Geographical variation in thermal requirements for insect development

Alois HONĚK

Research Institute of Plant Production, 161 06 Praha 6 – Ruzyně 507, Czech Republic

Lower development threshold, sum of effective temperatures, temperature, development length, egg, larva, pupa, total development

Abstract. Thermal constants, lower development threshold (LDT) and sum of effective temperatures (SET) were recalculated from literature data for 335 insect species. Included were only populations whose development rate was ascertained in at least 4 constant temperatures of $\leq 28°C$. Variation of thermal constants was investigated in relation to geographic origin of the populations to test the prediction that LDT will decrease and SET increase with increasing geographical latitude (Trudgill, 1995). In tropics (at $\leq$ 23°N or S), LDT was high with little geographic variation. In subtropical and temperate zones there was a significant trend for decreasing average LDT with increasing geographical latitude. SET increased with geographic latitude but the scatter of data was greater than in LDT. The geographic trends of variation in thermal constants conformed to the prediction but the scatter of data was large probably due to both eco-physiological differences between the species, and errors in estimating thermal constants of development.

INTRODUCTION

A simple way to describe the effect of temperature on insect development is the linear regression of development rate (reciprocal of development time) on temperature. This relationship is significant in a range of biologically favourable temperatures from about 2°C above the temperature at which the growth ceases to the upper temperature above which the development is negatively affected. Although the variation in developmental rate over the whole range of temperatures may be described by non linear relationships, use of linear regression is sufficient in most cases (Lamb, 1992). Linear regression enables calculation of the lower development threshold (LDT), a temperature at which development ceases, and sum of effective temperatures (SET), the number of heat units called degrees (dd) above LDT required to complete development. Knowing the linear relationship between development rate and temperature (R = aT + b, where R is development rate and T is temperature), the thermal characteristics of development may be calculated as LDT = –b/a and SET = 1/a. Thermal constants LDT and SET are convenient for comparing requirements of insect populations since they provide a good prediction of development time over a wide range of biologically significant temperatures.

Earlier we (Honěk & Kocourek, 1988, 1990) have demonstrated, for a number of different species, that LDT decreases with increasing SET. Generally, this negative LDT/SET relationship will be obtained if regression lines for two species cross in the range of biologically acceptable temperatures (Fig. 1). In this case the species with a lower LDT will have a higher SET (i.e. smaller slope of regression line since SET is its reciprocal) than the species with a higher LDT. Recently, Trudgill & Perry (1994) and Trudgill (1995) proposed a functional explanation for this relationship: cold adapted species of higher
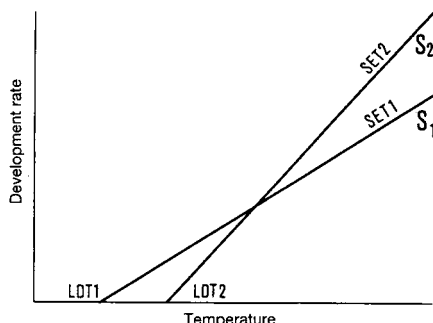
Fig. 1. Schematic representation of the relationship between development rate and temperature in a cold adapted species S1, and a warm adapted species S2. Species S1 has lower LDT and higher SET (the slope of regression line is inversely proportionate to the SET) than the species S2.

geographical latitudes (species S1 in Fig. 1) with a low LDT develop faster at low temperatures (below the point of intersection of both regression lines), while warm adapted species of lower geographical latitudes (species S2) with a high LDT develop faster at high temperatures. From this we may predict that (a) LDT will decrease with increasing geographic latitude, and (b) SET will increase with geographic latitude. While we will expect intuitively the first prediction, the second one appears less obvious.

In the past 7 years I have compiled a large data base of thermal constants of development of insect species. This data base now comprises 605 species belonging to 14 insect orders. Using this information we may test the predictions concerning geographical variation of thermal constants of insect development.

MATERIAL AND METHODS

Lower development threshold (LDT) and sum of effective temperatures (SET) were recalculated from literature data on duration of non-dormant development under constant temperatures. The data were extracted systematically from journals which frequently publish this type of information as well as other supplementary sources. I calculated LDT and SET from data on development duration at constant temperatures of $\leq 28°C$ (80°F) using the formulas indicated in the Introduction. To decrease the probability of including poor data I used only results calculated from ≥ 4 temperatures. The recalculated data, with the original references, were published by Honěk & Kocourek (1990) and Honěk (1996). Geographic origin of the investigated populations was either indicated in the original works, or I have assumed that the material was collected near the place where the experiments were done. In case of doubt as to the origin of a population the data were not considered in this analysis. After eliminating data suspect of being loaded by error, the number of species included in this study decreased to 335 (Appendix). When comparing average LDT and SET, I divided the populations into "tropical" (originating from 0–23°N or S), "subtropical" (from 24–39°N or S), and "temperate" (from $\geq 40°N$ or S). Stored product pests of tropical origin were included among the tropical species. Regressions of LDT or SET on geographical latitude were calculated for subtropical and temperate species (from $\geq 24°N$ or S). Within tropical zone, LDT does not seem to change substantially with geographic latitude. There were few data for tropical region which did not enable to test this general impression.

