Thermal requirements for development of aphidophagous *Coccinellidae* (Coleoptera), *Chrysopidae*, *Hemerobiidae* (Neuroptera), and *Syrphidae* (Diptera): some general trends

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Summary. The sum of effective temperatures (SET) and lower development threshold (LDT) were established for eggs and/or pupae of central European populations of 20 species of chrysopid, coccinellid, hemerobiid, and syrphid predators of aphids. LDT ranged between 5.6° and 12.2° C, SET between 38.3 and 140.9 day degrees (dd), with broad overlap among stages and taxa. When LDT was plotted against SET, the data for both eggs and pupae were scattered along a single regression line which predicted a 0.47° C decrease in LDT per 10 dd increase in SET ($r = -0.77$, $p < 0.001$). A regression calculated from published data from all over the world predicted a 0.24° C/10 dd decrease in LDT, and the data were more scattered ($r = -0.38$, $p < 0.01$). This is perhaps the first report on the functional relationship between LDT and SET at the interspecific level. The species and stages differed in typical development length (VDL) and in the extent of its deceleration by low temperatures (DD). DD increased with increasing VDL, but the relative effect of low temperature on development length (DD/VDL ratio) reflected thermal adaptations consistent with the life history of the species. Polyvoltine species were less affected by low temperatures than monovoltine species, particularly the thermophilic ones.

Key words: Temperature – Lower development threshold – Sum of effective temperatures – Voltinism – Life history

The importance of two thermal constants, the lower development threshold LDT (temperature when development ceases) and sum of effective temperatures SET (number of day degrees (dd) above LDT for completion of a development stage), for understanding insect life histories has long been recognized. Both reflect the temperature dependence of the rate of ontogenetic development. This may also be affected by factors such as photoperiod, food, or population density. Nevertheless, LDT and SET are good predictors of the timing of life history events, particularly in eggs and pupae whose development depends only on the rate of intrinsic processes. Much attention has been paid to predators of aphids, which show wide inter- and intraspecific (geographic) variation of thermal constants (Appendix 2). We established the constants for eggs and/or pupae of 20 species from a small geographic area. From these homo-

geneous data we were able to demonstrate a relationship between LDT and SET, whose existence and implications we discuss in this paper.

Methods

Experimental material originated from natural populations of central Bohemia. Ovipositing females or larvae before pupation were collected and kept under room conditions (20°–25° C, natural daylength). Freshly deposited egg batches or new pupae were removed at 4–10 h intervals and transferred, usually in batches of 5–10 of each species, into conditions of 15° (or 15.3°), 18°, 21°, and 24° C (with <0.1° C oscillations) and continuous darkness. Egg hatching or emergence from pupae were checked every 12 h, and the length of development was estimated with an accuracy of ±0.1 day. In *Chrysopa carnea*, we recorded the duration of the cocoon period and assumed that the pupal stage is 2/3 of its length (cf. Tauber and Tauber 1974). Average lengths of development were calculated as arithmetic means of observed values.

We used a medium range of temperatures where development length (DL) is inversely proportional to development temperature T (Howe 1967). Then development rate 1/DL is a linear function of T:

$$1/DL = aT + b$$

where a and b are regression parameters fitted to the average observed data for a species. From this, the lower development threshold LDT was calculated as T if $1/DL = 0$, i.e. as $LDT = -b/a$. The sum of effective temperatures SET was calculated as T if $1/DL = 1$ and $b = 0$, i.e. as $SET = 1/a$.

In evaluating the effect of temperature on life histories, we found it useful to calculate two derived characteristics: (1) Typical development length VDL calculated as

$$VDL = ((SET/(T_1 - LDT))^2 + (SET/(T_2 - LDT))^2)^{1/2}$$

and (2) Development deceleration DD caused by decreasing temperature calculated as

$$DD = \sin 45° |SET/(T_1 - LDT) - SET/(T_2 - LDT)|$$

T_1 and T_2 are development temperatures >LDT. Our procedure is presented on the insert of Fig. 2. DLs at $T_{15° C}$ and $T_{25° C}$ were plotted as rectangular coordinates of a point. VDL was calculated as the magnitude of the vector indicating the position of this point, and DD was the direc-

tion of the vector expressed as distance from the dotted line that indicates equal DLs at both temperatures.

