

Body size variation in insects: a macroecological perspective

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ABSTRACT

Body size is a key feature of organisms and varies continuously because of the effects of natural selection on the size-dependency of resource acquisition and mortality rates. This review provides a critical and synthetic overview of body size variation in insects from a predominantly macroecological (large-scale temporal and spatial) perspective. Because of the importance of understanding the proximate determinants of adult size, it commences with a brief summary of the physiological mechanisms underlying adult body size and its variation, based mostly on findings for the model species *Drosophila melanogaster* and *Manduca sexta*. Variation in nutrition and temperature have variable effects on critical weight, the interval to cessation of growth (or terminal growth period) and growth rates, so influencing final adult size. Ontogenetic and phylogenetic variation in size, compensatory growth, scaling at the intra- and interspecific levels, sexual size dimorphism, and body size optimisation are then reviewed in light of their influences on individual and species body size frequency distributions. Explicit attention is given to evolutionary trends, including gigantism, Cope's rule and the rates at which size change has taken place, and to temporal ecological trends such as variation in size with succession and size-selectivity during the invasion process. Large-scale spatial variation in size at the intraspecific, interspecific and assemblage levels is considered, with special attention being given to the mechanisms proposed to underlie clinal variation in adult body size. Finally, areas particularly in need of additional research are identified.

Key words: Bergmann's rule, clinal variation, compensatory growth, frequency distribution, gigantism, ontogeny, Rensch's rule, seasonality, sexual size dimorphism.

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I. INTRODUCTION

Body size is one of the most striking features of all organisms. Indeed, it is thought to be documented as frequently by biologists as human age is by reporters (Nee & Lawton, 1996). The apparency of body size has resulted in a tacit acceptance by many that it can be considered, for all practical purposes, a fixed, or an 'independent', variable in biological studies, strange as this might seem to evolutionary ecologists. Often this perspective is a matter of convenience, since so many physiological, life-history, and ecological traits are strongly related to size, and because, with due care (Hayes & Shonkwiler, 2006), these traits may be predicted from a measure of size. However, some recent approaches treat size as a fixed variable that has consequences for such other traits (see review in Brown *et al.*, 2004). By contrast, much of life-history theory considers size to be a continuously varying trait dependent on a variety of factors operating at different stages in an individual's life, and their integration (Roff, 1981, 2002; Bede, McNeil & Tobe, 2007). Most prominent amongst the proximate, physiological factors are differences in growth rate and the duration of important periods during juvenile growth, the regulatory basis for this variation, and regulatory differences in the rate and duration of cell proliferation (Nijhout, 2003; Emlen & Allen, 2004; Edgar, 2006; Nijhout, Davidowitz & Roff, 2006; Mirth & Riddiford, 2007). Amongst the ecological factors are the size-dependencies of production and mortality rates and the differences between capital and income breeders (Kirkendall & Stenseth, 1985; Kozłowski, Czarnolęski & Daňko, 2004; Teder, Tammaru & Esperk, 2008). These size-dependencies interact with the physiology of the animal, which in turn may also be related to genome size, cell size and membrane properties (Kozłowski, Konarzewski & Gawelczyk, 2003; Hulbert, 2003, 2008). The size-dependencies are also affected by the animal's environmental circumstances, which may alter mortality and production rates at various stages (Roff, 2002). Hence, natural selection continuously sculpts body size, which, nonetheless, tends also to be phylogenetically conservative (Gaston & Blackburn, 2000).

What form the size frequency distributions of populations and assemblages take as a consequence of these interactions, and how and why these distributions vary over large spatial and temporal scales form a major component of macroecology (Brown, 1995; Gaston & Blackburn, 2000; Brown *et al.*, 2004; Diniz-Filho *et al.*, 2007; Gaston *et al.*, 2008). Indeed, given the frequently marked relationships between body size and energy use, abundance, and geographic range size (e.g. Brown *et al.*, 2004; E.P. White *et al.*, 2007), body size variation has long been, and remains of central concern to macroecologists (Brown, 1995; Gaston & Blackburn, 1996; Blackburn & Gaston, 1999, 2001; Brown *et al.*, 2003; Olson *et al.*, 2009). In essence, macroecology is concerned with understanding the division of food and space among species at large spatial and temporal scales (Brown & Maurer, 1989), or, alternatively, with understanding the distribution and abundance of organisms at large spatial and temporal scales (Gaston & Blackburn, 2000). Although macroecological investigations encompass a wide variety of theoretical and empirical approaches (Brown, 1995, 1999; Blackburn & Gaston, 1998, 2003), often a distinction is drawn between univariate, bivariate and multivariate perspectives, and integration follows from joint consideration of the insights obtained from each (e.g. Gaston & Blackburn, 2000; McGill, 2003; Hui & McGeoch, 2008; E.P. White *et al.*, 2007; Storch *et al.*, 2008).

Given the extraordinary diversity of insects (Gaston, 1991*b*) and their preponderance amongst animals, at least at the species level, for any model or hypothesis which seeks to explain large-scale patterns in or concerning the evolution of size to claim wide applicability or primacy, it must apply as much to insects as to any other group of organisms. To assess the validity for such claims requires knowledge of the hypotheses and models in question as well as the empirical information on the insects. Unlike groups such as birds and mammals, for which macroecological patterns of body size variation and their underlying mechanisms have been well documented (Gaston & Blackburn, 2000; Smith *et al.*, 2004; Millien *et al.*, 2006), in insects several broader scale patterns and their likely underlying mechanisms remain

poorly synthesized. Here, we adopt a largely univariate macroecological perspective in critically reviewing a variety of empirical patterns in insect size variation, their likely mechanisms, and their downstream consequences. The univariate perspective most commonly concerns the form of and mechanisms underlying frequency distributions (Morse, Stork & Lawton, 1988; Hanski & Cambefort, 1991; Blackburn & Gaston, 1994*b*; Gaston & Blackburn, 2000), the ways in which these distributions (or their central tendencies) vary over space (e.g. Ashton, Tracy & De Queiroz, 2000; Millien *et al.*, 2006; Greve *et al.*, 2008) and time (e.g. Jablonski, 1997; Kingsolver & Pfennig, 2004), and the extent to which variation shows a phylogenetic signal (e.g. Smith *et al.*, 2004; Diniz-Filho *et al.*, 2007).

As is common in macroecology, we accept that the explanations for many patterns lie at lower levels in the biological hierarchy, whilst the consequences thereof may be most visible at higher levels (Gaston & Blackburn, 2000, see also Eldredge, 1986). Thus, physiological regulation of growth and development, in the context of life history, must necessarily play critical roles in setting final size, as well as allometric variation (Shingleton *et al.*, 2007). Without some comprehension of the biochemical and physiological basis of size determination in insects, and without considering the life-history consequences of size variation, many large-scale patterns of body size variation cannot readily be comprehended. Therefore, we begin with a brief overview of the biochemical and physiological bases of size determination, and draw on insights from life-history theory wherever appropriate. However, these topics are largely not the subject of the present review, and are well-represented in a large and growing literature (see e.g. reviews by Sehna, 1985; Nijhout, 1994, 2003; Oldham *et al.*, 2000; Roff, 2001, 2002; Davidowitz, D'Amico & Nijhout, 2003; Emlen & Allen, 2004; Dubrovsky, 2005; Gäde & Hoffmann, 2005; Edgar, 2006; Emlen, Lavine & Ewen-Campen, 2007; Mirth & Riddiford, 2007; Angilletta, 2009).

II. THE PHYSIOLOGY OF ADULT SIZE DETERMINATION

Although some, especially earlier, research concerned the physiology of adult size determination in non-holometabolous insects (see reviews in Nijhout, 1994, 2003), much recent work has focused on holometabolous species, specifically *Drosophila melanogaster* (Diptera) and *Manduca sexta* (Lepidoptera, Sphingidae). Different aspects of the determination of final adult size have been considered in these two species. In some cases it is clear that the mechanisms are similar, but in others this has not yet been verified. For example, the sequence of endocrine events leading up to critical weight are much better defined in *Manduca sexta* and other Lepidoptera than they are in *Drosophila melanogaster* (Mirth & Riddiford, 2007). Moreover, the extent to which the physiological control mechanisms of size, operating at both the local cellular and higher levels, can be generalised to

other insect species is not yet fully established (Nijhout, 2003; Parker & Johnston, 2006), but presumably they generalize in their most significant aspects.

(1) The developmental sequence of events

Because of much recent work on *Manduca sexta* that concerns both physiological and evolutionary aspects of body size variation (Nijhout, 1975; D'Amico, Davidowitz & Nijhout, 2001; Davidowitz *et al.*, 2003; Davidowitz, D'Amico & Nijhout, 2004; Davidowitz, Roff & Nijhout, 2005; Davidowitz & Nijhout, 2004; Nijhout *et al.*, 2006; Kingsolver, 2007), in the context of this review it is most useful to focus on events during the growth and development of this species. *Manduca sexta* typically has five larval instars (though see Kingsolver, 2007), and size within each is constrained by the sclerotized head capsule and by the soft integument's epicuticle. The initial mass of each instar is a multiple (usually constant) of that of the former instar, more generally known as Dyar's constant or rule. The size of the first instar is determined by egg size. In other species, egg size varies among populations, as it does among species. It is also phenotypically plastic, being sensitive to day length, temperature, nutrition and conditions experienced by the adult and also by the juvenile stage of the egg-laying adult, and it also responds to selection (Azevedo, French & Partridge, 1996; Ernstring & Isaaks, 1997, 2000; Blanckenhorn, 2000*a*; García-Barros, 2000; Fischer, Zwaan & Brakefield, 2002; Fischer *et al.*, 2003; Fischer, Bauerfeind & Fiedler, 2006; Stillwell & Fox, 2005; Fox & Czesak, 2006; Homeny & Juliano, 2007; Steigenga & Fischer, 2007). The growth ratio at each moult is determined by both cell size and number. Moulting is triggered by a well-known set of hormonal events including increases in prothoracicotropic hormone (PTTH) and ecdysteroids in the presence of juvenile hormone (JH).

In the last larval instar of *Manduca sexta* the typical sequence of events changes (Fig. 1). JH inhibits the secretion of PTTH and ecdysteroids during the early portion of the instar. Thereafter, JH secretion by the corpora allata ceases and the levels of juvenile hormone esterase (JHE), which breaks down JH, increase. When JH disappears, PTTH and ecdysteroid secretion are disinhibited. However, PTTH is only secreted during a photoperiodic gate that is controlled by a photoperiodic clock (this is not the case in *Drosophila melanogaster*—see Edgar, 2006). If this 8 h time window, which recurs daily, is closed, PTTH secretion does not occur and up to 16 h may pass before PTTH is secreted. Once this happens, PTTH stimulates ecdysteroid secretion, which then causes the larva to stop feeding, clear its gut of all content, and to wander in search of a suitable pupation site. Because pupae do not feed, the final mass of the last larval instar usually determines adult size. In many insect species adult feeding may lead to additional mass gain even though adult linear dimensions are fixed and, in a few others, circumstances during the pupal stage may affect adult mass (Fischer & Fiedler, 2002).

The larval mass at which JH secretion ceases is of considerable biological significance, and is termed the critical

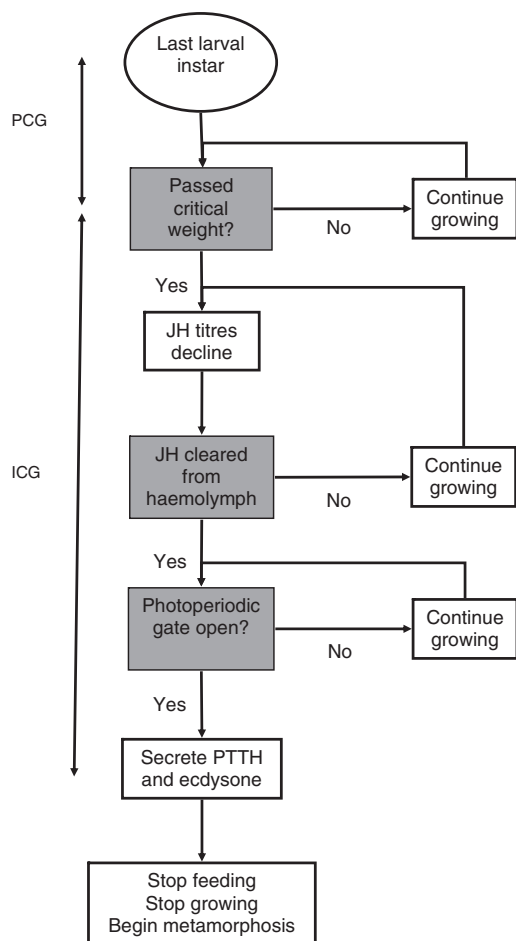


Fig. 1. The mechanisms controlling size in the final instar larvae of the tobacco hornworm, *Manduca sexta* (Lepidoptera, Sphingidae). The physiological points determining the timing of the cessation of growth are indicated by the shaded boxes. The extent of growth between these points determines final size. PCG = growth prior to critical weight, ICG = interval to cessation of growth, JH = juvenile hormone, PTTH = prothoracicotropic hormone. Redrawn from Nijhout *et al.* (2006).

weight (Nijhout *et al.*, 2006). This is not to be confused with the minimal viable weight, that below which individuals do not survive to pupation (Nijhout, 1975; Mirth & Riddiford, 2007). Once JH secretion ceases, the larva is irrevocably committed to a sequence of events that are independent of further growth or nutrition. The interval between attainment of critical weight and the secretion of PTTH (meaning full clearance of JH) is also of considerable significance in the context of adult size, and is known as the interval to the cessation of growth (ICG) (Davidowitz *et al.*, 2004). However, because the mechanisms linking critical size to increases in ecdysteroids have not been as well elucidated in other species, it has been suggested that the interval be more generally known as the terminal growth period (TGP) (Shingleton *et al.*, 2007). This usage may also facilitate models of static allometry that include investigations of the growth and development of the imaginal discs, which may differ

from overall size in the length of their terminal growth period (Shingleton, Mirth & Bates, 2008).

