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Temperature and development of central European species of *Amara* (Coleoptera: Carabidae)

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Key words. *Amara aenea*, *A. familiaris*, *A. similata*, *A. ovata*, *A. littorea*, *A. eurynota*, *A. fulvipes*, *A. chaudoiri incognita*, *A. equestris*, thermal constants, lower development threshold, sum of effective temperatures, rate isomorphy

Abstract. Development rates of the eggs of 9 species, larvae of 6 species and pupae of 6 species of the genus *Amara* (Coleoptera: Carabidae) were recorded at five constant temperatures between 17 and 28°C, and thermal constants for each development stage calculated. The lower development threshold varied between 9.2–13.5°C for different stages and species. Rate isomorphy, which implies the existence of a common temperature threshold for all development stages, was demonstrated in 5 species. The sum of effective temperatures differed between stages. On average the egg stage took 18%, the first larval instar 13%, second instar 13%, third instar 35% and pupa 21% of the total development time. A poor diet increased the SET of the larvae. The results are compared with published data on Carabidae.

INTRODUCTION

The duration of development is an insect life history trait, shaped by the environments in which the species live. As a consequence relating the variation in development time to geographic or climatic data makes an interesting macroecological study. Important in this context are the differences between closely related taxa. The best characteristics that describe the temperature requirements of a species with direct (non-dormant) development are the thermal constants, lower development threshold (LDT) and sum of effective temperatures (SET). LDT is the temperature at which development ceases, while SET is the number of heat units, day degrees (dd), above the LDT required for complete development. Thermal constants can be calculated assuming a linear relationship between temperature and development rate (reciprocal of development duration). This assumption is realistic for temperatures between 3–4 degrees above LDT and the temperature at which the development is the shortest. In this range of "ecologically relevant temperatures" insects spend most of their active lives (Howe, 1967).

Jarošík et al. (2002) demonstrated that LDT is constrained within a population of a species and does not differ between development stages. A manifestation of this constraint is isomorphy of the development rate, which means that the proportion of development time spent in a particular development stage does not change with temperature. The LDT, however, varies between taxa. A large data set, accumulated over the past 70 years (reviewed by Honěk & Kocourek, 1990; Honěk, 1996; Kiritani, 1997), reveals large differences between species and probably also between populations of the same species. However, for comparative studies this data should be used with caution. As LDT is a virtual value that is outside the range of ecologically relevant temperatures, its calculation involves an extrapolation of experimental data. This makes the estimation of LDT rather imprecise. For forecasting development times this lack of precision is not important (Jarošík et al., 2002). This is because the LDT and SET of a stage are intercorrelated. An error in LDT is accompanied by a corresponding and compensating error in SET, when the duration of development is calculated.

However, for comparative studies any error in LDT has serious consequences. The LDT calculated for a species from the literature often varies by several degrees. Different data sets are difficult to compare because of reported or concealed differences in experimental design. The bias is decreased when several species are compared using a uniform method. The variation in LDT values decreases because the experimental "noise" becomes small relative to the true differences between taxa. For the comparison of closely related taxa and/or those from a small area, data collected under identical conditions are indispensable. In contrast to LDT, SET varies between stages depending on a number of factors including food quality and quantity and body size (Honěk, 1999; Honěk et al., 2002).

The constraints and adaptive trends in thermal constants are best studied in groups of related species using an identical design. In this study the thermal constants of nine species of the genus *Amara* (Coleoptera: Carabidae) were determined. These species commonly occur on arable land where they are important predators of the seeds of weed plants (Thiele, 1977; Saska & Jarošík, 2001). However, the thermal requirements of carabids are little studied and reliable data are scarce. The data collected was used to test for rate isomorphy of development (Jarošík et al., 2002) and compare the thermal constants of closely related species.

