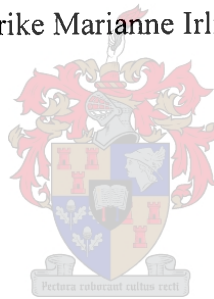# Insects, temperature and the metabolic theory of ecology

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DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature

Date   ....22/02/2007..........

ABSTRACT

Metabolism is a fundamental characteristic of all living organisms. That metabolic rate varies substantially between species and environments has long been recognized and the significance of this variance has gained renewed interest with the introduction of the metabolic theory of ecology (MTE). The theory states that variation in metabolism accounts for variation in a large number of organismal traits, such as development and speciation rates and a range of population parameters. This quantitative theory is based on the assumption that metabolic rate varies principally as a consequence of body mass and temperature. Thus the MTE can be divided into two main components, the mass component and the temperature component, both of which are heavily debated. The empirical values and theoretical explanations underlying the mass scaling of metabolic rate remain a subject of contention. To date, the temperature component, the Universal Temperature Dependence (UTD) of metabolism, has received far less attention than the mass component. In this study the effect of temperature on insect metabolic rate and development rate in the context of the MTE was investigated. The four main predictions of the MTE were examined: (i) the mean activation energy should not be significantly different from the mean value of 0.65 eV, with most values lying between 0.6 and 0.7 eV; (ii) little phylogenetic signal should be evident in the slopes of the rate-temperature relationships; (iii) slopes of the rate-temperature relationships should show minimal environmental variation; (iv) intra- and interspecific rate-temperature relationships should not differ. This study clearly illustrated that the first step in any assessment of the MTE must be to understand the artefacts that might be associated with the data collection, specifically the methods used to measure metabolic rates. Although the intraspecific activation energies were close to the predicted value of 0.65 eV, only 21-31% of all values fell within the predicted range. Consistent variation about the rate-temperature relationships was found in the form of a weak phylogenetic signal, explaining a small

proportion of the variation. A greater proportion of variance was however explained by a set of environmental variables, specifically geographic locality and environmental temperature. In the case of development rate the slopes of the interspecific relationship were typically lower than the mean slopes of the intraspecific relationships, while for metabolic rate this pattern was only apparent in some cases, depending on the method used to calculate the interspecific slopes. Furthermore, this study showed that the environmental temperature at which the insect was thought to live its adult life, or its entire development, plays a pivotal role in shaping the between species rate-temperature relationships. This study showed that the hard version of the UTD of metabolism does not appear to be supported by the data for insect metabolic and development rates, and thus the MTE is rejected. However, some support was obtained for the soft UTD as well as the evolutionary trade-off hypothesis.

OPSOMMING

Metabolisme is 'n basiese eienskap van alle lewende organismes. Dit is lankal bekend dat metaboliese tempo substantieel varieer tussen spesies en omgewings en die belangrikheid van hierdie verskil het nuutgevonde belangstelling met die inleiding van die Metaboliese Teorie van Ekologie (MTE) tot gevolg gehad. Die teorie verklaar dat variasie in metabolisme gee aanleiding tot variasie in 'n groot getal organismiese kenmerke, soos die tempo van ontwikkeling en soortvorming en 'n verskeidenheid van populasie parameters. Hierdie kwantitatiewe teorie mik op 'n verduideliking van hoe metaboliese tempo op grondvlak varieer as 'n gevolg van liggaamsmassa en temperatuur. Dus kan die MTE verdeel word in twee hoof komponente, die massa en die temperatuur komponent waarvan albei ernstig gedebateer word. Die empiriese waardes en teoretiese verduidelikings, wat die massa komponent onderlig, bly onderworpe aan bewering. Die temperatuur komponent, die Universele Temperatuur Afhanklikheid (UTA) van metabolisme het tot op datum veel minder aandag geniet as die massa komponent. In hierdie studie is die effek van temperatuur op insek metaboliese tempo en ontwikkelings tempo in die konteks van die MTE bestudeer. Die vier hoof voorspellings van die MTE was ondersoek: (i) die gemiddelde aktiverings energie behoort nie kenmerkend te verskil van die gemiddelde waarde van 0.65 eV met meeste waardes tussen 0.6 an 0.7 eV; (ii) min filogenetiese seine mag sigbaar wees in die hellings van die temperatuur-tempo verhoudings; (iii) die hellings van die temperatuur-tempo verhoudings mag minimale variasie wys as gevolg van omgewings veranderlikkes; (iv) intra- en interspesiefieke temperatuur-tempo verhoudings behoort nie te verskil nie. Hierdie studie illustreer duidelik dat die eerste stap in enige bepaling van die MTE is die begrip van die artefakte wat met die data versameling geassosieer mag word, spesifiek die metodes wat gebruik is om metaboliese tempo te bereken. Alhoewel die intraspesifieke aktiverings energieë na aan die voorspelde waarde van 0.65 eV was, het slegs 21-31% van al die waardes

binne die voorspelde reeks geval. Konstante variasie oor die temperatuur-tempo verhoudings was gevind in die vorm van swak filogenetiese seine wat n klein deel van die variasie verduidelik. 'n Groot deel van die variasie was verduidelik deur n stel omgewings veranderlikes, spesifiek geografiese lokasie en omgewings temperatuur. In die geval van ontwikkelings tempo was die hellings van die interspesifieke verhoudings tipies laer as die gemiddelde hellings van die intraspesifieke verhoudings, terwyl ten opsigte van metaboliese tempo hierdie patroon slegs in sekere gevalle bekend was, afhanklik van die metode wat gebruik is om die interspesifieke hellings te bereken. Verder het hierdie studie gewys dat die omgewings temperatuur waarby die insek skynbaar sy volwasse lewe uitleef of dat sy volkome ontwikkeling 'n wesenlikke rol speel in die vorming tussen spesies se temperatuur-tempo verhoudings. Hierdie studie het verder gewys dat die harde weergawe van die UTA van metabolisme blyk nie ondersteun te wees deur die data vir insek metaboliese en ontwikkelings tempos en dus word die MTE verwerp. Alhoewel 'n bietjie ondersteuning verwerf is vir die sagte UTA sowel as die evolusionêre kompromis hipotese.

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Chapter 1

General Introduction

Explaining global variation in biodiversity has been a major challenge for decades (Gaston, 2000; Ricklefs, 2004). Several large-scale patterns have been identified, of which the latitudinal gradient in species richness is probably the oldest and most well known (Gaston and Blackburn, 2000; Willig et al., 2003). However, the processes underlying these patterns remain controversial (Rohde, 1992; Gaston, 2000; Allen et al., 2003; Storch, 2003; Currie et al., 2004). Many ecological mechanisms have been proposed aiming at explaining large-scale patterns in species richness, which can be grouped into three main categories: null models, historical factors and ecological processes (Willig et al., 2003; Chown et al., 2004; Pimm and Brown, 2004).

The most recent, comprehensive approach to explaining global variation in biodiversity is the metabolic theory of ecology (MTE) (Brown et al., 2004). This quantitative theory states that metabolism, being the basis of ecology, controls ecological processes at all organizational levels, thus explaining much of biodiversity (West et al., 1997; Ritchie and Olff, 1999; Allen et al., 2002, 2006; Brown and Gillooly, 2003; Brown et al., 2003). Metabolism comprises the entire network of biochemical reactions, including anabolic and catabolic reactions, carried out by living cells that alter energy and materials to produce the required products to sustain life and to maintain a variety of life structures and functions (Schmidt-Nielsen, 1984; West et al., 1999a; Gillooly et al., 2001; Brown et al., 2004; Glazier, 2005). Furthermore, metabolic rate forms a basis for many biological activities at various levels of organization, thus setting the 'pace of life' (Brown et al., 2004; Glazier, 2005).

The metabolic rate of organisms is known to be affected by several important traits, such as body size (Peters, 1983; Schmidt-Nielsen, 1984), physiological status, feeding state or dehydration (Brown et al., 2004; Chown and Nicolson, 2004), and the activity state of the organisms (Schmidt-Nielsen, 1984; Cossins and Bowler, 1987; Spicer and Gaston, 1999). Probably the most important abiotic factor influencing metabolic rate in the inactive state over

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short time scales is temperature (Keister and Buck, 1964; Peters, 1983; Cossins and Bowler, 1987; Clarke and Johnston, 1999; Brown et al., 2004). Because the effects of temperature and body mass on biological processes, such as metabolic rate, are multiplicative (Gillooly et al., 2001; Brown et al., 2003), Gillooly et al. (2001) linked the metabolic rate (Y) of an organism to its body mass (M) and temperature (T), to construct the fundamental equation of the MTE:

$$Y = b_0 M^b e^{-E/kT} \tag{1}$$

The first part of the equation describes the mass component of the MTE, where b_0 is the species-specific normalization constant which is fitted empirically (Brown et al., 2004). The universal scaling exponent, b, is said to be indistinguishable from ¾, as explained by West et al. (1997). The second part of the equation describes the temperature component of the MTE, where T is the absolute temperature in degrees Kelvin, E is the mean activation energy of the respiratory complex in electron Volts (eV) and k is the Boltzmann's constant (8.617×10^{-5} eV/K). The empirically estimated activation energies for different organisms should all be similar, normally within a range of 0.6 – 0.7 eV (Gillooly et al., 2001; Brown et al., 2004). This component of the MTE was termed the 'Universal Temperature Dependence' (UTD) of metabolic rate (Gillooly et al., 2001).

The body size component of the fundamental equation

Organismal body size is an important variable since it affects the rates of all biological processes and structures at all hierarchical organizational levels (Peters, 1983; Schmidt-Nielsen, 1984; West et al., 1997; Brown et al., 2000, 2003). Moreover, many ecologically relevant physiological traits vary with organismal size (Peters, 1983; Schmidt-Nielsen, 1984). The relationship between metabolic rate and body size has long been recognized and is one of the most intriguing problems in ecology and physiology (McMahon and Bonner, 1983;

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Schmidt-Nielsen, 1984). Understanding how this relationship is formed is likely to have a substantial influence on all levels of biology (Suarez et al., 2004; Whitfield, 2004). The size of any living organism affects metabolic rate by setting the rate at which resources can be taken up and distributed. Body size also enforces geometric constraints on exchange surfaces as well as distribution networks (Brown et al., 2003). The relationship between mass and metabolic rate is typically characterized by an allometric equation:

$$Y = b_0 M^b \tag{2}$$

where Y is metabolic rate, b_0 the species specific normalization constant, M is body mass and b is the scaling exponent (Kleiber, 1932; West et al., 1997; Hochachka et al., 2003). By making use of logarithms, this equation becomes:

$$log\ Y = log\ b_0 + b\ log\ M \tag{3}$$

revealing a linear relationship with a slope of b and an intercept of b_0 (Schmidt-Nielsen, 1984; Brown et al., 2000). However, the exact value of the scaling exponent and the nature of the relationship between metabolic rate and body mass remain controversial.

In 1883 Rubner first proposed that the scaling exponent should have a value of ⅔. This relationship was suggested to be a result of simple surface to volume ratios and heat dissipation of mammals, a result of the 'surface law' (Keister and Buck, 1964; Peters, 1983; McMahon and Bonner, 1983; Schmidt-Nielsen, 1984; McNab, 2002; Chown and Nicolson, 2004). Years later, in his study on mammals and birds, Kleiber (1932) found that the relationship between basal metabolic rate and body mass had a slope of 0.74, a value not significantly different from ¾ (McMahon and Bonner, 1983; Schmidt-Nielsen, 1984). For

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decades researchers have proposed a variety of explanations for the scaling relationship, but little consensus was typically achieved (Heusner, 1991; West et al., 1997; Brown et al., 2000; Dodds et al., 2001; Hochachka et al., 2003; Agutter and Wheatley, 2004; Glazier, 2005).

The model proposed by West et al. (1997), aimed at describing the origin of the quarter-power scaling relationship, states that the exact value of the scaling relationship is the result of the rate at which organisms can take up resources from the environment and the rate at which these are distributed through the branching networks supplying various parts of the organism (West et al., 1997, 1999a, b, 2000, 2002). This is suggested to be applicable to all hierarchical levels. Examples of these branching hierarchical transport networks and internal exchange surfaces are the respiratory and circulatory systems of mammals and birds, insect tracheal systems, the vascular systems of plants and intracellular transport systems (West et al., 1997, 2000; Whitfield, 2001). This quantitative model is based on three general principles: First, a space-filling, hierarchical branching system is required to supply every part of the organism with the necessary materials. Second, the terminal unit of this branching network is size-invariant. Third, the energy required to transport the materials is minimized, a result of natural selection (West et al., 1997, 2000, 2002; West and Brown, 2005). In other words metabolic rate is largely supply-limited (Suarez et al., 2004).

However, a number of problems concerning the nutrient supply network model proposed by West et al. (1997) have been raised, resulting in the model being debated vigorously (Dodds et al., 2001; Agutter and Wheatley, 2004; Glazier, 2005; Etienne et al., 2006; see also the special forum in *Ecology* and *Functional Ecology* 2004 and the special issue of *The Journal of Experimental Biology* 2005). Some of the mathematical arguments of the nutrient supply network model have been criticized and it has thus been suggested that the model is flawed (Dodds et al., 2001; Agutter and Wheatley, 2004). Kozłowski and Konarzewski (2004) also argued that several of the model's assumptions seem unrealistic. Of

the assumptions, the size-invariance of the terminal branching units is apparently not in keeping with the mathematics of the model. To obtain the scaling coefficient of ¾, as the model predicts, this assumption has to be violated as the metabolic rate would otherwise scale isometrically with body mass. It was also noted that the model restricts the range of organismal body size, as larger animals would have blood volumes exceeding the body size (Banavar et al., 2002; Kozłowski and Konarzewski, 2004). Furthermore, the model has been criticized on the grounds of its limited range of applicability and its inability to explain the diverse array of scaling exponents so far obtained (Agutter and Wheatley, 2004; Glazier, 2005). Moreover, it has also been pointed out that some organisms lack fractal networks (Glazier, 2005) and that vascular, tracheal and cardiovascular systems do not conform to the assumptions of nutrient supply network model (Kozłowski and Konarzewski, 2004). However, West et al. (1997, 2002) argue that the model should be viewed as a "zeroth-order model", which only incorporates the most important features of the supply networks, and can be extended at later stages for more thorough analyses. Moreover, Etienne et al. (2006) took the nutrient supply network model and investigated its assumptions and the mathematics in more detail. They highlighted some problems and proposed ways to overcome them by reformulating the model, showing also that self-similarity is not required. However, the debate surrounding the nutrient supply network model is still far from being resolved (see Brown et al., 2005; Kozłowski and Konarzewski, 2005).

Besides the nutrient supply network model, several alternative models have been proposed, all aimed at explaining empirical scaling relationships. Banavar et al. (1999) proposed a single-cause model for the same scaling relationship, similar to the one proposed by West et al. (1997, 2002), stating that the scaling relationship is a result of the constraint body mass sets on the delivery of resources to the exchange sites. This model also suggests that the scaling relationship is a result of the internal, physical constraints set by the transport

systems. Similarly, it is also based on the idea that the transport networks minimize the volume of transport-fluid needed but that the demand on resources is met (Banavar et al., 1999, 2002; Whitfield, 2001; Glazier, 2005). However, the delivery-constraint model is simpler, in that the supply network does not necessarily have to be fractal. Importantly, Etienne et al. (2006) showed that this is the case with the nutrient supply network model too. McMahon and Bonner (1983) proposed a different explanation for the quarter-power scaling relationship between metabolic rate and organismal size. Their elastic similarity theory states that the scaling relationship can be explained by biomechanical adaptations to gravitational forces. A multiple-cause model, rather than the above single-cause models, was proposed by Darveau et al. (2002). The allometric cascade model states that the scaling exponent is a result of the joint effects of multiple contributors that control metabolic rate.

Besides these and other models which attempt to explain why metabolic rate scales to mass$^{3/4}$ (see Glazier, 2005), several models have been developed to account for other scaling exponents, in particular the exponent of $2/3$. This is probably the most well known allometric relationship which is based on simple geometric scaling resulting in exponents being multiples of $1/3$ (Brown et al., 2000; West et al., 1997). The basis of these exponents is said to be the result of the relationship between heat production and surface area of endotherms (Keister and Buck, 1964; Schmidt-Nielsen, 1984; Chown and Nicolson, 2004). Furthermore, this scaling relationship was suggested to be a result of the three-dimensionality of organisms (Whitfield, 2001).

An alternative explanation for the relationship between metabolic rate and body size was proposed by Kozłowski et al. (2003a, b). They based their model on the conclusion that there is no unique slope for this scaling relationship. The size optimization model proposed by Kozłowski et al. (2003a, b) is an extension of the model proposed by Kozłowski and Weiner (1997) in which they state that interspecific allometries are a by-product of selection through

evolutionary time, shaping intraspecific scaling relationships. The model suggests that the optimum body size would be the one at which fitness would be at its maximum, which in turn is governed by the size-dependence of mortality and production rates and determines the scaling relationship between metabolic rate and body mass (Kozłowski et al., 2003a, b). The body size optimization model is aimed at explaining the relationship between interspecific and intraspecific scaling relationships, which are said to differ as a result of differences in production and mortality rates between species (Kozłowski and Gawelczyk, 2002; Kozłowski et al., 2003a). Body size differences are generally a result of either an increase in the cell volume or the cell numbers, both of which will result in the scaling relationship between body size and size dependent traits to differ. Cell size was proposed to be determined by the genome size (Kozłowski et al., 2003b). While size increases mediated solely by cell number increases will generally result in metabolic rate scaling isometrically, i.e. $b = 1$, cell size mediated increases in body size will cause metabolic rate to increase less drastically resulting in a lower scaling exponent, b = ⅔ (Kozłowski et al., 2003a, b). The interspecific scaling exponents are said to fall between ⅔ and ¾, which is lower than the range of intraspecific slopes of ¾ and 1 (Kozłowski et al., 2003a). For those organisms making use of both strategies to alter body size the slope of the scaling relationship will fall between ⅔ and 1 (Kozłowski et al., 2003a, b). This model's predictions differ greatly from the nutrient supply network model, which predicts that the scaling exponent of metabolic rate is a constant ¾ for both interspecific as well as intraspecific allometries (West et al., 2002). However, it has been claimed that for vertebrates the within-species scaling exponents are lower than between-species exponents (Andrews and Pough, 1985; McNab, 2002).

Empirical evidence for the mass scaling exponent

The empirical value of the scaling exponent of the MTE is heavily debated, specifically, whether the mass scaling exponent is a multiple of ¼ or some other value. Metabolic rate, and its scaling relation with mass, has been investigated in a range of taxa and the debate on whether metabolic rate scales to ⅔ or ¾ with mass continues (Dodds et al., 2001; McNab, 2002). In a recent review Glazier (2005) stated that because many biological processes scale with mass^{¾} (e.g. West et al., 2001; Savage et al., 2004a; Gillooly et al., 2005) should count towards the idea of having found a universal scaling law, the quarter-power scaling law. However, Glazier (2005) also highlighted some problems concerning this relationship, suggesting that the law is not universal. Some of the problems he pointed out concerned the broad range of scaling exponents obtained by some scientists (e.g. Peters, 1983; Withers, 1992), the ignorance of other scaling exponents, and ignorance of intraspecific metabolic scaling. Thus the universality of the quarter-power scaling law remains questionable. For mammals, some studies have found support for a scaling exponent of ¾ (Kleiber, 1932; Savage et al., 2004b), while others have found scaling exponents that differ from ¾ (Heusner, 1991; Lovegrove, 2000; Dodds et al., 2001; Kozłowski et al., 2003a, b; White and Seymour, 2003, 2005a, b). The deviation in scaling exponents was suggested to be a possible result of microbial fermentation in artiodactyls which results in metabolic rates being elevated (White and Seymour, 2003, 2005a). Furthermore, difference in scaling exponents were also suggested to be caused by ecological types, taxa and body mass range examined in each study (Schmidt-Nielsen, 1984; Heusner, 1991; Lovegrove, 2000; McNab, 2002) as well as a range of extrinsic and intrinsic factors (see Glazier, 2005 for details). After reanalysing data from earlier studies Dodds et al. (2001) found that for smaller mammals the scaling exponents are generally closer to ⅔, while for larger mammals (larger than 500g) the scaling exponent is usually closer to ¾ (Glazier, 2005), possibly a result of differences in

geographical locations (Lovegrove, 2000). Studies on avian metabolic rate-mass scaling relationships (Kleiber, 1932; McKechnie and Wolf, 2004; McKechnie et al., 2006) have found that scaling exponents are more often closer to ⅔ than ¾ (Dodds et al., 2001; Glazier, 2005). Phenotypic plasticity, specifically in the case of captive-raised birds, was found to be a major contributor to variation in metabolic rate-mass scaling relationships (McKechnie et al., 2006).

To date, the majority of studies have examined scaling relationships in mammals and birds (Glazier, 2005), but for the scaling law to be universal, it should apply to all living organisms. While most work has so far focused on endotherms, the empirical work suggests that unicells as well as ectotherms follow the same trends (Robinson et al., 1983; West et al., 2002; West and Brown, 2005). Andrews and Pough (1985) found an interspecific mass scaling exponent significantly higher than ¾ for reptiles. It was found that temperature as well as ecological category plays a vital role in shaping the metabolic rate-mass relationship observed in squamates. Clarke and Johnston (1999) investigated the scaling relationship in teleost fish and found a slope significantly different from the expected values. Empirical work done on arthropods suggested that the slope of the relationship between metabolic rate and body mass is neither ⅔ nor ¾ (Lighton and Fielden, 1995; Lighton et al., 2001; Meehan, 2006), while another study found that mites, springtails and spiders combined have a scaling exponent of ¾ (Meehan, 2006). Furthermore, studies on insects also indicated that the scaling relationships differ significantly from the predicted values (Bartholomew and Casey, 1977; Lighton and Wehner, 1993; Hack, 1997; Davis et al., 1999; Duncan et al., 2002). However, one recent study on insect metabolic rate found that the scaling relationship has a slope not significantly different from ⅔ (Niven and Scharlemann, 2005). Using a larger dataset Chown et al. (2007) found that insect metabolic rate scaled as mass^{¾}, after correcting for phylogenetic non-independence, a procedure ignored by many previous studies (Clarke and Johnston,

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1999; Glazier, 2005; Seymonds and Elgar, 2002). Besides animals, the ¾-power scaling of metabolic rate and size has also been investigated and supported by some studies on plants (Enquist et al., 1998; Enquist and Niklas, 2001, 2002). Further evidence suggesting that metabolic rate does not scale to mass with an exponent of ¾ comes form work done on intraspecific comparisons (Hulbert and Else, 2004; Glazier, 2005). However, little work has been done on intraspecific scaling relationships as a result of the narrow body size ranges in fully grown animals (Chown et al., 2007). Heusner (1991) found that the intraspecific scaling exponent for mammals was not significantly different from ⅔. For squamate reptiles, Andrews and Pough (1985) observed an intraspecific mass scaling exponent of ⅔. However, the range of exponents included ¾. Bokma (2004) found that in fish the intraspecific scaling exponent was significantly different from both the ⅔ as well as the ¾ scaling exponents. Clarke and Johnston (1999) found similar results and also found no difference between interspecific and intraspecific scaling exponents in fish. One recent study on the intraspecific metabolic rate-mass scaling relationship for insects was conducted by Chown et al. (2007) in which they found that the slopes of the ants varied between values that were not significantly different from ⅔ to values not different from 1. In his review Glazier (2005) suggested that intraspecific exponents that deviate from ¾ could be a result of pure chance or due to measurement errors caused by the small body mass range or small available sample sizes. He further suggested that it is likely that different mechanisms drive the interspecific scaling relationship than the intraspecific ones, thus resulting in slopes differing in between- and within-species comparisons (Glazier, 2005). Furthermore, the significance of body mass scaling is vital in understanding processes at many biological levels despite the precise value of the scaling exponent (Peters, 1983).

The temperature component of the fundamental equation

Probably the most important abiotic factor influencing metabolic rate over short time scales is temperature (Keister and Buck, 1964; Peters, 1983; Cossins and Bowler, 1987; Clarke and Johnston, 1999; Brown et al., 2004). Temperature has a marked effect on metabolic rate, similar to temperature effects on the kinetics of chemical and biochemical reactions, generally resulting in an exponential increase in metabolic rate with increasing temperature until some upper level, set by thermal tolerance, is reached (Kleiber, 1932; Robinson et al., 1983; Brown et al., 2003). By altering the rates of biochemical reactions within an organism, temperature alters the metabolic rate of the whole organism (Gillooly et al., 2001; West and Brown, 2005), specifically so for ectotherms (Clarke and Johnston, 1999; Addo-Bediako et al., 2002; Glazier, 2005; Niven and Scharlemann, 2005). The effect of temperature on metabolism is generally expressed as a temperature coefficient (Q_{10} – the change in metabolic rate with a change of 10°C) (Keister and Buck, 1964; Cossins and Bowler, 1987). However, several concerns have been raised regarding the use of Q_{10} as a parameter describing the effects of temperature (Chaui-Berlinck et al., 2002, 2004). An alternative to the Q_{10} was originally proposed by Arrhenius (1889) and extended by Gillooly et al. (2001) who suggested that the temperature dependence of metabolic rate can be explained by the Boltzmann's factor:

$$e^{-E/kT} \tag{4}$$

where T is the absolute temperature in degrees Kelvin, E is the activation energy for metabolism in electron Volts (eV) and k is Boltzmann's constant (8.617×10^{-5} eV/K). This temperature dependence term is a rediscovery of the Arrhenius equation and van't Hoff's law (Arrhenius, 1889; Chown and Nicolson, 2004). The Boltzmann factor, together with the van't

Hoff-Arrhenius relationship, explains the effect temperature has on biological processes (Brown et al., 2004). The Boltzmann's factor is a well known factor widely used in physical chemistry, but it is not widely used in macroecological studies (Brown et al., 2003). The Arrhenius plot, showing the effect of temperature on the logarithmic value of the rate of the biological process of interest, yields a straight line, the slope of which provides the Arrhenius activation energy, which is the rate limiting factor for biochemical reactions (Keister and Buck, 1964; Hochachka and Somero, 2002). Within a range of 'biologically relevant' temperatures (between 0 – 40ºC) (Cossins and Bowler, 1987) the activation energies for different biological processes should all be similar, normally within a range of 0.6 – 0.7 eV (Gillooly et al., 2001; Brown et al., 2004). These predicted values are similar to the range of minimal energy levels required for biochemical reactions of metabolism to take place (Gillooly et al., 2001; Hochachka and Somero, 2002; Brown et al., 2004). Gillooly et al. (2001) referred to their equation as the 'Universal Temperature Dependence' (UTD) of metabolic rate as well as other biological rates and times, suggesting that temperature is one of the major factors underlying metabolic rate variation (Gillooly et al., 2002; Brown et al., 2004; Clarke, 2004; Savage et al., 2004b).

However, the idea and assumptions of the UTD of metabolism as proposed by Gillooly et al. (2001) have been criticized as it is known that several biochemical reactions appear to remain constant at a wide range of ecologically relevant temperatures and are thus considered to be independent of environmental temperature (Hochachka and Somero, 2002; Clarke, 2003, 2004, 2006; Clarke and Fraser, 2004). Furthermore, it has been argued that ATP demand, not temperature *per se*, is the factor driving metabolic rate (Darveau et al., 2002; Hochachka and Somero, 2002; Hochachka et al., 2003). An alternative to the UTD of metabolic rate was proposed by Clarke (2003, 2004), based on the idea that the relationship between metabolic rate and temperature is a result of evolutionary optimizations. This idea

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was termed the 'Evolutionary Trade-Off hypothesis' (ETO), and is based on the assumptions that metabolic rate is a result of the trade-offs between energetic requirements of a species, the temperature it experiences in its environment, and its lifestyle, not temperature *per se* as the UTD argues (Clarke, 2004, 2006). Furthermore, while the UTD suggests that the relationship between metabolic rate and temperature is the same for interspecific as well as intraspecific relationships (Brown and Sibly, 2006), the ETO states that between-species slopes of the logarithm of metabolic rate versus temperature are shallower than within-species slopes (Clarke and Fraser, 2004). Thus, Clarke (2004) suggested that two forms of the UTD hypothesis should be distinguished: the 'hard UTD' as proposed by Gillooly et al. (2001), which Clarke (2004) argues is not supported either empirically or theoretically, and the 'soft UTD' which can be thought of as a statistical description of the relationship between metabolic rate and temperature, but which can be used for large scale investigations of the implications of metabolic rate variation. However, the debate surrounding the UTD of metabolism continues (Clarke, 2006; Gillooly et al., 2006a).

