

Physiological mechanism governing slow and fast development in predatory ladybirds

ANTHONY F. G. DIXON^{1,2}, ALOIS HONĚK³
and VOJTECH JAROŠÍK^{4,5}

¹Department of Biodiversity Research, Global Change Research Centre AS CR, České Budějovice, Czech Republic, ²School of Biological Sciences, University of East Anglia, Norwich, U.K., ³Research Institute of Crop Production, Drnovská, Czech Republic, ⁴Faculty of Science, Department of Ecology, Charles University, Prague, Czech Republic and ⁵Department of Invasion Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice, Czech Republic

Abstract. Aphidophagous and coccidophagous ladybirds, similar to their prey, show marked differences in their pace of life (Dixon, 2000), in particular in their rate of development, with all stages of aphidophagous species developing much faster than those of coccidophagous species. Two hypotheses are proposed to account for the large difference in the pace of life of these two groups. These are that differences in the rate of development are a result of differences in lower temperature thresholds for development or the quality of their respective prey as food (Dixon *et al.*, 2011). Analysis of published results on the rates of development of the eggs of ladybirds indicates that the inverse relationships between the number of day-degrees required for development (K) and the lower temperature threshold for development (td_{\min}) of these two groups are significantly different. In particular, the respective td_{\min} overlap and K of the aphidophagous and coccidophagous species with a similar td_{\min} are, on average, 38 and 117 day-degrees (D°). The relationship between the rate of development (R) and temperature (T) for aphids reared on poor- or high-quality foods indicates that, although the value of td_{\min} of a species depends on food quality, K does not, showing that it is unlikely that K is governed by food quality. Thus, there is little support for differences in either the td_{\min} or food quality governing the difference in the pace of life of these two groups of ladybirds. The results indicate that the physiological mechanism that may govern the difference in the pace of life between these two groups is the number of day-degrees (K) needed to complete their development. The possible evolutionary reason for this is discussed.

Key words. Coccinellidae, food quality, geographical distribution, ladybirds, lower developmental threshold, pace of life, sum of effective temperatures.

Introduction

Although metabolic theory predicts that small species develop faster than large species and this is particularly well established for mammals (Bonner, 1966; Sibly & Brown, 2007), it is likely that factors other than size, such as food quality, lower temperature threshold for development (td_{\min}), number of

day-degrees required for development (K) and phylogeny, may also be important in determining the pace of life. In ladybird beetles, the life-history parameters of all the stages of aphidophagous species differ from those of coccidophagous species, and this is associated with the pace of life of their respective prey: either fast developing aphids or slow developing coccids (Dixon, 2000; Dixon *et al.*, 2011). Previous studies demonstrate that the fact that aphidophagous ladybirds develop much faster than coccidophagous species over a wide range of temperatures is not the result of a phylogenetic constraint or a difference in their size (Dixon *et al.*, 2011).

Correspondence: Professor Anthony Dixon, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, U.K. Tel.: +44 (0)1603 592269; e-mail: a.f.dixon@uea.ac.uk

There are two possible explanations for the difference in the pace of life of these two types of ladybird (Dixon *et al.*, 2011). The difference is associated in some way with a difference in the respective td_{\min} s of aphid- and coccid-eating ladybirds. They occur predominantly in temperate and subtropical and tropical regions, respectively, and are assumed to be adapted to the temperature conditions prevailing at these latitudes because td_{\min} increases with mean environmental temperature (Trudgill, 1995; Honěk, 1996a, b). Alternatively, the food quality of aphids and coccids could differ in terms of either limiting nutrients (Cohen & Brummett, 1997) and/or in the toxic chemicals that they sequester from their host plants (Dixon, 1998).