MATERIAL AND METHODS

Experimental material. The experiments on species of the genus *Amara* Bonelli were done in 2001 and 2002. Specimens

of species of the subgenus *Amara* Bonelli, *Amara aenea* (De Geer), *Amara similata* (Gyllenhal), *Amara ovata* (Fabricius), *Amara familiaris* (Duftschmid), *Amara littorea* C.G. Thomson, *Amara eurynota* (Panzer) and subgenus *Percosia* Zimmermann, *Amara equestris* (Duftschmid) were collected at Prague-Ruzyně in the Czech Republic (50°06' N, 14°15' E). Those of the subgenus *Zezea* Csiki, *Amara fulvipes* (Audinet-Serville) and *Amara chaudoiri incognita* Fassati were collected at Rybník near Levice, Slovakia (48°18' N, 18°34' E). These beetles were kept in pairs in glass Petri dishes (10 or 20 cm in diameter, 2 or 4 cm deep, filled to a depth of 1 or 2 cm with sieved garden soil moistened with tap water. All species were kept at 17.5 ± 1°C and a long-day photoperiod (16L : 8D). Twice a week the beetles were provided with pieces of larvae of *Tenebrio molitor* Linnaeus (Coleoptera: Tenebrionidae) and a mixture of seeds of herbaceous plants. The quality of the diet influences the rate of oviposition in granivorous species (Saska, unpubl.), therefore the dominant weed species that shed seeds during their respective oviposition periods were chosen as food: *Tripleurospermum inodorum* (L.) Schultz-Bip. and *Artemisia vulgaris* L. for *Amara eurynota* and *A. equestris* (autumn-breeders) and *Stellaria media* (L.) Vill. and *Capsella bursa-pastoris* (L.) Med. for the remaining (spring-breeders) species. To obtain eggs of approximately the same age, the soil was replaced and eggs removed daily.

Experimental temperatures. The duration of development of the egg, larva and pupa were recorded at 17, 19, 22, 25 and 28°C, which fluctuated at irregular intervals by ± 0.7°C around these means. These temperatures were considered to be "ecologically relevant temperatures" (Howe, 1967) for all the species. They were achieved at a tempered room (17°C) and in temperature conditioned boxes (other temperatures). To increase the precision of the temperature measurements, they were recorded at 1 h intervals, using dataloggers Tinytalk® placed within 10 cm of an experimental vial and enclosed in the glass container, which experienced conditions similar to those inside the Petri dishes. The average temperature during development of egg, pupa and each of the larval instars was calculated as an arithmetic mean of the logged data. It was calculated separately for each stage of each individual.

Establishing temperature effects. Eggs, 0–24 h old, were placed in glass Petri dishes (6 cm in diameter, 1.5 cm deep) filled to a depth of 0.4–0.5 cm with plaster of Paris mixed with charcoal. This layer was kept moist by adding daily several drops of tap water, which maintained a suitable humidity but did not cause the growth of moulds. The eggs were examined 3 times a day until they hatched. The larvae were reared individually in Petri dishes (6 cm in diameter, 1.5 cm deep) filled to a depth of 1 cm with sieved garden soil regularly moistened with drops of tap water. The food was placed on the substrate surface. Larvae of the subgenus *Amara* were fed with their preferred seeds: *C. bursa-pastoris* (*A. aenea*, *A. similata*, *A. ovata*, *A. littorea*) or *S. media* (*A. familiaris*) (Saska & Jarošík, 2001). The larvae of *A. fulvipes* and *A. chaudoiri* incognita were fed pieces of *T. molitor* larvae because their food preferences were unknown but previous results indicated they were carnivorous. Moulting of larvae, pupation, and emergence of adults were checked for daily. The development of larvae and pupae of the "autumn-breeding" species *A. eurynota* and *A. equestris* was not investigated because they were expected to undergo larval dormancy. In species of the subgenus *Amara*, duration of development of some individuals increased in the third instar because their legs, head capsule or urogomphi were encrusted with dirt and soil particles. This prevented the larvae from moulting and the development time increased. Data for these larvae were not used to calculate thermal constants.

