of food or haemolymph. Recently the control of crop-emptying has been carefully investigated in honeybees (*Apis mellifera carnica*), using unrestrained bees trained to collect defined amounts of sucrose solution (Roces and Blatt 1999; Blatt and Roces 2001, 2002). As in other insect species, crop-emptying rates measured by volume were inversely related to food concentration. Conversion to sugar transport rates showed that sugar left the crop at a constant rate, independent of food concentration but corresponding closely with the metabolic rate of the bees (Fig. 2.8). It is well known that the metabolic rate of honeybees depends on the reward rate at the food source (Moffat and Núñez 1997; see also Chapters 3 and 6). Haemolymph sugar homeostasis was maintained under all conditions except those involving dilute food and a high metabolic rate (induced by cold); haemolymph trehalose concentration then decreased. Crop-emptying is, therefore, adjusted to the energy demands of the bee, mediated by the trehalose concentration of its haemolymph.

We conclude this section on midgut physiology by considering phenotypic flexibility and whether there are reversible changes in gut surface area and absorption capacity depending on demand, as have been demonstrated in vertebrates (Diamond 1991; Weiss *et al.* 1998). Increased gut size helps to compensate for reduced food quality in grasshoppers (Yang and Joern 1994). Larval *M. sexta* reared on low protein diet allocate more tissue to midgut, although they still grow more slowly (Woods 1999). Woods and Chamberlin (1999) measured proline transport in the posterior midgut of *M. sexta* and found no response to dietary history (Fig. 2.9). They used flat sheet preparations bathed by asymmetrical salines designed to resemble *in vivo* conditions, and measured fluxes of ^{14}C-labelled L-proline, which was transported from lumen to haemolymph 15 times faster than in the reverse direction. However, leucine transport in brush border membrane vesicles from the midgut of *B. mori* (Lepidoptera, Bombycidae) is increased in starved larvae (Leonardi *et al.* 2001). In contrast to data from vertebrates (e.g. Weiss *et al.* 1998) showing upregulation of gut function in response to increased substrate levels, the compensatory responses described above in insects suggest possible upregulation of gut function in response to *declining* nutrients (Woods and Chamberlin 1999). Decreased secretion of digestive enzymes after exposure to low substrate concentrations, or decreased absorption of the products of hydrolysis, does not seem an efficient way to maximize the value of low-nutrient diets (Simpson *et al.* 1995). Passive absorption of nutrients provides a mechanism for matching the rate of absorption to the rate of hydrolysis (Pappenheimer 1993), so absorption

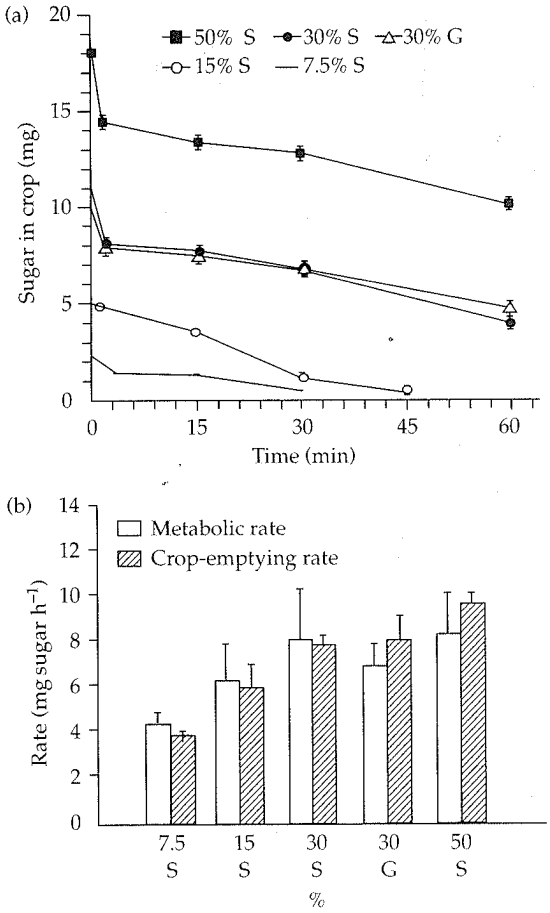

Figure 2.8 Crop-emptying rates and metabolic rates in honeybees collecting sugar solutions of different concentrations. (a) Sugar content of the crop as a function of time in bees which collected 30 µl of each sucrose (S) or glucose (G) concentration (means ± SD). (b) Comparison of crop-emptying and metabolic rates, both expressed as mg sugar h^{-1} (means ± SD). Only the rates for 7.5% sucrose were significantly different from the others.

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