In contrast to the plethora of studies on food quality and feeding specialization in herbivorous insects (Denno & McClure, 1983; Strong *et al.*, 1984; Berenbaum, 1990; Jaenike, 1990; Schoonhoven *et al.*, 1998), there are few such studies on carnivorous insects and these are mainly on parasitoids (Vinson, 1976, 1981, 1984; Arthur, 1981; Weseloh, 1981; Schultz, 1983). This is normally attributed to the widely held view that predators tend to be generalists precisely because they eat animals. Plant tissues are mostly poor in nitrogen and are often rich in nondigestible if not toxic materials, whereas animal flesh is assumed to provide an excellent balance of nutrients for another animal (Dout & DeBach, 1964; Bristow, 1988). That is, plant secondary chemistry is regarded as an important factor in the specialization of herbivores (Ehrlich & Raven, 1964) and, by implication, the supposed absence of chemical defences in animals results in the markedly lower specialization of predators. Rather than by chemical or other intrinsic characteristics of prey, predator–prey associations in insects are considered to be determined by ant attendance, characteristics of the habitat and/or the phenology, size or abundance of prey or natural enemies (Evans, 1982; Hagen, 1987; Tauber & Tauber, 1987; Hurd, 1988; Endler, 1991; Milbrath *et al.*, 1993; Nylin & Janz, 1993; Sih, 1993; Albuquerque *et al.*, 1997; Sloggett & Majerus, 2000). However, there is a well documented two-fold difference in the rate of development of ladybirds reared at the same temperature but on different species of similar prey such as aphids or coccids (Hodek, 1962; Blackman, 1967; Hodek & Honěk, 1996; Kalushkov, 1998; Sadeghi & Gilbert, 1999, 2000). In addition, the performance of ladybirds selected for better performance on poor-quality prey decreases on high-quality prey and vice versa. This trade-off in performance on prey of different qualities is homologous to that recorded for herbivorous insects feeding on plants of different qualities (Rana *et al.*, 2002). Accordingly, there is strong evidence that the food of both herbivorous and predatory insects varies similarly in quality and that both groups of insects respond similarly to differences in the quality of their food.

Studies are available indicating that food quality affects the thermal constants of Hemiptera and Lepidoptera (Honěk *et al.*, 2002; Kipyatkov & Lopatina, 2010). The only results available for ladybirds are for *Adalia bipunctata* reared on an artificial diet or on aphids over a range of temperatures. However, these are not suitable for testing the food quality hypothesis because, although the thermal requirements of the egg and

pupal stages differ slightly, they do not differ in the same way and the thermal constants for complete development do not differ on the two diets (Jalali *et al.*, 2010), possibly because the diets differ little in terms of their food quality, and mortality of the immature stages is generally high and even higher on the aphid than on the artificial diet. Assuming, as outlined above, that the response of insects to food quality is a general one and not specific to ladybirds, the data available for another group of insects (i.e. aphids) are used in the present study to test the hypothesis that the quality of the food of aphidophagous and coccidophagous ladybirds determines their pace of life.

The present study aims to determine the physiological mechanism that governs the rates of development of similar sized species with a similar td_{\min} in these two groups of ladybirds, in particular, whether this can be accounted for by either of the above explanations.

Materials and methods

Calculation of td_{\min} and K

The method used to calculate both K and the temperature at which td_{\min} is zero is well documented by Jarošík *et al.* (2002) and Kipyatkov & Lopatina (2010). In summary, the hyperbolic relationship between the number of days (D) taken to complete development at a range of temperatures (T) can be transformed into a linear form by using $1/D$ (i.e. R) rather than D . The transformed linear form of the relationship is:

$$R = a + bT \quad (1)$$

where a is a constant and b the coefficient of the linear relationship. When R is zero in Eqn (1) then:

$$td_{\min} = -a/b \quad (2)$$

and

$$K = D \times (T - td_{\min}) \quad (3)$$

Replacing D in Eqn (3) with the reciprocal of the development rate from Eqn (1) and taking into account that, according to Eqn (1), $a = b td_{\min}$ then:

$$K = 1/b \quad (4)$$

Although some studies indicate that the models of Lactin *et al.* (1995) and Brière *et al.* (1999) give better estimates of the temperature thresholds than other nonlinear models (Roy *et al.*, 2002; Kontodimas *et al.*, 2004), the study by Jalali *et al.* (2010) shows that these nonlinear models overestimate the upper developmental threshold and that experimental results are well described by the linear model proposed above, which also has the advantage of being easy to calculate and is the only model that provides an estimate of K (Kontodimas *et al.*, 2004)

The td_{min} and K required for the development of the eggs of aphidophagous and coccidophagous ladybirds

Although the relative food quality of aphids and coccids may differ, the eggs of each species of ladybird are likely to be well provisioned with the nutrients necessary for embryonic development. Therefore, data from the literature on the rate of development of eggs of ladybirds at different temperatures were used to determine whether there is an inverse relationship between K and td_{min} as recorded for other insects (Honěk & Kocourek, 1988, 1990; Imura, 1990; Kiritani, 1991; Frazer & McGregor, 1992; Trudgill, 1995; Honěk, 1996a, b; Kipyatkov & Lopatina, 2002; Ikemoto, 2003), and also whether the relationships for aphidophagous and coccidophagous ladybirds differ.

A survey of the literature provided datasets of the time that it takes the eggs of coccidophagous and aphidophagous ladybirds to hatch when maintained under at least four different temperatures falling within the range of the linear relationship between developmental rate and temperature. The data for the coccidophagous ladybirds include two species of *Chilocorus* belonging to the Chilocorini and three species of *Nephus* belonging to the Scymnini. The data for aphidophagous ladybirds include 21 species from 12 genera all belonging to the Coccinellini (Dixon *et al.*, 1997, 2011; Dixon, 2000; Mehrnejad & Jalali, 2004).

