Developmental Database for Phenology Models: Related Insect and Mite Species Have Similar Thermal Requirements

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ABSTRACT Two values of thermal requirements, the lower developmental threshold (LDT), that is, the temperature at which development ceases, and the sum of effective temperatures, that is, day degrees above the LDT control the development of ectotherms and are used in phenology models to predict time at which the development of individual stages of a species will be completed. To assist in the rapid development of phenology models, we merged a previously published database of thermal requirements for insects, gathered by online search in CAB Abstracts, with independently collected data for insects and mites from original studies. The merged database comprises developmental times at various constant temperatures on 1,054 insect and mite species, many of them in several populations, mostly pests and their natural enemies, from all over the world. We show that closely related species share similar thermal requirements and therefore, for a species with unknown thermal requirements, the value of LDT and sum of effective temperatures of its most related species from the database can be used.

KEY WORDS lower developmental threshold, base temperature, sum of effective temperatures, day degrees, rate of development

While birds and mammals produce metabolic heat, enabling them to grow and develop in a range of ambient temperatures by burning food, ectotherm organisms, that is, plants, fungi, bacteria, virus and virus-like organism, protists, and all animals except birds and mammals, rely on external sources of heat for their development. Because ectotherms require a certain combination of time and temperature, their development is a function of a given temperature and time over which it is acting. This time, called thermal or physiological, is the basis of phenology models that use two values of thermal requirements: 1) lower developmental threshold (LDT), that is, the temperature at which development ceases (also called based developmental temperature); and 2) the sum of effective temperatures (SET), that is, day degrees (DD) above the LDT necessary for a completion of a developmental stage (Ludwig 1928). A heat accumulation of DD above LDT enables prediction of the time at which the development of individual stages of a species will be completed. In insect and mites, the thermal accumulation is usually modeled by daily maximum and minimum temperatures, assuming the sine curve as an approximation of the diurnal temperature curve (Baskerville and Emin 1969, Allen 1976).

To create a phenology model of a species, it is necessary to obtain data on the thermal requirement of the modeled species. This requires a literature search for published thermal requirements, or, alternatively, because the application of the thermal requirements is often limited by the lack of available data, new laboratory experiments.

In literature, the base developmental temperatures (LDTs) are given separately for each developmental stage within a population of a species. This is so because, until recently, it was considered that within a species, each developmental stage has its own, specific lower developmental threshold. This understanding has changed when Jarošík et al. (2002) showed that the proportion of the developmental time, spent in individual developmental stages of a species, does not change with temperature. This means that within a population of a species, the LDT remains the same for all developmental stages. Consequently, when LDT is known only for any one of developmental stages of a species, this LDT can be used for all developmental stages of the species.

The existence of a common LDT within a species, called rate isomorphy (van Rijn et al. 1995), was first tested on insect and mites, using data on the duration of nondormant development for 426 populations of 349 species (Jarošík et al. 2002). Later it was shown that rate isomorphy occurs in all ectotherm animals (Jarošík et al. 2004), and different methods to tests for

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rate isomorphy were developed (Shi et al. 2010, Bonato et al. 2011). There are also indications that it might be applied to plants. The existence of rate isomorphy has important practical consequences because it can save a lot of experimental work. LDT can be established from the data on one stage, for example, in holometabolous insects having the true pupal stage preferably in the pupal stage in which the influence of factors other than temperature is minimal and where duration is usually longer than that of egg stage. SET may also be calculated from the duration of development at only one temperature (Jarošík et al. 2002, 2004). However, there is no remedy for missing values of SET based on rate isomorphy because missing value of SET for a stage of a species cannot be inferred from values of SET for a different developmental stage of the same species.

If rate isomorphy is common, there should be little variation in the LDT between stages and instars within species and populations. This is, however, not supported by the literature. Therefore, if rate isomorphy is a common feature, then a significant proportion of the variation in LDTs is illusory and possibly a consequence of how it is estimated from experimental data (Jarošík et al. 2002). The first source of error in estimating LDT is the precision in the measurement of developmental rates at low temperatures. At low temperatures, there may be differential mortality. The individuals with the fastest development complete their development early while the rest succumb to adverse conditions, especially when development is prolonged. The second reason is the imprecise measurement of developmental times at high temperatures. As developmental time decreases with temperature, the number of observations per stage also decreases if monitoring is made at constant intervals at low and high temperatures. To keep the same precision, 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 interval as temperature increases is the most probable source of bias in data collected at high temperatures. Any bias in measurements made at extreme temperature are crucial, as an important determinant of the slopes of the linear regressions, from which the LDTs are inferred, are the extreme values (see e.g., 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.