Throughout this paper we use the following abbreviations:

DD – deceleration of development due to low temperature (Fig. 2)
dd – day degree
DL – development length
LDT – lower development threshold
SET – sum of effective temperatures
T – temperature of development
VDL – typical development length (Fig. 2)

Results

Thermal constants of development

LDT and SET varied with species and stage (Appendix 1). LDTs of coccinellid eggs ranged between 8.2° and 11.4° C

(mean $10.3 \pm 1.1°$ C), and were significantly higher than in neuropteran egges (6.1°–10.0° C, mean $8.9 \pm 1.4°$ C). LDTs of coccinellid pupae were 8.4°–12.2° C (mean $10.5 \pm 1.5°$ C). They did not differ significantly from LDTs of coccinellid eggs, but were much higher than LDTs of syrphid pupae (5.6°–7.5° C, mean $6.5 \pm 0.9°$ C). SETs of coccinellid eggs (41.7–61.9 dd, mean 50.4 ± 7.6 dd) were significantly lower than SETs of neuropteran eggs (65.3°–100.0 dd, mean 83.7 ± 13.3 dd). SETs of coccinellid pupae (38.3–78.7 dd, mean 66.1 ± 14.1 dd) were similar to SETs of their eggs, but much lower than in syrphids (105.7–140.9 dd, mean 129.1 ± 16.1 dd).

When LDT was plotted against SET on rectangular coordinates (Fig. 1), LDT decreased proportionately to increasing SET. Data for both eggs and pupae were scattered along a common regression line, despite the physiological and morphometric differences of the stages. This relationship holds for both observed (Fig. 1 A) and published (Fig. 1 B) data. The dispersal of our data around the regres-

Appendix 1. The temperature characteristics of eggs and pupae in Bohemian populations of 20 species of aphidophagous predators

Species	Gen[b]	Average development length (days)				LDT	SET	VDL	DD	DD/VDL
		15° C[a]	18° C	21° C	24° C					
Eggs										
Chrysopidae										
Chrysopa carnea	P	10.9[a]	7.7	5.8	4.9	8.0	77.3	11.9	4.6	0.385
C. commata	P	14.6[a]	8.5	6.8	6.0	8.3	90.1	14.5	5.7	0.393
C. perla	P	14.9[a]	8.8	7.5	5.4	9.9	78.1	16.2	7.2	0.444
C. prasina	M	19.2[a]	11.6	8.8	7.0	10.0	97.3	20.5	9.2	0.447
C. septempunctata	P	11.8[a]	7.5	6.0	4.5	9.7	65.3	13.0	5.7	0.437
C. ventralis	M	17.7[a]	11.2	8.6	6.6	9.9	93.3	19.3	8.6	0.444
Coccinellidae										
Adalia bipunctata	P	8.6	5.7	4.1	3.0	10.5	41.7	9.7	4.5	0.466
Adonia variegata	P	9.4[a]	5.8	4.5	4.0	8.2	61.9	9.7	3.8	0.390
Coccinella quinquepunctata	M	13.1	8.1	5.3	4.0	11.4	51.3	14.7	7.4	0.503
C. septempunctata	M	10.9	7.0	4.6	3.9	10.2	52.9	11.6	5.3	0.454
Hippodamia septemmaculata	M	10.2	7.2	4.8	4.0	9.6	57.1	11.2	4.9	0.433
Propylea quatuordecimpunctata	M	10.4	6.3	–	3.3	11.0	43.3	11.3	5.5	0.486
Semiadalia undecimnotata	M	11.0[a]	6.0	4.2	3.5	10.9	44.5	11.3	5.4	0.482
Hemerobiidae										
Micromus angulatus	P	11.4[a]	7.5	5.8	4.6	9.2	68.0	12.5	5.2	0.420
M. variegatus	P	11.6[a]	7.9	6.6	5.7	6.1	100.0	12.4	4.2	0.338
Pupae										
Chrysopidae										
Chrysopa carnea[c]	P	30.7[a]	19.4	14.4	11.4	10.0	111.3	23.6	10.5	0.447
Coccinellidae										
Adalia bipunctata	P	13.2[a]	8.1	6.4	5.3	8.9	78.7	13.8	5.7	0.411
A. decempunctata	P	11.2[a]	6.7	5.9	–	8.4	71.9	11.7	4.6	0.396
Coccinella quinquepunctata	M	16.1[a]	9.4	7.4	5.2	11.0	69.4	18.0	8.8	0.486
C. septempunctata	M	17.0[a]	9.7	6.9	5.4	11.1	69.0	18.4	9.0	0.490
Propylea quatuordecimpunctata	M	11.4[a]	6.6	4.9	3.1	12.2	38.3	14.0	7.6	0.540
Semiadalia undecimnotata	M	16.4[a]	10.0	7.4	5.3	11.1	69.4	18.5	9.1	0.490
Syrphidae										
Episyrphus balteatus	P	14.5	10.1	7.4	6.6	7.5	105.7	15.3	5.7	0.371
Melanostoma mellinum	P	–	11.2	8.1	7.4	5.8	131.6	15.9	5.3	0.332
Scaeva pyrastri	P	18.0	13.0	–	–	7.2	140.9	19.7	7.2	0.367
Sphaerophoria scripta	P	15.5	11.0	8.2	7.9	5.6	138.1	16.3	5.4	0.328

