam 1975; Belovsky 1981, 1990), but this precludes fitness from changing gradually with intake of the constraining nutrient. An alternative approach for dealing with the need for multiple nutrients has been to base models on the principle of the complementarity of foods

(Rapport 1970; Covich 1972; Schmitz et al. 1998). However, this locates the analysis at the wrong level, since foods are not a currency in their own right, but vehicles for nutrients, which are the primary currencies.

Our aim here is first to enumerate for a two-dimensional nutrient space the possible simple fitness landscapes for the case that fitness costs increase continuously and smoothly with distance from the optimal point of intake. We show how an animal's needs for multiple nutrients can be assessed experimentally using direct measures of animal performance as the common currency, and a fitness landscape can then be constructed over nutrient intake space. Such a description can then be used to test the prediction that animals have evolved nutrient acquisition strategies that maximize fitness, for instance that when provided with nutritionally complementary foods they will select the mixture that brings them to a point of intake corresponding to the summit of the fitness landscape. We next explore these issues by surveying published data and reporting the results of a new experiment, on the leaf-feeding caterpillar *Spodoptera littoralis*. Our approach is descriptive in the first instance, but we argue that it will lead ultimately to models that can both explain and predict foraging decisions.

THEORY

In this section we construct and classify simple linear and quadratic fitness landscapes and locate the optimal strategies within them. Our approach is to construct each fitness landscape around a 'target' intake, which by definition is the point at which no fitness cost is incurred. Relative to this point, fitness is reduced with both nutrient deficits (as in conventional models) and surpluses. There is no reason, however, to suppose the cost functions relating deficits and surpluses to distance from the target are either the same, or necessarily independent, and they are therefore distinguished but allowed to interact. Following Tilman (1982), we assume that fitness costs increase gradually (i.e. continuously and smoothly) with distance from the target. It follows that fitness costs in the neighborhood of the target have a Taylor series expansion in terms of surpluses and deficits and their interactions, their squares, and so on.

In mathematical notation, writing S for surplus, D for deficit and ' a ' for the associated coefficients we have for the case of a single nutrient that:

$$\text{Fitness costs} = a_1S + a_2D + a_3S^2 + a_4D^2 + \dots \quad (1)$$

Equation (1) can readily be extended to the case of two nutrients, which for concreteness we shall take to be protein and carbohydrate (the two nutrient groups most strongly regulated by insect herbivores). In this case interaction terms ($S_{\text{protein}} \times D_{\text{carbohydrate}}$, $D_{\text{protein}} \times D_{\text{carbohydrate}}$, $S_{\text{protein}} \times S_{\text{carbohydrate}}$ and $D_{\text{protein}} \times S_{\text{carbohydrate}}$) must also be included. Such terms indicate the extent to which the costs of an excess or deficit of one nutrient depend upon the simultaneous presence of an excess or deficit of the other nutrient. Thus, for example, the fitness cost of an

ingested excess of carbohydrate might increase with the extent to which protein is undereaten.

In this formulation, the nature of the fitness landscape will be determined by details of the dependences of fitness costs on surpluses and deficits. We now consider various possibilities in order of complexity. Figure 1 shows the three simplest scenarios. The corresponding fitness contours in a two-dimensional nutrient space are shown in the left-hand column of Fig. 2a–c. The thick lines in the plots in the right-hand column of Fig. 2a–c show the optimal strategy for each case, i.e. the ‘ridge’ derived by joining the points of maximum fitness achievable by animals confined to a single food, where foods are represented as lines (‘rails’) radiating out from the origin with a slope equal to the ratio of carbohydrate to protein they contain. Where linear fitness costs predominate over quadratic and interaction costs (Fig. 1a), the fitness contours are straight parallel lines in each of the quadrants round the target intake (Fig. 2a). The optimal strategies (thick lines, Fig. 2a) correspond with feeding to either a horizontal or a vertical line that passes through the target, except where the feeding rail and the fitness contour are coincident.

The next simplest possibility is that quadratic fitness costs predominate over linear and interaction costs, as in Fig. 1b, c. If for each nutrient the cost of a deficit is the same as that of a surplus (symmetrical costs, Fig. 1b), then

the optimal strategy is to feed to an elliptical ridge (Fig. 2b). However there is no a priori reason to suppose that the fitness costs are symmetrical. Figure 2c shows the fitness contours for the case of asymmetrical costs (Fig. 1c). The fitness contours are now elliptical within, but not across each quadrant, and the fitness ridge is described by different ellipses in the upper left and lower right quadrants. An interesting feature that emerges from this analysis is that the asymmetrical nature of the fitness costs generally induces a bending outwards in the fitness ridge at the target. This does not occur if the fitness costs are symmetrical (contrast Fig. 2b, c).

So far (Fig. 2a–c) we have considered cases in which there are no interaction costs. In these cases, the fitness effects of one resource are independent of the fitness effects of others, and joint effects are obtained as the simple sum of individual effects. We now go on to consider how landscape shapes are affected by interactions between resources. Figure 2d shows an example of addition of an interaction cost to the symmetrical quadratic costs of Fig. 2b. Here, the costs of ingested deficits of either nutrient are ameliorated by surpluses of the other, such as might occur when the two nutrients are partly substitutable. This tilts the elliptic fitness contours as in Fig. 2d, and the optimal strategies become more linear than in Fig. 2b. In the limiting case the fitness contours become parallel straight lines (Fig. 3), indicating that

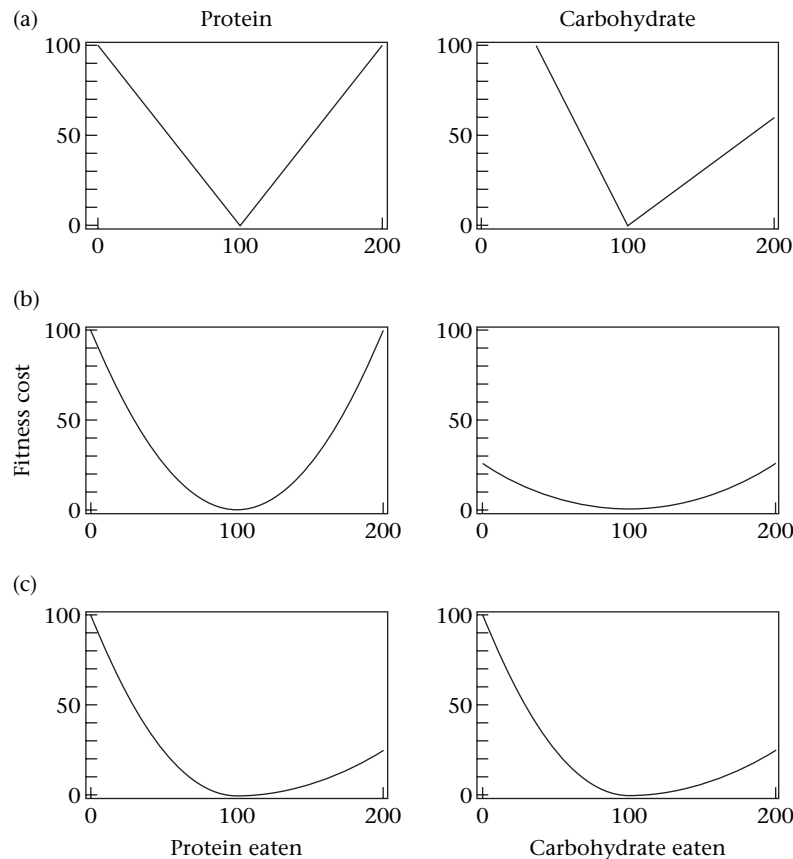


Figure 1. Three simple possibilities for the dependence of fitness costs on surpluses and deficits for protein and carbohydrate. The target intake of each nutrient is taken to be 100 units. (a) Linear costs; (b) symmetrical quadratic costs (by symmetrical costs we mean that the costs of surpluses are the same as those of deficits); (c) asymmetrical quadratic costs.

