DEVELOPMENTAL ISOMORPHY IN LADYBIRDS (COLEOPTERA: COCCINELLIDAE)

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Analysis of the time spent in the egg, larval and pupal stages by insects reveal a distinct pattern. Although, well fed individuals kept at high temperatures complete their development much faster than poorly fed individuals kept at low temperatures, nevertheless, they all spend the same proportion of the total time required for development in each developmental stage. Data will be presented that indicate that ladybirds conform to this pattern. All stages of development appear to have the same lower developmental threshold. If this is true than it will greatly facilitate practical studies on the development of ladybirds and improve our understanding of how selection has shaped their life history strategies and those of insects in general.

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INTRODUCTION

That the developmental rate of insects increases with temperature is described by many models. To the best of our knowledge, the most appropriate model is that of SHARPE & DE MICHELLE (1977), which predicts a linear relationship between the developmental rate and temperature in the middle of the temperature range. The linear part of the relationship corresponds to temperatures that are ecologically relevant for insect development, and gives the most reliable approximation of developmental rate (J. Polechová personnal communication). Here we show that the linear approximation is the most appropriate for ladybirds (Coleoptera: Coccinellidae), and introduce the notion of developmental isomorphy.

When data on duration of development are converted into its reciprocal, the developmental rate, the linear approximation of the relationship between the rate of development and temperature enables us to calculate two virtual constants: the sum of effective temperatures, *SET*, i.e. the amount of heat needed to complete a developmental stage, and the lower developmental threshold, *LDT*, i.e. the temperature below which development ceases (e.g., HODEK & HONĚK 1996, pag. 65-71). The thermal constants *SET* and *LDT* can be used for the timing of life-history events, the determination of pre-adult thermal requirements when forecasting and monitoring agricultural and forestry pests, assessing natural enemies suitable for biological control, comparing populations, and determining the effect of phylogeny, geography, body size, food and other constraints on the duration of development. Since LUDWIG (1928) introduced this method it has been widely used, and there are several reviews of the results, including those for ladybirds (HONĚK & KOCOUREK 1990; HONĚK 1996; HODEK &

HONĚK 1996; KIRITANI 1997; DIXON 2000).

If the proportion of total developmental time spent in a particular developmental stage does not change with temperature, than the *LDT* is the same for all developmental stages of a species, and it shows developmental isomorphy. Developmental isomorphy is known for 7 species of mites and 342 species from 11 insect orders (JAROŠÍK et al. 2002). Here developmental isomorphy is demonstrated in non-dormant ladybirds. We discuss how developmental isomorphy can greatly facilitate practical studies on the development of ladybirds.

MATERIAL & METHODS

The linear model

The linear approximation of the relationship between the developmental rate, *DR* (i.e. proportion of development occurring per unit time) and temperature, *t*, can be described as $DR = a + b.t$, where *a* is the intercept with the *y*-axis, and *b* the slope of the linear function. From this equation, the lower developmental threshold, *LDT,* i.e. the temperature when development ceases ($DR = 0$, $t = LDT$) can be estimated as $LDT = -a/b$. Graphically, *LDT* is the value at which the relationship intercepts the temperature axis. Using the relationship between *DR* and *t*, the sum of effective temperatures, *SET*, i.e. number of day degrees above the *LDT* necessary for the completion of a particular developmental stage, can also be estimated. At the moment of completion of a development stage, $DR = 1$ and $t = SET$. Then, shifting *y*-axis so that $a = 0$, $SET = 1/b$.

Reliability of linear vs. exponential models of developmental rates

To assess the suitability of a simple linear model for predicting thermal requirements, the accuracy of linear and exponential approximations of developmental rates were compared. Because the developmental rates at the very low and high temperatures for a species, where mortality sharply increases, are of little practical importance, only data for those temperatures where the mortality was lower than 10% of the maximum survivorship were included in the analysis. Then, the residuals of the linear and exponential approximations were compared using a paired T-test. The data used for this was that for *Hyperapsis notata* (DREYER et al. 1997), *Harmonia axyridis* (LAMANA & MILLER 1998), *Scymnus levaillanti* and *Cycloneda sanguinea* (ISIKBER 1999). These data sets are exceptional as they include the mortality experienced by the species at each temperature.

