

# **Intraspecific body size variation in insects**

**by**

**Emeline Jeanne Gouws**

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Supervisor: Prof S.L. Chown

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

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## ABSTRACT

This thesis investigates several aspects of intraspecific variation in the body sizes of insects. More specifically, it concerns how body size is distributed within populations of a species and how body size within populations varies over space and time. The motivation for this study is the relative paucity of information in the literature pertaining to how body size varies at the intraspecific level for insects, and what mechanisms might underlie this variation. In particular, it is shown that although a lognormal frequency distribution in body size is expected at all taxonomic levels, there is great variation in these body size frequency distribution patterns at the intraspecific level for insects. This study also highlights the need to consider all possible factors that might influence the pattern of body size frequency distributions, including sexual size dimorphism of a species, how many size classes or bins are used in the distributions and the sample size. Furthermore, if a better understanding of these patterns is sought, especially with regard to the mechanisms underlying how body size of a population is distributed, factors affecting the life history, physiological and ecological responses of individuals in a population need to be considered. This is also the case for geographical variation in body size of insects. Altitudinal variation in insect body size therefore, is of particular interest, and here it was used as the basis for an investigation of the possible mechanisms underlying clinal patterns in body size. Variation was found in the patterns observed for the beetle species considered in this study. Although one species (*Sternocara dentata*) did not vary significantly in mean size along the altitudinal gradient, *Thermophilum decemguttatum* and *Zophosis gracilicornis* both showed a decrease in size with altitude, contrary to what is expected from the temperature-size rule for ectotherms. The responses in the body sizes of the latter two species to several environmental variables along the altitudinal gradient, including mean annual temperature and some vegetation variables indicated that the size variation is subject to the combined effects of temperature, resource availability and resource acquisition. This finding provides support for the resource allocation switching curve mechanism (one of several alternative mechanisms) thought to underlie clinal size variation.

## OPSOMMING

Hierdie tesis ondersoek 'n verskeidenheid eienskappe van intra-spesifieke variasie in liggaams groottes van insekte. Die ondersoek is spesifiek gemik op hoe liggaams grootte versprei is binne populasies van 'n spesie en hoe liggaams grootte sodoende varieer oor tyd en ruimte. Motivering vir hierdie studie gaan gepaard met die onvoldoende informasie beskikbaar oor hoe liggaams grootte varieer tussen individue van 'n spesie en ook watter meganismes hierdie variasies tot grondslag kan hê. Alhoewel dit die verwagting is dat die liggaams grootte van alle taksonomiese vlakke 'n log-normale frekwensie verspreiding sal aanneem, is daar huidig 'n groot verskeidenheid patrone in die frekwensie verspreidings binne insek spesies. Hierdie studie beklemtoon dat daar 'n groot behoefte is daaraan om alle faktore wat moontlik die patrone van liggaams grootte frekwensie verspreidings in ag te neem. Hierdie faktore sluit in die seksuele dimorfisme in grootte, die hoeveelheid grootte klasse wat gebruik word, asook die aantal monsters wat gebruik word. Om hierdie patrone beter te verstaan, veral met betrekking tot die meganismes wat die liggaams grootte verspreiding van 'n spesie populasie veroorsaak, is dit nodig om faktore wat die lewens geskiedenis, fisiologie en ekologiese reaksies van individue in ag te neem. Dit is ook die geval vir geografiese variasie in die liggaam grootte van insekte. Daarom is die variasie in insek liggaams grootte met hoogte bo seespieël veral van belang en was hier gebruik in 'n ondersoek tot die meganismes wat geografiese variasie in liggaams grootte moontlik maak. Daar was weereens variasie teenwoordig tussen die patrone in liggaams grootte van die drie kewer spesies wat ondersoek is. Alhoewel een spesie glad nie betekenisvol gevarieer het met hoogte bo seespieël nie (*Stenocara dentata*), het *Thermophilum decemguttatum* en *Zophosis gracilicornis* albei verklein in liggaams grootte met hoogte bo seespieël. Die reaksies in liggaams grootte in die laasgenoemde twee spesies tot 'n verskeidenheid omgewings veranderlikes langs die hoogte gradiënt, soos byvoorbeeld gemiddelde jaarlikse temperature en sommige vegetasie veranderlikes, het daarop gedui dat die variasie in liggaams grootte moontlik onderworpe was aan die gekombineerde effekte van temperatuur, hulpbron beskikbaarheid en hulpbron verwerfing.

“Between the shores of the oceans and the summit of the highest mountain is a secret route that you must absolutely take before being one of the sons of earth.”

Khalil Gibran

“When we reach the mountain summits we leave behind all the things that weigh heavily on our body and our spirit. We leave behind all sense of depression; we feel a new freedom, a great exhilaration of the body no less than the spirit.”