To ease the search for thermal requirements, in this study we merged a previously published database of thermal requirements for insects (Nietschke et al. 2007) with independently collected data for insects and mites from further original studies. To assist in a rapid development of phenology models, using this merge database and the notion on rate isomorphy, we show how to assess the thermal requirements when the data for a particular species are not available.

Materials and Methods

To assist scientists and field practitioners in development of phenology models, we summarized a database of thermal requirements, DTR, for insects and mites (Supplemental Table S1, available online only; continuously updated version is available at https://secure.fera.defra.gov.uk/pratique/members/viewPackages.cfm?packageID = 112). This DTR was created by merging Insect Developmental Database, IDD (Nietschke et al. 2007; full version with 1,034 studies), containing thermal requirements for development of >500 insect species gathered by online search in CAB Abstracts (http://www.cabdirect.org/) between 1972 and 2004, with a database, independently collected from original studies by Alois Honěk and his colleagues (Honěk and Kocourek 1990; Honěk 1996a; Jarošík et al. 2002, 2004; Jarošík and Honěk 2007), containing 659 insect and mite species. The calculation of the values of LDTs and SETs, first described by Ludwig (1928), based on a linear relationship between the developmental rate (DR; i.e., proportion of development occurring per unit time) and temperature, t, using a linear equation $DR = a + bt$, from which the thermal requirements can be calculated as $\mathrm{LDT} = -a/b$ and $\mathrm{SET} = 1/b$ (e.g., Jarošík et al. 2002, 2004). The values in the database were often recalculated from the original studies, using only the range of temperatures for which the relationship between the rate of developmental (reciprocal value of developmental time) and temperature is actually linear. Consequently, the values of LDTs and SETs in the database cannot correspond to the values in the original studies.

To show the variation in the thermal requirements among populations within species, species within genera, genera within families, families within orders and among orders, taxonomic hierarchy was analyzed with LDTs and SETs as the response variables by nested analyses of variance on random factors (model II analysis of variance [ANOVA]; Sokal and Rohlf 1995). In this method, the larger the variance at a particular taxonomic level, the larger the possible lack of statistical independence below this level, because of a likely phylogenetic relatedness of species within the taxa (Harvey and Pagel 1991, Pyšek et al. 2009, Moravcová et al. 2010). The analyses were done by nested designs in mixed effect models using restricted maximum likelihood method (Crawley 2002, p. 673–676). To test at which levels of taxonomic hierarchy the amount of variance is statistically significant, a series of nested models included models 1) without taxonomy (i.e., a null model), 2) with only orders included, 3) with families nested within orders, 4) with genera nested within families and orders, and 5) species nested within genera within families and within orders. Individual populations within species were the error term. Calculations were done in S-PLUS v. 8.1.1 (TIBCO Software Inc.), using the functions *glm* (applied on all nested models except the null model), *gls* (applied on the null models to enable including the model with no random effect in nested likelihood ratio tests of random components; Zuur et al. 2009) and *anova* (to get values of likelihood ratio tests on the nested models). Before the analyses, the response variables were checked for normality and SETs log transformed to normalize the data. The analyses were first done for all data and then repeated excluding mites (order Acari and Mesostigmata from the class Arachnida), which are taxonomically distant from the rest of data, all belonging to insect (class Insecta).

