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Thermal requirements for development of predatory insects: Contributions of Alois Honěk, including data on three Nearctic species

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Abstract. This paper salutes Alois Honěk's outstanding contributions and collaborative work in ecology and entomology. First, we highlight two important aspects of his work – the experimental analysis of thermal responses in predaceous insects, and the elucidation of general trends in these responses. These areas of study are crucial for understanding how predators adapt to seasonal and long-term changes in their physical and biotic environments, as well as for managing predator-prey interactions in agricultural and horticultural settings. Second, we provide data on the thermal requirements for development of three North American species of predaceous lady beetles – *Cycloneda munda* (Say, 1835), *Hippodamia glacialis* (Fabricius, 1775), and *H. tredecimpunctata* (Linnaeus, 1758). We show that their thermal responses are similar to those of other aphid-feeding lady beetles; for complete preimaginal development, their T_b values (lower thermal temperatures) range from 10 °C to 11 °C, and their SET values (number of day degrees above T_b) vary from 252 °C to 284 °C days.

Key words. Developmental threshold, lower base temperature, Degree days, thermal time, thermal constant, phenology of insect predators.

INTRODUCTION

Investigation of poikilothermic thermal responses and their role in adapting predators to their physical and biotic environment has been a very important and fruitful area of Alois Honěk's research. In the first part of this paper we discuss some of the significant topics to which Honěk and his co-authors have contributed, and that, in some cases impinged on our own work.

In the second part of the paper, we present previously unpublished data on the thermal requirements for development of three predatory lady beetle species from North America, *Cycloneda munda* (Say), *Hippodamia glacialis* (F.), and *H. tredecimpunctata* (Say). Such information adds to the large body of comparative data that Honěk, his co-authors, and others developed; and, it extends our studies emphasizing the thermal biology of Nearctic predatory species.

CONTRIBUTIONS OF ALOIS HONĚK

Experimental analysis of thermal reaction

Through a series of widely cited papers beginning in the 1980s, Alois Honěk and his colleagues characterized the thermal responses of a substantial number and variety of insect species, especially predaceous ones. For example, Honěk & Kocourek (1988) determined the thermal requirements for development of 20 species of aphid predators (Coccinellidae, Chrysopidae, Hemerobiidae, and Syrphidae) from central Bohemia and compared these values to those for similar species from

†) Professor Maurice J. Tauber deceased on 6 October 2014.

around the world. And, in doing so, they documented an inverse relationship between the lower thermal threshold for development (T_b) and the Sum of Effective Temperatures (SET) [often referred to as degree days or the Thermal Constant (K)]. Later in a comprehensive worldwide study, Honěk & Kocourek (1990) documented a similar inverse relationship between T_b and SET in 294 species from nine insect orders. Interestingly, this pattern of trade-offs between T_b and SET values among species was also shown to occur among populations of a single species of North American lacewing predator, *Chrysopa oculata* Say (Tauber et al. 1987). In the lacewing study, the relationship was interpreted as a possible evolutionary constraint on the two parameters. Subsequently, in a series of significant publications, Honěk and co-authors presented interesting ideas of how such information could be used to explore physiological mechanisms and trade-offs underlying temperature-developmental rate relationships in plants and invertebrates (Jarošík et al. 2002, 2004, Trudgill et al. 2005, Dixon et al. 2009, 2013).

Thermal responses and community interactions

Many of Honěk's investigations were aimed at elucidating general patterns of poikilothermic thermal responses that impinge on the ecology, management, and conservation of arthropods (Honěk & Kocourek 1988, Honěk 1996a, Dixon et al. 2005, Nedvěd & Honěk 2012). Several papers demonstrated general trends in the thermal requirements for development of taxonomically diverse aphid predators within communities; these studies help provide a foundation for explaining the predators' characteristic patterns of seasonal occurrence and their interactions with prey. For example, based on the thermal requirements for development in two groups of predatory insects, syrphids and coccinellids, Dixon et al. (2005) proposed that differences in lower thresholds (T_b) for development serve as a mechanism for timing the characteristic patterns of the predators' seasonal occurrence with seasonally available aphid prey. T_b values of ~4 °C for syrphids, compared to an average T_b of ~10 °C for coccinellids, result in temporal separation of the two groups and their different seasonal patterns of prey usage.