Jan Christiaan Smuts

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# **Chapter 1**

## **General Introduction**

Of all organismal characteristics, body size is arguably the most significant and visible. Therefore, it has long been a subject of interest in the fields of ecology and physiological ecology (Peters, 1983; Calder, 1984; Gaston & Blackburn, 2000). Not only is body size one of the most obvious characteristics of an organism, but it is also known to correlate with many aspects of life history, morphology, and physiology (Peters, 1983; Calder, 1984), and ecological aspects such as species abundance and range size (Blackburn & Gaston, 1996a; Gaston & Blackburn, 2000). Additionally, the relative ease of determining body size has meant that it has been measured in a great number of animals (see for example Brown & Nicoletto, 1991; Blackburn & Gaston, 1994a, 1996b; Gaston & Blackburn, 1995, 1996; Novotný & Kindlmann, 1996; Poulin & Morand, 1997; Arita & Figueroa, 1999; Gardezi & da Silva, 1999). In most cases, body mass is the preferred body size measure used for studies of size variation because it is comparable on a universal scale between different families and orders of animals (Gaston & Blackburn, 2000). One possible disadvantage to using this trait, however, is that the mass of an individual varies over time. An alternative trait used is that of a linear variable, such as body length, but these measures are thought to have 'limited comparative value' (Gaston & Blackburn, 2000).

Variation in body size of vertebrates has thus far enjoyed most attention (birds, Blackburn & Gaston, 1994a, 1996b; Gaston & Blackburn, 1995, 1996 and mammals, Brown & Nicoletto, 1991; Arita & Figueroa, 1999; Gardezi & da Silva, 1999) and, although an increasing number of studies concerning body size has been undertaken for invertebrates (see for example Novotný & Kindlmann, 1996; Finlay *et al.*, 2006), information is still largely lacking, especially for insects. What is of great interest for insect species is that they range in body size (linear measurements) from the 139  $\mu\text{m}$  of the wingless males of a parasitic wasp species (*Dicopomorpha echmepterygis*,) to the largest species of goliath beetles and elephant beetles (*Goliathus goliatus*, *Goliathus regius*, *Megasoma elephas*, *Megasoma actaeon*, with sizes ranging from 11 – 16.7 cm, see Gahlhoff, 1998; Williams, 2001; Gaston & Chown, in press).

Variation in body size forms the foundation for a number of macroecological patterns, including Bergmann's rule, which describes an increase in body size with a decline in temperature (Bergmann, 1847; translated by James, 1970; but see Blackburn *et al.*, 1999)

and Cope's rule, which describes the tendency for animal groups to become larger over evolutionary time (Stanley, 1973; but see Jablonski, 1997) among others. However, the generality of these patterns remains controversial (Bergmann's rule, Geist, 1987, 1990; Paterson, 1990; Ashton *et al.*, 2000; Cope's rule, see Jablonski, 1997; Ashton, 2001), and it is likely that they will differ for different taxa (especially if one compares endo- and ectotherms, or vertebrates and invertebrates).

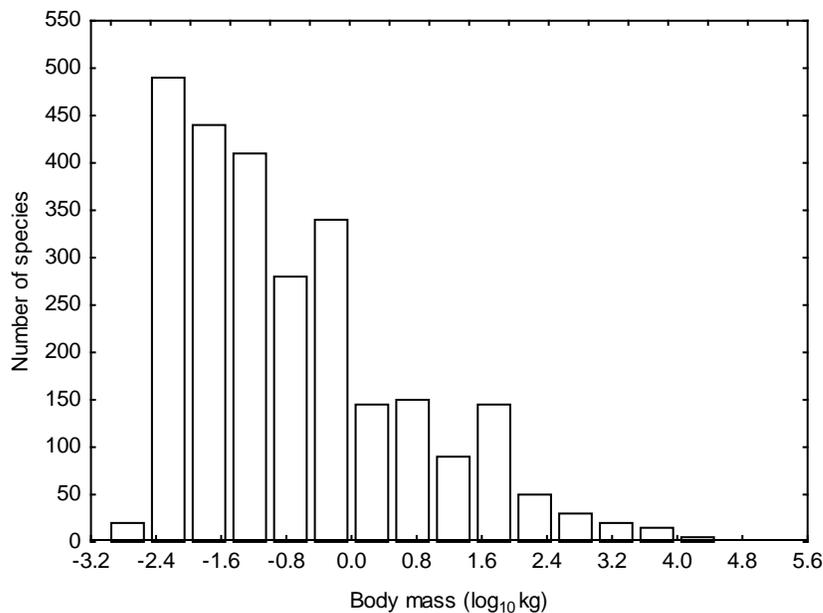
One method used for studying the structure and pattern of variation in body size within or between animal assemblages is the body size frequency distribution. Body size frequency distributions can be studied at either the interspecific or intraspecific level. Furthermore, their greatest use is in providing information on the ecological and evolutionary processes that govern the structure of animal assemblages, especially with regard to the underlying allometric, evolutionary and ecological constraints governing size variation (Bakker & Kelt, 2000; Smith *et al.*, 2004).