The effect of food quality on td_{min} and K

Although there is currently no suitable information available for ladybirds in the literature, there is detailed information for another insect, the black bean aphid *Aphis fabae* Scop., with respect to the time that it takes this species to complete its development when reared on either the broad bean *Vicia faba* var *aquadulce*, a high-quality food source, or on a synthetic diet, which is a low-quality food source. The time to complete development was recorded over a wide range of temperatures (Dharma, 1979). The synthetic diet used matched that described by Dadd & Krieger (1967) and the sterilization and subsequent encapsulation of the diet were carried out as described by Dadd *et al.* (1967). Aphids were reared on broad bean plants at 10, 15, 20, 25 and 30 °C and on the synthetic diet at 15, 20, 25, 28 and 30 °C (Dharma, 1979). Food quality was measured in terms of the weight and time that it took this aphid to develop on broad beans or the synthetic diet.

Statistical analysis

To test the relationships between the number of day-degrees required for development (K) and the lower temperature threshold for development (td_{min}) of the eggs of aphidophagous and coccidophagous ladybirds, the values of K were regressed on td_{min} with a different intercept and slope for aphid- and for coccid-eating species. To test the effect of food quality on both td_{min} and K , the rates of development (R) were regressed on temperature (T) with a different intercept and slope for each aphid diet. Parameters of these analyses of

covariance (ANCOVA) models were inspected for significance by deletion tests (Crawley, 1993). Deletion tests were repeated until minimal adequate models (MAMs) were established. In MAMs, all nonsignificant parameters are removed, and all the remaining parameters are significantly ($P < 0.05$) different from zero and from one another (Crawley, 1993). Differences in the mean K and td_{min} values of aphid- and coccid-eating aphids were tested using one-way analysis of variance.

Results

The relationships between td_{min} and K for the development of the eggs of aphidophagous and coccidophagous ladybirds

The ANCOVA and regression analysis of the relationships between K and td_{min} for the eggs of 21 species of aphidophagous and five species of coccidophagous ladybirds reveal that the relationships for these two groups of ladybirds differ and that the intercept of the relationship for coccidophagous ladybirds is greater than that for aphidophagous ladybirds ($P < 0.0001$) (Fig. 1). In particular, for overlapping td_{min} values, which do not differ significantly between the two groups of ladybirds ($F = 1.48$; d.f. = 1, 24; $P = 0.23$), the K values for aphidophagous and coccidophagous species differ markedly, being 38 and 117 D°, respectively ($F = 51.06$; d.f. = 1, 24; $P = 0.0001$). Also noteworthy is that, with an increasing value of td_{min} , K decreases significantly faster ($F = 5.64$; d.f. = 1, 22; $P < 0.05$) for coccidophagous than for aphidophagous species. However, the relationship for coccidophagous species is based on the results for only three species of one genus and two of another, and their respective points in Fig. 1 are well separated into two groups. The suggestion that the relationship for coccidophagous species is apparently decreasing faster than for aphidophagous species needs to be confirmed using a larger

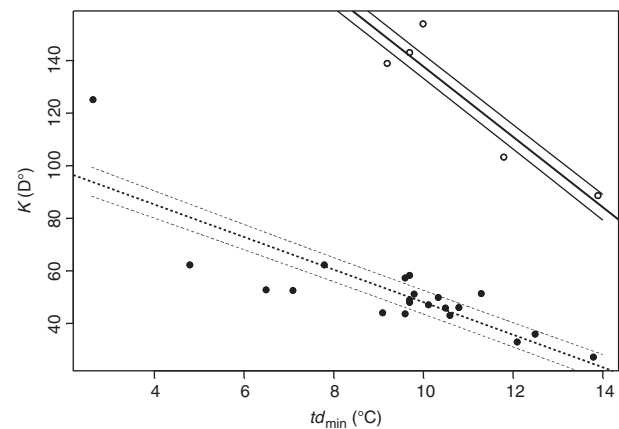


Fig. 1. The relationships between the sum of effective temperatures (K , day-degrees D°) and the lower developmental threshold (td_{min} , °C) for coccidophagous (○) and aphidophagous (●) ladybirds. Coccid-eating ladybirds: $K = 271.6$ to $13.4 td_{min}$; aphid-eating ladybirds: $K = 110.0$ to $6.2 td_{min}$ (fitted regression lines with 95% confidence intervals). The overall significance of the model is $F = 80.61$; d.f. = 3, 22; $P < 0.0001$; $R^2 = 0.92$.

