## 2.5 Growth, development, and life history

The amount and quality of food consumed by an insect determines its performance; in the larval stage this is measured as growth rate, development time, body mass, and survival, and in the adult as fecundity, dispersal, and survival (Slansky and Scriber 1985). In the previous section we examined some of the variation in food quality experienced by insect herbivores; now we turn to variation in nutritional needs of insects during growth, development and reproduction. Much of this section concerns trade-offs between competing fitness functions, and these become apparent as a result of developmental plasticity (i.e. environmentally caused variation within a single genotype during development; see also Chapter 5). Insects provide excellent opportunities for experimentation on the nutritional basis of life history trade-offs, so it is not necessary to rely on correlations to show causality.

Nutritional factors are important in explaining the success of holometabolous development. Caterpillars have high protein requirements for rapid tissue growth, but are relatively sedentary, while cockroaches or grasshoppers need more carbohydrate to sustain higher activity levels, but their growth rates are lower (Bernays 1986*b*; Waldbauer and Friedman 1991). Caterpillars have double the consumption rate, double the gut capacity, and ECD values which are 50 per cent higher than do acridids. They also produce and maintain much lighter integuments: The cuticle of acridids is 10 times as heavy, and up to 50 per cent of total dry mass excluding the gut contents (Bernays 1986*b*).

### 2.5.1 Development time versus body size

Three traits central to life history theory are closely interrelated: adult size, development time, and growth rate. It is commonly accepted that there is a trade-off between short development time and large adult size (assuming constant growth rates), but an organism that grows at a high rate can achieve both (Arendt 1997; Nylin and Gotthard 1998). These negative associations between traits are exacerbated by stressful conditions, suggesting competition between different organismal demands for limited resources. Physiological studies aimed at elucidating the mechanistic basis of life history trade-offs were reviewed recently by Zera and Harshman (2001).

Extending development time increases the risk of predation, but so can high growth rates which depend on increased feeding rates. Bernays (1997) clearly demonstrated the risks that caterpillars face from parasitoids and predators when they feed. Examination of feeding behaviour throughout the fourth and fifth instars of *Helicoverpa armigera* caterpillars shows that exponential growth is sustained more by increased ingestion rates than increased time spent feeding, especially during the late fifth instar which is most susceptible to bird predation (Barton Browne and Raubenheimer 2003). The fitness cost of high growth rate in terms of predation risk has been tested experimentally by using photoperiod to manipulate growth rate in the wood butterfly *Pararge aegeria* (Nymphalidae) (Gotthard 2000). Shorter day length induced slower growth, corresponding to late summer conditions when larvae enter diapause in the pupal stage, and this was accompanied by 30 per cent lower mortality due to a generalist predator, *Picromerus bidens* (Heteroptera, Pentatomidae), introduced to the cages. In seasonal environments development time is complicated by diapause, which only occurs in certain stages—this situation favours genotypes capable of plasticity in growth rate (Nylin and Gotthard 1998). Butterflies such as *P. aegeria* can either speed up their development to produce an additional generation before winter, or slow down and enter diapause. Gotthard (2000) distinguishes between the instantaneous mortality risk of the fast-growing caterpillars in his experiment, and their total mortality risk during the larval stage, which might actually be lower because of the shorter development time. Flexible growth strategies have recently been investigated in an alpine beetle, *Oreina elongata* (Chrysomelidae), and late season light conditions led to an increase in growth rate and shorter development time, but no change in prepupal weight (Margraf *et al.* 2003). The authors argue that if 'catch-up growth' occurs in this species, in which a short and unpredictable growing season might be expected to select for rapid growth, then it may be common in temperate insects.