## **BODY SIZE FREQUENCY DISTRIBUTIONS**

### **Interspecific body size frequency distributions**

Frequency distributions in general have been used with the purpose of statistically simplifying or clarifying information on the range of values for a given variable, such as body size (Elderton, 1938; Gardiner & Gardiner, 1979; Sokal & Rohlf, 1995). The interspecific body size frequency distribution refers to the distribution of the number of species of different sizes (often grouped in different size classes, see Sokal & Rohlf, 1995). It has been thoroughly explored for a range of taxa with patterns in the frequency distribution differing between them (Morse *et al.*, 1985; Morse *et al.*, 1988; Brown *et al.*, 1993; Blackburn & Gaston, 1994a, b; Cambefort, 1994; Chown & Steenkamp, 1996; Gaston *et al.*, 2001; Maurer *et al.*, 2004; Smith *et al.*, 2004). The patterns vary from being right-skewed, to bimodal, to symmetric or left-skewed (see Kozłowski & Gawelczyk, 2002). Of these, the right-skewed body size distribution is the most common for both untransformed and log-transformed body size data (e.g. Figure 1; see also Gaston & Blackburn, 2000; Kozłowski & Gawelczyk, 2002). This particular pattern has been found for birds (e.g. Blackburn & Gaston, 1994a, b), mammals (Brown *et al.*, 1993; Smith *et al.*,

2004) and insects (Morse *et al.*, 1985; Morse *et al.*, 1988; Cambefort, 1994). However, the skewness of a body size frequency distribution tends to be scale-dependent in the sense that the skew declines or the pattern changes at smaller scales (Bakker & Kelt, 2000; Kozłowski & Gawelczyk, 2002). One of the reasons for a decline in the skewness of a body size frequency distribution is thought to be that at the smaller scales there are fewer species and less chance for larger species to be present relative to the presence of smaller species. Therefore, body size distributions become more variable in shape at local scales (Kozłowski & Gawelczyk 2002).



**Figure 1.** Body size frequency distribution of the mammals of the world. Redrawn from Gardezi & da Silva (1999).

The shape of the distribution also varies between different systematic groups, for example differences in the shape of the body size distribution between classes and orders (Poulin & Morand, 1997; Maurer, 1998; Gardezi & da Silva, 1999). The superposition of size distributions of the smaller taxonomic hierarchies (e.g. orders), which vary in shape, is suggested to result in the right-skew of the distribution at the higher taxonomic levels (i.e. classes) (Kozłowski & Gawelczyk, 2002; see also Chown & Gaston, 1997 for ‘taxonomic inclusiveness’). More importantly, the optimization models discussed by

Kozłowski and Gawelczyk (2002) showed that intraspecific body size optimization predicts that the right-skew pattern would prevail over a diversity of other patterns. However, the patterns observed could and probably are also influenced by incomplete data sets and to a small extent, the size measure used (mass or length), causing a bias in the pattern.

Biases found in body size distributions are likely to be due to either the absence of species from the distribution, measurement error pertaining to the measures of body size, or to a bias in the capture of species with different body sizes (Blackburn & Gaston, 1994b). It would appear that the missing species are most often of small size as newly discovered species are generally small bodied (Blackburn & Gaston, 1994a, b, c, 1995; Gaston & Blackburn, 2000). Additionally, as more species are discovered, species body size distributions are bound to change in shape (Blackburn & Gaston, 1994c). Problems concerning measurement error are due mainly to measurement accuracy varying with body size, although biases here are likely to be small (Blackburn & Gaston, 1994b). One problem that might be common, though, is the use of single individual measurements as representative of a species, when this is unlikely to be the case (see Farrell-Gray & Gotelli 2005). Problems with body size measurements are also caused by the fact that especially in the higher taxa, animals have indeterminate growth, and therefore body size varies throughout their lifetimes (Blackburn & Gaston, 1994b). Lastly, species of certain body sizes are more susceptible to capture because they are rare, of low abundance or more likely to be caught by some sampling methods, therefore causing a bias in the size distribution (Blackburn & Gaston, 1994b).

### **Intraspecific body size frequency distributions**

Intraspecific size distributions concern the number of individuals of a particular species and how the body sizes of those individuals are distributed. Somewhat surprisingly, relatively little work has been done concerning intraspecific body size distributions of invertebrates compared to interspecific studies. Some insect studies that have reported intraspecific size distributions based on length measures include those done on an anthrophorid bee species (Alcock, 1984), neotropical *Anopheles* species (Lounibos, 1994), *Drosophila* (see David *et al.*, 1997), coccinellid species (Evans, 2000) and a

floodwater mosquito species (Gleiser *et al.*, 2000). Within these species, the body size frequency distributions ranged from being right-skewed for males of the anthrophorid bee, *Centris pallida* (Alcock, 1984), left-skewed for two mosquito malaria vector species, *Anopheles (Nyssorhynchus)* (Lounibos, 1994), normally distributed for *Drosophila melanogaster* females (David *et al.*, 1997) and two ladybird species (Evans, 2000), and varying from being right-skewed, to bimodal, to left-skewed and back to right-skewed for the floodplain mosquito *Aedes albifasciatus* during the rainy season (Gleiser *et al.*, 2000). However, statistical tests were rarely conducted to confirm the significance of the skewness of these distributions.