Regression: Eggs   LDT = –0.044 SET + 12.51, r = –0.640, n = 15
    Pupae   LDT = –0.058 SET + 14.35, r = –0.866, n = 11
    Total   LDT = –0.047 SET + 13.02, r = –0.770, n = 26

[a] The species was reared at T = 15.3° C
[b] Voltinism: M – monovoltine species P-polyvoltine species
[c] Development length of cocoon, SET calculated as in Methods
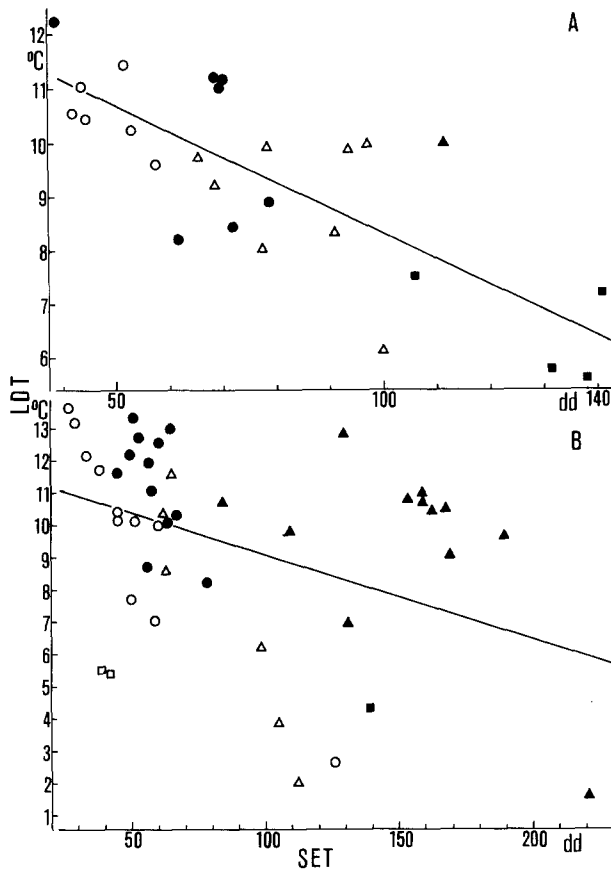
Fig. 1A, B. The relationship between sum of effective temperatures SET and lower development threshold LDT for eggs (*open symbols*) and pupae (*heavy symbols*) of aphidophagous species of A Bohemian populations (Appendix 1), and B populations from all over the world (Appendix 2). o ● Coccinellidae, △ ▲ Neuroptera, □ ■ Syrphidae
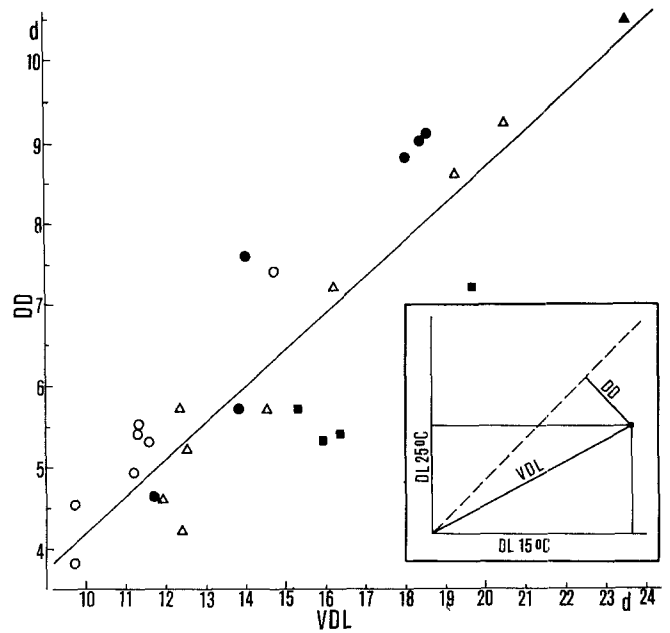

