Chapter 16

INSECT METABOLIC RATES

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SUMMARY

1 Insect metabolic rates are highly variable and are affected by environmental, behavioral, developmental, and evolutionary factors.

2 The effects of temperature on insect metabolic rates depend on their behavior, life-history stage, morphology, and size. In many cases, inactive insect metabolic rates increase with temperature in a manner consistent with the assumptions of the metabolic theory of ecology (MTE), but exceptions include insects that are flying, endothermic, or behaviorally thermoregulating. In these cases, metabolic rates may remain constant or decrease with increasing temperature.

3 Insect metabolic rates are not generally constrained by oxygen supply limitation.

4 The metabolic rates for behaviorally active insects may be elevated up to 30 times greater than their standard resting metabolic rates, an aerobic scope greater than the comparable range found among similarly sized vertebrates.

5 Nutritional state can have dramatic influences on insect metabolic rates, ranging from extreme diapause in response to starvation to nearly 10-fold increases in metabolic rate following feeding.

6 Metabolic rate correlates with insect body size both intra- and interspecifically. Individual insects as well as eusocial insect colonies share common hypometric scaling exponents, but there is extensive variation in the metabolic elevation (i.e., scaling intercept or normalization constant) of these allometric relationships. While some of this variation may be related to methodology and behavioral variation, it is likely that these patterns reflect previously unrecognized evolutionary differences in physiology and life history.

7 Extensions of MTE should include more physiological, behavioral, and evolutionary mechanisms. Future developments of MTE have great potential to identify a number of areas in which further research is highly needed including the evolution of insect endothermy, body size, eusociality, and metabolic symmorphosis.

16.1 INTRODUCTION

16.1.1 Insect physiological diversity

The insects are among the most species-rich, morphologically diverse, and physiologically complex groups of organisms on the planet. The number of documented insect species is between one and four million and some ecologists estimate that there are potentially as many as seven million species alive today (Wilson 1985; Gaston 1991). Insects have evolved adaptations that allow them to occupy terrestrial, aquatic, and

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aerial ecosystems and environments that vary in temperature, humidity, salinity, oxygenation, and resource abundance.

Insects exhibit an impressive range of sizes over ontogenetic development, within and between species. One of the smallest adult insects is the 20 μg whitefly (Hemiptera: Aleyrodidae). Seven orders of magnitude larger, the Goliath beetle (Coleoptera: Scarabaeidae) is one of the most massive individual insects at 50 g, larger than many birds and mammals. Among the shortest adult insects is a 0.1 mm springtail collembolan (Minelli et al. 2010). The longest may be the stick insect (Phasmatodea: Phasmatidae), which stretches over 0.5 m. Fossil records from the Paleozoic include giants such as the griffenfly (Protodonata: Meganeuridae) that had wingspans as long as 0.71 m (Grimaldi and Engle 2005). The sizes of eusocial insect superorganisms can be much larger. An average honeybee colony may weigh more than 10 kg and one single colony of ants may stretch over many square kilometers (Giraud et al. 2002). In addition to exhibiting broad variation in size, insects are among the most ecologically dominant taxa, filling crucial roles in ecosystem functioning including pollination, seed dispersal, and nutrient cycling (Fittkau and Klinge 1973; Janzen 1987). Recognizing the ecological and physiological diversity among the insects presents a great opportunity to advance the development of a comprehensive and mechanistic theory of metabolic ecology.

Insect metabolism is primarily aerobic and is fueled by catabolic substrates transported by an open circulatory system, oxidized within cells by oxygen that is directly transported from the environment in the gas phase to metabolizing tissues by a system of branching and interconnected air-filled tracheal conduits (Fig. 16.1). Although the transport capacity of the insect tracheal system was once thought to be limited by the passive mechanics of diffusive flux through stationary tubes, this is now known to be an antiquated paradigm (Chown and Nicolson 2004; Socha et al. 2010). An impressive number of active mechanisms achieve convection through tracheal systems, including convective pumping of air sacs by ventilatory muscles of the abdomen (Miller 1966; Socha et al. 2008), convection associated with thoracic volume changes during flight (Weis-Fogh 1967; Wasserthal 2001), ventilation associated with hemolymph transfer between compartments (Wasserthal 1996), and "suction ventilation" associated with the reduced tracheal pressures that occur when spiracles are closed (Miller 1981; Lighton et al. 1993; Hetz and Bradley 2005). Furthermore, the geometry of the tracheal system is sensitive to environmental conditions and exhibits both phenotypic plasticity and evolutionary responses to compensate for changing oxygen availability (Harrison et al. 2006b; Klok and Harrison 2009).

16.1.2 Measuring insect metabolic rates

Analyses of metabolic rate patterns in physiology and ecology rely on standardized conditions for measurement. In the field of mammalian biology, basal metabolic rate is relatively well defined as the metabolic rate of resting, non-digesting animals within their thermoneutral zone, the temperature range in which metabolic rate is constant (Hulbert and Else 2004). The field of insect physiological ecology does not have a thoroughly applied or well-defined set of criteria for standardizing metabolic rate measurements. To a large extent, this is not the result of researcher negligence but rather a consequence of the broad diversity of insect behaviors and physiology.

Defining criteria for standard metabolic rate is challenging in insects due to both behavioral and physiological issues. On the behavioral side, it can be difficult to get many insects to stop moving long enough to obtain stable metabolic measurements. For example, ants or bees removed from their colonies will often search ceaselessly for a way to rejoin their colonies. While it is possible to use movement sensors and chambers with short time constants to eliminate trials or time periods with locomotion, this approach can be challenging and is impossible for some species (Vogt and Appel 1999). Decapitation eliminates most insect locomotory movements, and some insects will continue to metabolize and exhibit regular discontinuous gas exchange cycles (DGC) following decapitation (Lighton et al. 1993); however, this terminal approach is not suitable for many studies and may cause other stresses that affect metabolic rate. A variety of studies have used respiratory patterns (exhibition of discontinuous gas exchange) as a way to determine when insects are in a "resting" state (Davis et al. 2000; Klok and Chown 2005; Lachenicht et al. 2010). Lower metabolic rates do increase the likelihood of discontinuous gas exchange (Contreras and Bradley 2009), but some insects can be quite active while exhibiting DGC and some simply never show such cycles, so this cannot be used as a uniform criterion for all insects. It

