reproduction comes from the supplementary yeast. Divergence in life history characters of O and B flies during selection are discussed by Simmons and Bradley (1997), and the O flies appear to have been selected for the ability to acquire nutrients. Harshman and Hoffman (2000), among others, have drawn attention to possible artefacts with laboratory selection in *Drosophila*, such as strong directional selection, constraints on normal behaviour such as dispersal, and an overabundance of food. The latter tends to favour adaptive responses involving the storage of energy reserves (glycogen and triacylglycerol), which are commonly measured in laboratory selection experiments, rather than conservation of energy by lowering metabolic rate, which might be more evident in the wild. Section 4.5 deals with laboratory evolution and comparative studies in relation to water balance of *Drosophila*.

Developmental trade-offs may not be apparent if larvae are provided with discrete resources (van Noordwijk and de Jong 1986). In mass-provisioning solitary Hymenoptera, adult body size is controlled by maternally provided resources in a protected environment (Klostermeyer *et al*. 1973). An energy budget for reproduction is easily constructed by collecting either intact provisions, or fully grown larvae and their faeces, from sealed brood cells. The pollen–nectar mixture provided by female solitary bees is a high-quality food, and high assimilation efficiencies have been measured in carpenter bees *Xylocopa capitata* (Anthophoridae) (Louw and Nicolson 1983) and leafcutter bees *Megachile pacifica* (Megachilidae) (Wightman and Rogers 1978). Female offspring receive larger provisions than males and are larger than males, and this greater investment has implications for the sex ratio of the offspring, males being cheaper to produce (Bosch and Vicens 2002). These authors verified the use of body size as an estimate of production costs in bees by showing that weight loss of *Osmia cornuta* (Megachilidae) throughout the life cycle did not differ significantly between the sexes, in spite of differences in metabolic rate, water content, cocoon construction, and development time. Male size dimorphism in bees (involving different size classes) is also controlled by female provisioning decisions (Tomkins *et al*. 2001). Similar relationships between provision weight and adult weight apply to solitary wasps, except that larvae are given prey such as paralysed spiders—nicely demonstrated by Marian *et al*. (1982) with energy budgets for a wasp nesting in the holes of electrical sockets. The digger wasp *Ammophila sabulosa* (Sphecidae) provisions cells with caterpillars of varying size, but offspring size is controlled by a flexible provisioning strategy which results in the same total weight of prey in each cell (Field 1992).

2.5.2 Developmental trade-offs between body parts

Metamorphosis allows resources to be redistributed among body compartments. Holometabolous insects are therefore ideal organisms for examining how resources accumulated during larval stages are allocated to reproductive or somatic tissues. Most of the growth of imaginal discs occurs in a closed system after the larva stops feeding. Removal of hind wing imaginal discs from larvae of a butterfly results in disproportionately large forewings, and use of juvenile hormone treatment to reduce horn development in male dung beetles, *Onthophagus taurus* (Scarabaeidae), leads to a compensatory increase in size of the compound eyes, which develop in close proximity to the horn (Nijhout and Emlen 1998). In these examples, competition between body parts is suggested by increased growth of one trait at the expense of growth in another, with no change in overall body size. Horn development is dimorphic in *O. taurus*, occurring only in males above a threshold size. The threshold is lower in populations subsisting on poor quality food (cow manure rather than horse dung) (Moczek 2002). In case-building caddis flies, larval resources can be manipulated by inducing them to build new cases and produce additional silk. Stevens *et al*. (2000) have demonstrated empirically that a short-lived caddis species preserves abdomen size (an index of reproductive allocation) at the expense of the thorax, while a long-lived species preserves thorax size in order to maintain longevity. This flexible trade-off between larval defence and adult body size again implies the partitioning of finite resources between parts of the body.