The above findings cast further light on work by other investigators. For example, Neuenschwander (1975) documented that the lower thresholds (T_b) for egg, larval and pupal development of the brown lacewing *Hemerobius pacificus* (Neuroptera: Hemerobiidae) were much lower than those for chrysopid, coccinellid, and lygaeid predators in California, thus synchronizing development with its aphid prey and providing an early seasonal advantage for *H. pacificus*. In a comparative study of the thermal responses of three lady beetle species, Obrycki and Tauber (1981) proposed that the lower developmental threshold of *Adalia bipunctata* (L.) allows it to become active earlier in the spring relative to two other predatory species, *Coccinella septempunctata* (L), and *Coccinella transversoguttata* (Brown), that have higher threshold values.

Thermal responses and climate change

Research on thermal responses, such as that of Alois Honěk and his colleagues, becomes especially pertinent to our current concern with global climate change (Thomson et al. 2010), which includes consistent increases in temperature. A thorough understanding of insect responses to warming conditions requires fundamental information on the thermal and photoperiodic responses of individual species (e.g., Bradshaw & Holzapfel 2008, Moore & Remais 2014.); it also requires an understanding of interspecific and intraspecific variation in these responses (e.g., Tauber & Tauber 1981, Tauber et al 1987, Bradshaw & Holzapfel 2008, Hoffmann & Sgrò 2011, Jarošík et al. 2011, 2014). For example, patterns of distribution, phenological traits, and numbers of generations per year, all of which serve to describe the seasonality of insect species, are influenced by developmental interactions with temperature. In this regard, the types of highly valuable studies that Honěk and his colleagues (e.g., Honěk 1996b, Dixon et al. 2009) conducted on the thermal characteristics of predatory species provide an important (thermal) component for exploring the effects of climate change on predaceous insects. Moreover, when such knowledge of the thermal and other responses of insect species is combined with long-term studies of predator communities (e.g., Honěk et al. 2014), it becomes possible to quantify and explain climate-based changes in the broader community structure.

Thermal Responses of Three North American Lady Beetle Species

In this section, we report on our developmental studies with three lady beetle species, whose thermal responses have not been published previously – *C. munda*, *H. glacialis*, and *H. tredecimpunctata*. Then, we compare their thermal requirements with the general patterns for predatory species that Alois Honěk and his colleagues described (Honěk & Kocourek 1988, 1990, Honěk 1996a, Dixon et al. 2005, Nedvěd & Honěk 2012). These findings extend our work on the thermal biology of predatory species in North America (Obrycki & Tauber 1978, 1981, 1982, Tauber & Tauber 1981, Tauber et al. 1987, Orr & Obrycki 1990, Obrycki et al. 1993).

The three lady beetle species feed on aphids in a wide range of agricultural and herbaceous habitats; they are members of a guild of aphid predators typically observed in surveys of lady beetles in North America (e.g., Hoffmann et al. 1997, Colunga-Garcia & Gage 1998, Elliot et al. 1998, Hesler & Kieckhefer 2008). *Hippodamia tredecimpunctata* has a Holarctic distribution; in North America it occurs from Newfoundland to South Carolina in the east, and from Alaska to California in the west (Gordon 1985). *Cycloneda munda* and *H. glacialis* are widely distributed in eastern North America (Gordon 1985). However, recent photo documentation of these species by citizen scientists indicates that their areas of distribution in North America have become reduced since Gordon's (1985) publication (data summarized by the Lost Ladybug Project http://www.lostladybug.org/index.php).

MATERIALS AND METHODS

Adult *C. munda, H. glacialis*, and *H. tredecimpunctata* were collected in the Ithaca, NY area (latitude = 42.44° N, longitude = 76.5° W). They were maintained at 23.9±1 °C and L:D 16:8 on a diet of pea aphids, *Acrythosiphon pisum* (Harris), and green peach aphids, *Myzus persicae* (Sulzer). The developmental studies were conducted with F_1 individuals reared from these field-collected adults.

