

# Temperature, food quality and life history traits of herbivorous insects

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Population dynamics of herbivorous insects are strongly influenced by temperature and host plant quality; an interaction generally thought to be mediated via effects of temperature on metabolic rate and altered energy requirements. However, recent research suggests the relationship between nutrition, temperature, host plant quality and life history traits that influence insect fitness are more complex than appreciated to date. In the laboratory, rates of development are most strongly influenced by temperature, while growth, body composition, and reproductive output are greatly affected by nutrition, notably the uptake of protein and carbohydrate. However, individual outcomes and consequently population responses in the field are not readily predicted from data on ambient temperatures and host plant chemical composition. The relative amounts of protein and carbohydrate gained from a host plant depends on complex interactions between plant cell structure and leaf chemistry, combined with plasticity in feeding behaviour, microclimate selection, digestive and assimilative physiology. For example, grasshoppers can exploit the temperature dependence of host plant quality to maintain nutritional homeostasis. Consequently, understanding environmental interactions such as leaf defences and patterns of foraging, and predicting the effects of climate change on insect populations, will be complex.

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**Current Opinion in Insect Science** 2015, **11**:63–70

This review comes from a themed issue on **Global change biology**

Edited by **Steven L Chown**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 10th November 2015

<http://dx.doi.org/10.1016/j.cois.2015.10.011>

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Herbivorous insect population dynamics are strongly affected by climate, principally through the consequences to food plant quality and temperature on physiological processes which influence the time taken to reach maturity (development rate), adult size and reproductive output. Fitness responses and associated life history traits vary with temperature and nutrition, reflecting both

short-term plastic responses and longer-term adaptation [1,2]. Historically temperature and nutrition have been thought to be linked via an animal's metabolic rate and the consequent effect on energy requirements; that is with increasing temperature relatively more energy is required to fuel growth and development [3–5]. However, substantial research has demonstrated that macronutrient *balance* (especially protein ( $P_{rot}$ ) and carbohydrate ( $C_{arb}$ )), rather than energy *per se*, strongly influences lifetime performance (growth, rates of development, survival and reproduction) of chewing herbivorous insects [2,6,7,8–10] (Figure 1).

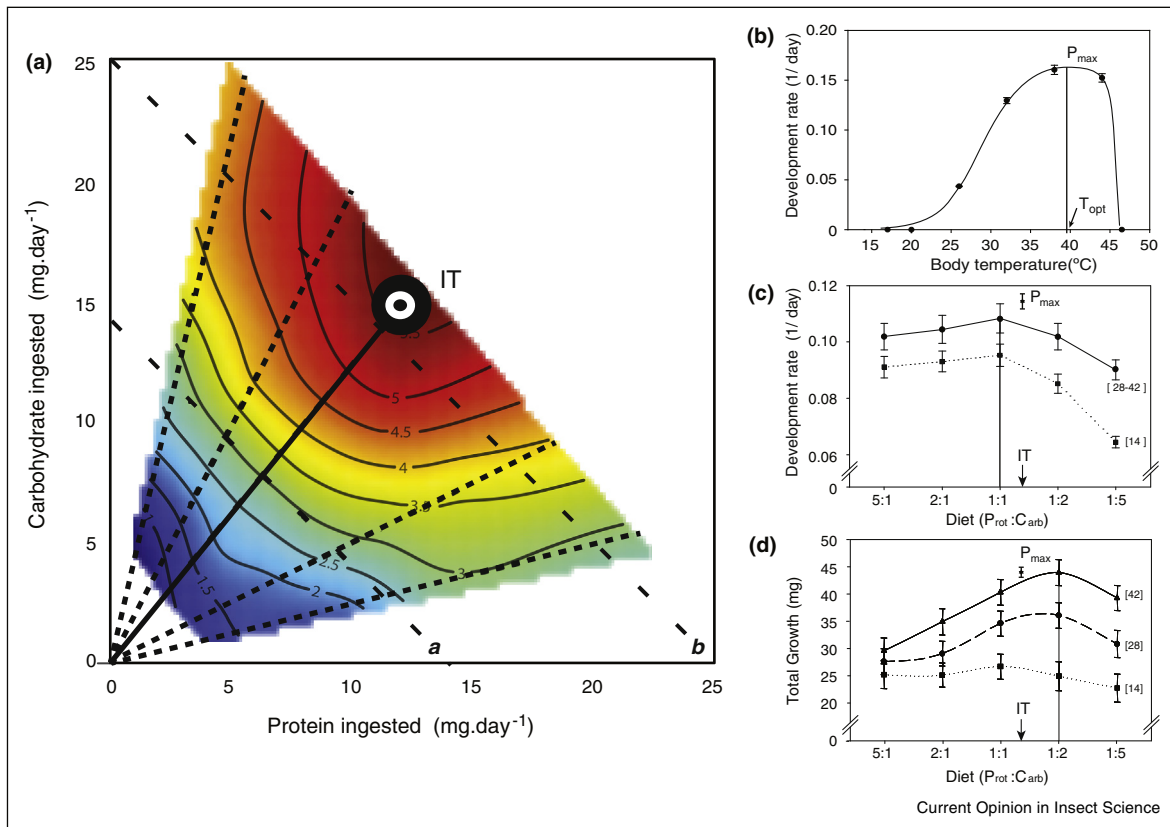
Temperature in turn interacts with macronutrient balance, as has been demonstrated in laboratory studies on lepidopterans and orthopterans [3,11,12]. However, despite being able to measure the interactions between temperature and nutrition in the laboratory, this information cannot be translated directly to outcomes in the field. For example, host plant quality varies with temperature (e.g. [13,14,15,16]) and the environment can be extremely thermally heterogeneous for small animals [17,18]. Because insects are able to adjust both body temperatures by selecting microclimates and their intake and utilization of nutrients by using feeding behaviour and post-ingestive physiology, they have considerable capacity to buffer against the effects of variable environments. This in turn makes interpreting preferences for temperature or host plants from low resolution field-based correlations difficult, to say the least.