Data processing. The thermal constants were calculated using the duration of development of stages of particular individuals (D) and mean temperatures (T). A linear relationship between development rate (1/D) and temperature (T): $1/D = aT + b$ was established, separately for each stage of development. From this the lower development threshold LDT (°C) was calculated as $-b/a$, and sum of effective temperatures SET (dd) as $1/a$. A linear relationship between development rate and mean temperature for each stage of each individual was calculated. That is, the thermal constants were calculated from data for particular individuals. This procedure differs from the usual method of calculating thermal constants, which uses the average development length for all the individuals reared at a particular temperature. We adopted this procedure because of (i) oscillations in the mean temperature around the average "constant" temperature (the average temperature was not the same for all individuals) and because (ii) some individuals were observed for only a part of their development. The variation in the duration of development and thermal constants between stages and species was tested by one-way ANOVA, with the thermal constants as dependent variables and development stage or species as factors. The differences between means were tested using a post-hoc LSD test (Sokal & Rohlf, 1981). The calculations were done using the commercial statistical program GLIM® 3.77. Throughout the paper, means are accompanied by ± standard errors of mean (SE).

Rate isomorphy. The data for species that completed development were tested for rate isomorphy. Average proportion of the total development time spent in the egg, larval and pupal stages at 17.5, 19.7, 25.0 and 27.2°C (i.e. average logged temperatures) were calculated. The proportions were plotted against temperature for each stage and species, and regressions of proportions on temperature calculated. The slopes of the regression lines were calculated. Rate isomorphy was tested for using (i) ANOVA, (ii) the slopes of the regressions (Jarošík et al., 2002) and (iii) the slope of the two most different regressions for each species. For the ANOVA, either species or stage was the factor and proportion the dependent variable. Whether the slopes of the regressions differed from zero was tested using t-test: t = slope of regression / SE of the slope (Crawley, 1993). For intraspecific comparison, the two most different regression lines were compared. The differences in proportions against temperature were tested whether the slope of this regression differed from zero using a t-test.

RESULTS

Thermal constants. The development rate increased proportionally with temperature and is well represented by a linear relationship. Data for all development stages were obtained for six species, *A. aenea*, *A. familiaris*, *A. fulvipes* (except the third instar), *A. littorea*, *A. ovata*, *A. similata* (Fig. 1). In *A. chaudoiri incognita*, *A. equestris* and *A. eurynota* only the development of the egg (Fig. 2) was investigated. Thermal constants (Table 1) varied between species and stages. The LDT varied between 9.2°C (*A. similata*, second instar larva) and 13.8°C (*A. fulvipes*, first instar larva). Mean value (± SE) for all stages (n = 32) was 11.1 ± 0.2°C. The maximum range in the LDT for a species was 3.2°C in *A. fulvipes*, the minimum 1.0°C in *A. ovata*. The mean values of the LDTs of the six species, whose complete development

TABLE 1. Lower development threshold LDT (°C) and sum of effective temperatures SET (day degrees) for egg, larval and pupal stages of nine species.

Species	Egg		Larva						Pupa	
			L1		L2		L3			
	LDT	SET	LDT	SET	LDT	SET	LDT	SET	LDT	SET
Amara aenea	10.4	70.9	12.4	47.7	12.2	61.6	10.9	147.1	12.6	70.5
Amara familiaris	10.9	71.5	9.7	51.9	10.7	46.0	9.7	118.9	11.8	69.2
Amara similata	9.3	97.2	10.3	47.9	9.2	53.4	9.5	152.9	11.0	82.5
Amara ovata	11.4	71.6	10.8	47.4	11.8	47.2	10.9	155.6	11.4	81.8
Amara littorea	11.7	59.9	9.8	60.8	11.0	52.1	12.1	139.7	9.9	109.1
Amara eurynota[1]	13.5	110.2	–	–	–	–	–	–	–	–
Amara fulvipes	12.2	56.6	13.8	54.1	10.6	100.9	–	–	12.0	99.9
Amara chaudoiri incognita	9.8	82.7	–	–	–	–	–	–	–	–
Amara equestris[1]	12.6	114.8	–	–	–	–	–	–	–	–

[1]autumn-breeding species

was monitored (Table 2), differed significantly between species (ANOVA: mean square MS = 4.82, $F_{5,23}$ = 3.68, p = 0.014) but not stages within species (ANOVA: MS = 0.88, $F_{4,24}$ = 0.42, p = 0.792). The range in LDT within a stage was between 2.6°C in the third instar and 4.2°C in the egg (mean = 3.3°C, SD = 0.8, n = 5). However, varia-