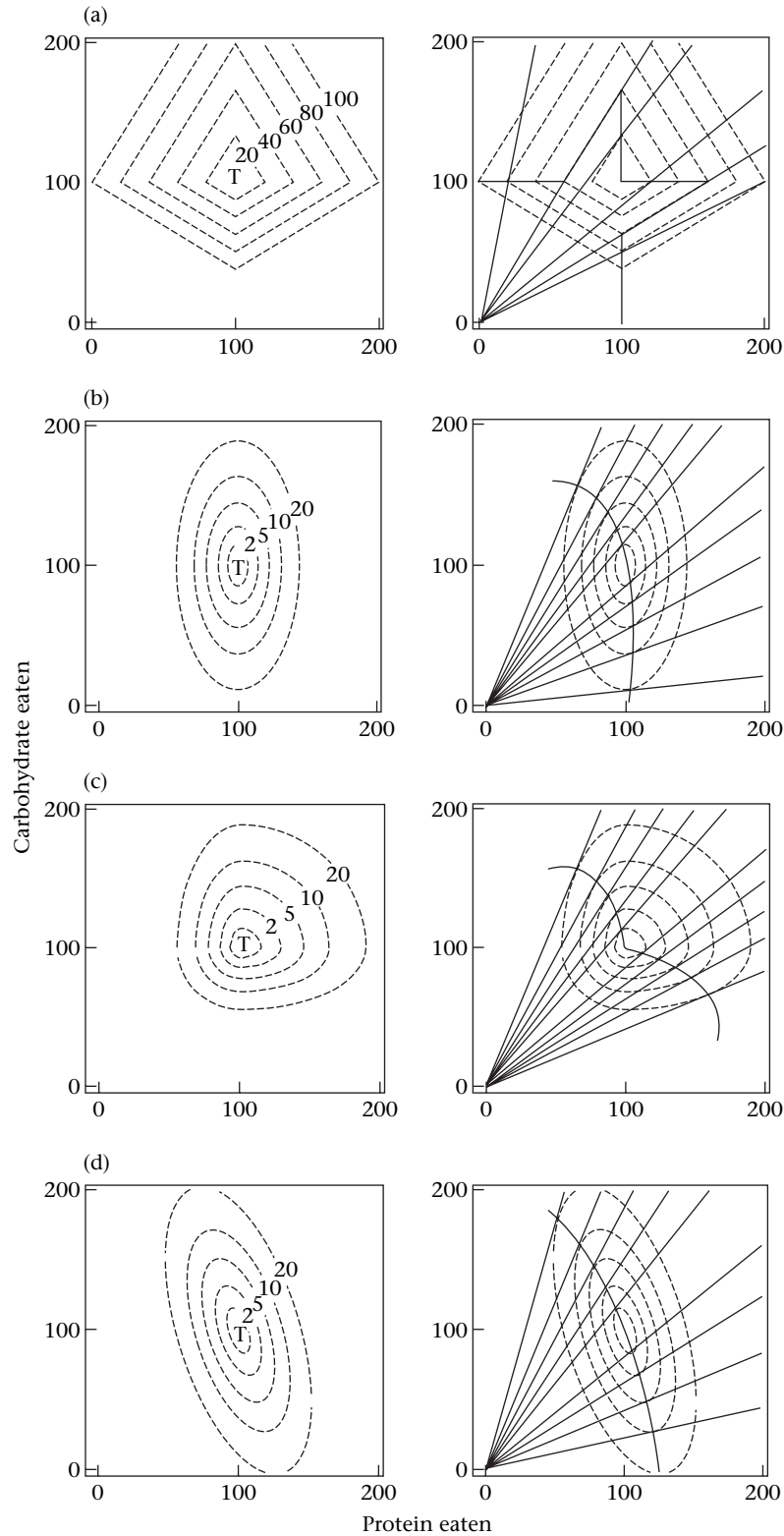


Figure 2. Implications for optimal strategy of the fitness costs shown in Fig. 1. Dashed lines in the left-hand panels are fitness contours. Numbers beside the fitness contours indicate the fitness cost on that contour. Only contours near the target intake, T, are shown. In the right-hand graphs thin lines represent selected feeding rails (food compositions), and thick lines optimal strategies, where maximum fitness is obtained. (a) Linear costs, as in Fig. 1a. The fitness contours are straight parallel lines in each of the quadrants around the target intake, T. (b) Symmetrical quadratic costs, as in Fig. 1b. The fitness contours are ellipses, and the optimal strategies (thick lines) are also ellipses. (c) Asymmetrical quadratic costs, as in Fig. 1c. The fitness contours are ellipses in each of the quadrants around T, and the optimal strategies are also ellipses in each quadrant. (d) Symmetrical quadratic with interaction costs. The fitness contours are now tilted ellipses, and the optimal strategies are more linear than in (b). The quadratic component of the fitness cost is the same as in (b).

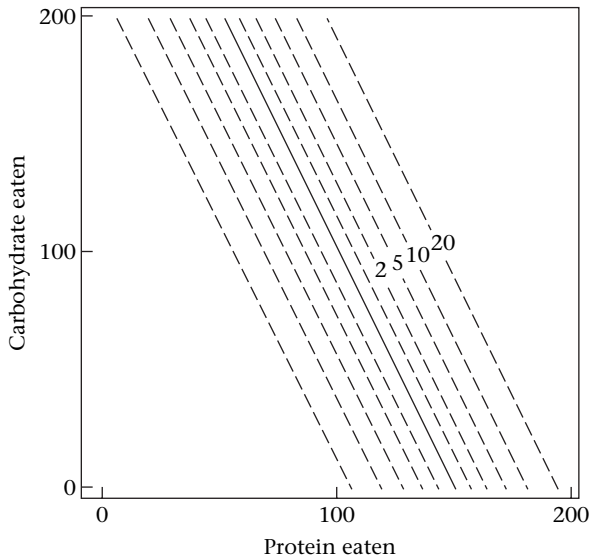


Figure 3. As in Fig. 2d, but with increased interaction costs the fitness contours become straight parallel lines.

protein and carbohydrate are in terms of fitness gains (although not necessarily physiologically) completely substitutable (Tilman 1982; Stephens & Krebs 1986). In this case fitness costs depend on the weighted sum of the quantities of protein and carbohydrate consumed. If the total is less than the target there is a deficit, if more a surplus; but for summed intakes equal to the target intake, there is a flat summit ridge in the fitness plane and the target is met at all points on this summit ridge. An example is given in Fig. 3.

If there are no interaction costs, as in Fig. 2a–c, then the optimal strategies intersect the axes at the coordinates of the target, i.e. at 100 units in the figures. However if there are interaction costs this is no longer the case, as can be seen in Figs 2d and 3. Interaction costs might also be added to the linear costs case of Fig. 2a, but this does not affect the conclusions. Interaction costs on their own are implausible and are not presented.

In summary, the main results are: (1) linear costs generally imply optimal strategies on horizontal or vertical lines through the target or, in some regions of nutrient space, on food rails (as in Fig. 2a); (2) symmetrical quadratic costs produce ellipsoidal optimal strategies as in Fig. 2b; (3) asymmetrical costs imply that the optimal strategy is discontinuous on the two sides of the target as in Fig. 2c; (4) if there are no interaction costs, as in Fig. 2a–c, then the optimal strategies intersect the axes at the coordinates of the target; and (5) the addition of an interaction term to quadratic costs changes this so that optimal strategies no longer intersect the axes at the coordinates of the target and can lie on a straight line, as in Fig. 3.