(2) Determinants of size variation

Adult size variation can clearly be determined by variation in the number of larval instars, the growth rate and duration of each (affecting the size increment at each moult), and growth rate and the timing of events during the last larval instar. In many species larval instar number is fixed, and indeed a general phyletic trend of reduced instar number and increased instar growth increment exists (Nijhout, 1994). However, growth rates and instar duration can be labile, as can instar number in some species (e.g. Shafiei, Moczek & Nijhout, 2001; Tammaru *et al.*, 2004; Esperk *et al.*, 2007; Kingsolver, 2007; Etile & Despland, 2008), although growth rate rarely reaches the physiological maximum (see Section III.1). In *Manduca sexta*, the final size of the last larval instar depends on five factors: initial size (which depends on egg size), growth rate, critical weight, the time required to clear JH, and the timing of the photoperiodic gate for PTTH secretion (Nijhout *et al.*, 2006). These factors all respond to selection (D'Amico *et al.*, 2001; Davidowitz *et al.*, 2005). The five factors can be simplified to three critical parameters that explain well most of the variation in size among different *M. sexta* strains (Nijhout *et al.*, 2006): critical weight (which is linearly related to growth increment), growth rate, and the ICG.

Among the many factors that induce phenotypic size variation, nutrition and temperature are most significant. Diet (quality and amount) affects growth rate, which in turn affects instar size. A decline in instar size on poor diets eventually leads to a lower critical weight. Diet quality also affects growth rate before and during the ICG, in the last larval instar, but importantly does not affect the duration of the ICG (Davidowitz *et al.*, 2004; Davidowitz & Nijhout, 2004). Temperature has a positive effect on growth rate, and also on the rate of biochemical reactions. This means that at higher temperatures not only is growth rate higher, but the rate at which JH is cleared by JHE increases, which in turn reduces the duration of the ICG (Davidowitz *et al.*, 2004, 2005). By contrast, critical weight is insensitive to temperature (Davidowitz & Nijhout, 2004). Total development time (larval duration) also declines exponentially with temperature. These differential responses to temperature and diet quality of the factors determining final size have considerable significance for understanding spatial and temporal variation in adult size, and we will return to them in Section VII.

Although much of the focus in *M. sexta* has been on the influence of diet quality and temperature on adult size variation, which can go a long way to explain patterns of size variation seen under laboratory (Atkinson, 1994) and field circumstances, day length may also have significant effects. Several studies have shown that egg size variation may be determined by day length, and that this interacts with other factors to influence egg size (e.g. Ernstring & Isaaks, 2000). Moreover, whether individuals find themselves at the start

or end of the growing season, as adjudicated by day length, has a substantial effect on the extent to which growth rate is altered, so influencing size and other factors such as static allometry (e.g. Gotthard, Nylin & Wiklund, 1999, 2000; Margraf, Gotthard & Rahier, 2003; Plaistow *et al.*, 2005).

(3) What controls adult size?

Size is likely to be under both local and more general proximate control. In *D. melanogaster* nutrition-dependent growth is controlled by insulin/insulin-like growth factor signalling (IIS), and has been the subject of much recent research (reviewed in Edgar, 2006; Mirth & Riddiford, 2007; see also Emlen *et al.*, 2007). Insulin-like peptides influence both growth rate and final adult size. The target of rapamycin (TOR) protein kinase is probably the most significant growth-regulatory target of insulin signalling, and again has been well studied. It responds to levels of ATP and amino acids, and is also sensitive to oxygen levels (as is growth rate and, in some species, adult size—see Harrison *et al.*, 2006). How the feedbacks operate between nutrition, IIS and TOR is a rapidly moving research field. The locus of nutrient sensing is especially significant, probably also involving the transcription factor Foxhead Box, class O (FOXO), the fat body, prothoracic gland, and imaginal discs. Juvenile hormone and ecdysteroids are likely also to play a role in the feedback. Indeed, Layalle, Arquier & Léopold (2008) have recently demonstrated in *D. melanogaster* that if the activity of TOR is reduced in the prothoracic gland, the ecdysone peak that signals the end of larval development no longer occurs. In consequence, the growth period is prolonged and size increases. However, much remains to be understood about how critical weight is assessed, how the relative significance of cell size and number is regulated, and how adult size is finally determined (Edgar, 2006; Mirth & Riddiford, 2007; Shingleton *et al.*, 2008).

III. ONTOGENETIC AND PHYLOGENETIC SIZE VARIATION

(1) Ontogenetic variation

Body mass and a characteristic linear dimension, such as head length or elytron length (e.g. Kaspari & Weiser, 1999), are often used interchangeably as measures of body size in insects. Although mass and linear dimensions may be strongly related ($\text{mass}^{0.33} \approx \text{length}$) (Hódar, 1996; Benke *et al.*, 1999; Mercer *et al.*, 2001; Powell & Franks, 2006), this need not always be so. Given constant linear dimensions, adult mass may vary depending on age, season, and the feeding and reproductive status of an individual. At times, such variation may lead to fundamental differences in the shape of body size frequency distributions assessed using mass and a linear dimension for the same population, even when measurement has been temporally and spatially constrained. For example, in both the apionid weevil *Setapion provinciale* and

the wasp *Trichilogaster acaciaelongifoliae* (Pteromalidae) the body size frequency distributions differ substantially depending on whether length or mass is measured (Fig. 2).

Likewise, during ontogenetic growth, mass increases, whilst many linear dimensions often remain fixed as a consequence of cuticular sclerotization (Sehnal, 1985; Strobbe & Stoks, 2004; Nijhout *et al.*, 2006). Such differential size increases may also be responsible for variation in the form and central tendency of size frequency distributions based on mass *versus* linear dimensions. They also have a variety of physiological consequences. The need for moulting is obviously one of the most significant given the physiological sequence of events required and the elevated risk of mortality. However, less fully appreciated is a probable reduction in the safety margin for gas exchange, which may, in turn, also account for the need to moult (Greenlee & Harrison, 2005): cuticle-lined tracheae and spiracles remain at a fixed size whilst tissue mass increases. However, the extent of this change in safety margin depends also on the capacity for tracheal ventilation of the species concerned, which might more than compensate for a reduced margin associated with fixed tracheal and spiracular sizes (Greenlee & Harrison, 2004; Harrison, Lafreniere & Greenlee, 2005). These interactions are important to consider when size variation associated with historical fluctuations in atmospheric oxygen concentration is being investigated.

During ontogeny, the increase in size from egg to adult can be more than two orders of magnitude. Typically, this variation has substantial implications for the resources used by growing individuals, often entailing fundamentally different approaches to acquisition at different life stages (e.g. Gaston *et al.*, 1991). Ontogenetic changes in insect body size also affect the kinds of predators that feed on different stages or instars. In anomalous emperor moth *Imbrasia belina* caterpillars the early instars are eaten by small predators such as insects and gleaning birds, the later instars by a variety of insectivorous birds, and the last instar by reptiles, mammalian carnivores and humans (Gaston, Chown & Styles, 1997).

Variation in size amongst individuals of a given species at a given life stage can also be marked. In many social species, size variation is determined by caste membership. Even within castes, variation may be substantial. More extreme cases include leaf-cutter ants *Atta* spp. and army ants *Eciton hamatum*, where workers range from 0.0025 to 0.0206 g, and from 0.0017 to 0.027 g, respectively (Feener, Lighton & Bartholomew, 1988; Rocas & Lighton, 1995). Some of this variation is a consequence of food availability to juvenile stages (Emlen & Nijhout, 2000; Peat *et al.*, 2005).

Within a season, final adult size, and therefore the form of size-frequency distributions, is strongly dependent on interactions among time constraints, resource allocation to growth and/or reproduction, mortality, physiological costs (such as those associated with oxidative damage), ageing, and food quality (Nylin & Gotthard, 1998; Blanckenhorn, 1999; Cichoń & Kozłowski, 2000; Scriber, 2002; De Block & Stoks, 2008). In several species, despite initially poor resource conditions, elevation of growth rate occurs such

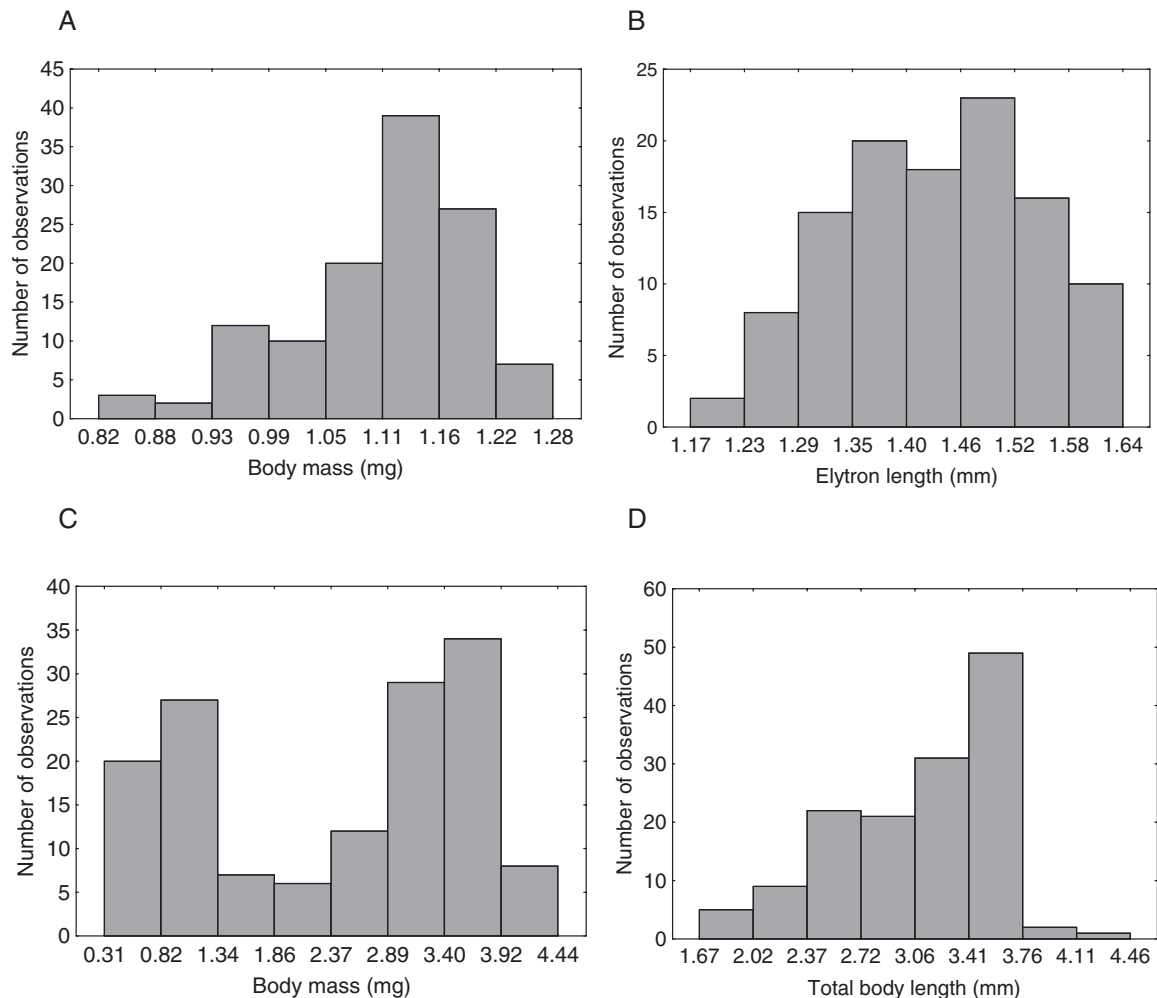


Fig. 2. Body size frequency distributions for: (A, B) *Setapion provinciale* (Coleoptera, Apionidae) and (C, D) *Trichilogaster acaciaelongifoliae* (Hymenoptera, Pteromalidae) based on both body mass and linear dimensions. Note the difference in the form of the distributions. In panel C, the bimodality arises from the much lighter males and heavier females. Redrawn from Gouws (2007).

that the final body sizes of adults show much less variation than might otherwise have been the case (Nylin & Gotthard, 1998; Gotthard, 2004; Gotthard *et al.*, 1999, 2000; Margraf *et al.*, 2003; Strobbe & Stoks, 2004). Nonetheless, additional growing time does not always serve to increase size (Kause *et al.*, 2001; Berner, Blanckenhorn & Körner, 2005), and may also be sex dependent (Plaistow *et al.*, 2005; Esperk *et al.*, 2007; Etile & Despland, 2008). Resource quality and the presence of predators often play a significant role in determining final size, whether this size is attainable given seasonal time constraints, and what the costs thereof might be (Scriber & Lederhouse, 1992; Scriber, 2002; Berner *et al.*, 2005; Stoks *et al.*, 2006b; De Block, McPeck & Stoks, 2008; Röder, Rahier & Naisbit, 2008). Although increased growth rates might be able to compensate for linear dimensions, mass may nonetheless be reduced under time constraints (Nylin & Gotthard, 1998; Strobbe & Stoks, 2004). At least in income breeders, adults can gain mass by feeding, reducing the significance of low emergence mass.