Egg masses from two to four *C. munda* and *H. glacialis* females were harvested daily and placed in one of five temperatures (15.6, 18.3, 21.1, 23.9, and 26.7, all ±1 °C) at L:D 16:8. Similarly, egg masses from *H. tredecimpunctata* females were collected daily, but placed in one of four temperatures (15.6, 18.3, 23.9, and 26.7 °C) at L:D 16:8. After hatching, first instars were moved to individual glass vials; they were fed pea aphids and checked for ecdysis daily. The number of individuals completing development at each temperature ranged from 3 to 45; one replicate group of individuals were reared at each temperature. The developmental times of the egg, each instar, and the pupa were recorded.

We used linear regression to examine the relationship between temperature and developmental rate [1/developmental time (days)] for each growth stage. The lower threshold for development was estimated by extrapolating the straight-line portion of the regression line between developmental rate and temperature to the x-axis. And, the Sum of Effective Temperatures (SET), °C Days, [= thermal constant (K)] was calculated from the equation $K=1/m$, where m is the slope of the regression line.

RESULTS

The mean preimaginal developmental time for *C. munda* ranged from 44 days with 29 % mortality at 15.6 °C, to 14.5 days with 0% mortality at 26.7 °C (Table 1). In comparison, relatively few (12%) *H. glacialis* completed development at 15.6 °C (Table 2); their mean preimaginal development time was 67 days (N=3). At 26.7 °C mortality decreased to 0 % and development was completed in a mean of 18 days (Table 2). The preimaginal development time of *H. tredecimpunctata* ranged from 50 days at 15.6 °C to 16 days at 26.7 °C (Table 3). Mortality was lowest at 23.9 °C (28%) and

Table 1. Developmental times (X±SD, days) and survival rates (%, n) of *Cycloneda munda* under a range of constant temperatures (±1 °C; L:D 16:8)

	15.6 °C	18.3 °C	21.1 °C	24.0 °C	26.7 °C
egg	7.4±0.5	4.4±0.5	4.3±0.5	3.6±0.5	2.8 ±0.4
first instar	7.1±1.5	4.8±0.8	3.8±0.8	3.1±0.5	1.8±0.6
second instar	5.0±1.2	3.0±0.7	2.65±0.8	1.8±0.5	1.4±0.5
third instar	4.3±1.2	3.0±0.6	2.7±0.6	2.0±0.6	1.6±0.5
fourth instar and prepupa	8.8±1.0	7.0±1.2	5.0±0.5	4.7±1.0	3.5±0.5
total larval stage	25.3±1.7	17.6±1.2	14.2±0.8	11.6±1.2	8.4±1.0
pupa	11.0±0.7	6.8± 0.5	6.1±0.4	3.9±1.3	3.3± 0.5
total preimaginal	43.7±2.1	28.6±1.2	24.6±1.0	19.0±1.4	14.5±0.8
% survival (n)	71 (28)	75 (24)	96 (26)	98 (46)	100 (25)

highest at 15.6 °C (70%) (Table 3). The rates of preimaginal development for all stages of each of the three species showed strong (R^2 >0.98) positive linear relationships with temperature (Table 4). Although the lower thresholds (T_b) for development of the embryo (oviposition to hatching) varied among the three species by 3.4 °C, those for larval and complete preimaginal development generally showed a considerably smaller range of variation. For example, the T_b value for total development differed among the three species by only 1.3 °C (10.0–11.3 °C) (Table 4). And, the estimated lower threshold for larval and pupal development for the three species fell between ~10 °C and 12 °C.

Similarly, the sum of effective temperatures (SET) for preimaginal development also had a relatively small span of variation among the three species. For total development, the SET values ranged from 252 °C to 284 °C Days.