Empirical evaluations of the UTD

The temperature component of the MTE has been less carefully explored than the mass scaling component. The UTD of biological rates was proposed by Gillooly et al. (2001) and subsequently tested for several taxa ranging from unicellular microbes to multicellular ectotherms, endotherms and plants. Initially, Gillooly et al. (2001, 2002) stated that the UTD predicted a wide range of activation energies (0.2 – 1.2 eV, with an average of 0.6 eV) applicable to all organisms. In subsequent work this was refined to a range of 0.6 – 0.7 eV, with an average of 0.65 eV (Brown et al., 2004; Gillooly et al., 2006a). To date, few studies have investigated the temperature component of the MTE. Although the UTD has not been confirmed yet, it has been applied in a number of studies, to either further develop the MTE or

to test the MTE and its underlying assumptions. Although the UTD was incorporated in studies to determine global biodiversity estimates (Allen et al., 2002), evolutionary rates (Gillooly et al., 2005; Allen et al., 2006), development rate (Gillooly et al., 2002) and metabolic rate (Gillooly et al., 2001; Meehan, 2006) few studies have tested the actual validity of the temperature term of the fundamental equation. The debate on whether the UTD is correct or not thus continues. Clarke (2003, 2004, 2006) pointed out a range of problems with this theory and proposed an alternative, the ETO. Meehan (2006) in his study on metabolic rate variation found that for litter and soil invertebrates the activation energy falls within the range of 0.2 and 1.2 eV, with some species having activation energies significantly different from the range of 0.6 – 0.7 eV, as predicted by Brown et al. (2004). Clarke and Johnston (1999) investigated the effect of temperature on metabolic rate of several fish species. They used three different statistical transformations to linearize the data, namely log/linear, log/log and Arrhenius models. The latter was observed to provide the best statistical description of the metabolic rate-temperature relationship in fish. Furthermore, Clarke and Johnston (1999) found some support for the ETO. To date, the MTE cannot be considered to be the unifying theory scientists have been seeking, as both the mass scaling and the temperature component of the MTE continue to be debated vigorously.

Implications of the MTE

The MTE does not only apply to metabolic rate and its variation, but can also be applied to investigate other biological processes (Brown et al., 2004). Mass-specific biological rates R, such as heart rate, developmental rate, mortality rate and rate of molecular evolution, can generally be described by:

$$R = cM^{-\frac{1}{4}} e^{-E/kT} \tag{5}$$

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Biological times D, such as turnover times for generations of individuals and metabolic substrates, as well as for ecosystem processes can generally be explained by the reciprocal of rates:

$$D = dM^{\frac{1}{4}} e^{E/kT} \tag{6}$$

where M is body mass, E is the mean activation energy of the respiratory complex, k is the Boltzmann's constant, T is absolute environmental temperature, and c and d being the species specific normalization constants (Gillooly et al., 2001; Brown et al., 2003, 2004; West and Brown, 2005).

Allen et al. (2002) employed the UTD to explain biodiversity gradients by making use of theoretical frameworks which explain richness and abundance gradients in terms of energetics. They extended the "energetic-equivalence rule" by including temperature and then applied it to predict changes in ectotherm species diversity along temperature gradients. The energetic equivalence rule states that the energy flux of a population per area unit will stay constant with body size. The rule was extended by incorporating environmental temperature in the form of biochemical kinetics of metabolism. Allen et al. (2002) explored both the effect of temperature as well as the effect of quarter-power scaling of mass on the variation of global biodiversity. The Boltzmann's constant of the model can account for large proportions of the variation observed in global diversity patterns (Brown et al., 2003). In their study, Allen et al. (2002, 2006) found support for the idea brought forward by Rohde (1992) that with increasing temperature developmental times become shorter. This again results in faster generation turnover and accelerated biochemical reactions, which eventually results in increased evolutionary rates and an increase in species richness (Rohde, 1992, 1999; Allen et al., 2006).

Furthermore, Kaspari et al. (2004) evaluated three hypotheses (energy-speciation, energy-abundance and area hypothesis) that can be applied to predict variations in species richness patterns in response to large and small-scale changes in the environment. Predictions of home range size and population density have also been investigated by making use of scaling relationships (Damuth, 1981; Belgrano et al., 2002; Enquist et al., 1998; 2002; Jetz et al., 2004). Furthermore, both Savage et al. (2004a) and Frazier et al. (2006) found that the MTE can be used to estimate population growth rates. A further model, based on quarter-power scaling, was introduced fairly recently, which can be used to model ontogenetic growth rates, development rates as well as the timing of life history events (West et al., 2001; Gillooly et al., 2002). However, after re-analyzing the assumptions of the ontogenetic growth models Makarieva et al. (2004) found that these models are unable to predict or even explain growth rates. This conclusion was based on the energy conservation law being violated should the assumptions be met. Moreover, rates of molecular evolution (Gillooly et al., 2005; Allen et al., 2006) as well as the structure and dynamics of food webs (Brown and Gillooly, 2003; Brown et al., 2004) can also be investigated using the MTE. Most recently, Gillooly et al. (2006b) used the MTE to predict the body temperatures of dinosaurs. These are just a few examples giving an indication of the implications and the extent to which the MTE can be used to describe a large range of organismal traits.

The third component of the MTE, resources, is not yet well understood (Brown et al., 2004; Whitfield, 2004). The role of nutrient stoichiometry, the ratios of resources which are the essential elements of life, in ecological scaling is yet to be determined (Agrawal, 2004). Limited resource supply is known to affect population density, biomass, and other traits, through its restricting effects on metabolic rate. Thus Brown et al. (2004) incorporated this term in their model:

$$X = aM^{-\frac{3}{4}} e^{-E/kT} [R] \qquad\qquad (7)$$

where X is the ecological parameter of interest, such as carrying capacity, M is body mass, E is the mean activation energy of the respiratory complex, k is the Boltzmann's constant, T is absolute environmental temperature, a being the species specific normalization constant and [R] represents the concentration of the limiting resources (Brown et al., 2004). Furthermore, Brown et al. (2003) stated that "stoichiometry influences many aspects of ecological structure and dynamics (Elser et al., 2000), including residual variation in ontogenetic growth rates not explained by body size and temperature (Gillooly et al., 2002)". This is likely to be a result of growth rates being dependent on organsimal chemical composition, specifically the nitrogen, carbon and phosphorous ratio (Woods et al., 2003, references therein).

This thesis

Arthropods, especially insects, make an excellent case study to test the MTE, as they are receiving an increased amount of attention in the present debate (reviewed in Chown et al., 2007). This is not surprising, as they are such an abundant and species rich group. Insects play a very significant roles in all ecosystems, from the low to high latitudes, and to date, macroecological and macrophysiological patterns are poorly understood in this group. It is estimated that there are 4 to 8 million extant insect species, of which only a small number have been described (Hawksworth and Kalin-Arroyo, 1995; Ødegaard et al., 2000; Novotny et al., 2002). Furthermore, many studies have been conducted on a large variety of insect physiological traits as well as their life histories, and the data are readily available in the published literature. Specifically metabolic and developmental rate measurements have been investigated on a large number of insect species. Thus the aim of this project is to determine, whether the MTE applies to insects. Chown et al. (2007) have found an interspecific scaling

exponent of ¾ in insects, but have argued that the intraspecific scaling values in ants, varying from 0.67 to 1.0, mean that the insect data are inconsistent with the mass component of the fundamental equation of the MTE. The aims of this work are therefore to determine whether the temperature term of the MTE also applies to insects, making use of metabolic rate and development rate-temperature relationships. By making use of the published literature dating back as far as 1900, with major emphasis on the last 50 years, the MTE and its applicability to insects can be investigated.

First, it will be determined whether there is any directional variance about the rate-temperature relationships. This will be done by investigating whether there is a pronounced phylogenetic signal present as well as the effect of environmental variables, such as temperature, on the rate-temperature relationships. Furthermore, the interspecific rate-temperature relationships will be compared to the intraspecific ones to determine whether there is a difference as the ETO predicts (Clarke, 2004), or whether they are identical, as the UTD predicts (Gillooly et al., 2001). The last test will be to determine whether the interspecific activation energies of the rate-temperature relationships fall within the range of values predicted by Brown et al. (2004).

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Chapter 2

Insect rate-temperature relationships: does the temperature

component of the metabolic theory of ecology apply?

INTRODUCTION

Metabolic rate is a fundamental characteristic of organisms which varies substantially among species and environments. The significance of this variation has long been appreciated (Calow, 1977; Schmidt-Nielsen, 1984; Spicer and Gaston, 1999; McNab, 2002). However, the scope of this significance has been broadened considerably by the metabolic theory of ecology (MTE). According to the MTE, variation in metabolic rate can account for much of the variation in population parameters, generation times and the mutation rates of organisms (Ernest et al., 2003; Gillooly et al., 2002, 2005; Savage et al., 2004a; Frazier et al., 2006), ultimately explaining variation in speciation rates across the planet and large-scale patterns in biodiversity (Allen et al., 2002, 2006, but see also Thomas et al., 2006). Although it is widely acknowledged that metabolic rate may vary for several reasons (Peters, 1983; Schmidt-Nielsen, 1984; Cossins and Bowler, 1987; Spicer and Gaston, 1999; Brown et al., 2004; Chown and Nicolson, 2004), the fundamental equation of the MTE posits that basal (or standard) metabolic rate varies principally as a consequence of organismal body mass and environmental temperature in the following manner (Gillooly et al., 2001; Brown et al., 2004):

$$Y = b_0 M^b e^{-E/kT} \tag{1}$$

where Y is metabolic rate, M is body mass, b a universal scaling exponent (¾), b_0 a taxon-specific constant, E the mean activation energy of the respiratory complex (≈ 0.65 electron Volts), k the Boltzmann's constant (8.617×10^{-5} eV/K), and T the absolute environmental temperature (in Kelvin).

Both the mass and temperature components of this fundamental equation of the MTE have been the subject of contention, although most of the attention has been focussed on the

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former (see Glazier, 2005). Empirical values of and theoretical explanations underpinning the mass scaling of metabolic rate have been questioned (e.g. Dodds et al., 2001; Banavar et al., 2002; White and Seymour, 2003; Agutter and Wheatley, 2004; Kozłowski and Konarzewski, 2004, 2005; McKechnie and Wolf, 2004), and the proponents of the MTE have replied (Allen et al., 2002; Savage et al., 2004b; Brown et al., 2005), with much of the dialogue still ongoing (West and Brown, 2005; Etienne et al., 2006; Makarieva et al., 2006; White et al., 2006). By contrast, discussion of the way in which temperature affects metabolic rate has been less extensive.

Gillooly et al. (2001) proposed that the many different reactions that comprise metabolic rate each depend on the concentration of reactants, their fluxes, and the kinetic energy of the system. The first two terms are accounted for by mass dependence because they are constrained by resource transportation described by the fractal nature of transport systems which lead to a mass-scaling of ¾ (see West et al., 1997). The third term therefore incorporates the major influence of temperature, which is in turn governed by simple Boltzmann kinetics (see also Brown et al., 2004; West and Brown, 2005). The activation energy, E, is apparently relatively invariant among organisms with a mean value of 0.65 eV. This temperature dependence term of the fundamental equation of the MTE has therefore been termed the 'Universal Temperature Dependence' (UTD) (Gillooly et al., 2001).

The validity of the UTD has subsequently been questioned on the grounds that organismal metabolism is very different to the conditions of simple systems, such as molecules in solution, for which the Boltzmann distribution provides a comprehensive description (Clarke, 2004; Clarke and Fraser, 2004). Moreover, as a result of changes in key enzymes among species, reaction rate is rendered relatively independent of environmental temperature (Hochachka and Somero, 2002). In consequence, although a positive relationship between temperature and metabolic rate should remain amongst species, this among-species

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relationship should apparently be different to the rate-temperature relationship within species. Indeed, Clarke (2004) argued that the UTD as described by Gillooly et al. (2001) (termed the hard UTD hypothesis) predicts a similar among- and within-species rate-temperature relationship, whereas the alternative, the evolutionary trade-off hypothesis (ETO) he proposed, predicts a steeper intraspecific relationship (see also Clarke, 2003). Clarke (2004) further proposed that two forms of the UTD hypothesis should be distinguished: a hard version as envisaged by Gillooly et al. (2001), and a soft version which can be thought of as little more than a statistical description of the metabolic rate-temperature relationship, but which can be used for large scale investigations of the implications of metabolic rate variation.

Gillooly et al. (2006) have responded to these criticisms. They argued that, notwithstanding the complexity of biochemical reactions, the UTD continues to explain a very large proportion of variation in mass-corrected metabolic rates, that whole-organismal metabolic rate does indeed reflect the statistical thermodynamics of many of the reactions that comprise metabolic rate, and that evolutionary adaptation, acclimatization and acclimation are reflected predominantly in changes to b_0 of the fundamental equation. They also noted that some variation about the rate-temperature relationships is to be expected, and therefore that the hard UTD hypothesis does not necessarily predict identical within- and among-species relationships. Clarke (2006) has responded to several of these arguments. More recently, Brown and Sibly (2006) have re-iterated this point, stating that 'this very general relationship holds both within and between species'.

According to the proponents of the MTE, other biological rates, such as heart rate, growth rate and development rate vary with mass and temperature in a similar fashion to that described for metabolic rate (Gillooly et al., 2001, 2002; West et al., 2001; Charnov and Gillooly, 2003; Brown et al., 2004). For example, embryonic development rate is considered a

function both of mass and of temperature, with the relationship being described, at its simplest as:

$$\frac{dm}{dt} = am^{3/4} \qquad (2)$$

where dm/dt is growth rate, m is embryonic mass, and a is a function of b_0 (the normalization factor for metabolic rate, see Gillooly et al., 2001), and the mass of a cell and the energy required to grow it (Gillooly et al., 2002). As might be expected, given that $a \propto b_0$, the temperature dependence of a is given by:

$$a(T) \propto \exp^{(-E/kT)} \qquad (3)$$

where E, k and T are as described for Equation 1. Like other aspects of the MTE, these ontogenetic growth models have also been vigorously criticized on several grounds (e.g. Ricklefs, 2003; Makarieva et al., 2004), and the proponents have replied (West et al., 2004). They have also indicated that post-embryonic growth is likely to show similar dependencies on mass and temperature (Gillooly et al., 2002; Brown et al., 2004). Nonetheless, as is the case with the universal temperature dependence of metabolic rate, investigations of the temperature dependence of development rate have been much less extensive than studies of the way in which development rate scales with size (though see Makarieva et al., 2004).

A critical, but perhaps not fully appreciated, point has emerged from these discussions: significant empirical tests of the fundamental equation of the MTE depend not so much on whether there is variation about the scaling and temperature terms, but what form that variation takes and whether it is in a consistent direction. Thus, the proponents of the MTE expect that, once the effects of temperature and mass on rates have been taken into

account, most of the remaining variation should be found in the normalization constant (Brown et al., 2004; Gillooly et al., 2006), with little directional variation about the slope of the rate-temperature and mass-scaling relationships. By contrast, alternative explanations, such as the ETO proposed by Clarke (2004) or the optimization hypothesis proposed by Kozłowski et al. (2003a, b) predict that variation should be found in the slopes of the relationships, and that directional variation in these slopes, especially among different levels in the genealogical hierarchy should be common. To date, only a single, controversial dataset on fish has been used to test these ideas in the context of the rate-temperature term of the fundamental equation of the MTE (Clarke, 2004; Gillooly et al., 2006).

Here, the temperature component of the MTE, as it applies to metabolic rate and development rate, and the form and directionality of variation about it are investigated using insects as model organisms. Given that insects are such a diverse and abundant group of animals, comprising over 70% of extant animal species (Hawksworth and Kalin-Arroyo, 1995; Ødegaard et al., 2000; Novotny et al., 2002), any universal model should apply to this group of animals. Specifically, for both metabolic rate and development rate the following predictions of the MTE are examined: (i) E should assume a mean value of 0.65 eV, with most values lying between 0.6 and 0.7 eV; (ii) little phylogenetic signal should be apparent in the slopes of the rate-temperature relationships; (iii) slopes of the rate-temperature relationships should show minimal environmental variation; (iv) intra- and interspecific rate-temperature relationships should not differ.

MATERIALS AND METHODS

Data collection

Temperature effects on metabolic rate and development rate have been extensively studied in insects (Addo-Bediako et al., 2002; Chown and Nicolson, 2004). To conduct a

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global investigation on the relationship between temperature and these two variables the published Anglophone literature dating back as far as 1900, with a major emphasis on the last 50 years, was examined. Only studies that measured metabolic or development rate at three or more constant temperatures were considered.

Metabolic Rate

From studies on adult insect metabolic rate-temperature relationships, the metabolic rate at each trial temperature, trial temperature, and body mass were extracted. For some species, the authors only published the regression equation of the metabolic rate-temperature relationships, which was then used to calculate the specific metabolic rates for each experimental temperature they had used. In studies that reported sex-related variation in metabolic rate-temperature relationships, the sex with the lower metabolic rate, together with its corresponding body mass was used. The experimental method used to measure metabolic rate was scored as closed or flow-through respirometry, as the former often results in higher estimates of metabolic rate (Lighton and Fielden, 1995; Addo-Bediako et al., 2002). Furthermore, wing status (flying or non-flying) was noted for each species (mostly determined secondarily from taxonomic literature) as it is known that the ability to fly is generally accompanied by elevated standard metabolic rates (Reinhold, 1999).

A study was excluded if data for any of the above variables were not given. Laboratory colonies were excluded to eliminate the possible effects of laboratory adaptation and acclimation (Harshman and Hoffmann, 2000; Terblanche et al., 2004a, 2005a, b), and studies that tested the effect of gas concentrations, diet or any other variables were not considered. Furthermore, when any doubt existed regarding the methods used, the quality of the data or the activity state of the animals, the data were excluded. If multiple data for the same species were obtained from the literature, the data from the locality most unrepresented

were chosen. This approach was necessarily iterative. Metabolic rates were converted to microwatts (μW) (Lighton, 1991; Chown et al., 2007) as a standard unit, assuming a respiratory quotient of 0.84, unless otherwise stated in the particular study. Furthermore, volumetric units were converted on the assumption of standard temperature and pressure (STP).

Development Rate

From studies of development rate-temperature relationships, development time (in days) at each trial temperature, trial temperature and life stage were extracted. If development times were given for several life stages they were summed to obtain times as close as possible to total development times (egg to adult development). In three cases, rate-temperature relationships of the various developmental stages of the same species were published separately. They were combined here to obtain developmental times of total egg-adult development as the methods and collection sites were identical. Where given, the adult body mass was also extracted from the study. However, because few developmental studies record body masses (Chown et al., 2002), these were secondarily determined from the primary literature where possible. For studies that investigated the effect of diet in conjunction with temperature, the developmental times were pooled and the geometric mean of all diets, excluding artificial diets, was used to calculate development rate-temperature relationships. If the effect of humidity on development was tested the humidity most beneficial for the species' development was chosen according to the authors' findings. If studies reported development rate for males and females separately the geometric mean of the rate-temperature relationship of the two sexes was used. For each study it was noted whether the animals were field-collected or reared for several generations in a laboratory.

A study was excluded if data for any of the above variables were not given. Studies that tested the effect of cold exposure prior to the development studies, unusual photoperiods, fluctuating temperatures or the effect of crowding were not considered. Furthermore, when any doubt existed regarding the methods used or the quality of the data, the study was excluded. If multiple data for the same species were obtained from the literature, field-collected animals were chosen first and then the locality least represented in the database. This procedure was necessarily iterative as the database developed.

For each species only the biologically relevant temperature range required for normal development was selected and temperatures detrimental to development were excluded. Although it is widely acknowledged that development rate and temperature show a non-linear relationship, and that this relationship is unimodal (e.g. Honěk and Kocourek, 1990; Birkemoe and Leinaas, 2000; Angiletta and Dunham, 2003), as are so many performance curves (Huey and Stevenson, 1979; Angilletta, 2006), the aim here was to investigate the relationship over its linear range, as has been done previously (Campbell et al., 1974; Lamb, 1992; Honěk and Kocourek, 1990; Honěk, 1996a, b; Jarošík et al., 2002), and as is implied by the metabolic theory of ecology. All developmental times (D) were converted to developmental rates ($^1/_D$). The slopes and intercepts of the relationships between temperature and non-transformed values of development rate were obtained by ordinary least-squares regression of each species individually (Somerfield et al., 2002).

For each study on metabolic or development rate the collection site was noted, and its latitudinal and longitudinal position recorded. If the latter were not presented in the original study, the information was obtained from an appropriate gazetteer. For studies that did not specifically state the geographic locality, and where the species range, as could be ascertained from the literature, was not at odds with the assumption, the authors address was used as the

locality. A suite of environmental variables were obtained from a high resolution, interpolated climate database (www.diva-gis.org) with a 1 km^2 resolution, and typically a time-series of 50 years (Hijmans et al., 2005). Mean annual temperature (MAT), mean annual precipitation (MAP), temperature of the warmest quarter (TWQ) and precipitation of the warmest quarter (PWQ) were extracted for this study for the particular grid within which each species' locality fell. Temperature and precipitation seasonality, calculated from the mean monthly data, were also obtained from the climate database.

Analyses

Intraspecific level

The slopes of the intraspecific relationships between temperature and natural logarithmic values of the metabolic and development rate were obtained by ordinary least-squares regression of each species separately (Somerfield et al., 2002). Because metabolic rate is strongly dependent on both temperature and body mass, it is often considered necessary to remove the effect of mass, to effectively determine the relationship between metabolic rate and temperature (Clarke and Johnston, 1999). The interspecific scaling exponent for insects is ¾ (Chown et al., 2007). Thus the metabolic rate of each species was divided by mass^{¾} resulting in mass specific metabolic rate (μW/g^{¾}). However, in the intraspecific analyses this is not strictly required because dividing through by constant mass will leave the slope of the power relationship unchanged. Intraspecific development rates for total egg-adult development were not mass corrected because most authors do not report masses of the species they investigated (for the 506 species finally used here, masses for 119 species were found). However, because final adult size and development rate are often negatively related (Atkinson, 1994, 1995; Angilletta and Dunham, 2003) it is also inappropriate to include a correction for size. In all cases, to obtain intraspecific activation energy (E) a least-squares

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linear regression of ln rate against inverse absolute temperature (1/kT) was used (see Cossins and Bowler, 1987).

Before proceeding with the investigations of variation in slopes (or activation energies) at this level, it was necessary to determine whether the slopes of the metabolic rate-temperature relationships are likely to be influenced by two artefacts associated with the method of data collection, and whether wing status had an effect on the slopes. It is widely known that activity of individuals during trials may confound estimates of standard metabolic rate (Schmidt-Nielsen, 1984; Chown and Nicolson, 2004). Closed-system respirometry often fails to account for activity and usually results in higher estimates of metabolic rate than real-time, open (flow-through) or similar methods (Lighton and Fielden, 1995). It was reasoned that higher temperatures would result in a higher probability of activity and therefore that for closed system methods slopes of the rate-temperature relationship would be steeper. Likewise, it was reasoned that where individuals were measured in groups, rather than individually, steeper rate-temperature slopes would also be found owing to increasing opportunities for disturbance of the whole group at higher temperatures or a greater proportion of the group being active. Previous studies have also noted that flying insects have higher metabolic rates than non-volant ones (Reinhold, 1999), but no investigations of consistent variation in rate-temperature relationships have been undertaken. In a similar vein, the difference between field and laboratory-acclimated animals in the development rate analyses was investigated because laboratory adaptation/acclimation has been commonly reported (Harshman and Hoffmann, 2000; Terblanche et al., 2004a, 2005a, b). In all cases generalized linear models assuming a normal distribution with a log-link function to examine differences among the groups defined above were used.

To determine whether the intraspecific activation energies had a mean of 0.65 eV and lay mostly between 0.6 and 0.7 eV, a single-sample t-test was applied and the proportion of

the empirical estimates lying between the values was determined, respectively. This was done separately for metabolic rate and development rate. To assess the extent of phylogenetic signal in the data a nested, hierarchical analysis of variance (nested ANOVA) with Satterthwaite's approximation for unequal sample sizes was used (Sokal and Rohlf, 1995; Addo-Bediako et al., 2000, 2002) to determine the significance of each level and the proportion of variation explained. Phylogenetic generalized least squares (PGLS), a more superior method to the one used here, and equivalent to phylogenetic independent contrast analyses (Chown et al., 2007), could not be run due to the lack of a complete phylogeny for insects and the difficulty of implementing this method. The extent of environmental variation in the data was examined using generalized linear models (GLZs) assuming a normal distribution with a log link function (McCullagh and Nelder, 1989). First, following Addo-Bediako et al. (2002), it was determined whether variation in the slopes of the rate-temperature relationships could be explained by latitude and hemisphere. However, latitude is a surrogate for environmental variation. Therefore, mean annual temperature and precipitation (MAT and MAP) together with the seasonality of these two variables were included with hemisphere in a second set of models. It has been argued that mean annual environmental data are not appropriate for use in macroecological studies because most insects are typically inactive during the winter, and that data from the activity season of the species should be used (see Addo-Bediako et al., 2002; Chown et al., 2003; Hodkinson, 2003). Therefore, the effect of temperature and precipitation of the warmest quarter (TWQ and PWQ) were also analysed in a third set of models. In all cases, if confounding or biologically important variables such as respirometry method or wing status were significant in the previous assessments, they were included in the models. In analyses incorporating environmental variables, only development rate-temperature relationships of field collected animals were included, as the latitudinal position for laboratory colonies does not necessarily indicate the true origin of the species and

as environmental temperature for the locality is not a representative of the temperatures experienced by the animals.

The models that best explained the variation in the rate-temperature relationships were selected using the Akaike Information Criterion (AIC). It is insufficient to simply choose the models with the lowest AIC values to compare the fit of competing models, as models might have similar AIC values. This contributes to model uncertainty, which cannot be ignored (Westphal et al., 2003). Akaike weights (w_i) on the other hand can be used to denote the support for a specific model (Burnham and Anderson, 2002; Johnson and Omland, 2004). As the difference between values is more important than the absolute AIC values itself, Akaike weights were calculated. Akaike weights take the AIC differences (Δ_i) into consideration. The calculated AIC weights indicate which model is the best fit model, or rather the probability that it provides the best fit to the data, by explaining the greatest amount of variation (Burnham and Anderson, 2002). Models with $w_i \geq 0.1$ give a set of candidate models to be used for further investigation (Burnham and Anderson, 2002; Westphal et al., 2003).