EXAMPLES FROM PUBLISHED DATA

Figure 4 shows some published examples of intake data in two-dimensional nutrient spaces with associated

performance consequences. The points labelled 'regulated intake' indicate bicoordinate nutrient intakes to which animals regulated when provided with one of several different complementary food pairings (see Raubenheimer & Simpson 1997). The most extensive studies indicating such regulation have been undertaken on the grass-specializing African migratory locust, *Locusta migratoria* (Simpson & Raubenheimer 2000). In each case in Fig. 4 it is apparent that animals performed best (by the measured criteria) at the regulated point of intake, and performance fell smoothly with distance away from this 'target'. The shape of the array for *Locusta* (Fig. 4a) appears to be ellipsoidal, as in Fig. 2b, and intake on the protein axis is about equal to the protein coordinate of the intake target, as expected in the absence of interaction costs. The decline in performance as one moves along the array away from the target is roughly ellipsoidal, the steeper decline to the left indicating that protein deficits are more serious than carbohydrate deficits in terms of locust survival. The situation for the highly polyphagous desert locust, *Schistocerca gregaria* (Fig. 4b) is rather similar except that the array resembles a tilted ellipse (Fig. 2d), indicating the presence of linear interaction costs. This is also indicated by the fact that intake on the protein axis is higher than the protein coordinate of the intake target. As for *Locusta*, the performance declines are ellipsoidal, with steeper decline to the left indicating that protein deficits are more serious than carbohydrate deficits. The array of layer hens, *Gallus gallus domesticus* (Fig. 4e) is similar to that of *Schistocerca* but the information available is more limited. The array of *Locusta* for salt mixture versus macronutrients (Fig. 4c) is vertical above the regulated intake point, indicating that salt overload is insignificant compared with protein/carbohydrate imbalance (cf. Fig. 2a). The array of the pea aphid, *Acyrtosiphon pisum* (Fig. 4d) is close to horizontal between amino acid intakes of 1 and 8 μg , indicating that in this range amino acid imbalance is unimportant compared to imbalance of carbohydrate (cf. Fig. 2a).

Hence, examples are seen of both horizontal and vertical arrays, compatible with the linear costs of Fig. 1a, together with cases that suggest quadratic costs both with and without interaction costs. Were arrays to be extended to encompass more markedly unbalanced foods, these relationships would break down in certain cases, indicating strongly nonlinear interaction costs at these extremes. For example, foods lacking protein cannot sustain survival in growing locusts, aphids or hens, and intake is commensurately low. A salt-free diet is also fatal to developing locusts.

In *Schistocerca* and the layer hen the arrays resembled the tilted ellipses of Fig. 2d, rather than the ordinary ellipses of Fig. 2b, indicating the existence of linear interaction costs, and it would be interesting to know what mechanism could be responsible. This question can be examined by comparing the optimal strategy curves in Fig. 2b, d, and noting that, far from the target, animals represented by Fig. 2d pay fewer fitness costs than would be paid by Fig. 2b animals with the same intakes. One possibility is that animals responding as in Fig. 2b are generalist feeders, and that the costs of surpluses are

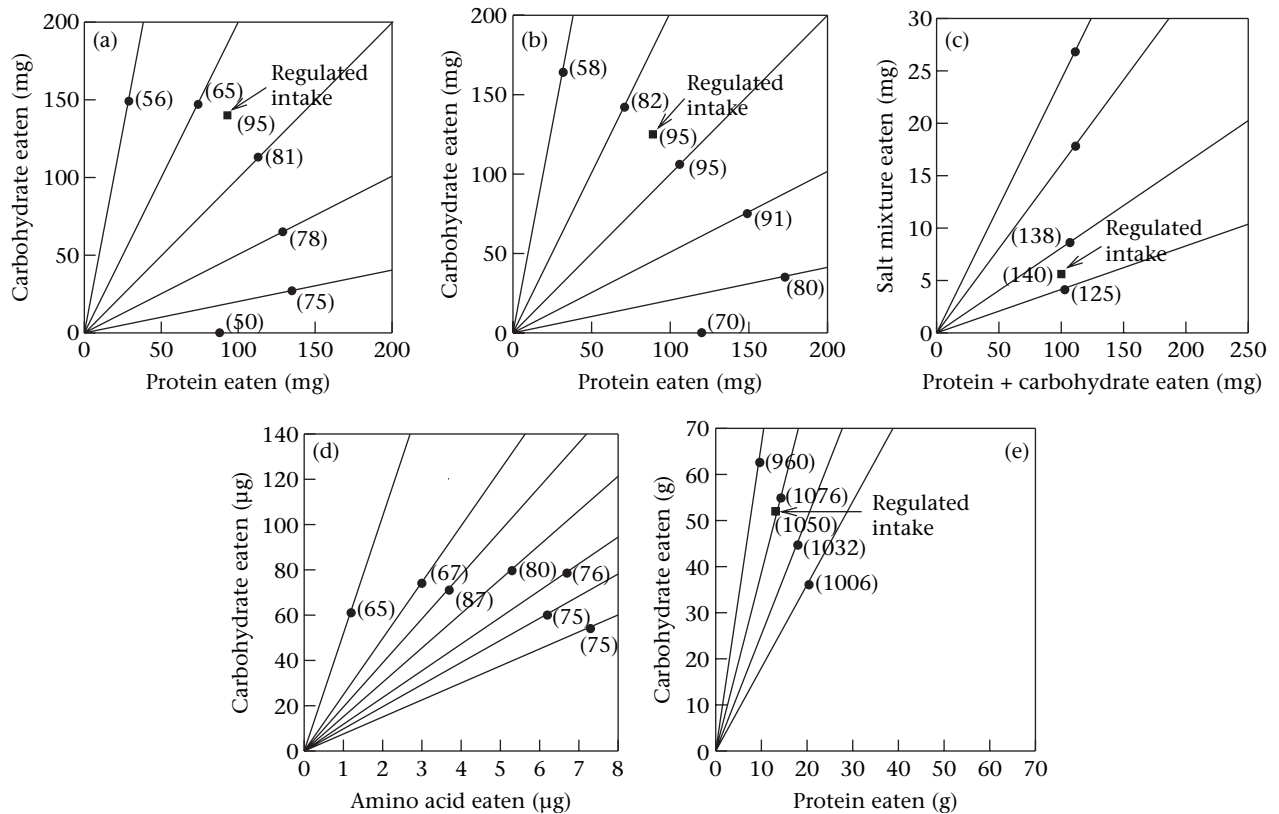


Figure 4. Examples of intake arrays with associated performance measurements. (a) and (b) Protein and carbohydrate intake in two species of locust, *Locusta migratoria* and *Schistocerca gregaria*, respectively (data from Raubenheimer & Simpson 1999, 2003). (c) Intake of salt versus protein + carbohydrate in *Locusta* (data from Trumper & Simpson 1993). (d) The array for pea aphids, *Acyrtosiphon pisum* (data from Abisgold et al. 1994). (e) The array for layer hens, *Gallus gallus domesticus* (Shariatmadari & Forbes 1993). 'Regulated intake' indicates the point to which animals regulated when provided with complementary food pairings (such regulation has not been measured for aphids, hence the lack of a point labelled as the target). Other points of intake lie on lines ('rails') radiating out from the origin at an angle that represents the ratio of the two nutrient groups in each food. Values beside intake points represent performance measures for the same insects. The performance measures recorded were: % survival in (a) and (b); dry mass growth (mg) in (c) (data not available for three points); dry mass growth (μg) in (d), and carcass dry mass (g) at the end of the experiment in (e).

discounted in generalists because they have a higher chance than specialists of finding a food providing a complementary nutrient (Simpson et al. 2001; Raubenheimer & Simpson 2003). A mechanistic explanation for why animals conforming to the pattern in Fig. 2d overeat protein on low-carbohydrate, high-protein foods relative to those following the pattern in Fig. 2b might be that the former have a greater capacity to deaminate protein than the latter. This could simultaneously reduce the surplus of amino acids in the blood, and provide reduced carbon to supplement the carbohydrate deficit incurred on the excess protein foods. At the other extreme, although they cannot convert carbohydrate to protein, when confined to high-carbohydrate, low-protein diets, animals conforming to Fig. 2d may have a greater capacity to store excess ingested carbohydrate as lipid (Raubenheimer & Simpson 2003).