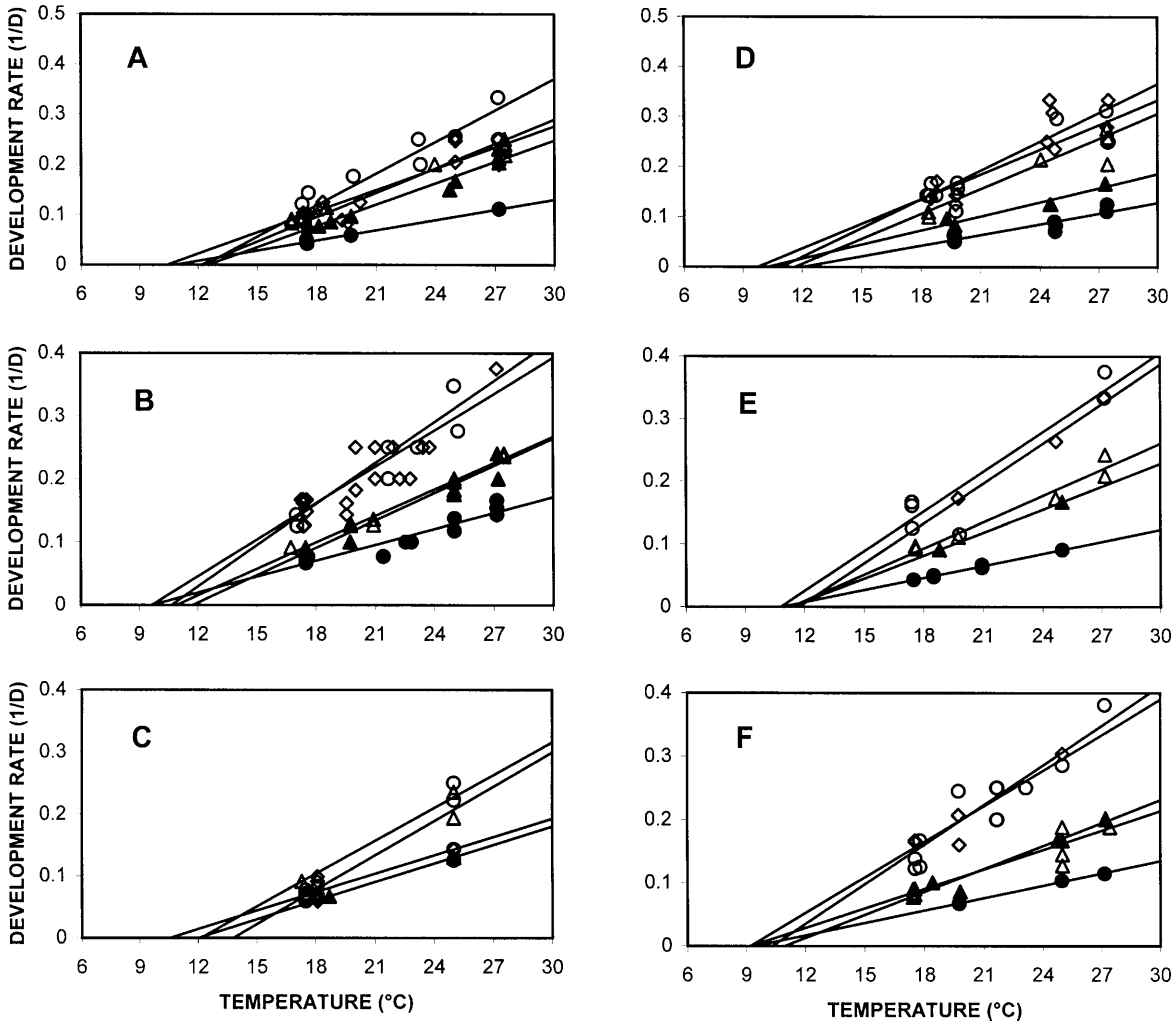

Fig. 1. Linear regression of development rate on temperature for eggs (△), first (○), second (◇), and third (●) instar larvae and pupae (▲) of six species of *Amara*: A – *A. aenea*; *B* – *A. familiaris*; C – *A. fulvipes*; D – *A. littorea*; E – *A. ovata*; F – *A. similata*.