DISCUSSION

In a recent review of thermal response studies, conducted between 1985 and 2010 on 44 populations of 25 species of Coccinellidae, Nedved & Honěk (2012) concluded that the range of T_b values was between 9 °C and 15 °C for most predacious Coccinellidae. The SET requirement to complete preimaginal development ranged from 200 to 320 °C days for aphid feeding species.

Table 2. Developmental times (X±SD, days) and survival rates (%, n) of *Hippodamia glacialis* under a range of constant temperatures (±1 °C; L:D 16:8)

	15.6 °C	18.3 °C	21.1 °C	24.0 °C	26.7 °C
egg	7.7±0.6	5.6±0.5	4.6±0.5	3.8±0.4	2.4±0.5
first instar	8.7±1.5	5.7±0.9	4.3±0.7	3.4±0.6	2.9±0.4
second instar	7.0±0.0	3.6±0.6	2.8±0.7	2.1±0.5	1.8±0.4
third instar	8.3±1.2	4.5±0.7	3.4±0.8	2.6±0.5	2.0±0.4
fourth instar and prepupa	19.3±1.2	10.3±1.0	7.5±0.8	5.5±0.6	4.4±0.6
total larval stage	43.3±0.6	23.9±1.4	17.9±1.7	13.6±0.8	11.0±0.5
pupa	19.7±0.1	10.6±0.7	7.3±0.6	5.8±0.7	4.6±0.6
total preimaginal	67.0±8.7	40.1±1.1	29.9±2.5	23.2±0.9	18.1±0.8
% survival (n)	12 (25)	69 (26)	73 (45)	80 (45)	100 (28)

Table 3. Developmental times and (X±SD, days) survival rates (%, n) of *Hippodamia tredecimpunctata* under a range of constant temperatures (±1 °C; L:D 16:8)

	15.6 °C	18.3 °C	24.0 °C	26.7 °C
egg	7.9±1.3	6.0±0.0	3.4±0.5	3.0±0.0
first instar	6.1±1.1	5.0±0.0	2.8±0.9	2.0±0.0
second instar	5.0±1.0	3.0±0.5	2.0±0.6	2.0±0.0
third instar	6.4±0.5	3.4±0.5	1.75±0.5	2.0±0.0
fourth instar and prepupa	12.2±2.0	7.8±0.8	4.4±0.6	3.0±0.0
total larval stage	29.8±2.4	19.2±1.4	10.9±0.7	9.0±0.0
pupa	12.7±1.0	7.1±0.6	4.5±0.7	4.0±0.0
total preimaginal	50.2±3.0	32.3±1.7	19.0±1.3	16.0±0.0
% survival (n)	30 (30)	64 (14)	72 (46)	40 (10)

Based on these data from 25 species of predaceous Coccinellidae, Nedved and Honěk (2012) calculated average SET > T_b values for egg (64°C days > 9.8°C), larvae (167°C days > 9.3°C), pupae (78 °C days >10.1 °C), and total preimaginal development (304 °C days > 10.1°C).

The thermal thresholds (T_b) for egg, larval, pupal and total preimaginal development of *C. munda, H. glacialis* and *H. tredecimpuntata* are similar to values reported above. The exception to this pattern is the relatively low (7.5°C) T_b value for *C. munda* (Table 4). Moreover, the three species have T_b values that fall well within the range (t = 9.0°C to 12.2°C) of those previously determined for six additional species from eastern North America (see Table 5). Interestingly, the SET values are similar among all of the North American Coccinellidae, except for *H. glacialis*, which has a higher value (284 °C days), than those of the other species, including the three reported here (see Table 5). However, the SET value for *H. glacialis* is within the range for predaceous Coccinellidae determined by Nedved & Honěk (2012). These data provide additional support for the generalization of Honek and colleagues that Coccinellidae are characterized by relatively high T_b values and somewhat variable SET values.

Comparative studies, such as those by Honěk and colleagues and the one here, on insect thermal requirements for development help provide a basis for examining the effects of climate change and predicting the action of natural enemies in biological control. Further studies of the seasonal biology of predatory species are needed to examine their temporal relationships with prey and with other predatory species.