For capital breeders, emergence mass is set by resource allocation in the immature stages. This difference between income and capital breeders affects the relationship between final size and size variation because in the latter a linear increase in fecundity with size is likely, whilst in the former behavioural performance constrains maximum size (Teder *et al.*, 2008). These differences have implications for the overhead threshold model for the relationship between age and size at maturity (see Day & Rowe 2002).

Compensatory (or catch-up) growth is associated with intrinsic physiological costs, such as developmental errors and oxidative damage, and extrinsic costs such as increased exposure to predators and/or parasitoids (Nylin, Gotthard & Wiklund, 1996; Arendt, 1997; Mangel & Munch, 2005; Stoks, De Block & McPeck, 2006a; De Block & Stoks, 2008). Hence, growth rates are often less than the physiological maximum. A recent life-history approach, incorporating the mortality consequences of body size and physiological damage has demonstrated the circumstances under which

compensatory growth will tend to arise (Mangel & Munch, 2005). In the absence of selection on components of growth and damage, it is likely to be rare. The relative likelihood of different forms of compensation is long-term > short-term \approx short-term + long-term > overshooting.

Size variation is not only a consequence of interactions between the genotype and proximate, environmental effects, but also has a strong phylogenetic component (e.g. Read & Harvey, 1989; Smith *et al.*, 2004). Somewhat surprisingly, this phylogenetic component has not been extensively explored (but see e.g. Brändle, Stadler & Brandl, 2000).

(2) Phylogenetic variation

Across the insects as a whole, the smallest species is apparently the mymarid egg-parasitic wasp *Dicopomorpha echmepterygis*, with an adult male body length of approximately 139 μm , and females 40% larger (Gahlhoff, 1998). However, it is likely that there are yet smaller species still to be found, given that most species of insects remain undescribed, the typically negative relationship between mass and date of description in insects (Blackburn & Gaston, 1994a; Gaston & Blackburn, 1994), and that this species was not described until 1997. Five beetle species are thought to be the largest insect species: the cerambycid *Titanus giganteus* (167 mm), the elephant beetles *Megasoma elephas* (137 mm) and *Megasoma actaeon* (135 mm), and the goliath beetles *Goliathus goliatus* and *G. regius* (110 mm) (Williams, 2001). This gives a range of body lengths for adult insects of three orders of magnitude. Across the beetles alone, species body lengths may vary to a similar extent, with the feather-winged beetles (Ptiliidae) being as small as 250 μm (Gahlhoff, 1998).

The reliance on length, rather than mass, as a measure of insect body size reflects a general practical constraint. Collection and storage methods often limit opportunities for the direct determination of fresh body masses, and most studies of macroecological patterns in insect body size have thus employed measures of characteristic linear dimensions. Nonetheless, direct body mass measurements for insects are common, and there is substantial interspecific mass variation across the group. It is at least six orders of magnitude, ranging from the thrips *Apterothrips apteris* on Marion Island at 0.00004 g (Mercer *et al.*, 2001) to the scarab beetle *Circellium bacchus*, which can weigh in excess of 10 g (Chown *et al.*, 1995). However, globally the range is probably seven orders of magnitude given the small size of some mymarid wasps. This range is greater than the approximately four orders of magnitude spanned by birds (Blackburn & Gaston, 1994b), similar to that of mammals (Smith *et al.*, 2004), but smaller than that of fish, which range from likely milligram masses (Kottelat *et al.*, 2006) to the basking and whale sharks which weigh several thousands of kilograms, so spanning eight or more orders of magnitude.

Along with a number of life-history traits, the body size of animals tends to show a strong signal associated with phylogeny and/or taxonomic grouping above the species level (i.e. among genera, families and orders) (Gaston & Blackburn, 2000). This also appears to be true of the

insects, although empirical studies are limited. Studies of individual orders in particular regions have found that substantial variation is partitioned above the species level (Brändle *et al.*, 2000). Using body masses from an updated database constructed to examine variance partitioning in physiological traits (much of which occurs at family and genus levels; Chown, Addo-Bediako & Gaston, 2002), and including only those taxa for which data were available for two or more subtaxa, taxonomic order accounts for 3% of the variation in body size, family for 38%, genus for 39%, and the remaining variation is partitioned at the species level. However, these data represent only 212 species and five orders. If the genus level is ignored and the same constraint is set, 590 species in 10 orders can be examined. In this case, order accounts for 15% of the variation, family for 23%, and the remaining 62% is partitioned at the genus and species level. Overall, this partitioning makes intuitive sense, given that within orders such as the Orthoptera, Coleoptera, Hemiptera, Hymenoptera and Lepidoptera, species take on a wide range of sizes (Fig. 3), whilst within a given family size ranges are smaller.

The benefits of large body size have been widely explored, and are known to include greater fecundity in females, access to mates in males and resource sequestration advantages (Honík, 1993; Lighton, Quinlan & Feener, 1994; Parker & Simmons, 1994; Blanckenhorn, 2000b; Rivero & West, 2002). These benefits can be affected by patterns of resource acquisition and allocation (Kemp & Alcock, 2003), and by differences among the sexes in the benefits of large size, their responses to selection, and correlations among these responses (e.g. Molumby, 1997; Alcock, Simmons & Beveridge, 2006; Fox & Czesak, 2006). For example, in the bruchid *Stator limbatus* fecundity selection is the main source of selection on female and male size on a host on which larval mortality is low. By contrast, on a poor host, selection *via* a female size, egg size, fitness path offsets the reduction in fecundity selection of female size, but not on the size of males (Fox & Czesak, 2006).

The benefits of small size have not been examined so thoroughly. These may include reduced viability costs of growth and development, enhanced agility and reduced detectability, lowered maintenance energy costs, reduced heat stress, reduced costs of reproduction, and increased scramble competitive ability (Blanckenhorn, 2000b, 2005; Moya-Laraño, El-Sayyid & Fox, 2007). The life-history costs of large size may be difficult to detect because they only become evident under stressful conditions, large individuals may die early, or a platykurtic function may link size to fitness (Reim, Teuschl & Blanckenhorn, 2006; Teuschl, Reim & Blanckenhorn, 2007). Reim *et al.* (2006) examined two contrasting metabolic hypotheses concerning the relative costs of a given body size. Large individuals could either be advantaged because they have relatively high energy use efficiency owing to the negative scaling of mass-specific metabolic rate (see also Blanckenhorn, Fanti & Reim, 2007b), or disadvantaged because they have higher absolute energy requirements (Blanckenhorn, 2005). Using

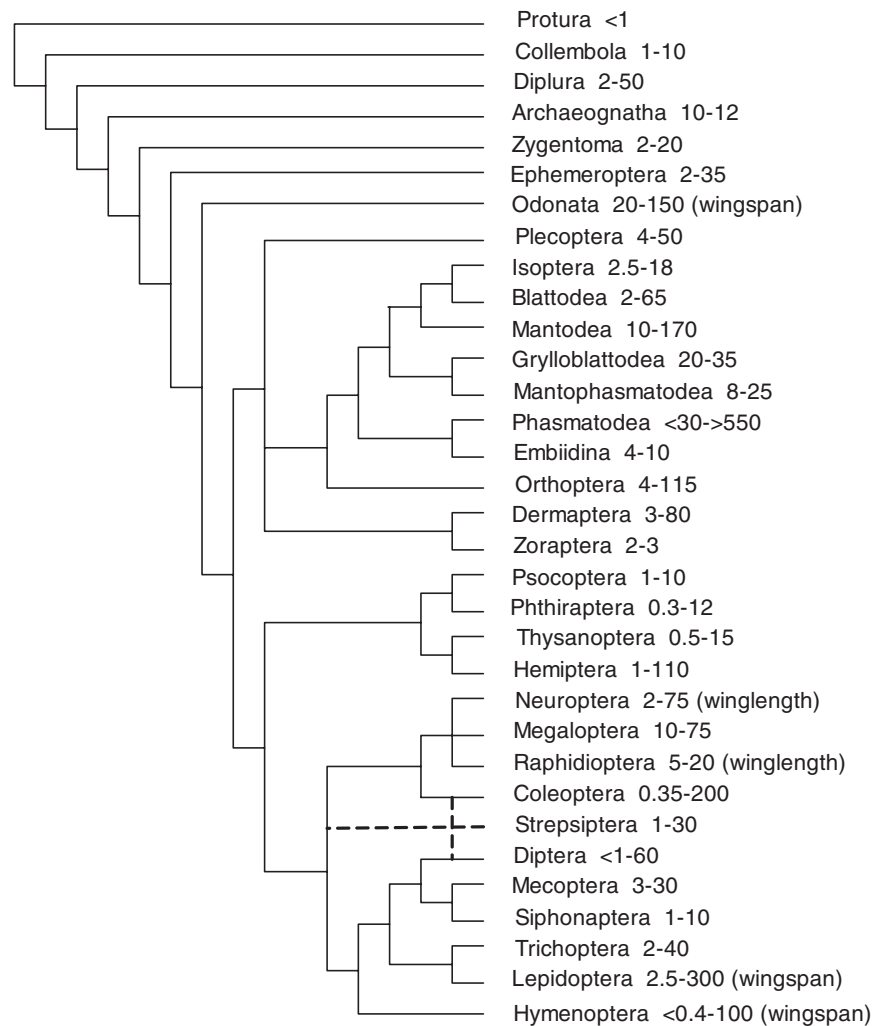


Fig. 3. Estimates of the minimum and maximum adult body lengths (mm) of species in different insect orders and close relatives, superimposed on a cladogram of their postulated relationships based on combined morphological and nucleotide sequence data. Broken lines indicate uncertain relationships. Cladogram from Gullan & Cranston (2005). Body size data from a variety of sources (available from the authors on request).

yellow dung flies *Scathophaga stercoraria* as model organisms the relative efficiency hypothesis could not be rejected (Reim *et al.*, 2006). In a further study of the same species, Teuschl *et al.* (2007) showed that large flies suffered greatest mortality under extreme food limitation, and were most susceptible to winter frost because of their long development times.

IV. BODY SIZE DISTRIBUTIONS

(1) Intraspecific

Despite a large literature on the factors influencing final adult size in insects, the body size frequency distributions of the individuals of particular species have been poorly documented. Moreover, knowledge thereof has typically resulted as a by-product of studies with other goals in mind.

Thus, many of the factors confounding the interpretation of body size frequency distributions, such as sample size and the choice of class size (or the width of classes used for constructing the frequency distribution) (Loder, Blackburn & Gaston, 1997) have not been considered in these studies. A range of shapes nonetheless characterise these distributions. In *Centris pallida* bees, intraspecific variation in head width is positively skewed (Alcock, 1984). In the longicorn *Phoracantha semipunctata*, elytron length does not deviate significantly from a normal distribution (Hanks, Paine & Millar, 2005), and this seems also to be the case in two coccinellid species (Evans, 2000), and in *Drosophila melanogaster* (David *et al.*, 1997). In adult *Anopheles* mosquitoes, wing length frequency distributions are significantly negatively skewed (Lounibos, 1994). Frequency distributions of masses seem to be equally rare. In six species of *Bombus*, size frequency distributions appear positively skewed (Peat *et al.*, 2005). Similarly, the size

distributions of adult leaf-cutter and army ants are distinctly non-normal, though this reflects the range of castes within each of the species (Feener *et al.*, 1988).

The most comprehensive single analysis yet undertaken of intraspecific body size frequency distributions in insects included 16 species, used both mass and a characteristic linear dimension as measures of size, and was careful to maintain sample sizes in the region of 100 individuals and to give appropriate consideration to size class choice (Gouws, 2007) (Fig. 2). For mass, nearly half of the distributions were significantly positively skewed, although log-transformation removed the skew in many cases. The remainder of the distributions showed little skew and were approximately normal. In the case of length, only two species showed a significant positive skew in their size frequency distributions. In the remainder, skew was either negative (two species) or not significant.

(a) Sexual size dimorphism

Although intraspecific body size frequency distributions often do not reveal sexual size dimorphism (SSD), males typically are smaller than females in insects (Fairbairn, 1997; Blanckenhorn *et al.*, 2007a). The opposite pattern is relatively uncommon (Teder & Tammaru, 2005), but is known from species such as the yellow dung fly (Kraushaar & Blanckenhorn, 2002) and the seed-feeding beetle *Stator limbatus* (Chrysomelidae: Bruchinae) (Stillwell & Fox, 2005). Moreover, in a range of species there is substantial male size polymorphism (in polymorphic ants and some other social Hymenoptera it is the females that are variable; Emlen & Nijhout, 2000). Intraspecific variation in SSD may well be a consequence of adaptive canalization of reproductive traits (Fairbairn, 2005).

Among species, it is commonly found that sexual size dimorphism increases with size when males are the larger sex, but declines with size when females are larger; this has been formalized as Rensch's rule (Abouhief & Fairbairn, 1997; Fairbairn, 1997; Blanckenhorn, 2000b). At the intraspecific level, this rule has been found in some species (Fairbairn, 2005). However, at this level, among-population SSD typically does not conform to the rule (Blanckenhorn *et al.*, 2006), and environmental conditions affect the degree rather than direction of SSD, often as a consequence of sex-related differences in growth and instar number (Teder & Tammaru, 2005; see also Esperk *et al.*, 2007; Etile & Despland, 2008). Where Rensch's rule is found, it seems likely that greater plasticity in males than in females, rather than sexual selection, might account for variation in sexual size dimorphism among populations (Fairbairn, 2005).