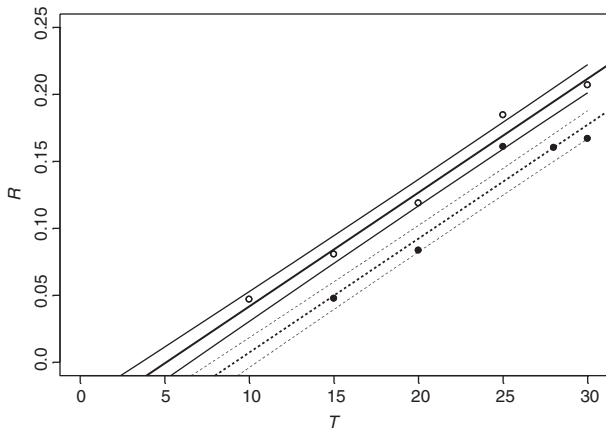


Fig. 2. Rate of development (R , 1/days) of *Aphis fabae* reared on bean (○) or a synthetic diet (●) at different constant temperatures (T). Bean: $R = -0.04 + 0.009 T$; synthetic: $R = -0.08 + 0.009 T$. $F = 83.38$; d.f. = 2, 7; $P < 0.0001$; $R^2 = 0.96$ (fitted regression lines with 95% confidence intervals).

dataset for coccidophagous species. Because the distributional ranges and, in particular, the td_{\min} for the species in these two groups of ladybirds overlap, it is clear that coccidophagous species require more day-degrees (K) to complete their development than aphidophagous species with the same td_{\min} .

The effect of food quality on td_{\min} and K

The analysis of the relationships between the rate of development (R) and temperature (T) for aphids reared on broad beans and an artificial diet indicates that the slopes of the two relationships are very similar ($F = 0.01$; d.f. = 1, 6; $P = 0.9$), although the intercepts differ very significantly ($F = 15.71$; d.f. = 1, 7; $P < 0.01$) (Fig. 2). Because the slopes are not significantly different, then food quality does not affect K but does affect td_{\min} , the value of which is significantly lower when aphids were reared on a high-quality diet.

The quality of the two diets was measured in terms of the adult weights achieved and the time that it took the aphid to complete its development. Both the weight and the time that it takes an aphid to complete its development, however, are also dependent on the temperature at which it is reared. Therefore, the means of the weights and developmental times were used (0.887 mg and 11.9 days and 0.311 mg and 13.8 days for broad bean and the artificial diet, respectively). Although, on average, they took 2 days longer to complete their development on the artificial diet, they were only slightly over a third of the weight of those reared on broad beans. Therefore, the nutritional quality of the artificial diet measured in these terms was considerably lower than that of broad bean plants. However, and more important for the argument being developed here, although the absolute time that they took to complete their development on the two diets differed, the number of D° that they require for development (K) at any temperature above their respective td_{\min} is the same ($K = 1/b = 111 D^\circ$). The fact that aphids take longer to complete their development

in terms of days on a synthetic diet is a result of their higher td_{\min} and the accumulation of D° at a slower rate than for aphids reared on bean plants.

Discussion

The inverse relationship between the sum of effective temperatures (K) and the lower temperature threshold for development (td_{\min}) has been reported previously (Honěk & Kocourek, 1988, 1990; Imura, 1990; Kiritani, 1991; Frazer & McGregor, 1992; Trudgill, 1995; Honěk, 1996a, b; Kipyatkov & Lopatina, 2002; Ikemoto, 2003). However, the finding that this relationship for aphidophagous and coccidophagous ladybirds differs significantly in elevation is novel. Previous analyses of the rates of development at different temperatures of the eggs and larvae of aphidophagous and coccidophagous ladybirds indicate that they differ in these two groups of ladybirds, with aphidophagous ladybirds developing much faster than coccidophagous species (Dixon *et al.*, 1997, 2011; Dixon, 2000). This difference in their rates of development is not the result of a phylogenetic constraint because the aphidophagous (*Scymnus*) and coccidophagous (*Nephus*) species in the robust tribe Scymnini (Magro *et al.*, 2010) also differ similarly in their rates of development (Dixon, 2000; Dixon *et al.*, 2011).

Although it needs to be confirmed, the faster decrease in K with an increase in td_{\min} for coccidophagous than for aphidophagous ladybirds indicates that, for overlapping td_{\min} values (Fig. 2), with an increase in td_{\min} , the rate of development of eggs of coccidophagous species increases faster than in aphidophagous species. Because td_{\min} increases with the mean environmental temperature (Trudgill, 1995; Honěk, 1996a, b), this might indicate that the adaptation to living in temperate versus subtropical and tropical regions might partly also account for the difference in the pace of life of aphidophagous and coccidophagous ladybirds inhabiting, respectively, mainly temperate and subtropical and tropical regions.