Table 4. Thermal requirements [T_b (= lower base temperature, °C) and SET (= sum of effective temperatures, °C days >T_b)] for development of three species of lady beetles from Ithaca, New York, USA

species	egg		larva		pupa		pre-imaginal	
	T_b	SET	T_b	SET	T_b	SET	T_b	SET
Cycloneda munda [a]	7.5	55	10.2	147	11.1	52	10.0	252
Hippodamia glacialis [b]	10.9	42	11.6	166	12.0	68	11.4	284
Hippodamia tredecimpunctata [c]	9.1	52	10.7	145	9.8	65	10.3	259

[a] Preimaginal development of *C. munda*: Y=0.00397×X–0.0396; (R^2=0.98); where Y=the rate of development (1/days) and X=temperature (°C);

[b] Preimaginal development of *H. glacialis*: Y=0.00352×X–0.04026 (R^2=0.99);

[c] Preimaginal development of *H. tredecimpunctata*: Y=0.00387×X–0.0399 (R^2=0.99).

Table 5. Thermal requirements [T_b (= lower base temperature, °C) and SET (= sum of effective temperatures, °C days >T_b)] for preimaginal development of selected species of predatory lady beetles in eastern North America. All species were fed the same aphid prey (*Acrythosiphon pisum* (pea aphids) and reared under comparable constant temperature conditions at L:D 16:8

species	T_b (°C)	SET (°C days >T_b)	reference
Adalia bipunctata	9.0	263	Obrycki & Tauber 1981
Coccinella septempunctata	12.1	197	Obrycki & Tauber 1981
Coccinella transversoguttata	12.2	218	Obrycki & Tauber 1981
Coleomegilla maculata	11.3	236	Obrycki & Tauber 1978
Cycloneda munda	10.0	252	reported here
Hippodamia convergens	12.0	230	Obrycki & Tauber 1982
Hippodamia glacialis	11.3	284	reported here
Hippodamia parenthesis	10.8	235	Orr & Obrycki 1990
Hippodamia tredecimpunctata	10.3	235	reported here

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REFERENCES

Bradshaw W. E. & Holzapfel C. M. 2008: Genetic response to rapid climate change: it's seasonal timing that matters. *Molecular Ecology* **17**: 157–166.

Colunga-Garcia M. & Gage S. H. 1998: Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environmental Entomology* **27**: 1574–1580.

Dixon A. F. G., Jarošík V. & Honěk A. 2005: Thermal requirements for development and resource partitioning in aphidophagous guilds. *European Journal of Entomology* **102**: 407–411.

Dixon A. F. G., Honěk A., Keil P., Kotela M. A. A., Sizling A. L. & Jarošík V. 2009: Relationship between the minimum and maximum temperature thresholds in insects. *Functional Ecology* **23**: 257–264.

Dixon A. F. G., Honěk A. & Jarošík V. 2013: Physiological mechanism governing slow and fast development in predatory ladybirds. *Physiological Entomology* **38**: 26–32.

Elliot N. C., Kieckhefer R. W., French B. W. & Lee J. H. 1998: A comparison of size, sex ratio, and dispersal in three coccinellids. *The Southwestern Entomologist* **23**: 137–145.

Gordon R. D. 1985: The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society* **93**: 1–912.

Hesler L. S. & Kieckhefer R. W. 2008: Status of exotic and previously common native coccinellids (Coleoptera) in South Dakota landscapes. *Journal of the Kansas Entomological Society* **81**: 29–29.

Hoffmann A. A. & Sgrò C. M. 2011: Climate change and evolutionary adaptation. *Nature* **470**: 479–485.

Hoffmann M. P., Orfanedes M. S., Pedersen L. H., Kirkwyland J. J., Hoebeke E. R. & Ayyappath R. 1997: Survey of lady beetles (Coleoptera: Coccinellidae) in sweet corn using yellow sticky cards. *Journal of Entomological Science* **32**: 358–369.

Honěk A. 1996a: Chapter 4. Life history and development. Pp.: 61–93. In: Hodek I. & Honek A. (ed.): *Ecology of Coccinellidae*. *Series Entomologica*. *Volume 54*. Boston: Kluwer Academic Publishers, 464 pp.

