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Photoperiod–Temperature Interaction—A New Form of Seasonal Control of Growth and Development in Insects and in Particular a Carabid Beetle, *Amara communis* (Coleoptera: Carabidae)

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Abstract—*Amara communis* larvae were found to develop significantly faster and to have higher growth rate at short-day (12 h) as compared to long-day (22 h) photoperiods at all used temperatures (16, 18, 20, and 22°C). The coefficient of linear regression of larval development rate on temperature was significantly higher at the short day than at the long day. The thermal developmental thresholds appeared similar at both photoperiods. Body weight of young beetles reared under different photoperiods was almost the same. Thus, photoperiod does not simply accelerate or decelerate insect development, but modifies the thermal reaction norm. At short days, larval development becomes faster and more temperature-dependent, which provides a timely completion of development at the end of summer. The analysis of literature data has allowed us to find the photoperiodic modification of thermal requirements for development in 5 insect orders: Orthoptera, Heteroptera, Coleoptera, Lepidoptera, and Diptera. Modification may result in significant changes in the slope of the regression line, and hence the sum of degree-days, and in the thermal developmental threshold. Consequently, the thermal requirements for development in many insects gradually vary during summer under the effect of changing day-length, which may have adaptive significance. Thus, the photoperiodic modification of thermal reaction norms acts as a specific form of seasonal control of insect development.

INTRODUCTION

The thermal and photoperiodic environmental conditions are the primary abiotic regulators of arthropod seasonal development. Rates of growth and development in insects, as well as in other ectotherms, directly depend on the environmental temperature, but may also be affected by other factors, such as photoperiod. Day-length acts indirectly by promoting induction and termination of diapause, and it is a reliable cue regulating seasonal cycles in insects. Furthermore, photoperiod affects such quantitative parameters as body weight and proportions, growth rate, and development time, sometimes causing additional larval instars [1, 2].

There are quite a few facts showing photoperiodic effects on the insect development time

[3−10]. The action of the day-length on the larval development time is described for more than 80 species in 10 orders. Most authors often studied the photoperiodic effect on insect development by using two day-length regimens (short and long) at single temperature, rarely at a pair of them. There are very few experiments performed at several photoperiods and temperatures. The traditional point of view is that different day-lengths can accelerate or decelerate insect development, which may be adaptively beneficial for synchronizing the life cycle with climatic seasonality [3, 5, 11]. The more recent advanced interpretation is based on considering adaptive reaction norms that reflect temperature-dependent development of insects at differing day-lengths [12, 13, 14].

Our studies on the linden bug *Pyrrhocoris apterus* at three photoperiods and five temperatures were the first to show that photoperiodic conditions do not simply accelerate or decelerate larval growth and development, as it was shown previously [15, 16], but do change the thermal reaction norm [17]. The short-day photoperiod accelerates nymphal development, as compared to the long-day one, at temperatures below 24°C, but at higher temperatures the pattern is reverse (Fig. 1). Thus, the photoperiodic effect is not straightforward: a certain day-length may accelerate development in comparison to other day-lengths at some temperatures and may decelerate it at other temperatures. It depends on the mutual position of the regression lines of development rate on temperature that describe the thermal reaction norm at various photoperiods. Furthermore, we found out that the slope of the regression line to the x-axis gradually becomes shallower, and the threshold lower, as day-length decreases; that is, development becomes less temperature-dependent. Therefore, the thermal reaction norm is modified as a whole, in the entire optimal range of temperatures, as natural day-length changes in the course of a season. It causes an adaptively beneficial acceleration of nymphal development as summer wanes, days become shorter, and temperatures fall, and allows new adults to emerge in time, as the species overwinters at this stage only. In the first half of summer, when days are long, a stronger sensitivity to temperature changes and faster development at higher temperatures may perhaps allow the second generation bugs
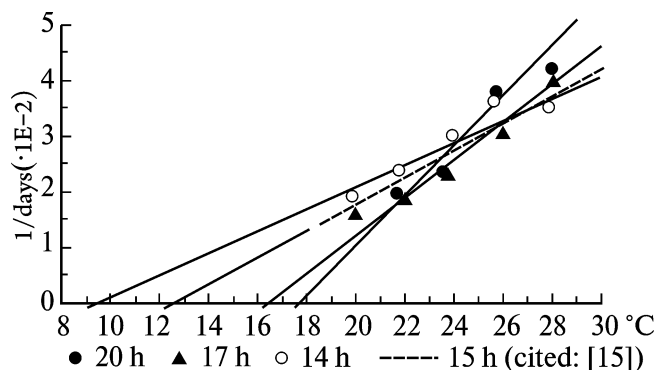

Fig. 1. Regression lines of development rate on temperature in the linden bug *Pyrrhocoris apterus* at different photoperiods [17]. From now on, x-axis is temperature, °C.

to emerge during warmer years in northern regions of the *P. apterus*' distribution range.

We obtained the same result with another species, the red poplar leaf beetle *Chrysomela populi* [18]. The short-day photoperiod has a marked effect on larval development by causing modification of the thermal reaction norm. Under short day conditions, larvae develop faster at lower temperatures, but slower at higher temperatures as compared to the long-day group; so, again, the slope of the regression line becomes shallower, and the threshold lower. Larval development in the red poplar leaf beetle is less sensitive to temperature change under short-day conditions, just as in the linden bug, which is apparently advantageous at the end of summer when days grow shorter and it turns colder. Therefore, larvae can complete development and pupate successfully. Adults would emerge before the onset of harsh conditions, and overwinter.

In this work we examine effect of photoperiod on thermal reaction norms in the ground beetle *Amara communis*. The Carabidae seem to be never studied in this aspect. *A. communis* is a widely distributed Palaearctic species, generally eurytopic, but preferably inhabiting meadows. Larvae and adults are mainly phytophagous, but may predate on small insects. *A. communis* is a spring-reproducing species with adults overwintering and larvae taking one summer to develop [19]. Thereby, we might expect some kind of short-day modification of thermal reaction norms in larvae late in season.