Following the sources of errors in rate isomorphy, for LDT of each population of a species, data measured for the longest developmental time, that is, for the total development (egg to adult and when not available, egg to egg) were used. If the data for the whole development were not available, that is, only data for several developmental stages of a species were known and the values varied, data for nonmobile developmental stages, that is, pupa were used. If data for the pupa were not available then data for egg were used. This supposes that values for nonmobile developmental stages are more precise than data for mobile and actively feeding stages, for example, nymphs for hemimetabolous and larvae for holometabolous insects (Honěk and Kocourek 1990, Jarošík et al. 2002). Data for larvae/nymphs were used only if no other developmental stages within a population of a species were available; where data for all larval/nymph stages were given, their average value was used. Where separate data from the same population for each sex were given, average value was used because males and females are known to have the same LDT (Jarošík et al. 2002). Negative LDTs were considered an artifact of calculation of the LDT values by linear regression, in which the slope is very sensitive to the effect of extreme values (Jarošík et al. 2002), and were not included. Overall, LDT data for insect and mites from 18 orders, 156 families, 613 genera, and 968 species (including several subspecies) in 2,393 populations were analyzed. For SET, only data for the whole egg to adult preimaginal development are used. Where separate data for each sex are given, males and females are evaluated as separate populations as males are known to develop faster than females (Jarošík and Honěk 2007). Overall, SET data are evaluated for 15 orders, 111 families, 405 genera, and 622 species (including several subspecies) in 1,339 populations.

Results

The database of thermal requirements (DTR) comprises developmental times at various constant temperatures on 1,054 species (including several subspecies), many of them in several populations, mostly pests and their natural enemies, from all over the world (Supplemental Table S1, available online only). The first column in the DTR is the valid scientific name of each species and its taxonomic affiliation, following the taxonomy used in IDD (Nietschke et al. 2007), with taxa listed alphabetically. Subsequent columns contain all available data on 1) base development temperature (LDTs); 2) upper developmental temperature (UDT; data available only for species from the original IDD database), that is, the temperature at which the development rate is maximal, corresponding to temperature above which an ectotherm stops development or at which development is adversely affected (i.e., some individuals still develop, but take longer to reach maturity and many die); 3) degree-days (DD) necessary for a completion of a particular developmental stage (egg, larva/nymph, pupa) and total developmental time (egg to adult/egg to egg) for each population (SET); and 4) overwintering stage (only for species from the original IDD database). The last columns contain locations where each population was studied, references, and for data originally summarized in IDD, abstracts of the studies.

The average LDT for the data from the DTR is 10.2°C (range, 0–28.1°C), and the distribution of LDT values is close to normal. Consequently, median value (a measure of central tendency; 50% values is smaller than the median and 50% is larger) is very close to the average (median = 10.3°C). Fifty percent of LDT values lie between 7.9 and 12.5°C and 90% between 3.6 and 16.5°C (Fig. 1). The average SET for completion of the total (egg to adult) development is 388.5 °DD with a range of values between 16.9 and 5,563.6 °DD. However, this distribution is strongly skewed to the left (cf. Fig. 2A with log transformed Fig. 2B), and median value (median = 316.5 °DD) is thus smaller than the average. Fifty percent of SET values lie between 201.1 and 472.7 °DD and 90% between 116.6 and 791.4 °DD (Fig. 2).

The variation among thermal requirements at all taxonomic levels was highly significant (Fig. 3). This means that the values of LDTs and SETs are hierarchically nested following species taxonomy, with the amount of variation successively decreasing from a model without including taxonomy, to models that include insect and mite orders, families, genera, and species. The pattern of variance partitioning however differs for LDT and SET (Fig. 3). For LDT, most variance is among families within orders and the variance then decreases to genera and species, but again increases for the individual populations among species. For SET, by far most variance is among orders; the variance remains virtually unchanged for families and genera, and then decreases to species and populations. When data for mites is excluded, the results of the variance partitioning remained virtually unchanged (results not shown).

Discussion

Our results on the similarity of thermal requirements of related species confirm, by rigorous statistically tests, previous indications on the similarity of thermal requirements for related species (Jarošík et al. 2002, Ikemoto 2003, Dixon et al. 2005, Kiritani 2006, Bonato et al. 2011). Because the taxonomical hierarchy was treated as a random effect, our inference on taxonomy can be applied to a wider population from which the species are derived, that is, to any species belonging to that genus, family, and order (Blackburn and Duncan 2001). Consequently, if the data on thermal requirements for a particular species are not listed

