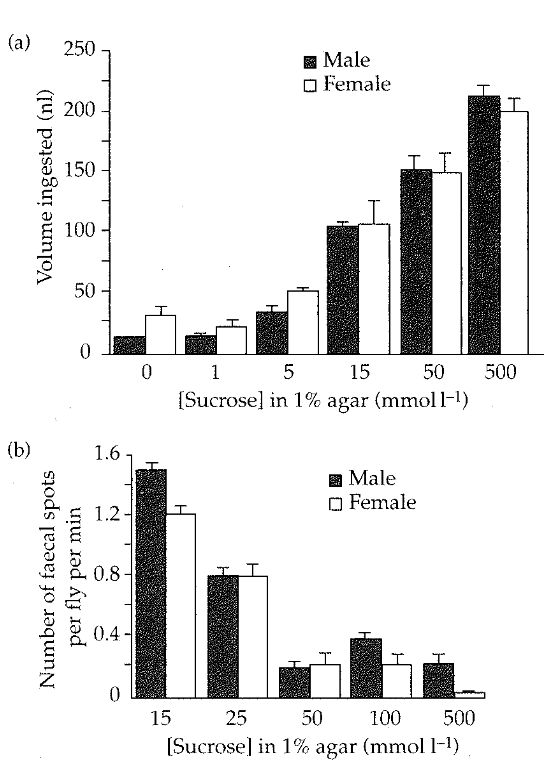

Figure 2.4 Responses of *Drosophila melanogaster* to diet concentration depend on feeding regime. (a) Volume ingested increases with sucrose concentration in flies deprived of food for 24 h and then fed for 5 min. Each column is the mean ± SE from four trials involving 20 flies each. (b) Excretion rate, measured as the number of faecal spots per min, decreases with sucrose concentration in flies fed *ad libitum*. Each column represents the mean ± SE from 5 trials of 50 flies each.

Source: Edgecomb *et al.* (1994).

ingested by insects are positively correlated with concentration in previously starved individuals offered single meals, but insects feeding *ad libitum* show compensatory feeding and the volume imbibed is then negatively correlated with concentration.

Regulation of load size may be more complex in social insects, which begin foraging with empty crops. Recently, Josens *et al.* (1998) investigated nectar feeding in the ant *Camponotus mus* by weighing foragers as they crossed a small bridge between the colony and the foraging arena, then weighing them again on the return trip. Crop load increased with increasing sucrose concentration to a maximum at about 1.5 M, then diminished because of viscosity effects. Workers carried up to 60 per cent of their own weight in the crop, but the loads were partial for either dilute or very concentrated solutions, when motivational state of the ants or physical properties of the solution played a role, respectively.

The central role of haemolymph in nutritional homeostasis was highlighted by Simpson and Raubenheimer (1993*b*). The haemolymph provides a continuous reading of the insects' nutritional and metabolic state: it integrates information on the time since the last meal, its size and quality, as well as current and recent demands by tissues. Feeding may be inhibited by high haemolymph osmolality or, more accurately, by high concentrations of specific nutrients such as amino acids or sugars. This feedback results from both previous and current meals. Haemolymph nutrient concentrations change during the course of a meal, as a result of nutrient absorption and secretion of dilute saliva. Movement of water from haemolymph to gut lumen can also be expected initially, down an osmotic gradient created by hydrolysis of macromolecules. Reynolds and Bellward (1989) showed that midgut water content of *M. sexta* was regulated between 87 and 91 per cent, even when dietary water content was much lower. Injections which increase haemolymph osmolality or amino acid concentration mimicked the effect of a high-protein meal and delayed the next meal in locusts (Abisgold and Simpson 1987). These authors did not find the same effect with high and low carbohydrate diets, probably because the products of carbohydrate digestion are rapidly removed from the haemolymph after absorption.

Hormonal involvement in feeding regulation is also likely. The diffuse endocrine cells of the locust midgut are more dense in the ampullae at the Malpighian tubule–gut junction, where they are perfectly positioned to monitor three key fluids; the midgut luminal contents, tubule fluid, and haemolymph (Zudaire *et al.* 1998). FMRFamide-like peptides are thought to be involved in digestive processes, and FMRFamide-like immunoreactivity of the ampullar endocrine cells was correlated with food quality, increasing as protein/carbohydrate composition of the diet shifted away from optimal.