The second aim of this work was to consider various published sources in search for the experimental data supporting the vast occurrence of photoperiodic modification of thermal reaction norms in insects.

MATERIALS AND METHODS

The experiments were carried out in 2009 at the Laboratory of Physiological and Evolutionary Ecology of Insects (St. Petersburg State University). *A. communis* beetles were collected from May 28 to June 30 using Barber pitfall traps in the park "Sergievka" (Stary Peterhof, St. Petersburg). The traps were visited daily.

Males and females were kept in couples at 20°C and the 22L:2D photoperiod, in 100-mm Petri dishes with wet sand on the bottom and some pieces of sphagnum moss for shelter. In total, there were 23 pairs of beetles. Adults and their larval progeny were fed with meadow grass seed mixture. Every day the beetles were supplied with food and checked for eggs, the latter being taken out of the substrate. Once checked, the sand and sphagnum were discarded and renewed, so that overlooked eggs, if they remained, could not be collected subsequently.

The eggs were laid singly into 40-mm Petri dishes, half filled with annealed and moistened sand, and then were distributed in a random manner among 8 experimental regimens. We used environmental chambers with constant temperatures of 16, 18, 20, and 22°C, and two photoperiods at each temperature, the short day 12L:12D and the long day 22L:2D. Temperature was maintained and measured with a precision of 0.1°C. The monitoring software logged temperature continually. Then, based upon the data logger readings, we calculated mean temperatures for each regimen and developmental stage. The resulting means differed from the set values by no more than ±0.1°C. The daily observations allowed determining the development time (*D*) for each stage with 0.5 d accuracy.

Newly emerged unfed adults were weighed by using a VL-210 electronic analytical balance with 0.1 mg precision. Pupae were not weighed to avoid possible injury, as we had to estimate their development time.

There is an approximately hyperbolic depen-dence of development time on temperature within the favorable thermal range. To transform this dependence into the linear one, we used reciprocal of development time (*D*), i.e., the development rate ($R = 1/D$) that expresses a portion of the whole development completed per unit time. The development rate was calculated for each individual in the experiment, and then the linear regression analysis was performed on the entire sample of development rates at all temperatures *T*, according to Kipyatkov and Lopatina [20], and the following parameters were evaluated: the constant *a* and the regression coefficient *b* from the equation $R = a + bT$, the threshold temperature for development ($T_0 = -a/b$) at which $R = 0$, and their corresponding statistical errors [21, 22].

The coefficient of linear regression *b*, also known as the thermolability coefficient [23, 24, 25] is a measure of how the rate changes as the temperature increases or decreases by 1°C ($b = \Delta R/\Delta T$). In this way, it describes the extent of dependence of development rate on temperature: the more the grade of a slope of the regression line to the x-axis (i.e., the bigger the *b* value), the stronger the dependence on temperature, and vice versa. The sum of degree-days, sometimes also termed the sum of effective temperatures, was calculated as reciprocal of the regression coefficient ($1/b$), its standard error estimated according to Campbell et al. [21].

Weighing newly emerged adults allowed assessment of the individuals' relative growth rate. We used the following formula [26, 27]: $RGR = (\ln P_D - \ln P_0)/D$, where P_0 is the egg weight (mg), P_D is adult weight (mg), *D* is larval development time (days), as growth occurs only at this stage. Therefore, this relative growth rate is daily weight gain per 1 mg of the initial body weight. Although this method is fairly approximate, it is nonetheless acceptable for detection of differences in growth rate if they exist. The *A. communis* eggs appeared very small and impossible to weigh by using our balance, so their weight was assumed to be 0.1 mg.

All described calculations and their basic statistical analysis were performed by using a self-designed form DevRate 4.4 (© V. E. Kipyatkov 1998−2010), realized in QuattroPro 9.0 (© Corel Corporation 1998−2000). Two regression lines for each stage under short and long day conditions were compared by slope (i.e., regression coeffi-

Table 1. Time of development of preimaginal stages in the ground beetle *Amara communis* under short and long-day conditions and at four temperatures

Photoperiod	Stage	Sample size	Temperature, °C			
			16	18	20	22
22L:2D	eggs	404	12.4 ± 0.12	9.8 ± 0.09	8.1 ± 0.08	7.1 ± 0.06
	larvae	138	41.3 ± 0.84	32.8 ± 0.41	27.9 ± 0.42	24.7 ± 0.38
	pupae	80	13.9 ± 0.21	11.7 ± 0.17	8.9 ± 0.13	7.5 ± 0.17
	total	80	66.6 ± 1.28	54.5 ± 0.45	44.8 ± 0.55	39.3 ± 0.46
12L:12D	eggs	391	12.6 ± 0.08	10.0 ± 0.09	8.1 ± 0.08	7.1 ± 0.06
	larvae	235	32.0 ± 0.32	26.1 ± 0.29	22.3 ± 0.36	19.8 ± 0.29
	pupae	153	13.7 ± 0.19	10.5 ± 0.18	8.9 ± 0.14	7.3 ± 0.12
	total	153	58.3 ± 0.45	46.7 ± 0.44	38.8 ± 0.39	33.8 ± 0.18

Note: The data are expressed as the mean values ± SD.