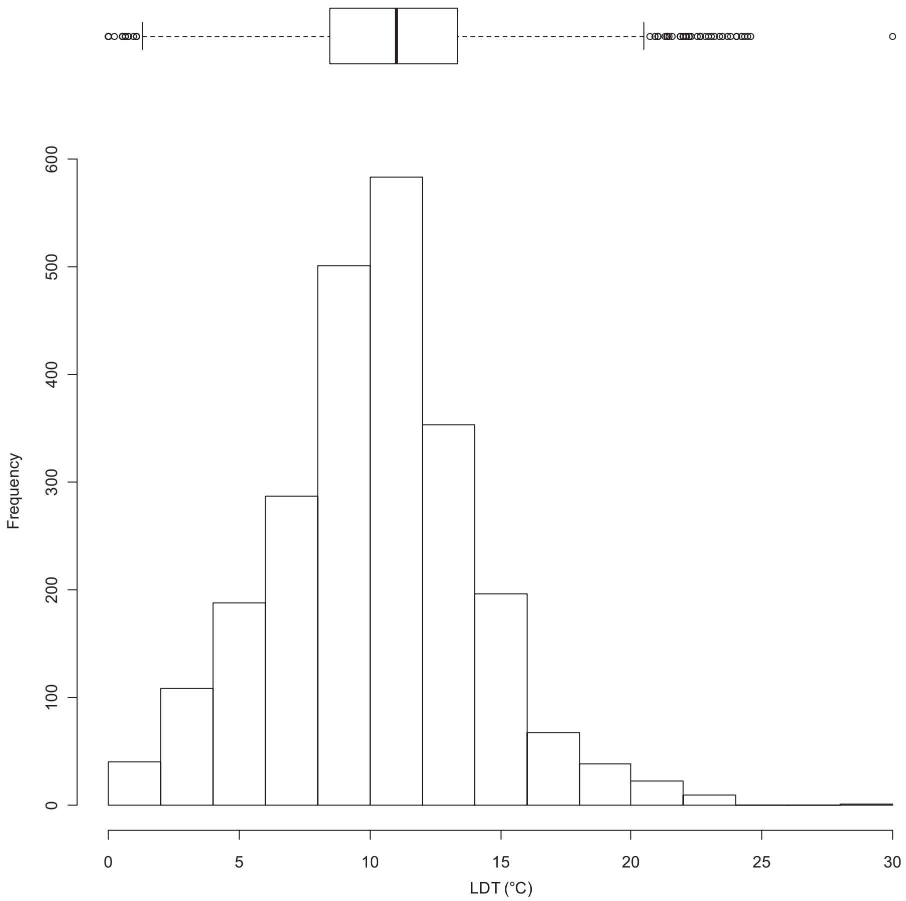

Fig. 1. Boxplot and frequency histogram of the values of the lower developmental threshold (LDT, °C) for 2,393 populations of 968 species in the Database of Thermal requirements (DTR; see Supplemental Table S1 [available online only] and https://secure.fera.defra.gov.uk/pratique/members/viewPackages.cfm?packageID = 112 for continuously updated version). In boxplot, the thick vertical line is the median; the box is defined by the 25th and 75th percentiles (i.e., lower and upper quartile). The dotted horizontal line has a length of 1.5 times of the difference between the percentiles; all points outside this range can be considered as outliers.

in the database, then a closely related species could be used to estimate the thermal requirements for risk analysis.

Moreover, the finding that the variation in LDT and SET decreases with decreasing taxonomic hierarchy directly infers that closely related species have similar thermal requirements. This may enable unknown thermal requirements for LDT and SET to be estimated from a phylogenetically close relative. This is an important finding because many exotic pests of phytosanitary importance originate from developing countries, where they may be poorly described and researched (e.g., Roques et al. 2009). To mitigate the impact of exotic pest introductions, researchers need these thermal requirements to build phenology and prediction models for pest surveillance and risk analysis (e.g., Magarey et al. 2011).

