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The significance of body size in the Orthoptera: a review

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Abstract

This review discusses body size and mass as they relate to the Orthoptera (crickets, katydids, grasshoppers) and the Phasmatodea (walkingsticks). It addresses the expression, causes and consequences of size in these insects. Topics include: methodological problems in body-size research, gravity *vs* surface forces, allometry and scaling, Dyar's law, ontogenetic scaling, size-invariant traits and nonallometric scaling, the influence of size on physiology, function, behavior, life history, mating, fecundity, population dynamics, ecology, and community, size-clines, Bergmann's rule, sexual size dimorphism, Rensch's rule, protandry, the environmental, genetic, and physiological control of size, the evolution of size and the influence of size on evolution. Hypotheses are presented to explain why insects remain small in comparison to other taxa.

Key words

body size, body mass, allometry, scaling, Dyar's law, life history, sexual size dimorphism, sexual selection, Bergmann's rule, Rensch's rule, protandry, season length, grasshoppers, crickets, katydids

Body size and mass are perhaps the most fundamental features of organisms because they influence nearly all aspects of biology. This is certainly true for the Orthoptera (grasshoppers, crickets, and katydids; ~ 24,300 species) (Orthoptera Species File) and the closely related Phasmatodea (walkingsticks; ~3,500 species) (Phasmida Species File). Body size within these two groups varies from tiny 2-mm long ant-inquiline crickets (Myrmecophilidae) (Otte & Alexander 1983, Vickery & Kevan 1985), to the longest insect known, the phasmid *Phobaeticus chani* from Borneo, which reaches 567 mm from extended fore tarsi to extended hind tarsi (Natural History Museum, London). The heaviest orthopteran is a giant weta, *Deinacrida heteracantha*, from New Zealand, with females weighing up to 71 g (Williams 2001). As such, these diverse insects range across 2.5 orders of magnitude for adult body length and 4.5 orders of magnitude for adult mass (from ~ 2 mg for the smallest *Myrmecophila* ant crickets to 71,000 mg for the largest weta) (Otte & Alexander 1983, Williams 2001). Hence, some wetas weigh an incredible 35,000 times as much as some ant crickets!

The widespread abundance and availability of Orthoptera and their great diversity in species, niche, life-history and body mass has made them an ideal group in which to study size and all of its manifestations, causes and consequences — from genetic and environmental influence, to allometry, physiology and performance, to sexual size dimorphism, community structure, and geographic size clines. This short review addresses these varied subjects, and is designed to serve as a reference starting point for future researchers interested in body size in the Orthoptera.

Why size and mass are important

Size and mass are important because they correlate strongly with fitness, because they directly or indirectly influence nearly all biological phenomena, and because a great many biological and physical factors influence size and mass. As such, size and mass are determinants of fitness and targets of natural selection. For researchers, size and mass are two easily obtained values that can encapsulate and predict a multitude of more difficult-to-obtain variables, such as metabolic rate, physiological condition, stress-resistance, immunocompetency, locomotor and dispersal abilities, fecundity, life history, mating system and mating success, abundance, competitiveness, community energy demands, types of predators, *etc.* (Woodward *et al*. 2005). Size is a key character for systematics and taxonomy, and phenotypic plasticity, geographic variability in size, and sexual size dimorphism have bedeviled these fields (Mayr 1969, Whitman & Agrawal 2009). Size-related traits serve as predictors of intra- and interpopulation genetic variability (Bégin & Roff 2004, Fabriciusova *et al*. 2008) and play a role in species conservation (Berggren 2008). Finally, size and mass are widely used to analyze selective variation, and are a major focus of evolutionary studies, including sexual selection.

Over the last century, researchers have compiled an impressive list of animal (mainly vertebrate) traits and processes that are influenced by, or correlated with, overall size or mass, or alternatively, factors and traits that influence size and mass. These are discussed in detail in Peters (1983), Schmidt-Nielsen (1984), Calder (1996), Brown & West (2000), Chown & Nicolson (2004), and others, and I direct the reader to these comprehensive treatments.

Body size and the insect's world: inertial *vs* viscous forces

A fundamental and underappreciated dynamic of body size for entomologists is its relation to inertial (gravitational) *vs* viscous (surface) forces (Vogel 1994). The physics of tiny objects are dominated by molecular cohesion and viscous forces, whereas larger objects are more affected by gravitational forces (Haldane 1929, Went 1968). Insect body sizes transcend this boundary. The smallest insects cannot escape from a droplet of water and are immobilized by electrostatic attraction. However, they can easily adhere upside-down on surfaces, drift in air currents, and are unharmed after falling. In contrast, large insects are dominated by gravity. They can easily escape wetting or electrostatic attraction, do not float in air, and can be harmed by falling. The morphologies, behaviors, life-histories, and overall strategies of insects must accommodate these size-dependent physical realities. Small insects must be designed to counter surface forces, and large insects must be designed to accommodate gravity. For example, most cricket and grasshopper eggs are deposited underground. When such soils are saturated, it is difficult for the tiny hatchlings to wiggle to the surface, because of the strong capillary forces binding the wet soil particles. The foam plug placed by female grasshoppers between the eggs and the soil surface may have, in part, evolved to counter this problem (Stauffer & Whitman 1997). During growth, most Orthoptera pass from a surface-cohesion world to a gravitational world.

Scaling and allometry

Scaling refers to how form, function and outcomes vary with body size and mass (Schmidt-Nielsen 1984, LaBarbera 1989, Brown & West 2000). Allometry is often reserved for relationships among morphological traits that are not isometric. Isometry results when morphological traits scale equally to one another, such that their relative sizes remain the same. Allometry results when traits scale disproportionally, such that their ratios change with overall body size. Allometries are usually modeled by the allometric equation $Y = aX^b$, where Y is a morphological (sometimes a physiological, behavioral, life-history, or ecological) variable (the dependent variable), a is a proportionality constant specific for that taxon and trait, X is size or mass (the independent variable), and the exponent b is the power function (the allometric exponent) that specifies the effect of mass or size on the dependent variable. A log transformation of the allometric equation gives the linear equation: $\log Y = \log a + b \log X$, which produces a straight line on log-log plot, in which b is the slope and a is the Y intercept at $X = \log 0$, and hence designates the magnitude of the dependent variable for an animal with a mass or size of one unit. If $b > 1$, then Y and X are positively related (positive allometry). If $b < 1$, then Y and X are negatively related (negative allometry); and if $b = 1$, then Y and X are isometric, in which case, the variables plot as a straight line on both linear and log-log plots. Small differences in b reflect large differences in the relationship of X to Y. Note that different authors use different symbols in the allometric equation (Schmidt-Nielsen 1984), and that the allometric exponent, b, is given in either decimal or fraction form (*e.g.*, $X^{0.75}$ *vs* $X^{3/4}$). Empirical allometric equations are typically obtained by fitting linear regressions to log-transformed data.

Scientists have discovered a phenomenal number of biological variables that scale to body size according to the allometric equation. These various relationships fill journals and books (Peters 1983, Schmidt-Nielsen 1984, Calder 1996, Brown & West 2000, Bonner 2006) and include morphological, physiological, life-history, ecological, and evolutionary relationships. For example, in spiders, exoskeleton mass scales with the 1.135 power of body mass (Anderson *et al.* 1979). In developing *Schistocerca gregaria* grasshoppers, mesotibial length scales to tibial diameter by the 1.25 power, and flexural storage stiffness of the hind tibia, scales to body mass to the 1.59 power (Katz & Gosline 1992). Among grasshopper species, hypoxic ventilation frequency, absolute tracheal system conductance, and mass-specific tracheal conductance scaled with mass to the 0.23, 0.73, and -0.23 powers, respectively (Greenlee *et al.* 2007). Walking velocity in beetles scales by ~ 0.32, and ingestion rates in forest-floor arthropods by 0.68 with body mass (Peters 1983). In insects, flight speed scales by O.86, and number of species by -1.74 with body length (Dudley 2000). Across terrestrial animals, species population density (number of individuals/km^2) scales with species mass by -0.98, but for invertebrates alone, by -0.54 (Peters 1983, Cyr 2000). Allometric equations are also used to model frequencies (for example of a behavior) as the dependent variable, and sexual size dimorphism, where the log of some aspect of male size is plotted against the log of female size (Blanckenhorn *et al.* 2007).

It would appear that everything scales with body size according to the allometric equation. However, that is not the case. Scaling is an extremely complicated subject and fraught with problems (Stern & Emlen 1999, Brown & West 2000, Emlen & Nijhout 2000). For example, scaling and allometry can apply to: 1) developmental changes within an individual (developmental allometry), 2) intraspecific differences among same-aged individuals within a population (static allometry) (Shingleton *et al.* 2007), 3) differences between intraspecific populations, or 4) interspecific differences (phylogenetic or evolutionary allometry). The first catagory deals with ontogeny in individuals (allometric growth, growth trajectories), and is proximally controlled by ontogenetic programs with environmental input. The second catagory represents to a great extent phenotypic plasticity (Emlen & Nijhout 2000), and the fourth is thought to represent evolutionary differences among species.