Sex-related differences in plasticity may also be the mechanism underlying a geographic version of Rensch's rule, whereby latitudinal clines in males are steeper than those in females (Blanckenhorn *et al.*, 2006). This link between clinal size variation (often termed Bergmann's rule—see below) and differential size variability among the sexes has not been well explored and the reasons for it remain obscure. In addition to variation in phenotypic plasticity, the link may

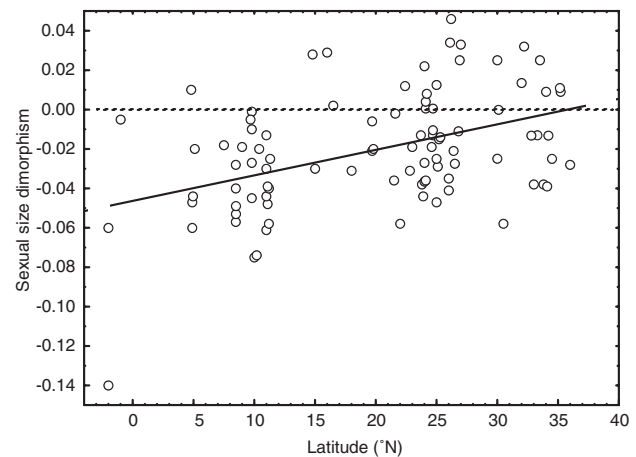


Fig. 4. Latitudinal variation in sexual size dimorphism of adults of the bruchid beetle *Stator limbatus*. Size units are arbitrary, above the dotted line females are larger, below it males are larger. Redrawn from Stillwell *et al.* (2007).

also be a consequence of stronger sex-specific selection on size associated with season length than selection as a consequence of temperature variation (Blanckenhorn *et al.*, 2006). The only study to investigate both latitudinal size variation and SSD in detail concerns the bruchid *Stator limbatus* in South, Central and North America (Stillwell, Morse & Fox, 2007). Adults of this species increase in size with latitude, and the slope of the relationship is steeper for females than it is for males. In consequence, SSD declines with increasing latitude (Fig. 4). The increase in size with latitude is correlated with increasing seed size, increasing seasonality, and declining moisture availability, suggesting that enhanced resistance to dry conditions and resource shortages, as well as resource availability are responsible for the cline. No correlation between size and several temperature variables was found, suggesting that the resistance hypothesis for size variation (i.e. better resistance to desiccation and/or resource shortages in larger individuals, see Cushman, Lawton & Manly, 1993; Chown & Gaston, 1999) is most significant in this species. Variation in SSD and latitude remained after the only significant environmental correlate of SSD was corrected for, suggesting either that varying sexual selection on males, or some other latitudinally varying difference in selection on males and females resulted in the latitudinal variation in SSD (Stillwell *et al.*, 2007). Further work is required to understand the interaction between latitudinal size variation and size variation among the sexes, and particularly how it varies among species that show increases or declines in size with latitude.

(b) Scaling

Acknowledging that there is substantial feedback between body size, physiological traits and life history variables (Blanckenhorn, 2000b; Emlen & Allen, 2004; Kozłowski *et al.*, 2004; Mirth & Riddiford, 2007; Shingleton *et al.*, 2007), the influence of intraspecific body size variation is pervasive.

Body size correlates with mortality from abiotic factors such as starvation, desiccation and low temperature (Lighton *et al.*, 1994; Arnett & Gotelli, 2003; Lehmann *et al.*, 2006; Colinet, Vernon & Hance, 2007), predation intensity (Nylin & Gotthard, 1998), predator guild composition (Gaston *et al.*, 1997), food particle size (Holter & Scholtz, 2005), fecundity (Honik, 1993; Taylor, Anderson & Peckarsky, 1998), mating and reproductive success (Stone, Loder & Blackburn, 1995; Taylor *et al.*, 1998), activity/foraging time (Stone, 1994; Cerdá & Retana, 2000), the outcome of intraspecific competition (Heinrich & Bartholomew, 1979), flight ability (Dudley, 2000a), and various aspects of morphology (e.g. Feener *et al.*, 1988; Green, 1999; Shingleton *et al.*, 2008; Eberhard, 2009). Where significant scaling relationships are documented they often show considerable variation, such that coefficients of determination are low, and are statistically weak owing to the small size range in many species, though morphological traits are typically an exception in this regard.

(2) Interspecific

Although data for insects have been employed in several classical studies of species-body size distributions (e.g. Hutchinson & MacArthur, 1959; May, 1978), understanding of such distributions for insects has been severely constrained by biased sampling; larger species are much better represented than smaller ones. Temporal trends in the sizes of those species being formally taxonomically described were first documented quantitatively for insects (Gaston, 1991a; Gaston & Blackburn, 1994; but see Cabrero-Sañudo & Lobo, 2003). In several groups, as progressively more species came to be described, the mean body sizes of those that were known decreased through time and the skewness of the observed species-body size distributions increased (Blackburn & Gaston, 1994a).

Nonetheless, reasonably well-documented species-body size distributions for major insect groups do not appear to differ markedly from those for other higher taxa. They are strongly right-skewed on untransformed axes, and typically approximately symmetric or still right-skewed when body size is logarithmically transformed, with departures from symmetry tending to become statistically more significant with increased numbers of species (e.g. Janzen, 1973; May, 1978; Morse *et al.*, 1988; Basset & Kitching, 1991; Hanski & Cambefort, 1991; Dixon, Kindlmann & Jarošík, 1995; Chown & Steenkamp, 1996; Basset, 1997; Novotný & Kindlmann, 1996; Novotný & Wilson, 1997; Brändle *et al.*, 2000; Hodkinson & Casson, 2000; Krüger & McGavin, 2000; Dixon & Hemptinne, 2001; Espadaler & Gómez, 2002; Ulrich, 2004; Agosta & Janzen, 2005; Finlay *et al.*, 2006). The vast majority of insect species are small, but the smallest species are not the most frequent. The greater numbers of small-bodied species do not, however, translate into simple negative relationships in insects between the species richness and body size of taxonomic groups (e.g. Katourakis *et al.*, 2001; Orme, Isaac & Purvis, 2002; Finlay *et al.*, 2006). Moreover, at a variety of scales, the species-body size distributions are similar, with peaks appearing at

four distinct body sizes, representing, in order of size, the Scolytidae and Chironomidae; Curculionidae, Staphylinidae and Chrysomelidae; Noctuidae; and Nymphalidae (Finlay *et al.*, 2006). The empirical data for the insects collected by Finlay *et al.* (2006) also fit the suggestion that small species are more widely dispersed, but do not suggest that the same applies to the largest species.

Mechanistic models, not always mutually exclusive, for the shape of species-body size distributions in general are based on (i) the distributions of optimal sizes resulting from an interspecific trade-off between production and mortality (Kozłowski & Weiner, 1997; Kindlmann, Dixon & Dostalkova, 1999); (ii) patterns of speciation and extinction rates (Dial & Marzluff, 1988; Maurer, Brown & Rusler, 1992); (iii) the world being larger, or the environment or resources being more finely sub-divided, for smaller species (Hutchinson & MacArthur, 1959; May, 1978; Shorrocks *et al.*, 1991); and (iv) patterns of dispersal (Chown, 1997; Etienne & Olff, 2004) (for further, more general discussion, see E.P. White *et al.*, 2007). For insects, the importance of the size structure of resources has attracted the most explicit attention for herbivores (influenced by plant size structure; Dixon *et al.*, 1995; Novotný & Wilson, 1997), predators (influenced by prey size structure; Dixon & Hemptinne, 2001) and parasites (influenced by host size; Johnson, Bush & Clayton, 2005, see also Tompkins & Clayton, 1999). In the last case, this relationship is known as Harrison's rule, but as with many such 'rules' (see discussion in Gaston, Blackburn & Spicer, 1998; Millien *et al.*, 2006; Gaston *et al.*, 2008) it is not always supported by empirical data (Johnson *et al.*, 2005). Nonetheless, it is difficult to escape the notion that, given the close relations between the sizes of many insects and those of the hosts and prey that they use, the size structure of the environment must have a profound influence on insect species-body size distributions (Morse *et al.*, 1985). This is not at odds with species-body size distributions being shaped by intraspecific trade-offs between production and mortality, because resources can be considered as affecting the production function (itself the difference between assimilation and respiration; Kozłowski & Gawelczyk, 2002).

Both at local and regional scales, the influence on species-body size distributions of transient or tourist species—those species present in an assemblage whose individuals obtain little if any of their nutrition directly or indirectly from resource bases that are present—has been a recurrent concern (e.g. Gaston *et al.*, 1993; Chown & Steenkamp, 1996). Likewise, at local scales, in insect assemblages the densities of species have typically been found at best to be weakly negatively related, and perhaps more frequently unrelated, to their body sizes (e.g. Morse *et al.*, 1988; Gaston *et al.*, 1993; Chown & Steenkamp, 1996; Krüger & McGavin, 2000). Evidence that this pattern generalises to greater spatial extents, let alone global scales, is scant (local studies alone may involve the identification of tens of thousands of individuals). However, those studies that have been conducted over greater extents provide little support for the notion that

there is any simple relationship between abundance and body size in insects (e.g. Gaston & Lawton, 1988; Gutiérrez & Menéndez, 1997).

The implications of interspecific size variation for physiological and life-history traits have been explored in a wide variety of studies, with the number and scope thereof ever increasing. Examples include various aspects of biochemistry (Darveau *et al.*, 2005a, b), stoichiometry (Fagan *et al.*, 2002; Woods *et al.*, 2004), metabolic rate (Chown *et al.*, 2007), gas exchange characteristics (Lighton, 1991; C.R. White *et al.*, 2007), wing loading and stroke frequency (Casey, May & Morgan, 1985; Darveau *et al.*, 2005b), post-flight cooling (Bartholomew & Epting, 1975), aspects of water balance (Lehmann, Dickinson & Staunton, 2000; Addo-Bediako, Chown & Gaston, 2001), population abundance (e.g. Gaston *et al.*, 1993), and rates of population increase (Gaston, 1988). In some cases, such as interspecific size variation in metabolic rate, development rate, and mortality, considerable feedback is likely, such that body size is as much a function of these variables as they are of body size at the intraspecific level (Kozłowski & Gawelczyk, 2002), so determining optimum body size and eventually the interspecific relationship. How these interactions might play out in insects is only beginning to be explored (Chown & Gaston, 1999; Blanckenhorn & Demont, 2004; Chown *et al.*, 2007). Much less seems to be known about other facets of body size scaling (or the lack thereof) at the interspecific level, such as that of polyunsaturated fatty acid content or membrane composition, tracheolar cross-sectional area, lipid content, critical oxygen tension, cuticle thickness, dispersal ability, geographic range size, and genetic variation, though some work has commenced (e.g. Greenlee, Nebeker & Harrison, 1997; Kaiser *et al.*, 2007).

V. VARIATION IN SIZE THROUGH TIME

(1) Evolutionary trends

Molecular evidence suggests that the insects arose from a common ancestor at the Silurian-Ordovician boundary approximately 434–421 million years before present (Myr BP) (Gaunt & Miles, 2002; Grimaldi & Engel, 2005). The fossil record for early insects and closely related groups is, however, poor. The earliest unrefuted evidence of insects in the fossil record is an archaeognathan from the Middle Devonian, and winged insects first appear in the fossil record in the Upper Carboniferous (*c.* 325 Myr BP; Shear & Kukalová-Peck, 1990). Oxygen availability probably influenced the early diversification of arthropods, and the diversity of insects began to increase only following the end of a low oxygen period, known as Romer's Gap (see Ward *et al.*, 2006), during the early Carboniferous (>325 Myr BP). Diversification was disrupted by notable, large extinction events, but continued to increase through to the present (Labandeira & Sepkoski, 1993; Labandeira, Johnson & Wilf, 2002; Wilf *et al.*, 2006), with some periods showing important patterns, such as

significant increases in herbivory during periods of high CO₂ partial pressure (Currano *et al.*, 2008).

(a) Oxygen and gigantism

Gigantism was taxonomically widespread in the late Palaeozoic, including amongst the Protodonata (wingspans may have ranged up to 710 mm), Paleodictyoptera (wingspans of up to 560 mm), Ephemeroptera (wingspans of up to 450 mm), Diplura, and Thysanura (Shear & Kukalová-Peck, 1990; Dudley, 1998; Wootton & Kukalová-Peck, 2000). Amongst the dragonfly clade, wingspans varied by a 24-fold range, compared with a sevenfold range amongst extant species (Wootton & Kukalová-Peck, 2000). One vigorously championed mechanism for the occurrence of gigantism during this period (which also occurred in other invertebrate and lower vertebrate groups) was hyperoxia and hyperbaria in the Palaeozoic atmosphere, leading to a relaxation of constraints on tracheal diffusion and the power demands of flight musculature in winged species (Miller, 1966; Dudley, 1998, 2000a, b). Oxygen availability would also have been enhanced in the aquatic larval stages of many of the groups, though gigantism was apparently also common in terrestrial species. This oxygen pulse hypothesis is consistent with the subsequent loss of these forms with increasing hypoxia in the late Permian (Huey & Ward, 2005), and the evolution of large size in at least one group (the mayfly family Hexagenitidae) during a second oxygen peak in the Cretaceous (Dudley, 2000b).