Similar to interspecific body size frequency distributions, the shape of intraspecific distributions is influenced by several factors. Such factors include the degree of sexual size dimorphism (SSD) of a species (see Teder & Tammaru, 2005), the sampling method and sample size, measurement error and the number of size class groupings (see Sokal & Rohlf, 1995; Loder *et al.*, 1997). Time and season of sampling would also influence the body size frequency distributions (Gleiser *et al.*, 2000). In insects, females are generally larger than males (Helms, 1994; Anholt, 1997; Fairbairn, 1997; Teder & Tammaru, 2005), although exceptions do occur (e.g. Kraushaar & Blanckenhorn, 2002). These differences in size between the sexes could lead to the males and females of a species having different size distributions, affecting the shape of the combined size distribution for that species. Furthermore, male individuals of several species, and the females of others, show a considerable degree of polymorphism in body size, especially in the form of exaggerated morphological traits of large individuals (Emlen & Nijhout, 2000). Moreover, Rensch's rule describes the general pattern where in taxa where males are the larger sex, SSD increases with body size, while it decreases in taxa where females are the larger sex. The occurrence of this pattern has been investigated for many taxa, including insects and has found substantial support (Abouhief & Fairbairn, 1997; Fairbairn, 1997). Nevertheless, Teder and Tammaru (2005) have recently shown that there is substantial intraspecific variation of SSD and that environmental conditions may strongly influence the degree of intraspecific SSD. Therefore, it is important to sample enough males and females of a species to give a true representation of the body size distribution of that

species and to overcome possible biases toward the body size distributions of a certain sex.

It is known that certain species of insect are more likely than others to be caught by certain sampling methods (see for example Uys & Urban, 1996). Consequently, it might be assumed that a bias could exist where within a species, larger or smaller individuals are more likely to be caught than the other when using a certain sampling method (see Blackburn & Gaston, 1994b for interspecific sampling bias). However, this bias would probably not have as significant an effect on the shape of the body size distribution within a particular species, as it would have at the interspecific level. A large sample size will give a more accurate representation of what the size frequency distribution would be for a given species, while changing the limits of the size classes used to construct the histogram of the size frequency distribution may for example alter the appearance of a distribution or even change the apparent position of the body size mode of the species (Sokal & Rohlf, 1995). As is the case for interspecific body size distributions, problems concerning measurement error are due mainly to measurement accuracy which varies with body size and over time, although the effects on intraspecific size distributions are not likely to be significant (see Blackburn & Gaston, 1994b).

## **SPATIAL AND TEMPORAL VARIATION IN BODY SIZE**

### **Spatial variation in body size**

#### *Latitudinal or altitudinal variation in body size*

Spatial variation in body size of animals has long been a subject of interest to ecologists (Rensch, 1938; Mayr, 1963; James, 1970; Gaston & Blackburn, 2000; Chown & Nicolson, 2004) and is encompassed in two rules, i.e. Bergmann's rule and James' rule. The best known is Bergmann's rule, which describes a larger body size in cooler environments among closely related homoeothermic animals (Bergmann 1847; translated by James, 1970). Therefore, the rule pertains to variation in body size between species of the same genus. It was later suggested by Rensch (1938) and Mayr (1963) that such variation also characterizes individuals of the same species. Following the suggestion of

James (1970) that inter- and intraspecific variation in body size should be considered separately, Blackburn *et al.* (1999) suggested that the intraspecific version of Bergmann's rule be called James's rule. Therefore, James' rule can broadly be defined as '...the tendency for geographical variation in mean body size within species...' (Blackburn *et al.*, 1999). They also suggested that Bergmann's rule be reformulated as '...the tendency for a positive association between the body mass of species in a monophyletic higher taxon and the latitude inhabited by those species' (Blackburn *et al.*, 1999). This proposed definition expands the rule to include both endo- and ectothermic animals and takes account of species not only within genera, but also at higher taxonomic levels, for example within families and orders.

These two rules clearly distinguish inter- and intraspecific spatial variation in body size, which have very different underlying mechanisms. Interspecific body size variation is an epiphenomenon of four factors, i.e. intraspecific variation in body size, variation in species richness, species identity and phylogenetic diversity, as well as species selection or replacement along a spatial gradient (Gaston & Chown, in press).