Interspecific level

For both metabolic rate and development rate interspecific rate-temperature relationships were also calculated. Previous assessments (e.g. Gillooly et al., 2001, 2002) have simply taken a single metabolic or development rate value (or set of values) at a specific experimental temperature (or a few temperatures) for a variety of species and then calculated the interspecific rate-temperature relationship for these species. This presumes that the experimental temperature used was somehow representative of the thermal environments commonly encountered by the species concerned. Although this seems a reasonable assumption, it was reasoned that the form of the interspecific relationship might be substantially affected especially if the experimental temperatures departed to any great extent

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or in any systematic fashion from environmental temperatures (see also Addo-Bediako et al., 2002; Chown et al., 2003; Hodkinson, 2003). In particular, it is not uncommon for studies from cool environments to use temperatures slightly warmer than the mean annual temperature, and those from warm environments to do the converse. Moreover, when dealing with studies for which a range of temperature data are available, it is not always clear which temperature should be selected as representative for the metabolic or development rate of that species, especially if authors do not report microclimate data, which is typically the case. Therefore, a range of approaches for determining the interspecific activation energy or slope of the rate-temperature relationship were adopted. Specifically:

1) For each species a metabolic or development rate measurement together with the specific experimental temperature was selected at random from the available data. These values were then used to determine an interspecific slope. This process was repeated a thousand times. The mean slope with its corresponding confidence intervals of this randomization was used for further investigation.

2) The slopes were calculated such that a metabolic or development rate value at the temperature closest to the MAT for each species was used as the dependent variable and temperature closest to MAT for each species as the independent variable.

3) Metabolic or development rate at the MAT for each species was determined by interpolation of the intraspecific rate-temperature relationship to provide the independent variable, and MAT was used as the independent variable.

4) Same procedure as in 2, but with TWQ.

5) Same procedure as in 3, but with TWQ.

6) For each species the median experimental temperature was selected. However, if no median was available, due to an even number of experimental temperatures, the temperature closest to MAT was selected.

In each case, activation energy was calculated from a least-squares linear regression of ln rate against inverse absolute temperature (1/kT). Mass-corrected data were used throughout which necessarily meant a substantial reduction in the development rate database: of the original 377 field collected species, 85 were used here. The extent to which the six interspecific activation energy values included 0.65 eV was examined by determining whether this value lay within the 95% confidence intervals. Thereafter, an assessment of the differences between the intraspecific and interspecific relationships was made by determining whether the 95% confidence intervals of the data for each of the levels overlapped, for each of the six interspecific relationships, for metabolic rate and for development rate, respectively.

RESULTS

Intraspecific level

The initial dataset on adult insect metabolic rate-temperature relationships contained 129 species, from 9 orders and 37 families (Appendices 1a and b). The mean slope of the metabolic rate-temperature relationship was significantly higher in studies where animals were examined in groups than where single individuals were used (8.95% variance explained, $\chi^2 = 12.10$, df = 127, p<0.001; Figure 1). After excluding studies that examined groups of individuals (Appendix 1a), the data base contained 91 species, in 8 orders and 22 families

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(Table 1, Appendix 1b), of which 30 species were collected in the southern hemisphere and 61 in the northern hemisphere (Figure 2).

Table 1: The number of species, orders and families for which metabolic rate-temperature relationships were obtained from the literature and were used for further analyses.

Order	Family	Species
Coleoptera	Carabidae	3
	Cicindelidae	1
	Coccinellidae	1
	Curculionidae	7
	Perimylopidae	2
	Scarabaeidae	7
	Scolytidae	1
	Tenebrionidae	4
Diptera	Asilidae	2
	Glossinidae	1
	Helcomyzidae	2
	Sphaeroceridae	1
Hemiptera	Cercopidae	1
	Cicadidae	2
Hymenoptera	Formicidae	36
Mantophasmatodea	Austrophasmatidae	1
Odonata	Libellulidae	3
Orthoptera	Acrididae	8
	Gryllidae	5
	Romaleidae	1
	Tettigoniidae	1
Siphonaptera	Pulicidae	1
Total	8	22	91

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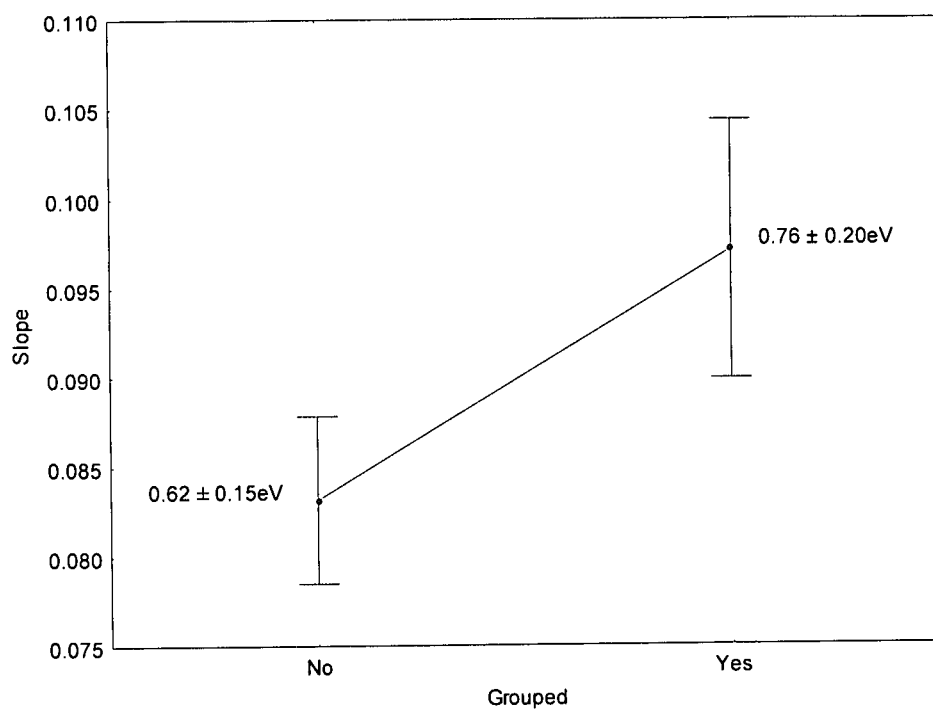
Figure 1: The effect of grouping on the relationship between metabolic rate (in $\ln \mu W/g^{3/4}$) and temperature. Vertical bars denote 95% confidence intervals. The mean ($\pm$ StDev) activation energy in electron Volts for each group is also given.
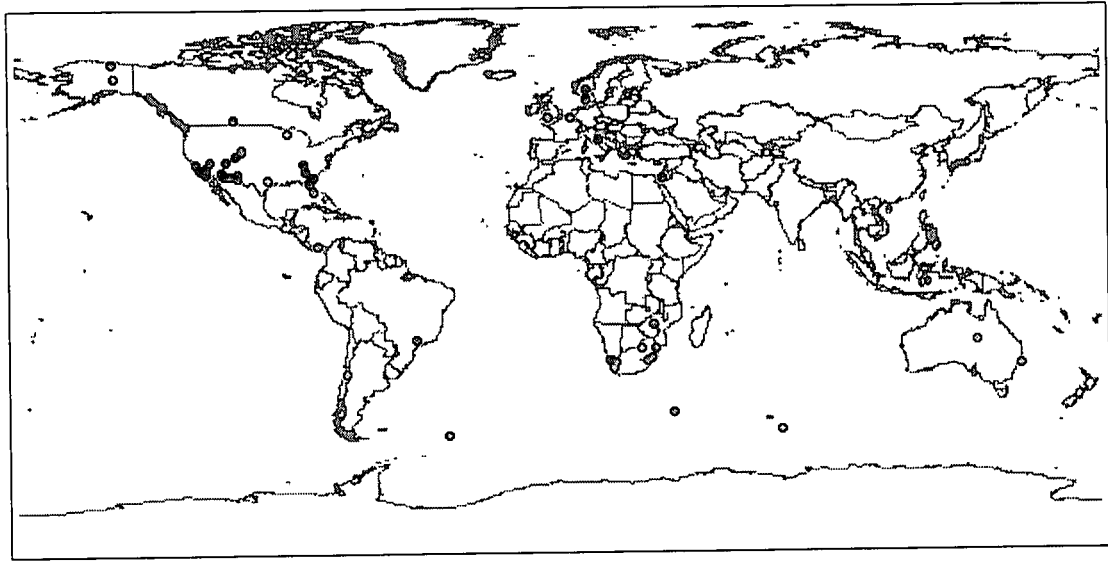
Figure 2: Global geographic extent of studies reporting metabolic rate-temperature relationships in 91 insect species.

Respirometry method likewise had an effect on the slopes of the rate-temperature relationships, with open system methods resulting in a shallower slope estimates and activation energies (8.72% variance explained, χ^2 = 8.30, df = 89, p<0.005, Figure 3). This distinction was therefore included as an independent categorical predictor variable in subsequent analyses. The ability to fly had no significant effect on the estimated slope of the metabolic rate-temperature relationships (χ^2 = 2.97, df = 89, p>0.05) and was thus not considered further in subsequent analyses.
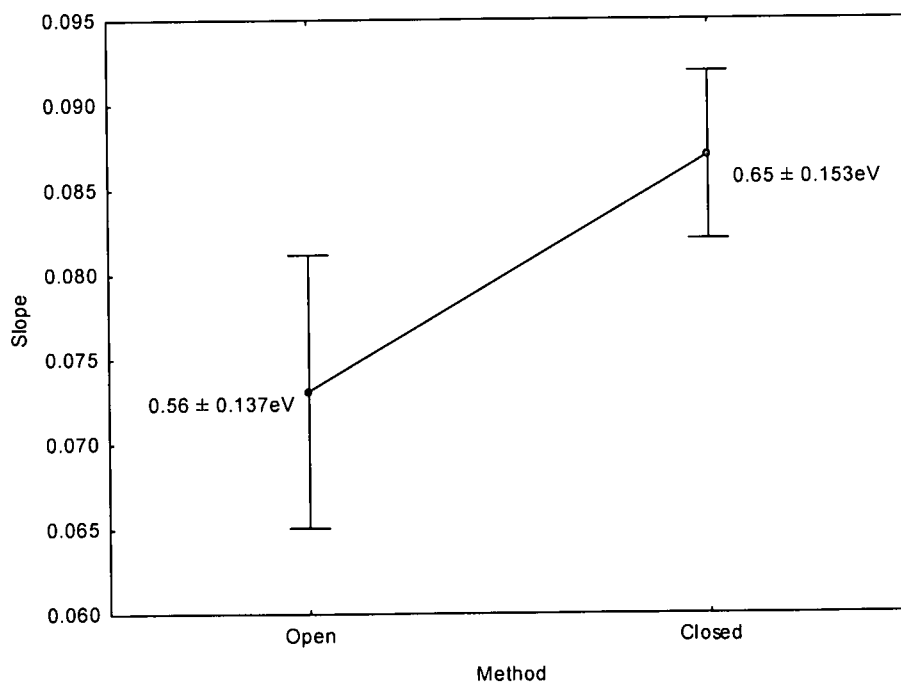
Figure 3: The method used to measure metabolic rate had a significant effect on the relationship between metabolic rate (in ln $\mu W/g^{3/4}$) and temperature. Vertical bars denote 95% confidence intervals. The mean ($\pm$ StDev) activation energy in electron Volts for each group is also given.

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For the development rate dataset a total of 753 species, from 15 orders and 132 families was obtained (Appendices 2a and b). For a total of 506 species, in 12 orders and 101 families (Table 2), total development time from egg to adult was obtained (Appendix 2a), while for the remainder of the species only partial development could be extracted from the published literature and these were thus excluded from subsequent analyses (Appendix 2b). Of the 506 species data for 377 species were from field-collected animals and data for 129 species were from laboratory-reared animals. No significant difference was found in the slopes of the development rate-temperature relationship between field collected and laboratory reared animals ($\chi^2 = 0.70$, df = 504, p>0.05, Figure 4). Of the field collected animals 67 species were collected in the southern and 310 in the northern hemisphere (Figure 5).

Table 2: The number of species, orders and families from which the development rate-temperature relationship was obtained for total egg to adult stage development.

Order	Family	Species
Blattodea	1	1
Coleoptera	20	111
Dermaptera	1	1
Diptera	19	75
Hemiptera	15	77
Hymenoptera	18	134
Lepidoptera	19	85
Neuroptera	2	6
Orthoptera	2	5
Psocoptera	1	1
Siphonaptera	1	2
Thysanoptera	2	8
Total 12	101	506

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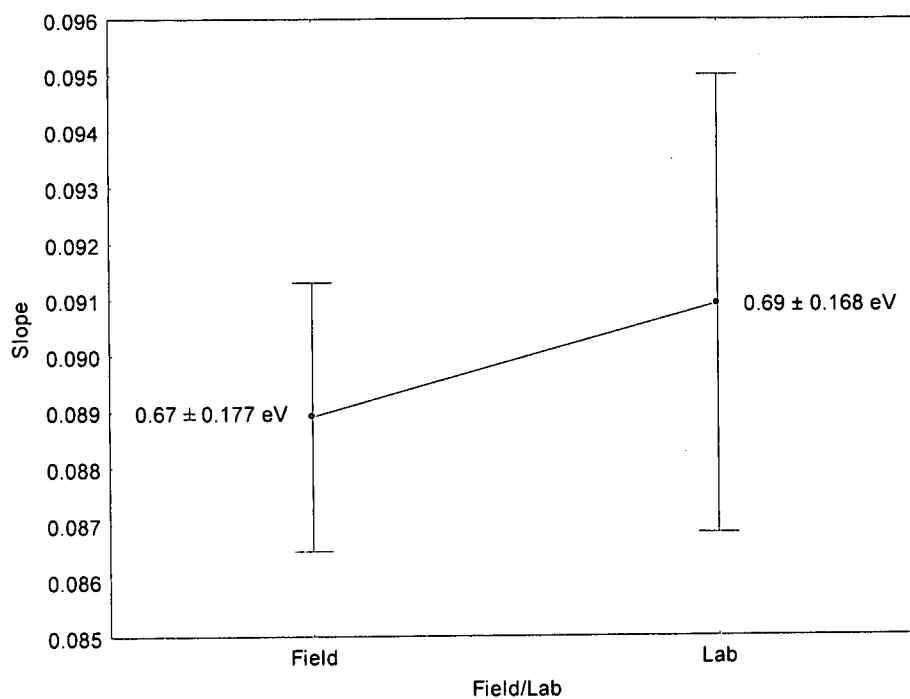
Figure 4: No significant difference was observed between the slope of the development rate-temperature relationships of field collected and laboratory reared animals. The mean (± StDev) activation energy in electron Volts for each group is also given.
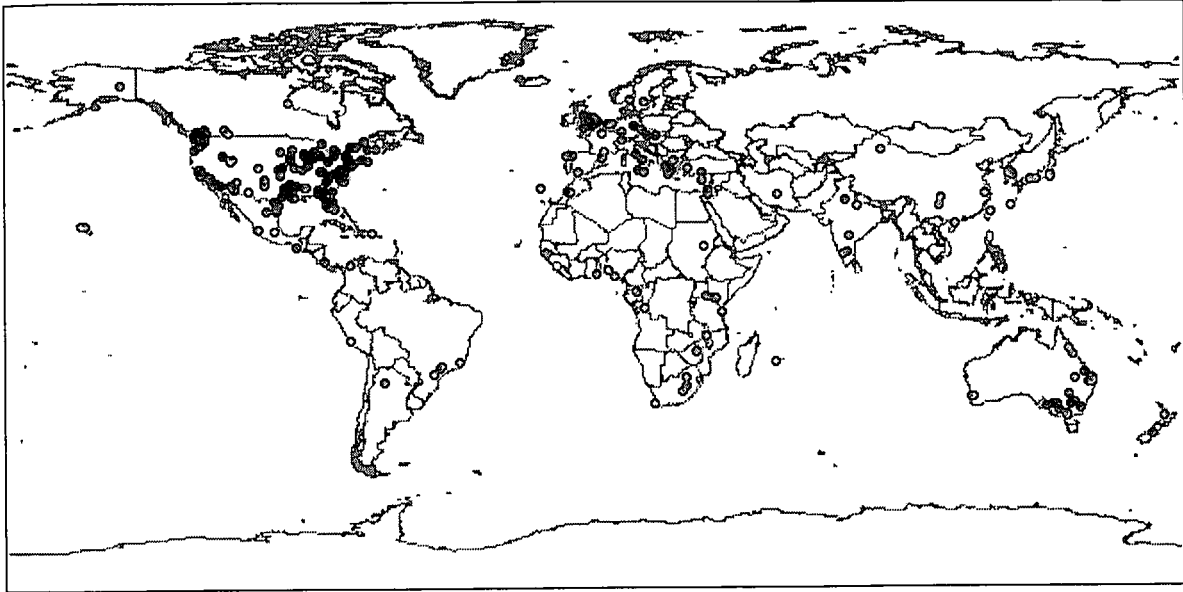
Figure 5: Global geographic extent of studies reporting development rate-temperature relationships for total egg to adult development in 377 insect species. Only the field collected animals were mapped.

The mean intraspecific activation energy of 0.62 ± 0.15 eV for the metabolic rate-temperature relationship was not significantly different from the mean predicted value of 0.65 eV (t = 1.759, df = 90, p>0.05), although only 31% of the values lay between 0.6 and 0.7 eV (Figure 6). In the case of the development rate-temperature relationship the mean activation energy (0.68 ± 0.17 eV) was significantly larger than the predicted value of 0.65 eV. However, the mean value still fell within the predicted range of 0.6 and 0.7 eV, but only 21% of the empirical values lay within this range (Figure 7).
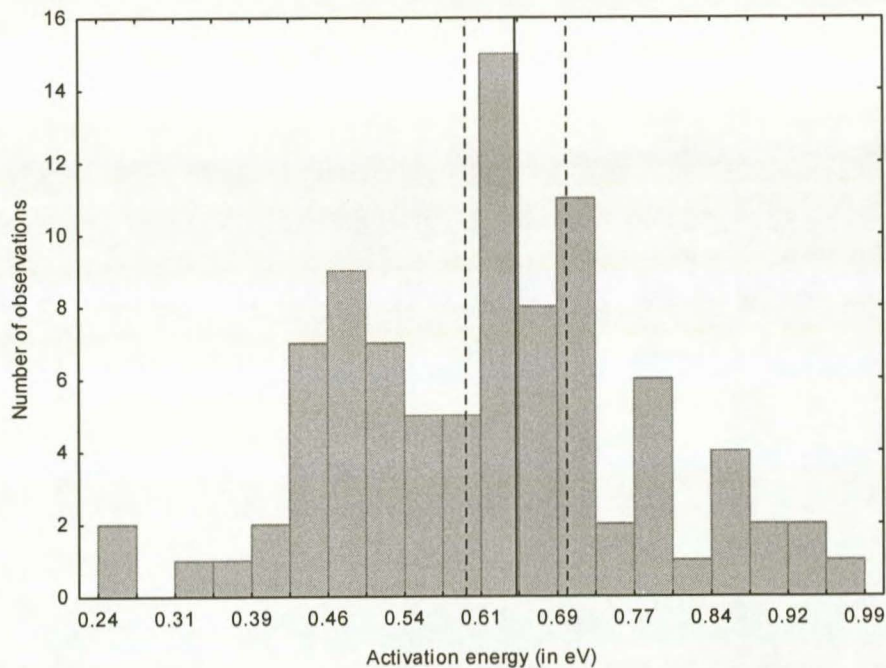
Figure 6: Frequency distribution of the intraspecific activation energies of the metabolic rate data compared with the predicted range of 0.6 – 0.7 eV. The solid line shows the predicted mean value of 0.65 eV and the dashed lines the 0.6 and 0.7 eV range.
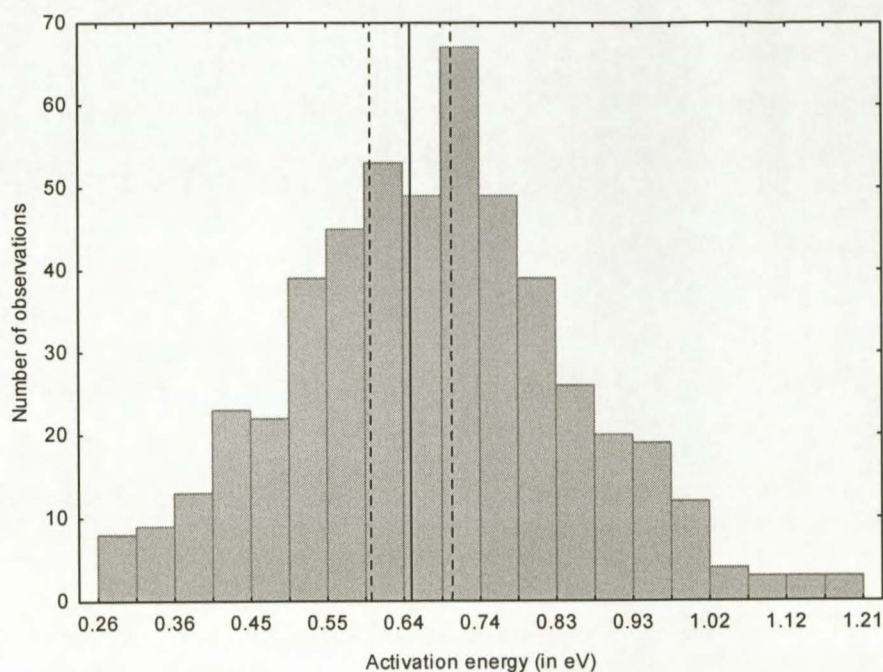
Figure 7: Frequency distribution of the intraspecific activation energies of the development rate data compared with the predicted range of 0.6 – 0.7 eV. The solid line shows the predicted mean value of 0.65 eV and the dashed lines the 0.6 and 0.7 eV range.

The nested ANOVA revealed little phylogenetic signal in the metabolic rate-temperature data because no significant proportion of the variance was partitioned at either the order ($F = 2.088$; df = 7; $p>0.05$) or the family levels ($F = 0.921$; df = 14; $p>0.05$). By contrast, a weak phylogenetic signal was detected in the relationship between development rate and temperature, where a small, but significant proportion of the variance was partitioned at the family level (6.0%, $F = 1.310$; df = 89; $p<0.05$) but not at the order level ($F = 1.037$; df = 11; $p>0.05$).

Significant systematic variation in both rate-temperature relationships was found. Geographic location in the form of absolute latitude and hemisphere was selected as the best fit model for both metabolic (Table 3) and development (Table 4) rate-temperature relationships. In both cases the rate-temperature relationships become steeper towards higher latitudes, showing distinct hemispheric differences. For metabolic rate-temperature relationships the increase in rate is steeper in the northern than in the southern hemisphere (Figure 8). The opposite was observed for the development rate-temperature relationships of the field collected animals, where the steeper, significantly positive relationship is found in the southern hemisphere (Figure 9). When annual environmental data were included, the positive influence of temperature seasonality together with the system used to measure metabolic rate formed the best fit model explaining 16.9% of the variance in the slopes of the metabolic rate-temperature relationships. Mean annual temperature together with hemisphere, with and without the system used, were also included in the best fit models (Table 3). In the case of the slopes of the development rate-temperature relationships, best fit annual environmental data models included temperature and precipitation seasonality together with mean annual temperature and hemisphere, although the variance explained was typically low, all of these variables showed a negative relationship with development rate-temperature relationships (Table 4). In the models investigating the environmental variables of the activity season, TWQ and hemisphere were included in most of the models, often with larger Akaike weights than in any of the other environmental models examined (Tables 3 and 4), although the signs of the estimates were typically in the same direction as in the other models. Both MAT and TWQ showed a consistent negative relationship with the rate-temperature relationships in all selected models.

Table 3: Generalized linear models (Normal error distribution with a log link function) of the influence of the explanatory variables on the slope of the relationship between metabolic rate (ln $\mu W/g^{3/4}$) and temperature. χ^2 = chi squared values, AIC = Akaike value, w_i = Akaike weight, %expl = percentage variance explained. MAT = mean annual temperature, TWQ = temperature of warmest quarter, N vs S = northern and southern hemisphere, system = closed or open system respirometry.

Predictor	df	Estimate ± SE	p	χ^2	AIC	w_i	% expl
Absolute Latitude	2	0.0070 ± 0.0019	0.0002	19.892	-459.13	0.474	19.64
N vs S		0.0771 ± 0.0269	0.0042				
Absolute Latitude	3	0.0060 ± 0.0019	0.0020	21.727	-458.96	0.436	21.24
N vs S		0.0690 ± 0.0275	0.0123				
System		-0.0417 ± 0.0314	0.1836				
Temp. Seasonality	2	0.0002 ± 0.0001	0.0020	16.805	-456.04	0.187	16.86
System		-0.0688 ± 0.0306	0.0246				
N vs S	3	0.0787 ± 0.0288	0.0064	17.633	-454.87	0.104	17.62
MAT		-0.0068 ± 0.0031	0.0289				
System		-0.0455 ± 0.0325	0.1611				
N vs S	2	0.0903 ± 0.0276	0.0011	15.592	-454.83	0.102	15.75
MAT		-0.0085 ± 0.0029	0.0035				
System	2	-0.0698 ± 0.0312	0.0255	13.337	-452.57	0.233	13.63
N vs S		0.0635 ± 0.0289	0.0283				
N vs S	3	0.0881 ± 0.0334	0.0084	15.223	-452.46	0.220	15.40
System		-0.0543 ± 0.0326	0.0955				
TWQ		-0.0051 ± 0.0037	0.1648				
N vs S	2	0.1081 ± 0.0312	0.0005	12.292	-451.53	0.138	12.63
TWQ		-0.0073 ± 0.0035	0.0365				

Table 4: Generalized linear models (Normal error distribution with a log link function) of the influence of the explanatory variables on the slope of the relationship between development rate (ln $^1/_D$) and temperature. χ^2 = chi squared values, AIC = Akaike value, w_i = Akaike weight, %expl = percentage variance explained. MAT = mean annual temperature, TWQ = temperature of warmest quarter, PWQ = precipitation of warmest quarter, N vs S = northern and southern hemisphere.

