of foraging activity, alternating with digestive phases when they rest in or on their tent, and these activity patterns can be electronically recorded under field conditions (Fitzgerald et al. 1988; Ruf and Fiedler 2002). The duration of both foraging bouts and digestive phases is inversely related to temperature in Eriogaster lanestris, which has an opportunistic feeding pattern in relation to thermal conditions. In contrast, another lasiocampid, the eastern tent caterpillar M. americanum, forages only three times a day, possibly because predation risk may outweigh the need for feeding efficiency. The effects of temperature on caterpillar foraging and growth are reviewed by Casey (1993) and Stamp (1993), but generalizations are difficult because such effects are intimately connected with the natural history of a species (which includes constraints due to predators and parasites).

The majority of caterpillar species are solitary, palatable, and cryptic and do not have the option of thermoregulation. Kingsolver (2000) measured peak consumption and growth rates around 35°C in fourth instar Pieris brassicae in the laboratory, and integrated these with the operative temperatures of physical models placed under leaves in a collard garden to demonstrate that infrequent high temperatures can make disproportionate contributions to caterpillar growth—because growth rates are so much faster at higher temperatures. In M. sexta, another thermoconformer (Casey 1976a), short-term consumption and growth rates show similar shallow thermal response curves, with  $Q_{10}$  values less than 2.0 for temperatures up to 34°C (Kingsolver and Woods 1997). When the thermal sensitivity of growth and its component processes in M. sexta was compared by measuring growth rate, consumption rate, protein digestion, methionine uptake, and respiration rate over the range 14-42°C, the thermal performance curve for growth rate was most similar to that for consumption rate, and declining growth above 38°C could not be ascribed to decreased digestion or absorption rates or increased respiration rates (Fig. 2.17). Reynolds and Nottingham (1985) similarly found that nutritional indices in M. sexta were unaffected by temperature, although chronic exposure resulted in smaller size at high temperatures.

## 2.6.2 Interactions with food quality

Caterpillars of M. sexta have again been used as a model system in examining nutritional interactions between temperature and dietary protein levels. Although low temperatures reduce rates of consumption and growth, low protein levels lead to increased consumption rates through compensatory feeding but may not affect growth rates. In short-term experiments (4 h), fifth-instar larvae of M. sexta failed to compensate for low protein levels at the most extreme temperatures of 14 and 42°C, but long-term experiments (duration of the fifth stadium) over a narrower temperature range showed little evidence of interactions between temperature and dietary protein (Kingsolver and Woods 1998). These authors suggest that compensatory feeding responses may be less effective in diurnally fluctuating temperatures than in the constant temperatures in which they are commonly examined. This study was extended by examining interactive effects on instars 1-3, 4, and 5 separately, and there were some striking differences between instars (Petersen et al. 2000). Mean growth rate was highest at 34°C during the first three instars but highest at 26°C during the fifth instar (the latter is the temperature at which laboratory colonies of M. sexta are maintained). Fifth instar caterpillars were surprisingly sensitive to high temperatures, which is significant in view of the fact that most studies of caterpillar nutritional ecology use this instar (Petersen et al. 2000). The gypsy moth is a spring-feeding forest insect which develops during a period of declining leaf nitrogen and increasing ambient temperatures. Lindroth et al. (1997) found interactive effects of temperature and dietary nitrogen on several performance parameters measured through the fourth instar, but there were no interactions over the larval period as a whole. The combination of poor quality food and low temperature can result in exceptionally slow growth and long life cycles, as in the Arctic caterpillar Gynaephora groenlandica (Lymantriidae) which has a development time of 7 years in spite of well developed basking behaviour (Kukal and Dawson 1989).

Temperature's effects become even more complex when allelochemicals or other trophic levels are

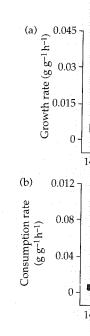


Figure 2.17 The theover the temperature (d) methionine absort Note: Growth and Consumer Source: Physiologica 7006-96117\$03.00.

involved. Stan caterpillars (M. between tempe phenolic, rutin. the most impordilution and rufunction of termoulting at low included in the control of the food quality, and caterpillars (M. Standard).