even after correction for phylogeny, allometry, and gut contents (which could dilute the body nitrogen content of herbivorous species). There is also a phylogenetic trend towards decreasing nitrogen content, with the more derived Lepidoptera and Diptera showing significantly lower nitrogen values than the Coleoptera and Hemiptera.

2.1 Method and measurement

2.1.1 Artificial diets

Artificial diets are widely used in nutritional studies. Often they are semi-synthetic and contain crude fractions of natural diets; for example, the widely used diet for rearing *Manduca sexta* (Lepidoptera, Sphingidae) larvae contains wheat germ, yeast, casein, and sucrose, together with salts, vitamins, and preservatives, combined with agar in water (Kingsolver and Woods 1998). For food specialists it may be necessary to include extracts of the host plant in the diet. The advantage of artificial diets is that single nutrients or allelochemicals can be omitted or their concentrations changed, and the effect on performance measured. An essential nutrient can be detected from the effects of its deletion on growth, development, or reproduction, but the determination of nutritional requirements tends to be laborious. Protein and carbohydrate are the major macronutrients, so lipids are generally minimal components of artificial diets, even those for wax moths (Dadd 1985). In compensatory feeding studies, animals may respond differently to diets diluted with water or indigestible agar (Timmins *et al.* 1988).

Artificial diets have certain limitations. They are based on purified proteins, such as the milk protein casein, which are probably easier to digest than plant proteins because they contain little secondary structure and are not protected by cell walls (Woods and Kingsolver 1999). Artificial diets are rich, and caterpillars raised on them have much higher fat contents than those fed on leaves (Ojeda-Avila *et al.* 2003). Laboratory selection experiments using *Drosophila* are influenced by the abundance of food, so that the responses of flies to various forms of selection have tended to involve energy storage rather than energy conservation (Harshman and Hoffman 2000). These diets are also much softer than plant material, and this can lead to a reduction in the size of the head and chewing musculature in caterpillars (Bernays 1986*a*). Experiments using natural forage are ecologically more realistic, but are complicated by the fact that plant tissue is highly variable in chemical composition and levels of nitrogen, water, and allelochemicals tend to covary. Nitrogen and phosphorus also covary in plant tissue (Garten 1976). The use of excised leaves is not recommended in assays of herbivory, because induced plant defences may reduce their nutritional quality (Olckers and Hulley 1994).

2.1.2 Indices of food conversion efficiency

Standard methods have been extensively used for quantifying food consumption, utilization, and growth in insects, especially phytophagous larvae (Waldbauer 1968; Scriber and Slansky 1981). The efficiency of food utilization is assessed using various ratios based on energy budget equations. Waldbauer, in his classic paper, defined three nutritional indices:

Approximate digestibility (or assimilation efficiency) $AD = (I - F)/I$;
Efficiency of conversion of ingested food (or growth efficiency) $ECI = B/I$;
Efficiency of conversion of digested food (or metabolic efficiency) $ECD = B/(I - F)$,

where I = dry mass of food consumed, F = dry mass of faeces produced, and B = dry mass gain of the insect. Performance is expressed in terms of relative (i.e. g per g) rates of consumption (RCR) and growth (RGR). Various interconversions between nutritional indices and performance rates are possible, for example, $RGR = RCR \times AD \times ECD = RCR \times ECI$. An insect may maintain its growth rate over various combinations of these parameters because there are trade-offs between rates and efficiencies, for example, a higher RCR lowers retention time and thus AD. Slansky and Scriber (1985) discussed the methodology and summarized an enormous amount of data on the nutritional performance of insects in different feeding guilds. Slansky (1993) recommended measuring food