similar-sized altricial birds and is achieved without the benefit of endothermy (Reynolds *et al.* 1985). The gut and its contents form 39 per cent of the mass of the caterpillar throughout the feeding period of the fifth instar. The transformation of leaf protein into insect tissue to achieve such rapid growth can be divided into four steps (Woods and Kingsolver 1999): consumption of leaves, digestion of protein into small peptides and amino acids, absorption of amino acids across the midgut epithelium, and construction of tissue. The last three steps are post-ingestive events which influence, and are influenced by, the rate of consumption.

In the continuous flow digestive system of a caterpillar, gut passage rates are equal to rates of consumption. Gut passage rates involve a trade-off between fast processing and thorough processing. Woods and Kingsolver (1999) used a chemical reactor model to predict the concentration profiles of proteins and their breakdown products along the midgut, and found that an intermediate consumption rate gave the highest rate of absorption. Reynolds (1990) reached the same conclusion using a model of optimal digestion (Sibly and Calow 1986): AD is optimized at the optimal retention time, which then determines the rate of consumption. Caterpillars, therefore, restrain food intake to an optimal level which maximizes the rate of nutrient uptake and the rate of growth (Reynolds *et al.* 1985). From measurements of food passage rates, midgut dimensions, proteolytic activity in the lumen (V_{max}), and the protein concentration giving half-maximal rates (K_m), Woods and Kingsolver (1999) predicted that protein is digested rapidly in the anterior midgut but absorption of breakdown products may be a limiting step. However, Reynolds (1990) measured rapid uptake of labelled amino acids in the anterior midgut, which would suggest post-absorptive rather than absorptive constraints on growth. Further studies should emphasize caterpillars eating leaves, because plant proteins differ from those in artificial diets, and undigested protein in leaf fragments will extend further along the midgut (Woods and Kingsolver 1999). Most caterpillars feed by leaf-snipping (their mandibles have cutting but not grinding surfaces) and few of the cells in the ingested tissue are crushed. However, AD values for carbohydrate and protein are surprisingly high, suggesting that nutrients are extracted when the cell walls become porous, and this digestive strategy is apparently as efficient as that of grasshoppers, which crush leaf tissues (Barbehenn 1992).

Evidence for restrained food intake also comes from behavioural observations on temporal patterns of feeding in caterpillars. The combination of meal durations and meal frequencies determines the proportion of time an insect spends feeding. This, combined with the instantaneous feeding rate, gives the overall consumption rate (Slansky 1993). The proportion of time spent feeding by *M. sexta* larvae is up to 80 per cent on tobacco leaves, compared to 25 per cent on artificial diet, the difference being due to relative water contents, although growth rates are identical on both diets (Reynolds *et al.* 1986). Bowdan (1988) examined the microstructure of feeding on tomato leaves using an electrical technique, and showed that larger caterpillars ate more by increasing bite frequency and the length of meals, but meal frequency was unchanged. The periods of inactivity even at high rates of consumption, and the compensatory feeding which occurs when artificial diet is diluted with water or cellulose (Timmins *et al.* 1988), confirm that caterpillars could consume more food than they do.

The feeding rhythms of caterpillars vary greatly because they depend on ecological factors as well as digestive processes. The caterpillar's task is to maximize growth rate while avoiding risk, and the risk from predators and parasitoids can be great. Bernays (1997) quantified the risk during continuous observation of two caterpillar species, and mortality was so high during feeding that there must be strong selection for rapid food intake. Predation will also increase considerably on nutritionally poor plants. Caterpillars undergo spectacular changes in body size with growth, with major effects on feeding ecology, behaviour, and predator assemblages (Reavey 1993; Gaston *et al.* 1997). Minimizing risk can involve changes in feeding habit as individuals grow: as body size increases there is a general trend from concealed feeding (leaf miners or gall formers, which suffer from space constraints) to spinning or rolling