However, these four categories are interconnected. Differential allometries exhibited in categories 3 and 4 are believed to be caused primarily by evolution altering allometric growth patterns (category 1) (Emlen & Nijhout 2000, Frankino *et al.* 2005, Shingleton *et al.* 2007). In contrast, different geographic environments acting on developmental allometry (category 1) may influence category 3 *via* phenotypic plasticity. Analyses of these different types of allometry should be kept separate, and readers should be cognizant as to which type of comparison is being made.

Many scaling relationships are not log-linear, and some are even discontinuous (Tomkins1999, Emlen & Nijhout 2000). Other traits are size-invariant, whereby $b = 0$. In addition, the slopes, intercepts, and shapes of plotted relationships can change, depending on how one defines both variables (*e.g.*, length *vs* mass *vs* surface area, or wet-, dry-, fed-, starved-, gravid-, nongravid-, or lipid-free mass) (see Blanckenhorn *et al.* 2007). Hence, one can derive different quantitative relationships by changing units.

Recent work has called into question many of the older scaling relationships, and even the value of the allometric equation itself. An example is ¾-power metabolic scaling in animals, which is taught in introductory textbooks as a metabolic law (Kleiber's law). Reexamination of metabolic scaling reveals numerous methodological and theoretical problems (Glazier 2005, da Silva *et al.* 2006). For example, metabolic rate scales to mass$^{0.92}$ across nymphal growth for *Melanoplus sanguinipes*, and by mass$^{1.06}$ among adults of 32 species of Orthoptera (Fielding & DeFoliart 2008). Both exponents were significantly greater than the 0.75 value given in the literature. Part of the problem is that animals can evolve to compensate for many size-dependent tradeoffs (see below).

Another problem is that most scaling work has been done on vertebrates. Arthropods differ substantially from vertebrates (molting, metamorphosis, exoskeleton, tracheae, cold-blooded, *etc.*), and these arthropod traits sometimes constrain or alter scaling-patterns. Hence, the rules developed for vertebrates (Peters 1983, Schmidt-Nielsen 1984, Calder 1996, Brown & West 2000) do not necessarily apply to insects. In addition, structures and processes change in function over evolutionary time, such as when locomotory structures evolve to also serve signaling, protective, predatory, mating, digging, construction, or feeding roles. Such adaptive changes in a few members of a large interspecific study group can be easily overlooked, yet can profoundly alter empirically derived conclusions about scaling patterns. Examples include the evolution of raptorial front legs in some katydids (Whitman *et al.* 1994) and the modification of male grasshopper legs for mating (Vincent, in prep.). Disparate species adaptations, compensatory mechanisms, and the unique characteristics of insects complicate scaling.

Despite these problems, an extraordinarily large number of traits scale with body size or mass in consistent ways that can be described mathematically either with the allometric equation or other models. These diverse relationships reflect important underlying developmental and evolutionary processes. The challenge is to determine their mechanistic and evolutionary basis, and to distill out the universal principles behind them.

Some scaling laws

At the most basic level, changes in size for inanimate, isometric (similar-shaped) objects, such as spheres, cylinders, and rods of uniform density, follow certain geometric laws. As isometric objects become increasingly larger, width and diameter vary directly with length, volume varies directly with mass, but mass and volume vary to the third power with length, *etc.* (Table 1). These relationships can be plotted on normal, semilog, or log-log scales to produce various linear or curvilinear patterns. Consistent divergence from isometry during development indicates allometry.

Table 1. Geometric scaling relationships for three-dimensional isometric bodies of uniform density (Bonner 2006).

Width, diameter, or circumference $\propto$ Length
Volume $\propto$ Mass
Volume or mass $\propto$ Length^3
Length, width, diameter, or circumference
$\propto$ Mass$^{1/3}$ or volume$^{1/3}$
Surface area $\propto$ Length^2
Surface area $\propto$ Volume$^{2/3}$ or Mass$^{2/3}$

Dyar's law

In the Orthoptera, most cuticular structures positively covary in size, both during growth and intraspecifically among different-sized individuals (Bégin & Roff 2004, Akman & Whitman 2008, Bidau & Marti 2008c, DeBano 2008, Lehmann & Lehmann 2008, but see Ciplak *et al*. 2008). Dyar's law (originally derived from caterpillar head capsules) suggests that each cuticular sclerite increases in linear dimensions by a constant ratio (Dyar's coefficient *or* growth coefficient) at each molt (Dyar 1890). For hemimetabolous insects, this ratio is about 1.3 (Cole 1980). Different ratios among species represent different growth strategies, and any change in the normal growth coefficient for a species during a particular molt presumably represents, either an environmental disruption, or an evolutionary adaptation in growth pattern (Sehnal 1985). Knowing the specific growth coefficient, the number of instars, and the adult size for a given species should allow estimation of sclerite sizes for hatchlings (or *vice-versa*). The square of Dyar's coefficient estimates the ratio of body surface between two successive instars (Sehnal 1985). A single Dyar's coefficient cannot accommodate the great diversity in insect growth patterns. However, size coefficients are useful when comparing differential growth and development patterns and strategies within and among species.

Ontogenetic scaling of morphology and physiology, and the ecological niche

As organisms grow, they must deal with the mechanical and physical challenges associated with increasing size. For organisms that display isometric growth, a doubling of a linear dimension will result in a fourfold increase in surface area and an eightfold increase in mass or volume (Table 1) (Hill 1950, McMahon 1984, Schmidt-Nielsen 1984). Such isometric growth would result in dramatic changes in performance and function over ontogeny. An example would be mass-specific decrease in strength, because maximum-force output of muscles scales proportionally to muscle cross-sectional area; but muscle cross-sectional area (and thus force output) increases proportionally less than mass, as size increases. Theoretically, organisms can circumvent the physical constraints of increasing body mass by either altering the rates of growth for given body parts (allometry), or undergoing ontogenetic shifts in behavior, life-history or ecology, that counter the negative effects of increased size (Dial *et al*. 2008). Insects do both.

Many insect traits scale smoothly with size or mass during development. However, unlike poikilothermic vertebrates, a great many traits in insects do not conform to theoretical scaling models, at least in terms of their physiological performance (Gabriel 1985a,b; Greenlee & Harrison 2004). In Orthoptera, some traits are size- or mass-invariant, and a great many physiological and functional traits exhibit punctuated changes that are believed to be driven by molting or ontogenetic shifts in ecology (Katz & Gosline 1992, 1993; Kirkton & Harrison 2006). For example, both African (*Schistocerca gregaria*) and American (*S. americana*) locusts exhibit punctuated developmental changes in several aspects of their locomotor performance, that are directly tied to differential predation pressures and dispersal behaviors between juveniles and adults (Katz & Gosline 1993, Kirkton & Harrison 2006). In *S. gregaria*, hind-femur growth in instars 1 to 4 is relatively isometric and absolute distance jumped is static. However, in the last nymphal instar and adult, hind-femur volume increases dramatically and jump distance triples (Gabriel 1985a,b; Bennet-Clark 1990), presumably because of different demands on adults *vs* nymphs (Kirkton & Harrison 2006). Similar scaling patterns for locomotor performance, endurance and respiratory rate are common for other Orthoptera.

Trophic performances in some grasshoppers also show sudden ontogeny changes linked to the exploitation of a different ecological niche by sexually mature adults. Maximum bite force in Eastern lubber grasshoppers (*Romalea microptera*), for example, increases only slightly throughout nymphal development, until 10 to 15 d after the final molt (Vincent, unpub.). At this time, adult females show an abrupt increase in maximum bite force, which enables them to feed on a wider range of foliage types in order to presumably offset the increased energetic requirements of oogenesis (Vincent 2006).