Based on the inverse relationship between K and td_{\min} and an analysis of data on the rates of development at different temperatures of closely-related species within a family or genus, Ikemoto (2003) suggests that there is a temperature (T_c) at which the duration of development (D_c) is the same for all the members of a particular taxon and that the optimal temperature for their development is T_c . Speciation within each taxon is seen as occurring in terms of a rotation about a fixed point (T_c , D_c) in the relationships between the developmental rate (R) and temperature (T), and that there is an intrinsic optimal temperature (T_c) for species with a common ancestor (Ikemoto, 2005; Bonato *et al.*, 2011). If this is the case, then the inverse relationship between K and td_{\min} should be common to all ladybirds and should not differ in elevation between groups, which indicates that, for the two groups of ladybirds in the present study, the T_c , D_c intersections differ. In addition, the expectation is that, if R is plotted against T for members of a genus of ladybirds such as *Coccinella* for which there is suitable data for four species and three geographically separated populations of one of the species, there would be one temperature at which all these species/populations have

the same rate of development, as is illustrated in Ikemoto (2003), but this is not the case as there is more than one T intersection between the relationships (A. F. G. Dixon, unpublished observations). It is also debatable whether there is an optimal temperature for the development of a species because each species is constrained by physiology and can only develop over a narrow range of temperatures (i.e. its thermal window) and it is likely that this window for each species is the optimal one, in terms of fitness, for a particular variable thermal environment (Dixon *et al.*, 2009). If this is the case, then the expectation is not for a single T_c , D_c but a cluster of such points for a particular thermal environment (e.g. the Tropics, etc.), with distinct differences in the positions of the various clusters in thermal space. However, it is unlikely that the thermal windows of organisms are only shaped by the thermal environments they occupy and, in particular, if there is a 'fixed point' (T_c, D_c), then, for any taxon, there can only be one relationship between K and td_{\min} , which is clearly not the case for ladybirds. Of the three hypotheses proposed by Ikemoto (2003), the one that is rejected (which suggests that speciation within a taxonomic group does not occur around one T_c , D_c) would appear to be a more accurate representation of the results reported in the present study for ladybirds.

The results of the present study indicate that there is a marked difference in the relationship between K and td_{\min} of the thermal windows for the development of eggs of ladybirds that feed on aphids and coccids, respectively. In particular, at any given temperature within their thermal windows, eggs of coccidophagous species develop more slowly than those of aphidophagous species because they require more day-degrees to complete their development. In addition, the rate of juvenile development and the size and fecundity of adult ladybirds is markedly affected by the quality of the food that they feed on (Hodek & Honěk, 1996; Dixon, 2000). Therefore, it is possible, as implied by Cohen & Brummett (1997), that the slow rate of development of coccid-eating ladybirds is a consequence of their feeding on poor-quality prey. Currently, there are insufficient data on the effects of food quality on the thermal windows of ladybirds. However, there are good grounds for assuming that all insects, if not all ectotherms, are likely to respond similarly to differences in food quality, and the reported results for black bean aphids reared on a poor-quality artificial diet and a high-quality food plant indicate that, although td_{\min} is significantly higher when reared on a low rather than on a high-quality diet, the slopes of the relationships between R and T are virtually the same on both the high- and low-quality diets. Therefore, K is not affected by food quality. Similar results are reported for the cereal aphid *Sitobion avenae* reared at a range of temperatures on the flag leaf or on ears of wheat. The food available to aphids reared on the ears of wheat is of a higher quality than that available to aphids reared on the flag leaves. As is the case with the black bean aphid, the quality of the food is indicated by differences in adult weights (1.4 and 1.1 mg) and also the time that it takes them to complete their development (7 and 8 days, respectively) on the ears and flag leaves. However, the number of day-degrees that they need for development on the two diets is the same (120 D°) (Watson, 1983). Assuming that the parameters of the

thermal windows of all ectotherms respond similarly to food quality, then it is unlikely that the great difference in the value of K for aphidophagous and coccidophagous ladybirds is a consequence of the differences in the nutritional quality of their prey.

If K is not determined by a physiological or phylogenetic constraint, food quality or an the thermal environment of an organism, then why does its value differ so strikingly in aphidophagous and coccidophagous ladybirds? The most likely explanation is that the K values of these two groups of ladybirds are the consequence of transformations occurring during the course of evolution that are adaptive in terms of being optimal for foraging for prey differing in spatial distribution, abundance and rates of population increase (Dixon, 2000; Borges *et al.*, 2006, 2011). However, because fitness is often viewed in terms of the potential rate of population increase, and because the development rate and population rate of an increase are correlated in both aphids and ladybirds (Dixon, 1998, 2000), it would appear to be advantageous for coccidophagous species of ladybirds to develop faster. However, this assumes that there are no constraints to coccidophagous ladybirds developing faster. It is possible that the constraint is an ecological one, as implied above. However, the evolutionary reason explaining why coccidophagous ladybirds do not develop as fast as aphidophagous ladybirds remains to be determined.