Surprisingly, the explained variance for LDTs among populations within a species was larger than among species within genera. This points to the impreciseness of measurements of LDTs at low and high temperatures, and to error amplification when LDTs are calculated by an ordinary linear regression between the rate of development and temperature (Jarošík et al. 2002). The calculation of LDTs can be refined by the use of reduced major axis (Ikemoto and Takai 2000) and nonlinear regressions (e.g., Sharpe and DeMichele 1977, Schoolfield et al. 1981, Ikemoto 2005, 2008, Shi et al. 2011a,b) but the use of the latter is limited by data availability. While the LDTs based on linear regressions can be calculated from three (and assessed from even two) values for constant temperatures and rates of development, the calculation of LDTs by nonlinear equations requires more values.

Also at higher taxonomic levels, taxonomy did not explain all the variation in thermal requirements. There is more variance explained by variation among families than among orders for LDTs. Moreover, there is virtually the same variation among genera and among families for SETs, and in addition little change in the pattern of the explained variance in the taxo-

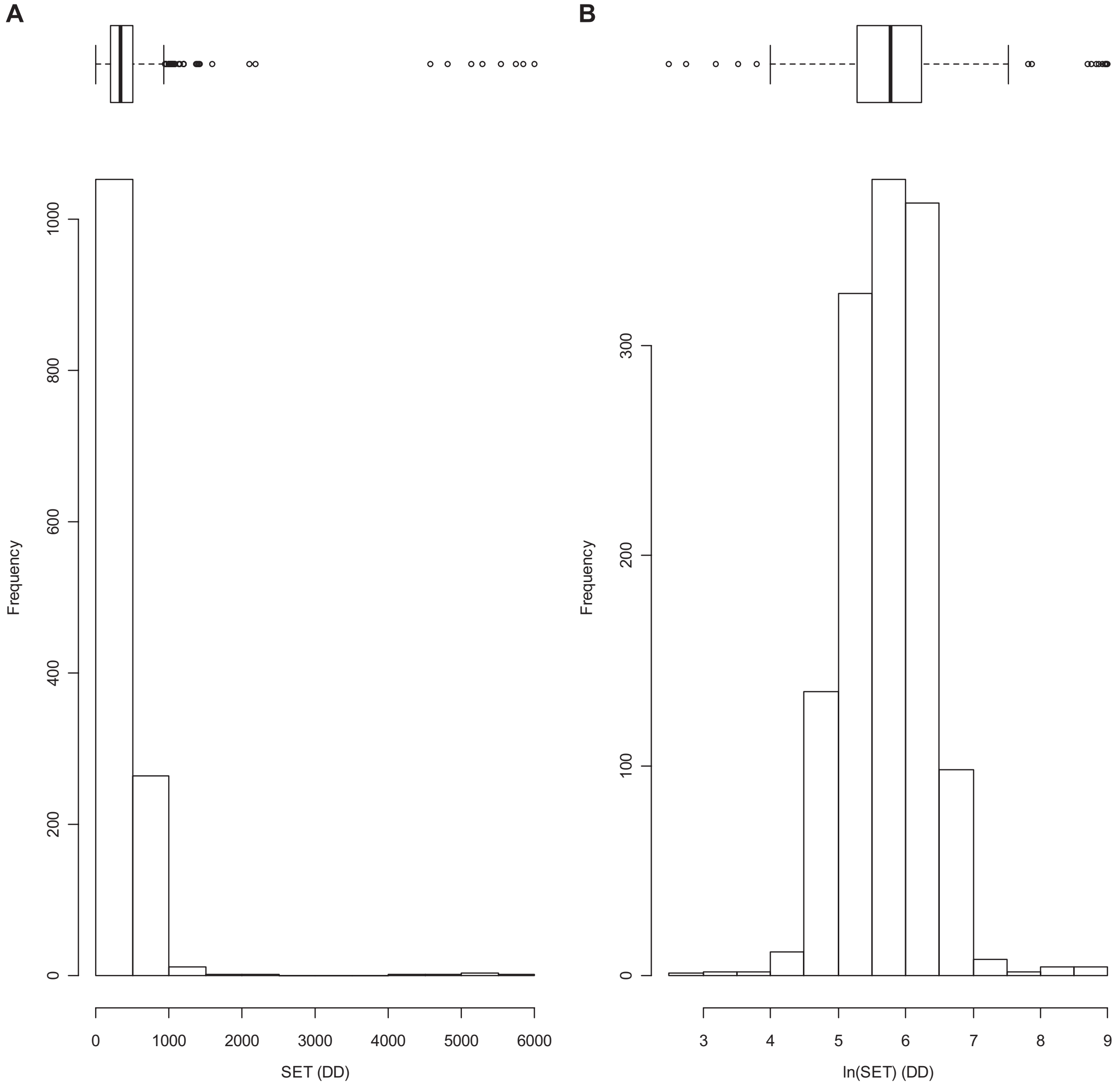

Fig. 2. Boxplot and frequency histogram of the values of the SETs above lower developmental thresholds °DD (A) and their natural logs (B) for 1,339 populations of 662 species in the DTR. Otherwise as in Fig. 1.

nomic distribution of variance when excluded data for mites, belonging to other class than insects. These results suggest that the estimation of thermal requirements based of taxonomic hierarchy could be further improved with one or more of the following covariates. First, inclusion of species phylogenetic relatedness instead of its approximation by species taxonomy could improve the precision of the prediction (Harvey and Pagel 1991, Desdevides et al. 2003, Pyšek et al. 2009, Dixon et al. 2009). The phylogenetic distance between the species might allow a researcher to quantify the likely uncertainty if data from a surrogate species is used for thermal requirements. Second, the prediction could