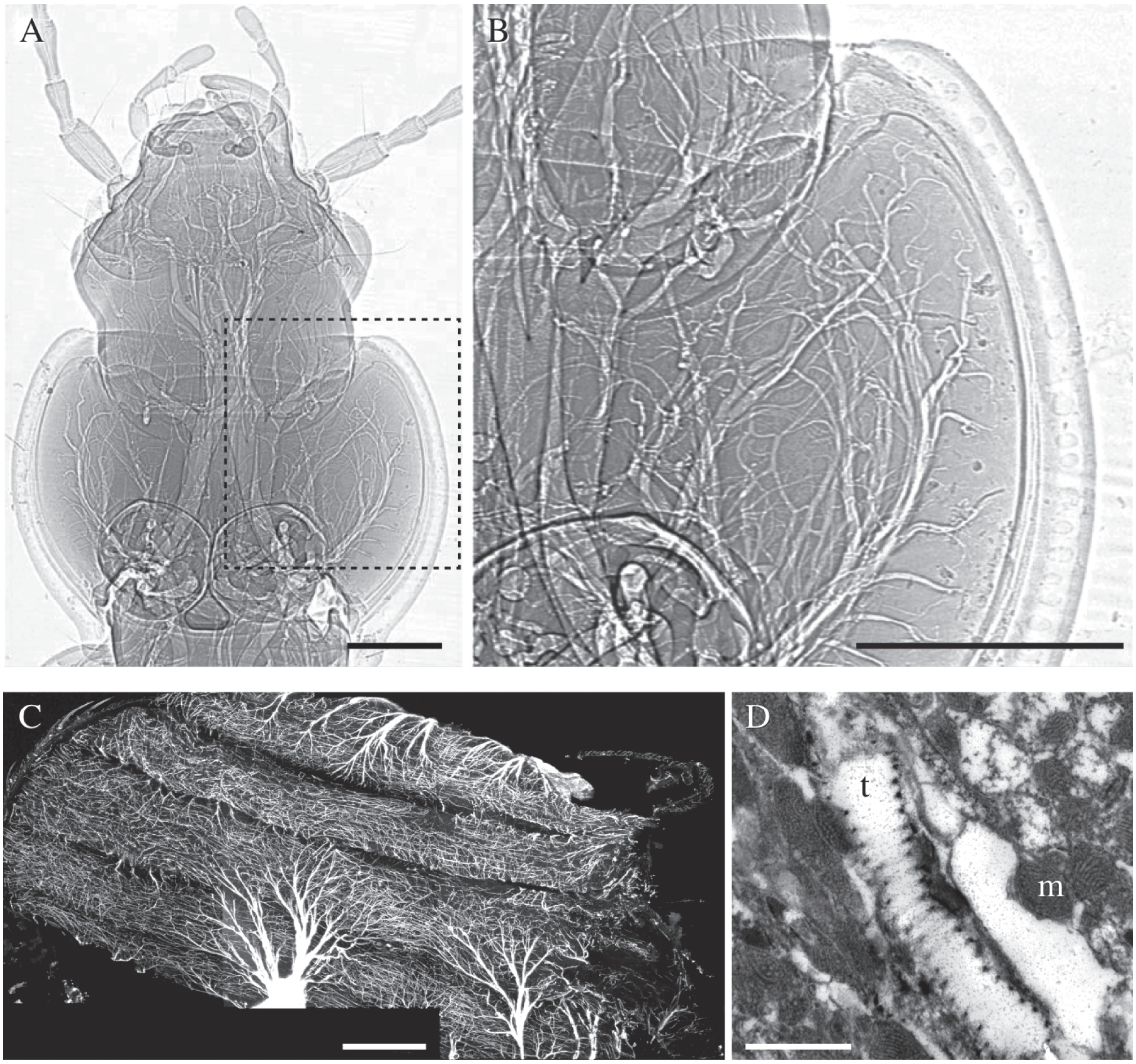

Figure 16.1 Insect tracheal systems provide the primary pathway for transporting oxygen from the environment to all of the metabolically active tissues within the body. (A) Synchrotron x-ray phase contrast image (Socha et al. 2007) of the head and thorax of the beetle, *Pterostichus stygicus*; scale bar: 1 mm. (B) Magnified view of the thorax from the region enclosed by the dotted lines in (A); scale bar: 1 mm (Socha et al. 2007). (C) Confocal microscopy image of the autofluorescent tracheae and tracheoles within the thoracic longitudinal flight muscle of a *Drosophila melanogaster* male; scale bar: 200 μm. (D) Transmission electron microscopy image of a single taenidia-reinforced tracheole (t) positioned near mitochondria (m) within the flight muscle of *Drosophila*; scale bar: 1 μm. Data for (C) and (D) were collected by the authors at the Bioimaging Facility in the School of Life Sciences at Arizona State University.

is often challenging to determine whether insects are in a post-absorptive state, as is commonly done for vertebrates, again because of the great diversity among insects. Some insects tolerate starvation very well, while in other species (e.g., honeybees), high metabolic rates lead to rapid utilization of nutrient stores and death after only a few hours of starvation at a temperature of 20 °C. The lack of a uniform definition for conditions for measurement of insect metabolic rates has two important implications. First, meta-analyses that compile data from various studies need to carefully consider such problems. Second, investigators should monitor and report behavior and time since feeding during all metabolic measurements of insects. Although variability of this sort might be expected to only add noise to analyses of metabolic rate allometry, it may also contribute bias; for example, smaller animals might be more likely to more rapidly exhaust metabolic reserves during a set period of starvation, and respiratory patterns can be size-dependent (Lighton 1991; Lighton and Berrigan 1995; Davis et al. 1999).

Another source of confusion can be terminology. Here we define isometric scaling as following the standard predictions of Euclidian geometry, with volumes scaling with mass^{1}, surface areas with mass$^{0.67}$, and linear dimensions (e.g., leg length) with mass$^{0.33}$. Despite these scaling exponents ranging from 0.33 to 1.0, they all represent isometric scaling. Hypermetric scaling refers to allometric patterns in which the dependent variable exhibits a significantly higher rate of change than predicted by isometry (e.g., leg length scaling with mass$^{0.5}$). Hypometric scaling refers to a significantly lower relationship than predicted by isometry (e.g., leg length scaling with mass$^{0.2}$). Since the vast majority of these patterns are nonlinear, and since the sign (positive or negative) of the scaling relationship does not by itself indicate the nature of the allometry, we have chosen to use the hypometric/hypermetric language to consistently classify the deviation of allometric relationships from the predictions of isometry.

16.2 ENVIRONMENTAL AND BEHAVIORAL EFFECTS ON INSECT METABOLIC RATES

16.2.1 Temperature

One of the primary environmental influences on insect metabolic rates is temperature. The effect of temperature, however, is highly complex and depends on behavior, life-history stage, morphology, and size. Most insects are poikilothermic ectotherms, meaning that their body temperatures vary and that the source of that variation is environmental. Nonetheless, many insects utilize behavioral thermoregulation to achieve relatively constant body temperatures over large parts of the day (Forsman 2000; Ruf and Fiedler 2002). A few insects are endothermic, often demonstrating considerable capacity for regulation of body temperatures using heat generated by the flight muscles (Heinrich 1992). Some social bee colonies that generate their own heat and a stable core colony temperature exhibit features consistent with homeothermic endothermy (Heinrich 1981; Southwick 1985). The ability of many insects to uncouple body temperature from air temperature contributes to some of the variation in how insect metabolic rate responds to air temperature (Fig. 16.2), an important factor to consider when extrapolating from climatic models to predicted insect energetics.

The temperature dependence of metabolic rates has been analyzed with two main approaches. The MTE proposes an Arrhenius expression with a single activation energy that hypothesizes a broadly applicable, exponential effect of temperature on rate processes (Gillooly et al. 2001, 2006a) in ectothermic poikilotherms (see Brown and Sibly, Chapter 2). The classic physiological approach focuses on measuring an organism's Q_{10}, defined as the factorial change in metabolic rate for a 10-degree temperature difference (Lighton 2008). In many cases, Q_{10} is not constant, but varies depending on the specific range of temperatures being modeled (Lighton 1989; Nielsen et al. 1999; Downs et al. 2008). The intraspecific variation in Q_{10} and the interspecific variation in MTE-modeled activation energy may be due to potential behavioral, acclimatory, and evolutionary effects that cause deviations in thermal response patterns away from simple exponential models (Chown et al. 2003; Nespolo et al. 2003; Clarke 2006; O'Connor et al. 2007).