Likewise, theory predicts that mass-specific gas-exchange rates in insects should vary inversely with increased body size, because of the difficulty of diffusing gases through increasingly long tracheae (Greenlee *et al*. 2007). Hence, in insects, aerobic capacity and performance should theoretically decline with increased body size (Tappan 1974). However, larger grasshoppers solve this problem through developmental or evolutionary compensation. Later instars and larger species tend to have relatively greater tracheal volumes and ventilation frequencies (Greenlee & Harrison 2004, Harrison *et al*. 2006, Lease *et al*. 2006, Greenlee *et al*. 2007, Kirkton 2007), and hence, often have a greater capacity to withstand hypoxia. Similarly, flightless Orthoptera have evolved different metabolic rates and tracheal systems than flying Orthoptera. Furthermore, the relationships between size or mass and gas exchange during development are not smooth, but sinusoidal. During a single grasshopper stadium, mass can double (doubling O_2 need), while tissue growth collapses the abundant and voluminous air sacs, thus decreasing tracheal and ventilatory capacity (Greenlee & Harrison 2004, Harrison *et al*. 2006, Lease *et al*. 2006). This precipitous decline in ability to exchange gas within each stadium is one hypothesis for what, proximally and ultimately, determines the timing of molting

(Harrison *et al*. 2006). Molting resets ventilatory capacity: newly molted Orthoptera are essentially empty, their volume filled with large air sacs. Mass and size do not scale smoothly in arthropods during development.

In summary, the 5- to 400-fold increase in body mass that takes place over the course of ontogeny in Orthoptera is not always smoothly coupled to physiological and ecological performance. Instead, performance often changes dramatically after the final molt, facilitating the exploitation of a radically different social and ecological niche in sexually mature, reproducing and dispersing adult animals. This contrasts with the more gradual changes in morphology, physiology, and ecology characteristic of vertebrate ontogeny, and likely explains why Orthoptera and other insects frequently do not conform to theoretical scaling models.

Physiology and performance

Despite variations in scaling patterns (above), it is clear that insect physiology, function, ecological performance, and behavior are strongly influenced by body mass and size (Dial *et al*. 2008). Within species, titers of various chemicals (lipids, carbohydrates, proteins, elements, *etc.*) change with instar and size, and these changes relate to both development and mass (Boswell *et al*. 2008, DeBano 2008). Absolute metabolic rate tends to increase with body size, during growth and also between different-sized adults within and among species (Fielding & DeFoliart 2008), whereas mass-specific metabolic rates tend to decrease with size. Hence, larger species are generally more metabolically efficient. Absolute ingestion and defecation rates increase with body size, as does diet breadth and ability to chew through tough food (Vincent 2006). Larger individuals often have greater food reserves and starvation resistance (Slansky 1985). Likewise, the intermolt fasting period increases with each successive molt and tends to be longer in larger females than smaller males (Rackauskas *et al*. 2006). Molting also takes longer in later (larger) instars. Large size increases overwinter survival in grasshopper nymphs, but the mechanism is unknown (Landa 1992).

Exceptionally large insects may have difficulty exchanging gasses and maintaining prolonged high aerobic activity (Lease *et al*. 2006). Among grasshopper species maximum tracheal conductance scaled with mass$^{\sim 0.7}$, but estimated ventilation (during hypoxia) scaled directly with mass (Greenlee & Harrison 2004, Greenlee *et al*. 2007). As previously mentioned, muscle strength varies with cross-sectional area, and larger species and individuals, with larger-diameter muscles, are stronger and can more easily manipulate their environment. Larger individuals are often more successful in intra- and interspecific competition (Joern & Klucas1993, Denno *et al*. 1995, Chase 1996, Branson 2008). But large grasshopper species may be more prone to intraspecific competition because of higher individual food requirements (Liu *et al*. 2007). Larger species can generally run, swim, and fly faster than small species (Dudley 2000), but smaller species are typically more mobile and agile (Slansky 1985, Kelly *et al*. 2008). However, size did not affect jump distance among grasshopper species (Kirkton & Harrison 2007).

In some species, vagility is a threshold trait based on size (Donelson *et al*. 2008): those individuals that fail to acquire enough resources during development are flightless. In other polymorphic species, vagility is primarily genetically determined (Zera 2009). Because locomotory costs decrease with size, but speed and duration increase (Roff 1992, Dudley 2000), Orthoptera species that migrate long distances should be larger than nonmigrating Orthoptera. Indeed, the largest grasshoppers known (*Tropidacris* spp., up to 30 g) are strong fliers (Rowell 1983, Carbonell 1986). However, within different species of locusts, gregarious phase (migratory) adults are often (but not always) smaller and lighter than solitary phase (nonmigrating) adults (Uvarov 1977). In these cases, load-reduction is thought to favor flight. Flight is also facilitated by differential allocation of resources: migrating and vagile species and individuals have relatively larger flight muscles, but smaller ovaries, or they delay oogenesis until after migration (Uvarov 1966, 1977; Zera 2009).

Body size determines predator types, and smaller Orthoptera species and earlier instars tend to be attacked by invertebrate predators; larger species and later instars are attacked by vertebrate predators (Whitman & Vincent 2008). Size also influences both predator tactics and prey defense strategies (Dial *et al*. 2008, Bateman & Fleming 2008). Burst acceleration and maneuverability during escape from predators decreases with size (Dudley 2000, Dangles *et al*. 2007, Dial *et al*. 2008).

Because body surface area increases by volume$^{0.67}$, larger insects have relatively lower surface/volume ratios, and hence are less susceptible to surface processes such as diffusion and heat transfer. Hence, larger individuals are generally less prone to desiccation (Winterhalter & Mousseau 2008) or osmotic disruption, and so can exploit hot and dry habitats. Large size in grasshoppers may possibly allow internal water recycling, when saturated air, made hot from the heat-generating flight muscles, passes from hot thoracic tracheae into the cool abdominal tracheae, causing condensation (Heinrich 1993). Some insects are heterothermic (= periodically endothermic), which gives them a great ecological advantage (Heinrich 1993). Larger bodies produce and retain more metabolic heat than smaller bodies, because mass-specific heat loss is inversely proportional to body mass (Chappell & Whitman 1990). Hence, large body mass is critical for effective insect endothermy, especially prolonged flight on cold days, and that is why insect heterotherms tend to be large (Heinrich 1981, 1993). This is also probably the reason why there are many cold-blooded, but no warm-blooded vertebrates under 2 to 3 g (Bartholomew 1981). Larger insects can also achieve and maintain higher temperatures during solar basking (Whitman 1987, Heinrich 1993). Of course, rates of warm-up and cooling in both basking and endothermic insects are inversely related to body size, and large insects may be restricted in activity in hot climates because of overheating (Bartholomew 1981, Heinrich 1993). These same size principles apply to groups of insects: by tightly aggregating (touching), groups of locusts may increase their body temperature during solar basking. Although evaporative cooling is not an option for small insects, some large- and medium-sized grasshoppers, with greater water reserves, apparently can evaporatively cool (Prange 1996, Roxburgh *et al*. 1996). Small size limits thermoregulation, but some Orthoptera may overcome such constraints by evolving either light or dark body colors for reducing or absorbing radiant energy (Chappell & Whitman 1990, Forsman 1999, Fielding & DeFoliart 2005). But, in general, effective thermoregulation requires large size.

Finally, size and body symmetry are thought to be indicators of overall condition, with larger and more symmetrical individuals often considered more fit (Simmons 1995, Simmons & Ritchie 1996, Thornhill & Møller 1998, Berggren 2008). Likewise, body size may relate to immunocompetence *via* two competing hypotheses: larger individuals may have lower immunity because both growth and the immune system compete for nutrients, creating a tradeoff (Arendt 1997). Alternatively, larger animals may be more successful at gaining resources, and such abilities allow greater allocation to both growth and immunity (see Ryder & Siva-Jothy 2001, Schmid-Hempel 2003). However Berggren (2008) found that symmetry increased and immune response decreased with increasing body size in a katydid, suggesting that larger individuals were more fit, but that size traded off with defense.

Life history and fecundity

In insects, life-history features (development time, growth rate, clutch size, egg size, interovipostion intervals, longevity, *etc.*) often correlate with body size, both between and within species (Roff 1992, 2002; Stearns 1992; Nylin & Gotthard 1998; Branson 2008; Hodin 2009). Because of limited time and resources during development and oogenesis, the various life-history components are thought to trade off against one another, such that a change in one trait necessitates a change in another, as when faster development is accomplished by decreasing adult body size. Over evolutionary time, populations are assumed to evolve toward an optimal combination of life-history components that best fits their specific environment (*i.e.*, produces high fitness). In addition, individuals exhibit plasticity during development, and can alter life-history traits, including body size, to match current or predicted environmental conditions (Whitman & Ananthakrishnan 2009).