RESULTS

A clear pattern, similar for eggs, larvae and pupae, resulted when LDT was plotted against geographical latitude of the origin of the populations (Fig. 2). In populations from $\geq 24°N$ or S (subtropical and temperate areas) the average LDT decreased with increasing geographical latitude. The decrease of LDT with increasing geographical latitude was significant in all development stages, eggs ($r^2 = 0.150$), larvae ($r^2 = 0.142$), pupae ($r^2 = 0.040$), as well as for total development ($r^2 = 0.121$). The decrease in LDT was associated with an opposite trend of SET which increased with geographic latitude (Fig. 2). However, the
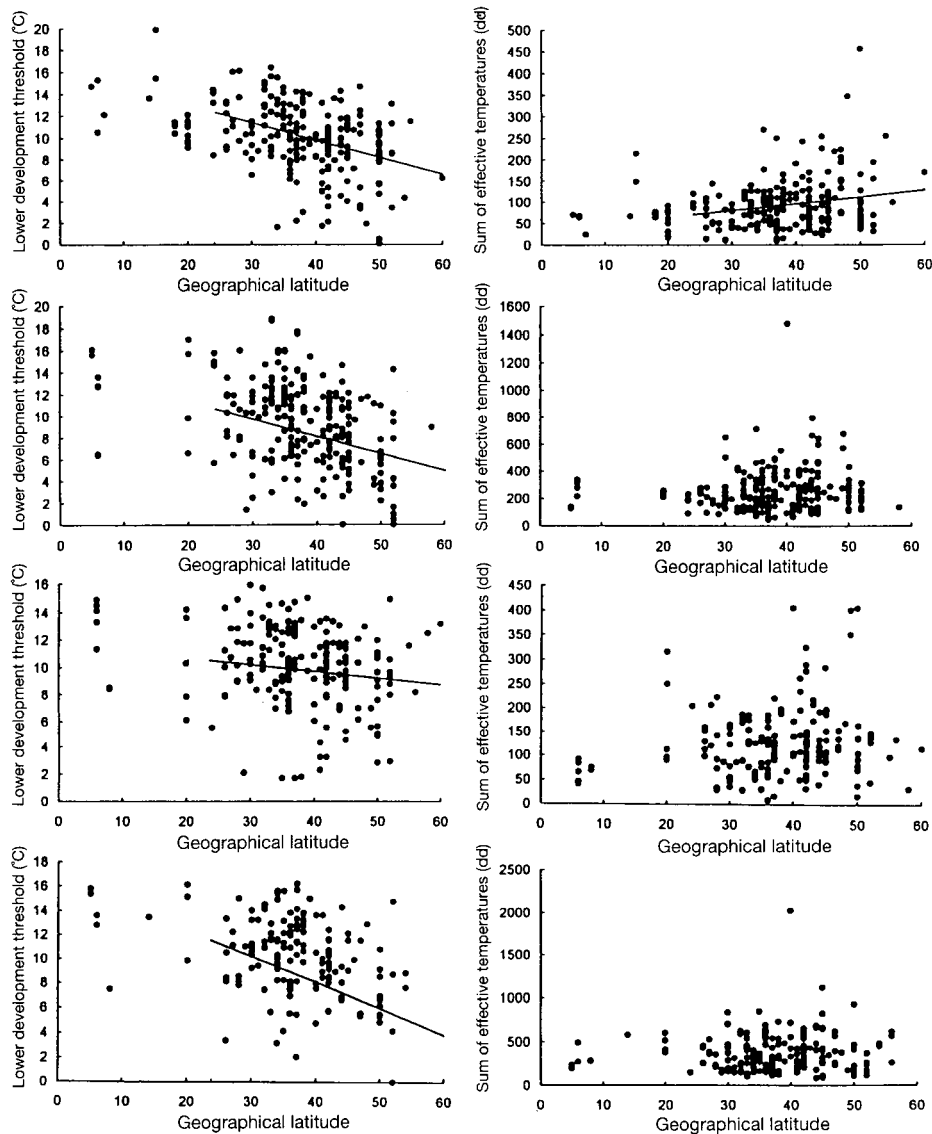
Fig. 2. Lower development threshold (left) and sum of effective temperatures (right) plotted against geographical latitude (°N or S) of the origin, in (from the top) eggs, larvae, pupae, and total development. Regression lines for data from $\geq 24°$ geographic latitude indicated when significant at $p < 0.05$.

