

Stoffolano (1995) has referred to the midgut as the least studied, but largest, endocrine tissue in insects.

2.2.3 Regulation of protein and carbohydrate intake

Waldbauer and Friedman (1991) defined self-selection of optimal diets as a continuous regulation of intake involving frequent shifts between foods. The fact that insects perceive nutritional deficiencies, and alter behaviour to correct them, has been clearly illustrated by application of the geometrical approach to protein and carbohydrate intake in *Locusta migratoria*. Many aspects of nutritional regulation in this species stem from interactions between these two macronutrients (Raubenheimer and Simpson 1999). Animals given a balanced diet, or two or more unbalanced but complementary diets, can satisfy their nutrient requirements (arrive at the same point in nutrient space) and achieve similar growth performances (Fig. 2.2). It must be emphasized that the nutritional needs reflected in intake targets are not static. A flight of 2 h duration moves the intake target of adult *L. migratoria* towards increased carbohydrate levels, and targets also vary as requirements change throughout development (Raubenheimer and Simpson 1999).

When fed unbalanced diets and prevented from reaching their intake targets, the grass-feeding species *L. migratoria* is less willing to eat an unwanted nutrient than the polyphagous *Schistocerca gregaria*, perhaps because the latter has a better chance of encountering new host plants of different composition (Raubenheimer and Simpson 1999). Put another way, the amount eaten of the unbalanced food should reflect the probability of encountering an equally and oppositely unbalanced food. This is supported by comparisons of nutritional regulation in solitary and gregarious phases of *S. gregaria* (Simpson *et al.* 2002). Solitary locusts are less mobile and encounter fewer host plants, and so experience less nutritional heterogeneity. Gregarious locusts, not subject to these constraints, ingest more of the excess nutrient in unbalanced foods. Locusts respond rapidly to nutritional deficiencies: compensatory selection for either protein or

carbohydrate was evident after a single deficient meal in *L. migratoria*, but not in another relatively sessile herbivore, *Spodoptera littoralis*, in which the response may take longer to develop (Simpson *et al.* 1990). Interactions between nutrients and allelochemicals in locust feeding are considered below (Section 2.4.3). On a more detailed level, *Phoetaliotes nebrascensis* grasshoppers are able to select individual amino acids from a background mixture of amino acids and sucrose applied to glass fibre discs (Behmer and Joern 1993, 1994). This selection is determined by nutrient requirements: Nymphs but not adults preferred diets high in phenylalanine (needed for cuticle production), while adult females but not males preferred high proline concentrations (probably because of the protein demands of egg production).

When diet selection was investigated in *Blattella germanica* (Blattaria, Blattellidae) using paired foods differing in protein and carbohydrate content, the intake target was biased towards carbohydrate because symbionts contributed to nitrogen balance, and cellulose digestion compensated for inadequate levels of soluble carbohydrate in diluted diets (Jones and Raubenheimer 2001). Kells *et al.* (1999) investigated the nutritional status of the same cockroach species in the 'field' (low income apartments). In spite of the reputation of cockroaches as successful generalists, the apartment diet was considered suboptimal (low in protein) compared to rodent chow because the uric acid content of field cockroaches was much lower. Stored uric acid is utilized by symbiont bacteria (see Section 2.4.2).

Nutritional homeostasis involves not only long-term regulation of feeding, but also of post-ingestive utilization. The geometric approach draws attention to the fact that regulating intake of one nutrient often involves ingesting, and then removing, excesses of another. There is so far little evidence in insects for pre-absorptive removal of excess nutrients by the most likely mechanisms of increasing gut emptying rate, decreasing enzyme secretion, or reducing absorption rates (for references see Simpson *et al.* 1995). Instead, the major site of differential regulation appears to be post-absorptive. Nymphs of *L. migratoria* feeding on unbalanced foods remove excess nitrogen by increased uric acid excretion (Fig. 2.3b) and excess

carbon by increased respiration. Excesses are removed chemically in either the midgut or the hindgut, so that the partially assimilated nutrients are not lost. Ingested nutrients are converted into oligosaccharides and honeydew.

2.3 Digestion of nutrients

Some digestive enzymes are secreted into the salivary gland and enter the gut anteriorly. Others are secreted into the midgut. Biochemical processes occur in the midgut. Occasionally, like the aphid, the midgut (Hemiptera) is involved in wishing to bats, Helicoverpa brought together transport, energy from all nutrients (Fig. 2.1). In the midgut, is fundamental to understanding

The midgut of an insect and its role in control. Insect midgut bacterium *E. coli* against certain diptera, Coleoptera, and crops expressed. The midgut proteases, is the columnar conformation of the brane in agrocytotoxic osmotic lysis (Pietrantoni) swelling in the target insect to the toxin (Escriche *et al.*) are most aff