consumption based on fresh weight as well as dry weight, otherwise compensatory feeding (see below) may not be evident when the foods differ in water content. Errors resulting from inaccurate measurement of food water content (especially leaves) are common and potentially serious.

Dry mass measurements (most of the data) can be converted for calculation of energy or nitrogen budgets (Wightman and Rogers 1978). ECI and ECD of a phytophage will be higher when expressed in terms of energy content than when expressed in dry mass because insect tissue has a higher energy content than plant tissue (Waldbauer 1968).

2.1.3 Use of a geometric framework

Ratio analyses in ecophysiology are problematic (Packard and Boardman 1988; Raubenheimer 1995; Beaupre 1995), and statistical problems can be avoided by direct analysis of measured variables. This approach has been convincingly advocated over the past decade by Simpson and Raubenheimer (Simpson and Raubenheimer 1993*a*; Simpson *et al.* 1995; Raubenheimer and Simpson 1999) for nutritional analysis in insects at both ingestive and post-ingestive levels. Their geometric approach has been valuable for demonstrating how animals eating unbalanced or suboptimal foods compromise between intakes of different nutrients, and is briefly explained here.

The concept of an 'intake target' provides a new way of looking at the regulation of nutrient intake (Simpson and Raubenheimer 1993*a*). Intake targets, which vary with growth or reproduction, are defined as the optimal amount and balance of nutrients that must be ingested for post-ingestive processes to operate at minimal cost to fitness. In the simplest case of two nutrients (such as protein and carbohydrate), with each represented as an axis on a two-dimensional graph, an insect given a single food type consumes a fixed proportion of nutrients so that its intake lies on a line passing through the origin, termed a 'rail' to suggest movement in a fixed direction (Fig. 2.2). The insect will not be able to achieve its intake target for the two nutrients if the rail does not pass through the origin. It may have to compromise by eating an

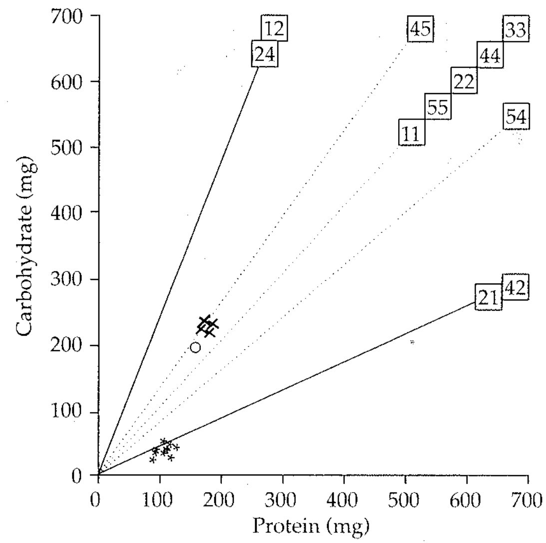

Figure 2.2 Geometric approach to nutrient intake in fifth-instar nymphs of *Locusta migratoria* fed a wide range of artificial diets.

Note: Nutrient consumption is shown as a bivariate plot of protein and carbohydrate consumption. Crosses indicate the intake target reached in experiments with various choices of foods (the circle is a separate estimate of the intake target). Asterisks indicate the growth target reached in no-choice experiments on different diets. Boxes at the end of the rails give the proportions of carbohydrate to protein. The intake target is close to a 1 : 1 ratio.

Source: Simpson and Raubenheimer (1993). *Philosophical Transactions of the Royal Society of London B.* **342**, 381–402, The Royal Society Publications.

excess of one nutrient or insufficient amounts of the other. But if the insect is allowed to choose between two foods containing different nutrient ratios (i.e. defining different rails), it will be able to attain any target lying within the nutrient space between the rails. This can be demonstrated by offering various combinations of paired diets.

Alternatively, nutrient balance can be achieved post-ingestively by removing nutrients which are in excess of metabolic requirements: this enables an insect to move across nutrient space from the intake target to the growth target (Fig. 2.2). This is also important in cases when the unbalanced foods are not complementary and it is impossible to reach the intake target. Post-ingestive aspects of nutrition can be examined by constructing utilization plots of nutrient output versus intake; a change in slope indicates the point above which ingested nutrient is not utilized (Fig. 2.3). Bicoordinate utilization plots