scatter of SET data was much greater than in LDT data. As a result, the relationship for subtropical and temperate regions was significant only in eggs ($r^2 = 0.034$), but not in larvae, pupae, or for total development. Geographic differences became manifest when populations were sorted into the classes according to the value of LDT (Fig. 3). Representatives
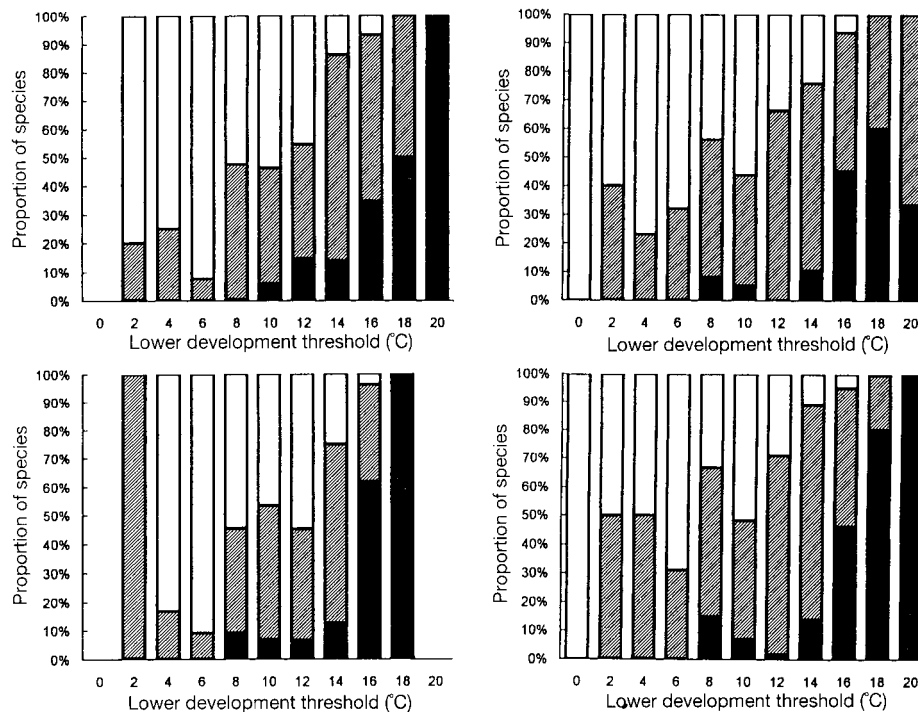
Fig. 3. Distribution of tropical species and stored product pests of tropical origin (open bars), subtropical species (shaded) and temperate species (black) in the groups assorted according to the value of lower development threshold, in eggs (top left), larvae (top right), pupae (bottom left) and for total development (bottom right). Regression lines for data from $\geq 24°$ geographic latitude indicated when significant at $p < 0.05$.

of the temperate zone prevailed among the species having a low LDT while inhabitants of the tropical zone (and stored product pests of tropical origin) dominated among the species with a high LDT. This trend was similar in particular development stages as well as for total development time. Average values of LDT for species of different climatic zones were significantly different (Table 1). The average LDT decreased from $12.9–13.7°C$ in tropical species, to $10.4–11.1°C$ in subtropical species and $7.8–9.3°C$ in temperate species, similarly in all development stages. The differences in average LDT between the geographical zones were statistically significant. By contrast, trends in variation of SET only partially conformed the prediction of monotonical increase with geographic latitude (Table 2). The average SET increased monotonically from tropical to temperate zone in eggs and pupae. In larvae and for total development, average SET increased from subtropical to temperate zones. However, average SET for tropical species was somewhat higher than in subtropical ones (see Discussion).

I have also tested the hypothesis that part of the scatter of the results is due to taxonomic heterogeneity of the material. As LDT of development stages within particular geographic zones were not significantly different (Table 1), I have pooled all LDT data and investigated the variation in Exopterygota, Endopterygota, and four endopterygotan orders
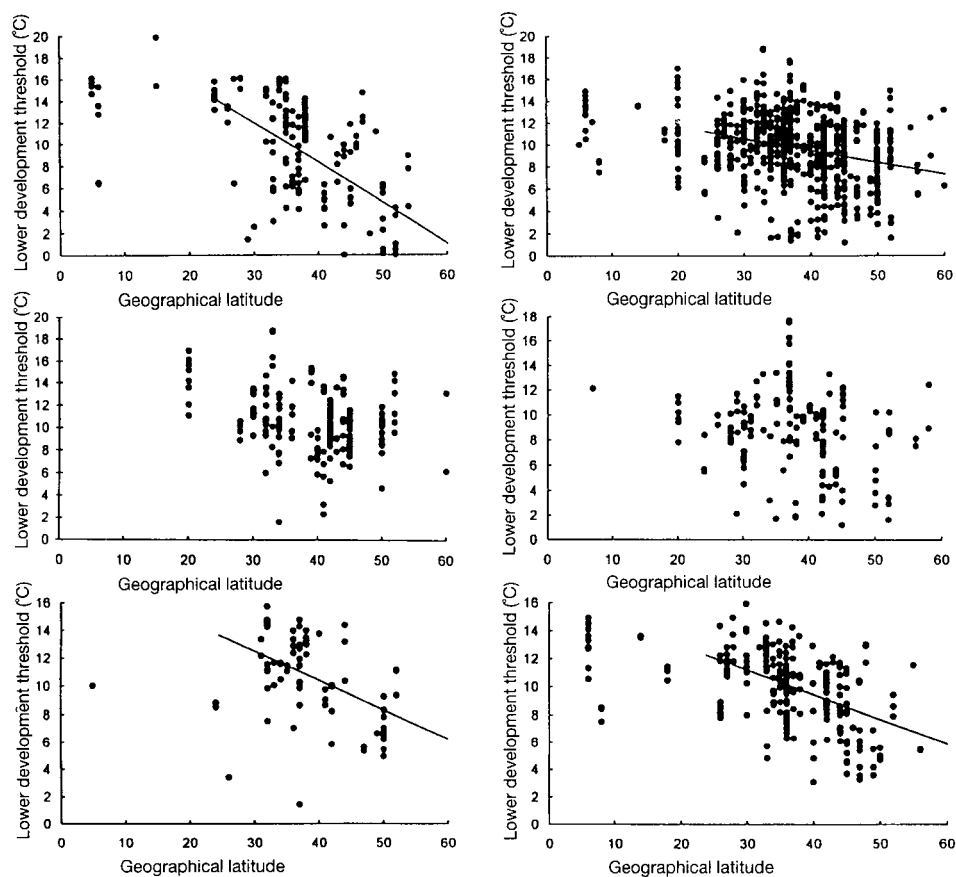
Fig. 4. Lower development threshold ploted against geographical latitude (°N or S) of the origin in Exopterygota (top left), Endopterygota (top right), Coleoptera (middle left), Diptera (middle right), Hymenoptera (bottom left) and Lepidoptera (bottom right). Pooled data for all developmental stages. Regression lines as in Fig. 2.