Fig. 2. The relationship between typical development length VDL and deceleration of development due to low temperature DD, in Bohemian populations of aphidophagous species. *Insert*: illustration of the method of calculation and meaning of VDL and DD – see Methods for explanation. Symbols as in Fig. 1

sion line was much smaller ($r = -0.770$, $p < 0.001$) than for all published cases ($r = -0.377$, $p < 0.01$). The regression for our pooled data (LDT = -0.047 SET + 13.02) predicted a greater decrease of LDT with increasing SET than that for published data (LDT = -0.024 SET + 11.48). In our data, the separate regressions for eggs (LDT = -0.044 SET + 12.51, $r = -0.640$) and pupae (LDT = -0.058 SET + 14.35, $r = -0.866$) differed slightly.

In coccinellids, the correlations between egg and pupal SET ($r = 0.185$) and LDT ($r = 0.368$) were not significant in the species we studied. For the published data (Appendix 2) they were virtually zero ($r = -0.109$ and -0.058, respectively).

Differences in development length

Typical development length differed among taxa and stages (Fig. 2). It was significantly smaller in coccinellid eggs (9.7–14.7, mean 11.4 ± 1.7 days) than neuropteran eggs (11.9–20.5, mean 15.0 ± 3.3 days), and coccinellid (11.7–18.5, mean 15.7 ± 2.9 days) and syrphid pupae (15.3–19.7, mean 16.8 ± 2.0 days). DD increased with VDL, and the variation of DD among taxa and stages showed the same trends as VDL.
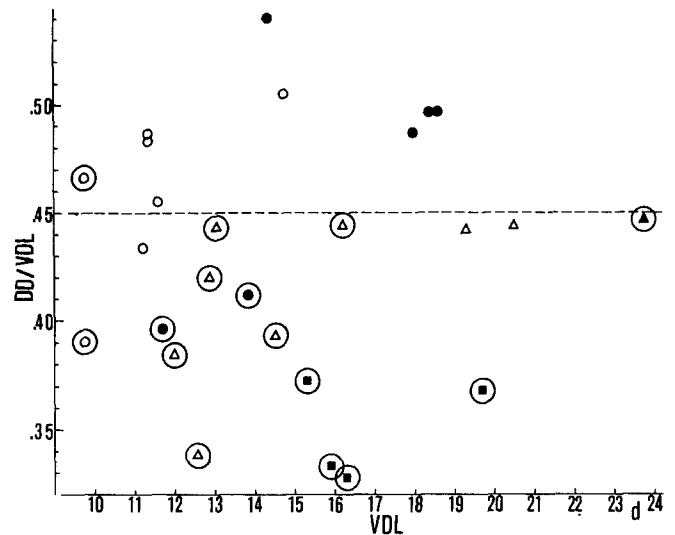

Fig. 3. The relationship between typical development length VDL and relative deceleration of development DD/VDL in Bohemian populations of aphidophagous species. *Circled* – polyvoltine species, *without circle* – monovoltine species. Symbols as in Fig. 1

The relative deceleration of development DD/VDL varied independently of VDL, between 0.328 and 0.540 in our species (Fig. 3). Polyvoltine species had low DD/VDL ratios (usually < 0.45), i.e. the rate of their development was less influenced by low temperatures than that of monovoltine species. This applied to both coccinellid eggs with short VDLs ans syrphid or chrysopid pupae with long development times. Pupae and eggs of monovoltine thermophilic coccinellids (*Coccinella quinquepunctata, C. septempunctata, Semiadalia undecimnotata*) both had high DD/VDL ratios.