In many cases, insect metabolic rates increase with temperature in a manner approximately consistent with the assumptions of the MTE (Fig. 16.2A; "inactive insects"). Typical fitted activation energy parameters for these cases are in the range of 0.5 to 0. 8, consistent with the findings of a recent meta-analysis using a much larger database of insect metabolic rates (Irlich et al. 2009) and with Q_{10} values in the range of 2–3.

These general patterns occur despite substantial variation in metabolic intensity. For example, similar thermal sensitivities of metabolic rate (i.e., slopes) are observed for scarab beetles and whiteflies, despite their very different metabolic rate at a given temperature (normalization constants, Fig. 16.2A). In the scarab study, only data from insects exhibiting DGC are included, probably explaining their relatively low metabolic rate (Davis et al. 2000), while the whitefly data are for feeding groups (Salvucci and Crafts-Brandner 2000).

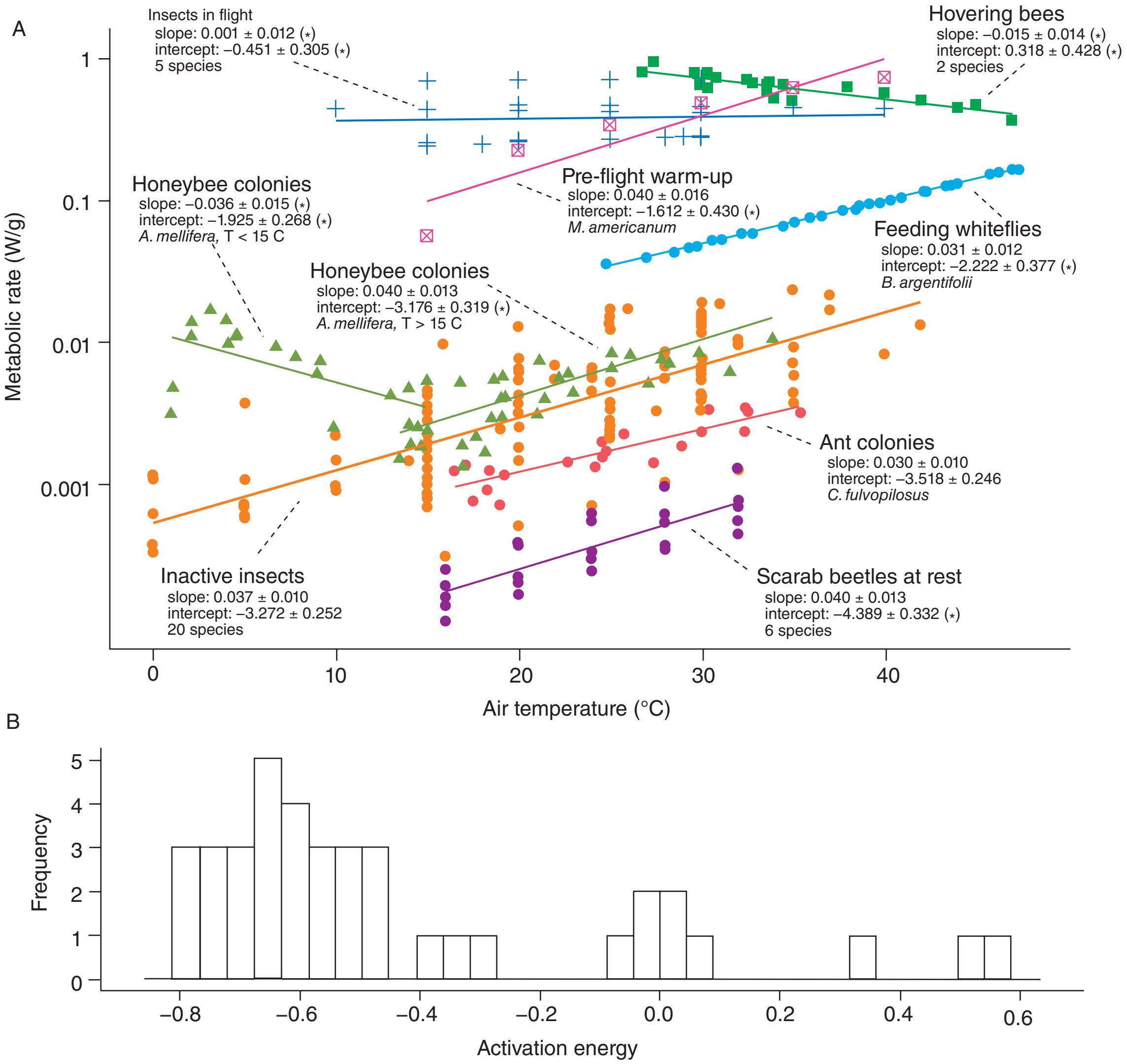

Figure 16.2 Insect metabolic rates are sensitive to temperature and dependent on behavioral and environmental factors. In (A), the mass-specific metabolic rates for 31 insect species from eight taxonomic orders and also ranging across eight orders of magnitude in body size are plotted as a function of air temperature. There is a common trend of insect metabolic rates increasing with temperature in the majority of sampled studies but there are also a number of exceptions. In particular, highly metabolically active, endothermic insects (e.g., endothermic flying insects, cold-exposed honeybee swarms) tend to show little effect of air temperature on metabolic rate, or even an inverse relationship. The coefficients of the linear regressions describing the rate–temperature relationships are provided with asterisks (*) indicating whether the slope or intercept of the fitted data are significantly ($p < 0.05$) different from the coefficients of the common regression parameters shared by the majority of inactive insects. Note that the intercept estimates and their standard error are in log-transformed units.

(B) Frequency distribution of activation energies of insects. Activation energies were obtained as the slopes of OLS regressions of the natural logarithm of mass-specific metabolic rate as a function of inverse absolute temperature for the 35 analyzed datasets. References for the data analyzed in (A) and (B) include: ant colonies (Lighton 1989), flying insects (Casey and Ellington 1989), hovering bees (Roberts et al. 1998; Harrison and Fewell 2002), honeybee colonies (Heinrich 1980), inactive insects (Casey 1977; Herreid et al. 1981; Chappell 1983, 1984; Morgan et al. 1985; Casey and Knapp 1987; Schultz et al. 1992; Vogt and Appel 1999; Fielden et al. 2004; Klok and Chown 2005; Terblanche and Chown 2007), pre-flight warm-up (Casey and Hegel-Little 1987), scarab beetles (Davis et al. 2000), and whiteflies (Salvucci and Crafts-Brandner 2000).

Despite the modal trend for thermal effects on metabolic rates to be relatively well predicted by MTE (Fig. 16.2B), there are some striking exceptions that illustrate potential dangers of not considering the physiological ecology of the species in question. While metabolic rates of social insect larvae or sleeping adults indicate fairly normal responses to temperature (Schmolz et al. 2002; Petz et al. 2004), endothermic flying insects or insect colonies can exhibit constant or even decreasing metabolic rate as temperature increases (Fig. 16.2A). Because flight (foraging) costs can be a significant fraction of total metabolic rate for such insects (Harrison and Fewell 2002), and metabolic rate during overwintering can affect survival of such colonies (Harrison et al. 2006a), it is important to consider these mammal-like thermoregulatory responses of metabolic rate to temperature when considering the effect of climate on these species. Diurnal behavioral thermoregulation can result in higher than expected responses of metabolic rate to air temperature (Casey and Knapp 1987), as can testing insects outside their normal thermal ranges (Schultz et al. 1992). Exposure to naturally occurring fluctuating temperature regimes can also induce stress (e.g., oxidative damage) that increases metabolic rates even where the average temperature decreases (Lalouette et al. 2010). Furthermore, some insects exhibit seasonal and intraseasonal variation in mass-specific and temperature-independent metabolic rate (McGaughran et al. 2009). In many of these cases, the biochemical/physiological mechanisms responsible for thermal responses that differ from MTE remain unknown.