TABLE 1. Average lower development threshold (± SE) in tropical (0–23°N or S), subtropical (24–39°N or S) and temperate (40–60°N or S) species, and number of populations included (in brackets).

	Tropical species	Subtropical species	Temperate species
Eggs	$12.94^{ac} \pm 0.46$	$11.07^{ab} \pm 0.26$	$8.73^{bc} \pm 0.28$
	(33)	(116)	(110)
Larvae	$13.45^{ac} \pm 0.67$	$10.40^{ab} \pm 0.30$	$7.76^{bc} \pm 0.32$
	(27)	(133)	(107)
Pupae	$13.14^{ac} \pm 0.50$	$10.66^{ab} \pm 0.30$	$9.28^{bc} \pm 0.29$
	(31)	(92)	(93)
Total development	$13.65^{ac} \pm 0.49$	$10.46^{ab} \pm 0.28$	$7.89^{bc} \pm 0.34$
	(38)	(140)	(89)

$^{a-c}$ the figures (in rows) accompanied by the same letter are different at p < 0.01, the figures in columns are not significantly different.

(Fig. 4). The taxonomic segregation showed the significant relationship (in populations from subtropical and temperate zones) for Exopterygota ($r^2 = 0.315$), Endopterygota ($r^2 = 0.059$), Hymenoptera ($r^2 = 0.227$) and Lepidoptera ($r^2 = 0.199$). The significance of results for total Coleoptera ($r^2 = 0.020$) and Diptera ($r^2 = 0.026$) was not improved. Regressions for pooled SET data could not be calculated since average set significantly differ between development stages (Table 2).

TABLE 2. Average sum of effective temperatures (± SE) in tropical (0–23°N or S), subtropical (24–39°N or S) and temperate (40–60°N or S) species, and number of populations included (in brackets).

	Tropical species	Subtropical species	Temperate species
Eggs	70.4[b]± 6.0	85.8 ± 3.9	99.6[b]± 6.5
	(33)	(116)	(110)
Larvae	257.6 ± 35.8	236.6[c]± 10.6	330.8[c]± 21.0
	(27)	(133)	(107)
Pupae	97.9[de]± 10.0	110.3[d]± 5.2	133.4[e]± 8.4
	(31)	(92)	(93)
Total development[a]	406.8 ± 35.9	387.1 ± 17.8	454.6 ± 34.3
	(38)	(90)	(64)

[a] Aphids and parasitic Hymenoptera not included.
[b-e] the figures in rows accompanied by the same letter, and all figures in columns are different at $p < 0.05$.

DISCUSSION

The data demonstrated a significant geographic variation in thermal characteristics of insect development. Lower development threshold decreased with increasing geographical latitude. This trend is in concert with the functional prediction (Trudgill & Perry, 1994; Trudgill, 1995) that implies higher development thresholds and lower sums of effective temperatures in warm (tropical) than cold adapted (temperate) species. It also satisfies intuitive expectations that will imply the absence of adaptations for development under cold conditions in tropical species. These adaptations will not be favoured by natural selection since they probably confer no advantage to their bearers. It should be noted that geographic trends in LDT revealed in this study appeared at inter-specific or even higher taxonomic level (most species were the only examples of genera or families). This fact may indicate that adaptations of the thermal requirements occur chiefly at inter-specific level. This is in accordance with some earlier results which provided no evidence for geographic variation of thermal constants at the species level (Tauber et al., 1987; Lamb & MacKay, 1988; Mogi, 1992; Groeters, 1992). However, contrary examples of intraspecific geographical variation of LDT and SET, consistent with functional predictions, are also available (Umeya & Yamada, 1973; Rae & Death, 1991).