Predictor	df	Estimate ± SE	p	χ^2	AIC	w_i	% expl
N vs S	2	-0.0584 ± 0.0194	0.0026	9.342	-1745.73	0.779	2.45
Absolute Latitude		0.0030 ± 0.0014	0.0287				
N vs S	1	-0.0376 ± 0.0172	0.0291	4.519	-1742.91	0.190	1.19
Absolute Latitude	1	0.0012 ± 0.0012	0.3465	0.898	-1739.29	0.031	0.24
Temp. Seasonality	4	-0.0002 ± 0.0001	0.0266	16.115	-1748.50	0.153	4.18
Prec. Seasonality		-0.0011 ± 0.0005	0.0368				
MAT		-0.0064 ± 0.0033	0.0519				
N vs S		-0.0313 ± 0.0197	0.1127				
Temp. Seasonality	3	-0.0002 ± 0.0001	0.0017	13.650	-1748.04	0.121	3.56
Prec. Seasonality		-0.0011 ± 0.0005	0.0380				
MAT		-0.0067 ± 0.0032	0.0412				
TWQ	2	-0.0080 ± 0.0032	0.0112	10.995	-1747.38	0.514	2.87
N vs S		-0.0381 ± 0.0171	0.0257				
TWQ	3	-0.0083 ± 0.0033	0.0110	11.093	-1745.48	0.199	2.90
N vs S		-0.0365 ± 0.0178	0.0407				
PWQ		0.00002 ± 0.0001	0.7549				
TWQ	1	-0.0079 ± 0.0032	0.0128	6.278	-1744.66	0.132	1.65
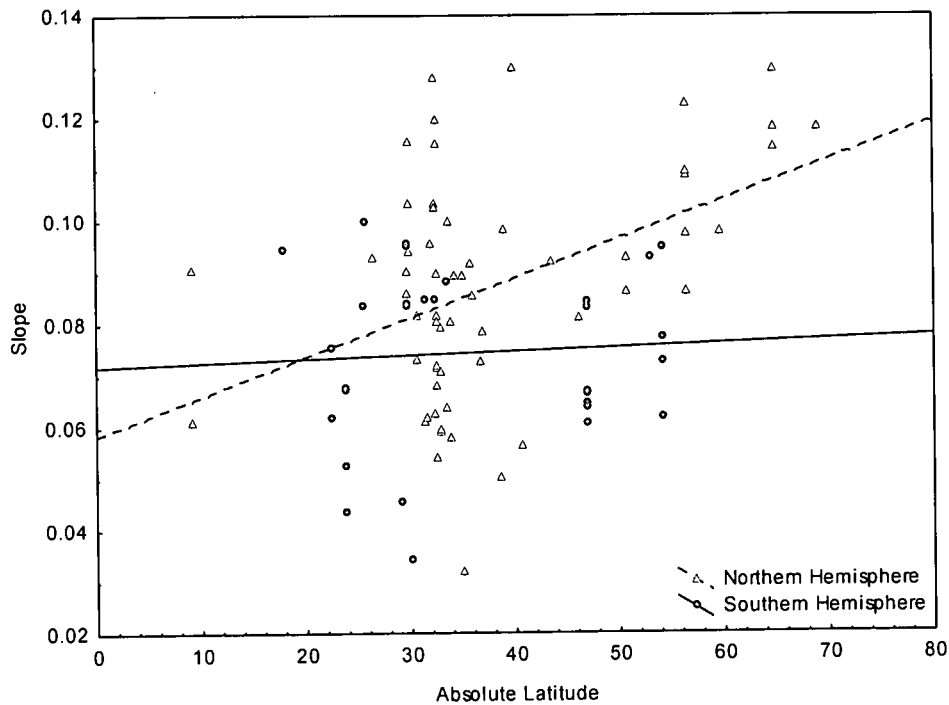
Figure 8: The slopes of the relationship between metabolic rate (in ln $\mu W/g^{3/4}$) and temperature plotted against absolute latitude. For the northern hemisphere the relationship between latitude and the slope of the relationship was significant ($R^2 = 0.185$, $p<0.05$), while for the southern hemisphere the relationship was not significant ($R^2 = 0.003$, $p>0.05$).
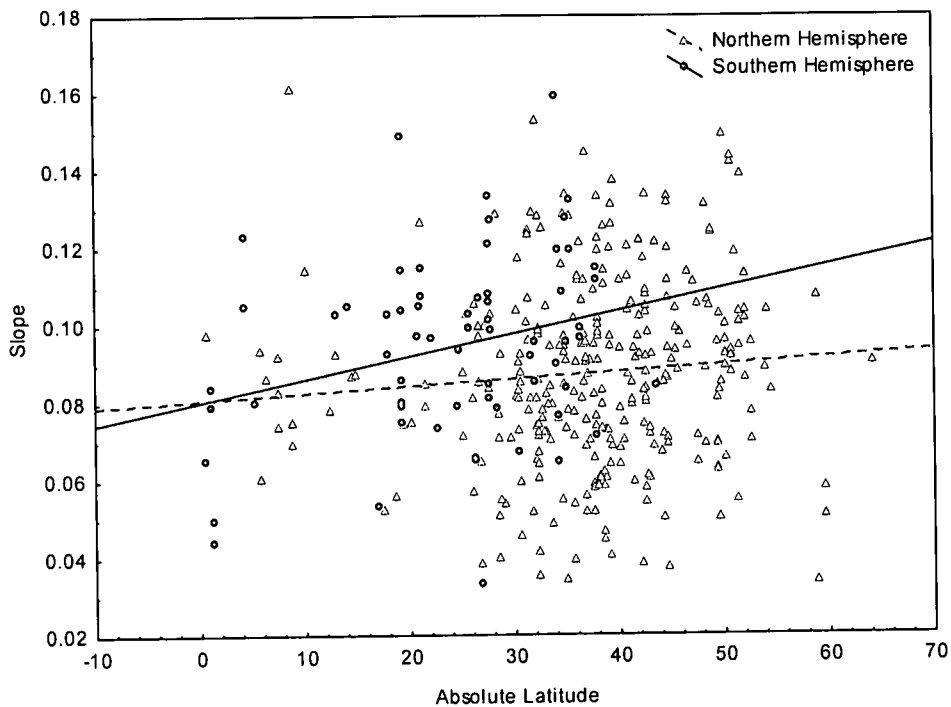
Figure 9: The slopes of the relationship between development rate (ln $^1/_D$) and temperature plotted against absolute latitude. For the northern hemisphere the development rate-temperature relationship was not significant ($R^2 = 0.006$, $p>0.05$) while for the southern hemisphere the relationship was significant ($R^2 = 0.068$, $p<0.05$).

Interspecific level

In the case of metabolic rate, the range of activation energy values predicted by the MTE did not overlap with the 95% confidence intervals of the calculated values for the randomly selected values, at TWQ, and at the median temperature, but not in the other cases (Figure 10). By contrast, the range of values predicted by the MTE did not overlap with the 95% confidence intervals of the interspecific activation energy for development rate in all cases with the exception of development rate interpolated to the mean annual temperature (Figure 11).

The 95% confidence intervals of the mean intraspecific activation energies for metabolic rate did not differ from the 95% confidence intervals of the interspecific activation energy in all but one of the cases. Only where metabolic rate at the temperature of the warmest quarter and this temperature were used to calculate the interspecific activation energy for metabolic rate was the interspecific value smaller than the mean intraspecific one (Figure 10). In the case of development rate, the upper 95% confidence interval of the interspecific activation energy was lower than the lower 95% confidence interval of the mean intraspecific activation energy in all cases except where the interspecific activation energy was calculated using development rate interpolated to the mean annual temperature and MAT (Figure 11).
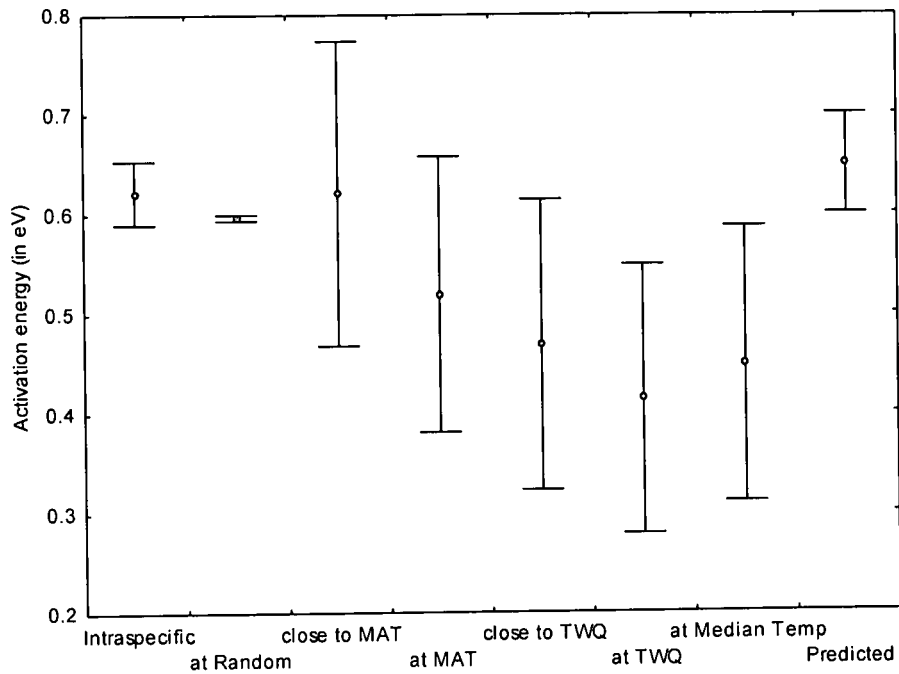
Figure 10: Mean and 95% confidence intervals of the intraspecific activation energies of the metabolic rate compared with the mean interspecific activation energies of metabolic rate and its 95% confidence intervals, calculated in six different ways. The intraspecific and interspecific ectivation energies were further compared to the predicted range of 0.6 – 0.7 eV. MAT = mean annual temperature, TWQ = temperature of the warmest quarter. See test for details.
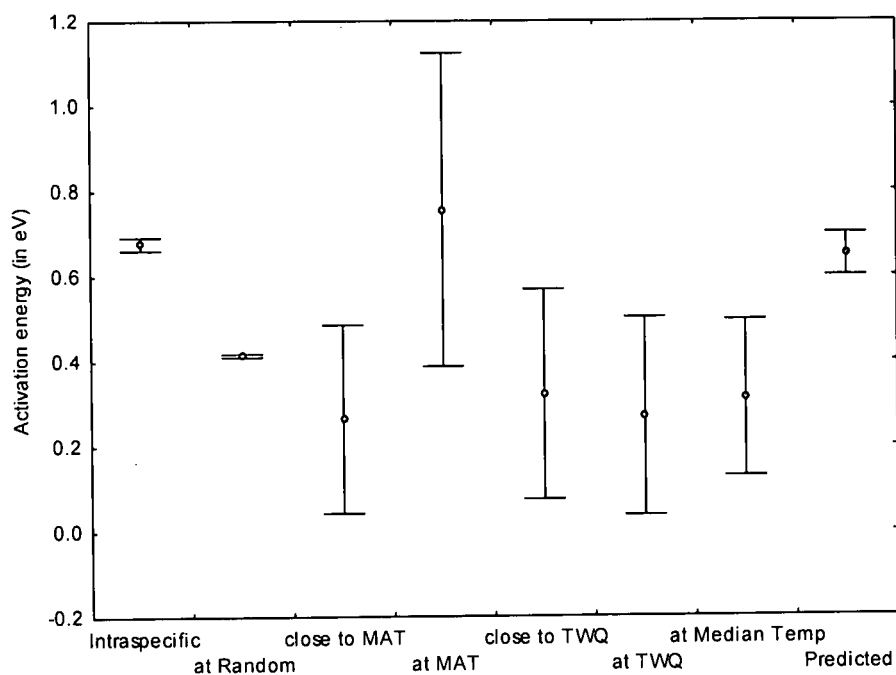
Figure 11: Mean and 95% confidence intervals of the intraspecific activation energies of the metabolic rate compared with the mean interspecific activation energies of metabolic rate and its 95% confidence intervals, calculated in six different ways. The intraspecific and interspecific ectivation energies were further compared to the predicted range of 0.6 – 0.7 eV. MAT = mean annual temperature, TWQ = temperature of the warmest quarter. See test for details.

DISCUSSION

According to the metabolic theory of ecology, vital rates vary largely as a consequence of body mass and temperature, with residual variation largely lying in the normalization constant b_0 (Gillooly et al., 2001, 2006; Brown et al., 2004). Moreover, the theory does not typically predict consistent variation in the form of the body size and temperature components of its fundamental equation, except perhaps in the case of the mass scaling of metabolic rate in mammals (Savage et al., 2004b), which is contentious (Kozłowski and Konarzewski, 2004; White and Seymour, 2004). Indeed, Clarke (2004, 2006) has argued that a substantial difference between the universal temperature dependence component of the fundamental equation, and other explanations for rate-temperature relationships at the whole-organismal level (such as his evolutionary trade-off hypothesis) is that the former posits equivalent slopes or activation energies, whilst the latter does not. This idea has been confirmed by the proponents of the MTE (Brown and Sibly, 2006), though not consistently so (Gillooly et al., 2006). Nonetheless, this prediction of intra- versus interspecific similarity in slopes of the rate-temperature relationship, as well as for little phylogenetic variation, and little consistent, directional environmental variation in the exponents of the fundamental equation of the MTE provide readily testable predictions of the idea that do not just concern the mean value of the exponents, which might be equally well predicted by a range of models (see discussions in Angilletta and Dunham, 2003; Kozłowski et al., 2003a, b; Clarke, 2004; Glazier, 2005; Chown et al., 2007).

This study showed that the first step in any assessment of the universal temperature dependence (UTD) of the MTE must be to understand the artefacts that might be associated with the data collection process. Here, it is clear that the method used to acquire metabolic rate data has a pronounced effect on the slope of the rate-temperature relationship and therefore on the activation energy. Indeed, studies that use groups of individuals are likely to

conclude that the slope of the relationship (or activation energy) is much steeper (larger) than it is in reality. The same is true of investigations that use closed versus open respirometry systems (see Lighton, 1991; Chown and Nicolson, 2004 for discussion of methods). It seems most likely that these results are the consequence of the fact that the closed system method cannot detect movement of individuals as readily as flow-through system methods (see Lighton and Fielden, 1995; Chown et al., 2003; Hodkinson, 2003; Terblanche et al., 2004b), and that movement rate increases with increasing temperature (Gilchrist, 1996; Deere and Chown, 2006). Therefore, rate temperature relationships are likely to be steeper when assessed using closed system methods. This effect is likely to be compounded when groups of individuals are used simply by probability of more individuals being active as temperature increases. This would suggest very steep values for rate-temperature relationship of the grouped animals which is indeed what was found. By contrast, little effect of laboratory adaptation or acclimation was found on the slope of the development rate-temperature relationship. In consequence, assessments of UTD must screen the data that are used carefully to avoid the introduction of likely confounding factors, or should at least explicitly take them into account in formal analyses. Investigations of the mass scaling component of the fundamental equation of the MTE have also shown that several confounding factors must be taken into account during empirical assessments thereof (McKechnie and Wolf, 2004; Farrell-Gray and Gotelli, 2005; White and Seymour, 2005; McKechnie et al., 2006; Chown et al., 2007).

Having taken confounding factors into account, this study showed that the mean intraspecific activation energies for both metabolic rate and development rate lay close to the values predicted by the MTE (Gillooly et al., 2001, 2002; Brown et al., 2004), and certainly well within the 0.6 – 0.7 eV range, although the mean for the latter was significantly larger than the 0.65 eV mean value predicted by the MTE. However, only 21-31% of the activation

energies fell within the 0.6 – 0.7 eV range. It is possible to interpret these results either as providing support for the MTE or as rejecting the idea, depending, unfortunately, on the perspective adopted. For example, the biochemical activation energies Gillooly et al. (2001) used to form the basis for their whole-organismal predictions varied between 0.2 and 1.2 eV; approximately the range found in this study (see Figures 6 and 7). Therefore, it might be argued that the present data support the UTD component of the fundamental equation of the MTE, but then the reasoning might be considered suspiciously circular. Alternatively, it might be argued that because so few of the intraspecific activation energies lie between 0.6 and 0.7, the UTD cannot be applied at the intraspecific level, especially since more recent statements by the proponents of the MTE have suggested that the activation energy should be reasonably tightly constrained between 0.6 and 0.7 eV (Brown et al., 2004; Gillooly et al., 2006). However, because such conclusions might be considered an assessment of the soft UTD hypothesis (i.e. statistical description hypothesis of Clarke, 2004), rather than the hard UTD hypothesis intended by Gillooly et al. (2001), it is necessary first to examine the outcomes of the tests of the consistent phylogenetic and environmental variation about these relationships, and the differences between the intra- and interspecific activation energies.

Unlike the situation for the scaling exponent of the fundamental equation of the MTE (see Kozłowski et al., 2003a, b; White and Seymour, 2003; Chown et al., 2007), little of the variation in the slopes of the rate-temperature relationships was accounted for by phylogenetic relatedness, at least as far as is suggested by the nested hierarchical analysis of variance. However, the nested ANOVA approach is a weak method of investigating the extent of phylogenetic signal (see Harvey and Pagel, 1991 for discussion of limitations of this approach). Moreover, it does not enable the form of the phylogenetic effect to be shown and taken into consideration. A comprehensive understanding of the influence of phylogeny on the present results will require a more sophisticated approach such as that provided by

phylogenetic generalized least squares. By contrast, for the metabolic rate-temperature data at least 20% of the variance was a result of consistent variation with latitude and hemisphere, mostly as a consequence of differences in the extent of seasonality among latitudes and hemispheres. Such consistent variation is larger than that estimated by Gillooly et al. (2006) from a previous investigation (Addo-Bediako et al., 2002) of a smaller data set, and is not predicted by the MTE. Moreover, it is consistent with the outcome of the previous investigation, which concluded that differences in climate (see also Bonan, 2002; Chown et al., 2004) and the opportunities for behavioural thermoregulation might account for the marked difference in the change of slope of the rate-temperature relationship with hemisphere. In the case of development rate, much less of the variation in the slope of the relationships was explained by environmental variables. Moreover environmental influences were more complicated than in the case of metabolic rate. However, consistent variation in the relationships was found, although it was in a different direction to that found for metabolic rate. Why this might be the case likely has to do with the range of environments encountered by all developmental stages (see discussions in Honěk, 1996a, b; Chown et al., 2002), and is beyond the scope of the present investigation. Nonetheless, it is clear that for both development rate and metabolic rate, consistent variation in the form of the rate-temperature relationship was present.

In the case of the difference between the interspecific and intraspecific activation energies or slopes, it was clear that in the case of development rate the slopes of the interspecific relationship were typically lower than the mean slopes of the intraspecific relationships, although the range of the latter encompassed the former. Likewise, the interspecific activation energy value tended to be lower than the $0.6 - 0.7$ eV predicted by the MTE, irrespective of the method used to calculate it. For metabolic rate, the converse appeared to be the case. Moreover, at least half of the calculated interspecific activation

energies had 95% confidence intervals that overlapped with the predicted $0.6 - 0.7$ eV value. Therefore, the interspecific and intraspecific activiation energies certainly did differ, and often in the direction predicted by Clarke (2003, 2004, 2006): i.e. the intraspecific slopes are steeper than the interspecific ones. However, this was dependent to some extent on the environmental temperature at which the insect was thought to live its adult life or its entire development.

Given that so many insect species in more temperate latitudes undergo some form of inactivity, quiescence or diapause during the winter months (Leather et al., 1993; Convey, 1996; Danks, 2002) it seems reasonable to suppose that temperature of the warmest quarter is a better predictor of the temperatures at which the animals find themselves growing and (in adults) metabolizing than mean annual temperature (Hodkinson, 2003). In turn, such an assumption presumes that all of the species examined are largely active in summer, that Stevenson Screen temperatures are a reasonable proxy for microclimates experienced and selected by insects (see Chown et al., 2003), and that the evolution of responses to deal with environmental extremes at other times of the year in no way constrains the temperature sensitivity of growth, development and metabolism to a certain range of values. Most of the studies used here did not provide explicit information on the activity times of the species they examined, nor the likely microclimates they inhabited. Therefore, it is difficult to determine the extent to which these assumptions are correct. Although it is well known that insects actively regulate their body temperatures in a wide variety of ways (reviewed in Heinrich, 1993; Chown and Nicolson, 2004), and that microhabitat selection can influence experienced ambient temperature considerably (Leather et al., 1993; Addo-Bediako et al., 2000; Pincebourde and Casas, 2006a, b) the extent to which this affects macrophysiological investigations at such a scale has not been thoroughly explored (see discussions in Chown et al., 2003; Hodkinson, 2003; Chown and Terblanche, 2007). Similarly, it is difficult to

determine what the likely influence is of biochemical strategies to avoid environmental stress on metabolism and ontogeny generally. Whilst some studies suggest that the stress phenotype results from considerable biochemical resculpting (e.g. Zachariassen, 1985; Bale, 2002; Storey, 2002; Storey and Storey, 2004), others emphasize the tight linkage between stressful and non-stressful conditions (Voituron et al., 2002; Makarieva et al., 2006). Therefore, it is not clear which temperature is the 'right' one to use when conducting interspecific examinations of rate-temperature dependence of the kind originally proposed by Gillooly et al. (2001). Clearly the choice can make a substantive difference, although in turn this depends on the trait under investigation. Future studies clearly need to be specific about the temperatures used, and some investigation of what are the most appropriate temperatures is required.

Bearing in mind these issues, the hard version of the UTD hypothesis does not appear to be supported by the data for insect metabolic and development rates. The large majority of the intraspecific values for activation energy lay outside the 0.6 – 0.7 eV range, as did many of the estimates of interspecific activation energy. Moreover, the inter- and intraspecific values differed for development rate and at least in one case for metabolic rate, and environmental variation in a consistent direction (i.e. not at random with respect to the central tendency) was found in the rate-temperature relationships. Therefore, the empirical data for insects do not support the MTE. Rather, at the least they support the soft version of the UTD, and more optimistically, they support the evolutionary trade-off hypothesis proposed by Clarke (2004). In the case of development rate, the lack of fit between the data and the MTE is perhaps not surprising given that Makarieva et al. (2004) are of the view that the formulation of the MTE for growth and development is problematic.

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Chapter 3

General Conclusion

The metabolic theory of ecology (MTE) has two main components, the mass component and the temperature component (Gillooly et al., 2001; Brown et al., 2004). Although a great deal of attention has been paid to the empirical values and theoretical explanations underlying the mass component (see Glazier, 2005), far less work has been done on testing the assumptions of the temperature component. For insects the mass component of the MTE was explicitly tested by Chown et al. (2007). They rejected the nutrient supply network model, the mechanism underlying the mass component (West et al., 1997; Brown et al., 2004), due to the large variation in intraspecific mass scaling exponents. Rather they found support for the size optimization model proposed by Kozłowski et al. (2003a, b). In this study, the temperature component, the Universal Temperature Dependence (UTD) of metabolism was investigated. Data on insect metabolic rate and development rate-temperature relationships were used to test the main predictions of the UTD. Support for the UTD was limited to the soft version, as proposed by Clarke (2004), while the hard version was rejected. Limited support for the evolutionary trade-off hypothesis, an alternative to the UTD proposed by Clarke (2004), was obtained. Due to the lack of support for both the mass and the temperature component, the MTE with its current assumptions was rejected for insects.

Rather than readdressing some of the assumptions and results obtained in this study, the aim of this section is to highlight several issues that have emerged from this data compilation study, several of which were previously highlighted by Chown et al. (2002). As in previous studies, the geographic extent to which studies were conducted on metabolic rate as well as development rate-temperature relationships is most concentrated in the Holarctic (see Addo-Bediako et al., 2000, 2002), with less than 25% of all studies used in this study collected in the southern hemisphere (Figure 1). Furthermore, little work has so far been done

on tropical species, with less than 15% of all species tested between 25°N and 25°S. Variation in the rate-temperature relationships was found to show pronounced hemispheric differences, mostly as a result of differences in the extent of seasonality among latitudes and hemispheres (Bonan, 2002; Chown et al., 2004).
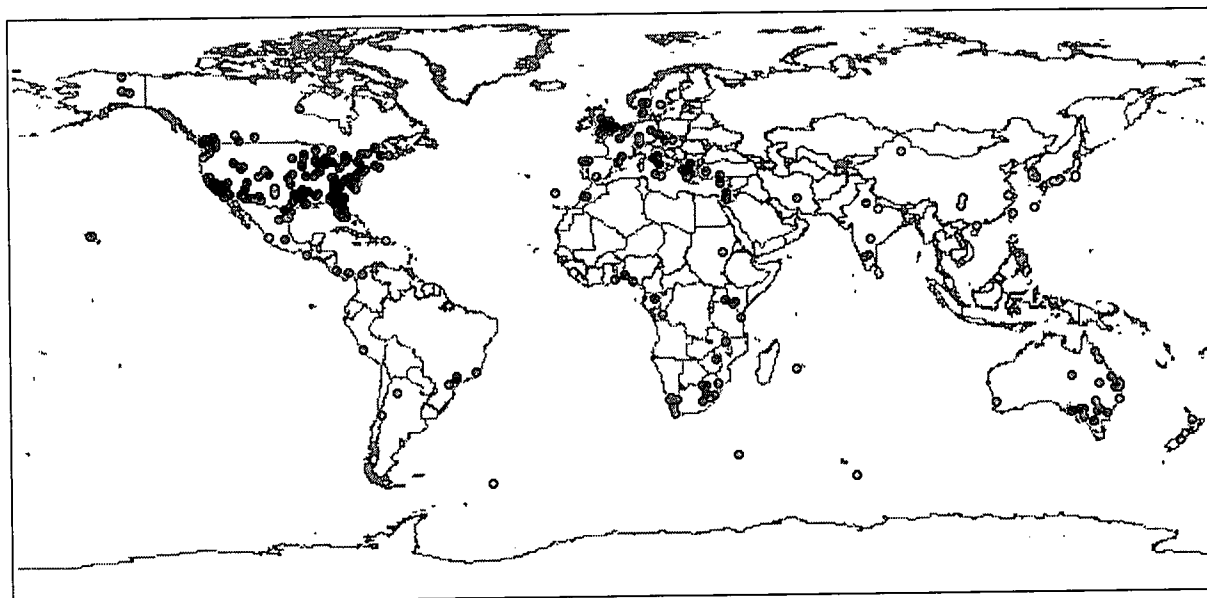
Figure 1: Global geographic extent of studies reporting metabolic and development rate-temperature relationships in 468 field collected insect species. A total of 371 species were collected in the northern hemisphere, while only 97 species were collected in the southern hemisphere.

A further issue raised by Chown et al. (2002) concerns the extent to which body masses are reported in studies, or rather the lack thereof. Several studies on insect metabolic rate-temperature relationships had to be excluded from analyses due to the lack of body masses. For insect development rate-temperature relationships adult body masses were obtained for less than 25% of all the species, most of which were obtained secondarily form other published studies. Body size influences a large range of physiological traits (Peters, 1983; Schmidt-Nielsen, 1984; Kozłowski and Weiner, 1997) and is thus of great importance. Development rate of ectotherms has been shown to negatively influence final adult body size (Atkinson, 1994, 1995; Angilletta and Dunham, 2003). This could have an impact on the rate-temperature relationships of insects, but is unlikely to affect the outcomes of this study.

The last issue raised concerns the environmental temperature experienced by insects. Most studies that investigated the effect of environmental temperature on organismal traits used the mean annual temperature of the locality where the animals were collected (e.g. Addo-Bediako et al., 2002; Veldtman and McGeoch, 2003; Lovegrove, 2003; Lardies et al., 2004; Frazier et al., 2006). However, it has been argued that annual temperature is not the best representative for insects as they are generally inactive during the cold winter months. Instead it was suggested that the temperature of their activity season should be used (Hodkinson, 2003) and some discussion of this matter has permeated the entire literature on insect macrophysiology (Addo-Bediako et al., 2002; Chown et al., 2003). This study has highlighted the fact that the selected environmental temperature can have a substantial effect on the outcomes. Thus, future studies need to be more specific about the temperatures used and some investigation of what are the most appropriate temperatures is required. Understanding the body temperatures of insects in the field is also significant for this reason. However, it does not seem wise at this stage to reject all macrophysiological studies using mean annual temperature. The veracity of these studies will depend both on the signal to noise ratio that

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APPENDIX 1a

Slopes of the relationships between metabolic rate (in ln μW/g$^{3/4}$) and experimental temperature for the insect species extracted from the published literature. The animals were measured in groups of two or more individuals simultaneously and were excluded from subsequent analyses. The temperature range (in °C) at which the metabolic rates were measured and body masses (in mg) are also given.