Testing of developmental isomorphy

The ratios of the times spent in each developmental stage at different constant temperatures (ºC) were recalculated from the data on duration of non-dormant development. In most cases, it was calculated as a ratio of time spent in a particular stage divided by the total pre-imaginal development, i.e., *(egg)/(egg+larva+pupa)*. However, data on a particular stage and an uncompleted total development, e.g., *(larva)/(larva+ pupa)* were also analysed. The calculations used data for three or more temperatures. The data was obtained from the studies listed in Table 1. All the 66 populations of 48 species and subspecies were analysed to avoid bias in favour of the hypothesis being tested. All the data for each particular stage evaluated fell within the range of the linear relationship between the rate of development and temperature.

Table 1
The species and source of the data used for determining developmental isomorphy.

Species	**Reference**	**Temp. (⁰C) #[1]**	**Range**
Adalia bipunctata (L.)	OBRYCKI & TAUBER (1981)	4	18.3-26.7
Adalia bipunctata (L.)	HONĚK & KOCOUREK (1988)	4	15-24
Adalia bipunctata (L.)	GURNEY & HUSSEY (1970)	3	16-24
Adalia flavomaculata DeGeer	MICHELS & BATEMAN (1986)	3	25-29
Brumus suturalis F.	DE FLUITER (1939)	5	23.1-32.2
Calvia quattuordecimguttata (L.)	LAMANA & MILLER (1995)	3	14-26
Calvia quattuordecimguttata (L.)	SEMYANOV (1980)	4	15-30
Cheilomenes sulphurea (Olivier)	OKROUHLÁ et al. (1983)	3	20-28
Chilocorus stigma (Say)	MUMA (1955)	3	16.7-26.7
Hyperaspis notata (Mulsant)	CORREJO et al. (1991)	3	22-30
Coccinella novemnotata Herbst	MCMULLEN (1967)	3	15.6-26.7
Coccinella quinquepunctata L.	HONĚK & KOCOUREK (1988)	4	15-24
Coccinella septempunctata (L.)	HONĚK &KOCOUREK (1988)	4	15-24
Coccinella septempunctata (L.)	HODEK (1958)	3	15-25
Coccinella septempunctata (L.)	BUTLER (1982)	4	17-25
Coccinella septempunctata (L.)	OBRYCKI & TAUBER (1981)	4	18.3-26.7
Coccinella septempunctata (L.)	XIA et al. (1999)	3	15-25
Coccinella septempunctata (L.)	TRITISCH (1997)	3	17-25
Coccinella septempunctata brucki Mulsant	KAWAUCHI (1983)	4	15-25
Coccinella septempunctata brucki Mulsant	KAWAUCHI (1979)	3	20-30
Coccinella septempunctata brucki Mulsant	SAKURAI et al. (1991)	3	22-30
Coccinella transversalis F.	VEERAVEL & BASKARAN (1996)	3	18-30
Coccinella transversoguttata Brown	OBRYCKI & TAUBER (1981)	4	18.3-26.7
Coccinella trifasciata L.	MILLER & LAMANA (1995)	5	18-34
Coccinella undecimpunctata L.	ERAKY & NASSER (1993)	4	14-26
Coelophora quadrivittata Fauvel	CHAZEAU (1981)	3	20-30
Coleomegilla maculata (DeGeer)	OBRYCKI & TAUBER (1978)	4	18.3-26.7
Coleomegilla maculata (DeGeer)	GURNEY & HUSSEY (1970)	3	16-24
Coleomegilla maculata lengi Timberlake	WRIGHT & LAING (1978)	4	19-25
Curinus coeruleus Mulsant	DIRAVIAM & VIRAKTAMATH (1991)	4	22.8-25.8
Cycloneda sanguinea (L.)	ISIKBER (1999)	4	20-27.5
Cycloneda sanguinea (L.)	GURNEY & HUSSEY (1970)	3	16-24
Delphastus catalinae (Horn)	HEMACHANDRA (1994)	3	20-26
Eriopis connexa (Germar)	MILLER & PAUSTIAN (1992)	4	14-26
Harmonia axyridis (Pallas)	KAWAUCHI (1979)	3	20-30
Harmonia axyridis (Pallas)	LAMANA & MILLER (1998)	5	14-30
Hippodamia convergens Guerin	BUTLER & DICKERSON (1972)	4	20-28.9
Hippodamia convergens Guerin	OBRYCKI & TAUBER (1982)	5	15.6-26.7
Hippodamia parenthesis (Say)	ORR & OBRYCKI (1990)	4	14-26
Hippodamia quinquesignata (Kirby)	KADDOU (1960)	3	15.6-30
Hippodamia sinuata Mulsant	MICHELS & BEHLE (1991)	4	15-30
Hippodamia variegata Goetz	MICHELS & BATEMAN (1986)	3	25-29
Hyperaspis notata Mulsant	DREYER ET AL. (1997)	5	18-32
Lemnia biplagiata (Swartz)	SEMYANOV & BEREZNAYA (1988)	3	20-30
Lioadalia flavomaculata (DeGeer)	BROWN (1972)	6	13-27
Menochilus sexmaculatus (F.)	KAWAUCHI (1979)	3	20-30
Menochilus sexmaculatus (F.)	VEERAVEL & BASKARAN (1996)	3	18-30