For insects, an intraspecific increase in size with latitude or altitude, i.e. James's rule, holds for the fruit fly species *Drosophila robusta* (Stalker & Carson, 1948), one desert darkling beetle species (Krasnov *et al.*, 1996), both larval and adult body sizes of the ant lion *Myrmeleon immaculatus* (Arnett & Gotelli, 1999a), wild caught individuals of two cactophilic fruit fly species, *Drosophila aldrichi* and *D. buzzati* (Loeschcke *et al.*, 2000), the burying beetle species, *Nicrophorus investigator* (Smith *et al.*, 2000) and workers of the holarctic ant species, *Leptothorax acervorum* (Heinze *et al.*, 2003). These studies all concerned either latitudinal or altitudinal body size variation, used as proxies for temperature. The occurrence of the body size trends described above has been ascribed to factors such as habitat productivity (Krasnov *et al.*, 1996), photoperiod effects, which act as a signal for an increase or decrease in growth rate during development (Arnett & Gotelli, 1999a), the seasonality of the environment and food availability together with temperature (Arnett & Gotelli, 1999b, 2003), resource limitation in arid environments (Loeschcke *et al.*, 2000) and selection for enhanced fasting endurance (Heinze *et al.*, 2003). Starvation resistance has been identified as one of the most important factors affecting intraspecific size variation in insects (Cushman *et al.*, 1993; Blackburn *et al.*,

1999). Responses in body size to different temperature regimes have enjoyed considerable attention in *Drosophila melanogaster*, where evolution in colder temperature conditions gives rise to larger individuals (Partridge *et al.*, 1994).

An opposite trend, namely an intraspecific decline in body size with an increase in latitude or altitude (thus temperature) has been found for insects, such as the field cricket, *Teleogryllus emma* (Masaki, 1967), the striped ground cricket, *Allonemobius fasciatus* (Mousseau & Roff, 1989; Mousseau, 1997), some darkling beetle species (Krasnov *et al.*, 1996), two grasshoppers, i.e. *Melanoplus sanguinipes* and *M. devastator* (Orr, 1996) and the weevil species *Ectemnorhinus viridis* (Chown & Klok, 2001; see also Chown & Klok, 2003). Masaki (1967) proposed that such a converse trend might be a result of the 'climatic selection on the genetic basis for duration of development'. In univoltine species, growing season length has been proposed to be the most important factor determining ultimate adult body size (Mayr, 1963; see also Masaki, 1967). Growing season length tends to be longer in lower latitudes (or altitudes), causing an increase in the time available for development and ultimately a larger body size (Mousseau, 1997). In a longer growing season, more than one generation could potentially be completed, which causes a 'saw-tooth' latitudinal body size pattern within a species (Masaki, 1967; Roff, 1980; Mousseau & Roff, 1989; Chown & Gaston, 1999). An increase in season length is expected to cause the generation time for one or more of the generations to increase, leading to an increase in body size (Roff, 1980). A consequent shift from being univoltine with a longer growing season, to being bivoltine with a shorter growing season, for instance, would result in a shift in body size, which will ultimately generate a saw-tooth geographical pattern in body size (Roff, 1980; Mousseau & Roff, 1989). It would appear, however, that the underlying factors influencing the observed patterns are more complex than is described above, with numerous factors contributing to these patterns.

Alternative mechanisms have been suggested by Chown and Gaston (1999) for the occurrence of these contrasting patterns. These authors proposed that the patterns are a result of the separate effects of temperature and the seasonality of an environment on body size. Therefore, for an increase in size with latitude (or altitude) to occur Chown and Gaston (1999) proposed that differential sensitivity of growth and development to

temperature (van der Have & de Jong, 1996) would be the most likely cause. A decrease in size with latitude (or altitude) would be associated with growing season length and developmental time (Chown & Gaston, 1999). However, several problems have been identified to underlie these predictions, including the recent rejection of the arguments presented by van der Have and de Jong (1996) about the differential sensitivity of growth and differentiation to temperature (see Kozłowski *et al.*, 2004; Gaston & Chown, in press). Furthermore, it has been pointed out that the explanations proposed by Chown and Gaston (1999) were not completely developed in the framework of life-history parameters (Gaston & Chown, in press). It has recently been shown by Blanckenhorn and Demont (2004) that empirical evidence does support the mechanisms proposed by Chown and Gaston (1999) (see also Chown & Klok, 2003). Therefore, the proposed mechanisms have been recast in the context of life history parameters, such as the models proposed by Roff (1980) and subsequently the models regarding switching curves resulting from optimization of resource acquisition and allocation, proposed by Kozłowski (1992) and Kozłowski *et al.* (2004) (see Gaston & Chown, in press).

Following the models proposed by Kozłowski (1992) and Kozłowski *et al.* (2004), the switch of resource allocation from growth to reproduction in a univoltine species, should occur when the optimal body size is reached. Several factors influence optimal body size, including season length, growth rate and time constraints (Nylin & Gotthard, 1998; Kozłowski *et al.*, 2004). With a decrease in season length, an increase in growth rate could be accomplished under time constraints, therefore leaving the change in optimal size to a minimum (relative to a longer growing season) and increasing the overall fitness of an organism (Nylin & Gotthard, 1998; Gaston & Chown, in press). Alternatively, for an increase in season length an increase in developmental time would be advantageous. However, following the models proposed by Roff (1980), developmental time will increase to the point where the addition of a second generation will be more beneficial than large size. Therefore, a saw-tooth pattern would result along with a change in the switching curve (Gaston & Chown, in press). Other important influential factors influencing geographical variation in body size and worth incorporating into these models include mortality, availability of resources and the ability

of an organism to resist starvation, especially where there is a diapausal or over wintering stage (Chown & Gaston, 1999; Arnett & Gotelli, 2003).