Although a diverse combination of life-history traits can be found in nature, general trends emerge. In the Orthoptera, development rate is often inversely related to adult body size, both within and between species (Fronstin & Hatle 2008, Lehmann & Lehmann 2008). There is also a tendency for higher survival and longer life spans in larger Orthoptera species (Uvarov 1977), and this influences fecundity because longer-lived adults can lay more eggs. In some species and populations, larger individuals live longer (Ovadia & Schmitz 2002, Miura & Ohsaki 2004, Judge *et al.* 2008), and in others, smaller individuals live longer (Rosetti *et al.* 2008, Donelson *et al.* 2008). Even the magnitude of size variation (*i.e.*, standard deviation) in a population may influence mean survival (Filin *et al.* 2008). In female insects, fecundity is usually positively correlated with body size (Honek 1993). This is the case in grasshoppers, where larger species tend to possess more ovarioles and lay larger clutches of larger eggs, but at longer intervals, than small species (Stauffer & Whitman 1997, Branson 2008). Within species, larger individuals usually lay larger clutches, and sometimes more clutches and larger eggs (Lewis 1984, Stauffer & Whitman 1997, Berner & Blanckenhorn 2006), and resorb fewer oocytes (Akman & Whitman 2008, DeBano 2008). However, these relationships vary among different populations and environmental conditions (Davidowitz 2008), and as mentioned above, exceptions abound. In some grasshopper species, larger individuals develop faster than small ones (Wall & Begon 1987, Ahnesjö & Forsman 2003, Berner & Blanckenhorn 2006).

Mating and reproduction

In many insects, including many Orthoptera, mating success is directly related to size or strength in males (Thornhill & Alcock 1983, Andersson 1994, Brown 2008, Hochkirch & Gröning 2008, McCartney & Heller 2008, Remis 2008, Sugano *et al.* 2008), or in females (Cueva del Castillo & Núñez-Farfán 2002, Rosetti *et al.* 2007, Brown 2008). Larger males often maintain larger territories, larger harems, or are better fighters (Leisnham & Jamieson 2004, Shackleton *et al.* 2005, Brown *et al.* 2006, Briffa 2008, Brown 2008, Jang *et al.* 2008), give larger nuptial gifts (Fedorka & Mousseau 2002), and produce larger spermatophores with more sperm (Wedell 1997, Schaus & Sakaluk 2001, Brown 2008), or produce them at a faster rate (Simmons 1988). Female crickets remove the small spermatophores from smaller males earlier than the large spermatophores from large males (Simmons 1986), and *Schistocerca americana* female grasshoppers remate later, after mating with a large or heavy male (Kosal & Niedzlek-Feaver 1997). Larger males may be better mate-guarders (Cueva del Castillo 2003, Cueva del Castillo & Núñez-Farfán 2008). Within specific Orthoptera taxa, calling quality (loudness, frequency, pulse rate, time spent calling, *etc.*) is often related to body size (Champagnon & Cueva del Castillo 2008, Judge *et al.* 2008, Ponce-Wainer & Cueva del Castillo 2008, Morris 2008, Römer *et al.* 2008). Such calls often attract more mates, and louder males win in intermale interactions (Greenfield 1997, Couldridge & van Staaden 2006, Mhatre & Balakrishnan 2008, Ponce-Wainer & Cueva del Castillo 2008). Hearing sensitivity in Orthoptera also correlates with body and tympanum size (Römer *et al.* 2008). Females often prefer larger males (Kosal & Niedzlek-Feaver 1997, Brown 1999, Lehmann & Lehmann 2007, Champagnon & Cueva del Castillo 2008), and females mating with larger males have been shown to have higher fecundity (Gwynne *et al.* 1984, Brown 1997, Fedorka & Mousseau 2002), or to produce larger offspring (Kosal & Niedzlek-Feaver 2007). In some species, males prefer larger females (Gwynne 1981, Kvarnemo & Simmons 1999). In other cases, body size determines alternative signaling, territorial, or mating strategies (Shelly & Greenfield 1989, Belovsky *et al.* 1996, Greenfield 1997), as when tiny males attempt to "sneak" matings or otherwise use alternative tactics to obtain mates (Cade 1980, Donelson & van Staaden 2005, Kelly 2005, Donelson *et al.* 2008, Moczek 2009).

In those species that exhibit large ranges in body size for both sexes, assortative mating sometimes occurs, whereby large males tend to mate with large females, and small males with small females (Cueva del Castillo *et al.* 1999). There are competing hypotheses for why and how this occurs, and for the fitness and evolutionary consequences of assortative mating (Crespi 1989). Size incompatibility may sometimes hinder copulation (Weissman *et al.* 2008).

Demographics and community structure

At the community level, body size influences the distribution and abundance of species (Cyr 2000, Allen *et al.* 2006). The Orthoptera follow the general rule for animals of a right-skewed (log-normal) distribution when species richness is plotted against species body size, with few small species, many medium-sized species, and some very large species (Fig. 1) (Eadie *et al.* 1987, Lewin 1987, Meyhew 2006, Whitman & Vincent 2008). As a result, in most terrestrial communities there tends to be a large number of "medium-sized" Orthoptera species. Some grassland and tropical habitats hold an incredible number of Orthoptera species at fairly high population densities (Uvarov 1977, Joern & Gaines 1990, Lockwood 1997), and it is not understood how so many similar-sized species can occupy a single community. Competition theory predicts that closely related sympatric species should diverge in body size, which reduces competition. For example, related, sympatric vertebrates often differ in body size by a factor of about 1.3, producing a graded size series among related species (Hutchinson 1959, Eadie *et al.* 1987, Lewin 1987). This clearly is not the case in Orthoptera, where many dozens of similar-sized, phytophagous species can co-exist in a single community, and sometimes in very high numbers.

Generally, smaller-sized animals have much higher population densities than do larger-sized animals (Calder 1996, Cyr 2000, White *et al.* 2007). However, this may not hold true for some groups of Orthoptera where aggregation and swarming (Uvarov. 1977, Lorch *et al.* 2005) or chemical defense lead to high local population densities in larger species (Whitman 1990).

Body size may influence population dynamics, competitive abilities, trophic interactions, and community structure (Belovsky 1986, Belovsky & Joern 1995, Ovadia & Schmitz 2002, Woodward *et al*. 2005, Filin & Ovadia 2007, Ovadia *et al*. 2007, Dial *et al*. 2008, Branson 2008, Filin *et al*. 2008). Size predicts amplitude of population fluctuations, because small species tend to be *r*-strategists, living a boom-or-bust lifestyle in unstable habitats (Price 1984, Speight *et al*. 1999). Early successional colonizers likewise tend to be small *r*-strategists with high dispersal ability (Picaud & Petit 2008). However, within species, winged individuals tend to be larger than nonwinged individuals (Zera & Denno 1997). Species size also influences mortality rates from predators and hence, the relative abundance of different-sized species (Branson 2005). Many "phytophagous" Orthoptera become more carnivorous in later instars as increased size and strength allow them to more easily overcome small arthropod prey (Whitman *et al*. 1994), and this alters community trophic relationships. Finally, evolutionarily older communities should contain larger species of Orthoptera, not only because diversity is thought to increase with ecosystem age, and higher diversity allows more outliers, but because of Cope's Law, which suggests that lineages increase in size over evolutionary time (Kingsolver & Pfennig 2004, 2007). Whether this is true for Orthoptera is still to be determined; Cope's law may not apply to insects (Newell 1949, LaBarbera 1989, see below).

Geographic patterns

Orthoptera body size varies spatially, both within and among species, with a tendency for warmer, drier, and long-season areas to contain relatively more large-sized species (Fig. 1) (Schoener & Janzen 1968; Makarieva *et al*. 2005a,b). Some Orthoptera follow Bergmann's rule, with larger individuals or species existing at higher latitudes and altitudes, but most Orthoptera follow the converse Bergmann's rule, with larger individuals and species at lower latitudes and altitudes (Mousseau 1997, Blanckenhorn & Dermont 2004, Berner & Blanckenhorn 2006, Bidau & Marti 2008b, Ciplak *et al*. 2008, Remis 2008). Which type of cline occurs may depend on overall body size and development time: larger insect species with longer development times tend to show converse Bergmann size clines, and smaller species with shorter development times tend to exhibit Bergmann size clines (Blanckenhorn & Demont 2004). This suggests that it is not season length that determines size clines, but