[1]Number of temperatures

Table 1 (continued)
The species and source of the data used for determining developmental isomorphy.

Species	Reference	Temp. (^{0}C) #[1]	Range
Olla v-nigrum (Mulsant)	KREITER (1985)	5	15-30
Pharoscymnus flexibilis (Mulsant)	SHARMA et al. (1990)	3	24-32
Pharoscymnus numidicus (Mulsant)	KEHAT (1967)	3	24-31
Propylea japonica (Thunberg)	KAWAUCHI (1979)	3	20-30
Propylea japonica (Thunberg)	KAWAUCHI (1983)	4	15-25
Propylea quatuordecimpunctata (L.)	HONĚK & KOCOUREK (1988)	3	15-24
Propylea quatuordecimpunctata (L.)	BAUMGAERTNER et al. (1987)	3	15.3-25.3
Scymnus apiciflavus Motschulsky	DE FLUITER (1939)	6	19.1-32.2
Scymnus frontalis (F.)	NARANJO et al. (1990)	3	15-26.2
Scymnus hoffmani Weise	ZHAO & WANG (1987)	4	18-30
Scymnus hoffmani Weise	KAWAUCHI (1983)	4	15-25
Scymnus interruptus (Goeze)	TAWFIK et al. (1973)	3	15.5-27.9
Scymnus levaillanti Mulsant	ISIKBER (1999)	5	17.5-27.5
Scymnus roepkei de Fluiter	DE FLUITER (1939)	6	19.1-32.2
Semiadalia undecimnotata (Schneider)	HONĚK & KOCOUREK (1988)	4	15-24
Stethorus bifidus Kapur	PETERSON (1993)	5	12.5-27.5
Stethorus punctillum Weise	BERKER (1958)	3	19-35.6
Stethorus japonicus H.Kamiya	TANAKA (1966)	13	17-29
Subcoccinella vigintiquatuorpunctata (L.)	ALI (1971)	3	18-28

[1]Number of temperatures

Angular transformed proportion of total developmental time spent in a particular stage was plotted against temperature, and the existence of developmental isomorphy inferred from a zero change in proportion. Temperature was first regressed with a different intercept and a different slope for each stage (using average proportion for replicated data due to origin or photoperiod), and the significance was then evaluated by simultaneous deletion test. Individual studies on populations of the same species were analysed separately because the results varied due to differences in experimental design. The calculations were performed using general linear modelling in GLIM v. 4 (FRANCIS et al. 1994).