More recently, however, and based on their work on a temperate cricket species, Walters and Hassal (2006) have shown that the temperature-size rule could also be explained by the biophysical model and its assumptions proposed by van der Have & de Jongh (1996). They illustrated that the explanations to the rule lie within the relationship between the minimum threshold temperature for development ( $TT_D$ ) and the minimum threshold temperature for growth ( $TT_G$ ) and not the slopes of the rates of change of development and growth with temperature, as was originally suggested by van der Have and de Jongh (1996).

The explanations suggested by these studies have been highly contested (see Kozłowski *et al.*, 2004) and the presence of one general explanation for the temperature-size rule in ectotherms has been rigorously evaluated and questioned (see Angilletta & Dunham, 2003). Here it is important to acknowledge that there is still no general consensus as to whether the occurrence of patterns such as a larger body size in colder environments (i.e. the temperature-size rule, Atkinson, 1994) is an adaptive response (Roff 1980; Kozłowski *et al.*, 2004) or is a result of 'physiological constraints' caused by temperature effects (van der Have & de Jongh, 1996; Walters & Hassal, 2006). Most likely, the occurrence of these patterns are a result of a more complex set of factors and not necessarily because of a single general explanation.

### **Temporal variation in body size**

Several researchers have reported how intraspecific body sizes of insect species vary within and between years and/or seasons (e.g. Sequeira & Mackauer, 1993; Yuval *et al.*, 1993; Gleiser *et al.*, 2000; Evans, 2000; Smith *et al.*, 2000). Species that have been studied thus far for seasonal variation in body size include *Drosophila* (Tantawy, 1964; Kari & Huey, 2000), tsetse flies (Rogers & Randolph, 1991), a parasitoid wasp species (Sequeira & Mackauer, 1993), mosquitoes (Yuval *et al.*, 1993; Gleiser *et al.*, 2000) and a beetle species (Ernsting & Isaaks, 1997). The effects of developmental temperature and food availability and quality are probably most influential in shaping the observed patterns. Studies done on interannual variation in body size of species, although

seemingly less common than those for seasonal variation, include work on an anthophorid bee species (Alcock, 1984), stoneflies (Haro *et al.*, 1994), burying beetles (Smith *et al.*, 2000) and ladybirds (Evans, 2000). In these examples, both evidence for and against interannual variation in body size has been found.

Within a season, adult body size is strongly dependent on the interactions of many life history traits and the processes or mechanisms which govern them. Here the effects of time constraints, resource availability and temperature on life history traits such as growth, development and mortality (or risk thereof) are the most prominent (Kozłowski, 1992; Ayres & Scriber, 1994; Nylin & Gotthard, 1998). In fact, several species are able to increase growth rate to compensate in body size for poor conditions (i.e. time constraints, temperature and food availability, e.g. Tseng, 2003; Strobbe & Stoks, 2004). Therefore individuals of these species can obtain final body sizes of less variance than would be expected otherwise (Nylin & Gotthard, 1998; Markgraf *et al.*, 2003; Tseng, 2003; Strobbe & Stoks, 2004). Conversely, it is not always the case that longer time for growth would result in a larger size being reached (Kause *et al.*, 2001). Rather, the quality and availability of resources throughout the season and extended periods of risk of predation, often has marked effects on the final body sizes that are reached within seasonal time constraints (Nylin & Gotthard, 1998; Kause *et al.*, 2001; Rodrigues & Moreira, 2004). These factors and their effects could very well also be important influentially for interannual variation in body size, in conjunction with the effects of other environmental factors such as for example annual rainfall.

## **AIMS OF THIS THESIS**

Because so few studies have been done concerning intraspecific body size distributions for insects, the first aim of this thesis is to investigate intraspecific body size (mass and length) distributions in insects. Of particular interest here is what the patterns of intraspecific body size distributions are for the different insect groups. As a consequence of this lack in studies concerning intraspecific patterns, it is impossible to make generalisations about the patterns of these distributions. Nevertheless, on theoretical grounds, one would expect the distribution of untransformed body size data where

individuals were collected from a single population from the same locality to be right-skewed and that a log transformation would remove the skew (May, 1981; Quinn & Keough, 2002). The right-skew is expected due to the influence of numerous factors which govern a populations' dynamics, including physical factors in their environment, their food supply, competition and predation (May, 1981).

Similarly, the number of studies of temporal variation in altitudinal body size patterns within a species is surprisingly small. Therefore, the second major aim of this thesis is to investigate the spatial (altitudinal) and short term temporal (yearly) variation in body length within three beetle species (*Stenocara dentata*, *Thermophilum decemguttatum*, and *Zophosis gracilicornis*). The three beetle species also represent two different trophic groups, with the carabid species being carnivorous feeding on other ground-dwelling insects (Scholtz & Holm, 1985; Picker *et al.*, 2002), and the two tenebrionid species being scavengers of dead animal and plant material, i.e. detritivores (Scholtz & Holm, 1985; Picker *et al.*, 2002).