TABLE 2. Mean lower development threshold LDT (°C) and sum of effective temperatures SET (day degrees) for particular development stages and species.

	n	LDT (mean ± SE)	SET (mean ± SE)
Development stage			
egg – pooled data	9	11.3 ± 0.5	81.7 ± 7.1
egg – spring-breeders	7	10.8 ± 0.4	72.9 ± 5.2
egg – autumn-breeders	2	13.1 ± 0.5	112.5 ± 2.3
first instar	6	11.1 ± 0.7	51.6 ± 2.1
second instar – pooled data	6	10.9 ± 0.4	60.2 ± 8.4
second instar – *A. fulvipes* excluded	5	11.0 ± 0.5	52.1 ± 2.8
third instar	5	10.6 ± 0.5	142.8 ± 6.6
pupa	6	11.5 ± 0.4	85.5 ± 6.5
Species			
Amara aenea	5	11.7 ± 0.4	79.6 ± 17.4
Amara familiaris	5	10.6 ± 0.4	71.5 ± 12.8
Amara similata	5	9.9 ± 0.3	86.8 ± 18.9
Amara ovata	5	11.3 ± 0.2	80.7 ± 19.9
Amara littorea	5	10.9 ± 0.5	83.7 ± 17,1
Amara fulvipes	4	12.2 ± 0.7	77.9 ± 13.0
Average	29	10.9 ± 0.3	80.2 ± 6.4

tion in the egg stage decreased when the mean LDT was calculated separately for spring breeding (10.8 ± 0.4°C) and autumn breeding species (13.1 ± 0.5°C), whose LDTs differed significantly ($t = 2.529$, $p < 0.01$).

The SET values (Table 1) differed between stages (MS = 6741.0, $F_{4,27} = 22.76$, $p = 2.56E\text{-}08$) but were similar between species (MS = 333.0, $F_{8,23} = 0.24$, $p = 0.979$). Variation within stages was thus lower than within species (Table 2). The SET of the egg stage varied between 56.6 dd (*A. fulvipes*) and 114.8 dd (*A. equestris*), and was significantly different for "spring" and "autumn--breeding" species ($t = 3.570$, $p < 0.01$). After separating these two groups the variation in SET was smaller (Table 2). The variation in SET in the second instar decreased after excluding *A. fulvipes*, whose development was prolonged by the unsuitable diet (Table 2). In species for which data for all stages were available variation within instars was lower (MS = 7001.0, $F_{4,20} = 47.69$, $p = 5.95E\text{-}10$) than within species (MS = 169.9, $F_{4,20} = 0.11$, $p = 0.978$). The multiple paired comparison test revealed that the SET for the first and second larval instars and for

TABLE 3. The differences in the SET for the different development stages of *A. aenea*, *A. familiaris*, *A. similata*, *A. ovata* and *A. littorea* between stages (LSD test: MS = 7001.0, $F_{4,20} = 47.69$, $p << 0.001$).

Stage	n	egg	L1	L2	L3	pupa
egg	5	0				
L1	5	NS	0			
L2	5	NS	NS	0		
L3	5	*	*	*	0	
pupa	5	NS	*	*	*	0

NS – not significant; * – significant at $p < 0.05$

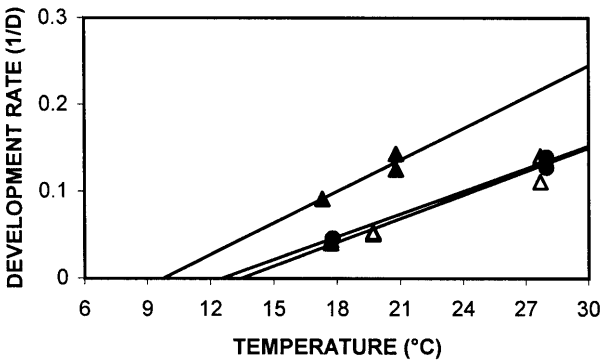

Fig. 2. Linear regression of development rate on temperature for eggs of *A. chaudoiri incognita* (▲), *A.equestris* (○), *A. eurynota* (△).

pupae and eggs were similar while that for the third instar differed significantly from all other instars (Table 3).