Although compelling, this hypothesis has not been well explored empirically or theoretically from the perspective of the changes in tracheolar density and gas exchange mechanics that might offset alterations in ambient oxygen availability (Dudley, 2000a, 2000b; Frazier, Woods & Harrison, 2001; Greenlee & Harrison, 2004; see also Schmitz & Harrison, 2004; Harrison *et al.*, 2006; Klok & Harrison, 2009). Moreover, the evolution of large size and its subsequent decline might also involve interactions between oxygen availability, geographic range size and thermal tolerance. Reductions in geographic range size are thought to have been precipitated both by warming and by a decline in atmospheric oxygen levels (Huey & Ward, 2005), and typically larger species require larger geographic ranges to avoid extinction. Aquatic stages may also have been compromised more than their terrestrial counterparts owing to differential changes in metabolic demand and oxygen flux (Huey & Ward, 2005; Makarieva, Gorshkov & Li, 2005), although flight metabolism in modern insects has a much lower critical PO₂ than resting metabolism (Rascón & Harrison, 2005). Hypoxic stress may also have lowered thermal tolerance (Pörtner, 2001) so reducing range sizes, especially if upper and lower thermal limits are decoupled as they appear to be in insects (Chown, 2001). However, the evidence for oxygen limitation of thermal tolerance in insects remains equivocal (Chown & Terblanche, 2007). Perhaps the most promising work in this area suggests that limitations to size are set by steeper scaling of the cross-sectional area of the tracheae in the legs (mass^{1.02}) than of the cross-sectional

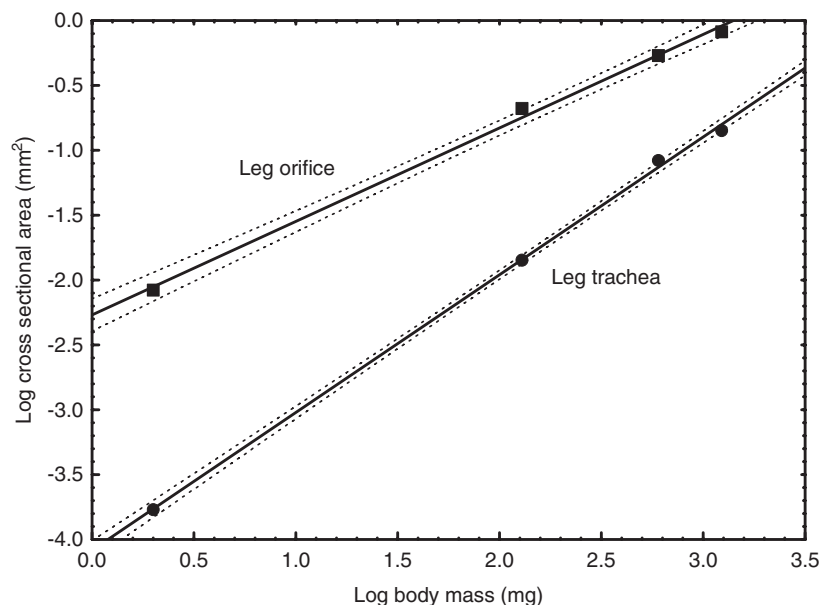


Fig. 5. Scaling of tracheal cross-sectional area (isometry— $\text{mass}^{1.02}$), and leg orifice (i.e. the opening from the body to the leg through which tracheae and haemolymph pass) cross-sectional area (shallow allometry— $\text{mass}^{0.77}$) in four species of tenebrionid beetles. The interaction of the two relationships could set the upper limit to size. Redrawn from Kaiser *et al.* (2007).

area of the leg opening to the main body cavity through which the tracheae and haemolymph must pass (the cross-sectional area of this opening (or orifice) scales as $\text{mass}^{0.77}$) (Kaiser *et al.*, 2007) (Fig. 5). These scaling differences mean that space available for tracheae in the legs may limit the size of an insect, and such limitations may well apply to other constrictions of the exoskeleton. Under experimental, hyperoxic conditions, insects reduce the dimensions of their tracheae, which suggests that during such conditions in the past, the constraints on large size may have been reduced substantially, so leading to gigantism (Kaiser *et al.*, 2007).

Alternative hypotheses include the evolution of large size as a defensive adaptation of Palaeozoic arthropods in response to predation by vertebrates, of which the majority at the time were insectivorous or predators on other vertebrates (Shear & Kukalová-Peck, 1990). Changes in size, particularly later reductions, might also have been mediated by changing mortality risks that must have been encountered by juvenile stages. In this context it is notable that the largest recent insects (extant or recently extinct) either typically spend the bulk of their lives as concealed feeders (e.g. beetle species in the Cerambycidae, Scarabaeidae, Dynastinae) or are restricted to oceanic islands where predation pressure may be lower (e.g. St Helena giant earwig *Labidura herculeana*, New Zealand giant weta *Deinacrida* spp.). In addition, the late Permian not only saw the loss of giant insects, but a mass extinction of insect diversity (Labandeira & Sepkoski, 1993). Assuming that before this decline most insect species were nonetheless small-bodied relative to the absolute giants, and that the largest bodied species were still comparatively uncommon, then even random losses of species with respect to body size would almost certainly have seen the loss of the

more giant forms. Which of these mechanisms is likely to have had the predominant role in promoting gigantism, and its subsequent disappearance, is difficult to determine, but the question deserves further exploration in the context of the factors determining final body size in insects.

(b) Cope's rule

A general empirical trend for selection acting on individual organisms predominantly to favour larger body size has been argued to translate, if unopposed, into a macroevolutionary trend toward increased size (Kingsolver & Pfennig, 2004). Such a pattern is known as Cope's rule. Clearly the existence of many large-bodied forms early in the evolution of the insects means that the rule has not been obeyed over the entire duration of the insects, either for the group as a whole, or for several major clades.

However, the picture may appear rather different if one focuses on the period post the Permian mass extinction. Endopterygote insects predominate in recent insect faunas, particularly those in the orders Coleoptera, Hymenoptera, Diptera and Lepidoptera (Gaston, 1991b). Although the ancestors of at least some of these groups were present in the Permian, they all underwent dramatic and continued diversification after the mass extinction event, and have continued to do so through to the present (Labandeira & Sepkoski, 1993; Gaunt & Miles, 2002). In all four orders it seems likely that the largest recent species are amongst, if not actually, the largest that have existed (Coleoptera: largest recent species detailed earlier; Hymenoptera: wasps in the genus *Pepsis* can reach a wingspan of 100 mm; Diptera: largest species is *Gauromydas heros* with a body length of about 60 mm; Lepidoptera: largest wingspan is that of the white

witch moth *Thysania agrippina* at 280 mm or more; Gauld & Bolton, 1988; Kons, 1998).

Within particular clades, phyletic size increase has been explored for only a single family, the carabids. Of the 34 groups examined, seven showed significantly positive correlations between body size and cladogram position (indicating phyletic size increase), two showed significantly negative relationships, and in the remainder there was no relationship between size and cladogram position (Liebherr, 1988). Although a macroevolutionary trend towards large size is thus uncommon in the family, it is not randomly distributed amongst taxa. Typically, phyletic size increase is associated with brachyptery, and with groups inhabiting stable environments, although the mechanisms responsible for this trend have not been fully explored.

(c) Evolutionary rates

Both the standing diversity and the history of the body size of insects plainly reveal how rapidly body size changes can evolve and how developmentally plastic they can be. This has also been demonstrated both indirectly and directly by a variety of laboratory selection experiments. In the former case, David *et al.* (1997) demonstrated that laboratory-reared *Drosophila melanogaster* show both a reduction in size and change in kurtosis of the size frequency distribution relative to their wild counterparts. In the latter, numerous experiments have shown that size changes can be effected rapidly within generations depending on external conditions such as food availability or oxygen tension (e.g. Emlen & Nijhout, 2000; Frazier *et al.*, 2001), and that selection can effect rapid size changes between generations (e.g. Gibbs, Chippindale & Rose, 1997).

In the field, rapid evolution of body size has been shown in *Drosophila subobscura* (Huey *et al.*, 2000). This species is native to the Old World, where it displays a positive cline in wing length with latitude. It was, however, introduced to North and South America, where it spread rapidly, evolving a cline in body size that largely converged on that observed in the Old World, although the way in which the variation in size was achieved is different. Thus, in North America, an increase in wing length with latitude has been achieved largely through changes in the relative length of the distal portion of vein IV, whereas in Europe lengthening is a consequence of a relative increase in length of the basal portion of this vein. Likewise, the threshold for horn development in the beetle *Onthophagus taurus* evolved rapidly, in opposite directions, in populations introduced to Western Australia and eastern North America from the Mediterranean region (Moczek & Nijhout, 2003).

(2) Ecological trends

(a) Intraspecific level

Seasonal variation in body size, in species where there is no period of diapause or quiescence, has been described *inter alia* for stoneflies (Haro, Edley & Wiley, 1994), blackflies (Colbo & Porter, 1979; Baba, 1992), *Drosophila* spp. (Tantawy,

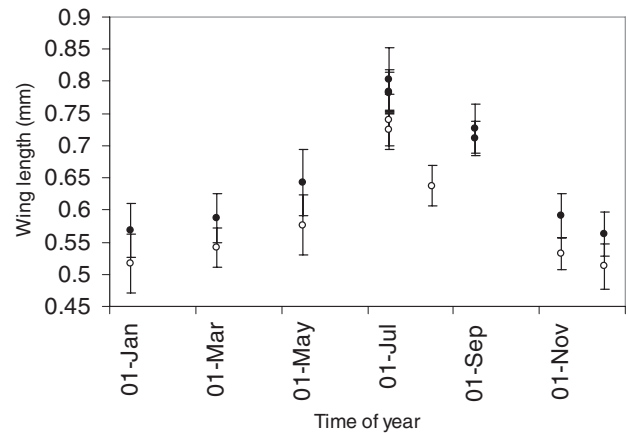


Fig. 6. Seasonal variation in means \pm S.E.M. wing length (mm) of female (filled symbols) and male (open symbols) *Simulium chutteri* (Diptera, Simuliidae) collected over the course of a single year along the Orange River in South Africa (data from Myburgh, 2001). July is the lowest temperature period of the year.

1964; Kari & Huey, 2000), mosquitoes (Yuval *et al.*, 1993), tsetse flies (Rogers & Randolph, 1991), beetles (Ernsting & Isaaks, 1997), a parasitoid wasp (Sequiera & Mackauer, 1993), a bee (Alcock, Simmons & Beveridge, 2005), and butterflies (Rodrigues & Moreira, 2004) (see Fig. 6). In the majority of these cases developmental temperature has the most significant influence on body size, such that size tends to be largest at the lowest temperatures. Kari & Huey (2000) suggested that in *D. subobscura* resource availability and/or stressful abiotic conditions probably also influence the seasonal pattern (see also Baba, 1992). This is in keeping with many investigations of resource competition and the effects of stress on insects (e.g. Hirschberger, 1999; Vessby, 2001; Warren *et al.*, 2006), and with mechanistic investigations of the response of insects to resource deprivation (e.g. Blanckenhorn, 1999; Mirth & Riddiford, 2007). Such developmental phenotypic plasticity is not uncommon in insects (for recent review and discussion of phenotypic plasticity see DeWitt & Scheiner, 2004; Ghalambor *et al.*, 2007; Angilletta, 2009).

Interannual variation in size has also been investigated in several species (Alcock, 1984; Evans, 2000; Smith *et al.*, 2000). Typically, this variation is not substantial (Fig. 7), and the likely causes have not been systematically explored. The ultimate mechanisms may well be similar to those responsible for spatial variation in size (see below), such as differences in selection intensity and direction (e.g. Kingsolver *et al.*, 2007). Clearly, size changes must be mediated by a variety of proximate physiological mechanisms which determine final adult size (see Section II.2 above). For example, in *Manduca sexta* an evolutionary increase in body size after 220 generations in the laboratory was a consequence of elevated growth rate, increased critical weight, and a prolonged ICG, or the interval between the critical weight

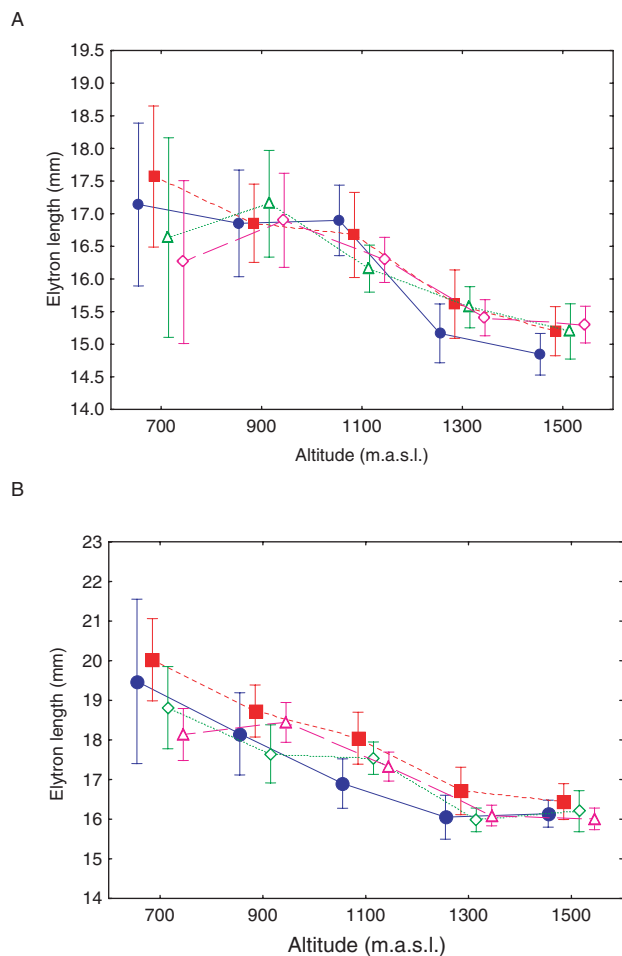


Fig. 7. Elytron length variation (mean \pm 95% C.I.) in (A) males and (B) females of the carabid beetle *Thermophilum decemguttatum* along the western slopes of the Cederberg in South Africa. Four years are shown (solid line and filled circles–October 2002; broken line and solid squares–October 2003; dashed line and open triangles–October 2004; broken line and open diamonds–October 2005). Redrawn from Gouws (2007).

and prothoracicotropic hormone secretion (D'Amico *et al.*, 2001).