To reach a general conclusion, all the data was then tested using meta-analysis, a statistical synthesis of the results of separate, independent experiments (HEDGES & OLKIN 1985; GUREWITCH & HEDGES 1993; COOPER & HEDGES 1994). The outcome of each analysis was represented by a quantitative index (the effect size), which is independent of sample size, and the null hypothesis that the overall effect size indicates a zero slope was tested. The assumption that the individual analyses share a common population effect size was tested by the homogeneity statistic Q (SHADISH & HADDOCK 1994). Details of the statistical procedure are described in JAROŠÍK et al. (2002).

RESULTS

Linear vs. exponential models of developmental rate

For the four ladybird species for which there is sufficient data on developmental rate and mortality, the linear model gave a better fit ($R^2 = 0.991 \pm 0.0102$) than the exponential ($R^2 = 0.973 \pm 0.0194$) ($t = 2.62$; $df = 3$; $P < 0.05$) (Table 2). That is, the simple linear model is the best for practical purposes.

Table 2
Comparison of explained variance (R^2) obtained by fitting exponential (exp) and linear (lin) approximations to the relationships between developmental rate and temperature in 4 species of ladybirds.

Species	Stage	R^2 *lin*	R^2 *exp*
Cycloneda sanguinea	Pupa	0.990	0.960
Harmonia axyridis	Pupa	0.999	0.976
Hyperaspis notata	Egg - Adult	0.998	0.999
Scymnus levaillanti	Pupa	0.977	0.957
Average		0.991	0.973
Standard error		0.0102	0.0194

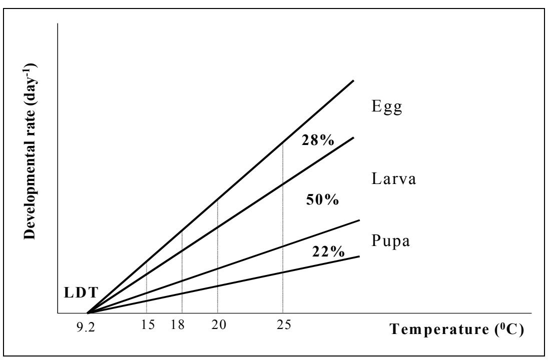

Fig. 1. Effect of temperature (t) on rate of development (RD) within the linear range of the relationship for Propylea japonica. Data from Kawauchi (1983). The population is isomorphic and spent 28% of total development in egg, 50% in larva, and 22% in pupa at temperatures 15, 18, 20 and 25 ^{0}C. All developmental stages have a common lower developmental threshold (LDT = 9.2) and for assessment of the number of day-degrees above the LDT necessary for completion of a particular development stage the sum of effective temperatures can be determined at any temperature within the linear range.

Developmental isomorphy

Combining statistically the results of the 68 studies in a meta-analysis indicated the overall prevalence of developmental isomorphy in ladybirds (the overall weighted average effect size: 7.10E-04 with 95% confidence interval from –2.94E-03 to 4.36E-03; homogeneity statistic Q = 0.64, df = 65, p = 1). That is, all the populations and species showed developmental isomorphy.

Developmental isomorphy in ladybirds implies no change in the proportion of time spent in a particular developmental stage with change in temperature. It is illustrated for *Propylea japonica* in Fig. 1. Therefore, within the temperature ranges with a linear relationship between *RD* and *t*, for each species there is (1) a proportional *SET* for completion of each developmental stage at each temperature and (2) a common *LDT* for all developmental stages.

DISCUSSION

Linear vs. non-linear models of developmental rate

There are three categories of models of the relationship between temperature and duration of development in insects and other ectotherms (HONĚK 1999): (i) *Non-linear*. The objective of this kind of data fitting is the description of the developmental rate over a wide range of temperatures (e.g. STINNER et al. 1974; HAGSTRUM & MILLIKEN 1991). This type of model gives a good fit to the data, but the parameters have little biological meaning. (ii) *Non-linear incorporating physiological and biochemical constants*. These not only describe but also attempt to explain the relationship in terms of physiological mechanisms (e.g. LOGAN et al. 1976; SHARPE & DEMICHELLE 1977; SCHOOLFIELD et al. 1981; WAGNER et al. 1984, 1991). (iii) *A linear approximation*.