Species	Family	Order	Mass (mg)	Slope	Temp range Min	Max	Reference
Chauliognathus marginatus	Cantharidae	Coleoptera	33.00	0.0817	22.0	34.0	Menhinick, 1967
Diabrotica 12-*punctata*	Chrysomelidae	Coleoptera	19.50	0.0742	22.0	34.0	Menhinick, 1967
Maecolaspis flavida	Chrysomelidae	Coleoptera	12.30	0.0719	22.0	34.0	Menhinick, 1967
Pantomorus taeniatulus	Curculionidae	Coleoptera	14.70	0.0872	22.0	34.0	Menhinick, 1967
Conoderus aversus	Elateridae	Coleoptera	13.50	0.0652	22.0	34.0	Menhinick, 1967
Collops 4-*maculatus*	Melyridae	Coleoptera	9.00	0.1044	22.0	34.0	Menhinick, 1967
Bothrotes fortis	Tenebrionidae	Coleoptera	162.00	0.1382	22.0	34.0	Menhinick, 1967
Asilus sp.	Asilidae	Diptera	37.80	0.1072	22.0	34.0	Menhinick, 1967
Proctacanthus sp.	Asilidae	Diptera	405.00	0.1287	22.0	34.0	Menhinick, 1967
Clastoptera xanthocephala	Cercopidae	Hemiptera	2.10	0.0578	22.0	34.0	Menhinick, 1967
Prosapia bicincta	Cercopidae	Hemiptera	28.50	0.0858	22.0	34.0	Menhinick, 1967
Cuerna costalis	Cicadellidae	Hemiptera	22.20	0.0796	22.0	34.0	Menhinick, 1967
Deltocephalus sp.	Cicadellidae	Hemiptera	20.10	0.1206	22.0	34.0	Menhinick, 1967

Appendix 1a continued

Species	Family	Order	Mass (mg)	Slope	Temp range Min	Max	Reference
Gyponana sp.	Cicadellidae	Hemiptera	1.80	0.0796	22.0	34.0	Menhinick, 1967
Alydus eurinus	Coreidae	Hemiptera	30.00	0.0923	22.0	34.0	Menhinick, 1967
Alydus pilosulus	Coreidae	Hemiptera	27.00	0.0882	22.0	34.0	Menhinick, 1967
Harmostes reflexulus	Coreidae	Hemiptera	17.10	0.0889	22.0	34.0	Menhinick, 1967
Ormenis septentrionalis	Fulgoridae	Hemiptera	15.60	0.1038	22.0	34.0	Menhinick, 1967
Stictocephala diminuta	Membracidae	Hemiptera	16.80	0.0906	22.0	34.0	Menhinick, 1967
Vanduzea leata	Membracidae	Hemiptera	5.40	0.1048	22.0	34.0	Menhinick, 1967
Lygus lineolaris	Miridae	Hemiptera	6.00	0.0771	22.0	34.0	Menhinick, 1967
Acrosternum hilaris	Pentatomidae	Hemiptera	294.00	0.0706	22.0	34.0	Menhinick, 1967
Euschistus servus	Pentatomidae	Hemiptera	123.00	0.0954	22.0	34.0	Menhinick, 1967
Hymenarcys nervosa	Pentatomidae	Hemiptera	30.00	0.1808	22.0	34.0	Menhinick, 1967
Solubea pugnax	Pentatomidae	Hemiptera	54.00	0.0620	22.0	34.0	Menhinick, 1967
Thyanta custator	Pentatomidae	Hemiptera	63.00	0.1109	22.0	34.0	Menhinick, 1967
Sinea diadema	Reduviidae	Hemiptera	42.00	0.1061	22.0	34.0	Menhinick, 1967
Zelus cervicalis	Reduviidae	Hemiptera	33.00	0.1118	22.0	34.0	Menhinick, 1967
Apis mellifera	Apidae	Hymenoptera	66.00	0.1636	22.0	34.0	Menhinick, 1967
Chelaner rothsteini	Formicidae	Hymenoptera	0.75	0.1088	10.0	35.0	Davison, 1987
Chelaner whitei	Formicidae	Hymenoptera	6.00	0.0888	10.0	35.0	Davison, 1987
Dorymyrmex pyramicus	Formicidae	Hymenoptera	0.90	0.1044	22.0	34.0	Menhinick, 1967

Appendix 1a continued

Species	Family	Order	Mass (mg)	Slope	Temp range		Reference
					Min	Max	
Pogonomyrmex badius	Formicidae	Hymenoptera	6.60	0.0811	10.0	40.0	Golley & Gentry, 1964
Megachile mendica	Megachilidae	Hymenoptera	78.00	0.1069	22.0	34.0	Menhinick, 1967
Osmia sp.	Megachilidae	Hymenoptera	198.00	0.1189	22.0	34.0	Menhinick, 1967
Campsomeris plumipes	Scolytidae	Hymenoptera	147.00	0.0883	22.0	34.0	Menhinick, 1967
Noctuidae sp.	Noctuidae	Lepidoptera	99.00	0.0847	22.0	34.0	Menhinick, 1967
Mesothemia sp.	Libellulidae	Odonata	420.00	0.0806	22.0	34.0	Menhinick, 1967

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APPENDIX 1b

Slopes of the relationships between metabolic rate (in ln $\mu W/g^{3/4}$) and experimental temperature of the insects used in this study, together with the temperature range (in °C) and body mass (in mg) used. These are the metabolic rate-temperature relationships of animals that were measured individually and used for analyses.

Species	Family	Order	Mass (mg)	Slope	Temp range Min	Temp range Max	Reference
Abax ater	Carabidae	Coleoptera	244.69	0.0864	5.0	25.0	Chaabane et al., 1999
Carenum sp.	Carabidae	Coleoptera	4167.50	0.0673	20.0	35.0	Duncan and Dickman, 2001
Cerotalis sp.	Carabidae	Coleoptera	567.80	0.0437	20.0	40.0	Duncan and Dickman, 2001
Cicindela longilabris	Cicindelidae	Coleoptera	118.00	0.0815	15.0	30.0	Schultz et al., 1992
Hippodamia convergens	Coccinellidae	Coleoptera	17.00	0.0897	0.0	40.0	Acar et al., 2001
Bothrometopus elongatus	Curculionidae	Coleoptera	1.80	0.0646	2.5	25.0	Chown et al., 1997
Bothrometopus parvulus	Curculionidae	Coleoptera	3.60	0.0610	5.0	25.0	Chown et al., 1997
Bothrometopus randi	Curculionidae	Coleoptera	13.80	0.0640	5.0	30.0	Chown et al., 1997
Canonopsis sericeus	Curculionidae	Coleoptera	60.35	0.0930	0.0	15.0	Klok and Chown, 2005
Ectemnorhinus marioni	Curculionidae	Coleoptera	6.30	0.0669	2.5	25.0	Chown et al., 1997
Ectemnorhinus similis	Curculionidae	Coleoptera	25.50	0.0833	5.0	30.0	Chown et al., 1997
Palirhoeus eatoni	Curculionidae	Coleoptera	6.80	0.0666	5.0	30.0	Chown et al., 1997

Appendix 1b continued

Species	Family	Order	Mass (mg)	Slope	Temp range Min	Max	Reference
Hydromedion sparsutum	Perimylopidae	Coleoptera	23.50	0.0621	5.0	20.0	Sømme et al., 1989
Perimylops antarcticus	Perimylopidae	Coleoptera	14.50	0.0728	5.0	20.0	Sømme et al., 1989
Pleocoma australis	Scarabaeidae	Coleoptera	1000.00	0.0920	5.0	25.0	Morgan, 1987
Scarabaeus galenus	Scarabaeidae	Coleoptera	1470.00	0.0836	16.0	32.0	Chown and Davis, 2003
Scarabaeus gariepinus	Scarabaeidae	Coleoptera	1130.00	0.0952	16.0	32.0	Chown and Davis, 2003
Scarabaeus hippocrates	Scarabaeidae	Coleoptera	2010.00	0.0842	16.0	32.0	Davis et al., 2000
Scarabaeus rusticus	Scarabaeidae	Coleoptera	1060.00	0.1001	16.0	32.0	Chown and Davis, 2003
Scarabaeus striatum	Scarabaeidae	Coleoptera	790.00	0.0956	16.0	32.0	Davis et al., 2000
Scarabaeus westwoodi	Scarabaeidae	Coleoptera	1800.00	0.0836	16.0	32.0	Chown and Davis, 2003
Ips acuminatus	Scolytidae	Coleoptera	2.84	0.0981	10.0	20.0	Gherken, 1985
Cryptoglossa verrucosa	Tenebrionidae	Coleoptera	700.00	0.0896	10.0	30.0	Cooper, 1993
Eleodes armata	Tenebrionidae	Coleoptera	917.00	0.0320	10.0	30.0	Cooper, 1993
Heleus waiti	Tenebrionidae	Coleoptera	713.00	0.0526	20.0	40.0	Duncan and Dickman, 2001
Pterohelaeus sp.	Tenebrionidae	Coleoptera	246.80	0.0677	20.0	40.0	Duncan and Dickman, 2001
Pilica formidolosa	Asilidae	Diptera	200.00	0.0610	22.0	37.0	Morgan et al., 1985
Promachus sp.	Asilidae	Diptera	180.00	0.0908	22.0	37.0	Morgan et al., 1985
Glossina morsitans orientalis	Glossinidae	Diptera	22.34	0.0947	6.0	41.0	Rajagopal and Bursell, 1966
Paractora dreuxi	Helcomyzidae	Diptera	19.17	0.0846	5.0	30.0	Chown, 1997
Paractora trichosterna	Helcomyzidae	Diptera	13.26	0.0948	2.0	25.0	Chown, 1997

Appendix 1b continued

Species	Family	Order	Mass (mg)	Slope	Temp range Min	Max	Reference
Antrops truncipennis	Sphaeroceridae	Diptera	2.21	0.0774	2.0	25.0	Chown, 1997
Neophilaenus lineatus	Cercopidae	Hemiptera	5.74	0.0931	10.0	25.0	Hinton, 1971
Cystosoma saundersii	Cicadidae	Hemiptera	1158.00	0.0850	10.0	25.0	Mac Nally and Doolan, 1982
Diceroprocta apache	Cicadidae	Hemiptera	622.00	0.0641	30.0	42.1	Hadley et al., 1991
Aphaenogaster cockerelli	Formicidae	Hymenoptera	14.16	0.1280	5.0	35.0	Nielsen, 1986
Atta laevigata	Formicidae	Hymenoptera	15.00	0.0621	5.0	35.0	Beraldo and Mendes, 1982
Atta sexdens rubropilosa	Formicidae	Hymenoptera	15.00	0.0755	5.0	35.0	Beraldo and Mendes, 1982
Camponotus fulvopilosus	Formicidae	Hymenoptera	43.00	0.0850	10.0	40.0	Lighton, 1989
Camponotus herculeanus	Formicidae	Hymenoptera	26.85	0.1182	5.0	25.0	Nielsen, 1986
Camponotus laevigatus	Formicidae	Hymenoptera	57.45	0.0717	5.0	25.0	Nielsen, 1986
Camponotus sp.	Formicidae	Hymenoptera	46.23	0.0728	5.0	25.0	Nielsen, 1986
Camponotus vafer	Formicidae	Hymenoptera	13.53	0.1034	5.0	35.0	Nielsen, 1986
Camponotus vicinus	Formicidae	Hymenoptera	52.90	0.0580	10.0	40.0	Lighton, 1988
Crematogaster californica	Formicidae	Hymenoptera	1.43	0.0594	20.0	40.0	Schilman et al., 2005
Dorymyrmex insanus	Formicidae	Hymenoptera	0.59	0.0806	20.0	40.0	Schilman et al., 2005
Forelius foetidus	Formicidae	Hymenoptera	0.30	0.1026	15.0	35.0	Nielsen, 1986
Forelius mccooki	Formicidae	Hymenoptera	0.27	0.0709	20.0	40.0	Schilman et al., 2005
Formica fusca	Formicidae	Hymenoptera	4.45	0.0864	5.0	25.0	Jensen and Nielsen, 1975
Formica fusca var. *subaenescens*	Formicidae	Hymenoptera	4.04	0.1294	5.0	25.0	Nielsen, 1986

Appendix 1b continued

Species	Family	Order	Mass (mg)	Slope	Temp range Min	Temp range Max	Reference
Formica occulta	Formicidae	Hymenoptera	3.90	0.0900	5.0	25.0	Nielsen, 1986
Formica perpilosa	Formicidae	Hymenoptera	11.73	0.0681	15.0	35.0	Kay and Whitford, 1975
Formica pratensis	Formicidae	Hymenoptera	6.08	0.1091	15.0	30.0	Jensen and Nielsen, 1975
Lasius niger	Formicidae	Hymenoptera	1.84	0.1098	5.0	25.0	Jensen and Nielsen, 1975
Lasius sitiens	Formicidae	Hymenoptera	0.87	0.1199	5.0	25.0	Nielsen, 1986
Leptogenys nitida	Formicidae	Hymenoptera	1.71	0.0456	20.0	30.0	Duncan and Crewe, 1993
Leptothorax acerovorum	Formicidae	Hymenoptera	1.11	0.1183	5.0	25.0	Nielsen, 1986
Linepithema humile	Formicidae	Hymenoptera	0.44	0.0542	20.0	40.0	Schilman et al., 2005
Messor capitatus	Formicidae	Hymenoptera	9.25	0.0923	10.0	40.0	Nielsen and Baroni-Urbani, 1990
Myrmica alaskensis	Formicidae	Hymenoptera	2.73	0.1145	5.0	25.0	Nielsen, 1986
Myrmica rubra	Formicidae	Hymenoptera	2.40	0.0976	5.0	25.0	Jensen and Nielsen, 1975
Novomessor cockerelli	Formicidae	Hymenoptera	3.21	0.0816	15.0	35.0	Kay and Whitford, 1975
Pogonomyrmex californicus	Formicidae	Hymenoptera	4.17	0.1151	15.0	35.0	Kay and Whitford, 1975
Pogonomyrmex desetorum	Formicidae	Hymenoptera	6.63	0.0805	15.0	35.0	Kay and Whitford, 1975
Pogonomyrmex maricopa	Formicidae	Hymenoptera	11.07	0.0621	5.0	45.0	Ettershank and Whitford, 1973
Pogonomyrmex occidentalis	Formicidae	Hymenoptera	9.00	0.0564	10.0	40.0	Rogers et al., 1972
Pogonomyrmex rugosus	Formicidae	Hymenoptera	14.85	0.0628	5.0	45.0	Ettershank and Whitford, 1973
Solenopsis invicta	Formicidae	Hymenoptera	2.95	0.0819	15.0	40.0	Elzen, 1986
Solenopsis xyloni	Formicidae	Hymenoptera	0.50	0.0595	20.0	40.0	Schilman et al., 2005

Appendix 1b continued

Species	Family	Order	Mass (mg)	Slope	Temp range Min	Max	Reference
Tetramorium caespitum	Formicidae	Hymenoptera	0.76	0.1228	5.0	25.0	Jensen and Nielsen, 1975
Trachymyrex smithi neomexicanus	Formicidae	Hymenoptera	3.03	0.0720	15.0	35.0	Kay and Whitford, 1975
Karoophasma biedouwensis	Austrophasmatidae	Mantophasmatodea	94.22	0.0342	10.0	25.0	Chown et al., 2006
Erythrodiplax connata	Libellulidae	Odonata	51.67	0.0904	20.0	40.0	May, 1979
Miathyria marcella	Libellulidae	Odonata	175.67	0.0843	20.0	40.0	May, 1979
Pachydiplax longipennis	Libellulidae	Odonata	192.50	0.0862	15.0	40.0	May, 1979
Bootettix punctatus	Acrididae	Orthoptera	141.15	0.0785	10.0	40.0	Mispagel 1978
Encoptolophus sordidus costalis	Acrididae	Orthoptera	174.60	0.0865	10.0	25.0	Bailey and Riegert, 1973
Melanoplus bivittatus	Acrididae	Orthoptera	1800.00	0.1299	15.0	35.0	Harrison and Fewell, 1995
Melanoplus sanguinipes	Acrididae	Orthoptera	295.00	0.0794	13.0	42.0	Chappel, 1983
Taeniopoda eques	Acrididae	Orthoptera	2043.00	0.0959	15.0	30.0	Quinlan and Hadley, 1993
Trimerotropis pallidipennis	Acrididae	Orthoptera	174.60	0.0502	25.0	40.0	Massion, 1983
Trimerotropis saxatilis	Acrididae	Orthoptera	135.88	0.1001	15.0	32.0	Duke and Crossley, 1975
Trimerotropis suffusa	Acrididae	Orthoptera	297.50	0.0985	25.0	40.0	Massion, 1983
Anurogryllus arboreus	Gryllidae	Orthoptera	377.00	0.0941	10.0	30.0	Prestwich and Walker, 1981
Hophlosphyrum griseus	Gryllidae	Orthoptera	38.93	0.0882	7.0	27.0	Nespolo et al., 2003
Oceanthus celerinicus	Gryllidae	Orthoptera	53.00	0.1157	10.0	35.0	Prestwich and Walker, 1981
Oceanthus quadripunctatus	Gryllidae	Orthoptera	49.00	0.1035	10.0	35.0	Prestwich and Walker, 1981

Appendix 1b continued

Species	Family	Order	Mass (mg)	Slope	Temp range Min	Temp range Max	Reference
Pteronemobius fasciatus	Gryllidae	Orthoptera	78.51	0.0858	15.0	25.0	van Hook, 1971
Romalea guttata	Romaleidae	Orthoptera	2921.00	0.0929	15.0	30.0	Hadley and Quinlan, 1993
Orchelimum fidicinium	Tettigoniidae	Orthoptera	303.42	0.0610	20.0	30.0	Smalley, 1960
Xenopsylla ramesis	Pulicidae	Siphonaptera	0.16	0.0731	10.0	30.0	Fielden et al., 2004

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APPENDIX 2a

Slopes of the relationships between development rate (ln $^1/_D$) and experimental temperature of the insects used in this study, together with the temperature range (in °C) used. Given are all the species for which total egg to adult development rate-temperature relationships were obtained.

Species	Family	Order	Slope	Temp range Min	Max	Reference
Periplaneta fuliginosa	Blattidae	Blattodea	0.0950	20.0	35.0	Benson et al., 1994
Stegobium paniceum	Anobiidae	Coleoptera	0.1305	17.5	25.0	Lefkovitch, 1967
Cylas puncticollis	Apionidae	Coleoptera	0.1033	18.6	31.2	Nteletsana et al., 2001
Prostephanus truncatus	Bostrichidae	Coleoptera	0.0748	22.0	32.0	Bell and Watters, 1982
Rhizopertha dominica	Bostrichidae	Coleoptera	0.0992	22.0	34.0	Birch, 1945
Callosobruchus maculatus	Bruchidae	Coleoptera	0.0605	25.0	35.0	Lale and Viddal, 2003
Callosobruchus rhodesianus	Bruchidae	Coleoptera	0.0977	20.0	30.0	Giga and Smith, 1983
Callosobruchus subinnotatus	Bruchidae	Coleoptera	0.0530	25.0	35.0	Lale and Viddal, 2003
Amara aenea	Carabidae	Coleoptera	0.1007	17.0	28.0	Saska and Honěk, 2003
Amara familiaris	Carabidae	Coleoptera	0.0899	17.0	28.0	Saska and Honěk, 2003
Amara fulvipes	Carabidae	Coleoptera	0.1066	17.0	28.0	Saska and Honěk, 2003
Amara littorea	Carabidae	Coleoptera	0.0926	17.0	28.0	Saska and Honěk, 2003
Amara ovata	Carabidae	Coleoptera	0.0965	17.0	28.0	Saska and Honěk, 2003

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Amara similata	Carabidae	Coleoptera	0.0899	17.0	28.0	Saska and Honěk, 2003
Monochamus carolinensis	Cerambycidae	Coleoptera	0.0931	22.0	30.0	Pershing and Linit, 1986
Cassida rubiginosa	Chrysomelidae	Coleoptera	0.0743	21.1	32.5	Ward and Pienkowski, 1978
Cerotoma arcuatus	Chrysomelidae	Coleoptera	0.0735	18.0	32.0	Nava and Parra, 2003
Crioceris asparagi	Chrysomelidae	Coleoptera	0.0940	10.0	32.0	Taylor and Harcourt, 1978
Diorhabda elongata	Chrysomelidae	Coleoptera	0.0721	20.0	35.0	Herrera et al., 2005
Galerucella calmariensis	Chrysomelidae	Coleoptera	0.0978	15.0	25.0	McAvoy and Kok, 2004
Galerucella pusilla	Chrysomelidae	Coleoptera	0.0856	15.0	27.5	McAvoy and Kok, 2004
Gastrophysa viridula	Chrysomelidae	Coleoptera	0.0658	18.0	28.0	Honěk et al., 2003
Leptinotarsa decemlineata	Chrysomelidae	Coleoptera	0.0916	15.0	29.0	Logan et al., 1985
Oulema melanopus	Chrysomelidae	Coleoptera	0.0985	8.0	30.0	Guppy and Harcourt, 1978
Pyrrhalta luteola	Chrysomelidae	Coleoptera	0.0952	15.6	32.2	King et al., 1985
Adalia bipunctata	Coccinellidae	Coleoptera	0.0804	15.6	29.4	Obrycki and Tauber, 1981
Calvia quatuordecimguttata	Coccinellidae	Coleoptera	0.1116	10.0	26.0	LaMana and Miller, 1995
Chilocorus nigritus	Coccinellidae	Coleoptera	0.1126	20.0	30.0	Ponsonby and Copland, 1996
Coccinella novemnotata	Coccinellidae	Coleoptera	0.1052	15.6	32.2	McMullen, 1967
Coccinella septempunctata	Coccinellidae	Coleoptera	0.1262	14.0	23.0	Katsarou et al., 2005
Coccinella transversoguttata richardsoni	Coccinellidae	Coleoptera	0.0883	18.3	29.4	Obrycki and Tauber, 1981

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Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Coccinella trifasciata	Coccinellidae	Coleoptera	0.0868	18.0	34.0	Miller and LaMana, 1995
Coleomegilla maculata lengi	Coccinellidae	Coleoptera	0.1215	19.0	27.3	Wright and Laing, 1978
Diomus austrinus	Coccinellidae	Coleoptera	0.0975	20.0	30.0	Chong et al., 2005
Epilachna varivestis	Coccinellidae	Coleoptera	0.0871	15.0	27.0	Fan et al., 1992
Eriopis connexa	Coccinellidae	Coleoptera	0.1126	14.0	26.0	Miller and Paustian, 1992
Harmonia axyridis	Coccinellidae	Coleoptera	0.0946	14.0	34.0	LaMana and Miller, 1998
Hippodamia convergens	Coccinellidae	Coleoptera	0.1313	14.0	23.0	Katsarou et al., 2005
Hippodamia parenthesis	Coccinellidae	Coleoptera	0.1025	14.0	30.0	Orr and Obrycki, 1990
Hippodamia sinuata	Coccinellidae	Coleoptera	0.0784	15.0	25.0	Michels and Behle, 1991
Lioadalia flavomaculata	Coccinellidae	Coleoptera	0.0997	13.0	32.0	Brown, 1972
Nephus bisignatus	Coccinellidae	Coleoptera	0.0692	15.0	32.5	Kontodimas et al., 2004
Nephus includens	Coccinellidae	Coleoptera	0.0907	15.0	32.5	Kontodimas et al., 2004
Oenopia conglobata contaminata	Coccinellidae	Coleoptera	0.0905	17.5	30.0	Mehrnejad and Jalali, 2004
Propylea dissecta	Coccinellidae	Coleoptera	0.0387	20.0	35.0	Omkar, 2004
Pullus mediterraneus	Coccinellidae	Coleoptera	0.0815	15.0	30.0	Ba M'Hamed and Chemseddine, 2001
Rhyzobius lophanthae	Coccinellidae	Coleoptera	0.0769	15.0	30.0	Stathas, 2000
Rodolia cardinalis	Coccinellidae	Coleoptera	0.1216	14.0	26.0	Grafton-Cardwell et al., 2005

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Scymnus levaillanti	Coccinellidae	Coleoptera	0.0607	20.0	35.0	Uygun and Atlihan, 2000
Stethorus japonicus	Coccinellidae	Coleoptera	0.1121	15.0	30.0	Mori et al., 2005
Stethorus punctillum	Coccinellidae	Coleoptera	0.1116	14.0	30.0	Roy et al., 2002
Cryptolestes ferrugineus	Cucujidae	Coleoptera	0.0856	22.0	35.0	White and Bell, 1994
Cryptolestes pusillus	Cucujidae	Coleoptera	0.0953	20.0	32.5	Currie, 1967
Anthonomus eugenii	Curculionidae	Coleoptera	0.0856	15.0	30.0	Toapanta et al., 2005
Anthonomus grandis thurberiae	Curculionidae	Coleoptera	0.0955	15.0	30.0	Fye et al., 1969
Anthonomus signatus	Curculionidae	Coleoptera	0.0504	15.6	30.0	Clarke and Howitt, 1975
Aubeonymus mariaefranciscae	Curculionidae	Coleoptera	0.1092	20.0	26.0	Marco et al., 1997
Bagous affinis	Curculionidae	Coleoptera	0.1023	18.0	32.0	Godfrey and Anderson, 1994
Baris lepidii	Curculionidae	Coleoptera	0.0733	15.0	27.0	Sherrod et al., 1982
Calandra oryzae	Curculionidae	Coleoptera	0.1266	18.2	29.1	Birch, 1945
Conotrachelus nenuphar	Curculionidae	Coleoptera	0.0924	17.0	28.0	Lan et al., 2004
Cylas formicarius elegantulus	Curculionidae	Coleoptera	0.1532	20.0	27.0	Mullen, 1981
Euhrychiopsis lecontei	Curculionidae	Coleoptera	0.0911	15.0	29.0	Mazzei et al., 1999
Gonipterus scutellatus	Curculionidae	Coleoptera	0.0923	10.5	26.8	Santolamazza-Carbone et al., 2006
Hylobius pales	Curculionidae	Coleoptera	0.0490	21.0	28.0	Salom et al., 1987
Hypera brunneipennis	Curculionidae	Coleoptera	0.0823	15.0	26.7	Butler and Ritchie, 1967
Hypera meles	Curculionidae	Coleoptera	0.1052	12.0	35.0	Chan et al., 1990

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Hypera postica	Curculionidae	Coleoptera	0.1046	12.0	32.0	Guppy and Mukerji, 1974
Listronotus oregonensis	Curculionidae	Coleoptera	0.1207	12.7	23.9	Simonet and Davenport, 1981
Listronotus texanus	Curculionidae	Coleoptera	0.1055	17.5	30.0	Woodson and Edelson, 1988
Otiorrhynchus sulcatus	Curculionidae	Coleoptera	0.0442	15.0	24.0	Stenseth, 1979
Sitophilus granarius	Curculionidae	Coleoptera	0.0623	20.0	30.0	Campbell et al., 1976
Sitophilus oryzae	Curculionidae	Coleoptera	0.0825	20.0	28.0	Ryoo and Cho, 1988
Cybocephalus micans	Cybocephalidae	Coleoptera	0.0742	20.0	36.0	Blumberg and Swirski, 1982
Cybocephalus nigriceps nigriceps	Cybocephalidae	Coleoptera	0.0655	24.0	36.0	Blumberg and Swirski, 1982
Dermestes ater	Dermestidae	Coleoptera	0.0330	25.0	35.0	Coombs, 1981
Dermestes frischii	Dermestidae	Coleoptera	0.1135	20.0	30.0	Amos, 1968
Dermestes haemorrhoidalis	Dermestidae	Coleoptera	0.0927	20.0	30.0	Coombs, 1979
Dermestes maculatus	Dermestidae	Coleoptera	0.0851	20.0	30.0	Richardson and Goff, 2001
Trogoderma anthrenoides	Dermestidae	Coleoptera	0.1286	20.0	35.0	Burges and Cammell, 1964
Trogoderma glabrum	Dermestidae	Coleoptera	0.0559	26.7	35.0	Archer and Strong, 1975
Trogoderma variabile	Dermestidae	Coleoptera	0.0521	23.9	37.8	Partida and Strong, 1975
Trogoderma versicolor	Dermestidae	Coleoptera	0.1105	20.0	35.0	Hadaway, 1955
Laricobius nigrinus	Derodontidae	Coleoptera	0.1051	9.0	18.0	Zilahi-Balogh et al., 2003
Collops vittatus	Malachiidae	Coleoptera	0.1253	22.8	32.2	Butler and Wardecker, 1973
Typhaea stercorea	Mycetophagidae	Coleoptera	0.1036	20.0	30.0	Jacob, 1988