EXPERIMENT

A limitation of the examples in Fig. 4 is the incomplete coverage of performance data across nutrient space. In an

attempt to obtain better coverage we carried out an experiment using final-stage larval *Spodoptera littoralis*, a generalist leaf-feeding caterpillar.

Sampling the performance landscape more fully requires measuring the consequences of restriction to different regions of intake in the nutrient plane. It is straightforward to restrict animals to suboptimal balances of intake by providing diets that differ from the target nutrient ratio. It is also possible to achieve experimentally restricted intake within a given nutrient ratio by limiting the amount of food provided or, alternatively, by manipulating nutrient density of the foods (our chosen method for this experiment). Far more difficult, however, is to force animals to overeat a food (and hence cross the fitness hill and descend the other side) without resorting to invasive techniques, which greatly complicate the measurement of performance. In the present experiment, we attempted to achieve this by providing a subset of the animals from each P:C ratio treatment with foods that were unusually nutrient dense, but not so concentrated that they would be rejected. Such foods might be less phagostimulatory than less-concentrated foods (Simpson

& Raubenheimer 1996), but could none the less result in the ingestion of excess nutrient because they elicit lower levels of inhibitory feedbacks from stretch receptors in the gut per unit of nutrient eaten than do more concentrated foods (Simpson 1995). To moderate any acute effects of the highly concentrated foods, we simultaneously provided the insects in these treatments with a moderately concentrated food. In this way, we hoped to coerce, rather than force, the animals to overingest nutrient, and measure the associated fitness consequences.

Methods

Final-instar larvae were provided with one of 35 foods varying in protein and digestible carbohydrate concentration and ratio. In an additional five treatments larvae were allowed to select between complementary food resources (henceforth, the self-selecting treatment), to establish whether and to which point they would regulate their intake of protein and carbohydrate.

Caterpillars were reared on a wheat-germ based, semi-artificial diet until the final (sixth) larval stadium. For no-choice treatments, 350 newly moulted sixth-instar larvae were weighed to the nearest 0.1 mg and each was placed in its own 9-cm-diameter petri dish with a preweighed block (weighing ca. 1.5 g) of one of 35 chemically defined diets. Foods contained one of five ratios of protein (a 3:1:1 mix of casein, peptone and albumen) to digestible carbohydrate (sucrose): 5:1, 2:1, 1:1, 1:2 or 1:5. Foods also differed in their concentration of protein + carbohydrate through the addition of indigestible cellulose. There were seven such dilutions: P + C = 42, 33.6, 25.2 or 16.8% by dry mass. In an attempt to cause the caterpillars to overingest nutrient, we included an additional three treatments per protein:carbohydrate ratio where insects were provided with a pair of foods, one of which was highly and the other moderately concentrated (see above): P + C = 63% + 42%; 84% + 42%; 84% + 63%. Remaining dietary ingredients (salts, vitamins, cholesterol and linoleic acid) totalled 4% dry weight in all foods. Dry ingredients were suspended at a 1 to 6 ratio in 1% agar solution. Insects were maintained at $27 \pm 5^\circ\text{C}$ under a 14:10 light:dark photoregime.

In the self-selecting treatments, 60 newly moulted, final-instar larvae were each provided with a pair of nutritionally complementary food blocks, containing the following protein to carbohydrate ratios (%P:%C): 35P:7C with 21P:21C; 28P:5.6C with 21P:21P; 28P:5.6C with 16.8P:16.8C; 21P:4.2C with 21P:21C; or 21P:4.2C with 16.8P:16.8C.

Food was replaced each day and uneaten food was removed and dried to constant mass. We calculated consumption as the difference between initial food mass (estimated from initial wet mass) and final dry mass. Insects were maintained until pupation, with the time of pupation being recorded to the nearest 6 h. Pupae were wet-weighed and wet mass growth across the stadium was calculated. Growth rate was measured as wet mass growth/stadium duration. Those insects that died were recorded but removed from analyses of intake and growth.

Results

Mean points of intake on the 35 single-diet treatments were spread across nutrient space in a pattern that reflected both the ratio of macronutrients in the diet and their concentration (Fig. 5a). For presentation, we chose as a performance measure % survival within a treatment multiplied by mean rate of development (wet mass grown divided by stadium duration). This enabled the combined effects of two of the major determinants of fitness in Lepidoptera (e.g. Honek 1993) to be superimposed as a performance value on the intake plot in Fig. 5a. For statistical testing, however, we analysed survival and growth rate separately, to distinguish the individual contributions of these variables to any effects on the performance index. We return to the individual contributions of growth and development time in a later section.

It is evident from Fig. 5a that we were successful in our aim of extending the data coverage of nutrient space. In particular, the caterpillars had only a partial capacity to compensate for dilution of the diet with cellulose, which therefore served as a constraint to nutrient intake. Additionally, and importantly, the animals on the excess-carbohydrate foods overingested nutrients, providing us with an opportunity to assess the costs of ingested nutrient excesses.

When following the intake points along the line for the 1:5 ratio of protein to carbohydrate (Fig. 5a), it is apparent that performance rose with increasing nutrient intake up to the point for the 42% P + C concentration (where it reached a maximum still 30% below that seen at the overall peak of the landscape), but increased consumption beyond this resulted in declining performance (survival: $\chi^2_3 = 18.2$, $P < 0.001$; growth rate: $F_{3,33} = 1.68$, NS). This provides clear evidence for costs of carbohydrate excesses, independent of protein deficit. Intake along the 1:2 diet rail also showed increasing, then declining performance (survival: $\chi^2_3 = 9.9$, $P < 0.02$; growth rate: $F_{3,33} = 0.66$, NS). On the remaining food ratios (1:1, 2:1 and 5:1 %P:%C) there is also evidence for a fall in performance at the highest nutrient intakes: this downturn becomes increasingly pushed up against a maximal intake within each rail. It proved impossible to get the larvae to eat more than a certain total amount of nutrients on these higher-protein ratio foods. This clumping of intake points for the most concentrated foods on each rail indicates a strictly imposed intrinsic (behavioural) constraint to nutrient intake. Forcing animals to ingest in excess of this would require invasive techniques with associated problems of interpreting fitness responses (see above).

The performance surface plotted in Fig. 5a has a summit ridge running diagonally from approximately 100 mg P, 200 mg C to 250 mg P, 50 mg C, interpolating within which leads to a predicted summit point in the region of 170 mg P, 125 mg C. The next question was whether caterpillars provided with the opportunity to regulate their intake of carbohydrate and protein defended a point of intake, and whether this point lay in the region of the peak on the performance landscape. Earlier work had shown that final-stadium *S. littoralis* provided with food