Table 2. Thermal reaction norms for preimaginal development in the ground beetle *Amara communis* under short- and long-day conditions

Photoperiod	Stage	Sample size	Regression coefficient, $°C^{-1} \cdot d^{-1}$	Threshold, °C	Sum of degree-days, $°C \cdot d$
22L:2D	eggs	404	0.01025 ± 0.000233	8.0 ± 0.25	98 ± 2.2
	larvae	138	0.00279 ± 0.000150	7.1 ± 0.67	359 ± 19.3
	pupae	80	0.01085 ± 0.000606	9.6 ± 0.57	92 ± 5.2
	total	80	0.00181 ± 0.000078	7.8 ± 0.52	552 ± 23.9
12K:12D	eggs	391	0.01081 ± 0.000233	8.7 ± 0.23	93 ± 2.0
	larvae	235	0.00332 ± 0.000126	6.5 ± 0.49	302 ± 11.5
	pupae	153	0.01079 ± 0.000468	9.3 ± 0.44	93 ± 4.0
	total	153	0.00215 ± 0.000054	7.9 ± 0.28	465 ± 11.7

Note: The data are expressed as the mean values ± SD.

cient *b*) and threshold using the *t*-test, standard values of these parameters specified. Development times of all stages, adult weights, and relative growth rates were compared with ANOVA and non-parametric Kruskall-Wallis ANOVA, because distributions often deviated from normality and there was a correlation between means and variances [28]. Dependence between two quantities was measured by using Pearson's correlation. Statistical analyses were performed with Statistica 7.1 (© StatSoft, Inc. 1984–2006).

RESULTS

Duration of all developmental stages of the ground beetle *A. communis* at two photoperiods

and four temperatures, and parameters characterizing its temperature-dependent development are presented in Tables 1 and 2. Table 3 summarizes results of comparisons of development times, body weights, and relative growth rates among all thermal and photoperiodic regimens by using two-way factorial ANOVA and Kruskal-Wallis ANOVA.

Both statistical tests revealed a significant effect of photoperiod on larval development time, total development time from oviposition to adult eclosion, and the growth rate. The temperature–photoperiod interaction is significant for all three mentioned traits. It means that there is a difference in functional dependence of development time and rate on temperature under the short- and long-day conditions.

Table 3. The effect of photoperiod on time of development of different stages, adult body weights, and relative growth rates by results of ANOVA and Kruskal-Wallis ANOVA

Parameters	Effect of photoperiod		Temperature–photoperiod interaction (ANOVA)
	ANOVA	Kruskal-Wallis	
Development time			
Eggs	$F_{1.794} = 1.82$ $p = 0.1774$	$H = 0.5295$ $p = 0.4668$	$F_{3.794} = 1.80$ $p = 0.1463$
Larvae	$F_{1.372} = 516.47$ $p = 0.0000$	$H = 56.4908$ $p = 0.0000$	$F_{3.372} = 10.45$ $p = 0.0000$
Pupae	$F_{1.232} = 4.76$ $p = 0.0302$	$H = 0.7380$ $p = 0.3903$	$F_{3.232} = 2.74$ $p = 0.0441$
Total development	$F_{1.232} = 399.23$ $p = 0.0000$	$H = 15.3162$ $p = 0.0001$	$F_{3.232} = 3.15$ $p = 0.0257$
Adult weight	$F_{1.205} = 2.54$ $p = 0.0580$	$H = 1.6947$ $p = 0.1930$	$F_{3.205} = 1.24$ $p = 0.2978$
Relative growth rate	$F_{1.205} = 251.21$ $p = 0.0000$	$H = 45.5995$ $p = 0.0000$	$F_{3.205} = 5.17$ $p = 0.0019$
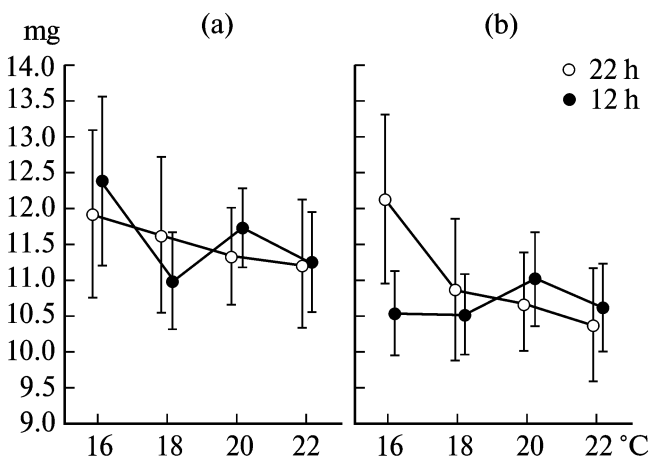
Fig. 2. Body weight (vertical axis, mg) in *Amara communis* at different temperatures and photoperiods. White circles—day, black circles—night. (a) Females, (b) males. Vertical bars designate confidence intervals at $p \leq 0.05$.

According to ANOVA, there was a weak, but significant photoperiodic effect on pupal development time, although it was not confirmed by the Kruskal-Wallis test (Table 3). There was no effect of photoperiod on eggs.

The short-day photoperiod accelerated larval development in the ground beetle, on average, by 20.7%, and, as a consequence, reduced the total

development time, on average, by 13.5% at all used temperature regimes (Table 1).

ANOVA and Kruskal-Wallis ANOVA did not reveal any effect of temperature or photoperiod on adult weight. However, the body weight had a slight decreasing tendency for the temperature rise from 16 to 22°C under long-day conditions, which was more pronounced in males ($F_{3, 37} = 4.594$, $p < 0.0084$, $H = 7.5165$, $p = 0.057$) (Fig. 2). There was a strong and significant correlation between the male weight and temperature ($r = -0.48$; $p < 0.05$), yet it was absent under short-day conditions (Fig. 2).

The only factor significantly affecting body weight was sex ($F_{1, 205} = 11.26$, $p < 0.0009$; $H = 21.71$, $p < 0.0000$): all regimes put together, females were heavier than males, on average, by 1 mg (11.5 and 10.7 mg, respectively).

ANOVA and Kruskal-Wallis ANOVA revealed a weak, but significant relationship between sex and pupal development time ($F_{1, 205} = 8.53$, $p = 0.0039$; $H = 3.7303$, p = 0.053). Female pupae developed a little faster, although the difference was negligible (Fig. 3).

There were no sex differences in development time. We also found no correlation between the larval or pupal development time and adult weight as well as between the larval and pupal develop-

ment times.