(b) Interspecific and assemblage levels

The average body sizes of species in insect assemblages tend to decline with ecological succession, both at individual sites through time as succession progresses and across sites of different successional status (e.g. Steffan-Dewenter & Tschamtker, 1997; Siemann, Haarstad & Tilman, 1999; Braun, Jones & Perner, 2004). This is despite the species richness of different groups increasing, decreasing, and remaining approximately stable. A similar trend in body size tends to occur along gradients of increasing disturbance (e.g. Blake *et al.*, 1994; Grandchamp, Niemelä & Kotze, 2000; Braun *et al.*, 2004). Both patterns probably result from changes in the environmental constraints on body size, particularly those associated with vegetational complexity

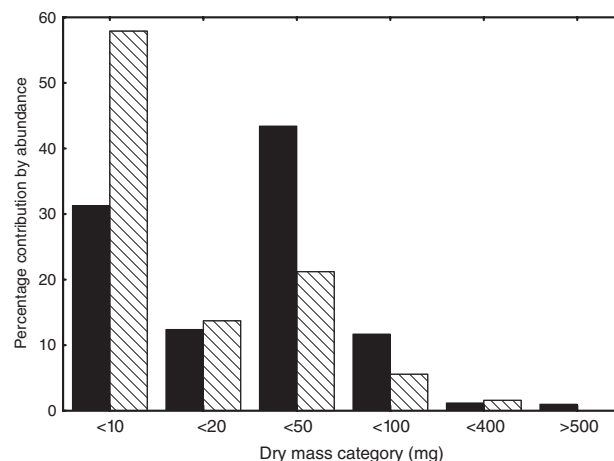


Fig. 8. Body size differences in the dung beetle assemblages occupying a dry savanna (filled bars) and a nearby area heavily invaded by *Prosopis glandulosa* (Fabaceae) (hatched bars) in the Northern Cape of South Africa. Note the predominance of small-bodied species in the invaded site. Data from Steenkamp & Chown (1996).

and stability. However, dramatic changes in vegetation structure, such as those associated with the transformation of landscapes by invasive alien species, can also have substantial impacts on assemblage body size distributions. Typically, large species are lost from the assemblage, probably as a consequence of flight impairment by dense vegetation and a change in resource availability (Steenkamp & Chown, 1996; Coetzee, van Rensburg & Robertson, 2007) (Fig. 8). By contrast, the relationship between habitat fragmentation effects and size is often weak or not significant. For example, Didham *et al.* (1998) found no variation in mean size among beetle species that responded differently to forest fragmentation in Brazil. Idiosyncratic responses of different-sized beetles to habitat alteration were found in the Atherton Tablelands of Australia (Grimbacher, Catterall & Kitching, 2008). In a forest fragmentation experiment, involving 80–100 yr old Eucalyptus regrowth forest, Davies, Margules & Lawrence (2000) similarly found no relationship between response to fragmentation and body size in ground-dwelling beetles. Among the reasons for the variation in responses are the likelihood of large size benefiting desiccation tolerant species in relatively dry, small forest fragments on the one hand, but small body size reducing extinction risk on the other (Grimbacher *et al.*, 2008). Nonetheless, it should be recognized that the relationship between size and extinction risk is indirect and complicated by size-related variation in abundance, population growth rate and population fluctuations (Davies *et al.*, 2000).

Two analyses have also demonstrated that the likelihood of island invasion by insects might well be size dependent, thus having a significant influence on size distributions. A negative relationship between the probability of establishment of an insect invader accidentally or intentionally introduced to the British Isles and its body size has been reported (Lawton & Brown, 1986), and a similar pattern was found within

higher taxa for the insects of sub-Antarctic Marion Island (Gaston, Chown & Mercer, 2001). Convincing explanations for this pattern are yet to be found, but may have to do with relationships between body size, abundance, and probability of detection by humans, who serve as vectors *via* transport of the species by vehicle.

VI. VARIATION IN SIZE THROUGH SPACE

(1) Intraspecific patterns

The two primary patterns of spatial variation in body size are those concerned with latitudinal and altitudinal gradients. Recent reviews have documented patterns for both gradients (Chown & Gaston, 1999; Blanckenhorn & Demont, 2004; Dillon, Frazier & Dudley, 2006). In many species, body size, usually measured as characteristic linear dimensions, increases with latitude (Table 1). Altitudinal size variation has been investigated in a smaller number of species (Table 2), and size increases have been documented in several of these (Dillon *et al.*, 2006). Often, the patterns are not simply a consequence of plasticity because size variation is retained when populations are maintained under common garden conditions (James, Azevedo & Partridge, 1995; Arnett & Gotelli, 1999b; Huey *et al.*, 2000; Loeschcke, Bundgaard & Barker, 2000; Blanckenhorn *et al.*, 2006; Stillwell *et al.*, 2007), and the genetic basis of spatial size variation is now starting to be explored (Weeks, McKechnie & Hoffmann, 2002).

Size increases with latitude and altitude are often referred to as Bergmann's rule (Chown & Gaston, 1999; Blanckenhorn & Demont, 2004), although the original application of this term by Bergmann was to interspecific, rather than intraspecific patterns. Despite the proposal that the intraspecific version be termed James' rule, to distinguish it from the more complex interspecific situation (see below) (Blackburn, Gaston & Loder, 1999), this usage has not been widely adopted. Rather, positive relationships between size and latitude are still known as Bergmann clines and the opposite as converse Bergmann clines (Blanckenhorn *et al.*, 2006).

Converse Bergmann clines (i.e. size declines with latitude) have been documented in several species (Table 1). In some of them, the declines are not constant, but take the form of a saw-tooth cline, such that increasing season length leads to increasing body size until two generations can be incorporated within a season, at which point the body size declines precipitously (Roff, 1980; Masaki, 1996). Altitudinal declines in size have also been documented (Table 2). Again, these patterns have been shown to have a strong genetic basis.

The proximate and ultimate explanations for these opposing size clines is the subject of a large, contentious and growing literature, and we consider this in more detail in Section VII. However, despite the complexity of this debate, by definition it only pertains to a relatively small number of species: those with geographic ranges that typically cover tens of degrees of latitude or hundreds (but often thousands) of metres of altitude (Gaston *et al.*, 2008). These are the

'common' species in macroecology, which constitute a small proportion of any given higher taxon. Range size frequency distributions are usually strongly right-skewed, such that the majority of species are rare (Gaston & Blackburn, 2000), and this is true of insects too (Gaston & Chown, 1999). Therefore, questions regarding latitudinal and altitudinal patterns in size variation only apply to a small number of species, and discussions of the significance of, and relationships between, various ecogeographic rules (e.g. Blanckenhorn *et al.*, 2006; Gaston *et al.*, 2008) at the intraspecific level especially must necessarily concern a small proportion of insect diversity.

(2) Interspecific and assemblage patterns

The entomological literature also has its share of investigations of multispecies body size clines. These take two forms, distinguished by Gaston *et al.* (2008) as interspecific and assemblage analyses. Interspecific analyses treat different species as separate data points, typically plotting average size against the position (usually the midpoint) of the range of that species on a latitudinal or altitudinal gradient. In assemblage analyses the data points are different areas (sites), and typically the average size of the species occurring in an area is plotted against the position of that area on a latitudinal or altitudinal gradient. Whilst related, in as much as they can be derived from the same sites by species matrix, interspecific and assemblage approaches document rather different things. The former captures how between-species variation in body size changes with the distribution of those species across the landscape, and the latter captures how variation in the body size composition of species assemblages changes across the landscape. For assemblage analyses, increases (Hawkins & Lawton, 1995), declines (Barlow, 1994) or no simple change (Hawkins, 1995) in size with latitude have been documented, whilst for interspecific analyses, increases (Moreteau *et al.*, 2003) and declines (Diniz-Filho & Fowler, 1998) with latitude have been found.

Several adaptive arguments have been proposed (and debated) for such spatial change in average body sizes, with the most common hypothesis being that it is driven by enhanced tolerance of starvation or desiccation (Cushman *et al.*, 1993; Kaspari & Vargo, 1995; Blackburn *et al.*, 1999; Chown & Gaston, 1999). However, interspecific body size clines, especially if expressed as means for a given geographic location, are much more difficult to interpret than intraspecific geographic size variation. Interspecific clinal size variation is a consequence of geographic changes in the location and shape of the interspecific species-body size distribution. Thus, the form of interspecific or assemblage size clines depends on beta diversity (the spatial pattern of species gains and losses), as well as the form of the intraspecific size clines of the species that are retained across more than two sites. Therefore, clines could take virtually any form. The latter has been demonstrated several times, as has the influence of spatial turnover of higher taxa on the form of the interspecific or assemblage size cline (Hawkins & Lawton, 1995; Chown & Klok, 2003; Brehm & Fiedler, 2004).

Table 1. The direction of latitudinal size variation in insects at the intraspecific, interspecific and assemblage levels. * = no size range data could be extracted. Negative = decline in size with increasing latitude.

Taxon	Higher taxon	Direction	Dependent variable	Size range	Source
Intraspecific					
<i>Myrmica rubra</i>	Hymenoptera	Curvilinear	Mass	3.0–3.4 mg	Elmes <i>et al.</i> (1999)
<i>Enallagma cyathigerum</i>	Odonata	Curvilinear	Forewing length	19.7–24.1 mm	Johansson (2003)
<i>Carabus nemoralis</i>	Coleoptera	Negative	Elytron length	14.5 mm	Blanckenhorn & Demont (2004)
<i>Dicaelus purpuratus</i>	Coleoptera	Negative	Length	20–28 mm	Park (1949)
<i>Glossina palpalis</i>	Diptera	Negative	Wing cell size	1.3–1.7 mm	Rogers & Randolph (1991)
<i>Aquarius remigis</i>	Hemiptera	Negative	Total length	12–16 mm	Brennan & Fairbairn (1995)
<i>Aphantopus hyperantus</i>	Lepidoptera	Negative	Wing length	16.5–24 mm	Nylin & Svard (1991)
<i>Coenonympha arcania</i>	Lepidoptera	Negative	Wing length	15–20 mm	Nylin & Svard (1991)
<i>Coenonympha hero</i>	Lepidoptera	Negative	Wing length	13.5–15.5 mm	Nylin & Svard (1991)
<i>Coenonympha pamphilus</i>	Lepidoptera	Negative	Wing length	12.5–17.5 mm	Nylin & Svard (1991)
<i>Coenonympha tullia</i>	Lepidoptera	Negative	Wing length	15–22 mm	Nylin & Svard (1991)
<i>Erebia ligea</i>	Lepidoptera	Negative	Wing length	18–25 mm	Nylin & Svard (1991)
<i>Heodes virgaureae</i>	Lepidoptera	Negative	Wing length	13–17 mm	Nylin & Svard (1991)
<i>Lasiommata maera</i>	Lepidoptera	Negative	Wing length	22–28 mm	Nylin & Svard (1991)
<i>Lymantria dispar</i>	Lepidoptera	Negative	Wing length	24–30 mm	Blanckenhorn (2006)
<i>Papilio canadensis</i>	Lepidoptera	Negative	Mass	600–900 mg	Ayres & Scriber (1994)
<i>Pararge aegeria</i>	Lepidoptera	Negative	Wing length	19–25 mm	Nylin & Svard (1991)
<i>Acheta veletis</i>	Orthoptera	Negative	Body length	14–26 mm	Alexander & Bigelow (1960)
<i>Caledia captiva</i>	Orthoptera	Negative	Pronotum length	3.8–5.2 mm	Groeters & Shaw (1996)
<i>Chorthippus brunneus</i>	Orthoptera	Negative	Mass	4.5–6.0 mg	Telfer & Hassall (1999)
<i>Teleogryllus emma</i>	Orthoptera	Negative	Head width	5.2–7.3 mm	Masaki (1967)
<i>Hipparchia semele</i>	Lepidoptera	None	Wing length	21.5–30 mm	Nylin & Svard (1991)
<i>Lasiommata megera</i>	Lepidoptera	None	Wing length	18.5–24.5 mm	Nylin & Svard (1991)
<i>Lasiommata petropolitana</i>	Lepidoptera	None	Wing length	1–22 mm	Nylin & Svard (1991)
<i>Lyacaena helle</i>	Lepidoptera	None	Wing length	12–15 mm	Nylin & Svard (1991)
<i>Lyacaena phlaeas</i>	Lepidoptera	None	Wing length	11–17 mm	Nylin & Svard (1991)
<i>Maniola jurtina</i>	Lepidoptera	None	Wing length	18–26 mm	Nylin & Svard (1991)
<i>Palaeocrysophamus hippothoe</i>	Lepidoptera	None	Wing length	14–17 mm	Nylin & Svard (1991)
<i>Phyllotreta striolata</i>	Coleoptera	Positive	Elytron length	2.0 mm	Blanckenhorn & Demont (2004)
<i>Stator limbatus</i>	Coleoptera	Positive	Elytron length/width	*	Stillwell <i>et al.</i> (2007)
<i>Drosophila aldrichi</i>	Diptera	Positive	Thorax length	*	Loeschcke <i>et al.</i> (2000)
<i>Drosophila buzzatii</i>	Diptera	Positive	Thorax length	*	Loeschcke <i>et al.</i> (2000)
<i>Drosophila kikkawi</i>	Diptera	Positive	Wing length	9.7 mm	Karan <i>et al.</i> (1998)
<i>Drosophila melanogaster</i>	Diptera	Positive	Wing area	1.4–2.2 mm ²	James <i>et al.</i> (1997)
<i>Drosophila melanogaster</i>	Diptera	Positive	Wing length	1.37–1.61 mm	Imasheva <i>et al.</i> (1994)
<i>Drosophila melanogaster</i>	Diptera	Positive	Mass	0.9–1.1 mg	David & Bocquet (1975)
<i>Drosophila melanogaster</i>	Diptera	Positive	Thorax length	1.1–1.6 mm	Hoffmann <i>et al.</i> (2001)
<i>Drosophila melanogaster</i>	Diptera	Positive	Wing: thorax size ratio	1.35–1.55	Azevedo <i>et al.</i> (1998)
<i>Drosophila melanogaster</i>	Diptera	Positive	Thorax length	0.92–1.10 mm	James <i>et al.</i> (1995)
<i>Drosophila serrata</i>	Diptera	Positive	Wing length	0.9–1.4 mm	Hallas <i>et al.</i> (2002)
<i>Drosophila simulans</i>	Diptera	Positive	Mass	*	David & Bocquet (1975)
<i>Drosophila subobscura</i>	Diptera	Positive	Wing length	2.22–2.61 mm	Calboli <i>et al.</i> (2003)
<i>Drosophila subobscura</i>	Diptera	Positive	Wing length	2.3–3.2 mm	Gilchrist & Huey (2004)
<i>Drosophila subobscura</i>	Diptera	Positive	Wing length	0.8–0.95 mm	Huey <i>et al.</i> (2000)
<i>Drosophila subobscura</i>	Diptera	Positive	Wing width	0.89–1.5 mm	Gilchrist <i>et al.</i> (2004)
<i>Musca domestica</i>	Diptera	Positive	Wing length	2–6 mm	Bryant (1977)
<i>Scathophaga stercoraria</i>	Diptera	Positive	Hind tibia length	2.7–3.7 mm	Blanckenhorn & Demont (2004)
<i>Zaprionus indianus</i>	Diptera	Positive	Mass	0.13–0.12 mg	Karan <i>et al.</i> (2000)
<i>Pemphigus populitransversus</i>	Homoptera	Positive	Wing length	2 mm	Blanckenhorn & Demont (2004)
<i>Apis mellifera</i>	Hymenoptera	Positive	Forewing length	9.15 mm	Daly <i>et al.</i> (1991)
<i>Apis mellifera</i>	Hymenoptera	Positive	Wing length	8–10 mm	Alpatov (1929)
<i>Leptothorax acervorum</i>	Hymenoptera	Positive	Thorax length	1.05–1.15 mm	Heinze <i>et al.</i> (1998)
<i>Leptothorax acervorum</i>	Hymenoptera	Positive	Thorax length	0.98–1.18 mm	Heinze <i>et al.</i> (2003)
<i>Nomia melanderi</i>	Hymenoptera	Positive	Mass	130–180 mg	Rust (2006)
<i>Myrmeleon immaculatus</i>	Neuroptera	Positive	Body mass	0.019–0.1 g	Arnett & Gotelli (2003)
<i>Myrmeleon immaculatus</i>	Neuroptera	Positive	Head width	1.19–1.25 mm	Arnett & Gotelli (1999a)