Rate isomorphy. The proportions of time spent in a particular stage (Table 4) varied significantly between stages (ANOVA using data for particular larval instars: MS = 0.039, $F_{4,20} = 84.16$, $p = 3.21E\text{-}12$) but not between species (MS = 6.0E-06, $F_{4,20} = 0.001$, $p = 0.999$). Average proportions of time (mean ± SE) spent in the egg stage, first, second and third larval instar, and pupal stage was 18.2 ± 1.3%, 12.6 ± 1.0%, 13.4 ± 1.2%, 34.5 ± 1.3%, and 21.4 ± 0.8%, respectively. The larval stages took 60.4 ± 1.7% of the total development time. The slopes of the regression lines of proportion on temperature were not significantly different from zero for all stages and species (Fig. 3). Maximum departure from a slope of zero was found for the eggs of *A. similata* ($t = 1.46$, $p > 0.2$), the least for the pupae of *A. aenea* ($t = 0.01$, $p > 0.5$). The slopes of the regressions for particular development stages were not significantly different in any species. The greatest departure from a slope of zero was observed in *A. littorea* ($t = 0.77$, $p > 0.5$).

Food and mortality. Generally, the mortality of eggs, first and second instar larvae was low, except for species of the subgenus *Zezea* fed on *T. molitor* larvae. As this unsuitable diet decreased the development rate of the larvae, thermal constants for *A. chaudoiri incognita* (all stages) and *A. fulvipes* (the third instar) were not calculated.

DISCUSSION

Although Carabidae are well studied the effect of temperature on their development has only been studied in

TABLE 4. Proportions of total development spent in particular stages of development in five *Amara* species.

	Egg	Larva				Pupa
		L1	L2	L3	Total	
Amara aenea	0.15	0.13	0.17	0.35	0.65	0.20
Amara familiaris	0.21	0.13	0.13	0.31	0.57	0.22
Amara similata	0.22	0.11	0.12	0.34	0.56	0.22
Amara ovata	0.18	0.13	0.12	0.37	0.62	0.20
Amara littorea	0.15	0.14	0.13	0.36	0.62	0.23