16.2.2 Oxygen and supply limitation

Metabolism represents a balance between energy supply and demand integrated across the many tissues and systems within an organism. Energy is generated primarily by catabolism of fuels using oxygen transported by the tracheal system. One foundational concept of MTE is the proposition that allometric scaling of metabolic rate reflects a resource supply constraint (West et al. 2001). Alternatively, or additionally, the hypometric scaling of metabolic rate with body mass could relate to body-size related scaling of energy demand (Ricklefs 2003; Seibel and Drazen 2007). One way to consider the matching of oxygen supply and demand is to consider how metabolic rate is affected by ambient changes in oxygen supply. To model this effect, it can be useful to consider the classic mass balance equation of respiratory physiology:

$$VO_2 = G \cdot \Delta P_{O_2} \tag{16.1}$$

in which VO_2 indicates an organism's oxygen consumption rate, G the conductance of the respiratory system, and ΔPO_2 the partial pressure gradient for oxygen from atmosphere to mitochondria. G is a measure of the capacity of the respiratory system to transport oxygen, and in this simplified case represents the combination of both diffusive and convective conductance (Buck 1962). If ambient oxygen level is slowly lowered, and ΔPO_2 drops, animals will typically increase the conductance of their respiratory system (in the case of insects, by opening spiracles and increasing ventilation) to maintain a constant VO_2. Over this range, the organism is within its safety margin for oxygen transport and is not supply limited. The organism's critical pO_2 for that particular function is defined as the pO_2 when oxygen becomes limiting and below which VO_2 decreases (Fig. 16.3). We know from work

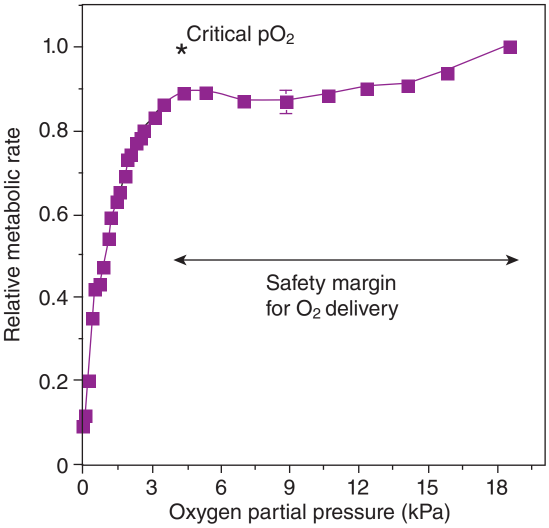

Figure 16.3 To quantify the safety margin for oxygen delivery, organism function can be measured over a range of oxygen partial pressures; the partial pressure (pO_2) at which the activity measure significantly decreases is referred to as that organism's critical oxygen partial pressure. The critical pO_2 for the metabolic rate of adult *D. melanogaster* is 3 kPa or at about 85% less oxygen than normal, with a safety margin of 18 kPa O_2 (Van Voorhies 2009).

with isolated mitochondria (Gnaiger and Kuznetsov 2002) that mitochondria themselves need very little oxygen to perform maximally (less than 1 kPa) so at the critical pO_2, the average ΔPO_2 is likely approximately equivalent to the atmospheric pO_2. Under these circumstances, the maximal capacity of the respiratory system to conduct oxygen, $G_{\max}$, can be estimated as VO_2/critical pO_2 (Harrison 1997). Conductance varies with behavior; for example, it is much higher during insect flight than at rest due to recruitment of more active methods of ventilation (Harrison 1997). Comparison of critical pO_2 values for a given behavior across insects of different sizes can provide a direct way to test whether the ratio of oxygen supply to demand changes with body size. To our knowledge, insects are the only taxonomic group in which there have been systematic tests of the effect of body size on respiratory conductance and critical pO_2.

Most inactive insects exhibit very low critical pO_2 values (Fig. 16.4), clearly indicating that resting metabolic rate is not oxygen-limited. However, critical pO_2 values do tend to be higher when metabolic rate is elevated, as during flight (Fig. 16.4). When comparisons are made controlling for behavior and developmental stage, there is no evidence that critical pO_2 values are higher in larger insects, and mass-specific tracheal conductances at least match the scaling of metabolic rate. Thus there is no evidence that oxygen demand outstrips supply as insects increase in size (Greenlee and Harrison 2004a, 2005; Harrison et al. 2005; Greenlee et al. 2007, 2009). However, there is a tendency for juvenile insects tested later within the development of a single instar (when mass increases without molting) to have much higher critical pO_2 values, suggesting that size increases without molting and resizing of the tracheal system might lead to oxygen supply limitation (Greenlee and Harrison 2004b, 2005).

While oxygen supply seems to meet demand as insects increase in size, this may occur because larger insects exhibit an increased investment in respiratory structure. Larger tenebrionid beetle species have a greater fraction of their body devoted to the tracheal system, and extrapolations of these trends suggest that this pattern could explain oxygen limitations on insect size (Kaiser et al. 2007). Similar hypermetric patterns

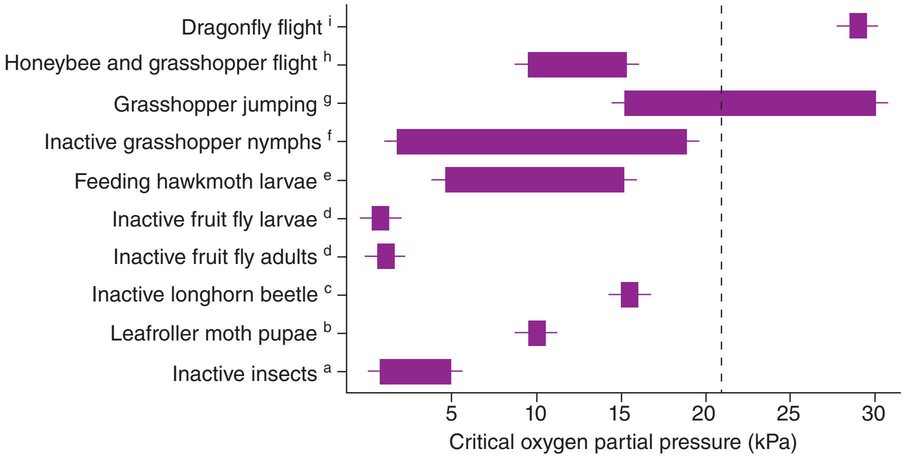

Figure 16.4 Insects often exhibit an impressively broad safety margin for maintaining measures of activity (e.g., O_2 consumption, CO_2 emission, performance) in spite of reduced partial pressures of oxygen in their environment. This figure plots the range of critical pO_2 in the literature for a diverse range of insects and their behaviors. Critical pO_2 tends to be higher in active insects. In cases where hyperoxic values are reported, this indicates that the measure of activity (i.e. dragonfly CO_2 emission and grasshopper jumping performance) increased in hyperoxia relative to normoxia. Normal pO_2 is 21 kPa, as indicated by the dotted line. The letter superscript associated with each row indicates the reference for that dataset: a (Harrison et al. 2006b), b (Zhou et al. 2000), c (Chappell and Rogowitz 2000), d (Klok et al. 2010), e (Greenlee and Harrison 2005), f (Greenlee and Harrison 2004a), g (Kirkton et al. 2005), h (Joos et al. 1997; Rascón and Harrison 2005), and i (Harrison and Lighton 1998).

of tracheal investment have been observed in grasshoppers during ontogeny (Harrison et al. 2005; Greenlee et al. 2009). The increased investment in respiratory structure in larger insects suggests that body size influences metabolic rate via evolutionary tradeoffs such as reduced proportions of active tissues per unit volume in larger insects (Harrison et al. 2010).