Honěk A. 1996b: Geographical variation in thermal requirements for insect development. *European Journal of Entomology* **93**: 303–312.

Honěk A. & Kocourek F. 1988: Thermal requirements for development of aphidophagous Coccinellidae, Chrysopidae, Hemerobiidae, and Syrphidae – 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* **117**: 401–439.

Honěk A., Martinkova Z., Kindlmann P., Ameixa O. M. C. C. & Dixon A. F. G. 2014: Long-term trends in the composition of aphidophagous coccinellid communities in Central Europe. *Insect Conservation and Diversity* **7**: 55–63.

Jarošík V., Honěk A. & Dixon A. F. G. 2002: Developmental rate isomorphy in insects and mites. *American Naturalist* **160**: 497–510.
Jarošík V., Kratochvil L., Honěk A. & Dixon A. F. G. 2004: A general rule for the dependence of developmental rate on temperature in ectothermic animals. *Proceedings of the Royal Society of London*, *Series B* **271**: S219–S221.
Jarošík V., Honěk A., Magarey R. D., & Skuhrovec J. 2011: Developmental database for phenology models: Related insect and mite species have similar thermal requirements. *Journal of Economic Entomology* **104**: 1870–1876.
Jarošík V., Kumar G., Omkar & Dixon A. F. G. 2014: Are thermal constants constant? A test using two species of ladybird. *Journal of Thermal Biology* **40**: 1–8.
Lost Ladybug Project. URL: www.lostladybug.org/index.php.
Moore J. L. & Remais J. V. 2014: Developmental models for estimating ecological responses to environmental variability: Structural, parametric, and experimental issues. *Acta Biotheoretica* **62**: 69–90.
Nedved O. & Honěk A. 2012: Chapter 3 Life history and development. Pp.: 54–109. In: Hodek I., van Emden H. F. & Honek A. (eds.): *Ecology and Behaviour of the Ladybird Beetles* (*Coccinellidae*). West Sussex: Wiley-Blackwell, 561 pp.
Neuenschwander P. 1975: Influence of temperature and humidity on the immature stages of Hemerobius pacificus. *Environmental Entomology* **4**: 215–220.
Obrycki J. J., Orr D. B., Orr C. J., Wallendorf M. & Flanders R. V. 1993: Comparative biology of three populations of Propylea quatuordecimpunctata (Coleoptera: Coccinellidae). *Biological Control* **3**: 27–33.
Obrycki J. J. & Tauber M. J. 1978: Thermal requirements for development of *Coleomegilla maculata* (Coleoptera: Coccinellidae) and its parasite Perilitus coccinellae (Hymenoptera: Braconidae). *Canadian Entomologist* **110**: 407–412.
Obrycki J. J. & Tauber M. J. 1981: Phenology of three Coccinellid species: Thermal requirements for development. *Annals of the Entomological Society of America* **74**: 31–36.
Obrycki J. J. & Tauber M. J. 1982: Thermal requirements for development of Hippodamia convergens (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America* **75**: 678–83.
Orr C. J. & Obrycki J. J. 1990: Thermal and dietary requirements for development of Hippodamia parenthesis (Coleoptera: Coccinellidae). *Environmental Entomology* **19**:1523–1527.
Tauber C. A., Tauber M. J. & Nechols J. R. 1987: Thermal requirements for development in Chrysopa oculata: A geographically stable trait. *Ecology* **68**: 1479–1487.
Tauber M. J. & Tauber C. A. 1981: Seasonal responses and their geographic variation in Chrysopa downesi: ecophysiological and evolutionary considerations. *Canadian Journal of Zoology* **59**: 370–376.
Thomson L. J., Macfadyen S. & Hoffmann A. A. 2010: Predicting the effects of climate change on natural enemies of agricultural pests. *Biological Control* **52**: 296–306.
Trudgill D. L., Honěk A., Li D. & van Straalen N. M. 2005: Thermal Time – concepts and utility. *Annals of Applied Biology* **146**: 1–14.