There is great scatter in the LDT and SET data, particularly in the temperate zone. This variation may have two sources: (1) Ecophysiological differences between the species living at the same geographical latitude, and (2) errors of estimation of the thermal constants. I suppose that an important factor in decreasing the variation is to select the groups of species according to ecological criteria. Seasonality of development may be an important factor associated with variation of thermal constants in species of temperate zone (Honěk & Kocourek, 1988). I suppose that also selecting species of similar size may decrease the

variation, since body size is related to several physiological characteristics that are important in temperature adaptation, e.g. duration of development and thermoregulation. The results revealed that the scatter of LDT was in some cases decreased by selecting data on the basis of taxonomic similarity. As the choice of species included in this study is not random (usually there are practical reasons to investigate temperature characteristics of a species), a taxonomic selection may be associated with selecting species of particular ecological requirements. An example may be Hymenoptera where the development time was ascertained chiefly in parasitoids, mostly of small size. Trends in average SET for tropical, subtropical and temperate species (Table 2) is another example of complicating factors. The data for eggs and pupae, i.e. stages when development occurs with no growth in biomass, conform the prediction and SET increases monotonically with geographic latitude. By contrast, duration of larval development (SET) depends on the rate of body growth. This is affected particularly by availability, and efficiency of digestion and conversion of food. Duration of larval stage is correlated with food specialisation. Given the same difference between initial and final larval size, the duration of development will differ in herbivors, predators and parasites, and this variation may be more important than differences associated with thermal adaptation. The data available for groups with different food specialisations are not evenly distributed with respect to geographic latitude. Stored product pests growing relatively slowly (due to water poor feeding substrates) are overrepresented among tropical species. This may be one of the reasons that made average SET of tropical species longer than in the subtropical ones. The association between taxonomy and ecological specialisation makes the analysis of relative importance of taxonomic and ecophysiological causes of the scatter of LDT and SET data difficult.

On the other hand, a considerable proportion of variation is undoubtedly due to errors made in estimation of thermal characteristics. Errors of this type could not be completely corrected by a posteriori selection of the data. In this study we eliminated LDT and SET data based on 2 or 3 temperatures only. Another method to eliminate some probably inaccurate results is to look at standard error of the LDT, i.e. the precision of its estimation. Our parallel study (Honěk & Janáček, in prep.) revealed that the precision of estimation varies largely. Thus for total development data used in this study, standard error of LDT varied between 0.1–7.2°C, and only 53% of data had standard error of the LDT smaller than 2°C. The investigation of literature data may be improved by using combinations of various methods of elimination of probably wrong results, as well as more sophisticated statistics (Honěk & Jarošík, in prep.). However, an intensive comparative study is needed to establish the precise quantitative expression of the geographic trends indicated by this study. Estimating the development time under uniform conditions (Honěk & Kocourek, 1988) and a deliberate selection of species may substantially decrease the scatter of data.

This study confirmed the geographical variation of LDT and SET predicted from the functional relationship between thermal constants and adaptation to temperature conditions. We obtained statistically significant results despite the relatively small number of species included and a probably biased selection of the material with respect to ecological requirements. This justifies further research on geographic variation of thermal constants.

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APPENDIX

The species included in this study as eggs (e), larvae (l), pupae (p) and total development length(t).

Coleoptera: *Adalia bipunctata* (L.) (e,l,p,t), *Adonia variegata* (Goeze) (e,l,p), *Anthonomus signatus* Say (l), *Anthraenus verbasci* (L.) (e,p), *Baris lepidii* Germar (e,l,p,t), *Bubas bison* (L.) (e), *Chilocorus bipustulatus* (L.) (e,l,p,t), *C. kuwanae* Silverstein (e,l,p,t), *Chrysomela populi* L. (e,l,p,t), *Coccinella quinquepunctata* L. (e,p), *C. septempunctata* L. (e,l,p,t), *C. transversoguttata* Brown (e,l,p), *Coelopalorus foveicollis* (Blair) (e,l,p,t), *Coleomegilla maculata* (DeGeer) (e,l,p,t), *Collops vittatus* (Say) (e), *Copris hispanus* L. (e), *Costelytra zealandica* (White) (e,p), *Crioceris asparagi* (L.) (e,l,p,t), *Cryptolestes pusillus* Schoenherr (l,p,t), *Cybocephalus micans* Reitter (e,l), *Dendroctonus ponderosae* Hopkins (e,l,p,t), *Dermestes frischi* (Kugelberg) (e), *D. haemorrhoidalis* Kustler (e), *D. lardarius* L. (p), *Diabrotica virgifera* (e,l,p), *Dytiscus alascanus* Balfour-Browne (e), *Epilachna varivestis* Mulsant (e,l,p), *Eriopis connexa* Mulsant (e,l,p,t), *Galeruca sardoa* (Gené) (l,p), *Glischrochilus quadristriatus* (Say) (e,p), *Gnathocerus maxilosus* (F.) (t), *Hippodamia convergens* Guérin-Ménéville (e,l,p,t), *H. parenthesis* (Say) (e,l,p,t), *H. septemmaculata* (DeGeer) (e), *H. sinuata* Mulsant (e), *Hylobius pales* (Herbst) (e,l), *Hypera meles* (F.) (e,l,p,t), *H. postica* (Gyllenhal) (e,l,p,t), *Ips calligraphus* (Germar) (e,l,p,t), *Leptinotarsa decemlineata* Say (e,l,p,t), *Lioadalia flavomaculata* (DeGeer) (e,l,p,t), *Listronotus oregonensis* (LeConte) (e,l,p,t), *L. texanus* (Stockton) (e,l,p,t), *Oryzaephilus acuminatus* Halstead (e,l,p,t), *Otiorrhynchus sulcatus* F. (e,p), *Oulema melanopus* (L.) (e,l,p,t), *Palorus laesicollis* (Fairmaire) (e,l,p,t), *P. ratzeburgi* (Wissmann) (e,l,p,t), *P. subdepressus* (Wollaston) (e,l,p,t), *Phyllotreta vittata* (F.) (l,p), *Propylea japonica* (Thunberg) (e,l,p,t), *P. quatuordecimpunctata* (L.) (p), *Prostephanus truncatus* (Horn) (e,l,p,t), *Rhyzopertha dominica* (F.) (e,l,p,t), *Scymnus hoffmani* (e,l,p,t), *Semiadalia undecimnotata* (Schneider) (e,p), *Tribolium castaneum* (Herbst) (e,p), *T. confusum* Duval (e,p), *T. madens* (Charpentier) (e,l,p,t), *Trichosirocalus*