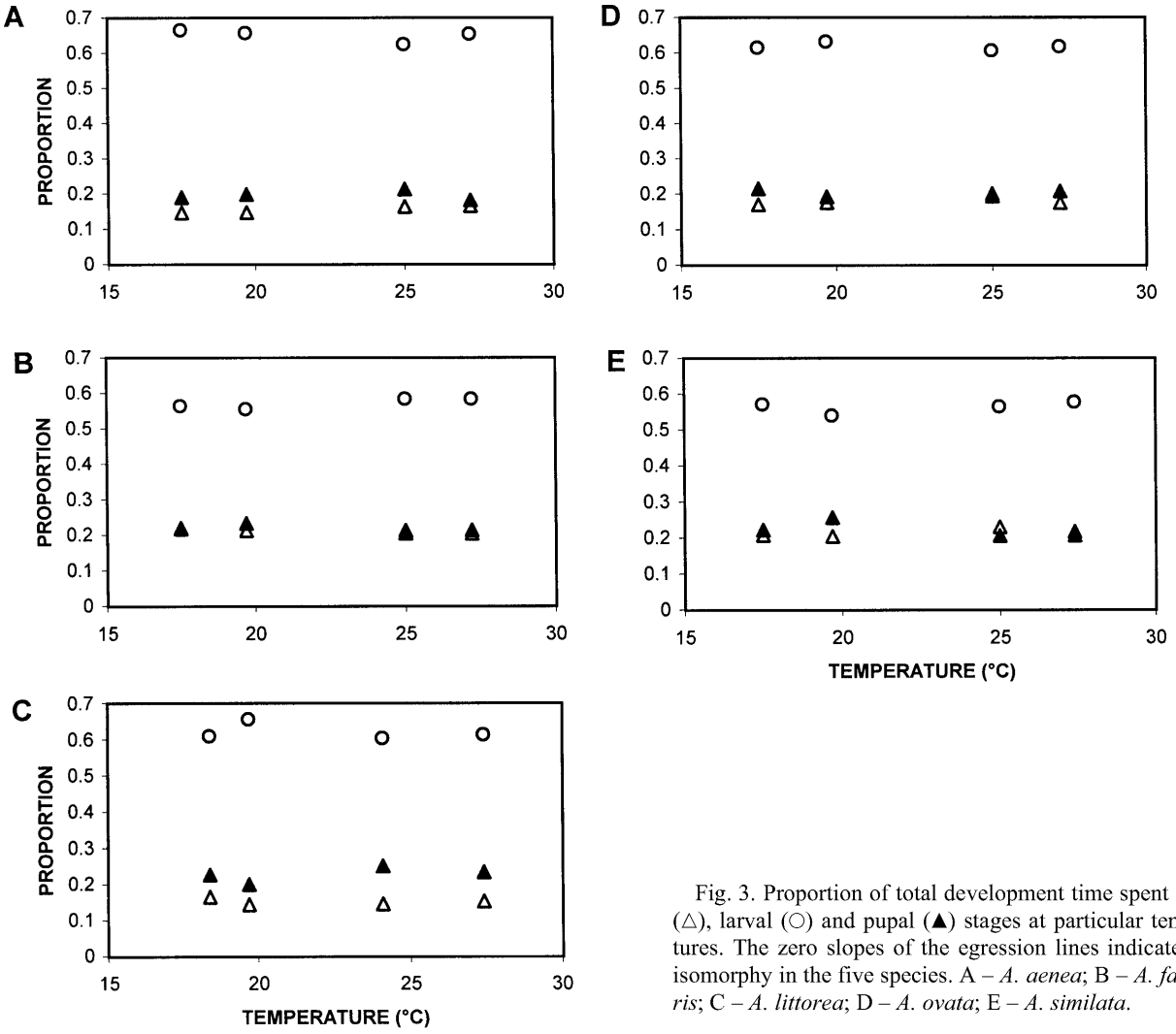

Fig. 3. Proportion of total development time spent in egg (△), larval (○) and pupal (▲) stages at particular temperatures. The zero slopes of the egression lines indicates rate isomorphy in the five species. A – *A. aenea*; B – *A. familiaris*; C – *A. littorea*; D – *A. ovata*; E – *A. similata*.

few species (Balachowsky, 1962; Paarmann, 1966; Luff, 1973; Ferenz, 1975; Hůrka, 1975; Luff, 1975; Sota, 1986; Jensen, 1990; Paarmann, 1994; van Dijk, 1994). From this information the thermal constants for at least one stage were estimated in only 11 species (Table 5). Those for other species are confounded by fluctuating temperature regimes, dormancy or changing food quality. This study doubles the available knowledge by providing data for a further nine species.

TABLE 5. Thermal constants for carabids calculated from data in the literature.

Species	Egg		Larva								Pupa		Reference
			L1		L2		L3		Total				
	LDT	SET	LDT	SET	LDT	SET	LDT	SET	LDT	SET	LDT	SET	
Zabrus tenebrionoides (Goeze)	12.9	118.3											Balachowsky, 1962
Pterostichus quadrifoveolatus Letzner	9.7	77.8	10.7	90.8	10.0	92.1	7.6	210.0			8.6	102.9	Paarmann, 1966
Pterostichus oblongopunctatus (Fabricius)	8.6	88.1	5.8	104.1							8.0	103.4	Paarmann, 1966
Pterostichus madidus (Fabricius)	2.0	285.1					1.9	1819.0			1.6	235.6	Luff, 1973
Pterostichus nigrita (Paykull)[1]									6.7[3]	419.7[3]			Ferenz, 1975
Pterostichus nigrita (Paykull)[2]									6.5[3]	375.5[3]			Ferenz, 1975
Pterostichus melanarius (Illiger)											7.9	139.9	Hůrka, 1975
Nebria brevicollis (Fabricius)											4.0	129.9	Luff, 1975
Carabus yaconinus Bates	5.6	151.1							1.5	597.5	5.7	157.3	Sota, 1986
Bembidion lampros (Herbst)	9.5	93.2							6.1	340.9	7.2	113.7	Jensen, 1990
Pterostichus adstrictus Escholtz	5.5	119.4	6.6	81.5							7.8	97.1	Paarmann, 1994
Poecilus versicolor (Sturm)[4]									8.5	411.0	5.5	135.9	van Dijk, 1994
Poecilus versicolor (Sturm)[5]									7.6	358.8	4.8	133.7	van Dijk, 1994