16.2.3 Locomotion

The metabolic rates of behaviorally active insects range from 3 to 30 times resting rates, and the maximal mass-specific metabolic rates of active insects can be more than double those of maximally active, similarly sized mammals or birds (Harrison and Roberts 2000). Flying insects exhibit the highest metabolic scopes and flight metabolic rates are approximately 10 times greater than maximal metabolic rates for running insects of a similar size (Full 1997). In some endothermic insects, transitions from rest to activity are associated with strong increases in body temperature, leading to very high metabolic scopes. For example, it has been reported that stridulating katydids (Stevens and Josephson 1977) and running beetles (Bartholomew and Casey 1977) exhibit metabolic scopes in the range of 50 to 100-fold during these behaviors as they endothermically warm their bodies by up to 20 °C.

Metabolic rates increase linearly with running speed (Weier et al. 1995; Lipp et al. 2005) and peak metabolic rates among running and flying insects scale on average with $M^{0.86}$ (Full 1997). Metabolic rates during flight have been reported to scale with $M^{0.9}$, but the degree of this allometry is likely influenced by the tendency of larger endothermic insects to have higher body temperatures and flight metabolic rates than smaller insects (Niven and Scharlemann 2005). Mechanical power output (usually estimated from the kinematics of limb or wing movements and dynamic models) scales isometrically with body size in running insects and either isometrically or hypermetrically in flying insects (Full 1997). This pattern (increasing mechanical power output relative to metabolic power input) suggests that the relative efficiency (mechanical power output/metabolic power input) of locomotion increases with insect body size. If efficiency is defined as the ratio of locomotory power output to metabolic power input, isometric scaling of power output and input would predict that efficiency is invariant with mass ($M^{0.0}$). For insects in general, efficiency scales hypermetrically (relative to the isometric prediction) with mass$^{0.12}$ and even more dramatically for honeybees, locomotory metabolic efficiency scales with $M^{0.45}$ (Harrison and Roberts 2000).

16.2.4 Nutrition and feeding

The metabolic costs of insect foraging are usually tightly linked to the energetics of locomotion. In honeybee colonies, the energetic costs of foraging are approximately 30% of the estimated whole-colony metabolic rate, but this fraction is likely much lower in terrestrial foraging species such as ants (Harrison and Fewell 2002). However, the metabolic rates of stationary ants (*Atta sexdens rubropilosa*) during leaf-cutting may be more than 30 times their inactive metabolic rate, yielding a similar aerobic scope to flight (Roces and Lighton 1995).

Metabolic rates typically increase in response to feeding and these increases may scale with both body size and meal type. The metabolic costs of post-feeding digestion can be quantified by the elevation of metabolic rate relative to baseline, the postprandial metabolic scope (3.3 for insects) and also by the net energy expended for the duration of the specific dynamic action response (SDA), which ranges among the insect groups studied from 0.00025 to 0.102 kJ (Secor 2009). Across a broad range of invertebrate taxa, SDA scales with $M^{0.31}$, meal-mass$^{0.72}$, and meal-energy$^{0.32}$; for comparison, among mammals, SDA scales with $M^{0.32}$, meal-mass$^{0.7}$, and meal-energy$^{1.21}$ and among reptiles SDA scales with $M^{-0.08}$, meal-mass$^{1.13}$, and meal-energy$^{1.06}$ (Secor 2009). Among insects, the kissing bug (*Rhodnius prolixus*) exhibits the highest postprandial metabolic scope (10-fold increase in whole-organism metabolic rate) as well as the greatest SDA (0.102 kJ) following feeding on a blood meal (Bradley et al. 2003). The specific dynamic action for migratory locust (*Locusta migratoria*) nymphs is in the four- to fivefold range (Gouveia et al. 2000). In addition to effects of being fed or not, the characteristics of the diet can also affect metabolic rate. A high-carbohydrate diet is linked to increased metabolic rates in honeybees (Blatt and Roces 2001). In locusts, increased carbohydrate : protein intake can lead to strong elevation in metabolic rates, probably to dispose of excess energy in the diet and allow intake and assimilation of needed quantities of protein (Zanotto et al. 1997; Gouveia et al. 2000).

Restricted nutritional resource supply can have a range of effects on insect metabolic rates. Foraging honeybees given richer (higher carbohydrate) rewards exhibit higher metabolic rates during periods of foraging that include both flight and non-flight (Balderrama et al. 1992), suggesting that in this species, metabolic rate is positively influenced by nutritional supply. Similarly, starvation may decrease metabolic rates or impair flight performance (Goldsworthy and Coupland 1974; Matsura 1981; Stoks et al. 2006), but this is not always the case. In the African fruit beetle (*Pachnoda sinuata*), voluntary flight performance and duration is not inhibited by 15–30 days of starvation (Auerswald and Gäde 2000). Reduced water supply can elevate metabolic rate in growing insect larvae (Martin and Van't Hof 1988) but does not affect the overall metabolic rate of adult locusts (Loveridge and Bursell 1975). One of the reasons for the complex pattern of nutrient-supply effects on insect metabolic rates is the fact that there are often plastic physiological responses to resource deprivation including dramatic shifts in the metabolic pathways and nutrient substrates used to fuel metabolism, often without affecting overall metabolic rates (Djawdan et al. 1997; Juliano 1986; Auerswald and Gäde 2000; Renault et al. 2002; Sinclair et al. 2011). However, both comparative and artificial selection studies suggest that an evolutionary response to starvation and water stress may involve reduced mass-specific metabolic rate (Harshman et al. 1999; Marron et al. 2003).

At the extreme of environmental nutrient restriction, insects may utilize torpor and diapause to survive long dearth periods, reducing metabolic rates for extended periods of time by more than 98% (Schneiderman and Williams 1953; Hahn and Denlinger 2010). A meta-analysis of the metabolic rate scaling for insect eggs, larvae, and pupae (62.4 $M^{0.77}$) shows a similar hypometric exponent but a significantly reduced intercept (normalization constant) relative to the allometry (363 $M^{0.86}$) for the corresponding adult resting metabolic rates (Guppy and Withers 1999).