horridus (Panzer) (e), *Trogoderma anthrenoides* (Sharp) (e,l), *T. inclusum* LeConte (t), *Typhaea stercorea* (L.) (e,l,p,t); **Dermaptera:** *Nala lividipes* (Dufour) (e); **Diptera:** *Aedes campestris* Dyar & Knab (l,p), *Agromyza frontella* (Rondani) (e,l,p,t), *Anastrepha ludens* (Loew) (e,p,t), *Bradysia impatiens* (Johannsen) (e), *Ceratitis capitata* (Wiedemann) (e,l,p,t), *Compsilura concinnata* (Meigen) (l,p), *Contarinia nasturtii* (Kieffer) (e), *C. sorghicola* (Coquillet) (t), *Culex quinquefasciatus* Say (l,p), *C. theilieri* Theobald (e,l,p,t), *Culicoides mississippiensis* Hoffman (e,l,p,t), *C. variipennis* (Coquillet) (e,l,p,t), *Culiseta inornata* (l), *Cystiphora schmidtii* (Rubsamen) (e,l), *Dacus cucurbitae* Coquillet (e,p), *D. oleae* (Gmelin) (e,l,p,t), *D. dorsalis* Hendel (e), *Dasyneura brassicae* Winnertz (p,t), *Delia coarctata* Fallen (l), *D. florilega* (Zetterstedt) (e,l), *D. platura* (Meigen) (e,l), *Drosophila lutescens* Okada (t), *D. melanogaster* (Meigen) (t), *D. takahashi* Sturtevant (t), *D. simulans* Sturtevant (t), *Episyrphus balteatus* (DeGeer) (p), *Exorista mella* (Walker) (p), *Haematobia irritans exigua* deMeijere (e,t), *H. thirouxi potans* (Bezzi) (e,l,p,t), *Hippelates bishoppi* Sabrosky (e,l,p,t), *H. pallipes* (Loew) (e,l,p,t), *H. pusio* Loew (e,l,p,t), *Hylemya antiqua* (Meigen) (l,p), *Hypoderma bovis* (L.) (p), *H. lineatum* (de Villers) (p), *Chromatomyia syngenesiae* (Hardy) (t), *Leptopilina boulardi* Barbotin (t), *Liriomyza bryoniae* (Kaltenbach) (e,l,p), *L. trifolii* Burgess (e,l,p,t), *Lixophaga diatraeae* (l,p), *Lucilia cuprina* (Wiedemann) (e), *Mayetiola destructor* (Say) (e,l,p), *Musca autumnalis* DeGeer (t), *M. vetustissima* Walker (e,p), *Odagmia ornata* (Meigen) (p) *Oscinella frit* (L.) (e,l,p,t), *Psila rosae* (F.) (e,l,t), *Psorophora confinnis* Lynch Arribalzaga (l,p), *Sarcophaga crassipalpis* Macquart (l), *Sepedon fuscipennis* Loew (e,l,p,t), *Simulium kawamurae* Matsumura (p), *S. nigritarse* Coquillet (p), *S. noelleri* Friedrichs (p), *Sphaerophoria scripta* (L.) (p), *Tipula subnodicornis* Zetterstedt (p), *Toxorhynchites brevipalpis* (e), *T. rutilus septentrionalis* (Dyar) (e,l,p,t), *Winthemia fumiferanae* Totham (e,l); **Ephemeroptera:** *Colobursicoides* sp. near *haleuticus* (e), *Ecdyonurus dispar* (Curtis) (e), *E. picteti* Meyer-Dur (e), **Heteroptera:** *Acanthomia tomentosicollis* Stål (e,l,t), *Acrosternum hilare* (Say) (e,l,t), *Adelphocoris lineolatus* (Goeze) (l), *Anasa tristis* DeGeer (e,l,t), *Biprorulus bibax* (Breddin) (e,l,t), *Calocoris norvegicus* (Gmelin) (t), *Cermatulus nasalis* (Westwood) (e), *Corythucha ciliata* (Say) (e), *Creontiades dilutus* (Stål) (e,l,t), *Diplonychus japonicus* Vuilefroy (l), *D. major* Esaki (l), *Geocoris punctpes* (Say) (e), *Gerris commatu*s Drake & Hottes (t), *G. pingreensis* Drake & Hottes (t), *Chlorochora uhleri* Stål (e), *Jalysus spinosus* (Say) (l), *Lygus hesperus* Knight (l), *L. lineolaris* (Palisot de Beauvois) (e,l,t), *Nabis americoferus* (Carayon) (e,l,t), *N. roseipennis* (Reuter) (e,l,t), *N. rufusculus* (Reuter) (e,l,t), *Nysius vinitor* Bergroth (e,l,t), *Oechalia schellenbergii* (Guérin-Ménéville) (e), *Orius majusculus* (Reuter) (l), *Rhinacola fronticollis* (Reuter) (e); **Homoptera:** *Acyrthosiphon kondoi* Shinji (l,t), *A. pisum* (Harris) (l,t), *Adelges piceae* (Ratzeburg) (e), *Aonidiella aurantii* (Mask) (t), *Aphis fabae* (Scopoli) (l,t), *Austroasca viridigrisea* (Paoli) (l), *Bemisia tabaci* (Gennadius) (e,t,), *Chionaspis pinifoliae* (Fitch) (e), *Circulifer opacipennis* (Lethierry) (e,l,t), *Diuraphis noxia* (Mordvilko) (l,t), *Drepanosiphum acerinum* (Walker) (l,t), *D. platanoidis* (Schrank) (l,t), *Graminella nigrifirons* (Forbes) (e,l,t), *Hyperomyzus lactucae* (L.) (l,t), *Laodelphax striatellus* (Fallén) (e,l), *Longistigma liquidambarus* (Takahashi) (l,t), *Macrosiphum euphorbiae* (Thomas) (l,t), *Metopolophium dirhodum* (Walker) (l,t), *Myzus persicae* (Sulzer) (l,t), *Nephotettix cincticeps* Uhler (e,l), *N. malayanus* Ishihara & Kavase (e,l), *N. nigropictus* Stål (e,l), *N. virescens* Distant (e,l), *Nilaparvata lugens* (Stål) (e,l), *Peregrinus maidis* (Ashmead) (l), *Phenacoccus herreni* Cox & Williams (e,l,t), *Psylla pyricola* Forster (e), *Rhopalosiphum maidis* (Fitch) (l,t), *R. padi* (L.) (l,t,), *Saissetia oleae* (Olivier) (e), *Schizaphis graminum* (Rondani) (l,t), *Sitobion avenae* (F.) (l,t), *Sogatella furcifera* (Horvath) (l), *Spissistilus festinus* (Say) (l), *Typhlocyba froggatti* Baker (e,l,t) *Viteus vitifoliae* (Fitch) (e); **Hymenoptera:** *Anagyrus pseudococci* (Girault) (t), *Anaphes flavipes* (Forster) (e,l,p,t), *Anisopteromalus calandrae* (Howard) (t), *Apanteles* sp. group *ultor* (t), *A. fumiferanae* Viereck (p), *A. subadinus* Blanchard (e,l,p,t), *Aphelinus asychis* Walker (t), *A. mali* (Haliday) (p), *A.* sp. near *varipes* (t), *Aphidius ervi* Haliday(t), *A. smithi* Sharma (t), *A. sonchi* Marshall (t), *A. matricariae* Haliday (t), *Aphytis mellinus* DeBach (e,l,p,t), *Brachymeria lasus* (Walker) (p,t), *Coccobius fulvus* (Compére & Annecke) (t), *Copidosoma truncatellum* (Dalman) (t), *Dendrocerus niger* (t), *Diaretiella rapae* (M'Intiosh) (t), *Diglyphus isaea* Walker (t), *Diprion pallipes* (Fallén) (l), *D. pini* (L.) (e), *Edovum putleri* Grissell (t), *Encarsia tricolor* Foerster (l,t), *Eurytoma amygdali* Enderlin (e,p), *Gonatocerus cincticipitis* Sahad (t), *Goniozus legneri* Gordh (p,t), *Leptomastidea abnormis* (Girault) (t), *Leptomastix dactylopi* Howard (t), *Megachile rotundata* (F.) (e,l), *Metaphycus swirskii* Annecke & Mynhardt (t), *Microctonus aethiopoides* Loan (l,p), *Microplitis rufiventris* Kokujev (p,t), *Muscidifurax raptor* Grant & Sanders (t), *Patasson lameerei* Debauche (t), *Perilitus coccinellae* (Schrank) (p,t), *Praon pequedorum* (t), *Pteromalus venustus* Walker (e), *Solenopsis invicta*