The relative growth rate was significantly different between the two photoperiodic regimes (Table 3, Fig. 4): both in males and in females it was higher under short day conditions.

Table 2 combines parameters of linear regression of development rate on temperature in preimaginal stages of *A. communis* under short- and long-day conditions. Pairwise comparisons of the thresholds and regression coefficients using *t*-test resulted in the following. Within a given stage, temperature thresholds did not differ between the photoperiods. The pupal thresholds were the highest both under the long ($9.6 \pm 0.57°C$) and under the short day conditions ($9.3 \pm 0.44°C$), differing significantly from thresholds of other stages ($p < 0.001$). The regression coefficients, as well as the sums of degree-days, of eggs and pupae did not differ from each other and between the photoperiodic regimes. These were the fastest stages with the highest sensitivity to temperature change and the lowest sum of degree-days ($98-92$ °C·d). Larvae had the longer development that was less temperature-dependent. Their thresholds and regression coefficients at both day-lengths were significantly lower than those in eggs and pupae ($p < 0.001$).

Figure 5 shows the regression lines of development rate on temperature for the long- and short-day larvae and pupae. The lines for pupae run much steeper than those for larvae, as their development rate and regression coefficients are higher. The regression line for the short-day pupae runs somewhat higher and in parallel to that for the long-day group. Therefore, within the optimal thermal range pupal development rate was generally higher under short-day conditions as compared to the long-day ones, although the difference proved to be insignificant. The regression line for the short-day larvae makes a greater angle, whereas the line for the long-day larvae is less inclined to the x-axis. Their thresholds lie quite close to each other (Fig. 5). Accordingly, the short-day larvae have the higher development rate at favorable temperatures than the long-day ones. The regression coefficient for the larvae at the 12-h light (0.00332 ± 0.000126 °C^{-1}·d^{-1}) is significantly higher than that at the 22-h light (0.00279 ± 0.000150 °C^{-1}·d^{-1}), and the sum of degree-days is lower (302 ± 11.5 and 359 ± 19.3°C·d, respective-
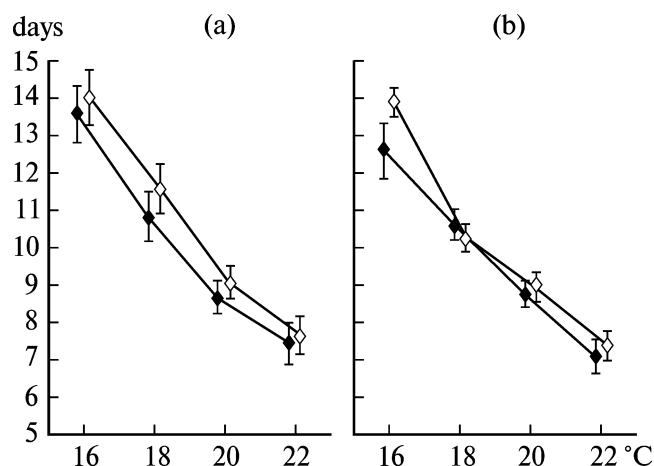

Fig. 3. Pupal development time in males (white circles) and females (black circles) of *Amara communis* at different temperatures and photoperiods. (a) 22L:2D, (b) 12L : 12D. Vertical bars designate confidence intervals at $p \leq 0.05$.
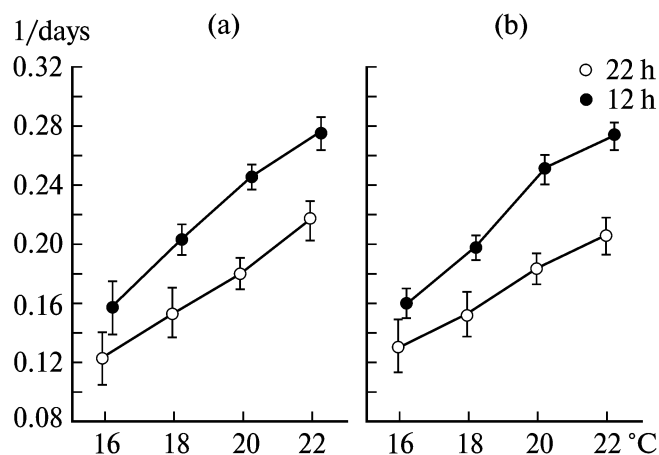

Fig. 4. Relative growth rate in larvae of *Amara communis* at different temperatures and photoperiods. (a) Females, (b) males. Vertical bars designate confidence intervals at $p \leq 0.05$.

ly). Comparing the thermal reaction norms for the total development between photoperiods gives the same result, as the mean fraction of the larval stage was 61.1% and 56.7% under long and short day conditions, respectively, i.e. this stage accounts for more than half of the duration of development in this ground beetle.

DISCUSSION

Our experiments showed a considerable effect of the day-length on the development time
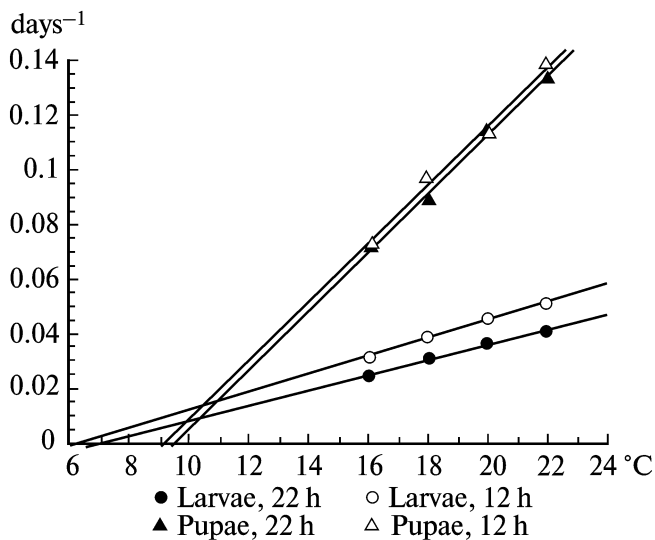
days^{-1}

Fig. 5. Regression lines of development rate (ordinate) on temperature (abscissa) in larvae and pupae of *Amara communis* at two photoperiods.

in the ground beetle *A. communis.* The short-day photoperiod caused the more rapid development in larvae at all used temperatures. It did not affect duration of egg development and very weakly accelerated development of pupae, the latter also might be a residual effect of the photoperiod experienced by larvae. Eggs and pupae develop in the soil, and probably cannot receive light stimuli.