Several hypotheses have been proposed to explain the patterns of variation found in ectotherms. Here I aim to gain insight into whether the pattern of body size variation is only an epiphenomenon of the differential effects of temperature on growth and development (van der Have & de Jongh, 1996; Walters & Hassal, 2006) or whether it is a consequence of natural selection (Roff, 1980; Kozłowski *et al.*, 2004) which might be responsible for the altitudinal patterns of body size variation in these three beetles. Furthermore, Makarieva *et al.* (2005) recently proposed another, alternative explanation based on a temperature independent minimum value of mass specific metabolic rate.

Subsequently, because any study on the adult body sizes of beetles really concerns the effects of environmental variables on the larval stages during their development (Krasnov *et al.*, 1996), several other morphological features are examined to gain insight into altitudinal variation in morphology. As no studies have thus far considered the patterns of spatial autocorrelation in these traits, despite the fact that such autocorrelation is likely and important (see Lennon 2000 for a discussion of spatial autocorrelation) an investigation is conducted concerning the spatial autocorrelation of body length of the beetles to ascertain whether it is spatial structure, environmental variation, or their interaction that accounts for most variance in body size (see Legendre & Legendre,

1998). To this end, relationships between size variation and several biologically meaningful environmental variables are also sought to provide insight into the possible mechanisms responsible for the size clines, if such relationships exist at all. In addition, I explore the consistency of the body size clines for the beetle species between the different years of sampling.

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## **Chapter 2**

### **Intraspecific body size frequency distributions of insects**

## INTRODUCTION

Body size influences numerous aspects of the life history, morphology, physiology and ecology of individuals and species (Peters, 1983; Calder, 1984; Blackburn & Gaston, 1996a, 1999; Gaston & Blackburn, 2000). In turn, these variables may feed back to influence the body size of a species or individual, especially via the size-dependence of production and mortality rates (Kozłowski & Weiner, 1997; Kozłowski & Gawelczyk, 2002; Kozłowski *et al.*, 2003). One of the most significant ways of investigating these interactions and how they structure the size of assemblages or of species is by examining the form of the body size frequency distribution (BSFD). Based on the form of this distribution, a range of hypothetical mechanisms have been proposed and tested to account for its shape (Brown *et al.*, 1993; Blackburn & Gaston, 1994a, 1996a; Chown & Gaston, 1997; Kozłowski & Weiner, 1997; Maurer, 1998a; 1998b; Kozłowski & Gawelczyk, 2002). Therefore, it is no surprise that the BSFD has enjoyed considerable attention at both the inter- and intraspecific levels, and especially for vertebrate taxa (Brown *et al.*, 1993; birds, Blackburn & Gaston, 1994b,c; Gaston & Blackburn, 1995, 1996; Polo & Carascal, 1999; Blackburn & Gaston, 1994a, 1996b; and mammals, Brown & Nicoletto, 1991; Arita & Figueroa, 1999; Gardezi & da Silva, 1999; Bakker & Kelt, 2000; Maurer *et al.*, 2004; Smith *et al.*, 2004). How the BSFD is likely to change with both partial and comprehensive studies, at different spatial scales, and at different taxonomic levels is now reasonably well understood (Gaston & Blackburn, 2000).

However, for insects knowledge of BSFDs is not as well developed. Although the interspecific BSFD has been examined in a wide variety of insect assemblages (Hutchinson & MacArthur, 1959; Morse *et al.*, 1985; Cambefort, 1994; Novotný & Kindlmann, 1996; Chown & Steenkamp, 1996; Gómez & Espadaler, 2000; Dixon & Hemptinne, 2001; Espadaler & Gómez, 2002; Gaston *et al.*, 2001; Ulrich, 2006), investigations of the intraspecific BSFD are comparatively rare. Moreover, knowledge thereof has typically been an incidental function, or by-product, of studies with other goals in mind (e.g. Alcock, 1984; Lounibos, 1994; David *et al.*, 1997; Evans, 2000; Gleiser *et al.*, 2000; Tatsuta *et al.*, 2004). In consequence, in these studies sample sizes are often small and little effort is made to distinguish the sexes despite the fact that substantial sexual size dimorphism is typical of insects (Teder & Tammaru, 2005; Gaston

& Chown, in press). Moreover, statistical analyses of the form of these BSFDs are rarely reported, and where this is done it seems likely that small sample sizes and inattention to issues such as size class selection and sampling season are likely to confound the outcomes (see discussion in Sokal & Rohlf, 1981; Loder *et al.*, 1997; Gleiser *et al.*, 2000). Nonetheless, understanding the form of the BSFD is a first step in assessing the likely mechanisms that might underlie such distributions (Kozłowski & Gawelczyk, 2002).