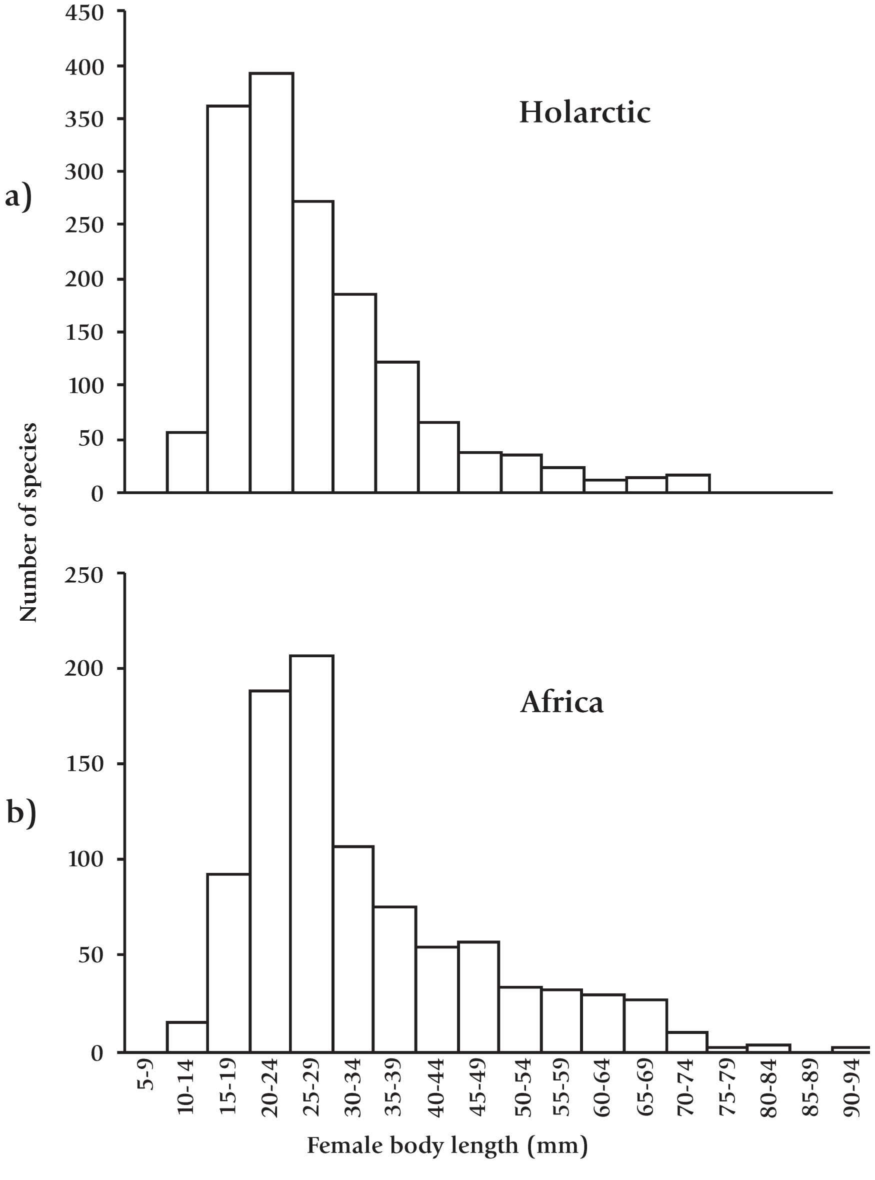

Fig. 1. Number of species *vs* female body length for grasshoppers from: a) USSR, Europe, Canada and USA combined (Bei-Bienko & Mishchenko 1963, 1964; Harz 1975; Vickery & Kevan 1985; Capinera *et al.* 2004) b) North Africa, Congo, Angola, and Madagascar combined (Chopard 1943; Dirsh 1962, 1963a,b, 1966, 1970).

season length in relation to development time (Chown & Gaston 1999); *i.e.*, some tiny, fast-developing insects are simply not constrained by the cooler temperatures and shorter seasons that occur at high latitudes, because even under these conditions, they can easily complete their lifecycles. In contrast, large-sized species, with long development times, can only survive in short-season habitats by reducing development time, which is normally accomplished by reducing adult size (Fronstin & Hatle 2008, Lehmann & Lehmann 2008). That season length, and not temperature *per se*, drives some insect size clines is suggested by the size clines that correlate with rainfall patterns (Lehmann & Lehmann 2008). However, other factors, such as population densities, forage, local pathogens, and interspecific competition, could also influence size clines (Ciplak *et al*. 2008, Lehmann & Lehmann 2008).

In addition to size variation across large geographic areas, individual species sometimes vary dramatically in body size across relatively small distances (Atkinson & Begon 1987a,b; Huizenga *et al.* 2008), and these differences could be due to genes and/or the environment (Telfer & Hassall 1999, see below). Genetic polymorphisms and phenotypic plasticity can create platykurtic or even bimodal size distributions within populations (Ahnesjö & Forsman 2003, Cherrill 2005, Donelson *et al.* 2008).

Evolution, diversification, and extinction

In animals in general, small species tend to diversify faster (LaBarbera 1989), and large species tend to go extinct at higher rates (Kingsolver & Pfennig 2007). This is thought to be because small species have more generations per unit time and also exist at higher population densities than large species. High abundance increases the opportunity for rare mutations and adaptive genetic combinations, while mutations and short generation times favor rapid adaptive evolution and lowered probability of extinction (Bonner 2006).

Evolutionary change in overall body size has a profound effect on the evolution of other traits. This is especially true for shape and function, because as discussed above, shape and physiology must change to accommodate new sizes, and because size change alters performance. Examples might include shorter, thicker legs to support larger body mass, or compressed bodies or greatly enhanced tracheal trunks or ventilatory muscles to increase gas exchange in larger insects. Molting, likewise becomes a problem in larger, heavier insects, because of the need to extract longer appendages from the old cuticle, and the gravitational deformation of the soft, newly molted individual. For those Orthoptera that hang when molting, heavier bodies require stronger tarsal hooks. Evolutionary increases in mass may preclude flight. The evolution of smaller body size likewise requires evolutionary accommodation in other traits, such as a reduction in ovariole number and clutch size, or an increase in relative egg size (see Parker & Begon 1986). For example, the tiny 2-mm long ant crickets produce eggs singly, each about 1/3 the size of the adult (Schimmer 1909). Organ complexity also generally increases with species' body size (Bonner 2006). In sum, evolutionary changes in body size require changes in numerous other traits, and alter ecological relationships, and in this way may facilitate macroevolution (Hanken & Wake 1993, Koehl 2000).

Likewise, assortative mating by size may help preserve genetic and phenotypic variation, and even promote speciation (Crespi 1989). Environmentally induced size variation within and among populations may promote the evolution of size variation followed by speciation, as different sizes come under different size-selective pressures (Whitman & Agrawal 2009). Similarly, sexual size dimorphism may promote speciation (see Butler *et al*. 2007).

What determines body size?

Size is determined by genes, the environment, and their interaction. Blanckenhorn (2009) suggests that about 30 to 40% of body-size variation in populations is heritable, and the remainder represents phenotypic plasticity, *i.e.*, the action of environmental factors on phenotype during development (see Whitman & Ananthakrishnan 2009). Teasing out the underlying genetic *vs* environmental causes of intraspecific body-size variation requires careful laboratory experimentation, including "common garden experiments", whereby different populations are reared under identical conditions (Telfer & Hassall 1999, Berner & Blanckenhorn 2006, Fronstin & Hatle 2008), often combined with a formal genetic analysis of known family design (Bégin & Roff 2004).

In Orthoptera, nearly every environmental factor known has been shown to influence body size, mass, and growth rate during development, including nutrition (Fielding & Defoliart 2008, Judge *et al.* 2008, Strengbom *et al.* 2008, Unsicker *et al*. 2008, Branson 2008, Davidowitz 2008), elements and minerals (McFarlane 1976), toughness of food (Thompson 1992, 1999), temperature (Whitman 1986, Atkinson & Begon 1988, Walters & Hassell 2006, de Jong & van der Have 2009), solar radiation (Begon 1983, Schädler & Witsak 1999), female age and date of oviposition (Cherrill 2002), season and hatching date (Atkinson & Begon 1988; Cherrill 2002, 2005), disease (Streett & McGuire 1990), parasites and parasitoids (Danyk *et al.* 2005), predator threat (Danner & Joern 2003, 2004; Whitman & Blaustein 2009), moisture (Farrow 1975, McCluney & Date 2008), photoperiod (Dingle *et al*. 1990, Kim 2008), toxins (Roberts & Olson 1999, Rathinasabapathi *et al*. 2007, Augustyniak *et al*. 2008), tactile stimulation (Simpson & Sword 2009), possibly interspecific competition (Belovsky 1986, Chase & Belovsky 1994, Belovisky & Joern 1995), and intraspecific factors, such as competition, stress, pheromones, population densities and isolation (Uvarov 1966, 1977; Fielding 2004, Simpson & Sword 2009, Berggren 2008, Branson 2008). Parental and even grandparental conditions can influence offspring size via transgenerational effects in locusts (Maeno & Tanaka 2008, Tanaka & Maeno 2008, Simpson & Sword 2009) and crickets (Weigensberg *et al*. 1998, Roff & Sokolovska 2004). Interestingly, although there is a general belief that cold rearing temperatures produce large body size in insects (the temperature-size rule) (Atkinson 1994, Van Voorhies 1996, Angilletta & Dunham 2003), many Orthoptera actually produce smaller individuals at cold rearing temperatures (Roe *et al.* 1985, Whitman 1986, Mousseau 1997, Telfer & Hassall 1999). Which pattern occurs may depend on the difference in minimum temperature thresholds for growth *vs* development (Walters & Hassall 2006). At a given low temperature, if growth can occur, but development cannot, then cold temperatures will produce a large size.