Models of type (ii) are often theoretically correct, but not tractable for most ecologists. In addition, only relatively recent models of this type (e.g. LACTIN et al. 1995) enable one to calculate lower developmental threshold. On the other hand, the type (iii) linear approximation within the range of temperatures ecologically relevant to where an insect lives, is a reliable model, and can be easily used to calculate two virtual constants: the lower developmental threshold, *LDT* (the temperature below which development ceases), and the sum of effective temperatures, *SET* (the amount of heat needed for completing a developmental stage). This greatly simplifies modelling. Therefore, we argue against non-linear models for practical purposes, and advocate the simple linear model. We believe that the simple linear model of the relationship between developmental rate and temperature gives the best approximation of *LDT* and *SET* in insects.

The existence of a common LDT for all the developmental stages of a species

When the data for ladybirds were plotted against temperature, the developmental isomorphy hypothesis was supported by a zero change in the proportion of the total developmental time spent in a particular stage of a development. Developmental isomorphy in the overall pattern of the data thus indicates that all the developmental stages of each ladybird species have a common LDT. If so, there should be little variation in the *LDT* between stages and instars within a species, and within populations of individual species. This is not supported by the literature on ladybird development (HONĚK & KOCOUREK 1990; HONĚK 1996; HODEK & HONĚK 1996). Therefore, if developmental isomorphy is a common feature of ladybirds, then a significant proportion of the variation in *LDT*s within species is illusory and possibly a consequence of how it is estimated from experimental data.

What are the sources of error in estimating *LDT*? First, the values of developmental rate obtained at extreme (high or low) temperatures may violate developmental isomorphy (JAROŠÍK et al. 2002). At low temperatures there may be differential mortality. The individuals with the fastest development complete their development but the rest are more likely to succumb to adverse conditions, because their development is prolonged. Second, imprecise measurement of developmental time, particularly at high temperatures. As developmental rate increases with temperature, the number of observations per stage should also increase. To measure the rate of development with the same precision at low and high temperatures, the time interval must be proportional to the length of the development stage at each temperature. This is not the case in most studies (SHAFFER 1983; VAN RIJN et al. 1995). A constant monitoring is the most probable source of bias in data collected at high temperatures.

Even if *LDT*s are calculated from data collected over a range of ecologically relevant temperatures, and the regression of development rate on temperature is linear, the accuracy of the estimates is affected by errors in the estimates of the developmental rate (CAMPBELL et al. 1974). The low precision of *LDT*s is obvious from their standard errors (CAMPBELL et al. 1974), which are typically between 1-3 ^{0}C (J. JANÁČEK & A. HONĚK, unpublished data). Crucial from a statistical point of view is any bias in the measurements made at extreme temperatures. Important determinants of the slopes of the linear regressions, from which the *LDT*s are inferred, are the extreme values (see CRAWLEY 1993, p. 78-82). Therefore, a relatively small bias in the developmental rates measured at extreme temperatures will cause a large shift in the *LDT*. Poor estimates of developmental rate are most likely at high temperatures because the precision with which the duration of development is measured is poor and the error large (development rate is the reciprocal of duration of development).

CONCLUSIONS

The existence of rate isomorphy in ladybirds has important practical implications for the timing of life-history events. The experimental procedure for determining the thermal development constants, *LDT* and *SET*, can be simplified. The lower developmental threshold can be determined based on data for one stage, preferably the pupa, which is little affected by factors other than temperature, and has a duration usually longer than that of the egg stage. *SET* may also be calculated from the duration of development at one temperature (Fig. 1). Thus more effort can be invested in greater precision in determining the length of development.

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