Table 1. (Cont.)

Taxon	Higher taxon	Direction	Dependent variable	Size range	Source
<i>Allonemobius fasciatus</i>	Orthoptera	Sawtooth	Femur length	5.6–6.8 mm	Mousseau & Roff (1989)
<i>Pteronemobius taprobanensis</i>	Orthoptera	Sawtooth	Head width	1.7–1.95 mm	Masaki (1978)
Interspecific					
Butterflies	Lepidoptera	Negative	Forewing length	17.5–21 mm	Hawkins & Lawton (1995)
Butterflies	Lepidoptera	Negative	Forewing length	19–23 mm	Hawkins & Lawton (1995)
Termites	Isoptera	None	Colony size	*	Porter & Hawkins (2001)
Butterflies	Lepidoptera	None	Forewing length	18.5–19 mm	Hawkins & Lawton (1995)
Ants	Hymenoptera	Positive	Body length	4.5–6.5 mm	Cushman <i>et al.</i> (1993)
Butterflies	Lepidoptera	Positive	Forewing length	18–21 mm	Hawkins & Lawton (1995)
Bees	Hymenoptera	Variable	Body length	7–15 mm	Hawkins (1995)
Assemblage					
Butterflies	Lepidoptera	Curvilinear	Forewing length	17–23 mm	Hawkins & Lawton (1995)
Butterflies	Lepidoptera	Negative	Forewing length	17–23 mm	Hawkins & Lawton (1995)
Butterflies	Lepidoptera	Negative	Wingspan	36–56 mm	Barlow (1994)
Butterflies	Lepidoptera	None	Forewing length	17–23 mm	Hawkins & Lawton (1995)
Ants	Hymenoptera	Positive	Colony size	*	Kaspari & Vargo (1995)
Ants	Hymenoptera	Positive	Body length	4.5–6.5 mm	Cushman <i>et al.</i> (1993)
Butterflies	Lepidoptera	Positive	Forewing length	17–23 mm	Hawkins & Lawton (1995)
Bees	Hymenoptera	Variable	Body length	7–15 mm	Hawkins (1995)

What has perhaps not been as clearly recognized is that adaptive explanations at the assemblage level make the implicit assumption either that the average body size of the assemblage is being optimised, or that a certain size is optimal for a given reason, and will be achieved irrespective of species-specific life-history variation. Both scenarios seem unlikely, except under the condition that there is an optimal body size for a given higher taxon (e.g. Brown, Marquet & Taper, 1993), which seems entirely unlikely (Chown & Gaston, 1997; Kozłowski & Gawelczyk, 2002).

VII. MODELS FOR ADULT CLINAL SIZE VARIATION

Many models exist which examine the relationship between age and size at maturity and the associated trade-offs which limit the scope of variation seen in natural populations. Several of these, as well as a variety of other, sometimes less mathematically formal approaches, have been used in attempts to explain the existence of clines in body size. Much of the focus has been on the increase in size with latitude or altitude, which is sometimes also known as the temperature-size rule, owing to the tendency for organisms to develop to larger sizes when reared at lower temperatures (Atkinson, 1994), and which has also been called a puzzle for life historians (Berrigan & Charnov, 1994). The underlying mechanistic explanations for size clines continue to be contentious, with several authors expressing the view that the reasons for 'Bergmann clines' remain unclear (Angilletta & Dunham, 2003; Blanckenhorn & Demont, 2004; Blanckenhorn *et al.*, 2006; Kingsolver *et al.*, 2007).

Before discussing the various explanations for changing adult size with changing altitude and latitude (and season),

it is important to recognize that few of these explicitly make a formal connection to investigations of the proximate physiological mechanisms for size variation discussed in Section II. Often this connection is implied, but explicit discussion of variation in critical weight, rate of growth prior to and after the critical weight, and duration of the ICG is uncommon. Where such discussion does take place, it is usually driven by those investigating the proximate physiological mechanisms as a means to explain spatial patterns in size variation (see e.g. Davidowitz & Nijhout, 2004; Nijhout *et al.*, 2006). In consequence, here, the various explanations proposed for size variation will be reviewed as they have been presented by their proponents. Thereafter, integration with mechanistic physiological explanations will be provided in the context of a general model for size variation.

Essentially, the explanations for size clines can be thought of as those that are explicitly adaptive and those that involve some form of biophysical constraint that may or may not be the subject of selection. The biophysical constraints generally concern the temperature sensitivity of different aspects of organismal development, such as growth *versus* differentiation (e.g. van der Have & de Jong, 1996), and have the closest connections to the proximate physiological mechanisms determining size. The most prominent of the constraint-based explanations for positive size clines (or Bergmann's clines) are the differential sensitivity of growth and development (van der Have & de Jong, 1996), and to some extent the difference in the temperature thresholds of growth and development (Walters & Hassall, 2006; see also de Jong & van der Have, 2008). Following re-assessment of the former, Walters & Hassall (2006) concluded that the slope of the rate-temperature curve is of much less significance than the relative position of its threshold. However, they also argued that selection for increases or declines in body size operates through variation in the relative positions of the

Table 2. The direction of altitudinal size variation in insects at the intraspecific, interspecific and assemblage levels. Negative = decline in size with increasing altitude.

Taxon	Higher taxon	Direction	Dependent variable	Size range	Source
Intraspecific					
<i>Adesmia metallica</i>	Coleoptera	Negative	Elytron length	9–15 mm	Krasnov <i>et al.</i> (1996)
<i>Bothrometopus gracilipes</i>	Coleoptera	Negative	Body length	4.4–4.9 mm	Chown & Klok (2003)
<i>Canonopsis sericeus</i>	Coleoptera	Negative	Body length	10.0–10.7 mm	Chown & Klok (2003)
<i>Ectemnorhinus viridis</i>	Coleoptera	Negative	Body length	4.9–6.6 mm	Chown & Klok (2003)
<i>Erodus edomitus</i>	Coleoptera	Negative	Elytron length	8–12 mm	Krasnov <i>et al.</i> (1996)
<i>Zophosis complanata</i>	Coleoptera	Negative	Elytron length	6.5–12 mm	Krasnov <i>et al.</i> (1996)
<i>Scathophaga stercoraria</i>	Diptera	Negative	Hind tibia length	2.5–3.5 mm	Blanckenhorn (1997)
<i>Myrmeleon immaculatus</i>	Neuroptera	Negative	Head width	1.19–1.25 mm	Arnett & Gotelli (1999a)
<i>Teleogryllus emma</i>	Orthoptera	Negative	Head width	5.3–7.4 mm	Masaki (1967)
<i>Omocestus viridulus</i>	Orthoptera	Negative	Hind femur length	9–14 mm	Berner & Blanckenhorn (2006)
<i>Xanthippus corallipes</i>	Orthoptera	Negative	Mass	1.9–3.1 g	Ashby (1997)
<i>Bothrometopus brevis</i>	Coleoptera	None	Body length	3.7–4.2 mm	Chown & Klok (2003)
<i>Phlebotomus papatasi</i>	Diptera	None	Wing length	2.26–2.52 mm	Belen <i>et al.</i> (2004)
<i>Sepsis cynipsea</i>	Diptera	None	Head width	0.9–1.0 mm	Blanckenhorn (1997)
<i>Drosophila robusta</i>	Diptera	Positive	Wing length	3.1–3.2 mm	Stalker & Carson (1948)
<i>Bothrometopus elongatus</i>	Coleoptera	Positive	Body length	2.8–3.4 mm	Chown & Klok (2003)
<i>Bothrometopus parvulus</i>	Coleoptera	Positive	Body length	3.7–5.0 mm	Chown & Klok (2003)
<i>Ectemnorhinus marioni</i>	Coleoptera	Positive	Body length	4.7–5.3 mm	Chown & Klok (2003)
<i>Ectemnorhinus similis</i>	Coleoptera	Positive	Body length	5.9–8.0 mm	Chown & Klok (2003)
<i>Nicrophorus investigator</i>	Coleoptera	Positive	Elytron length	8.8–9.8 mm	Smith <i>et al.</i> (2000)
<i>Sepidium dathan</i>	Coleoptera	Positive	Elytron length	7.5–12.5 mm	Krasnov <i>et al.</i> (1996)
<i>Drosophila buzzatii</i>	Diptera	Positive	Thorax length	*	Dahlgard <i>et al.</i> (2001)
<i>Drosophila mediopunctata</i>	Diptera	Positive	Size	*	Bitner-Mathé & Klaczko (1999)
<i>Lutzomyia intermedia</i>	Diptera	Positive	Size	0.31–0.40 mm	Marcondes <i>et al.</i> (1999)
<i>Musca domestica</i>	Diptera	Positive	Size	2.6 mm wing	Bryant (1977)
<i>Amegilla sapiens</i>	Hymenoptera	Positive	Mass	250–400 mg	Stone (1993)
<i>Apis mellifera</i>	Hymenoptera	Positive	Forewing length	8.3–9.5 mm	Ruttner <i>et al.</i> (2000)
<i>Hemideina maori</i>	Orthoptera	Positive	Head length	10–22 mm	Koning & Jamieson (2001)
<i>Melanoplus sanguinipes</i>	Orthoptera	Positive	Mass	0.2–0.6 g	Rourke (2000)
Interspecific					
Nymphalidae	Lepidoptera	Curvilinear	Forewing length	15–90 mm	Hawkins & DeVries (1996)
Pieridae	Lepidoptera	Negative	Forewing length	10–40 mm	Hawkins & DeVries (1996)
Riodinidae	Lepidoptera	None	Forewing length	10–30 mm	Hawkins & DeVries (1996)
Papilionidae	Lepidoptera	Positive	Forewing length	30–70 mm	Hawkins & DeVries (1996)
Assemblage					
Curculionidae	Coleoptera	Curvilinear	Body length	3.7–8.5 mm	Chown & Klok (2003)
Insects	Insecta	Curvilinear	Length	*	Janzen <i>et al.</i> (1976)
Curculionidae	Coleoptera	Negative	Body length	3.7–5.1 mm	Chown & Klok (2003)
<i>Hegeter</i> sp.	Coleoptera	Negative	Size	*	De Los Santos <i>et al.</i> (2000)

temperature thresholds for growth (TT_G) and development (TT_D), and that the relative benefits of changes in these values are dependent on season length. This makes their model much more like the adaptive explanations discussed below. A further constraint model concerns interactions between whole-organismal and cellular oxygen supply (Makarieva *et al.*, 2005). In this model, mass-specific metabolic rate increases more rapidly with temperature than does cellular metabolic flux. To maintain energy budget, cell size must decline with increasing temperature. Presuming constant cell number (which is by no means a certainty, see review in Chown & Gaston, 1999), declining cell size should lead to declining body size. Alternatively, if metabolic rate is held constant, *via* adaptive differentiation among populations,

larger size can be achieved by increasing whole-organismal metabolic flux and cell size. Using similar arguments and assuming constant minimum metabolic rates, this model also proposes a constraint explanation for interspecific size increases with temperature in terrestrial organisms, but the converse in aquatic ones (Makarieva *et al.*, 2005). The authors also argue that their intraspecific model is superior to those which require consideration of seasonality, because there is apparently no cost of extension of life cycles to several years at high latitudes, and because no quantitative approach has been developed to demonstrate how changes in season length might effect changes in body size.