Removal or addition of individuals in a population, such as size-biased immigration or migration, can alter size distributions during a single season. Also, size-specific mortality within or between populations can alter size distributions, such as when natural enemies kill a disproportionate number of certain size classes.

A substantial portion of intraspecific size variability is genetic (Bailey *et al.* 2007), and in some cases can be traced to specific chromosome polymorphisms, such as inversions and B-chromosomes (Colombo *et al.* 2004, Rosetti *et al.* 2008, Remis 2008). Likewise, different size traits (*e.g.*, body mass, femur length, pronotum length, wing length, *etc.*) are influenced by different genes on different chromosomes, and are sometimes sex-linked) (Reinhold 1994). This allows different structures to evolve independently, as in the case of cricket wing and ovipositor lengths (Bégin & Roff 2004). Body size in Orthoptera has moderate to high heritability (Simons & Roff 1994, Mousseau 1997, Ryder & Siva-Jothy 2001, Ahnesjö & Forsman 2003, Bégin & Roff 2004, Fedorka *et al.* 2007), strongly correlates with fitness (Ryder & Siva-Jothy 2001, Blanckenhorn 2009), and is thus under strong selection (Fedorka & Mousseau 2002, Kingsolver & Pfennig 2007, Hall *et al.* 2008).

Numerous factors select for large or small size in Orthoptera, and these sort into natural- and sexual-selection factors (Bidau & Marti 2008c, Cueva del Castillo & Núñez-Farfán 2008, Hochkirch & Gröning 2008, Lehmann & Lehmann 2008). Fecundity, sexual selection, contest competition, desiccation, high temperature (see Winterhalter & Mousseau 2008), low mortality rates, and predictable, stable, long-season environments, are thought to select for large size, such as in *K*-selected species (Price 1984, Telfer & Hassall 1999, Fedorka & Mousseau 2002). In contrast, predators, time constraints (season lengths), high mortality rates, unpredictable and variable habitats, and low-food scramble-competition habitats, are thought to select for small body size, such as in *r*-selected species (Roff 1992, 2002; Stearns 1992; Blanckenhorn 2000, 2009). In pigmy grasshoppers, body color is thought to influence size evolution (Ahnesjö & Forsman 2003). There may also be a tendency for isolated, small populations to lose genetic diversity and evolve small body size (Adis *et al.* 2008, Berggren 2008). Body-size selection is obviously different in males *vs* females, and in populations living in disparate geographic areas (see below).

Of course, size interactions are complex, and there are many exceptions to the above generalities. For example, in some cases, predators may select for large, not small, insect size (Whitman & Vincent 2008), sexual selection may select for small males (Weissman *et al.* 2008), and unstable habitats may select for large-sized individuals that are better able to disperse or resist starvation. Overall, evidence suggests that Orthoptera populations can rapidly adapt (evolve) body size to match their specific habitats (Telfer & Hassell 1999, Remis 2008).

An organism represents an integration of thousands of separate functions and interactions, all of which must integrate harmoniously to produce a successful functioning phenotype of high fitness (Pigliucci & Preston 2004, Canfield & Greene 2009). Because size is intimately connected with so many traits, any change in size disrupts any number of important physiological and functional processes (Vincent & Lailvaux 2008). As discussed above, a change in body size may alter food requirements, metabolic rate, gas exchange, desiccation resistance, development time, flight capability, predator load, *etc.* Strong genetic correlations of body size with numerous other traits that are already near adaptive peaks and closely linked to fitness, should act to slow evolutionary change in size (*e.g.*, Cortese *et al.* 2002, Bégon & Roff 2004). Likewise, negative correlations between the degree of size change and other beneficial functions should select for greater canalization against phenotypic plasticity in size (Price *et al.* 2003, Pigliucci & Preston 2004).

In contrast, strong antagonistic or mutualistic pleiotropy may favor evolutionary change in size (*e.g.*, Ryder & Siva-Jothy 2001). Given strong genetic correlations, selection on any of a vast number of other traits may act to alter body size, as an indirect, associated response (Fedorka & Mousseau 2002). Many cases of intra- or interspecific evolutionary change in size (such as gene-based size clines) probably represent selection on size-related traits, and not size *per se*. The classic example is the evolution of small body size in short-season habitats, where rapid development is thought to be the trait under selection. In this case, reduced size is a secondary consequence of moving developmental switches to earlier phases of the growth curve (Nijhout & Davidowtz 2009) in order to complete the life cycle prior to habitat failure. Likewise, Bégin and Roff (2004) posit that body size in crickets is driven in part by selection on diapause and calling song. A challenge for evolutionary biologists is separating actual targets of selection from correlated secondary effects, and understanding how species maintain functional coherence and phenotypic integration during size evolution (Vincent & Lailvaux 2008).

It is interesting that insects usually solve the problem of a short season by evolving rapid development, but do it in different ways, with different repercussions for body size (Telfer & Hassall 1999). Some Orthoptera counter short growing seasons by laying large eggs, which hatch into large nymphs, which then develop rapidly into small adults (Masaki 1967, Parker & Begon 1986, Dingle & Mousseau 1994, Orr 1996, Stauffer & Whitman 1997, Telfer & Hassall 1999, Hassall *et al*. 2006). In other species, rapid development (and resulting small adult size) is accomplished by reducing the number of molts (Stauffer & Whitman 1997, Cherrill 2005, Berner & Blanckenhorn 2006), or by evolving brachypterism (Uvarov 1966, 1977; Bellinger & Pienkowski 1987). Other species evolve dark body color, which allows them to thermomaximize by solar basking, thereby speeding development without having to reduce body size (Whitman 1988, Chappell & Whitman 1990), or perhaps even enabling increased size (Ahnesjö & Forsman 2003). Some high-altitude and high-latitude grasshoppers alter metabolic rates to speed development (Dingle *et al*. 1990, Fielding 2004), and others evolve 2-y or even 3-y life-cycles (Salt 1949, Batcheler 1967, Uvarov 1977). Alaskan *Melanoplus sanguinipes* grasshoppers combine faster growth, small adult size, and a 2-y life-cycle, in their northern short-season environments; rapid growth is accomplished by increasing assimilation or allocation rates (Fielding & Defoliart 2007).

In some cases, it is not season length *per se*, but season length per generation that appears to determine adult body size. For example, the cricket, *Allonemobius fasciatus*, is univoltine in its northern range, and these northern populations exhibit a converse Bergmann's size cline. However, at a lower latitude, where it is warm enough to support two generations a year, body size is smaller. This sudden decrease in body size corresponds to the transition from univoltine to bivoltine life cycles, because now two generations must fit into the single season (Mousseau & Roff 1989). This pattern can be repeated at even lower latitudes that can fit three generations per y, and produces a "sawtooth" pattern when body size is plotted on latitude (Walker & Masaki 1989).

Sexual size dimorphism (SSD)

Sexual size dimorphism (SSD) occurs in a species when the mean sizes of the sexes differ (Fig. 2). SSD varies among Orthoptera taxa, but is generally female-biased (females are larger). In a comprehensive study, Hochkirch and Gröning (2008) found that virtually all of 1106 Caelifera species and 82% of 390 Ensifera species, showed female-biased SSD. Only 13% of Ensifera species exhibited male-biased SSD. For example, male *Scapteriscus* mole crickets are larger than females, possibly because bigger males produce louder, more attractive calls, and are selected for by females (Forrest 1983, Loher & Dambach 1989). Overall, female Caelifera averaged 37% (range: -20 to +140%) larger than males, and female Ensifera averaged 9% larger than males (-20 to +40%) (Hochkirch & Gröning 2008).

At least three hypotheses attempt to explain SSD and these derive,

Fig. 2. Adult male and female *Purpuraria erna* Enderlein (Pamphagidae) from Fuerteventura Islands, Canary Islands, Spain, showing extreme sexual size dimorphism. Photo courtesy of Heriberto López. See back cover.

in part, from the different roles of males and females in reproduction (*i.e.*, expensive eggs *vs* inexpensive sperm) (Fairbairn 1997, Blanckenhorn 2000, Fairbairn *et al*. 2007, Fedorka *et al.* 2007, Cueva del Castillo & Núñez-Farfán 2008, Hochkirch & Gröning 2008, McCartney & Heller 2008): 1) Fecundity selection on females should select for large female size, because female reproductive fitness is strongly correlated with female body size (see above, Honek 1993). 2) Sexual selection *via* male-male interactions, female choice, or the need to overpower resistant females (Andersson 1994, Cueva del Castillo & Núñez-Farfán 2008) may produce SSD. 3) Natural selection, including intersexual competitive exclusion or different ecological niches for males *vs* females, may produce SSD. These selective forces interact in complex ways to produce different types of SSD. Note that individuals that choose a large mate often enjoy higher fitness (Gwynne *et al*. 1984, Brown 1999), thus favoring both the evolution of large size and size discrimination in mating.