(p), *Telenomus chloropus* Thomson (t), *T. podisi* Ashmead (t), *Trichogramma chilonis* Ishii (t), *T. pretiosum* Riley (e,l,p,t), *Trichoporia popei* (Muesebeck) (t), *Trissolcus basalis* (Wollaston) (t), *T. oenone* (Dodd) (t), *Orthomicus erosus* (Wollaston) (p); **Lepidoptera:** *Agrotis fucosa* Butler (e), *A. ipsilon* Hufnagel (e,l,p,t), *Amyelois transitella* (Walker) (e), *Ancylis comptana* (Froelich) (e,l,p,t), *Anticarsia gemmatalis* Hübner (p), *Argyrogramma albostriata* (Bremer & Grey) (t), *Argyrotaenia velutinana* (Walker) (e,l,p,t), *Autographa californica* (Speyer) (e,l,p), *Cacoecimorpha pronubana* (Hübner) (e,l,p,t), *Cadra cautella* (Walker) (e,l,p,t), *Choristoneura occidentalis* Freeman (e,l,p,t), *C. rosaceana* (Harris) (e,l,p), *Cnaphalocoris medinalis* Guenée (e,l,p,t), *Coelophora laricella* (Hübner) (e), *Corcyra cephalonica* (Stainton) (e,t), *Crambus trisectus* (e,p), *Crocidosema plebejana* (Zeller) (e,l,p,t), *Diaphania nitidalis* (Stoll) (e,l,p,t), *Diatraea grandiosella* Dyar (e,l,t), *D. saccharalis* (F.) (e), *Ephestia calidella* (Guenée) (e,p), *E. figuliella* Gregson (e,l,p,t), *E. kuehniella* Zeller (e,l,p,t), *Epichoristoides acerbella* (Walker) (e,l,p,t), *Epiphyas postvittana* (Walker) (e,l,p,t), *Eudocima salaminia* (Cramer) (e,l,p,t), *Euproctis chrysorrhoea* L. (p), *Grapholitha funebrana* Treitschke (e,p), *G. molesta* (p), *Harrisinia brillians* Barnes & McDunnough (e,l), *Heliothis armigera* (Hübner) (e,l,p), *H. zea* Boddie (l,p,t), *H. subflexa* (Guenée) (e,l,p), *H. virescens* (F.) (e,l,p,t), *Heterocampa guttivitta* (Walker) (l), *Homadaula anisocentra* Meyrick (e,l), *Hymenia recurvalis* (F.) (e,l), *Hyphantria cunea* Drury (e,l,p), *Keiferia lycopersicella* (Walsingham) (e,l), *Lithocolletis blancardella* (F.) (e,p,t), *L. pomonella* (Zeller) (e,l,p,t), *Lymantria dispar* L. (l,p), *Mamestra configurata* Walker (e,l,p,t), *Maruca testualis* Gayer (p), *Merophyas divulsana* (Walker) (r,l,p,t), *Mycalesis perseus* (F.) (e), *M. sirius* (F.) (e), *M. terminus* (F.) (e), *Mythimna convecta* (Walker) (e), *Orgyia pseudotsugata* (McDunnough) (l), *Ostrinia nubilalis* (Hübner) (e,l,p,t), *Palpita unionalis* (Hübner) (e), *Pandemis heparana* (Dennis & Schiffermüller) (p), *Papainema nebris* (Guenée) (e,l,p,t), *Papilio glaucus* L. (l), *Pararge aegeria* (L.) (t), *Pectinophora gossypiella* (Saunders) (e,l,p,t), *Peridroma saucia* (Hübner) (e,l,p,t), *Phlogophora meticulosa* (L.) (l,p), *Pieris brassicae* (L.) (e,l), *P. rapae* (L.) (l), *Plathypena scabra* (F.) (e,l,p,t), *Platynota flavedana* Clemens (e,l,p,t), *P. idaeusalis* (Walker) (e,l,p,t), *Plodia interpunctella* (Hübner) (l,p), *Plutella xyllostella* (L.) (e,l,p,t), *Pseudaletia unipuncta* (l,p,t), *Simyra henrici* (l,p) *Spodoptera exigua* (Hübner) (e,l,p), *S. frugiperda* (Smith) (t), *S. littoralis* (Boisduval) (e,p), *S. litura* (F.) (e,l,p,t), *Trichoplusia ni* (Hübner) (e,l,p,t), *Tyria jacobeae* (L.) (l); **Neuroptera:** *Anomalochrysa frater* Perkins (e,l,p,t), *A. maclachlani* Blackburn (e,l,p,t), *Chrysopa carnea* Stephens (e,p), *C. commata* Kis & Ujhelyi (e), *C. harrisii* Fitch (e,l,p,t), *C. oculata* Say (e,l,p,t), *C. perla* (L.) (e), *C. prasina* Burmeister (e), *C. septempunctata* Wesmael (e), *C. ventralis* Curtis (e), *Hemerobius pacificus* Banks (e,l,p,t), *Micromus angulatus* Stephens (e), *M. tasmaniae* (Walker) (e,l,p,t), *M. variegatus* (F.) (e); **Odonata**: *Enallagma ebrium* (Hagen), *E. vernale* Gloyd (e), *Leucorrhinia glacialis* Hagen (e); **Orthoptera:** *Gryllus commodus* Walker (e), *Chortoicetes terminifera* Walker (e), *Paulinia acuminata* (DeGeer) (e), *Schistocerca gregaria* (Forskal) (e); **Plecoptera:** *Skwala parallela* (Frison) (e); **Thysanoptera:** *Haplothrips victoriensis* Bagnall (e,l,t), *Scirothrips dorsalis* Hood (e,l,t), *Thrips imaginis* Bagnall (e,l), *T. obscuratus* (Crawford) (e,l,t), *T. tabaci* Lindeman (e,l,t).