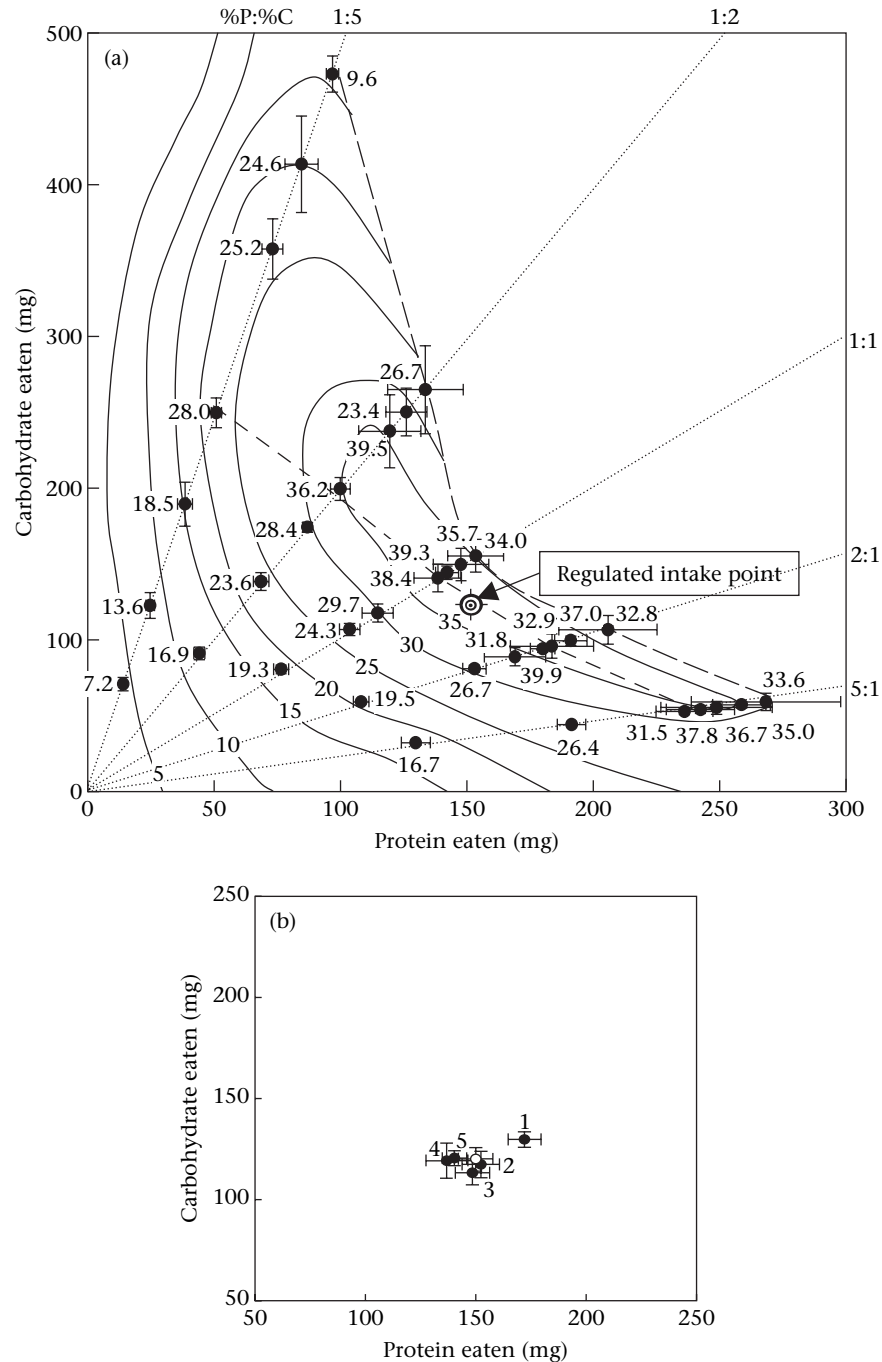


Figure 5. (a) Results of an experiment in which *Spodoptera littoralis* were fed chemically defined diets over the final larval stadium. Thirty-five treatment groups were provided with a single food and were thus restricted in their intake to the ratio of protein to carbohydrate present in the food, while five treatments were able to select between complementary food pairings. See text for details of treatment regimes. Points on the graph represent nutrient intake (bicoordinate mean \pm SE for 10 caterpillars), while the number beside each point gives performance calculated as the mean wet-mass growth rate of the insects (mg grown/day) multiplied by % surviving to pupation. The point labelled 'regulated intake point' is the combined mean for the 58 caterpillars ($N = 11$ or 12 per treatment) that were provided with one of the five choice treatments (see Fig. 5b for individual treatment values). Performance contours were fitted to the surface using SigmaPlot. Note how the performance surface is consistent with a tilted ellipse, indicative of quadratic costs with an interaction term, and how the regulated point of intake measured from self-selecting larvae lies within the region of the summit on the fitness surface. The short-dashed line indicates the values for the treatments in which the total of protein and carbohydrate in the diet was 42%. This concentration provided near maximal performance within each protein:carbohydrate ratio. The long-dashed line shows the upper limit to nutrient intake, beyond which insects would not go. (b) Mean \pm SE points of intake for the five choice treatments, as well as the overall mean (\circ) used in Fig. 5a. Treatments are numbered according to the order of presentation in the Methods. Each mean value differed highly significantly from the expected intake were insects to have fed indiscriminately between the two foods (MANCOVA contrasts between observed and expected values for protein and carbohydrate intake, with insect mass at the beginning of the stadium as a covariate, gave $F_{2,104}$ ranging from 35.62 to 60.45, all $P < 0.0001$). Pairwise contrasts among observed

pairings in which one food contained protein but no carbohydrate, and the other carbohydrate but no protein, regulated their intake to a protein to carbohydrate ratio of 65:35 (Simpson et al. 1988). We thus provided larvae with one of five different complementary food pairings, all of which encompassed the predicted position of the intake target, but in each case would require a unique combination of consumption of the two foods to reach a given point of protein–carbohydrate intake. Were larvae to have apportioned their feeding between the two dishes indiscriminately, the five treatment groups would have arrived at quite different points of nutrient intake. Instead, intake points converged in nutrient space, indicating strong regulation of both nutrients (Fig. 5b). This point lay at 150 mg P, 125 mg C, on the ridge of the performance landscape close to the predicted position of the summit point (Fig. 5a).

Having established the position of maximal performance through coincidence between two independent measures, growth and survivorship on the one hand, and dietary selection behaviour on the other, we could next fit the Taylor series expansion model. Fixing the intake target at 150 mg P, 125 mg C and fitting a quadratic model with interaction terms (as befits the shape of the landscape, a tilted ellipse) gives the following.

$$\begin{aligned} \text{Fitness (growth} \times \text{survival)} &= 34.2 - 0.00141 \text{ PD}^2 \\ &- 0.00073 \text{ PS}^2 - 0.00204 \text{ CD}^2 \\ &- 0.00031 \text{ CS}^2 + 0.0005 \text{ PD} \times \text{CD} - 0.00095 \text{ PD} \times \text{CS} \\ &- 0.0027 \text{ PS} \times \text{CD} + 0.0004 \text{ PS} \times \text{CS} \end{aligned}$$

where P is protein and C carbohydrate, D is deficit and S is surplus, relative to the intake target. Statistical results are provided in Table 1.

GENERAL DISCUSSION

Our approach has features in common with that introduced by Tilman and colleagues into the resource exploitation literature, following earlier work by Monod (1950). In a theoretical synthesis, Tilman (1982) considered the link between the availability of multiple resources and the growth rate of the population of consumers of those resources. Increasing availability produces a graded increase in population growth rate (see e.g. Figure 2 in Tilman 1982). When organisms require more than one resource there are a number of ways in which they could jointly affect population growth rate (cf. Ricklefs & Miller 1999). Tilman (1982) classified resources as essential if they limit population growth rate independently of one another, so that the effects of one have no interaction

Table 1. Taylor series expansion model fitted to the data in Fig. 5a, with intake target at 150 mg protein and 125 mg carbohydrate

Predictor	Coefficient	SE	T	P
Constant	34.193	1.144	29.88	<0.0005
PD ²	−0.00141	0.000237	−5.94	<0.0005
PS ²	−0.00073	0.000995	−0.73	0.471
CD ²	−0.00204	0.000457	−4.47	<0.0005
CS ²	−0.00031	0.000069	−4.43	<0.0005
PD × CD	0.00050	0.000739	0.67	0.508
PD × CS	−0.00095	0.000345	−2.77	0.010
PS × CD	−0.0027	0.001484	−1.81	0.081
PS × CS	0.0004	0.8100	0.00	1.000

P = protein, C = digestible carbohydrate, D = deficit of intake relative to the intake target, S = surplus intake. R² = 0.848; overall significance of the regression model: F_{8,26} = 18.15, P < 0.0005.

with the effects of others, and substitutable if one resource may be substituted for another.