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Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Carpophilus dimidiatus	Nitidulidae	Coleoptera	0.1018	20.0	30.0	Porter, 1986
Glischrochilus quadrisignatus	Nitidulidae	Coleoptera	0.0713	15.0	30.0	Mussen and Chiang, 1974
Maladera matrida	Scarabaeidae	Coleoptera	0.0858	20.0	29.0	Harari et al., 1998
Onitis caffer	Scarabaeidae	Coleoptera	0.1596	15.0	25.0	Edwards, 1986
Popillia japonica	Scarabaeidae	Coleoptera	0.1375	20.0	25.0	Ludwig, 1928
Dendroctonus ponderosae	Scolytidae	Coleoptera	0.1060	15.0	25.0	Bentz et al., 1991
Ips avulsus	Scolytidae	Coleoptera	0.0880	20.0	35.0	Wagner et al., 1988
Ips calligraphus	Scolytidae	Coleoptera	0.0928	15.0	35.0	Wagner et al., 1987
Ips confusus	Scolytidae	Coleoptera	0.0695	15.0	35.0	Berryman and Stark, 1962
Ips typographus	Scolytidae	Coleoptera	0.0715	15.0	33.0	Wermelinger and Seifert, 1998
Ahasverus advena	Silvanidae	Coleoptera	0.1132	17.5	30.0	Jacob, 1996
Oryzaephilus acuminatus	Silvanidae	Coleoptera	0.0972	20.0	32.5	Jacob, 1981
Oryzaephilus surinamensis	Silvanidae	Coleoptera	0.0784	20.0	35.0	Jacob and Fleming, 1990
Alphitobius diaperinus	Tenebrionidae	Coleoptera	0.1161	20.0	35.0	Rueda and Axtell, 1996
Coelopalorus foveicollis *(=Palorus foveicollis)*	Tenebrionidae	Coleoptera	0.1080	20.0	32.5	Halstead, 1967
Gnathocerus maxillosus	Tenebrionidae	Coleoptera	0.0925	20.0	32.5	Ntifo and Nowosielski-Slepowron, 1973

Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Latheticus oryzae	Tenebrionidae	Coleoptera	0.0867	27.5	37.0	Nowosielski-Slepowron and Aryeetey, 1980
Palorus laesicollis	Tenebrionidae	Coleoptera	0.1250	15.0	22.5	Halstead, 1967
Palorus ratzeburgii	Tenebrionidae	Coleoptera	0.0962	20.0	32.5	Halstead, 1967
Palorus subdepressus	Tenebrionidae	Coleoptera	0.0925	20.0	32.5	Halstead, 1967
Pterohelaeus alternatus	Tenebrionidae	Coleoptera	0.0653	24.4	30.2	Allsopp, 1981
Pterohelaeus darlingensis	Tenebrionidae	Coleoptera	0.0659	24.4	30.2	Allsopp, 1981
Tribolium castaneum	Tenebrionidae	Coleoptera	0.0870	25.0	35.0	Abdelsamad et al., 1988
Tribolium confusum	Tenebrionidae	Coleoptera	0.1211	20.0	32.5	Howe, 1960
Tribolium freemani	Tenebrionidae	Coleoptera	0.0874	25.0	32.5	Imura and Nakakita, 1984
Tribolium madens	Tenebrionidae	Coleoptera	0.1416	20.0	35.0	Howe, 1962
Nala lividipes	Labiduridae	Dermaptera	0.1212	22.0	32.5	Simpson, 1993
Agromyza frontella	Agromyzidae	Diptera	0.0812	15.0	25.0	Mellors and Helgesen, 1978
Chromatomyla syngenesiae	Agromyzidae	Diptera	0.0853	16.0	25.0	Cheah, 1987
Liriomyza bryoniae	Agromyzidae	Diptera	0.0865	15.0	25.0	Minkenberg and Helderman, 1990
Liriomyza huidobrensis	Agromyzidae	Diptera	0.0996	15.0	25.0	Lanzoni et al., 2002
Liriomyza trifolii	Agromyzidae	Diptera	0.0929	15.0	30.0	Leibee, 1984
Ophiomyia centrosematis	Agromyzidae	Diptera	0.0794	20.0	35.0	Talekar and Lee, 1988
Delia florilega	Anthomyiidae	Diptera	0.0721	15.0	30.0	Throne and Eckenrode, 1986

Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Delia platura	Anthomyiidae	Diptera	0.0606	15.0	35.0	Throne and Eckenrode, 1986
Calliphora vicina	Calliphoridae	Diptera	0.0699	15.8	23.3	Anderson, 2000
Eucalliphora latifrons	Calliphoridae	Diptera	0.0694	15.8	23.3	Anderson, 2000
Lucilia sericata	Calliphoridae	Diptera	0.1315	17.0	25.0	Grassberger and Reiter, 2001
Phaenicia pallescens	Calliphoridae	Diptera	0.0647	19.0	35.0	Ash and Greenberg, 1975
Phaenicia sericata	Calliphoridae	Diptera	0.0929	19.0	35.0	Ash and Greenberg, 1975
Phormia regina	Calliphoridae	Diptera	0.0520	15.0	35.0	Byrd and Allen, 2001
Protophormia terraenovae	Calliphoridae	Diptera	0.0695	15.0	35.0	Grassberger and Reiter, 2002
Aphidoletes aphidimyza	Cecidomyiidae	Diptera	0.0747	15.0	25.0	Havelka, 1980
Contarinia nasturtii	Cecidomyiidae	Diptera	0.1040	15.0	25.0	Readshaw, 1965
Contarinia sorghicola	Cecidomyiidae	Diptera	0.0598	20.0	34.0	Baxendale et al., 1984
Cystiphora schmidti	Cecidomyiidae	Diptera	0.0924	15.0	30.0	Moore, 1987
Feltiella acarisuga	Cecidomyiidae	Diptera	0.0989	15.0	27.0	Gillespie et al., 2000
Mayetiola destructor	Cecidomyiidae	Diptera	0.0597	15.6	26.7	Foster and Taylor, 1975
Culicoides mississippiensis	Ceratopogonidae	Diptera	0.0539	15.0	25.0	Davis et al., 1983
Culicoides variipennis	Ceratopogonidae	Diptera	0.0583	20.0	30.0	Mullens and Rutz, 1983
Chironomus crassicaudatus	Chironomidae	Diptera	0.1289	15.0	22.5	Frouz et al., 2002
Chironomus tepperi	Chironomidae	Diptera	0.1089	12.5	27.5	Stevens, 1998
Glyptotendipes paripes	Chironomidae	Diptera	0.0403	22.5	32.5	Lobinske et al., 2002

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Hippelates bishoppi	Chloropidae	Diptera	0.0827	18.3	35.0	Karandinos and Axtell, 1967
Hippelates pallipes	Chloropidae	Diptera	0.0397	23.9	35.0	Karandinos and Axtell, 1967
Hippelates pusio	Chloropidae	Diptera	0.0538	23.9	35.0	Karandinos and Axtell, 1967
Oscinella frit	Chloropidae	Diptera	0.0874	17.5	27.5	Tolley and Niemczyk, 1988
Aedes albopictus	Culicidae	Diptera	0.0466	22.0	30.0	Alto and Juliano, 2001
Aedes campestris	Culicidae	Diptera	0.0341	23.0	27.0	Tauthong and Brust, 1976
Anopheles gambiae	Culicidae	Diptera	0.0901	18.0	28.0	Bayoh and Lindsay, 2003
Anopheles quadrimaculatus	Culicidae	Diptera	0.1311	12.1	27.2	Huffaker, 1944
Culex annulirostris	Culicidae	Diptera	0.0814	20.0	35.0	Mottram et al., 1986
Culex tarsalis	Culicidae	Diptera	0.0552	15.0	35.0	Reisen, 1995
Culex theileri	Culicidae	Diptera	0.0674	15.0	33.0	Van der Linde et al., 1987
						Van der Linde and Mitchell 1991
Toxorhynchites brevipalpis	Culicidae	Diptera	0.0804	20.0	30.0	Trpis, 1972
Toxorhynchites rutilus septentrionalis	Culicidae	Diptera	0.1040	13.0	31.0	Trimble and Lund, 1983
Drosophila iri	Drosophilidae	Diptera	0.1050	17.0	28.0	Cohet et al., 1980
Drosophila lutescens	Drosophilidae	Diptera	0.0776	15.0	27.0	Kimura et al., 1994
Drosophila melanogaster	Drosophilidae	Diptera	0.0858	12.0	30.0	McKenzie, 1978
Drosophila prostipennis	Drosophilidae	Diptera	0.0882	15.0	27.0	Kimura et al., 1994

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Drosophila simulans	Drosophilidae	Diptera	0.1235	12.0	28.0	Cohet et al., 1980
Drosophila takahashii	Drosophilidae	Diptera	0.0974	15.0	27.0	Kimura et al., 1994
Drosophila trilutea	Drosophilidae	Diptera	0.0716	15.0	25.0	Kimura et al., 1994
Drosophila yakuba	Drosophilidae	Diptera	0.0981	14.0	28.0	Cohet et al., 1980
Haematobia irritans exigua	Muscidae	Diptera	0.0750	17.5	30.0	Cook and Spain, 1981
Haematobia thirouxi potans	Muscidae	Diptera	0.0989	15.0	30.0	Fay, 1985
Musca autumnalis	Muscidae	Diptera	0.0806	13.8	34.7	Moon, 1983
Musca domestica	Muscidae	Diptera	0.1019	16.0	31.0	Lysyk and Axtell, 1987
Musca vetustissima	Muscidae	Diptera	0.0986	18.0	28.0	Vogt et al., 1990
Ophyra aenescens	Muscidae	Diptera	0.0849	17.0	30.0	Lefebvre and Pasquerault, 2004
Ophyra capensis	Muscidae	Diptera	0.1240	17.0	30.0	Lefebvre and Pasquerault, 2004
Stomoxys calcitrans	Muscidae	Diptera	0.1152	15.0	30.0	Gilles et al., 2005
Stomoxys niger niger	Muscidae	Diptera	0.1078	15.0	30.0	Gilles et al., 2005
Piophila casei	Piophilidae	Diptera	0.0826	15.0	32.0	Russo et al., 2006
Psila rosae	Psilidae	Diptera	0.0676	12.5	20.0	Stevenson, 1981
Parasarcophaga (Liopygia) ruficornis	Sarcophagidae	Diptera	0.0592	19.0	31.0	Amoudi et al., 1994
Bradysia impatiens	Sciaridae	Diptera	0.0733	12.8	23.9	Wilkinson and Daugherty, 1970
Sepedon fuscipennis	Sciomyzidae	Diptera	0.0842	15.0	30.0	Barnes, 1976

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Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Episyrphus balteatus	Syrphidae	Diptera	0.1022	10.0	20.0	Ankersmit et al., 1986
Merodon equestris	Syrphidae	Diptera	0.1423	10.0	21.5	Collier and Finch, 1992
Exorista mella	Tachinidae	Diptera	0.0729	20.0	27.2	Butler et al., 1968
Leschenaultia adusta	Tachinidae	Diptera	0.0729	15.0	30.0	Jackson et al., 1970
Palexorista laxa	Tachinidae	Diptera	0.1007	15.0	30.0	Jackson et al., 1976
Voria ruralis	Tachinidae	Diptera	0.0607	20.0	30.0	Jackson et al., 1969
Anastrepha suspensa	Tephritidae	Diptera	0.0969	15.0	30.0	Prescott and Baranowski, 1971
Bactrocera cucurbitae	Tephritidae	Diptera	0.0753	16.0	32.0	Vargas et al., 1996
Bactrocera dorsalis	Tephritidae	Diptera	0.0543	19.0	34.0	Yang et al., 1994
Bactrocera latifrons	Tephritidae	Diptera	0.0912	16.0	29.0	Vargas et al., 1996
Ceratitis capitata	Tephritidae	Diptera	0.0875	16.0	29.0	Vargas et al., 1996
Dacus tryoni	Tephritidae	Diptera	0.0535	20.0	30.0	Bateman, 1967
Rhagoletis completa	Tephritidae	Diptera	0.0697	8.0	24.0	Kasana and AliNiazee, 1994
Tipula subnodicornis	Tipulidae	Diptera	0.0834	7.0	15.0	Butterfield, 1976
Aleurocanthus woglumi	Aleyrodidae	Hemiptera	0.0816	20.0	34.0	Dowell and Fitzpatrick, 1978
Aleyrodes proletella	Aleyrodidae	Hemiptera	0.1009	15.0	25.0	Iheagwam, 1978
Bemisia argentifolii	Aleyrodidae	Hemiptera	0.1000	15.0	30.0	Yang and Chi, 2006
Bemisia tabaci	Aleyrodidae	Hemiptera	0.0705	20.0	29.0	Powell and Bellows, 1992
Trialeurodes abutilonea	Aleyrodidae	Hemiptera	0.0355	23.9	35.0	Butler, 1967

Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Trialeurodes vaporariorum	Aleyrodidae	Hemiptera	0.0548	15.0	32.0	Greenberg et al., 2000
Lyctocoris campestris	Anthocoridae	Hemiptera	0.0928	17.0	29.0	Parajulee et al., 1995
Orius insidiosus	Anthocoridae	Hemiptera	0.1226	20.0	28.0	Isenhour and Yeargan, 1981
Orius sauteri	Anthocoridae	Hemiptera	0.0975	15.0	30.0	Nagai and Yano, 1999
Orius tristicolor	Anthocoridae	Hemiptera	0.0418	20.0	35.0	Butler, 1966a
Xylocoris flavipes	Anthocoridae	Hemiptera	0.1179	20.0	30.0	Arbogast, 1975
Acyrthosiphon kondoi	Aphididae	Hemiptera	0.0975	7.2	26.7	Summers et al., 1984
Acyrthosiphon pisum	Aphididae	Hemiptera	0.1017	10.0	25.0	Lamb and MacKay, 1988
Aphis gossypii	Aphididae	Hemiptera	0.0659	15.0	30.0	Kersting et al., 1999
Aphis pomi	Aphididae	Hemiptera	0.0651	10.0	30.0	Carroll and Hoyt, 1986
Brevicoryne brassicae	Aphididae	Hemiptera	0.0594	15.0	25.0	Satar et al., 2005
Diuraphis noxia	Aphididae	Hemiptera	0.0690	12.0	27.0	Kieckhefer and Elliott, 1989
Drepanosiphum acerinum	Aphididae	Hemiptera	0.0960	6.0	20.0	Wellings, 1981
Drepanosiphum platanoidis	Aphididae	Hemiptera	0.0776	6.0	20.0	Wellings, 1981
Dysaphis plantaginea	Aphididae	Hemiptera	0.1044	11.6	19.5	Blommers et al., 2004
Lipaphis erysimi	Aphididae	Hemiptera	0.0679	15.0	30.0	Liu and Yue, 2001
Macrosiphum avenae	Aphididae	Hemiptera	0.0857	11.0	23.0	Kieckhefer et al., 1989
Metopolophium dirhodum	Aphididae	Hemiptera	0.0605	10.0	20.0	Dean, 1974
Rhopalosiphum padi	Aphididae	Hemiptera	0.0739	10.0	25.0	Dean, 1974

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Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Sitobion avenae	Aphididae	Hemiptera	0.0706	10.0	25.0	Acreman and Dixon, 1989
Austroasca viridigrisea	Cicadellidae	Hemiptera	0.0791	20.0	32.0	Page, 1983
Cicadulina mbila	Cicadellidae	Hemiptera	0.1032	17.3	30.1	Rose, 1973
Cicadulina parazeae	Cicadellidae	Hemiptera	0.0930	23.0	30.0	Rose, 1973
Cicadulina storeyi	Cicadellidae	Hemiptera	0.0928	23.0	30.0	Rose, 1973
Empoasca fabae	Cicadellidae	Hemiptera	0.0914	13.0	29.0	Simonet and Pienkowski, 1980
Eutettix tenellus	Cicadellidae	Hemiptera	0.1036	18.3	33.3	Harries and Douglass, 1948
Graminella nigrifrons	Cicadellidae	Hemiptera	0.1041	18.0	30.0	Larsen et al., 1990
Acanthomia tomentosicollis	Coreidae	Hemiptera	0.0920	20.0	34.0	Egwuatu and Taylor, 1977
Anasa tristis	Coreidae	Hemiptera	0.1066	20.0	31.1	Fargo and Bonjour, 1988
Aonidiella aurantii	Diaspididae	Hemiptera	0.1130	15.0	30.0	Kennett and Hoffmann, 1985
Gerris buenoi	Gerridae	Hemiptera	0.0634	18.5	26.0	Spence et al., 1980
Gerris comatus	Gerridae	Hemiptera	0.0961	15.0	26.0	Spence et al., 1980
Gerris paludum insularis	Gerridae	Hemiptera	0.0909	15.0	35.0	Park, 1988
Gerris pingreensis	Gerridae	Hemiptera	0.0815	15.0	26.0	Spence et al., 1980
Geocoris atricolor	Lygaeidae	Hemiptera	0.0732	26.7	35.0	Dunbar and Bacon, 1972
Geocoris pallens	Lygaeidae	Hemiptera	0.1284	20.0	30.0	Butler, 1966a
Geocoris punctipes	Lygaeidae	Hemiptera	0.0979	20.0	30.0	Butler, 1966a
Nysius vinitor	Lygaeidae	Hemiptera	0.1085	20.0	32.0	Kehat and Wyndham, 1972

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Oncopeltus fasciatus	Lygaeidae	Hemiptera	0.1145	23.0	31.0	Baldwin and Dingle, 1986
Creontiades dilutus	Miridae	Hemiptera	0.0850	19.0	31.0	Foley and Pyke, 1985
Deraeocoris brevis	Miridae	Hemiptera	0.0987	15.0	32.0	Kim and Riedl, 2005
Dicyphus hesperus	Miridae	Hemiptera	0.0837	14.0	27.0	Gillespie et al., 2004
Lygus desertus	Miridae	Hemiptera	0.0745	20.0	30.0	Butler, 1970a
Lygus elisus	Miridae	Hemiptera	0.0797	10.0	35.0	Bommireddy et al., 2004
Lygus hesperus	Miridae	Hemiptera	0.0673	15.0	35.0	Champlain and Butler, 1967
Lygus lineolaris	Miridae	Hemiptera	0.0889	16.0	28.0	Khattat and Stewart, 1977
Macrolophus pygmaeus	Miridae	Hemiptera	0.0833	15.0	27.5	Perdikis and Lykouressis, 2002
Pseudatomoscelis seriatus	Miridae	Hemiptera	0.0457	23.9	35.0	Gaylor and Sterling, 1975
Rhinacloa forticornis	Miridae	Hemiptera	0.0715	25.0	30.0	Butler, 1970b
Nabis americoferus	Nabidae	Hemiptera	0.1338	15.0	27.0	Braman et al., 1984
Nabis roseipennis	Nabidae	Hemiptera	0.0984	15.0	30.0	Braman et al., 1984
Nabis rufusculus	Nabidae	Hemiptera	0.0912	18.0	30.0	Braman and Yeargan, 1988
Acrosternum hilare	Pentatomidae	Hemiptera	0.1195	18.0	27.0	Simmons and Yeargan, 1988
Biprorulus bibax	Pentatomidae	Hemiptera	0.0925	20.0	32.5	James, 1990
Cermatulus nasalis	Pentatomidae	Hemiptera	0.0970	20.0	30.0	Awan, 1988
Euschistus conspersus	Pentatomidae	Hemiptera	0.0473	21.0	32.0	Toscano and Stern, 1976
Oebalus pugnax	Pentatomidae	Hemiptera	0.0822	21.0	30.0	Naresh and Smith, 1983

Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Oechalia schellenbergii	Pentatomidae	Hemiptera	0.0751	20.0	35.0	Awan, 1988
Podisus acutissimus	Pentatomidae	Hemiptera	0.1156	15.0	30.0	Stoner et al., 1974
Podisus maculiventris	Pentatomidae	Hemiptera	0.0670	15.0	33.0	Drummond et al., 1984
Podisus sagitta	Pentatomidae	Hemiptera	0.0790	19.0	33.0	De Clercq and Degheele, 1992
Phenacoccus herreni	Pseudococcidae	Hemiptera	0.1617	18.0	25.0	Herrera et al., 1989
Phenacoccus manihoti	Pseudococcidae	Hemiptera	0.0742	20.0	27.0	Lema and Herren, 1985
Saccharicoccus sacchari	Pseudococcidae	Hemiptera	0.1488	20.0	30.0	Rae and De'ath, 1991
Psylla pyricola	Psyllidae	Hemiptera	0.0505	10.0	26.7	McMullen and Jong, 1977
Pristhesancus plagipennis	Reduviidae	Hemiptera	0.1073	22.5	30.0	James, 1992
Sinea confusa	Reduviidae	Hemiptera	0.0994	20.0	30.0	Butler, 1966a
Zelus renardii	Reduviidae	Hemiptera	0.0347	25.0	35.0	Ali and Watson, 1978
Zelus socius	Reduviidae	Hemiptera	0.0726	20.0	30.0	Butler, 1966a
Corythucha cydoniae	Tingidae	Hemiptera	0.0407	20.6	37.7	Neal and Douglass, 1990
Corythucha morrilli	Tingidae	Hemiptera	0.1292	20.0	25.6	Stone and Watterson, 1985
Stephanitis pyrioides	Tingidae	Hemiptera	0.0646	20.6	31.7	Neal and Douglass, 1988
Aphelinus asychis	Aphelinidae	Hymenoptera	0.1009	14.0	26.0	Lee and Elliott, 1998
Aphelinus gossypii	Aphelinidae	Hymenoptera	0.0712	15.0	30.0	Tang and Yokomi, 1995
Aphelinus semiflavus	Aphelinidae	Hymenoptera	0.0959	15.6	29.4	Force and Messenger, 1964
Aphelinus sp. nr. *Varipes*	Aphelinidae	Hymenoptera	0.0791	14.0	30.0	Prinsloo and du Plessis, 2000

Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Aphelinus spiraecolae	Aphelinidae	Hymenoptera	0.0773	15.0	30.0	Tang and Yokomi, 1995
Aphelinus varipes	Aphelinidae	Hymenoptera	0.0580	20.0	30.0	Röhne, 2002
Aphytis chrysomphali	Aphelinidae	Hymenoptera	0.0651	20.0	30.0	Abdelrahman, 1974
Aphytis melinus	Aphelinidae	Hymenoptera	0.0771	20.0	30.0	Abdelrahman, 1974
Encarsia citrina	Aphelinidae	Hymenoptera	0.0752	17.5	27.5	Matadha et al., 2004
Encarsia perniciosi	Aphelinidae	Hymenoptera	0.0715	20.0	28.0	McClain et al., 1990
Encarsia tricolor	Aphelinidae	Hymenoptera	0.0943	14.0	28.0	Avilla and Copland, 1988
Eretmocerus eremicus	Aphelinidae	Hymenoptera	0.0696	16.3	30.9	Tullett et al., 2004
Aphidius ervi pulcher	Aphidiidae	Hymenoptera	0.0883	10.3	25.9	Campbell and Mackauer, 1975
Aphidius matricariae	Aphidiidae	Hymenoptera	0.0796	11.0	26.0	Miller and Gerth, 1994
Aphidius platensis	Aphidiidae	Hymenoptera	0.0508	15.0	24.0	Hofsvang and Hågvar, 1975
Aphidius smithi	Aphidiidae	Hymenoptera	0.0926	10.3	25.9	Campbell and Mackauer, 1975
Aphidius sonchi	Aphidiidae	Hymenoptera	0.0915	12.5	26.0	Liu and Hughes, 1984
Ephedrus californicus	Aphidiidae	Hymenoptera	0.0629	17.6	26.4	Cohen and Mackauer, 1987
Lysiphlebia japonica	Aphidiidae	Hymenoptera	0.0729	10.0	25.0	Deng and Tsai, 1998
Lysiphlebia mirzai	Aphidiidae	Hymenoptera	0.0860	10.0	25.0	Liu and Tsai, 2002
Lysiphlebus testaceipes	Aphidiidae	Hymenoptera	0.1031	10.0	26.0	Royer et al., 2001
Praon pequodorum	Aphidiidae	Hymenoptera	0.1437	10.3	19.7	Campbell and Mackauer, 1975
Cephalonomia stephanoderis	Bethylidae	Hymenoptera	0.1056	17.0	32.0	Infante et al., 1992

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Goniozus legneri	Bethylidae	Hymenoptera	0.1258	17.0	30.0	Butler and Schmidt, 1985
Prorops nasuta	Bethylidae	Hymenoptera	0.0876	18.0	30.0	Infante, 2000
Apanteles fumiferanae	Braconidae	Hymenoptera	0.0946	12.5	26.0	Régnière, 1984
Apanteles glomeratus	Braconidae	Hymenoptera	0.1194	13.9	30.0	Nealis et al., 1984
Apanteles ornigis	Braconidae	Hymenoptera	0.1336	15.0	20.0	Johnson et al., 1979
Apanteles rubecula	Braconidae	Hymenoptera	0.1323	13.9	30.0	Nealis et al., 1984
Apanteles scutellaris	Braconidae	Hymenoptera	0.0566	23.9	35.0	Cardona and Oatman, 1975
Apanteles sp. group *ultor*	Braconidae	Hymenoptera	0.0525	20.0	29.0	Al-Maliky et al., 1988
Apanteles subandinus	Braconidae	Hymenoptera	0.0915	15.6	32.2	Cardona and Oatman, 1975
Apanteles yakutatensis	Braconidae	Hymenoptera	0.0378	21.0	31.0	Madar and Miller, 1983
Bracon mellitor	Braconidae	Hymenoptera	0.0695	15.6	37.8	Barfield et al., 1977
Chelonus blackburni	Braconidae	Hymenoptera	0.0745	20.0	32.2	Jackson et al., 1978
Chelonus inanitus	Braconidae	Hymenoptera	0.0812	20.0	36.0	Rechav and Orion, 1975
Chelonus sp. nr. *curvimaculatus*	Braconidae	Hymenoptera	0.0785	20.0	33.0	Hentz et al., 1998
Chelonus texanus	Braconidae	Hymenoptera	0.0858	15.0	35.0	Butler, 1966b
Cotesia marginiventris	Braconidae	Hymenoptera	0.1633	15.0	25.0	Sourakov and Mitchell, 2001
Cotesia melanoscela	Braconidae	Hymenoptera	0.0853	15.0	30.0	Gould and Elkinton, 1990
Cotesia urabae	Braconidae	Hymenoptera	0.0842	15.0	25.0	Allen and Keller, 1991
Dendrosoter sulcatus	Braconidae	Hymenoptera	0.1071	15.0	30.0	Jones and Stephen, 1994

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Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Diaeretiella rapae	Braconidae	Hymenoptera	0.0615	10.0	30.0	Hayakawa et al., 1990
Dolichogenidea eucalypti	Braconidae	Hymenoptera	0.0959	15.0	25.0	Allen and Keller, 1991
Macrocentrus grandii	Braconidae	Hymenoptera	0.1168	15.0	30.0	Dittrick and Chiang, 1982
Microplitis rufiventris	Braconidae	Hymenoptera	0.0949	15.0	30.0	Hutchison et al., 1986
Opius sp.	Braconidae	Hymenoptera	0.1003	15.6	29.4	Tyron and Poe, 1981
Perilitus coccinellae	Braconidae	Hymenoptera	0.0940	15.6	26.7	Obrycki and Tauber, 1978
Peristenus stygicus	Braconidae	Hymenoptera	0.0424	20.0	30.0	Butler and Wardecker, 1974
Praon palitans	Braconidae	Hymenoptera	0.0757	18.3	26.7	Force and Messenger, 1964
Spathius pallidus	Braconidae	Hymenoptera	0.1246	15.0	30.0	Jones and Stephen, 1994
Trioxys utilis	Braconidae	Hymenoptera	0.0918	15.6	26.7	Force and Messenger, 1964
Dendrocerus niger	Ceraphronidae	Hymenoptera	0.0938	14.8	25.9	Campbell and Mackauer, 1975
Brachymeria lasus	Chalcididae	Hymenoptera	0.0906	18.0	32.0	Mao and Kunimi, 1994
Trichopria atrichomelinae	Diapriidae	Hymenoptera	0.0837	15.0	30.0	O'Neill, 1973
Trichopria popei	Diapriidae	Hymenoptera	0.0548	20.0	30.0	O'Neill, 1973
Acerophagus coccois	Encyrtidae	Hymenoptera	0.0754	20.0	30.0	Herrera et al., 1989
Anagyrus pseudococci	Encyrtidae	Hymenoptera	0.1119	14.0	32.0	Daane et al., 2004
Copidosoma koehleri	Encyrtidae	Hymenoptera	0.0994	15.0	29.0	Horne and Horne, 1991
Epidinocarsis diversicornis	Encyrtidae	Hymenoptera	0.0698	18.0	30.0	Herrera et al., 1989
Leptomastidea abnormis	Encyrtidae	Hymenoptera	0.1109	18.0	30.0	Tingle and Copland, 1988