Social insect colonies are particularly well adapted to maintaining physiological homeostasis in response to variation in environmental resource availability. For example, workers within the colony vary their foraging activity in response to the nutritional demands of the brood (Sorensen et al. 1985; Dussutour and Simpson 2009) and many species harvest and store resources (Hölldobler and Wilson 1990). Colonies may also catabolize somatic tissue to survive resource scarcity and environmental stress (Wilson 1971; Sorensen et al. 1983; Schmickl and Crailsheim 2001). In the acorn ant (*Temnothorax rugatulus*), decreases in activity levels and increases in trophallaxis (mouth-to-mouth food transfer) are hypothesized to facilitate this species' remarkable ability for colonies to survive greater than eight months of starvation (Rueppell and Kirkman 2005). Kaspari and Vargo observed a hypermetric allometry for the duration of queen survival in the fire ant (*Solenopsis invicta*) which scaled with the size of the colony as $M^{0.21}$ (Kaspari and Vargo 1995). This capacity for resilience has been hypothesized as one of the factors involved in the evolution of eusociality, caste ratios, and variation in colony size (Michener 1964; Wilson 1968; Bouwma et al. 2006).

16.3 CORRELATIONS BETWEEN BODY SIZE AND METABOLIC RATE

16.3.1 Developmental allometries

Insect larvae represent excellent, albeit relatively unexplored, model systems for investigating the interface between physiology and ecology. As for adults, larval insects are quite diverse. Many insect larvae live underground, in leaf litter, or in decaying fruits and likely experience a range of hypoxic environments, but others (e.g., many lepidopteran larvae) forage on leaves in normoxia. Many insect larvae are solitary, but other species rear brood cooperatively, such as the bessbug (*Odontotaenius disjuctus*) which raise larvae in communal galleries carved out of decaying wood. While most insect larvae are terrestrial, some are aquatic, and of these, some have open (e.g., mosquito) and others closed (e.g., caddis fly) tracheal systems. Some aquatic insect larvae (e.g., the chironomids) have evolved the use of hemoglobin for oxygen transport (Oliver 1971). The diversity of these environments and behaviors as well as the general paucity of literature data make it difficult to draw broad conclusions about the energetics of insect larvae.

Insect larvae metabolic rate allometries have been investigated on an intraspecific basis for a number of insect species that can be easily reared. While many of these studies report hypometric scaling exponents, there is weak support for a canonical 0.75 exponent. Growing honeybee larvae increase in mass by more than 400-fold in only 4 days and exhibit metabolic rates that scale with mass$^{0.9}$ (Petz et al. 2004). Larvae of the tobacco hornworm (*Manduca sexta*) span three orders of magnitude in body mass and exhibit CO_2 emission rate scaling with a mass exponent that ranges from 0.77 (Alleyne et al. 1997) to 0.98 across the entire larval stage (Greenlee and Harrison 2005). However, individual instars show different patterns of metabolic rate scaling; as larvae grow within an instar, the mass-specific CO_2 emission decreases with age/size among early instars, but it increases with size in final larval instar (Greenlee and Harrison 2005) (see also Kerkhoff, Chapter 4, Fig. 4.1B). Similarly in grasshoppers, the pattern of CO_2 emission rate scaling varies within different instars with exponents ranging between 0.45 and 0.91 (Greenlee and Harrison 2004b), while across its entire development, metabolic rate scales with the exponent 0.73 (Greenlee and Harrison 2004a). Larvae of the flour beetle (*Tribolium castaneum*) exhibit mass-specific metabolic rates that decrease by over 90% during less than 12 days of development (Medrano and Gall 1976) and the hemimetabolous milkweed bug exhibits a 38% decrease in mass-specific metabolic rate from the first instar to adult (Niswander 1951).

Insect development from larvae to adults is associated with complex changes in body form and physiology in addition to alteration in body size. Metabolic rate scaling patterns may depend on the nature of these changes. Adult holometabolous insects are often substantially smaller than the terminal larval instar and the few studies available suggest that they have greater resting and maximal metabolic rates. Adults of vinegar flies (*D. melanogaster*) (Klok et al. 2010), fire ants (*S. invicta*) (Vogt and Appel 1999), and honeybees (*A. mellifera*) (Lighton and Lovegrove 1990; Petz et al. 2004) exhibit mass-specific metabolic rates approximately twice as high as their larvae. Are the higher mass-specific metabolic rates in adults due to their smaller size? If the adults and larvae are assumed to belong to a common mass-scaling allometry, then the ratio of their mass-specific metabolic rates can be calculated by:

$$\frac{B_2}{B_1} = \frac{B_0 M_2^{\alpha-1}}{B_0 M_1^{\alpha-1}} = \left(\frac{M_2}{M_1}\right)^{\alpha-1} \tag{16.2}$$

where symbols are defined as in equation 2.1. Equation 2.6 can be rearranged to solve for the mass ratio (ΔM) that would be necessary to generate an observed ratio in metabolic rate (ΔB):

$$\Delta M = \frac{M_2}{M_1} = (\Delta B)^{\frac{1}{\alpha-1}} \tag{16.3}$$

If the whole-animal scaling exponent (α) is 0.75, then we can predict what difference in masses would generate the observed ratio in mass-specific metabolic rates:

$$\Delta M = \Delta B^{-4} \tag{16.4}$$

In the case of a two-fold difference in mass-specific metabolic rates, the mass ratio would have to be 0.0625 for allometry to predict the observed difference in mass-specific metabolic rates. In other words, the adult stages of the ant, bee, and fly species mentioned above would have to be 94% smaller than their larval forms (or the larvae 16.67 times larger than the adults) for simple mass-scaling to explain the two-fold higher mass-specific metabolic rates in adults relative to larvae. Since adults are only approximately 10–30% less massive than larvae, the relatively high adult mass-specific metabolic rates are not simple allometric consequences of smaller body mass. An alternative ultimate explanation for the higher mass-specific metabolic rates of adults may be analogous to the higher metabolic rates of flying relative to non-flying adult insects (Reinhold 1999). The complex changes (e.g., in body tissue composition and tracheal system structure) that take place during metamorphosis in the holometabolous pupal stage apparently also enable fundamental changes in resting metabolic rate.

16.3.2 Intraspecific allometries

The relatively low range in masses among adults of a single species makes it difficult to accurately test for an intraspecific correlation between mass and adult insect metabolic rates in many species (Vogt and Appel 1999; Van Voorhies et al. 2004). Ants are somewhat exceptional in this regard, with some species exhibiting substantial variation in worker size. For example, the dry masses of *Pheidologeton diversus* workers vary by more than 500-fold (Hölldobler and Wilson 1990). In most cases, it appears that metabolic rates of such workers scale hypometrically with mass, with homogenous slopes ranging from 0.55 to 0.83 (Chown et al. 2007; see also Kerkhoff, Chapter 4, Fig. 4.1A).