[1]Germany; [2]Sweden; [3]constants for total development of larva and pupa; [4]low food supply; [5]high food supply.

The range in the LDTs calculated for *Amara* species was 9.2–13.8°C (Table 1). With the exception of the eggs of *Zabrus tenebrionoides* (Goeze) (Balachowsky, 1962) *Pterostichus quadrifoveolatus* Letzner (Paarmann, 1966) and *Bembidion lampros* (Herbst) (Jensen, 1990), and the first and second instars of *P. quadrifoveolatus* (Paarmann, 1966), the previous studies resulted in LDTs that were lower than those recorded for *Amara* species in this study (Table 5).

The variation in the LDT of the different stages of *Amara* species was smaller than that recorded in *Carabus yaconinus* Bates (Sota, 1986) or *Bembidion lampros* (Jensen, 1990) but similar to that in *P. quadrifoveolatus* (Paarmann, 1966). The test for rate isomorphy detected five species for which the assumption of an identical LDT for all the species could not be rejected. The test indicated that the intraspecific variation in the LDT of the different stages of these species (1.0–2.3°C) resulted from an experimental bias in the data. This supports the prediction of Jarošík et al. (2002). However, the distribution of rate isomorphy in taxa, which have different life cycles (Danks, 1987) or show temperature acclimation (Precht et al., 1973), requires further study.

Low interspecific variation in the LDT of *Amara* species (although significant) is consistent with the assumption that the development threshold of taxonomically related species may be constrained (Dixon et al., 1997). However the species with similar LDTs are all spring breeders. To determine the effect of life history spring and autumn breeding species were compared. For *Amara* species the thermal constants of the egg stage of both groups differed. In autumn breeding species the LDT is higher and the SET greater than in spring breeders. One might expect an opposite trend since low LDT would facilitate egg development in the cool weather of autumn. Thus in larvae of *C. yaconinus* the low LDT could be an adaptation to low temperatures (Sota, 1986). An example of this type of adaptation is seen in the autumn breeding neuropteran genus *Micromus* (Hemerobiidae) (Szentkiralyi, 1986). In Central Europe, the LDT for egg development in this genus is significantly lower (7.3 ± 1.1°C) than in spring and summer breeding species of the family Chrysopidae (9.3 ± 0.3°C) (Honěk & Kocourek, 1988). However, the opposite trend in *Amara* species may have an ecological significance. This is supported by the existence of a high LDT and SET in another autumn-breeding species, *Z. tenebrionoides* (Balachowsky, 1962). High thermal requirements for egg development may postpone the hatching of eggs deposited during a warm period in late summer. The delay in hatching results in timing of larval development occurring just before the overwintering period when the third instar larvae enter an obligatory diapause.

The first and second instars of all five species fed the same suitable diet had similar development times (and SET), whereas that of the third instar was 2–3 times longer. This distribution of development times between larval instars is typical of carabid species whose larvae develop without dormancy (Hůrka, 1988). The proportion of the total development time spent in a particular stage (Table 4) is near to the average values established for Coleoptera, that is, 18% for egg and 20% for pupal stages (Honěk & Kocourek, 1990).

The development rate of *Amara* species fed a poor diet is decreased slightly in the first instar, and more so in the second and third instars (Saska & Jarošík, 2001). In this study the development rate of *A. fulvipes* and *A. chaudoiri incognita* progressively decreased from the second instar onwards. The marked effect of food quality on development rate (and SET) is typical for phytophagous species (e.g. Honěk et al., 2002). In contrast, in the carnivorous *Poecilus versicolor* (Sturm) (Table 5) the effect of food on SET is small (van Dijk, 1994).

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