Why do Orthoptera have small males? Small males may benefit from lower predation rates or food requirements (Blanckenhorn 2000), from reduced ecological competition with females, from greater agility or mobility (Kelly *et al*. 2008), or from rapid development and protandry (Bidau & Marti 2008c, Hochkirch & Gröning 2008), allowing males to reach adulthood and be ready to mate when the females mature (Wiklund 1995). In cases where early maturing males (Cueva del Castillo & Núñez-Farfán 1999, Morby & Ydenberg 2001) or late-maturing females (Cueva del Castillo & Núñez-Farfán 2002) have greater reproductive success, protandry may be under strong selection. Hence, sexual selection, natural selection, or their interaction, can produce SSD (Bidau & Marti 2008c, Cueva del Castillo & Núñez-Farfán 2008, Hochkirch & Gröning 2008). High genetic covariance among traits within and between the sexes is thought to retard adaptive sexual differentiation or, at least, place an upper limit on SSD (Lande & Arnold 1983, Reeve & Fairbairn 1996, Fedorka *et al*. 2007). However, studies testing this in Orthoptera, suggest such may not be the case (Vincent & Lailvaux 2008). Hence, phenotypic integration may not always constrain the evolution of SSD.

In the Orthoptera, female-biased SSD can be accomplished in different ways (Jarošík & Honek 2007). It is often produced by increasing the number of instars for females or reducing it in males (Berner & Blackenhorn 2006, Esperk *et al*. 2007, Bidau & Marti 2008c, Hochkirch & Gröning 2008). For example, male *Acrostira euphorbiae* grasshoppers have four nymphal instars and females have six, allowing the small, 3-cm long adult males to mature 2 to 3 months before the large, 6-cm females (López *et al*. 2007). However, in many dimorphic Orthoptera, males and females undergo a similar number of molts, but males restrict growth and have shorter intermolt intervals, producing protandry.

Other dimorphic orthopteran species do not show protandry, and instead, small males reach adulthood at about the same time as females. It is interesting that in such species, males and females tend to have identical egg and hatchling size and mass, and nymphal development rates, yet adult males eclose at substantially smaller size and mass than females. Are males inferior in that they are unable to feed, assimilate, and grow as fast as females? Most likely, females are under greater selection than males for large size, because of fecundity selection, and thus maintain high growth rates. Indeed, life history theory suggests that growth rates for most animals should be near physiological maxima (Arendt 1997). However, this may not be the case for males. Males presumably could evolve to grow as fast and as large as females, but, for males of many species, there are probably advantages to growing slowly, remaining small, and delaying maturation to match that of females. Hence, in such cases, growth-maximization and development-time selection may be primarily on females, and males may be simply "coasting". If, indeed, males gain viability (= higher survival) by slowing growth and remaining small, whereas females suffer higher mortality by growing fast and large, then we would predict male-biased sex ratios in adults (assuming an equal sex ratio at hatching). Note that protandry is not always coupled with small-size selection in males. Sometimes there is selection for both protandry and large male size (Cueva del Castillo & Núñez-Farfán 1999).

Among related species, the degree of SSD sometimes varies with overall body size (Abouheif & Fairbairn 1997). Rensch's rule (originally derived for vertebrates) states that across related species, SSD will increase with increasing body size when the male is the larger sex, and decrease with increasing average body size when the female is the larger sex (Rensch 1960, Blankenhorn *et al.* 2007, Bidau & Marti 2008). Note that in both cases, male body size increases relative to female size in larger species. Neither Ensifera, Califera, nor Phasmatodea follow Rensch's rule, and in the latter two groups, SSD actually increases in larger-sized species (Sivinski 1978, Blanckenhorn *et al.* 2007, Hochkirch & Gröning 2008).

Among insects at the interpopulation level (different geographic populations within species), no clear pattern in regard to Rensch's rule emerges (Blanckenhorn *et al.* 2007, Bidau & Marti 2008). Some individual species follow the rule (*e.g.*, Lehmann & Lehmann 2008), and others do not. And, within single populations of Orthoptera, a converse Rensch's pattern was observed when individuals from the same population were reared under different conditions (food, temperature, *etc.*) (Teder & Tammaru 2005). This is possibly because, unlike males, females may already be growing as fast as possible (see above), and thus, growth and development in females may be more sensitive to environmental factors than in males (Teder & Tammaru 2005). Under poor conditions (whether in nature or the laboratory), female Orthoptera are more strongly affected than males, reducing SSD. In contrast, under good conditions, SSD increases. Thus, within individual populations, SSD increases with overall body size. However, applying Rensch's rule at the intrapopulation level may be inappropriate, because it represents environmental effects on individual development (phenotypic plasticity), as opposed to gene-controlled evolutionary effects between species. SSD may also be related to the size of nuptial gifts provided by males to females (Cueva del Castillo & Núñez-Farfán 2008). Phenotypic plasticity in instar number (perhaps as an adaptive response to variable environmental conditions), may facilitate the evolution of subsequent SSD (Esperk *et al.* 2007).

What keeps insects small?

This has long been a favorite question of biologists, and even more so now that most studies show directional selection for larger size in animals, including insects (Fedorka *et al*, 2007, Kingsolver & Pfennig 2007, Winterhalter & Mousseau 2008). Clearly biologists are overlooking something, otherwise all insects and other animals would be large (Blanckenhorn 2000, Weissman *et al.* 2008). Hypotheses for what ultimately limits insect size include: 1) **Exoskeleton**. Larger bodies require proportionally heavier exoskeletons; heavier, more costly exoskeletons eventually preclude further size increase (Currey 1967, Schmidt-Nielsen 1984, Price 1997, Greelee *et al.* 2007). Also, larger volumes require internal skeletons for tissue support (*e.g.*, tentoria), making molting (of internal cuticle) difficult. 2) **Gas exchange.** Exchange to deep tissues is difficult in large bodies. As a consequence, larger insects are presumed to require ever-increasing and complicated tracheal systems, which eventually limit the ability for additional size increase (Miller 1966, Tappan 1974, Kirkton 2007). Giant insects during the hyperoxic Carboniferous Period, support this hypothesis (Dudley 1998, 2000; Flueck *et al.* 2007). However, the safety margin for gas exchange in grasshoppers actually increases with instar, and insects seem to be able to counter large size with increased ventilation (Greenlee & Harrison 2004). 3) **Flight.** Flight may be necessary for evolutionary persistence in insect species, yet flight becomes increasingly difficult with larger size. Hence flight capability may limit size increase in insects. Indirect supportive evidence is that giant flying insects were present during the Carboniferous, when hyperoxia and perhaps greater atmospheric density made flying easier (Dudley 1998, 2000). 4) **Molting.** Insect size is limited by the deformation of soft tissues during and immediately following ecdysis. During molting, cohesive forces preserve the shapes of small insects, but gravitational forces deform large bodies, making increased size impossible for molting terrestrial animals. That many aquatic and marine arthropods are substantially larger than terrestrial arthropods supports this idea. Water supports soft bodies, reducing gravitational deformation, allowing substantially larger body sizes for marine and aquatic arthropods (McGavin 2001). 5) **Vertebrate predation.** This limits the size of insects because vertebrate predation rates increase with insect body size (McGavin 2001, Whitman & Vincent 2008). 6) **Vertebrate competition.** The ecological niches for larger-sized animals are already filled by vertebrates, which are better competitors in those size-defined niches. 7) **Open circulatory system.** Insects cannot maintain adequate flow of blood at larger sizes, because they lack a vascular system (Greenlee *et al.* 2007). 8) **Time limits to growth or life-cycle.** Insects are limited in body size, because they must complete development within a certain time frame, defined by temperature and season length, and increased body size would require increased development time (Gotthard *et al.* 2007). 9) **Increasing mortality with age**, where natural enemies or other mortality agents selects for rapid development and hence, small size (Gotthard *et al.* 2007). 10) **Metabolic rates**. Each clade has a minimum mass-specific metabolic rate, below which life is not possible (Makarieva *et al.* 2005a,b). The fact that mass-specific metabolic rates fall as mass increases, sets an upper limit to body mass. In insects, these various hypothesized limits on the evolution of large body size may counter Cope's law, the trend for increased body size in clades over evolutionary time.