Neither photoperiodic nor thermal conditions had a substantial effect on the beetle weight. However, under the long day conditions, the body weight tended to decrease with temperature rise from 16 to 22°C, especially in males (Fig. 3). There was no such tendency under the short day. The earlier studies on *A. communis* from St. Petersburg and Arkhangelsk at the 22L:2D photoperiod did not find any temperature effect on body weight [29].

The female pupae developed a little faster than the male ones, although females were heavier, on average, by 1 mg. We weighed newly emerged adults only, but supposed that the female pupae were heavier as well. Similar sexual differences in the development time and body weight were found in the common fruit fly *Drosophila melanogaster* [30] and the butterfly *Bicyclus anynana* [31]: the female pupae were heavier, but developed faster than the male ones. Small-sized pupae of the western spruce budworm *Chroristoneura occiden-*

talis also took longer to develop [32]. A reverse relationship was revealed in the swallowtail *Papilio polyxenes* [33] and the melon fly *Dacus cucrbitae* [34]: the smaller male pupae developed faster than the large female ones. More rapid development of smaller pupae was also described in the blow-fly *Calliphora vicina*, sex undetermined [35], and in workers of Myrmica ants [36].

The *A. communis* growth rate was significantly higher under short-day conditions in comparison to the long-day ones, which is not surprising, assuming similar weights throughout all regimes and the faster development of the short-day larvae.

Photoperiod did not affect the thermal thresholds for development in all the stages, of which the pupal ones were the highest. The regression coefficients (and sums of degree-days) did not differ between eggs and pupae and, in these cases, between photoperiods (Table 2). However, the regression coefficient in the short-day larvae as compared to the long-day ones was higher (0.00332 ± 0.000126 °C^{-1}·d^{-1} and 0.00279 ± 0.000150 °C^{-1}·d^{-1}, respectively), and the sum of degree-days lower (302 ± 11.5 and 359 ± 19.3 °C·d, respectively). This is our most important result. The same effect was found when comparing the thermal reaction norms for total development under different photoperiodic conditions, as the fraction of the larval stage in preimaginal development was about 60%.

Therefore, the short-day photoperiod does not merely accelerate larval development—it modifies the thermal reaction norm, increasing the angle of the regression line to the x-axis (Fig. 5). At the same time, the threshold temperatures remain quite similar. In other words, there is a short-day-promoted increase in the developmental sensitivity to temperature change. This may be adaptively beneficial, as the faster larval development at the end of summer, at a time when the day-length decreases, allows the more efficient use of heat sources and successful timely pupation. Adults would emerge before the onset of adverse conditions, and then overwinter. As the day-length gradually diminishes, the sum of degree-days decreases without shifting the threshold to the right. Thus, during its range expansion to the High North, *A. communis* is able to inhabit seemingly unsuitable biotopes providing less heat than the long-day sum
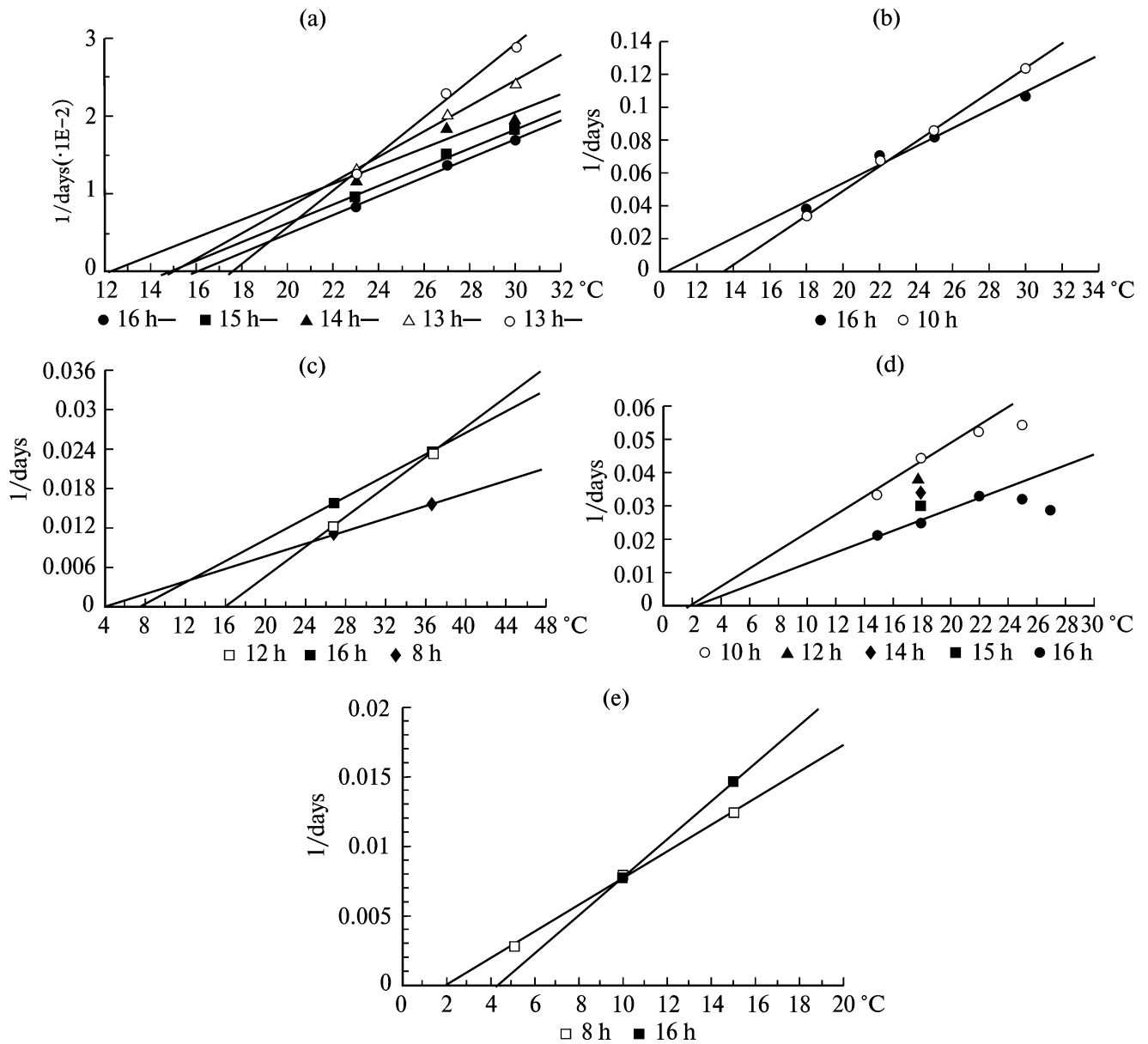
Fig. 6. Regression lines of development rate (ordinate) on temperature (abscissa) at different photoperiods in several insect species, calculated and plotted for the data from various publications. (a) Larval development in the cricket *Dianemobius (Pteronemobius) fascipes*, from [38]; (b) larval development in the lady beetle *Coccinella septempunctata brucki*, from [39]; (c) larval development in the acridid *Acrotylus insubricus*, from [40]; (d) development of the III instar larvae of the lady beetle *Epilachna admirabilis*, data from [41]; (e) total preimaginal development in the rove beetle *Quedius pellax*, from [42].