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Leptomastix dactylopii	Encyrtidae	Hymenoptera	0.0923	20.0	30.0	Tingle and Copland, 1988
Ooencyrtus anasae	Encyrtidae	Hymenoptera	0.0974	20.8	26.6	Tracy and Nechols, 1987
Ooencyrtus sp. nr. *anasae*	Encyrtidae	Hymenoptera	0.0948	20.8	26.6	Tracy and Nechols, 1987
Tachinaephagus zealandicus	Encyrtidae	Hymenoptera	0.0968	16.0	25.0	Ferreira de Almeida et al., 2002
Gronotoma micromorpha	Eucoilidae	Hymenoptera	0.0957	15.0	30.0	Abe and Tahara, 2003
Leptopilina boulardi	Eucoilidae	Hymenoptera	0.1108	18.3	26.7	Hertlein, 1986
Aprostocetus vaquitarum	Eulophidae	Hymenoptera	0.0562	20.0	30.0	Ulmer et al., 2006
Chrysocharis parksi	Eulophidae	Hymenoptera	0.0446	21.1	32.2	Christie and Parrella, 1987
Cirrospilus pictus	Eulophidae	Hymenoptera	0.0612	16.0	26.0	Lo Pinto et al., 2005
Cirrospilus sp. nr. *lyncus*	Eulophidae	Hymenoptera	0.1173	10.0	30.0	Urbaneja et al., 1999
Cirrospilus vittatus	Eulophidae	Hymenoptera	0.0746	15.0	30.0	Urbaneja et al., 2002
Citrostichus phyllocnistoides	Eulophidae	Hymenoptera	0.0746	15.0	30.0	Urbaneja et al., 2003
Colpoclypeus florus	Eulophidae	Hymenoptera	0.0800	15.0	25.0	Milonas and Savopoulou-Soultani, 2000b
Diglyphus intermedius	Eulophidae	Hymenoptera	0.0841	15.5	26.7	Patel and Schuster, 1983
Diglyphus isaea	Eulophidae	Hymenoptera	0.0932	15.0	25.0	Minkenberg, 1989
Edovum puttleri	Eulophidae	Hymenoptera	0.0874	15.6	29.4	Obrycki et al., 1987
Hyssopus thymus	Eulophidae	Hymenoptera	0.1141	16.0	28.0	Syme, 1972
Pediobius furvus	Eulophidae	Hymenoptera	0.0656	20.0	30.0	Duale, 2005

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Pnigalio soemius	Eulophidae	Hymenoptera	0.1131	10.0	30.0	Bernardo et al., 2006
Quadrastichus haitiensis	Eulophidae	Hymenoptera	0.1147	20.0	30.0	Castillo et al., 2006
Thripobius semiluteus	Eulophidae	Hymenoptera	0.0824	15.0	30.0	Bernardo et al., 2005
Solenopsis invicta	Formicidae	Hymenoptera	0.0837	24.5	35.0	Porter, 1988
Campoletis sonorensis	Ichneumonidae	Hymenoptera	0.0520	20.0	30.0	Isenhour, 1986
Diadromus collaris	Ichneumonidae	Hymenoptera	0.0732	15.0	30.0	Liu et al., 2001
Hyposoter exiguae	Ichneumonidae	Hymenoptera	0.0588	15.5	32.2	Browning and Oatman, 1981
Venturia canescens	Ichneumonidae	Hymenoptera	0.1023	15.0	30.0	Eliopoulos and Stathas, 2003
Megachile rotundata	Megachilidae	Hymenoptera	0.1220	22.0	29.0	Kemp and Bosch, 2000
Osmia lignaria	Megachilidae	Hymenoptera	0.0598	18.0	29.0	Bosch and Kemp, 2000
Anagrus atomus	Mymaridae	Hymenoptera	0.0904	16.0	24.0	Agboka et al., 2004
Anagrus giraulti	Mymaridae	Hymenoptera	0.0626	20.0	32.0	Meyerdirk and Moratorio, 1987
Anaphes nitens	Mymaridae	Hymenoptera	0.1342	10.4	20.1	Santolamazza-Carbone et al., 2006
Gonatocerus ashmeadi	Mymaridae	Hymenoptera	0.0860	15.0	30.0	Pilkington and Hoddle, 2006
Gonatocerus tuberculifemur	Mymaridae	Hymenoptera	0.0337	24.5	27.5	Virla et al., 2005
Patasson lameerei	Mymaridae	Hymenoptera	0.1250	7.2	26.7	Leibee et al., 1979
Stethynium sp.	Mymaridae	Hymenoptera	0.0961	15.0	25.0	Jacob et al., 2006
Amitus fuscipennis	Platygastridae	Hymenoptera	0.0729	15.0	30.0	De Vis et al., 2002
Anisopteromalus calandrae	Pteromalidae	Hymenoptera	0.1291	20.0	30.0	Smith, 1992

Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Asaphes lucens	Pteromalidae	Hymenoptera	0.0924	14.8	25.9	Campbell and Mackauer, 1975
Catolaccus grandis	Pteromalidae	Hymenoptera	0.0753	18.0	33.0	Morales-Ramos and Cate, 1993
Dibrachys boarmiae	Pteromalidae	Hymenoptera	0.0815	15.0	32.5	Mehrnejad, 2003
Dinotiscus dendroctoni	Pteromalidae	Hymenoptera	0.1240	15.0	25.0	Jones and Stephen, 1994
Heydenia unica	Pteromalidae	Hymenoptera	0.0783	15.0	30.0	Jones and Stephen, 1994
Muscidifurax raptor	Pteromalidae	Hymenoptera	0.0784	15.6	32.2	Ables et al., 1976
Muscidifurax raptorellus	Pteromalidae	Hymenoptera	0.1039	14.8	30.9	Lysyk, 2001a
Muscidifurax zaraptor	Pteromalidae	Hymenoptera	0.1494	15.2	29.8	Lysyk, 2001b
Nasonia vitripennis	Pteromalidae	Hymenoptera	0.0893	15.0	30.0	Grassberger and Frank, 2003
Pteromalus venustus	Pteromalidae	Hymenoptera	0.0855	20.0	30.0	Whitfield and Richards, 1985
Spalangia cameroni	Pteromalidae	Hymenoptera	0.0917	20.0	30.0	Mann et al., 1990
Spalangia endius	Pteromalidae	Hymenoptera	0.0965	18.0	32.2	Ables et al., 1976
Spalangia gemina	Pteromalidae	Hymenoptera	0.1364	15.0	30.0	Geden, 1997
Trichomalopsis sarcophagae	Pteromalidae	Hymenoptera	0.1191	15.0	30.0	Lysyk, 1998
Urolepis rufipes	Pteromalidae	Hymenoptera	0.1081	20.0	30.0	Smith and Rutz, 1986
Telenomus chloropus	Scelionidae	Hymenoptera	0.1082	15.0	30.0	Orr et al., 1985
Telenomus chrysopae	Scelionidae	Hymenoptera	0.1147	15.6	26.7	Ruberson et al., 1995
Telenomus cyamophylax	Scelionidae	Hymenoptera	0.0937	15.0	30.0	Foerster and Butnariu, 2004
Telenomus lobatus	Scelionidae	Hymenoptera	0.1199	15.6	26.7	Ruberson et al., 1995

Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Telenomus reynoldsi	Scelionidae	Hymenoptera	0.0992	18.0	33.0	Cave and Gaylor, 1988
Telenomus utahensis	Scelionidae	Hymenoptera	0.0738	20.0	35.0	Jubb and Watson, 1971
Trissolcus basalis	Scelionidae	Hymenoptera	0.0851	18.3	32.2	Powell et al., 1981
Trissolcus brochymenae	Scelionidae	Hymenoptera	0.0798	17.0	32.0	Torres et al., 2002
Trissolcus euschisti	Scelionidae	Hymenoptera	0.1005	18.0	30.0	Yeargan, 1983
Trissolcus oenone	Scelionidae	Hymenoptera	0.1196	15.0	30.0	James and Warren, 1991
Lathromeris ovicida	Trichogrammatidae	Hymenoptera	0.1256	18.0	30.0	Chabi-Olaye et al., 2004
Trichogramma acacioi	Trichogrammatidae	Hymenoptera	0.0848	15.0	35.0	Pratissoli et al., 2004
Trichogramma bournieri	Trichogrammatidae	Hymenoptera	0.0441	18.0	34.0	Haile et al., 2002
Trichogramma chilonis	Trichogrammatidae	Hymenoptera	0.1050	13.0	34.0	Haile et al., 2002
Trichogramma evanescens	Trichogrammatidae	Hymenoptera	0.1032	13.0	34.0	Haile et al., 2002
Trichogramma exiguum	Trichogrammatidae	Hymenoptera	0.1050	15.0	30.0	Harrison et al., 1985
Trichogramma minutum	Trichogrammatidae	Hymenoptera	0.1074	14.0	27.0	Lawrence et al., 1985
Trichogramma ostriniae	Trichogrammatidae	Hymenoptera	0.1139	17.0	24.0	Wang et al., 2004
Trichogramma pretiosum	Trichogrammatidae	Hymenoptera	0.0977	18.0	32.0	Pratissoli and Parra, 2000
Trichogramma sp. nr. *mwanzai*	Trichogrammatidae	Hymenoptera	0.0498	18.0	34.0	Haile et al., 2002
Uscana mukerjii	Trichogrammatidae	Hymenoptera	0.0552	20.0	33.0	Kapila and Agarwal, 1995
Acrolepiopsis assectella	Acrolpiidae	Lepidoptera	0.1077	12.0	20.0	Åsman, 2001
Hyphantria cunea	Arctiidae	Lepidoptera	0.0932	18.0	27.0	Gomi et al., 2003

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Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Carposina sasakii	Carposinidae	Lepidoptera	0.0813	15.5	30.0	Kim et al., 2001
Cochylis hospes	Cochylidae	Lepidoptera	0.0616	22.0	28.0	Barker and Enz, 1993
Chilo sacchariphagus	Crambidae	Lepidoptera	0.1051	17.0	30.0	Goebel, 2006
Crambus trisectus	Crambidae	Lepidoptera	0.0642	21.1	32.2	Banerjee, 1969
Aproaerema modicella	Gelechiidae	Lepidoptera	0.0395	25.0	35.0	Shanower et al., 1993a
Keiferia lycopersicella	Gelechiidae	Lepidoptera	0.0845	14.0	35.0	Lin and Trumble, 1985
Pectinophora gossypiella	Gelechiidae	Lepidoptera	0.0928	20.0	32.0	Raina et al., 1977
Phthorimaea operculella	Gelechiidae	Lepidoptera	0.0970	15.0	32.0	Horne and Horne, 1991
Sitotroga cerealella	Gelechiidae	Lepidoptera	0.0829	20.0	30.0	Hansen et al., 2004
Lithocolletis blancardella	Gracillariidae	Lepidoptera	0.1320	10.0	20.0	Johnson et al., 1979
Phyllonorycter blancardella	Gracillariidae	Lepidoptera	0.0735	15.0	25.0	Trimble, 1994
Lymantria dispar	Lymantriidae	Lepidoptera	0.0725	5.0	30.0	Gray et al., 1995
Bedellia somnulentella	Lyonetiidae	Lepidoptera	0.0584	18.3	29.4	Parrella and Kok, 1977
Agrotis ipsilon	Noctuidae	Lepidoptera	0.0944	18.3	26.7	Luckmann et al., 1976
Anticarsia gemmatalis	Noctuidae	Lepidoptera	0.0875	15.6	32.2	Johnson et al., 1983
Calophasia lunula	Noctuidae	Lepidoptera	0.1004	18.0	30.0	McClay and Hughes, 1995
Copitarsia decolora	Noctuidae	Lepidoptera	0.1054	9.7	29.5	Gould et al., 2005
Eudocima salaminia	Noctuidae	Lepidoptera	0.1336	15.0	27.0	Sands et al., 1991
Heliothis virescens	Noctuidae	Lepidoptera	0.0990	17.5	32.0	Butler and Hamilton, 1976

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Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Heliothis zea	Noctuidae	Lepidoptera	0.0879	17.5	34.0	Sharpe et al., 1981
Lacanobia subjuncta	Noctuidae	Lepidoptera	0.1056	20.0	30.0	Doerr et al., 2002
Mamestra configurata	Noctuidae	Lepidoptera	0.0900	8.0	28.0	Bailey, 1976
Mythimna convecta	Noctuidae	Lepidoptera	0.0714	15.0	33.0	Smith, 1984
Papaipema nebris	Noctuidae	Lepidoptera	0.0790	12.8	23.9	Levine, 1983
Peridroma margaritosa	Noctuidae	Lepidoptera	0.0799	15.0	32.0	Snyder, 1954
Peridroma saucia	Noctuidae	Lepidoptera	0.0691	10.0	30.0	Shields, 1983
Plathypena scabra	Noctuidae	Lepidoptera	0.0757	15.6	29.4	Hammond et al., 1979
Pseudaletia unipuncta	Noctuidae	Lepidoptera	0.0994	13.0	29.0	Guppy, 1969
Sesamia calamistis	Noctuidae	Lepidoptera	0.0791	20.0	35.0	Shanower et al., 1993b
Sesamia nonagrioides	Noctuidae	Lepidoptera	0.0610	20.0	30.0	Fantinou et al., 2003
Simyra henrici	Noctuidae	Lepidoptera	0.0684	18.3	32.2	Decker and Maddox, 1971
Spodoptera exigua	Noctuidae	Lepidoptera	0.0965	18.0	33.0	Ali and Gaylor, 1992
Spodoptera frugiperda	Noctuidae	Lepidoptera	0.0764	21.0	33.0	Ali et al., 1990
Spodoptera litura	Noctuidae	Lepidoptera	0.0527	20.0	35.0	Ranga Rao et al., 1989
Trichoplusia ni	Noctuidae	Lepidoptera	0.1155	16.6	27.2	Toba et al., 1973
Uraba lugens	Noctuidae	Lepidoptera	0.1277	15.0	25.0	Allen and Keller, 1991
Danaus chrysippus	Nymphalidae	Lepidoptera	0.0991	19.0	29.0	Zalucki, 1982
Danaus plexippus	Nymphalidae	Lepidoptera	0.1273	17.0	25.0	Zalucki, 1982

Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Ectomyelois ceratoniae	Phycitidae	Lepidoptera	0.0736	20.0	30.0	Cox, 1976
Ephestia calidella	Phycitidae	Lepidoptera	0.1343	15.0	30.0	Cox, 1974
Ephestia figulilella	Phycitidae	Lepidoptera	0.0911	17.5	30.0	Cox, 1974
Catopsilia pomona	Pieridae	Lepidoptera	0.1039	21.0	28.2	Jones et al., 1987
Eurema brigitta	Pieridae	Lepidoptera	0.0751	19.0	32.0	Jones et al., 1987
Eurema hecabe	Pieridae	Lepidoptera	0.0862	18.5	29.0	Jones et al., 1987
Eurema herla	Pieridae	Lepidoptera	0.1144	19.0	28.0	Jones et al., 1987
Eurema laeta	Pieridae	Lepidoptera	0.0795	19.0	32.5	Jones et al., 1987
Eurema smilax	Pieridae	Lepidoptera	0.0803	17.9	32.4	Jones et al., 1987
Pieris brassicae	Pieridae	Lepidoptera	0.0626	20.0	30.0	David and Gardiner, 1962a, b
Homadaula anisocentra	Plutellidae	Lepidoptera	0.1013	19.0	30.0	Bastian and Hart, 1991
Plutella xylostella	Plutellidae	Lepidoptera	0.1176	8.0	28.0	Liu et al., 2002
Anagasta kuehniella	Pyralidae	Lepidoptera	0.0711	20.0	27.5	Siddiqui and Barlow, 1973
Cadra cautella	Pyralidae	Lepidoptera	0.1015	15.5	30.0	Burges and Haskins, 1964
Corcyra cephalonica	Pyralidae	Lepidoptera	0.1034	17.5	35.0	Cox et al., 1981
Diaphania nitidalis	Pyralidae	Lepidoptera	0.1038	15.5	29.4	Elsey, 1980
Diatraea grandiosella	Pyralidae	Lepidoptera	0.0708	18.3	32.2	Whitworth and Poston, 1979
Diatraea lineolata	Pyralidae	Lepidoptera	0.0573	22.0	31.0	Rodríguez-del-Bosque et al., 1989
Diatraea saccharalis	Pyralidae	Lepidoptera	0.0783	22.0	30.0	King et al., 1975

Appendix 2a continued

Species	Family	Order	Slope	Temp range		Reference
				Min	Max	
Dioryctria amatella	Pyralidae	Lepidoptera	0.1320	15.0	30.0	Hanula et al., 1984, 1987
Eldana saccharina	Pyralidae	Lepidoptera	0.0795	30.0	35.0	Shanower et al., 1993
Ephestia kuehniella	Pyralidae	Lepidoptera	0.0859	15.0	25.0	Jacob and Cox, 1977
Euzopherodes vapidella	Pyralidae	Lepidoptera	0.0607	20.0	33.0	Ashamo and Odeyemi, 2001
Evergestis rimosalis	Pyralidae	Lepidoptera	0.0878	15.0	35.0	Mays and Kok, 1997
Herpetogramma licarsisalis	Pyralidae	Lepidoptera	0.1149	15.0	25.0	Jensen and Cameron, 2004
Ostrinia nubilalis	Pyralidae	Lepidoptera	0.1119	12.8	29.4	Matteson and Decker, 1965
Plodia interpunctella	Pyralidae	Lepidoptera	0.0953	17.0	32.0	Na and Ryoo, 2000
Pararge aegeria	Satyridae	Lepidoptera	0.0783	13.0	25.0	Nylin et al., 1993
Dasyses rugosella	Tineidae	Lepidoptera	0.0937	20.0	33.0	Ashamo and Odeyemi, 2004
Adoxophyes orana	Tortricidae	Lepidoptera	0.0809	14.0	25.0	Milonas and Savopoulou-Soultani, 2000a
Ancylis comptana	Tortricidae	Lepidoptera	0.0975	14.0	30.0	Gabriel and Obrycki, 1990
Argyrotaenia velutinana	Tortricidae	Lepidoptera	0.1285	10.0	25.0	Hawthorne et al., 1988
Choristoneura occidentalis	Tortricidae	Lepidoptera	0.1183	10.0	25.0	Reichenbach and Stairs, 1984
Choristoneura rosaceana	Tortricidae	Lepidoptera	0.1203	14.0	26.0	Gangavalli and AliNiazee, 1985
Crocidosema plebejana	Tortricidae	Lepidoptera	0.1060	14.0	31.0	Hamilton and Zalucki, 1991
Cydia pomonella	Tortricidae	Lepidoptera	0.0902	14.8	29.6	Howell and Neven, 2000
Epiphyas postvittana	Tortricidae	Lepidoptera	0.1120	11.5	25.0	Danthanarayana, 1975

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Grapholitha molesta	Tortricidae	Lepidoptera	0.0385	18.3	35.0	Chaudhry, 1955
Lobesia botrana	Tortricidae	Lepidoptera	0.1216	14.0	26.0	Briere and Pracros, 1998
Merophyas divulsana	Tortricidae	Lepidoptera	0.1083	11.3	27.5	Allsopp et al., 1983
Platynota flavedana	Tortricidae	Lepidoptera	0.0798	15.6	29.4	David et al., 1989
Platynota idaeusalis	Tortricidae	Lepidoptera	0.0738	15.6	29.4	David et al., 1989
Rhyacionia frustrana	Tortricidae	Lepidoptera	0.0948	14.0	34.0	Haugen and Stephen, 1984
Zeiraphera canadensis	Tortricidae	Lepidoptera	0.0707	12.0	28.0	Régnière and Turgeon, 1989
Harrisina brillians	Zygaenidae	Lepidoptera	0.1449	17.9	28.5	Roltsch et al., 1990
Anomalochrysa frater	Chrysopidae	Neuroptera	0.0951	11.4	28.0	Tauber at al., 1992
Anomalochrysa maclachlani	Chrysopidae	Neuroptera	0.1269	15.6	23.4	Tauber et al., 1990
Chrysopa carnea	Chrysopidae	Neuroptera	0.0642	20.0	32.2	Butler and Ritchie, 1970
Chrysopa harrisii	Chrysopidae	Neuroptera	0.1092	18.3	26.7	Tauber and Tauber, 1974
Chrysopa oculata	Chrysopidae	Neuroptera	0.1033	15.6	26.7	Tauber et al., 1987
Hemerobius pacificus	Hemerobiidae	Neuroptera	0.0589	13.3	26.7	Neuenschwander, 1975
Chorthippus brunneus	Acrididae	Orthoptera	0.0552	25.0	40.0	Walters and Hassall, 2006
Chortoicetes terminifera	Acrididae	Orthoptera	0.0904	25.9	36.0	Gregg, 1983
Melanoplus femurrubrum	Acrididae	Orthoptera	0.0707	26.5	38.0	Bellinger and Pienkowski, 1989
Melanoplus sanguinipes	Acrididae	Orthoptera	0.0908	21.0	36.0	Fielding, 2004
Gryllulus domesticus	Gryllidae	Orthoptera	0.1392	23.0	35.0	Busvine, 1955

Appendix 2a continued

Species	Family	Order	Slope	Temp range Min	Max	Reference
Liposcelis bostrychophila	Liposcelididae	Psocoptera	0.0709	20.0	32.5	Wang et al., 2000
Ctenocephalides felis	Pulicidae	Siphonaptera	0.1091	13.0	32.0	Silverman et al., 1981
Spilopsyllus cuniculi	Pulicidae	Siphonaptera	0.0991	15.0	30.0	Cooke and Skewes, 1988
Gynaikothrips ficorum	Phlaeothripidae	Thysanoptera	0.0764	15.0	30.0	Paine, 1992
Frankliniella fusca	Thripidae	Thysanoptera	0.0511	20.0	35.0	Lowry et al., 1992
Frankliniella occidentalis	Thripidae	Thysanoptera	0.0796	15.0	30.0	Gitonga et al., 2002
Megalurothrips sjostedti	Thripidae	Thysanoptera	0.0842	15.0	30.0	Gitonga et al., 2002
Thrips major	Thripidae	Thysanoptera	0.0947	12.0	25.0	Stacey and Fellows, 2002
Thrips obscuratus	Thripidae	Thysanoptera	0.0845	10.0	27.0	Teulon and Penman, 1991
Thrips palmi	Thripidae	Thysanoptera	0.0900	15.0	30.0	McDonald et al., 1999
Thrips tabaci	Thripidae	Thysanoptera	0.0892	12.0	28.0	Stacey and Fellows, 2002

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APPENDIX 2b

Slopes of the relationships between development rate (ln $^1/_D$) and experimental temperature of the insects used in this study, together with the temperature range (in °C) used. Given are all the species for which development rate-temperature relationships were obtained for incomplete egg to adult development. For each species the developmental stage is indicated as follows: e = egg, l = larvae, n = nymph, p = pupae; numbers indicate the larval or nymphal instars.

Species	Family	Order	Life Stage	Slope	Temp range Min	Max	Reference
Blattella germanica	Blattellidae	Blattodea	n l	0.1244	21.0	30.0	Stejskal et al., 2003
Acanthoscelides obtectus	Bruchidae	Coleoptera	e	0.0947	17.5	30.0	Howe and Currie, 1964
Amara chaudoiri incognita	Carabidae	Coleoptera	e	0.0835	17.0	28.0	Saska and Honěk, 2003
Amara equestris	Carabidae	Coleoptera	e	0.1119	17.0	28.0	Saska and Honěk, 2003
Amara eurynota	Carabidae	Coleoptera	e	0.1263	17.0	28.0	Saska and Honěk, 2003
Phoracantha semipunctata	Cerambycidae	Coleoptera	e	0.1402	15.0	25.0	Bybee et al., 2004
Aphthona abdominalis	Chrysomelidae	Coleoptera	e	0.1037	15.0	35.0	Fornasari, 1995
Aphthona lacertosa	Chrysomelidae	Coleoptera	l 3-last, p	0.0928	12.0	26.0	Skinner et al., 2004
Aphthona nigriscutis	Chrysomelidae	Coleoptera	l 3-last, p	0.1046	12.0	26.0	Skinner et al., 2004
Bruchus obtectus	Chrysomelidae	Coleoptera	l, p	0.0910	17.3	31.1	Menusan, 1936

Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Temp range Max	Reference
Bruchus pisorum	Chrysomelidae	Coleoptera	l, p	0.1404	16.2	29.6	Smith and Ward, 1995
Diabrotica barberi	Chrysomelidae	Coleoptera	l, p	0.1021	15.0	27.0	Woodson and Jackson, 1996
Diabrotica longicornis	Chrysomelidae	Coleoptera	e	0.0680	17.5	30.0	Chiang and Sisson, 1968
Diabrotica undecimpunctata howardi	Chrysomelidae	Coleoptera	p	0.0775	16.0	33.0	Fisher, 1986
Diabrotica virgifera zeae	Chrysomelidae	Coleoptera	l, p	0.1147	15.0	27.0	Woodson and Chandler, 2000
Entomoscelis americana	Chrysomelidae	Coleoptera	e	0.1238	5.0	30.0	Lamb et al., 1984
Pyrrhalta viburni	Chrysomelidae	Coleoptera	l, p	0.0752	17.0	27.0	Weston and Diaz, 2005
Adalia decempunctata	Coccinellidae	Coleoptera	p	0.1068	15.0	21.0	Honěk and Kocourek, 1988
Adonia variegata	Coccinellidae	Coleoptera	e	0.0939	15.0	24.0	Honěk and Kocourek, 1988
Coccinella californica	Coccinellidae	Coleoptera	e	0.1877	12.0	20.0	Frazer and McGregor, 1992
Coccinella quinquepunctata	Coccinellidae	Coleoptera	e, p	0.1262	15.0	24.0	Honěk and Kocourek, 1988
Coccinella undecimpunctata	Coccinellidae	Coleoptera	e	0.1965	12.0	20.0	Frazer and McGregor, 1992
Cycloneda polita	Coccinellidae	Coleoptera	e	0.1649	12.0	20.0	Frazer and McGregor, 1992
Hippodamia septemmaculata	Coccinellidae	Coleoptera	e	0.1071	15.0	24.0	Honěk and Kocourek, 1988
Propylea quatuordecimpunctata	Coccinellidae	Coleoptera	e, p	0.1334	15.0	24.0	Honěk and Kocourek, 1988
Semiadalia undecimnotata	Coccinellidae	Coleoptera	e, p	0.1243	15.0	24.0	Honěk and Kocourek, 1988
Artipus floridanus	Curculionidae	Coleoptera	l, p	0.0679	15.0	35.0	Tarrant and McCoy, 1989