In the following perspective we elaborate upon some of these key issues. First we look at what has been learnt from laboratory experiments on lepidopterans and orthopterans regarding the life history consequences of temperature and nutrition from the use of synthetic diets, and then show how temperature affects the digestion of plant leaves. Next we demonstrate how this laboratory-gained knowledge translates to a field situation. Then, finally, we briefly discuss how an understanding of how insects 'work' might impact ecological research, and highlight where research is needed.

## The interactive influence of temperature and nutrients on rates of development and growth in the laboratory

The thermal reaction norms for development are very similar for all insects, with development rates increasing exponentially to a maximum, plateauing, then

Figure 1



**(a)** Australian plague locust (*Chortoicetes terminifera*) performance over the 5th instar at 32 °C. The average daily rate of protein and carbohydrate ingestion over the entire 5th stadium have been plotted against growth rate × survival (data from [55]). The response surface has been visualized by fitting nonparametric thin-plate splines using the `FIELDS` package in R (version 4.3.0.2) [9]. The symbol labelled 'IT' is the intake target, which is the ratio and rate protein and carbohydrate ingested when able to self-compose ingesta. The two dashed lines labelled (a) and (b) represent isocaloric intakes. Between the origin and line (a) performance will be improved most by increasing the rate of nutrient intake regardless of ratio (as indicated by the contours being almost parallel with line (a); whereas if nutrient intake rate is maximized, performance is improved by the ratio of C<sub>arb</sub> to P<sub>rot</sub> ingested, as illustrated by the contour lines crossing line (b) and running in the direction of the different C<sub>arb</sub> to P<sub>rot</sub> ratios (dotted lines). When feeding from synthetic diets, protein and carbohydrate ingestion equals that absorbed across the gut wall [3]. Differences in nutrient (C<sub>arb</sub> and P<sub>rot</sub>) intake were generated by diluting food with indigestible cellulose so that the nymphs were unable to increase intake sufficiently (compensatory feeding) to maintain nutrient intake. Performance curves for development rate given **(b)** body temperature, **(c)** diet 'quality', and growth given **(d)** diet 'quality' for the Australian plague locust. The performance curves (c and d) show the effects of both P<sub>rot</sub>:C<sub>arb</sub> ratio and concentration. Australian plague locusts at a constant 32 °C were confined to one of 15 diets over the final nymphal stadium. Five different P<sub>rot</sub>:C<sub>arb</sub> ratios at three different concentrations (or densities) were used; for example the 1:1 diets consisted of 7% P<sub>rot</sub> with 7% C<sub>arb</sub> (7P:7C) and 14P:14C and 21P:21C (*sensu* [8]) (data from [56]). Rates of development and growth are optimized at different P<sub>rot</sub>:C<sub>arb</sub> (P<sub>max</sub>) and when allowed to self-compose their protein and carbohydrate intake to achieve the intake target, nymphs select a ratio that is a compromise between these two different optimas (arrow) [labelled, P<sub>max</sub> (★)]. Similarly shaped performance curves for development and growth with diet are found for the orthopteran, *Locusta migratoria* [21,56] and the lepidopteran, *Spodoptera littoralis* [8,57]. Symbols represent the LSM means (±SE) for 40 locusts with lines linking means for each concentration.

dropping off abruptly (Figure 1b) [4,19,20]. At a single temperature, the rates of juvenile development and growth of both orthopterans and lepidopterans vary in response to the amounts of P<sub>rot</sub> and C<sub>arb</sub> ingested (Figure 1c,d) (e.g. [7<sup>o</sup>,8,21]). Both development rate and growth are retarded when all nutrients are in concentrations that are so low in the food that overall nutrient intake is retarded, and when C<sub>arb</sub> is supplied in excess of P<sub>rot</sub> requirements, development rates are reduced but mass is greatest (Figure 1c,d).

Rates of development increased with temperature for two orthopterans, *Locusta migratoria* and *Melanoplus femurrubrum* [3,22] and a lepidopteran, *Spodoptera exigua* [11]. However, growth responses were study specific. Adult body size (mass and hind femur length) and pupal mass, for *M. femurrubrum* and *S. exigua* respectively, were similar regardless of temperature [11,12]. However, adult *L. migratoria* were the same size and body composition at 38 °C and 32 °C but were smaller (mass and hind femur length) at 26 °C [3].

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