of degree-days [37].

The pattern of the photoperiodic modification of thermal reaction norms in *A. communis* is entirely different from what we found in the linden bug *Pyrrhocoris apterus* and the red poplar leaf beetle *Chrysomela populi* [17, 18]. In the latter cases, short-day conditions promoted a decrease

both in the regression coefficient and in threshold, i.e., the larval development became more temperature-dependent as compared to the long-day group (Fig. 1). Therefore, we found another type of modification of thermal reaction norms promoted by the decreasing day-length late in season.

To ascertain how widespread such modification

is, we performed a review of published data on the insect development time at different temperatures and photoperiods by using our method that allows assessment of the photoperiodic effect on thermal reaction norms. The authors of the papers cited below did not question this issue, and their aims also were different. Often we had to take the data from the graphs plotted for other purposes.

Very interesting are the results of Kidokoro and Masaki [38] on the nymphal development of the ground cricket *Dianemobius (Pteronemobius) fascipes* at three temperatures and five photoperiods. We transformed them into regression equations of development rate on temperature. As seen from Fig. 6a, a decrease in the day-length from 16 to 14 h is accompanied by a full-range acceleration of development and lowering of the threshold, whereas the angle between the regression line and the x-axis probably remains the same, i.e., the degree of thermal sensitivity of development rate does not change. However, as the day-length declines further from 13 to 12 h, the pattern changes: now the regression coefficient and threshold increase, so that the nymphal development under the 12-h light is the most dependent on temperature. Possibly, these cricket nymphs are still able to find warmer habitats in Japan in September to complete their development successfully (the more so, as they can bask in the sun), and then adults could lay eggs before winter. We suppose that it would be advantageous in autumn to develop more rapidly under warm conditions, even though there is a deceleration of development at lower temperatures.

Here is one more remarkable example. We calculated the linear regression parameters for the development rate of the *Coccinella septempunctata brucki* larvae (the seven-spotted lady beetle subspecies inhabiting Central Japan) under the long-day (16L:8D) and short-day conditions (10L:14D). The data were taken from Sakurai et al. [39]. The regression line for the short-day larvae runs steeper than that for the long-day individuals (Fig. 6b). Their developmental threshold is also higher. It means that development under the short-day conditions is more sensitive to temperature changes. The short-day photoperiod accelerates development at higher temperatures, and so the long-day photoperiod does at lower temperatures: unlike what was described for the linden bug

(Fig. 1) and the red poplar leaf beetle. Apparently, like in the previous case of *D. fascipes*, the ladybug larvae can find warmer habitats in autumn to complete development. The overwintered adults oviposit in spring, and larvae develop successfully at lower temperatures and growing day-length. Newly emerged adults undergo summer diapause.

We also found a modification of the thermal reaction norms in the acridid *Acrotylus insubricus* from Egypt, studied at two temperatures of 27 and 37°C and three photoperiods: 8L : 16D, 12L : 12D, and 16L : 8D [40]. This insect develops continuously throughout the year without diapause in Egypt. The longest development was observed by the authors under the winter day-length of 8 h. Judging from the mutual position of the regression lines (Fig. 6c), which we plotted based on the primary data from the paper, the nymphal development in winter is characterized by a very low degree of temperature-dependence and a low threshold. The line is less inclined to the x-axis as compared to the others, which indicates the highest sum of degree-days. However, such response makes development possible at much lower winter temperatures than what nymphs experience during summer and autumn. In spring and summer, as the day-length increases to 16 h, the slope of the regression line and the threshold also increase, the sum of degree-days lowers. Development is accelerated at temperatures below 37°C. As the season proceeds, the temperature-dependence and the threshold of the nymphal development further increase (the regression line for 12L : 12D photoperiod runs even steeper than that for 16L : 8D); therefore, at the 12-h day-length, development is decelerated at temperatures below 37°C. The authors noted that nymphal development at 27°C was longer at the 12L : 12D photoperiod than at 16L : 8D. However, there is a simultaneous acceleration of development at temperatures above 37°C: it is still very hot in Egypt in September, and nymphs can bask in the sun, so such acceleration may be adaptively beneficial. The sensitivity to temperature change and the threshold appeared higher at 12-h light than at the long-day regime, like in *C. septempunctata brucki* (Fig. 6b). Then, as temperatures fall and day-length declines, the slope and threshold gradually return to their winter position.