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Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Max	Reference
Baris coerulescens	Curculionidae	Coleoptera	l	0.1286	10.0	30.0	Lerin and Koubaiti, 1998
Ceuthorhynchidius horridus	Curculionidae	Coleoptera	l	0.0677	10.0	21.0	Kok et al., 1975
Diaprepes abbreviatus	Curculionidae	Coleoptera	e, p	0.1080	22.0	30.0	Lapointe 2000, 2001
Hylobius transversovittatus	Curculionidae	Coleoptera	e	0.1149	15.0	27.5	McAvoy and Kok, 1999
Neochetina bruchi	Curculionidae	Coleoptera	e	0.0738	20.0	30.0	DeLoach and Cordo, 1976
Neochetina eichhorniae	Curculionidae	Coleoptera	e	0.0546	20.0	35.0	DeLoach and Cordo, 1976
Otiorhynchus ovatus	Curculionidae	Coleoptera	p	0.0816	12.0	30.0	Umble and Fisher, 2000
Pachnaeus opalus	Curculionidae	Coleoptera	e	0.0894	15.0	35.0	Tarrant and McCoy, 1989
Pantomorus cervinus	Curculionidae	Coleoptera	e	0.0860	15.0	35.0	Tarrant and McCoy, 1989
Pissodes yunnanensis	Curculionidae	Coleoptera	e, p	0.0807	15.0	25.0	Zhang et al., 2004
Rhinocyllus conicus	Curculionidae	Coleoptera	l, p	0.1194	22.0	26.0	Smith and Kok, 1985
Sophrorhinus gbanjaensis	Curculionidae	Coleoptera	e	0.0836	25.0	30.0	Daramola, 1978
Trichosirocalus horridus	Curculionidae	Coleoptera	e	0.1254	7.0	25.0	McAvoy and Kok, 1985
Anthrenocerus australis	Dermestidae	Coleoptera	e, l	0.0727	15.0	25.0	Gerard and Ruf, 1997
Anthrenus verbasci	Dermestidae	Coleoptera	e, p	0.1385	15.0	25.0	Blake, 1958
Dermestes lardarius	Dermestidae	Coleoptera	l, p	0.0763	15.0	30.0	Coombs, 1978
Dermestes peruvianus	Dermestidae	Coleoptera	l, p	0.1524	15.0	25.0	Coombs, 1979
Trogoderma granarium	Dermestidae	Coleoptera	l, p	0.0624	25.0	35.0	Hadaway, 1955
Trogoderma inclusum	Dermestidae	Coleoptera	l, p	0.0638	23.9	32.2	Strong, 1975

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Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Temp range Max	Reference
Trogoderma simplex	Dermestidae	Coleoptera	l, p	0.0928	21.1	32.2	Strong and Mead, 1975
Aphodius tasmaniae	Scarabaeidae	Coleoptera	e	0.0997	16.0	25.0	Maelzer, 1961
Bubas bison	Scarabaeidae	Coleoptera	e	0.0861	15.0	25.0	Kirk and Kirk, 1990
Copris hispanus	Scarabaeidae	Coleoptera	e	0.0998	15.0	30.0	Kirk and Kirk, 1990
Liriomyza sativae	Agromyzidae	Diptera	p	0.0767	15.6	32.2	Tyron and Poe, 1981
Coenosia tigrina	Anthomyiidae	Diptera	l, p	0.0783	15.0	25.0	Morris and Cloutier, 1987
Delia coarctata	Anthomyiidae	Diptera	l	0.1013	5.0	20.0	Jones, 1978
Hylemya brassicae	Anthomyiidae	Diptera	e, p	0.0724	15.2	21.1	Eckenrode and Chapman, 1971
Hylemya platura	Anthomyiidae	Diptera	e, p	0.1222	7.6	19.0	Sanborn et al., 1982
Cochliomyia macellaria	Calliphoridae	Diptera	e	0.0815	17.8	37.2	Melvin, 1934
Lucilia australis	Calliphoridae	Diptera	e	0.0496	23.3	31.7	Melvin, 1934
Lucilia cuprina	Calliphoridae	Diptera	p	0.0983	15.0	30.0	Dallwitz, 1984
Lucilia unicolor	Calliphoridae	Diptera	e	0.0540	13.3	34.4	Melvin, 1934
Sitodiplosis mosellana	Cecidomyiidae	Diptera	l, p	0.0762	15.7	27.5	Wise and Lamb, 2004
Cricotopus bicinctus	Chironomidae	Diptera	l	0.0959	10.0	20.0	Mackey, 1977
Cricotopus sylvestris	Chironomidae	Diptera	l	0.0964	10.0	20.0	Mackey, 1977
Phaenopsectra flavipes	Chironomidae	Diptera	l	0.0838	10.0	20.0	Mackey, 1977
Polypedilum convictum	Chironomidae	Diptera	l	0.1006	10.0	20.0	Mackey, 1977
Rheotanytarsus photophilus	Chironomidae	Diptera	l	0.1054	10.0	20.0	Mackey, 1977

Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Max	Reference
Synorthocladius semivirens	Chironomidae	Diptera	l	0.0934	10.0	20.0	Mackey, 1977
Aedes aegypti	Culicidae	Diptera	l, p	0.0415	20.0	35.0	Tun-Lin, 2000
Aedes dorsalis	Culicidae	Diptera	l, p	0.0688	21.0	30.0	Parker, 1979
Aedes sollicitans	Culicidae	Diptera	l, p	0.0884	12.0	32.0	Shelton, 1973
Aedes triseriatus	Culicidae	Diptera	l, p	0.0857	15.0	23.0	Shelton, 1973
Aedes vexans	Culicidae	Diptera	l, p	0.1225	15.0	25.0	Slater and Pritchard, 1979
Anopheles albimanus	Culicidae	Diptera	l, p	0.0825	20.0	29.0	Shelton, 1973
Culex pipiens pallens	Culicidae	Diptera	l, p	0.0988	15.0	28.0	Mogi, 1992
Culex quinquefasciatus	Culicidae	Diptera	l, p	0.1005	15.0	28.0	Mogi, 1992
Culex restuans	Culicidae	Diptera	l, p	0.0522	15.0	29.0	Shelton, 1973
Culex salinarius	Culicidae	Diptera	l, p	0.1112	12.0	23.0	Shelton, 1973
Culiseta inornata	Culicidae	Diptera	l, p	0.0457	15.0	26.0	Shelton, 1973
Psorophora columbiae	Culicidae	Diptera	l, p	0.0887	16.0	34.0	McHugh and Olson, 1982
Psorophora confinnis	Culicidae	Diptera	l, p	0.0963	18.3	32.2	Gunstream and Chew, 1967
Glossina morsitans orientalis	Glossinidae	Diptera	p	0.1187	16.0	29.0	Phelps and Burrows, 1969
Siphona irritans	Muscidae	Diptera	e, l	0.0887	18.3	30.0	Depner, 1961
Cephenemyia trompe	Oestridae	Diptera	p	0.0982	12.0	26.5	Nilssen, 1997
Hypoderma bovis	Oestridae	Diptera	p	0.1023	16.0	28.0	Pfadt et al., 1975
Hypoderma lineatum	Oestridae	Diptera	p	0.1229	18.0	26.0	Pfadt et al., 1975

Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Temp range Max	Reference
Hypoderma tarandi	Oestridae	Diptera	p	0.0991	12.0	26.5	Nilssen, 1997
Tetanops myopaeformis	Otitidae	Diptera	l	0.1566	10.0	25.0	Whitfield, 1984
Megaselia scalaris	Phoridae	Diptera	e, l	0.1000	15.0	25.0	Prawirodisastro and Benjamin, 1979
Liopygia (Sarcophaga) argyrostoma	Sarcophagidae	Diptera	l, p	0.0652	15.0	35.0	Grassberger and Reiter, 2002
Parasarcophaga knabi	Sarcophagidae	Diptera	l, p	0.0717	18.0	32.0	Woolcock, 1975
Sarcophaga (Liosarcophaga) tibialis	Sarcophagidae	Diptera	l	0.0630	10.0	35.0	Villet et al., 2006
Sarcophaga crassipalpis	Sarcophagidae	Diptera	l, p	0.0928	15.0	30.0	Chen et al., 1987
Wohlfahrtia pachytyli	Sarcophagidae	Diptera	l, p	0.0666	20.0	35.0	Price and Brown, 2006
Scathophaga stercoraria	Scathophagidae	Diptera	l, p	0.0898	10.0	25.0	Blanckenhorn, 1997
Ilione albiseta	Sciomyzidae	Diptera	l, p	0.1372	17.0	23.0	Gormally, 1987
Pherbellia cinerella	Sciomyzidae	Diptera	l, p	0.0743	14.0	26.0	Gormally, 1987
Boophthora erythrocephala	Simuliidae	Diptera	p	0.0956	11.0	21.0	Prügel, 1988
Odagmia ornata	Simuliidae	Diptera	p	0.1097	6.0	21.0	Prügel, 1988
Simulium arcticum	Simuliidae	Diptera	e	0.1369	3.0	18.0	Shipp and Whitfield, 1987
Melanostoma mellium	Syrphidae	Diptera	p	0.0691	18.0	24.0	Honěk and Kocourek, 1988
Sphaerophoria scripta	Syrphidae	Diptera	p	0.1061	15.0	21.0	Honěk and Kocourek, 1988

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Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Max	Reference
Compsilura concinnata	Tachinidae	Diptera	l, p	0.0877	15.6	26.7	Fusco et al., 1978
Lixophaga diatraeae	Tachinidae	Diptera	l, p	0.0903	16.0	30.0	King and Martin, 1975
Myiopharus doryphorae	Tachinidae	Diptera	l, p	0.0844	20.0	30.0	López et al., 1997
Myiopharus sp	Tachinidae	Diptera	l, p	0.0301	24.0	34.0	López et al., 1997
Sturmiopsis inferens	Tachinidae	Diptera	l, p	0.0435	27.0	33.0	David et al., 1981
Winthemia fumiferanae	Tachinidae	Diptera	e, l	0.0802	12.0	27.5	Hébert and Cloutier, 1990
Dacus cucurbitae	Tephritidae	Diptera	e, l	0.0795	15.6	29.4	Keck, 1951
Dacus dorsalis	Tephritidae	Diptera	e	0.1212	13.9	29.4	Messenger and Flitters, 1958
Rhagoletis cerasi	Tephritidae	Diptera	p	0.1104	10.0	23.7	Baker and Miller, 1978
Rhagoletis pomonella	Tephritidae	Diptera	p	0.1090	15.0	27.0	Reissig et al., 1979
Baëtis rhodani	Baëtidae	Ephemeroptera	e	0.1243	4.0	22.0	Elliott, 1972
Coloburiscoides sp.	Coloburiscidae	Ephemeroptera	e	0.0915	10.0	25.0	Brittain and Campbell, 1991
Ecdyonurus dispar	Heptageniidae	Ephemeroptera	e	0.1637	5.0	20.0	Humpesch, 1980
Ecdyonurus insignis	Heptageniidae	Ephemeroptera	e	0.1569	10.0	20.0	Humpesch, 1980
Ecdyonurus picteti	Heptageniidae	Ephemeroptera	e	0.1609	5.0	15.0	Humpesch, 1980
Ecdyonurus torrentis	Heptageniidae	Ephemeroptera	e	0.1661	5.0	20.0	Humpesch, 1980
Ecdyonurus venosus	Heptageniidae	Ephemeroptera	e	0.1534	5.0	20.0	Humpesch, 1980
Rhithrogena cf. hybrida	Siphlonuridae	Ephemeroptera	e	0.1132	5.7	20.0	Humpesch, 1982
Rhithrogena semicolorata	Siphlonuridae	Ephemeroptera	e	0.1803	5.0	19.5	Humpesch and Elliott, 1980

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Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range		Reference
					Min	Max	
Aphis fabae	Aphididae	Hemiptera	l	0.1050	11.5	22.5	Tsitsipis and Mittler, 1976
Aphis nasturtii	Aphididae	Hemiptera	n	0.0956	10.0	27.0	Wang et al., 1997
Aphis punicae	Aphididae	Hemiptera	n	0.0997	17.5	27.5	Bayhan et al., 2005
Aphis spiraecola	Aphididae	Hemiptera	n	0.0614	10.0	28.0	Wang and Tsai, 2000
Chromaphis juglandicola	Aphididae	Hemiptera	l, p	0.1680	15.0	20.0	Nowierski et al., 1983
Hyperomyzus lactucae	Aphididae	Hemiptera	n	0.0813	12.5	24.0	Liu and Hughes, 1987
Macrosiphum albifrons	Aphididae	Hemiptera	n	0.0847	9.8	24.2	Frazer and Gill, 1981
Macrosiphum euphorbiae	Aphididae	Hemiptera	n	0.0529	10.0	25.0	Barlow, 1962
Myzus persicae	Aphididae	Hemiptera	n	0.1136	6.2	24.7	Liu and Meng, 1999
Nasonovia ribisnigri	Aphididae	Hemiptera	n	0.0959	8.0	24.0	Diaz and Fereres, 2005
Pemphigus populitransversus	Aphididae	Hemiptera	n	0.0906	10.0	26.4	Royer et al., 1999
Rhopalosiphum maidis	Aphididae	Hemiptera	n	0.0800	11.0	26.0	Elliott et al., 1988
Rhopalosiphum nymphaeae	Aphididae	Hemiptera	n	0.0374	18.3	26.7	Ballou et al., 1986
Rhopalosiphum rufiabdominalis	Aphididae	Hemiptera	n	0.0623	15.0	30.0	Tsai and Liu, 1998
Schizaphis graminum	Aphididae	Hemiptera	n	0.1038	11.0	23.0	Walgenbach et al., 1988
Toxoptera citricida	Aphididae	Hemiptera	n	0.1336	8.0	25.0	Tsai and Wang, 1999
Toxoptera graminum	Aphididae	Hemiptera	l, p	0.0996	10.0	26.7	Headlee, 1914
Jalysus spinosus	Berytidae	Hemiptera	n	0.0973	15.9	29.5	Elsey and Lam, 1978

Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Temp range Max	Reference
Philaenus spumarius	Cercopidae	Hemiptera	e	0.1108	10.0	25.0	Chmiel and Wilson, 1979
Erythroneura elegantula	Cicadellidae	Hemiptera	n	0.0834	16.0	30.5	Olsen et al., 1998
Erythroneura ziczac	Cicadellidae	Hemiptera	n	0.0931	16.0	29.5	Olsen et al., 1998
Cimex lectularius	Cimicidae	Hemiptera	e	0.1385	13.0	20.0	Johnson, 1940
Cyrtomenus bergi	Cydnidae	Hemiptera	e, n 1,3,5	0.1445	18.0	25.0	Riis et al., 2005
Peregrinus maidis	Delphacidae	Hemiptera	n	0.0994	15.6	26.7	Tsai and Wilson, 1986
Hemiberlesia rapax	Diaspididae	Hemiptera	n	0.1155	13.7	24.6	Blank et al., 2000
Unaspis citri	Diaspididae	Hemiptera	n	0.0563	21.0	28.0	Arias-Reverón and Browning, 1995
Spissistilus festinus	Membracidae	Hemiptera	n	0.0861	18.3	29.4	Spurgeon and Mack, 1990
Calocoris norvegicus	Miridae	Hemiptera	n 1-4	0.1018	10.0	25.0	Purcell and Welter, 1990
Campylomma verbasci	Miridae	Hemiptera	e	0.1206	12.9	25.8	Judd and McBrien, 1994
Adelges piceae	Phylloxeridae	Hemiptera	e	0.1317	7.0	25.0	Amman, 1968
Planococcus citri	Pseudococcidae	Hemiptera	e	0.1098	13.0	29.4	Laflin and Parrella, 2004
Aphelinus mali	Aphelinidae	Hymenoptera	l, p	0.1295	12.0	24.0	Trimble et al., 1990
Meteorus gyrator	Braconidae	Hymenoptera	l, p	0.1299	10.0	25.0	Bell et al., 2003
Microctonus aethiopoides	Braconidae	Hymenoptera	l, p	0.1007	12.8	26.7	Morales and Hower, 1981
Neodiprion fulviceps	Diprionidae	Hymenoptera	e	0.0776	15.0	26.0	Tisdale and Wagner, 1990
Neodiprion sertifer	Diprionidae	Hymenoptera	e	0.1153	12.5	25.0	Régnière, 1984

Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Max	Reference
Habrobracon juglandis	Encyrtidae	Hymenoptera	e	0.1095	13.0	32.0	Davidson, 1942
Psyllaephagus bliteus	Encyrtidae	Hymenoptera	e, l	0.0730	22.0	30.0	Daane et al., 2005
Tetrastichus julis	Eulophidae	Hymenoptera	l, p	0.0982	12.8	26.7	Gage and Haynes, 1975
Anastatus semiflavidus	Eupelmidae	Hymenoptera	e	0.0870	20.0	35.0	Mendel et al., 1989
Eurytoma amygdali	Eurytomidae	Hymenoptera	e, p	0.1337	15.0	25.0	Plaut, 1972
Myrmica rubra	Formicidae	Hymenoptera	l 3	0.1211	16.0	25.0	Elmes and Wardlaw, 1983
Myrmica ruginodis	Formicidae	Hymenoptera	l 4	0.1330	16.0	25.0	Elmes and Wardlaw, 1983
Myrmica sabuleti	Formicidae	Hymenoptera	l 5	0.0862	16.0	25.0	Elmes and Wardlaw, 1983
Myrmica scabrinodis	Formicidae	Hymenoptera	l 6	0.1112	16.0	25.0	Elmes and Wardlaw, 1983
Nomia melanderi	Halictidae	Hymenoptera	l last, p	0.1281	21.0	29.0	Stephen, 1965
Bathyplectes curculionis	Ichneumonidae	Hymenoptera	e, l	0.0846	15.0	26.7	Butler and Ritchie, 1967
Glypta fumiferanae	Ichneumonidae	Hymenoptera	l, p	0.0982	14.9	23.4	Lysyk and Nealis, 1988
Pteromalus puparum	Pteromalidae	Hymenoptera	p	0.0970	17.0	30.0	Nealis et al., 1984
Tyria jacobaeae	Arctiidae	Lepidoptera	l	0.0710	18.3	26.7	Isaacson, 1973
Coleophora laricella	Coleophoridae	Lepidoptera	e	0.1214	12.8	22.2	Quednau, 1967
Chilo orichalcociliellus	Crambidae	Lepidoptera	l	0.0491	25.0	31.0	Ofomata et al., 2000
Chilo partellus	Crambidae	Lepidoptera	l	0.0344	25.0	31.0	Ofomata et al., 2000
Anarsia lineatella	Gelechiidae	Lepidoptera	e	0.0703	21.1	32.0	Brunner and Rice, 1984
Orgyia pseudotsugata	Lymantriidae	Lepidoptera	l, p	0.0679	15.0	30.0	Beckwith, 1982

Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Temp range Max	Reference
Autographa biloba	Noctuidae	Lepidoptera	l, p	0.0727	20.0	30.0	Beach and Todd, 1988
Autographa californica	Noctuidae	Lepidoptera	l, p	0.0868	18.0	30.0	Miller et al., 1984
Autographa gamma	Noctuidae	Lepidoptera	l, p	0.1015	13.0	25.0	Hill and Gatehouse, 1992
Heliothis armiger	Noctuidae	Lepidoptera	p	0.0935	20.0	32.0	Foley, 1981
Orthosia hibisci	Noctuidae	Lepidoptera	l, p	0.1118	7.7	20.4	Judd et al., 1994
Panolis flammea	Noctuidae	Lepidoptera	e	0.0942	5.0	25.0	Leather, 1994
Spodoptera littoralis	Noctuidae	Lepidoptera	p	0.0967	20.0	30.0	Rivnay and Meisner 1965
Heterocampa guttivitta	Notodontidae	Lepidoptera	e, l	0.0730	15.6	26.7	Martinat and Allen, 1987
Quadricalcarifera punctatella	Notodontidae	Lepidoptera	l	0.0770	15.0	24.0	Kamata and Igarashi, 1995
Aglais urticae	Nymphalidae	Lepidoptera	l, p	0.1072	15.0	25.7	Bryant et al., 1999
Hypolimnas bolina	Nymphalidae	Lepidoptera	l, p	0.0676	21.0	30.0	Kemp, 2000
Inachis io	Nymphalidae	Lepidoptera	l, p	0.0930	15.0	25.7	Bryant et al., 1999
Mycalesis perseus	Nymphalidae	Lepidoptera	e	0.0938	17.0	30.0	Braby and Jones, 1994
Mycalesis sirius	Nymphalidae	Lepidoptera	e	0.0930	17.0	30.0	Braby and Jones, 1994
Mycalesis terminus	Nymphalidae	Lepidoptera	e	0.1149	17.0	26.0	Braby and Jones, 1994
Polygonia c-album	Nymphalidae	Lepidoptera	l, p	0.0971	15.0	25.7	Bryant et al., 1999
Vanessa atalanta	Nymphalidae	Lepidoptera	l, p	0.0931	15.0	25.7	Bryant et al., 1999
Papilio glaucus	Papilionidae	Lepidoptera	l	0.0697	18.0	30.0	Scriber and Lederhouse, 1983
Elasmopalpus lignosellus	Phycitidae	Lepidoptera	l, p	0.1273	20.0	27.0	Holloway and Smith, 1976

Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Temp range Max	Reference
Pieris rapae	Pieridae	Lepidoptera	l, p	0.0800	15.0	31.0	Jones et al., 1987
Amyelois transitella	Pyralidae	Lepidoptera	e, p	0.1102	16.7	32.2	Sanderson et al., 1989
Ephestia cautella	Pyralidae	Lepidoptera	e, p	0.0884	20.0	30.0	Bell, 1975
Ephestia elutella	Pyralidae	Lepidoptera	e, p	0.0976	15.0	30.0	Bell, 1975
Galleria mellonella	Pyralidae	Lepidoptera	l last, p	0.0552	24.0	34.0	Stairs, 1978
Ostrinia furnacalis	Pyralidae	Lepidoptera	l, p	0.1016	15.0	30.0	Goto et al., 2001
Callosamia promethea	Saturniidae	Lepidoptera	e	0.0906	15.0	30.0	Ludwig and Anderson, 1942
Platysamia cecropia	Saturniidae	Lepidoptera	e	0.0722	15.0	32.5	Ludwig and Anderson, 1942
Samia walkeri	Saturniidae	Lepidoptera	e	0.1082	15.0	25.0	Ludwig and Anderson, 1942
Telea polyphemus	Saturniidae	Lepidoptera	e	0.0828	15.0	32.5	Ludwig and Anderson, 1942
Archips argyrospillus	Tortricidae	Lepidoptera	e	0.0723	12.5	27.5	Judd et al., 1993
Choristoneura fumiferana	Tortricidae	Lepidoptera	e, l	0.0957	10.0	30.0	Régnière, 1987
Choristoneura pinus pinus	Tortricidae	Lepidoptera	l, p	0.1106	14.9	23.4	Lysyk and Nealis, 1988
Pandemis heparana	Tortricidae	Lepidoptera	l, p	0.1280	13.0	22.0	de Reede and de Wilde, 1986
Chrysopa commata	Chrysopidae	Neuroptera	e	0.0964	15.0	24.0	Honěk and Kocourek, 1988
Chrysopa perla	Chrysopidae	Neuroptera	e	0.1068	15.0	24.0	Honěk and Kocourek, 1988
Chrysopa prasina	Chrysopidae	Neuroptera	e	0.1101	15.0	24.0	Honěk and Kocourek, 1988
Chrysopa septempunctata	Chrysopidae	Neuroptera	e	0.1038	15.0	24.0	Honěk and Kocourek, 1988
Chrysopa ventralis	Chrysopidae	Neuroptera	e	0.1075	15.0	24.0	Honěk and Kocourek, 1988

Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Temp range Max	Reference
Micromus angulatus	Hemerobiidae	Neuroptera	e	0.0993	15.0	24.0	Honěk and Kocourek, 1988
Micromus variegatus	Hemerobiidae	Neuroptera	e	0.0770	15.0	24.0	Honěk and Kocourek, 1988
Lestes eurinus	Lestidae	Odonata	l	0.0809	15.0	30.0	Lutz, 1968
Angaracris barabensis	Acrididae	Orthoptera	e	0.0988	15.0	35.0	Hao and Kang, 2004b
Aulocara elliotti	Acrididae	Orthoptera	n	0.0513	27.0	40.0	Kemp and Dennis, 1989
Austroicetes cruciata	Acrididae	Orthoptera	e	0.1338	16.1	30.3	Birch, 1942
Calliptamus abbreviatus	Acrididae	Orthoptera	e	0.1514	15.0	30.0	Hao and Kang, 2004a
Chorthippus dubius	Acrididae	Orthoptera	e	0.1114	15.0	35.0	Hao and Kang, 2004b
Chorthippus fallax	Acrididae	Orthoptera	e	0.0762	20.0	35.0	Hao and Kang, 2004a
Dociostaurus maroccanus	Acrididae	Orthoptera	e	0.0682	20.0	30.0	Quesada-Moraga and Santiago-Álvarez, 2000
Locusta migratoria migratorioides	Acrididae	Orthoptera	n	0.0356	23.9	43.3	Hamilton, 1950
Melanoplus bivittatus	Acrididae	Orthoptera	e	0.1064	12.0	33.0	Fisher, 1994
Melanoplus differentialis	Acrididae	Orthoptera	e	0.0944	12.0	33.0	Fisher, 1994
Nomadacris septemfasciata	Acrididae	Orthoptera	n	0.0270	26.7	37.8	Hamilton, 1936
Oedaleus asiaticus	Acrididae	Orthoptera	e	0.1176	15.0	35.0	Hao and Kang, 2004b
Omocestus haemorrhoidalis	Acrididae	Orthoptera	e	0.1328	15.0	30.0	Hao and Kang, 2004a
Omocestus viridulus	Acrididae	Orthoptera	n	0.1038	25.0	35.0	Willott and Hassall, 1998

Appendix 2b continued

Species	Family	Order	Life Stage	Slope	Temp range Min	Max	Reference
Schistocerca gregaria	Acrididae	Orthoptera	e	0.0986	19.7	35.1	Hunter-Jones, 1986
Taeniopoda eques	Acrididae	Orthoptera	l, p	0.0803	25.0	35.0	Whitman, 1986
Acheta configuratus	Gryllidae	Orthoptera	n	0.0653	23.0	33.0	Ghouri and McFarlane, 1958
Acheta domesticus	Gryllidae	Orthoptera	n	0.0899	23.0	35.0	Ghouri and McFarlane, 1958
Acheta veletis	Gryllidae	Orthoptera	e	0.0561	22.8	32.8	Bigelow, 1960
Gryllodes sigillatus	Gryllidae	Orthoptera	n	0.1004	23.0	35.0	Ghouri and McFarlane, 1958
Gryllulus commodus	Gryllidae	Orthoptera	e	0.1215	19.4	31.5	Browning, 1951
Gryllus bimaculatus	Gryllidae	Orthoptera	e, l	0.1012	23.0	34.0	Behrens et al., 1983
Paulinia acuminata	Pauliniidae	Orthoptera	n	0.0845	25.0	32.0	Thomas, 1980
Monistria discrepans	Pygomorphidae	Orthoptera	n	0.0595	25.0	35.0	Allsopp, 1977
Metrioptera roeseli	Tettigoniidae	Orthoptera	e	0.1052	18.0	30.0	Ingrisch, 1986
Pholidoptera griseoaptera	Tettigoniidae	Orthoptera	e	0.0890	18.0	30.0	Ingrisch, 1986
Ruspolia differens	Tettigoniidae	Orthoptera	e	0.0947	18.0	33.0	Hartley and Ando, 1988
Ruspolia nitidula	Tettigoniidae	Orthoptera	e	0.0638	20.0	30.0	Hartley and Ando, 1988
Capnia atra	Capniidae	Plecoptera	e	0.0900	4.0	20.0	Brittain et al., 1984
Mesocapnia oenone	Capniidae	Plecoptera	e	0.0885	2.0	15.0	Brittain and Mutch, 1984
Taeniopteryx nebulosa	Taeniopterygidae	Plecoptera	e	0.1068	2.0	23.7	Brittain, 1977
Xenopsylla cheopis	Pulicidae	Siphonaptera	l	0.0624	18.0	29.0	Mellanby 1933

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