Appendix 2. Temperature characteristics of geographic populations of aphidophagous species from all over the world. Standard values recalculated from published data on development length at 10°–25° C

Species	Origin	Eggs		Pupae		References
		LDT	SET	LDT	SET	
Chrysopidae						
Chrysopa carnea	Germany	3.8	104.4	–	–	Bänsch 1964
	USA Arizona	10.3	61.8	10.7	83.7[a]	Butler and Ritchie 1970
	USA Kentucky	8.6	62.2	6.0	130.9	Sheldon and MacLeod 1974
C. harrisii	USA New York	11.5	64.8	12.9	129.1	Tauber and Tauber 1974
C. oculata	Canada	–	–	10.7	158.5	Nechols et al. 1987
	USA Washington	–	–	9.0	169.4	Nechols et al. 1987
	USA New York	–	–	10.8	153.1	Nechols et al. 1987
	USA Utah	–	–	10.4	162.9	Nechols et al. 1987
	USA Colorado	–	–	9.7	178.6	Nechols et al. 1987
	USA Texas	–	–	10.8	158.1	Nechols et al. 1987
	USA Florida	–	–	10.5	168.1	Nechols et al. 1987
C. perla	Germany	6.2	98.3	9.8	108.9[a]	Hinke 1975
Coccinellidae						
Adalia bipunctata	USA New York	7.8	50.4	10.0	63.3	Obrycki and Tauber 1983
Cheilomenes sulphurea	laboratory	10.0	60.0	12.5	60.0	Okrouhlá et al. 1983
Coccinella septempunctata	Czechoslovakia	11.7	38.5	11.9	56.8	Hodek 1958
	USA New Jersey[c]	–	–	11.0	57.8	Obrycki and Tauber 1983
	USA New Jersey[c]	13.2	29.0	13.3	51.2	Butler 1982
C. septempunctata bruckii	Japan	10.2	44.6	13.0	64.8	Kawauchi 1983
	Japan	13.6	27.0	–	–	Butler 1982
	Japan	–	–	12.2	50.4	Sakuratani et al. 1986
C. transversoguttata	USA New York	7.0	58.3	10.3	66.1	Obrycki and Tauber 1983
Coleomegilla maculata	USA New York	10.2	44.9	11.6	45.9	Obrycki and Tauber 1978
Hippodamia convergens	USA Arizona	10.1	45.7	8.3	77.9	Butler and Dickerson 1972
	USA New York	9.7	48.1	11.1	62.2	Obrycki and Tauber 1982
Propylea japonica	Japan	12.1	33.2	8.7	56.5	Kawauchi 1983
Scymnus hoffmani[b]	Japan	2.6	125.7	12.7	52.6	Kawauchi 1983
Hemerobiidae						
Hemerobius pacificus[d]	USA California	2.0	111.8	1.6	221.4[e]	Neuenschwander 1975
Syrphidae						
Metasyrphus corollae	Norway	5.6	38.4	4.3	138.4	Benestad 1970
Scaeva pyrastri	Germany	5.4	42.3	–	–	Bänsch 1964

Regression: Eggs $LDT = -0.094\ SET - 14.16,\ r = -0.782,\ n = 19$
Pupae $LDT = -0.028\ SET - 13.10,\ r = -0.549,\ n = 25$
Total $LDT = -0.024\ SET - 11.48,\ r = -0.377,\ n = 44$

[a] Calculated as 2/3 of cocoon development length
[b] Coccidophagous
[c] Populations introduced from Europe
[d] Data on development length at 4.4° C included
[e] Calculated under assumption that pupal stage takes 4/5 of cocoon development length

Discussion

We found a functional relationship between LDT and SET at the interspecific level. It is perhaps the first time that this relationship, probably of quite general application (Honěk and Kocourek unpublished work), has been established. At the intraspecific level, it is paralleled by relationships among thermal characteristics of geographic populations (Nechols et al. 1987; Tauber et al. 1987). For seven North American populations of *Chrysopa oculata* we obtained $LDT = -0.036\ SET + 16.24,\ r = -0.650$ (from recalculated data given in Appendix 2). The correlation was not significant due to low numbers, but it does seem to follow the interspecific trend. We have no evidence concerning the biochemical and physiological basis of this phenomenon. The formal description of the relationship, however, allows some insight into the strategies of thermal adaptation of aphidophagous species.