Acknowledgements

A.F.G.D and A.H. were funded in part by project 522/08/1300 of the Grant Agency of the Czech Republic. V.J. was supported by grant no. 206/09/0563 (Czech Science Foundation) and LC 06073 (Czech Ministry of Education, Youth and Sports) and by the institutional resources of the Czech Ministry of Education, Youth and Sports. A.F.G.D. also acknowledges financial support from grant LC 06073 (Czech Ministry of Education) and the CzechGlobe Centre for Global Climate Change Impacts Studies, Reg. No. CZ.1.05/1.1.00/02.0073.

References

- Albuquerque, G.S., Tauber, M.J. & Tauber, C.A. (1997) Life history adaptations and reproductive costs associated with specialization in predaceous insects. *Journal of Animal Ecology*, **66**, 307–317.
- Arthur, A.P. (1981) Host acceptance by parasitoids. *Semiochemicals* (ed. by D.A. Nordlund, R.L. Jones and W.J. Lewis), pp. 97–120. John Wiley & Sons, New York, New York.
- Berenbaum, M.R. (1990) Evolution of specialization in insect-umbellifer associations. *Annual Review of Entomology*, **35**, 319–343.
- Blackman, R.L. (1967) Selection of aphid prey by *Adalia bipunctata* L. and *Coccinella 7-punctata* L. *Annals of Applied Biology*, **59**, 331–338.
- Bonato, O., Ikemoto, T., Shi, P. *et al.* (2011) Common-intersection hypothesis of development rate lines of ectotherms within a taxon revisited. *Journal of Thermal Biology*, **36**, 422–429.
- Bonner, J.T. (1966) *Size and Cycle: An Essay on the Structure of Biology*. Princeton University Press, Princeton, New Jersey.