Since population growth rate is often used as a fitness measure, there has been a need to apply a version of Tilman’s resource exploitation theory, which had mainly plants in mind, to the analysis of the foraging patterns of animals with multiple nutrient requirements. Indeed, efforts have been made to integrate consumer resource theory with optimal foraging theory. For example, Tilman (1988) plotted hypothetical fitness landscapes, superimposed a linear consumption constraint, and then identified the strategy with highest fitness that satisfies the consumption constraint. Vincent et al. (1996) provided a mathematical formulation of Tilman’s graphical models based on Holling’s (1959) disc equation and broadened the models to include aspects of community ecology (density-dependent habitat selection) as well as optimal foraging theory. More recently, Whelan et al. (2000) built upon these models by incorporating modulation of digestive physiology in response to consumer resource dynamics and season.

Our approach has been to construct a fitness landscape around a ‘target’ intake, at which minimal fitness cost is incurred. Following Tilman (1982), we suppose that fitness costs change gradually with nutrient imbalances, and this leads to a natural classification of possible fitness landscapes based on Taylor series approximations of landscape shape. In some cases there are no interaction costs (Fig. 2a–c), in others the presence of interactions can result in resources being substitutable (Fig. 3). The simplest possible landscapes are pyramids (Fig. 2a), corresponding to linear costs, and these generally produce optimal strategies on horizontal or vertical lines through the target. Symmetrical quadratic costs produce ellipsoidal optimal strategies as in Fig. 2b, and asymmetrical costs imply that the optimal intake array is concave in shape, bending outward in the neighbourhood of the target, as in

points of protein and carbohydrate intake following MANCOVA were as follows: treatment 1 versus 2 (F_{2,51} = 2.05, P = 0.139); treatment 1 versus 3 (F_{2,51} = 3.11, P = 0.053); treatment 1 versus 4 (F_{2,51} = 9.12, P = 0.0004); treatment 1 versus 5 (F_{2,51} = 6.97, P = 0.002); treatment 2 versus 3 (F_{2,51} = 0.18, P = 0.834); treatment 2 versus 4 (F_{2,51} = 4.22, P = 0.02); treatment 2 versus 5 (F_{2,51} = 3.05, P = 0.056); treatment 3 versus 4 (F_{2,51} = 4.67, P = 0.014); treatment 3 versus 5 (F_{2,51} = 3.60, P = 0.0344); treatment 4 versus 5 (F_{2,51} = 0.12, P = 0.890). When the required Bonferroni correction is made to the critical P value (0.05/10 = 0.005), the only differences that are significant are between treatments 1 and 4 and 1 and 5.

Fig. 2c. If there are no interaction costs, as in Fig. 2a–c, then the optimal strategies intersect the axes at the coordinates of the target; the addition of interaction to quadratic costs changes this so that optimal strategies no longer intersect the axes at the coordinates of the target.

The available data (Figs 4, 5) fit well with this classification of fitness landscapes. There are examples of both horizontal and vertical arrays, compatible with the linear costs of Fig. 2a, and cases that correspond to quadratic costs. Three cases suggest the existence of interactions (Fig. 4b, e, Fig. 5).

Substitutable resources were defined graphically by Tilman (1982) as in our Fig. 3, but this and his use of the term ‘essential resources’ are, in reality, not clear. For example, if forced to balance undereating carbohydrate against overeating protein by being restricted to a diet with a higher than optimal ratio of protein to carbohydrate, locusts, caterpillars and aphids have the capacity to deaminate protein to gain limiting carbon skeletons for growth and to fuel respiration (Raubenheimer & Simpson 1993, 2003; Thompson & Redak 2000; Wilkinson et al. 2001). In other words, protein (or amino acids in the case of aphids) can be substituted for carbohydrate, although the reverse is not the case. Nevertheless, if provided with pure protein or amino acids, all aphids die, and locusts either die or suffer in their growth and development. Also, if provided with the opportunity to regulate intake of both nutrient groups by selecting between complementary foods, these animals will do so. Hence, at the level of the regulatory systems for feeding behaviour the two macronutrients are not substitutable, but under severe dietary imbalance they are rendered partially, and asymmetrically, substitutable by postingestive physiological processes. It therefore seems preferable when dealing with animal foraging strategies to make a distinction in terms of the presence or absence of interaction costs as we have done here, rather than essentiality of resources.

Nonalignment of Regulation Points

In our experiment on *S. littoralis*, the point of regulated protein and carbohydrate intake coincided with the summit of the performance landscape (Fig. 5a). Were this not to be the case, it would indicate one of two things: either the fitness landscape had been mismeasured, or the animals truly were behaving maladaptively. Considering the first of these, it may be that the chosen performance measures were not on their own sufficiently strong determinants of fitness under natural conditions. They might, for example, exclude ecological costs such as time- and/or consumption-dependent mortality from predation, parasitism or disease (Bernays 1997; Lima 1998; Hutchings et al. 2000), which have become incorporated into the operation of regulatory mechanisms over evolutionary time. This is a useful feature as it provides an opportunity in our models to test directly for the appropriateness of the chosen currency, rather than merely assume it. Indeed, it might be argued that once likely laboratory measures have been exhausted, the extent and direction of any remaining misalignment of laboratory-

derived fitness surfaces and points of regulated intake could be used to predict such ecological costs.

A second reason why the regulated intake point may not align with the performance peak is that there is a mismatch between evolved regulatory mechanisms and the current environment; that is, even though animals are regulating their nutrient intake, they are doing so to a region in nutrient space that is maladaptive in a changed environment. For example, the regulated point may include a component for ‘anticipated’ nutrient expenditure, which is harmful if not used. Such cases might explain why humans (I.A.R.C. 2002), and some animals kept under captivity (e.g. Schwitzer & Kaumanns 2001), fail to downregulate intake in response to lowered exercise levels: it is not that there is a failure to regulate intake, but the regulatory system has evolved to anticipate a present or future level of energy expenditure, which if not used is deposited as fat, with associated fitness costs.

A more extreme but related scenario would be that in which a change in environment results in the loss of the ability to regulate nutrient intake at all, by distorting or circumventing the operation of regulatory mechanisms. An example of this would be the recently hypothesized positive feedback driving obesity in modern humans, in which the tendency to overeat fat and carbohydrate caused by the extremely high nutrient density and palatability of modern processed foods, relative to our ancestral diet, interacts with the powerful leverage over intake exerted by the mechanisms regulating protein intake (Simpson et al. 2003). In this context, note that the only way we could cause our caterpillars to ‘go over the top’ was to provide them with extremely nutrient-dense foods, and only then for carbohydrate.

Description versus Prediction

It is apparent that our approach relies on providing a detailed description of the shape of the fitness landscape (or at least measures of performance variables that serve as fitness surrogates), before predicting optimal behaviour, or, in reverse, a detailed description of nutritional regulation is needed to predict the shape of the fitness landscape. We would argue that, in the first instance, this is necessary if the aim of the modelling exercise is to explain behaviour as well as to predict it. (Here we fully concur with Illius et al.’s (2002, page 468) view that ‘The heuristic value of models lies not in their ability to make accurate predictions, but in their ability to make predictions for the right reasons.’) Studies over recent years have shown that the position of the intake target and the extent to which animals will overeat nutrients in excess against others in deficit (‘rules of compromise’ as defined by Raubenheimer & Simpson 1993) cannot yet be predicted a priori. That said, ecological and life history correlates have begun to emerge from comparative analysis of these variables for different species and phenotypes (Simpson & Raubenheimer 1993; Simpson et al. 2001; Raubenheimer & Simpson 2003). Once such more general patterns have been established, it will become possible to construct predictive models on the basis of less complete information.