The modification of thermal reaction norms is possible not only when adults overwinter, such as in *P. apterus*, *Ch. populi*, *A. communis*, and *C. septempunctata brucki*, but also in the species with overwintering larvae. For instance, the lady beetle *Epilachna admirabilis* from Japan [41] overwinters as IV instar larvae, and in the III instar there is a photoperiodic modification of thermal reaction norms for development, which is similar to one described above for *A. communis*: the short-day conditions (10L : 14D) have an accelerating effect at the four experimental temperatures, as compared to long-day (16L : 8D). Our calculations show that the slope of the regression line becomes steeper at the short day, whereas the threshold remains the same (Fig. 6d), i.e., the way it is in *A. communis*. We performed the regression analysis using only three temperatures, as there was an obvious deviation from linearity at 26°C. The author also obtained the data on larval development time under the three intermediate photoperiods (12L : 12D, 14L : 10D, and 15L : 9D) at 18°C, which indicate a possible graduation in thermal reaction norm changes in response to decreasing the day-length.

The North-American rove beetles *Quedius pellax* (Staphylinidae) with larval development during winter and an adult summer diapause were shown to have photoperiodic control of development time in the III instar [42]. The authors found that development was faster under the long-day conditions (16L : 8D) as compared to the short day (8L : 16D). The threshold temperature for total development was noted to increase from 1.8 to 4.2°C, and the sum of degree-days to decrease from 1086 to 205°C·d with growing day-length (Fig. 6e). Thus, here we observe a change in the functional dependence of development rate on temperature, as days grow longer in spring and early summer. There is a very weak temperature-sensitivity of development in winter, and the regression line runs shallower, the threshold being low. Preimaginal development is possible at temperatures below 8°C. Then, with growing day-length in spring, development becomes more temperature-dependent and is accelerated at temperatures above 8°C, the slope and threshold increase. Such response facilitates the timely completion of larval development and adult transition to diapause in summer.

Similar modification of thermal reaction norms may be observed in IV instar larvae of the tree hole breeding mosquito *Ochlerotatus triseriatus*. Their development begins early in spring. Under short day conditions (12L:12D), the larval development rate weakly depends on temperature, but this dependence becomes more pronounced at the long day (16.5L : 7.5D) [43]. We can conclude that the day-length variation in nature promotes the modification of thermal reaction norms, so that larval development is more sensitive to temperature change in spring and early summer. Both the slope and threshold would probably increase in response to increasing day-length, as described above for *Q. pellax*.

Gotthard at al. [13, 14] used another approach for studying thermal reaction norms at different day-lengths. They measured growth rate in *Lasiommata maera* caterpillars at three temperatures and two photoperiods (14L : 10D and 17L : 7D) in autumn, before overwintering, and afterwards in spring. The authors did not calculate the linear regression equations and determined the thresholds for growth rate under different photoperiodic conditions. They revealed an increase in growth rate of the II instar larvae and in its degree of dependence to temperature under short-day conditions. Late in season, caterpillars must moult into the III instar rapidly to undergo diapause at this stage. In spring, after larval overwintering in the field, the authors estimated growth rate again, this time in the final (IV) instar caterpillars. The reaction norm appeared to change, as this time the increase in growth rate and in its degree of dependence on temperature was found under long-day conditions. Thereby, we may come to the conclusion about adaptively beneficial seasonal changes in thermal reaction norms: the higher slope and threshold are observed under long day conditions at the beginning of summer, and at short days in autumn. A similar response was discussed above in *C. septempunctata brucki*.

Other examples of photoperiodic modification of thermal reaction norms we found by analyzing the published sources listed in our previous paper [17].

In all such cases, the authors stated the developmental acceleration or deceleration phenomenologically, without paying attention to the in-

teraction of two ecological factors, temperature and photoperiod. The fact of the thermal modification of photoperiodic reaction norms is well-established: the temperature is known to affect the incidence of diapause and the critical photoperiod for diapause induction [3, 5, 6, 11]. We argue that photoperiod, in turn, also can modify the thermal reaction norm: the development rate depends on temperature to a varying extent at different day-lengths. Therefore, the threshold temperature, the slope of the regression line, and the sum of degree-days can be controlled by photoperiod.

Such photoperiodic modification of thermal reaction norms is a widespread phenomenon in insects, as can be seen from our results and the reconsideration of the previous data by different authors. It is confirmed in 5 insect orders: Orthoptera, Heteroptera, Coleoptera, Lepidoptera, and Diptera.

It is possible to outline some general patterns of the photoperiodic modification of thermal reaction norms.

(1) *A gradual decrease both in the slope and in the threshold as days grow shorter*, i.e., a decrease in the sensitivity of development rate to temperature changes, as the season proceeds. Development is accelerated under short day conditions at lower temperatures, below the intersection point of the regression lines, and under long day conditions at higher temperatures, above this point. We revealed this form of modification in the linden bug *Pyrrhocoris apterus* (Fig. 1) and in the red poplar leaf beetle *Ch. populi* [17, 18]. We also found a gradual decline in the degree of temperature-dependence of development with decreasing day-length analyzing some previous works [17], specifically in the grasshopper *Melanoplus sanguinipes* [44], bugs *Graphosoma lineatum* [8] and *Palomena prasina* [45]. Unfortunately, the experiments with these bugs were performed at the 15-h or more daily light, so it is not certain whether this pattern would hold at shorter photoperiods.