In some insects, intraspecific variation is associated with morphological allometries that produce surprising

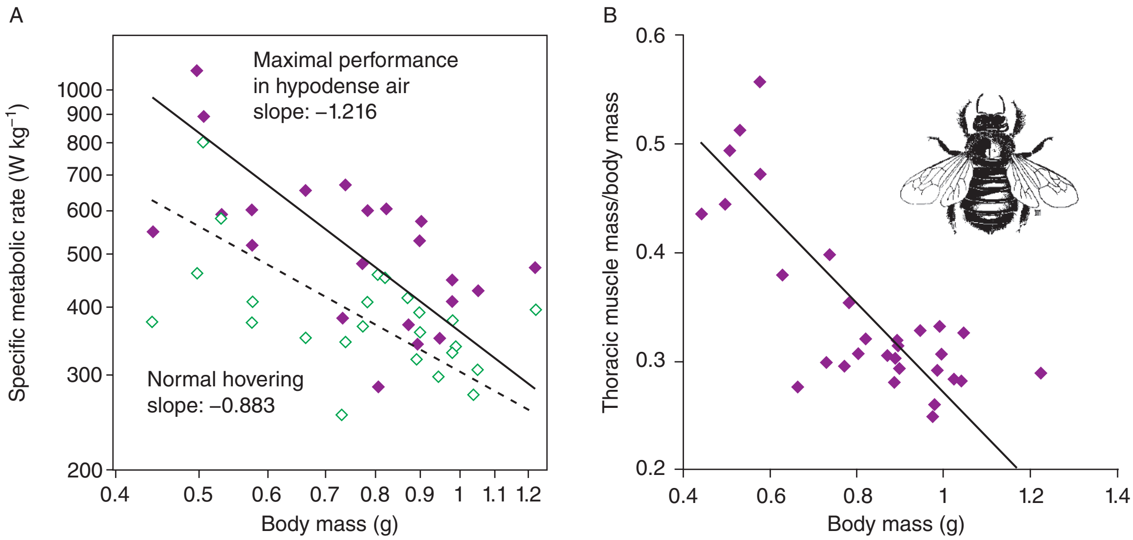

Figure 16.5 The allometry of body composition provides insight into the unusual intraspecific hypometric scaling of metabolic rate with body size in the carpenter bee, *Xylocopa varipuncta*. This figure, adapted from Roberts et al (2004), shows in (A) that body mass-specific metabolic rates decrease very strongly with body mass (so whole-organism rates scale with $M^{-0.22}$ for maximal performance in hypodense air and $M^{0.12}$ for normal hovering). This pattern occurs because the relative content of thorax muscle mass (the major site of oxygen consumption during flight) decreases with body size (B).

patterns in metabolic rate scaling and locomotory performance. Among female carpenter bees, flight metabolic rate scales hypometrically with mass$^{0.12}$ (Fig. 16.5A), a very low scaling exponent. When these bees exhibit their maximal performance, flying in the lowest density air possible (to stay aloft in thin air requires more power), the scaling exponent is –0.22, meaning that both the mass-specific and absolute metabolic rates are lower in larger individuals than smaller individuals. The reduced mass-specific metabolic rate and flight performance of larger bees in this species is explained by variation in the relative amount of flight muscle, the primary site of oxygen consumption in flying bees. In this species, larger females have proportionally larger abdomens (Fig. 16.5B) and likely larger ovaries. As a consequence, larger individuals have significantly lower ratios of flight muscle to body mass, lower mass-specific metabolic rate, and reduced scopes for flight performance and metabolic rate (Roberts et al. 2004).

16.3.3 Social insect colonies

Social insect colonies are intriguing organisms from the perspective of MTE because they span multiple levels of biological organization. Individuals within the colony may be expected to exhibit hypometric scaling of metabolic rate with mass, but whole colonies are made up of physically independent individuals at different developmental stages and engaged in a wide variety of different tasks and behaviors. Thus, whole-colony metabolic rate should scale linearly with mass, depending proportionally on the number of individuals in the colony. Surprisingly, social insect colonies exhibit hypometric intraspecific scaling of metabolic rate with colony mass (Fig. 16.6). Intriguingly, while the three social insect datasets illustrated in Figure 16.6 exhibit hypometric metabolic rate scaling consistent with the pattern for individual insects, they are each hypothesized to do so for different reasons. Honeybee clusters maintain a relatively constant core temperature when air temperature falls; mass-specific metabolic rates and mass-specific heat loss from the cluster falls in larger clusters due to a reduced surface area to volume ratio (Southwick et al. 1990). In the polymorphic ant *Pheidole dentata*, lower mass-specific colony metabolic rates arise from larger colonies having a greater fraction of larger “major” workers (Shik 2010). In a harvester ant species with monomorphic workers, *Pogonomyrmex californicus*, it is

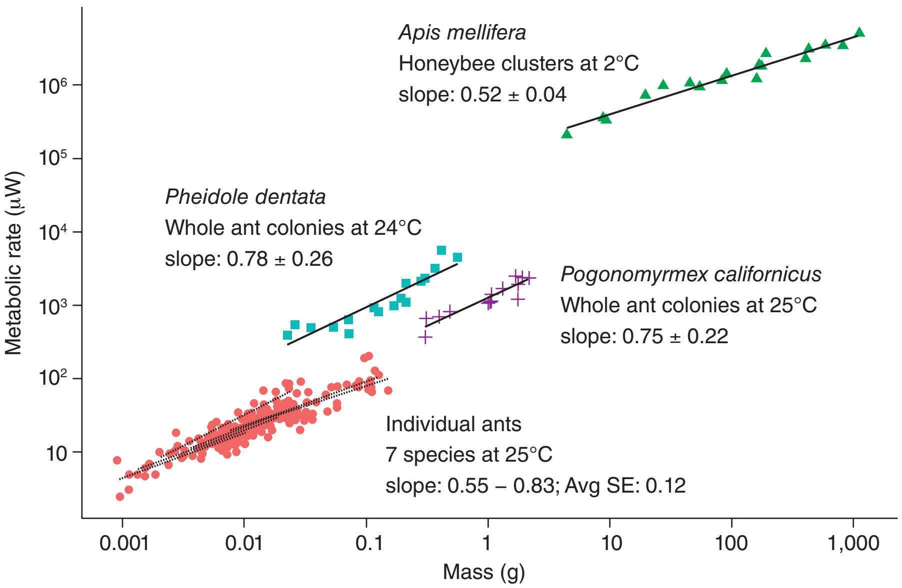

Figure 16.6 Allometry of colony metabolic rate in three colonial species compared with individual metabolic rate in seven solitary species. Social insect colonies, like individual insects, exhibit metabolic rates that scale hypometrically with mass. This figure combines intraspecific data for individual ants (Chown et al. 2007), two functioning whole ant colony species (Shik 2010; Waters et al. 2010), and thermoregulating honeybee clusters (Southwick et al. 1990). The OLS regression results for each group are displayed above (slopes are given with standard errors) and the overall model, which fits a separate slope and intercept for each species, has an $r^2 = 0.99$. The average homogenous slope was 0.62 and the only species that show significantly higher than average scaling slopes are *Eciton hamatum* (slope: 0.83, $p < 0.003$) and *P. dentata* (slope: 0.78, $p < 0.002$).

hypothesized that a lower mass-specific colonial metabolic rate in larger colonies may be due to larger colonies having a lower fraction of active workers (Waters et al. 2010). The similar hypometric scaling patterns with disparate mechanisms do suggest common underlying ecological/evolutionary forces that can be addressed by varied mechanisms in different species. Social insect colonies may be particularly useful for investigating mechanisms responsible for metabolic scaling patterns due to the capacity to more easily manipulate and measure specific components of the superorganism than is possible with individual organisms.

16.3.4 Interspecific allometries

On an interspecific basis, insect metabolic rates scale with $M^{3/4}$ (Chown et al. 2007) as in mammals (Karasov, Chapter 17). Analysis of the intercept (or normalization constant) of this relationship indicates that insects have low metabolic rates relative to mammals. After accounting for the effects of mass (the scaling exponent) and temperature (by adjusting insect rates from 25 °C to 37 °C following the activation energy method), insect metabolic rates are approximately half those reported for mammals (Fig. 16.7A). This pattern fits with the ectothermic nature of most insects; ectothermic vertebrates also have lower metabolic rate than mammals at the same body temperature (Hulbert and Else 2000).