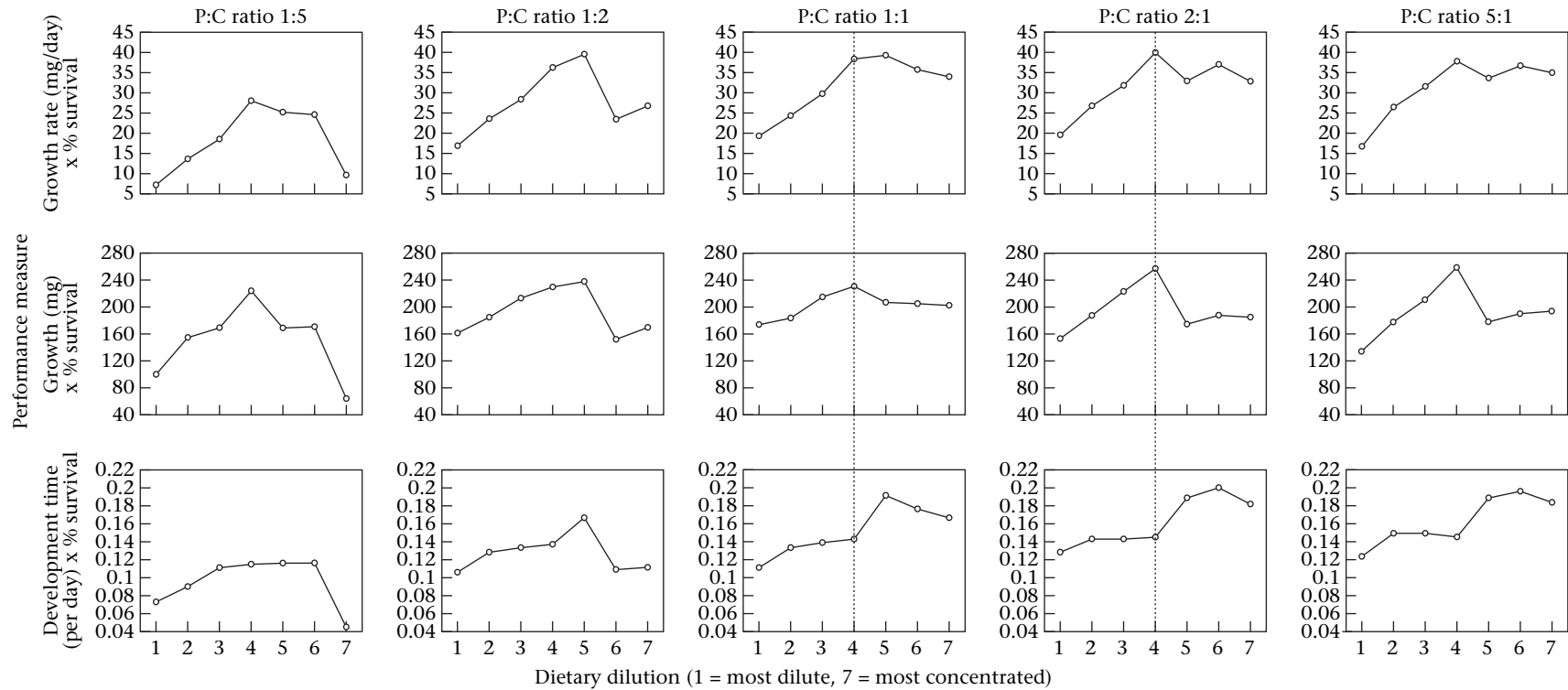


Figure 6. Plots in which the performance index from Fig. 5a (growth rate \times % survival) is broken down into growth \times % survival and the reciprocal of development time \times % survival. Data are means for the 35 treatment groups in which caterpillars were restricted to a diet of fixed P:C ratio and nutrient density. Caterpillars were allowed to self-select among complementary foods. The point to which they regulated their nutrient intake is indicated with dotted vertical lines (i.e. a ratio of 1.2:1 and a dilution value of 4 (42% protein + carbohydrate)).

Time and Toxins

As presented, our models do not deal explicitly with time costs. That time costs shape patterns of foraging, ingestion, postingestive processing, growth and development is likely to be true (Illius et al. 2002), although it need not be, nor can the form of the cost functions be predicted in advance (e.g. time minimization, rate maximization, etc.); rather, it is an empirical question (e.g. Herbers 1981). At least under laboratory conditions, animals such as our herbivorous insects readily pay substantial time costs to regulate nutrient intake, for example locusts eat five times more of a fivefold diluted diet (Raubenheimer & Simpson 1993), although work on other animals has shown that under natural conditions foraging patterns are influenced by level of predation risk (Lima 1998).

By using growth rate in our performance index in Fig. 5a, we have implicitly assumed costs for development time. One way of exploring these costs is to consider growth and development time separately. This is done for the caterpillar experiment in Fig. 6, where it can be seen that for low P:C ratios (1:5 and 1:2) growth and the reciprocal of stadium duration were closely correlated, such that diets sustaining high growth also produced short development times. However, at higher P:C ratios, the two variables became uncoupled. Growth was highest very close to the regulated intake point, whereas development time continued to fall as diets were made more protein biased. Except for a possible indirect effect of development time on survival, this indicates that caterpillars regulated their protein and carbohydrate intake to maximize growth, irrespective of development time.

The other temporal aspect that we have not addressed here is changes over time in the position of the intake target. We have presented the intake target as a point, integrated over a particular period during an animal's life. In reality, the intake target moves, tracking a trajectory over physiological, developmental, seasonal and evolutionary timescales (Simpson & Raubenheimer 1993; Raubenheimer & Simpson 1999). As the target shifts, so too will the fitness landscape. A recent advance in formalizing changing cost-benefit functions of food intake over an animal's life history is the model of Yearsley et al. (2002), and integration of our approach with theirs seems to offer considerable potential.

Another cost of feeding that we have omitted from the present analyses, but which is readily incorporated, is the deleterious effect of toxins, such as plant secondary metabolites (Simpson & Raubenheimer 2001b; Behmer et al. 2002).

From Individuals to Ecological Niches

Lastly, fitness landscapes can also be interpreted in terms of ecological niches. Fitness is often measured by population growth rate (pgr); thus fitness landscapes can be viewed as pgr landscapes. Following Birch (1953), Maguire (1973), Hutchinson (1978) and Tilman (1982), Caughley et al. (1988), Sibly & Hone (2002) and Sibly et al. (2003) have argued that populations persist where

$pgr \geq 0$, thus the $pgr = 0$ contour in nutrient space defines aspects of the organism's ecological niche. Our hope is that laboratory measurements of ecological niches can be used to provide the basis for predictions about the habitats in which organisms will be found in the field.

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References

- Abisgold, J. D., Simpson, S. J. & Douglas, A. E. 1994. Nutrient regulation in the pea aphid *Acyrtosiphon pisum*: application of a novel geometric framework to sugar and amino acid consumption. *Physiological Entomology*, **19**, 95–102.
- Behmer, S. T., Raubenheimer, D. & Simpson, S. J. 2001. Frequency-dependent food selection in locusts: a geometric analysis of the role of nutrient balancing. *Animal Behaviour*, **61**, 995–1005.
- Behmer, S. T., Simpson, S. J. & Raubenheimer, D. 2002. Herbivore foraging in chemically heterogeneous environments: nutrients and secondary metabolites. *Ecology*, **83**, 2489–2501.
- Behmer, S. T., Cox, E., Raubenheimer, D. & Simpson, S. J. 2003. Food distance and its effect on nutrient balancing in a mobile insect herbivore. *Animal Behaviour*, **66**, 665–675.
- Belovsky, G. E. 1981. Food selection by a generalist herbivore: the moose. *Ecology*, **62**, 1020–1030.
- Belovsky, G. E. 1990. How important are nutrient constraints in optimal foraging models or are spatial/temporal factors more important? In: *Behavioural Mechanisms of Food Selection* (Ed. by R. N. Hughes), pp. 255–278. Berlin: Springer-Verlag.
- Bernays, E. A. 1997. Feeding by lepidopteran larvae is dangerous. *Ecological Entomology*, **22**, 121–123.
- Berthoud, H.-R., Seeley, R. J. (Eds). 2000. *Neural and Metabolic Control of Macronutrient Intake*. Boca Raton: CRC Press.
- Birch, L. C. 1953. Experimental background to the study of the distribution and abundance of insects. I. The influence of temperature, moisture and food on the innate capacity for increase of three grain beetles. *Ecology*, **34**, 698–711.
- Bowen, S. H., Lutz, E. V. & Ahlgren, M. O. 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology*, **76**, 899–907.
- Caughley, G., Grice, D., Barker, R. & Brown, R. 1988. The edge of the range. *Journal of Animal Ecology*, **57**, 771–785.
- Chambers, P. G., Simpson, S. J. & Raubenheimer, D. 1995. Behavioural mechanisms of nutrient balancing in *Locusta migratoria* nymphs. *Animal Behaviour*, **50**, 1513–1523.
- Covich, A. 1972. Ecological economics of seed consumption by *Peromyscus*: a graphical model of resource substitution. *Transactions of the Connecticut Academy of Arts and Sciences*, **44**, 71–93.
- Diaz, J. A. 1995. Prey selection by lacertid lizards: a short review. *Herpetological Journal*, **5**, 245–251.
- Hanley, T. A. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). *Oikos*, **79**, 209–218.
- Herbers, J. M. 1981. Time resources and laziness in animals. *Oecologia*, **49**, 252–262.

- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist*, **91**, 385–398.
- Honek, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, **66**, 483–492.
- Houston, A. I. & McNamara, J. 1999. *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.
- Hutchings, M. R., Kyriazakis, I., Papachristou, T. G., Gordon, I. J. & Jackson, F. 2000. The herbivore's dilemma: trade-offs between nutrition and parasitism in foraging decisions. *Oecologia*, **124**, 242–251.
- Hutchinson, G. E. 1978. *An Introduction to Population Ecology*. New Haven: Yale University Press.
- Illius, A. W., Tolkamp, B. J. & Yearsley, J. 2002. The evolution of the control of food intake. *Proceedings of the Nutrition Society*, **61**, 465–472.
- I.A.R.C. (International Agency for Research on Cancer, WHO). 2002. *Weight Control and Physical Activity Handbook, Vol. 6*. Lyon: IARC Press.
- Kyriazakis, I., Emmans, G. C. & Whittemore, C. T. 1991. The ability of pigs to control their protein intake when fed three different ways. *Physiology and Behavior*, **50**, 1197–1203.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, **27**, 215–290.
- Maguire, B. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. *American Naturalist*, **107**, 213–246.
- Monod, J. 1950. La technique de culture continue; theorie et applications. *Annales Institute Pasteur*, **79**, 390–410.
- Pulliam, R. H. 1975. Diet optimisation with nutrient constraints. *American Naturalist*, **109**, 765–768.
- Rappaport, D. J. 1970. Optimal foraging for complementary resources. *American Naturalist*, **116**, 324–346.
- Raubenheimer, D. & Simpson, S. J. 1993. The geometry of compensatory feeding in the locust. *Animal Behaviour*, **45**, 953–964.
- Raubenheimer, D. & Simpson, S. J. 1997. Integrative models of nutrient balancing: application to insects and vertebrates. *Nutrition Research Reviews*, **10**, 151–179.
- Raubenheimer, D. & Simpson, S. J. 1999. Integrating nutrition: a geometrical approach. *Entomologia Experimentalis et Applicata*, **91**, 67–82.
- Raubenheimer, D. & Simpson, S. J. 2003. Nutrient balancing in grasshoppers: behavioural and physiological correlates of diet breadth. *Journal of Experimental Biology*, **206**, 1669–1681.
- Raubenheimer, D. & Tucker, D. 1997. Pairing of visual cues with the separate consumption of protein and carbohydrate. *Animal Behaviour*, **54**, 1449–1459.
- Ricklefs, R. E. & Miller, G. L. 1999. *Ecology*. 4th edn. New York: W. H. Freeman.
- Schmitz, O. J., Cohon, J. L., Rothley, K. D. & Beckerman, A. P. 1998. Reconciling variability and optimal behaviour using multiple criteria in optimization models. *Evolutionary Ecology*, **12**, 73–94.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics*, **2**, 369–404.
- Schwitzer, C. & Kaumanns, W. 2001. Body weights of ruffed lemurs (*Varecia variegata*) in European zoos with reference to the problem of obesity. *Zoo Biology*, **20**, 261–269.
- Shariatmadari, F. & Forbes, J. M. 1993. Growth and food intake responses to diets of different protein contents and a choice between diets containing two concentrations of protein in broiler and layer strains of chicken. *British Poultry Science*, **34**, 959–970.
- Sibly, R. M. & Hone, J. 2002. Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 1153–1170.
- Sibly, R. M., Hone, J., Clutton-Brock, T. (Eds). 2003. *Wildlife Population Growth Rates*. Cambridge: Cambridge University Press.
- Simpson, S. J. 1995. The control of meals in chewing insects. In: *Regulatory Mechanisms in Insect Feeding* (Ed. by R. F. Chapman & J. de Boer), pp. 137–156. New York: Chapman & Hall.
- Simpson, S. J. & Raubenheimer, D. 1993. A multi-level analysis of feeding behaviour: the geometry of nutritional decisions. *Philosophical Transactions of the Royal Society of London, Series B*, **342**, 381–402.
- Simpson, S. J. & Raubenheimer, D. 1996. Feeding behaviour, sensory physiology and nutrient feedbacks: a unifying model. *Entomologia Experimentalis et Applicata*, **80**, 55–64.
- Simpson, S. J. & Raubenheimer, D. 2000. The hungry locust. *Advances in the Study of Behavior*, **29**, 1–44.
- Simpson, S. J. & Raubenheimer, D. 2001a. A framework for the study of macronutrient intake in fish. *Aquaculture Research*, **32**, 421–432.
- Simpson, S. J. & Raubenheimer, D. 2001b. The geometric analysis of nutrient-allelochemical interactions: a case study using locusts. *Ecology*, **82**, 422–439.
- Simpson, S. J. & White, P. R. 1990. Associative learning and locust feeding: evidence for a 'learned hunger' for protein. *Animal Behaviour*, **40**, 506–513.
- Simpson, S. J., Simmonds, M. S. J. & Blaney, W. M. 1988. A comparison of dietary selection behaviour in larval *Locusta migratoria* and *Spodoptera littoralis*. *Physiological Entomology*, **13**, 225–238.
- Simpson, S. J., Raubenheimer, D., Behmer, S. T., Whitworth, A. & Wright, G. A. 2001. A comparison of nutritional regulation in solitary- and gregarious-phase nymphs of the desert locust *Schistocerca gregaria*. *Journal of Experimental Biology*, **205**, 121–129.
- Simpson, S. J., Batley, R. & Raubenheimer, D. 2003. Geometric analysis of macronutrient intake in humans: the power of protein? *Appetite*, **41**, 123–140.
- Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Thompson, S. N. & Redak, R. A. 2000. Interactions of dietary protein and carbohydrate determine blood sugar level and regulate nutrient selection in the insect *Manduca sexta* L. *Biochimica Biophysica Acta*, **1523**, 91–102.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton, New Jersey: Princeton University Press.
- Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton, New Jersey: Princeton University Press.
- Trumper, S. & Simpson, S. J. 1993. Regulation of salt intake by nymphs of *Locusta migratoria*. *Journal of Insect Physiology*, **39**, 857–864.
- Vincent, T. L. S., Scheel, D., Brown, J. S. & Vincent, T. L. 1996. Trade-offs and coexistence in consumer-resource models: it all depends on what and where you eat. *American Naturalist*, **148**, 1038–1058.
- Whelan, C. J., Brown, J. S., Schmidt, K. A., Steele, B. B. & Wilson, M. F. 2000. Linking consumer-resource theory and digestive physiology: application to diet shifts. *Evolutionary Ecology Research*, **2**, 911–934.
- Wilkinson, T. L., Minto, L. B. & Douglas, A. E. 2001. Amino acids as respiratory substrates in aphids: an analysis of *Aphis fabae* reared on plants and diets. *Physiological Entomology*, **26**, 225–228.
- Yearsley, J., Hastings, I. M., Gordon, I. J., Kyriazakis, I. & Illius, A. W. 2002. A lifetime perspective on foraging and mortality. *Journal of Theoretical Biology*, **215**, 385–397.