

Classic examples of the trade-off between body size and development time are seen in male butterflies which emerge first (protandry) and are consequently smaller than females (Lederhouse *et al.* 1982). However, the assumption that both sexes are growing at the same rate is not always true. Males of *Pieris napi* which develop directly instead of entering diapause are under severe time constraints and respond to selection for large size and protandry by increasing their growth rate (Wiklund *et al.* 1991).

Prolonged development can be viewed as a means of increasing food consumption on sub-optimal foods (Slansky 1993). If *M. sexta* are exposed to low dietary protein levels as early instars, low growth rates persist in the fifth instar even after transfer to a better diet (Woods 1999). Fig. 2.14 demonstrates how supernumerary moults by larvae of the African armyworm *Spodoptera exempta* (Noctuidae) enable them to reach the same final size when they are reared on poor quality grasses (Yarro 1985). Some female insects undergo an additional larval instar in order to store more nutrients for oogenesis (e.g. Stockoff 1993). The seed beetle *Stator limbatus* (Bruchidae) varies by an order of magnitude in adult body size, due to resource competition between multiple larvae in a single seed, but egg sizes do not differ much and a longer

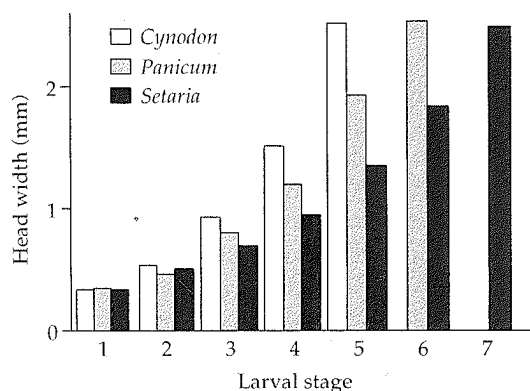


Figure 2.14 Effects of food quality on size and number of larval instars in *Spodoptera exempta* (Noctuidae). Super-numerary moults are used to achieve final body size (measured as head width) in larvae feeding on two nutritionally poor grasses, *Panicum* and *Setaria*. Source: Data from Yarro (1985).

development time allows the initially smaller progeny of small females to pupate at the same size as those of large females (Fox 1997). This can be considered another example of 'catch-up growth'.

Laboratory selection experiments using *Drosophila* have been a powerful research tool for demonstrating life history trade-offs, such as that between extended longevity and early female reproduction. In laboratory-reared *D. melanogaster*, increased food quality or quantity is correlated with an increase in reproduction and decrease in longevity and starvation resistance. This suggests that the trade-off between reproduction and survival can be manipulated by diet. Simmons and Bradley (1997) used supplementary live yeast to explore the quantitative basis of this trade-off in long-lived (O) and control (B) populations of *D. melanogaster*. Diet enrichment caused both O and B females to produce more eggs, and both lines showed reduction in energy stores. However, the trade-off is not quantitative (Fig. 2.15): Decreasing somatic storage does not account for increasing egg production, and most of the additional energy allocated to

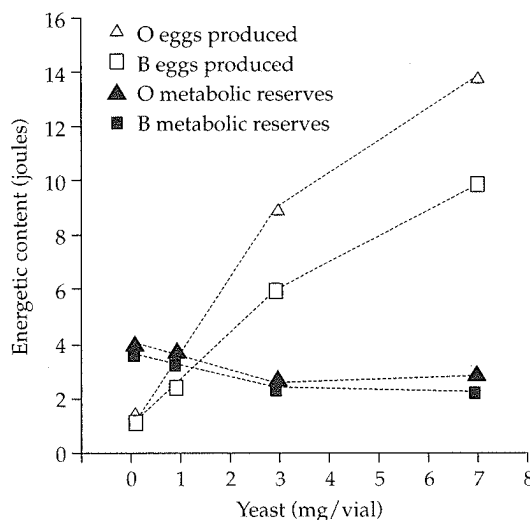


Figure 2.15 Changes in reproductive and somatic energy (joules) in female *Drosophila melanogaster* in response to supplementary yeast in the diet. Energy content was calculated for the eggs produced and the lipid and carbohydrate reserves in long-lived (O) and control (B) populations.

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