females normally show increased fecundity, and histolysis of flight muscles coincides with ovarian growth in long-winged female crickets. These correlations have been interpreted as demonstrating a fitness trade-off between flight ability and reproduction, but are not sufficient to prove a causal relationship. However, recent nutritional studies provide unequivocal evidence for this fitness trade-off. Gravimetric feeding trials on *Gryllus* species have demonstrated that ovarian growth in flightless morphs (either natural or hormonally engineered) may be due either to increased food consumption or to relative allocation of the same quantity of absorbed nutrients, depending on the species. Only the latter situation represents a trade-off (Zera and Harshman 2001). Thus, reduced nutrient input can magnify a trade-off, whereas an increase in nutrients can eliminate it. This has been emphasized by measuring nutritional indices for three morphs of *G. firmus* (long-winged, short-winged, and flightless morphs with histolysed flight muscles). Values of ECD were significantly elevated in both types of flightless morph: compared to the flight-capable morph, flightless morphs converted a greater proportion of absorbed nutrients into body mass, mainly ovarian mass, and allocated a smaller proportion to respiration. Low-nutrient diets increased the discrepancy in ECD values, indicating that the trade-off between respiration and early reproduction was magnified (Zera and Brink 2000). Lipid accumulation in the first few days of adult life results in triglyceride reserves which are 30–40 per cent greater in the flight-capable morphs of *G. firmus*, and the magnitude of this difference suggests that limited space in the abdomen could also be a factor in the trade-off between lipid accumulation and ovarian growth (Zera and Larsen 2001). Newly emerged male and female dragonflies, *Plathemis lydia* (Libellulidae), are similar in mass and the mass of individual body parts, but the abdomens of females then increase fivefold in mass owing to ovarian development, and the thoraxes of males increase 2.5-fold in mass as a result of flight muscle growth (Marden 1989). Such a high investment in the thorax carries a cost in that gut mass and body fat content are minimal in territorial male dragonflies.

The widespread occurrence of flightlessness and wing polymorphism in insects suggests that flight carries substantial fitness costs in the construction, maintenance, or operation of wings and flight muscles. This is borne out by differences in respiration rate between the pink flight muscle of fully winged *G. firmus* and the white muscle of the short-winged adults or of long-winged adults after flight muscle histolysis (Zera *et al.* 1997). The flying insects surveyed by Reinhold (1999) had resting metabolic rates which were about three times those of non-flying insects. Wing polymorphism is a type of dispersal polymorphism, and Roff (1990), in reviewing the ecology and evolution of flightlessness in insects, concluded that secondary loss of wings is more frequent among females because of the trade-off with fecundity and is most likely in stable environments. Males remain mobile to find mates, and habitat fragmentation may select for rapid evolutionary change in flight-related morphology in both sexes, seen in an increased investment in the thorax as habitat area declines (Thomas *et al.* 1998).

2.6 Temperature and growth

2.6.1 Thermal effects on feeding and growth

In ectotherms, higher temperatures increase growth rates and decrease development times, and generally result in smaller adult body sizes (Atkinson 1994; Atkinson and Sibly 1997). In *Drosophila*, small body size resulting from development at high temperatures is due mainly to decreases in cell size (Partridge *et al.* 1994), although changes in cell number can also be involved (reviewed in Chown and Gaston 1999). The selective advantage of smaller size at higher temperatures, or larger size at lower temperatures, has long been considered obscure (Berrigan and Charnov 1994). Indeed, several authors have considered larger size at low temperatures an epiphenomenon of differences in the responses of growth and of differentiation to temperature, and therefore not adaptive at all (Chapter 7). Likewise, Frazier *et al.* (2001) have recently demonstrated interactive effects of hypoxia and high temperature on the development of *D. melanogaster*, and a

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