Amongst the adaptive explanations, those based on von Bertalanffy's growth equation have generally been

rejected owing to their logical problems (Day & Taylor, 1997; Kozłowski *et al.*, 2004; Makarieva, Gorshkov & Li, 2004), and lack of empirical support for their predictions (Angilletta & Dunham, 2003). Perhaps the simplest of the remaining explanations, and one that has not typically been formulated numerically, is the starvation resistance (or more generally, resistance) hypothesis. Although originally used in an interspecific context, it can be applied just as readily intraspecifically (e.g. Stillwell *et al.*, 2007). The idea essentially posits that large individuals at higher latitudes may be better able to survive starvation (or desiccation) than small individuals, hence species should tend to be larger at high latitudes (Cushman *et al.*, 1993). One way in which this might occur is if the scaling of maintenance metabolic rate over winter has a lower exponent than the scaling of reserve storage. Such relative scaling does not seem implausible, and may even explain why colony size clines are found in some colonial insects (Kaspari & Vargo, 1995; but see also Porter & Hawkins, 2001). When examined from a scaling perspective, the starvation resistance hypothesis is readily identified as a specific case of a more general set of optimal resource allocation models (Kozłowski *et al.*, 2004).

If these resource allocation models are considered together with models explaining sawtooth clines in size (Roff, 1980), they can provide a comprehensive explanation for both increases and declines in size with latitude and altitude in the context of changes in both temperature and season length. The relative independence of season length and temperature as factors influencing size, and the significance of generation time relative to season length in determining whether season length or temperature will have the most significant influence on size, was mooted originally by several authors (Nylin & Gotthard, 1998; Chown & Gaston, 1999), and has now garnered considerable empirical support (Fischer & Fiedler, 2002; Chown & Klok, 2003; Blanckenhorn & Demont, 2004).

In essence, the combined model may be described as follows. Assume simple switching and growth curves for a univoltine insect, where the adult ages (although it can be ignored here, tissue repair and maintenance will make a difference to the form of the growth and switching curves; Kozłowski *et al.*, 2004), and dies at the end of the season (Fig. 9). Under season length T , switching curve a , and growth curve A , optimal body size is A' . At this size resources should be switched from growth to reproduction (see Kozłowski *et al.*, 2004). Assume now that season length declines by some increment (T to $T - 1$) because of a poleward shift in latitude. Because life expectancy is zero at the end of the season, the switching curve shifts to the left (b), and given the same growth rate, optimal final size is reduced to A'' . Experimental reductions in nutrient quality or availability typically result in reduced growth rate and size (including reduced critical weight), presumably *via* insulin signalling, so demonstrating the proximate physiological path. It is also simple to see the size-related fitness advantages associated with an increase in development time should season length increase (from $T - 1$ to T), as might be

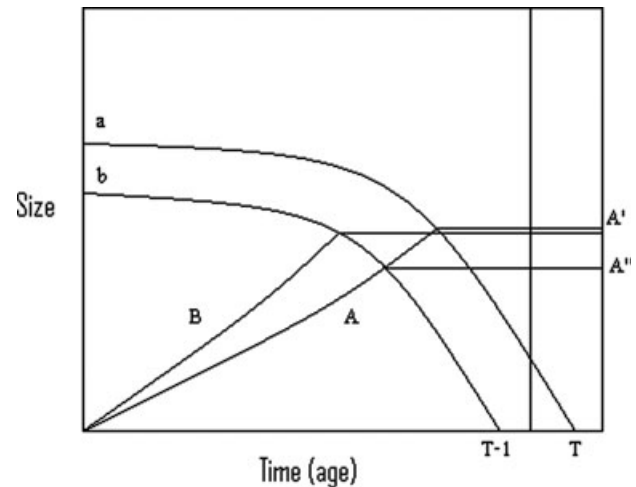


Fig. 9. Switching curve and growth curves for a model species (after Kozłowski *et al.*, 2004). The switching curves a and b show where the switch should be from growth to reproduction and decline to zero at the end of the season. Two growth curves A and B are also shown. A decline in season length from T to $T - 1$ will mean that the switching curve must shift to the left, which with constant growth rate will result in a decline in body size (A' to A''). An increase in growth rate (A to B) can compensate for the change in switching curve, but this has fitness implications. Increases in season length from $T - 1$ to T should result in an increase in size (although reductions in growth rate are not uncommon). This size increase will cease when the fitness benefits of a second generation outweigh those of large size as in Roff's (1980) model.

expected if moving towards the equator. However, as Roff (1980) has shown, there is a point at which the fitness advantage of large size is outweighed by the advantage of the addition of a second generation. Size then declines in the first tooth of a saw-tooth pattern because of the reduction in time for growth (i.e. there is a substantial change to the switching curve). As season length increases so additional generations can be added, each time with a declining reduction in development period, and so in body size. Once there is no longer any decline in development period with the addition of generations, the population is essentially composed of multivoltine, short-lived individuals living in a seasonal environment.

For multivoltine animals, Kozłowski *et al.*'s (2004) models for aseasonal conditions apply because they perceive reduced seasonality owing to the fast life cycle relative to the season length. These models are based on temperature-related differences in the body size-dependence of resource acquisition rate and metabolic rate (so giving rise to size-related changes in production rate), and the influence of mortality rate and its temperature dependence on optimal size. Under a wide range of conditions, and assuming several different forms of change in the coefficients and exponents of the size dependence of acquisition rate and metabolic rate, increases in size with declining temperature are optimal. Moreover, from a simple, proximate physiological

Table 3. Predictions of hypotheses proposed to explain spatial size variation in insects

Hypothesis	I	II	III	IV	V
Description	Proximate biophysical model ¹	Temperature threshold hypothesis ²	Optimal resource allocation model ³	Minimum metabolic rate ⁴	Starvation resistance ⁵
Size cline	+	-/+	-/+	-/+	+
Differences in scaling of rates	No	No	Yes	No	Yes
Relationship between length of unfavourable season and size	No	- when cline -	- when cline -	No	+
Larval mortality factors	No	No	Yes	No	No
Constant <i>versus</i> variable cell number	No	No	No	Yes	No
Sex-related differences	No	Yes	Yes	No	Yes

¹Van der Have & de Jongh (1996); ²Walters & Hassall (2006); ³Kozłowski *et al.* (2004); ⁴Makarieva *et al.* (2005); ⁵Cushman *et al.* (1993)

perspective, declining temperature prolongs the ICG and developmental time, in an exponential manner (leaving the critical weight unaffected), and leads to a linear decline in growth rate. The outcome is a decline in body size with increasing temperature under a wide range of conditions (see Section II and Davidowitz & Nijhout, 2004). The range of conditions under which such negative relationships between size and temperature are found might be wider than Kozłowski *et al.* (2004) or Davidowitz & Nijhout (2004) suggested because countergradient variation, with shorter development times leading to large final size, is not uncommon in insects (Ayres & Scriber, 1994; James *et al.*, 1995; Arendt, 1997; Blanckenhorn & Demont, 2004). However, which of the factors determining adult size (e.g. growth rate, duration of ICG, critical weight) are the subjects of selection has not yet been investigated.

A notable, and supported, empirical prediction of the optimal resource allocation model is a relationship between the direction of size clines and body size: smaller species with relatively faster development times that are unlikely to face nutritional constraints should tend to show Bergmann size clines, and indeed this is what has been found (Chown & Gaston, 1999; Blanckenhorn & Demont, 2004). Moreover, seasonal size variation is typical of such species too, and is almost by definition not applicable to species that do not have multiple generations annually. Nonetheless, some studies do not find support for the significance of variation in season length for variation in final adult size (Cabanita & Atkinson, 2006). Moreover, others have suggested that direct selection on traits that have different responses to temperature, such as wing length and thorax size in *Drosophila melanogaster*, may explain clinal variation in adult size (Hoffmann *et al.*, 2007).

If the resistance hypothesis (starvation or desiccation) is not subsumed within the resource allocation models, at least five models have been proposed to account for intraspecific clinal variation in adult size (Table 3). Most of these models predict some kind of relationship between size and temperature, and most of the predictions can, at least to some extent, be accommodated within what is known of

the proximate, physiological factors affecting final adult size (see Section II). Therefore, these models may prove difficult to distinguish empirically. Indeed, no studies to date have attempted to do so, either from a strong inference perspective, or using an information theoretic approach. Nonetheless, the models all make a variety of ancillary predictions which would render them amenable to such approaches (Table 3). The proximate biophysical model and starvation resistance hypothesis predict only an increase in size with latitude/altitude. They may be distinguished by the fact that the former makes no prediction about the scaling of metabolic rate *versus* resource stores. If only phenotypic data on size are available, then the former does not make any prediction regarding season length, whereas the latter predicts a positive relationship between length of the unfavourable season and size. The temperature threshold and optimal resource allocation models make the opposite prediction. However, they can be distinguished by the fact that the latter predicts a strong influence of mortality factors on size. The minimum metabolic rate model predicts constant *versus* varying cell numbers depending on the cline and can therefore readily be separated from the other hypotheses, especially given that cell size proxies (ommatidia, wing cells) (e.g. Blanckenhorn & Llaurens, 2005; Chown *et al.*, 2007) can be readily assessed. The proximate biophysical model and minimum metabolic rate models make no prediction for difference among the sexes, whereas such differences are implicit in the other models.

Of course, few of the explanations for size clines, and even fewer of the tests thereof make an attempt to couple the evolutionary ecological aspects of these models with the proximate physiological factors affecting size variation. This is perhaps the weakest area of the field at present. Whilst not all systems will lend themselves to such investigation, explicit coupling of field and laboratory investigations of model species (recognizing that differences may sometimes arise between the field and laboratory—Fairbairn, 2005; Kingsolver, 2007) and non-model species will help demonstrate which explanations for

size variation are likely to be the most general (see also Feder, 2007). Moreover, it should also be recognized that, at least at the intraspecific level, more than one set of circumstances might lead to spatial variation in size. After all, animals have to contend with variation in diet, water availability, temperature, and predators simultaneously (Elton, 1930). In consequence, it is too early yet to call off the documentation of intraspecific spatial variation in insect adult size, especially if this is undertaken either in the context of an explicit, strong inference assessment of the explanations for size variation, or in the context of how intraspecific variation relates to patterns at the interspecific and assemblage levels (see also Gaston *et al.*, 2008).

VIII. CONCLUSIONS

- (1) Much is known about the way in which natural selection leads to size variation at the individual level, how this translates to sexual size dimorphism, and how, in turn, individual-level variation leads to clinal variation within and between species and among assemblages at large scales.
- (2) Despite this considerable body of theoretical and empirical work, several fundamental aspects of large-scale size variation in insects remain poorly understood. For example, individual (i.e. population-level) body size frequency distributions remain relatively poorly investigated. Likewise, body mass variation across the insects as a whole and within each of the orders has not been thoroughly documented. Indeed, how variation is partitioned at various levels of the taxonomic hierarchy, or how significant is the phylogenetic signal in body mass variation remains unclear.
- (3) To a large extent this situation is a consequence of the fact that mass data are concealed within a wide range of papers. One solution would be the development of an online database for standardized insect body size data (for example length, mass and wingspan, and their variances). Such online databases are common in the fields of genomics and proteomics, and no good reason exists why the same approach should not be developed for macroecology.
- (4) Investigations of clinal variation in size also need to make a clearer distinction between intraspecific, interspecific and assemblage-level analyses. Whilst these three levels can be thought of as different elements of a species by sites matrix (Gaston *et al.*, 2008), this is rarely done. Nonetheless, such a distinction is necessary because both the methods required to document the patterns and the mechanisms underlying size variation (or lack of it) differ at each of these levels, although obviously what happens at one level may influence the others.
- (5) At the intraspecific level, a relatively neglected component of research is the role of plasticity in

generating and maintaining size clines relative to the importance of specialist phenotypes (see Angilletta, 2009 for a more general review). Moreover, a strong inference approach, or one using model selection based on information theory (see e.g. Johnson & Omland, 2004; Angilletta, 2009) sorely needs to be applied to the question of the mechanism underlying intraspecific clines in body size. At present, several competing hypotheses exist to explain clinal variation, yet few studies have attempted simultaneously to assess these.

- (6) Several other challenges remain. Of these, two strike us as most significant. First, the mechanistic basis by which oxygen concentration might influence insect size is not well understood. Whilst it is assumed that limits to diffusion and convection are the basis of oxygen-related size variation, recent empirical work suggests that the situation may be more complex (e.g. Klok & Harrison, 2009). In addition, oxygen limitation of geographic range size, and a positive relationship between body size and range size, might explain the disappearance of giant insects. A more direct physiological mechanism might do likewise, as might a simple sampling mechanism. Again, these alternatives are rarely explored simultaneously. Second, few studies have sought to determine whether other macroecological patterns typical of vertebrates, such as the Island rule (Palmer, 2002), apply to insects. If macroecological patterns are to be considered general, then they should apply to insects as much as to other taxa.

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