Two aspects of thermal adaptation

The meaning of the thermal constants appear when we consider the properties of the relationship:

$$DL = SET/(T - LDT)\ \text{for}\ T > LDT$$

The rate of development has two aspects:
(1) The length of development per se. DL will increase if (a) SET icreases, and (b) T decreases ($T \rightarrow LDT$).
(2) The rate at which development is retarded by a decrease of temperature. Suppose the decrease of T by a decrement $\delta T < (T - LDT)$ causes the increase of DL to $DL' > DL$.
(a) The effect of δT will decrease ($DL'/DL \rightarrow 1$) with increasing SET. (b) The effect of δT will increase if the difference between $(T - \delta T)$ and LDT decreases ($T - \delta T - LDT \rightarrow 0$). In other words, the effect of temperature decrease is small when it occurs far above LDT.

We may now investigate the meaning of the empirically determined co-variation of thermal characteristics (Fig. 1). The negative linear relationship between SET and LDT suggests that the species tend to maintain similar DLs and compensate for high SET by decreasing LDT. The compensation is not perfect, and along the regression line the DLs of the species increase from left to right. The scatter of species values around the regression line, i.e. the change of DL with constant SET, reflect specific adaptive changes of DL and its sensitivity to temperature decrease. Species below the regession line have shorter DLs and are less sensitive to temperature change than those above it. The species least affected by low temperatures are those to the right of the regression, i.e. those with high SET and low LDT.

Thermal adaptations at the species level

The adaptive strategies of aphidophagous species include adjustment of DL and sensitivity to temperature decrease to the demands of timing the life cycles and adaptation to habitat conditions.

Eggs of aphidophagous species reveal adaptive differences in DL. Syrphids make use of the very rapid development resulting from conspicuously low LDTs accompanied by low SET (Appendix 2). Their eggs are laid in large aphid colonies which offer abundant food but may soon disappear (Ito and Iwao 1977; Sanders 1979). Coccinellid eggs have greater DL, and the females start to lay eggs at rather low aphid densities (Honěk 1980). Aphid abundance becomes appropriate for development of larvae only when the first eggs hatch. Coccinellid eggs, with similar SET, have higher LDT than syrphid ones. Chrysopids, particularly Chrysopa carnea, may deposit eggs long before aphids arrive. The eggs hatch after a long period and are adapted to persistence in the field, e.g. by egg stalks which may give some protection against predation.

By contrast, the development of pupae of aphidophages is subject to fewer constraints. The resulting adults are capable of flight and may find food elsewhere. Before pupation, the larva can also minimize temperature effects on pupal DL by selecting appropriate warm sites for pupation. The pupae usually have a greater DL than the eggs.

The adaptations keeping the effects of temperature decrease to a minimum mainly concern the species which develop under a wide range of temperature conditions. In bivoltine species, the second generation encounters the low temperatures of late summer. In fact, the DD/VDL ratio was smaller in polyvoltine species than in monovoltine ones which develop at the optimum period of the season. The insensitivity to low temperatures is achieved by decreasing LDT. In Hemerobiidae specialized for autumn reproduction (Szentkirályi 1986) low LDT was accompanied by high SET.

Preference for cool habitats also require minimization of low temperature effects on DL. The syrphids investigated in this study often inhabit dense plant stands with cold microclimates. They have smaller DD/VDL ratio than thermophilic coccinellids (Coccinella septempunctata, C. quinquepunctata) which inhabit sparse insolated stands of the same crops (Honěk 1983).

Apparently there are constraints on the extent of adaptation through change of LDT and SET. They result from specific morphological and physiological properties of stages and taxonomic groups. Further knowledge concerning the physiological basis of the functional relationship between LDT and SET is needed.

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