(2) *An increase both in the slope and in the threshold under short day conditions.* Development is accelerated at short photoperiods at higher temperatures, above the intersection point, and under long-day conditions at lower temperatures, below the point (Fig. 6b). This pattern of the thermal reaction norm modification we found in the lady beetle *C. septempunctata brucki* according to the data from Sakurai et al. [39]. Seasonal changes in thermal reaction norms in *L. maera* are probably similar to this type.

(3) *The short-day-promoted acceleration of development in the full temperature range.* The regression line makes a greater angle to the x-axis under short-day conditions, but the threshold remains almost the same. This pattern is described in the present paper and was also found in *E. admirabilis* (Fig. 6d), according to the data of Hoshikawa [41].

(4) *An increase both in the slope and in the threshold under long-day conditions in the winter and early spring species.* Under winter conditions with very short photoperiods, development is accelerated at lower temperatures, the regression line runs shallower and the threshold is low, i.e., development is weakly temperature-dependent (Fig. 6e). Then, as days grow longer, development is accelerated at higher temperatures, the regression line gets more inclined to the x-axis, and the threshold increases, i.e., development becomes more temperature-sensitive. This type of the photoperiodic modification of thermal reaction norms was described above, based on external sources, for *Q. pellax* [42] and *O. triseriatus* [43].

(5) Using the data of Kidokoro and Masaki [38] who used a broad range of photoperiods, we found a complex form of the photoperiodic modification of thermal reaction norms in the cricket *D. fascipes.* This is the most extensively studied species, and it is possible to track the modification of its reaction norms throughout the entire season. First, as day-length decreases to 14 h, the threshold gradually shifts to the left, the slope of the regression line remains more or less constant (Fig. 6a). A further decrease in day-length to 12 h promotes a steepening of the slope and an increase in the threshold, i.e., development becomes more temperature-dependent, like in *C. septempunctata brucki* (Fig. 6b).

Another complex form of the photoperiodic modification of thermal reaction norms we found by analyzing external sources, in the acridid *A. insubricus* [40]. As day-length increases in spring and early summer, reaching 16 h, the slope and threshold also increase, like in *Q. pellax* (Figs. 6b, 6e). Later, with the day-length reduced to 12 h, the slope and threshold still increase, and the re-

sulting pattern reminds of that in *C. septempunctata bruckii* and *D. fascipes* (Figs. 6a, 6b). The further day-length reduction to 8 h (winter) promotes sharpening of the angle between the regression line of development rate on temperature and the x-axis, i.e., development becomes less temperature-dependent.

It is obvious, however, that the more extensively studied species, the more complex this modification.

It is to be noted that photoperiod does not always modify thermal reaction norms. For example, the day-length has no effect on larval development in the leaf beetle *Gastrophysa viridula* [46] and only slightly affects development in the lady beetle *Stethorus gilvifrons* [47].

The finding of the photoperiodic modification of thermal reaction norms is of considerable theoretical importance. The absence or the limitation of the intraspecies geographic variation of thermal reaction norms remains one of the unsolved problems in evolutionary ecology, yet the theory of life history predicts that such variation should exist [48]. Geographic differences in thermal reaction norms proved to be statistically significant in a few cases only [20, 48], and still they were incomparably small, for example, with respect to the latitudinal differences in photoperiodic reaction [49]. Why is it so? The authors addressing this question proposed several hypotheses [20, 48–50], a detailed review of which would be inappropriate here. On the basis of our results, we can suggest one more explanation.

Insects adapt to their environment in various ways. Natural selection may lead to changes in thermal reaction norms, and different populations would reveal significant differences in laboratory under conditions of a common-garden experiment. Instead of this, or in addition to this, the photoperiodic modification of thermal reaction norms can arise and evolve. In such a case, thermal reaction norms in the geographic populations, studied using traditional methods, would differ a little, and the photoperiodic modification would become more important, providing more rapid and precise adjustment of the life cycle to the environmental conditions at a given latitude, as it changes the degree of dependence of development rate on temperature in keeping with increasing or decreasing day-length. Therefore, the insignificance of the geographic variation of thermal reaction norms may be explained in part by the vast occurrence of their photoperiodic modification.

The photoperiodic modification of thermal reaction norms is to be taken into account when attempting comparative studies. For example, Hon k analyzed the published data on thermal reaction norms in several hundreds of insect species and revealed correlations between the threshold and sum of degree-days [51, 52, 53] as well as between these parameters and latitude [54]. Nevertheless, these correlations were typically weak, sometimes insignificant, and accompanied by a great dispersion of data. The author suggested [54] that this dispersion might be due to methodical discrepancies in assessment of thermal reaction norms by different authors and unintended inclusion of diapausing stages, as well as interspecies differences in body size, trophic preferences, and biology on the whole. Now we can enlarge this list by adding the photoperiodic modification of thermal reaction norms, ignored by previous authors.

Our results are important from a practical standpoint. For example, the sum of degree-days is widely used in phenological studies and prediction of the number of generations of a certain species during a season, in the analyses of biotopic distribution or geographical spreading of species. Traditionally this parameter has been considered constant and species-specific. In the light of our results, it becomes obvious that one cannot simply rely on the published values of the threshold and sum of degree-days obtained under a single photoperiod or, even more so, under unknown conditions. The possibility of the photoperiodic modification of thermal reaction norms must be kept in mind because both the threshold and sum of degree-days may increase, decrease or remain constant in response to the changing day-length in the course of the season.

CONCLUSION

The photoperiodic effect on insect development is not merely accelerating or retarding. Changes in day-length modify thermal reaction norms for development. The photoperiodic modification of thermal reaction norms in different species is ex-

hibited in various ways. It may appear as the significant changing of the slope of the regression line or the threshold temperature, or both. This means that the adaptive changes, mostly gradual ones, in insect thermal reaction norms may occur in the course of the season, promoted by the changes under photoperiodic conditions. The photoperiodic modification of thermal reaction norms is a specific form of regulation of seasonal development in insects.

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