

leaves, to external feeding in late instars. In bigger caterpillars the surface area of gut for absorption is relatively less in relation to the volume of gut contents. Rates tend to decrease with increasing body size but efficiencies do not (Slansky and Scriber 1985). AD does not vary with size in *M. sexta*, remaining about 60 per cent throughout the fifth instar, but retention time increases. Correction of the body mass component in nutritional indices for the presence of food in the gut reduces their value only slightly (Reynolds *et al.* 1985).

2.2.2 Regulation of meal size: volumetric or nutritional feedback

The physiological regulation of meal size can potentially include sensory stimuli (either positive or negative), volumetric feedback via stretch receptors in the gut or body wall, haemolymph composition (osmolality or the concentration of individual nutrients), available reserves, and neuropeptides, many of which are known to affect contractile activity of the gut (Gäde *et al.* 1997). Unravelling causal relationships is far from simple. For chewing insects, the most detailed information comes from acridids, in which volumetric feedback from stretch receptors in the gut is important in terminating a meal (reviewed by Simpson *et al.* 1995). These receptors are located in both the crop and ileum, those in the latter being stimulated by the remains of the previous meal. It is also likely that rapid changes in haemolymph osmolality and nutrient concentration inhibit further feeding. Locusts fed high-protein diets exhibited much greater increases in haemolymph osmolality and amino acid concentrations during a meal than those on low-protein diets, and the result was a longer interval until the next meal (Abisgold and Simpson 1987). Feeding stops when inhibitory feedbacks force excitation below the feeding threshold, and increasing inhibition during a meal is reflected in declining ingestion rates (Simpson *et al.* 1995). Volumetric feedbacks are less obvious in caterpillars, which lack the capacious crop of acridids, and meal size in *Manduca* may depend on feedback from nutrients in the gut lumen. Injection of soluble diet extract into the midgut lumen inhibited feeding, while an injection of xylose

solution of the same osmolality did not (Timmins and Reynolds 1992).

Carbohydrate feeding is best understood in Diptera, although it is also fundamental to the aerial success of adult Lepidoptera and Hymenoptera, all three orders depending on a variety of liquid carbohydrate resources as immediate energy for flight (Stoffolano 1995). These insects have evolved an expandable and impermeable crop (diverticular in Diptera and Lepidoptera, linear in the Hymenoptera) located in the abdomen. The blowfly *Phormia regina* (Calliphoridae) has been used as an experimental model, and it is clear that information from abdominal stretch receptors ends the meal. Not surprisingly, the regulation of feeding behaviour has also been thoroughly investigated in blood feeders, especially mosquitoes, where nectar meals are directed to the crop and blood meals to the midgut but both kinds of meal are terminated by abdominal distension (reviewed by Davis and Friend 1995).

Meal quality and feeding regime also influence crop filling. The Australian sheep blowfly *Lucilia cuprina* ingests greater volumes of dilute glucose solutions by taking larger and more frequent meals (Simpson *et al.* 1989). Crop volume at the end of a meal was similar in *L. cuprina* ingesting 0.1 and 1.0 M glucose, due to volumetric inhibition. However, the flies maintained on 1.0 M glucose had fuller crops at the beginning of a meal because dilute solutions empty from the crop more rapidly (see Section 2.3.3) and can be ingested in greater quantity. Evaporative losses caused by bubbling behaviour in *Rhagoletis pomonella* (Diptera, Tephritidae) reverse the volumetric inhibition, permitting feeding to continue on dilute solutions (Hendrichs *et al.* 1992). Some confusion in the literature has arisen because researchers have used insects in very different nutritional states. Feeding behaviour varies greatly between insects fed *ad libitum* and those which are deprived of food and then offered single meals, as elegantly demonstrated by Edgecomb *et al.* (1994) for *Drosophila melanogaster* feeding on sucrose-agar diets. Flies fed *ad libitum* maintained much smaller crop volumes than food-deprived flies fed a single meal, and responded differently to sucrose concentrations up to 0.5 M (Fig. 2.4). In general, the volumes of sugar solution

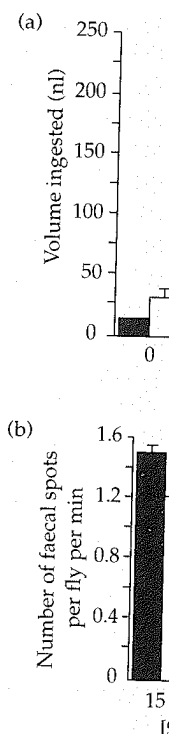


Figure 2.4 Response of flies to sucrose concentration. Flies were starved for 24 h and then fed for 15 min on four trials involving 20 flies per trial. The number of faecal spots per fly per min is the mean \pm SE from 5 trials.

ingested by insects increases with sucrose concentration in single meals. Flies offered single meals show compensatory increases in the number of faecal spots imbibed is the concentration.

Regulation of meal size in social insects, with the exception of honeybees, is not well understood. In honeybees, crop size is regulated by the amount of food ingested. Recently, it was shown that nectar feeding in honeybees involves weighing foragers before and after feeding between the colonies, weighing them again after feeding, and increased with the