be refined by inclusion of species traits that are known to affect species LDTs and SETs. Specifically, body mass (Honěk 1996a, 1999) and food specialization (Honěk 1999) are known to affect the thermal requirements of insect orders differently, and the effect of food specialization is known to interact with temperature for the locations from which the tested species originated (Honěk 1996b). Third, latitude, used as a surrogate for climate, affects LDT (Trudgill 1995, Honěk 1996b).

Our suggestion that closely related species share similar thermal requirements is related to the finding that closely related species share a common intrinsic optimum temperature and duration of development, which can be manifested by a negative relationship between their SETs and LDTs (Ikemoto 2003). From evolutionary point of view, this finding may suggest that species developing from a common ancestor can radiate to new environments with different temperature conditions, forming a related species group with different LDTs and rates of development (Ikemoto

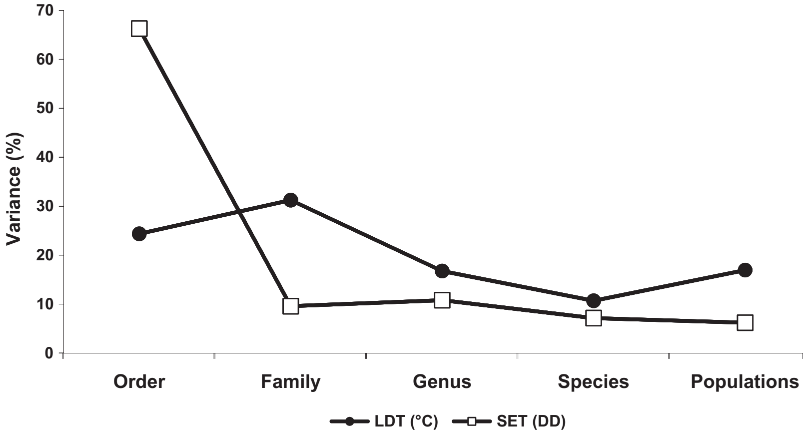

Fig. 3. Taxonomic distribution of the variance in successive taxonomic levels for LDT (°C) and for SET, °DD in the DTR. Likelihood ratio (*LR*) tests of significant variance on nested models for LDT: 1) among orders versus without taxonomy $LR = 271.52$; 2) families within orders versus orders $LR = 1016.12$; 3) genera within families versus families $LR = 578.51$; 4) species within genera versus genera $LR = 165.58$. LR tests of significant variance on nested models for SET: 1) among orders versus without taxonomy $LR = 733.85$; 2) families within orders versus orders $LR = 601.63$; 3) genera within families versus families $LR = 393.93$; 4) species within genera versus genera $LR = 140.50$. Populations within species are error terms. All *LR* tests are highly significant ($P < 0.0001$).

2003). The intrinsic optimum temperature thus could be used as an indicator for classifying phylogenetic relatedness (Ikemoto 2005), and there are also indications that it can be used for testing of developmental rate isomorphy (Bonato et al. 2011).

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