Physiological mechanism for body size determination

There is much current interest in understanding the physiological and developmental mechanisms that produce and determine body size. In one respect, there are three ways to alter adult body size: alter egg size, growth rates, or development rate (which alters the amount of time to grow) (Roff 1992, Stearns 1992). These factors are intimately interconnected by tradeoffs, and must be examined in unison (Blanckenhorn 2009). Among the Orthoptera, these three traits vary widely and are largely under genetic and physiological control. At the molecular/physiological level, rapid progress is being made in understanding the mechanisms and pathways that produce size and how individuals know when to stop growing (Nijhout 2003a,b; Stern 2003; Shingleton *et al.* 2007; Riddiford 2008; Moczek

2009; Nijhout & Davidowitz 2009). Physiological regulation of, and environmental influence on body size represent proximal control of body size, whereas natural selection represents ultimate control of size, and both must be considered for an overall understanding of size (deJong & van der Have 2009. Genes transcribe ultimate factors into proximate factors.

Unanswered questions

Body size has been intensely studied during the last half century. However, researchers are still attempting to understand the proximate and ultimate determinants of size, the consequence of size, and the size patterns that we see in nature. What regulates body size over evolutionary time? How do selective factors change during development and from year-to-year, and what is the role of random and rare, but extremely strong, selective events in shaping body size (see Winterhalter & Mousseau 2008)? Which characters are actually being selected, and which simply covary as size evolves? Perhaps most size evolution is really just a byproduct of strong selection on genetically correlated traits. If one size is optimal for a given '*bauplan*', then why do we find both minute and large species living adjacent to one another (*e.g.*, pigmy grasshoppers *vs* normal grasshoppers, and pigmy mole crickets *vs* large mole crickets)? Why do some Orthoptera species in the same general geographic area follow Bergmann's rule, and others the converse Bergmann's rule? Are chemically defended grasshopper species larger than palatable species, and why? What is the role of phenotypic plasticity in body size evolution? Does size determine behavior (Dial *et al.* 2008)? Why do some taxa exhibit strong female-biased sexual size dimorphism, and others do not? What is the relationship between body size and flight? How can a single grassland support dozens of species of similar-sized grasshopper – don't they compete (*e.g.*, Behmer & Joern 2008)? These questions await answers. However, with their widespread abundance, life-history variability, and size range, the Orthoptera are ideal candidates for testing hypotheses about the causes, evolution, and adaptive value of body size.

Some methodological problems in body-size research

Body size research is complicated, given the vast number of proximate and ultimate factors that influence size. It is difficult to recognize, let alone control for, these myriad factors in any experimental design, and most researchers ignore such aspects as acclimation, symbiotic microorganisms and parental effects. Insects quickly alter their physiology (acclimate) to different conditions, and this can influence all life-history traits, including size (Whitman 2009). Because of differential phenotypic plasticity among populations, common garden experiments should include multiple treatments that mimic the conditions from each geographic area (*e.g.*, Bégin & Roff 2004). Virtually all natural and laboratory populations of Orthoptera are infected by numerous, diverse gut symbionts and sublethal pathogens that alter growth, development, body size, fecundity, vitality, *etc*. (Mead *et al*. 1988, Streett & McGuire 1990, Hinks & Erlandson 1994, Dillon & Dillon 2004). Furthermore, different Orthoptera populations may interact differently with the same microorganism. Hence, the same pathogen may strongly influence body size in one geographic population and not another. Yet, few consider accompanying microorganisms when studying orthopteran body size. Likewise, although parents influence offspring size through transgenerational effects (Stauffer & Whitman 1997, Fox & Czesak 2009), such effects are seldom accounted for. There is a tendency for laboratory colonies of Orthoptera to evolve small size over time (Adis *et al*. 2008) or to acquire sublethal pathogens, which reduce the body size of laboratory insects. Hence, laboratory rearing can alter body size, and the problem increases the longer the colony has been in the lab. Also, researchers must be cognizant that rare but powerful selective events may shape size evolution, but go undetected during the typical 1 to 3-y field study. Finally, interspecific comparisons should be corrected for phylogenies (Harvey 2000). Few studies consider such factors.

Size-sampling is also problematic (Hochkirch & Gröning 2008), because larger individuals are usually easier to find or trap (Akman *et al*. 2007). At different times of day or season, or under certain weather conditions, certain sizes may be more conspicuous and thus more likely to be sampled (Akman *et al*. 2007). Size-specific mortality or dispersal rates alter population size distributions, and this problem may increase over the course of the season. Hence, sampling of different populations should be undertaken under similar environmental conditions and similar developmental stages when possible. Sex influences sampling. Larger males may call more than smaller males, males may be conspicuously searching for mates, or gravid (larger-bodied) females may be searching for oviposition sites, and may thus be more apparent. Likewise, adult mass and body length change over the 24-h period, and over days, as newly eclosed adults put on mass. Mass does not vary smoothly with size, because of intermittent molting. Within each instar, tissue growth collapses air sacs, changing mass and expanding the abdomen, increasing body length, but not size of individual sclerites such as the thorax or femur (Lease *et al*. 2006). Also, Orthoptera often stop feeding and empty their guts before molting (Rackauskas *et al*. 2006). Individual female *Romalea microptera* grasshoppers can vary in mass by nearly 2 g and body length by nearly 1 cm, depending on recency of feeding (Whitman unpub.). Mass changes with physiological and reproductive condition. Mass and body length cycle with egg-laying in females, (Kriegbaum 1997, DeBano 2008), and with mating in males that pass large spermatophores. For example, male *Ephippiger ephippiger* katydids can lose 40% of their body mass during mating (Busnel & Dumortier 1955). Most size measurements are made on dead museum specimens, whose abdomens have shrunk.

Finally, we plead with researchers to always measure multiple structures, because of the complex allometries among different structures (Bidau & Marti 2008b,c; Ciplak *et al.* 2008), and also to take multiple measurements of the same structure on the same specimen, and to double-check data. About 5% of measurements recorded by students in my lab are erroneous, the error occurring either during the measurement itself or during data entry. Therefore, we always have two different students measure each structure, and repeat their measurements, until both agree. Likewise, we always double check database entries, and remeasure extreme outliers when possible. For paired structures, we measure both. In adult lubber grasshoppers, the left and right hind femora normally differ by 1 mm, and sometimes by as much as 5 mm. Researchers should check and calibrate equipment at least weekly, if not more frequently. Also, we urge researchers to always specify exactly how total body length is measured in both males and females, and to provide illustrations. Different authors measure body length to the end of the abdomen, ovipositor, cerci, wings, or to the distal end of the hind femora, and in some cases they do not tell how size was measured at all. This makes it difficult to compare sizes by different authors. Finally, authors should record wet mass at specific life stages, for example, immediately after molting or just prior to or after oviposition.

Conclusion

As George Bartholomew (1981) proclaimed, it is only a slight overstatement to say that the most important attribute of an animal, both physiologically and ecologically, is its size. As this review suggests, size has not only a direct effect on a vast number of physiological, functional, and ecological processes, but it serves as a great central node through which nearly all physiological and environmental factors must pass. Nutrition, toxins, photoperiod, temperature, competition, disease and predator threat all converge to alter a single trait – body size. Size, in turn, alters countless functional and performance attributes, including feeding requirements, feeding abilities, competitive ability, locomotion, antipredator defense, mating success, fecundity, *etc.* – each of these making their own contribution to fitness. Innumerable positive and negative feedback loops return consequence to cause, such as when favorable nutrition or temperature produce large size, which alters an individual's ability to acquire nutrition or heat. Size acts as a central converter, transforming numerous factors into others, including fitness factors, and converting in both directions. Size represents ecological pleiotropy.

The centrality of body size as a responding entity to both the immediate environment and to long-term selection, and also as a determinant of manifold functional and fitness outcomes, places body size at the intersection of nearly all scientific fields. Indeed, a comprehensive understanding of size requires integrating genetics, molecular biology, physiology, development, phenotypic plasticity, behavior, ecology, biogeography, and evolution, including both natural and sexual selection. And, a comprehensive understanding of physiology, ecology, behavior, and sexual and natural selection requires an understanding of size. It is this great tangle of interconnections that makes size research so vexing, but so interesting.

Caveat

There are exceptions to nearly every relationship discussed in this review. For example, body size does not always predict physiology, spermatophore size or sperm number (McCartney *et al*. 2008), displacement performance (Picaud & Petit 2008), or follow a clear size cline with altitude or latitude (Adis *et al*. 2008, Ciplak *et a*l. 2008, Lehmann & Lehmann 2008). Some traits and some environmental factors are rarely associated with body size variation. However, the fact that the various factors discussed here are, at least sometimes, related to size, requires their consideration.

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