- Borges, I., Soares, A.O. & Hemptinne, J.-L. (2006) Abundance and spatial distribution of aphids and scales select for different life histories in their ladybird beetle predators. *Journal of Applied Entomology*, **130**, 461–464.
- Borges, I., Soares, A.O., Magro, A. & Hemptinne, J.-L. (2011) Prey availability in time and space is a driving force in life history evolution of predatory insects. *Evolutionary Ecology*, **25**, 1307–1319.
- Brière, J.F., Pracros, P., Le Roux, A.Y. & Pierre, J.S. (1999) A novel rate model of temperature-dependent development for arthropods. *Environmental Entomology*, **28**, 22–29.
- Bristow, C.M. (1988) What makes a predator specialize? *Trends in Evolution and Ecology*, **3**, 1–2.
- Cohen, A.C. & Brummett, D.L. (1997) The non-abundant nutrient (NAN) concept as a determinant of predator–prey fitness. *Entomophaga*, **42**, 85–91.
- Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell Science, U.K.
- Dadd, R.H. & Krieger, D.L. (1967) Continuous rearing of aphids of the *Aphis fabae* complex on sterile diet. *Journal of Economic Entomology*, **60**, 1512–1514.
- Dadd, R.H., Krieger, D.L. & Mittler, T. (1967) Studies on artificial feeding of the aphid *Myzus persicae* (Sulzer). IV. Requirements for water soluble vitamins and ascorbic acid. *Journal of Insect Physiology*, **13**, 249–272.
- Denno, R.F. & McClure, M.S. (1983) *Variable Plants and Herbivores in Natural and Managed Systems*. Academic Press, New York, New York.
- Dharma, T.R. (1979) *Fecundity and size in the black bean aphid, Aphis fabae Scop.* PhD Thesis, University of East Anglia.
- Dixon, A.F.G. (1998) *Aphid Ecology*, 2nd edn. Chapman and Hall, U.K.
- Dixon, A.F.G. (2000) *Insect Predator–Prey Dynamics: Ladybird Beetles and Biological Control*. Cambridge University Press, U.K.
- Dixon, A.F.G., Hemptinne, J.-L. & Kindlmann, P. (1997) Effectiveness of ladybirds as biological control agents: patterns and processes. *Entomophaga*, **42**, 71–83.
- Dixon, A.F.G., Honek, A., Keil, P. *et al.* (2009) Relationship between the minimum and maximum temperature thresholds for development in insects. *Functional Ecology*, **23**, 257–264.
- Dixon, A.F.G., Agarwala, B., Hemptinne, J.-L. *et al.* (2011) Fast–slow continuum in the life history parameters of ladybirds revisited. *European Journal of Environmental Science*, **1**, 61–66.
- Doutt, R.L. & DeBach, P. (1964) Some biological control concepts and questions. *Biological Control of Insect Pests and Weeds* (ed. by P. DeBach), pp. 118–142. Reinhold Publishing Co., New York, New York.
- Ehrlich, P.R. & Raven, P.H. (1964) Butterflies and plants: a study in co-evolution. *Evolution*, **18**, 586–608.
- Endler, J.A. (1991) Interaction between predators and prey. *Behavioural Ecology* (ed. by J.R. Krebs and N.B. Davis), pp. 169–196. Blackwell Scientific Publications, U.K.
- Evans, E.W. (1982) Timing of reproduction by predatory stinkbugs (Hemiptera: Pentatomidae): pattern and consequences for a generalist and specialist. *Ecology*, **63**, 147–158.
- Frazer, B.D. & McGregor, R.R. (1992) Temperature dependent survival and hatching rate of eggs of seven species of Coccinellidae. *Canadian Entomologist*, **124**, 305–312.
- Hagen, K.S. (1987) Nutritional ecology of terrestrial insect predators. *Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates* (ed. by F. Slansky Jr and J.G. Rodriguez), pp. 533–577. John Wiley & Sons, New York, New York.
- Hodek, I. (1962) Essential and alternative foods in insects. *Transactions of the XIth International Congress of Entomology* (ed. by H. Strouhal and M. Beier), Vol. 2, pp. 696–698. Austria.
- Hodek, I. & Honěk, A. (1996) *Ecology of Coccinellidae*. Kluwer Academic Publishers, The Netherlands.
- Honěk, A. (1996a) Geographical variation in thermal requirements for insect development. *European Journal of Entomology*, **93**, 303–312.
- Honěk, A. (1996b) The relationship between thermal constants for insect development. *Acta Societatis Zoologicae Bohemicae*, **60**, 115–152.
- Honěk, A. & Kocourek, F. (1988) Thermal requirements for development of aphidophagous Coccinellidae (Coleoptera), Chrysopidae (Neuroptera), and Syrphidae (Diptera): some general trends. *Oecologia*, **76**, 455–460.
- Honěk, A. & Kocourek, F. (1990) Temperature and development time in insects: a general relationship between thermal constants. *Zoologische Jahrbücher Abteilung für Systematik, Ökologie und Geographie der Tiere*, **117**, 401–439.
- Honěk, A., Jarošík, V., Martinkova, Z. & Novak, I. (2002) Food induced variation in thermal constants of development and growth of *Autographa gamma* (Lepidoptera: Noctuidae) larvae. *European Journal of Entomology*, **99**, 241–252.
- Hurd, L.E. (1988) Consequences of divergent egg phenology to predation and coexistence in two sympatric, congeneric mantids (Orthoptera: Mantidae). *Oecologia*, **76**, 549–552.
- Ikemoto, T. (2003) Possible existence of a common temperature and common duration of development among members of a taxonomic group of arthropods that underwent speciation adaptation to temperature. *Applied Entomology and Zoology*, **38**, 487–492.
- Ikemoto, T. (2005) Intrinsic optimum temperature for development of insects and mites. *Environmental Entomology*, **34**, 1377–1387.
- Imura, O. (1990) Thermal requirements for development of stored-product insects. *Tribolium Information Bulletin*, **30**, 58–68.
- Jaenike, J. (1990) Host specialization in phytophagous insects. *Annual Review of Ecology and Systematics*, **21**, 243–273.
- Jalali, M.A., Tirry, L., Arbab, A. & De Clercq, P. (2010) Temperature-dependent development of the two-spotted ladybeetle, *Adalia bipunctata*, on the green peach aphid, *Myzus persicae*, and a facultitious food under constant temperatures. *Journal of Insect Science*, **10**, 124.
- Jarošík, V., Honěk, A. & Dixon, A.F.G. (2002) Developmental rate isomorphy in insects and mites. *American Naturalist*, **160**, 497–510.
- Kalushkov, P. (1998) Ten aphid species (Sternorrhyncha: Aphididae) as prey for *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, **95**, 343–349.
- Kipyatkov, V.E. & Lopatina, E.A. (2002) Reaction norm in response to temperature may change to adapt rapid brood development to boreal and subarctic climates in *Myrmica* ants (Hymenoptera: Formicidae). *European Journal of Entomology*, **99**, 197–208.
- Kipyatkov, V.E. & Lopatina, E.A. (2010) Intraspecific variation of thermal reaction norms for development in insects: new approaches and prospects. *Entomological Review*, **90**, 163–184.
- Kiritani, K. (1991) Potential impacts of global warming on insects. *Insectarium*, **28**, 212–223.
- Kontodimas, D.C., Eliopoulos, P.A., Stathas, G.J. & Economou, L.P. (2004) Comparative temperature-dependent development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae), preying on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae): evaluation of a linear and various non-linear models using specific criteria. *Environmental Entomology*, **33**, 1–11.
- Lactin, D.J., Holliday, N.J., Johnson, D.L. & Craigen, R. (1995) Improved rate model of temperature-dependent development by arthropods. *Environmental Entomology*, **24**, 68–75.
- Magro, A., Lecompte, E., Magne, F. *et al.* (2010) Phylogeny of ladybirds (Coleoptera: Coccinellidae): are the subfamilies monophyletic? *Molecular Phylogenetics and Evolution*, **54**, 833–848.