Examination of the intercept of metabolic rate allometries (referred to as metabolic coefficient, intensity, elevation or normalization constant) has the potential to reveal evolutionary differences in the metabolic physiology of different animal taxa. Among invertebrates, ticks and scorpions have been shown to exhibit significantly lower metabolic rates than other "typical" arthropods, possibly contributing to the high abundance of these species in some regions (Lighton

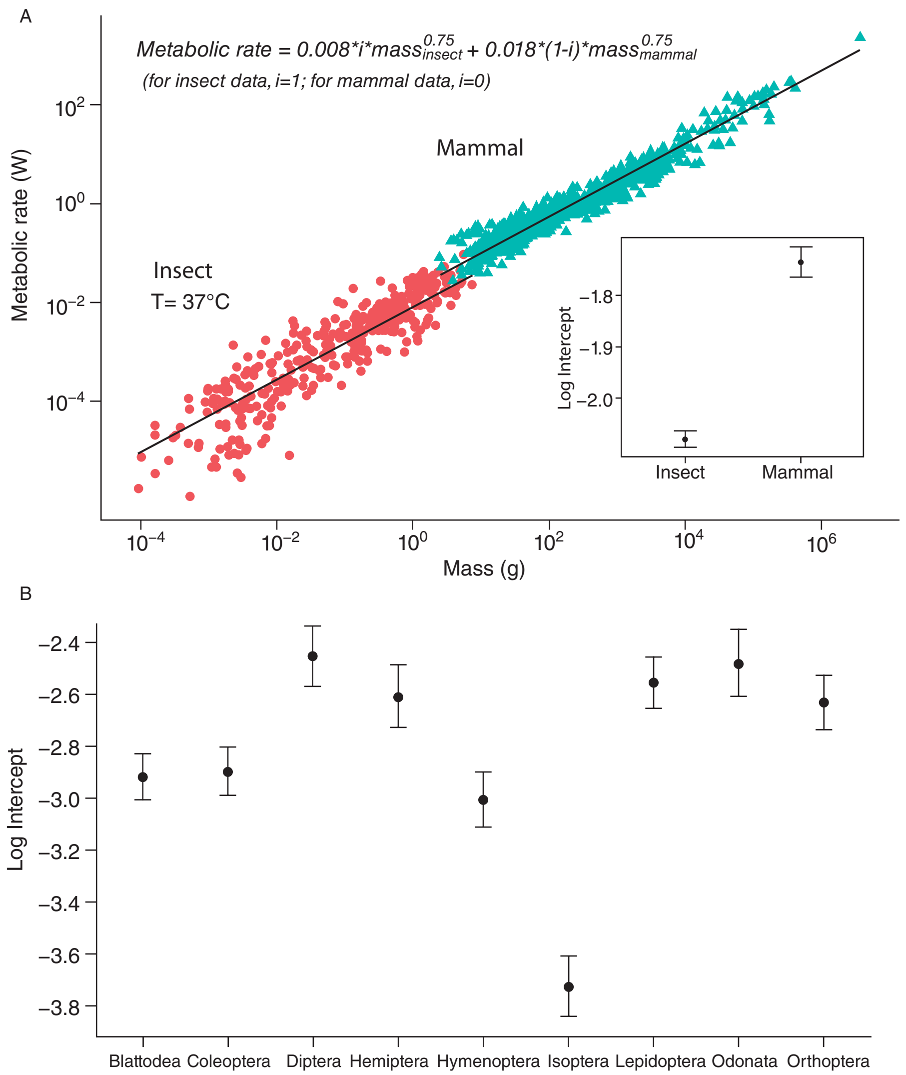

Figure 16.7 The hypometric scaling of inactive insect metabolic rates (Chown 2007) is generally consistent with the pattern observed for mammals (Savage et al. 2004b); both taxa exhibit similar 3/4-power scaling slopes but insects have lower intercepts or normalization constants. In (A) the metabolic rates for 391 insect species have been adjusted using the Arrhenius equation to 37 °C, a standard mammalian body temperature (see Brown and Sibly, Chapter 2). Independent of mass, inactive insects have metabolic rates about two times lower than inactive mammals with the same body temperature (figure inset displays the intercept values from the OLS regression on log-log data). (B) The interspecific data on insect metabolic rates at 25 °C (Chown 2007) can be analyzed by taxonomic order. A linear model that fits unique slopes and intercepts for each order was not a significantly better model than one that preserved a common slope (0.72 ± 0.2 SE) but allowed for variation in intercepts by order. The maximum intercept (Diptera, 3.5 mW) was more than 18 times greater than the minimal intercept (Isoptera, 0.19 mW). Part of this variation may be due to behavioral variation among "inactive" insects, and methodological variation among researchers, but the data suggest substantial order-level variation in inactive metabolic rates among insects.

et al. 2001). Similarly, predatory ant-lion larvae which build pits in which to capture prey exhibit common hypometric metabolic rate scaling exponents but with intercepts depressed lower than insects in general and even lower than similarly sized sit-and-wait predatory spiders (Lucas 1985; Van Zyl et al. 1997). The normalization constant (y-intercept on log-log plots) of the scaling relationship for different insect orders varies by 18-fold (Fig. 16.7B). While some of this variation may be related to methodology and behavioral variation among the taxa, it is likely that these order-level patterns at least partially reflect previously unrecognized evolutionary differences in physiology and life history.

16.4 BROADER IMPLICATIONS

The diversity of insect structure and function provides a powerful tool for testing physiological, ecological, and evolutionary predictions of MTE. While the general equations of MTE seem to fit the modal responses of insects, and thus may be very useful for community and ecosystem ecology, behavioral and physiological divergences of individual species and taxa from the general theory of MTE are considerable. The temperature dependence of insect metabolic rates is highly variable, and as previously discussed, frequently depends on important ecological variables including behavior and thermal preferences. The temperature dependence of insect metabolic rates can also be highly subject to thermal acclimation and adaptation (Chown and Nicolson 2004). All of these factors are critical to developing predictive models for how insect populations will respond to global-scale changes in climate (Dillon et al. 2010).

Applications of MTE may be able to help address some of the great unanswered questions in insect metabolic ecology. What biophysical forces or ecological pressures have driven the evolution of insect endothermy? What are the constraints on behavior and physiological performance imposed by body size? Have the biomechanics of the insect exoskeleton or tracheal system influenced the evolution of insect size, and if so, what is the role of metamorphosis in mediating these potential constraints? How do behavioral and developmental regulation within social insect colonies influence the scaling of supply and demand in these physically independent but functionally integrated systems?

Future mechanistic developments of MTE may also help to explain sources of variation in mass- and temperature-independent metabolic intensity, both among distinct insect taxa and on a larger scale between insects, birds, and mammals. In addition, studying the energetics of insects is tremendously important for ecology and agriculture. As predators, scavengers, detritovores, and herbivores, insects play enormously important roles in ecosystem functioning, so that more energy flows through an ecosystem due to the activity of insects than from the activity of vertebrates (Andersen and Lonsdale 1990). Economic growth and stability may depend on understanding the thermal preferences, metabolic rates, and behaviors of insect pollinators (Potts et al. 2010). By moving beyond broad assumptions and universal characterizations, MTE has the potential not only to integrate fields as diverse as insect ecophysiology and biofluid transport dynamics, but also to reveal questions of basic and fundamental importance to agriculture, biomechanics, ecology, and evolution.

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