- Mehrnejad, M.R. & Jalali, M.A. (2004) Life history parameters of the coccinellid beetle, *Oenopia conglobata contaminata*, an important predator of the common pistachio psylla, *Agonoscena pistaciae* (Hemiptera: Psylloidea). *Biocontrol Science and Technology*, **14**, 701–711.
- Milbrath, L.R., Tauber, M.J. & Tauber, C.A. (1993) Prey specificity in *Chrysopa*: an interspecific comparison of larval feeding and defensive behavior. *Ecology*, **74**, 1384–1393.
- Nylin, S. & Janz, N. (1993) Oviposition preference and larval performance in *Polygonia c-album* (Lepidoptera: Nymphalidae): the choice between bad and worse. *Ecological Entomology*, **18**, 394–398.
- Rana, J.S., Dixon, A.F.G. & Jarošik, V. (2002) Costs and benefits of prey specialization in a generalist insect predator. *Journal of Animal Ecology*, **71**, 15–22.
- Roy, M., Brodeur, J. & Cloutier, C. (2002) Relationship between temperature and developmental rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdanieli* (Acarina: Tetranychidae). *Environmental Entomology*, **31**, 177–187.
- Sadeghi, H. & Gilbert, F. (1999) Individual variation in oviposition preference, and its interaction with larval performance in an insect predator. *Oecologia*, **118**, 405–411.
- Sadeghi, H. & Gilbert, F. (2000) Aphid suitability and its relationship to oviposition preference in predatory hoverflies. *Journal of Animal Ecology*, **69**, 771–784.
- Schoonhoven, L.M., Jermy, T. & Loon, J.J.A. (1998) *Insect–Plant Biology*. Chapman & Hall, U.K.
- Schultz, J.C. (1983) Impact of variable plant defensive chemistry on susceptibility of insects to natural enemies. *Plant Resistance to Insects* (ed. by P.A. Hedin), pp. 37–54. American Chemical Society, Washington, District of Columbia.
- Sibly, R.M. & Brown, J.H. (2007) Effects of body size and lifestyle on evolution of mammal life histories. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 17707–17712.
- Sih, A. (1993) Effects of ecological interaction on forager diets: competition, predation risk, parasitism and prey behaviour. *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour* (ed. by R. N. Hughes), pp. 182–211. Blackwell Scientific Publications, U.K.
- Sloggett, J.J. & Majerus, M.E.N. (2000) Habitat preferences and diet in them predatory Coccinellidae (Coleoptera): an evolutionary perspective. *Biological Journal of the Linnean Society*, **70**, 63–88.
- Strong, D.R., Lawton, J.H. & Southwood, R. (1984) *Insects on Plants*. Blackwell Scientific Publications, U.K.
- Tauber, C.A. & Tauber, M.J. (1987) Food specificity in predaceous insects: a comparative ecophysiological and genetic study. *Evolutionary Ecology*, **1**, 175–186.
- Trudgill, D.L. (1995) Why do tropical poikilothermic organisms tend to have higher threshold temperature for development than temperate ones? *Functional Ecology*, **9**, 136–137.
- Vinson, S.B. (1976) Host selection by insect parasitoids. *Annual Review of Entomology*, **21**, 109–133.
- Vinson, S.B. (1981) Habitat location. *Semiochemicals* (ed. by D.A. Nordlund, R.L. Jones and W.J. Lewis), pp. 51–77. Wiley, New York, New York.
- Vinson, S.B. (1984) Parasitoid–host relationship. *Chemical Ecology of Insects* (ed. by W.J. Bell and R.T. Cardé), pp. 205–233. Chapman & Hall, New York, New York.
- Watson, S.J. (1983) *Effects of weather on the numbers of cereal aphids*. PhD Thesis, University of East Anglia.
- Weseloh, R.M. (1981) Host location by parasitoids. *Semiochemicals* (ed. by D.A. Nordlund, R.L. Jones and W.J. Lewis), pp. 79–95. John Wiley & Sons, New York, New York.

Accepted 16 September 2012

First published online 20 November 2012