Therefore, the aim of this study is to investigate explicitly intraspecific body size frequency distributions for a range of insect taxa, taking into account the need for adequate sampling, assessments within rather than between seasons, and the likely influences of sexual size dimorphism. Of particular interest is what form the intraspecific BSFDs will take. One might expect a lognormal distribution on the grounds that growth is a multiplicative process, and independent multiplicative effects will lead to a lognormal distribution (May, 1981). However, this expectation presumes little interaction between individuals and identical growth conditions (Gaston & Chown, in press), and does not take into account the fact that individual size is the outcome of a life history switch between growth and reproduction under different environmental circumstances (Kozłowski *et al.*, 2004).

## **MATERIALS AND METHODS**

When considering body size distributions within a species, it is important to keep in mind that individuals from different populations (e.g. populations from different altitudinal sites) will vary in their mean body sizes, both spatially and temporally, as does mean density (Pielou, 1977). A population should also be sampled over a short-term temporal scale (i.e. days) because the dynamics of a population (for example birth and death rates) govern abundance and could therefore influence the shape of the size frequency distribution of a population (see Pielou, 1977). Therefore, in this study sampling of all the individuals for a given species was undertaken from the same population or from one location during the same day or week of sampling. All species were collected in the Western Cape Province of South Africa (Table 1). Only species from which 100 or more individuals could be collected from the same location were included in this study, and

each species was sampled according to the method considered most effective for sampling it (Uys & Urban, 1996; Scholtz & Holm, 1985). In total 16 species, representing seven insect orders, were finally investigated (Table 1).

Both body mass and one or more body length (including total length and head width) measures were used to obtain size frequency distributions for these variables to account for any differences between mass and length distributions. The various merits and demerits of each of these measures have been discussed in the literature (see for example Gaston & Blackburn, 2000). Linear measurements might show less variation than mass in insects because growth is not continuous and mass might fluctuate depending on the age of the organism and its feeding status (e.g. Strobbe & Stoks, 2004). However, mass is directly comparable across a wide range of taxa irrespective of their body form, whilst linear measurements do not lend themselves entirely to such among-taxon comparisons (e.g. stick insects vs. beetles).

The wet mass of the individuals of each species was determined using Mettler Toledo UMX2 or AX504 (Mettler-Toledo GmbH, Laboratory & Weighing Technologies, Greifensee, Switzerland) microbalances, both in the field and in the laboratory. Thereafter, these individuals were preserved (in alcohol or frozen) for future measurement. Body length or an appropriate surrogate variable (see e.g. Weiser & Kaspari 2006) was measured using a StereoLEICA MZ 7.5 (Leica Microsystems, Wetzlar, Germany) microscope, fitted with an ocular micrometer.

A minimum of one hundred individuals per species was collected from the different sites. This ensured a more accurate representation of the size distribution of each species, therefore also accounting for sexual size dimorphism. Subsequently, the sex of each individual from each species was determined by dissection, to account for variance in body size between the sexes. Sexual size dimorphism was then analyzed using generalised linear models (GENMOD procedure, SAS Institute Inc., Cary, NC, USA: GLZ, Type III models, assuming a normal distribution and a log link function; McCullagh & Nelder, 1989; Quinn & Keough, 2002). During the study, ten specimens from each species were measured repeatedly when 0 %, 33%, 50%, 66% and 100% of all collected individuals of a species had been measured. This procedure was used to gauge the repeatability of the measurement process and measurement accuracy. Repeatability

was determined using the intraclass correlation coefficient ( $\tau$ , Krebs, 1999), obtained from the analysis of variance (ANOVA) and the equation for repeatability (Lessells & Boag, 1987; Krebs, 1999):

$$\tau = s^2_A / (s^2 + s^2_A) \quad (1)$$

where  $s^2_A$  is the among-group variance and  $s^2$  is the within-group variance, where  $\tau$  lies between 0 and 1. A  $\tau$ -value nearer to 1 implies that the measurement is accurate; while values nearer to 0 imply that the measurements are inaccurate, i.e. showing high variance for the same measurement.

#### *Data analysis*

To investigate intraspecific frequency distributions of the species, both untransformed and log-transformed data were used for analysis. The log transformation was applied because it has been suggested that BSFDs should show a lognormal distribution (May, 1981). Body size class (or bin size and number) is known to influence BSFDs (Loder *et al.*, 1997). Therefore, the number of bins for the BSFD of each species was chosen using Sturges rule, which can be represented as:

$$k = 1 + \log_2 n \quad (2)$$

and the method proposed by Scott (1979), which is can be represented as:

$$h = 3.49sn^{-1/3} \quad (3)$$

where  $k$  is the number of bins,  $n$  is the sample size and  $s$  standard deviation of the sample (Sturges, 1926; Scott, 1979). Although it has been pointed out that Sturges rule is not the most appropriate measure to determine the number of bins, it has been found to be relatively effective for sample sizes that are smaller than 200 (Hyndman, 1995).

**Table 1** The 16 insect species collected for this study, representing seven insect orders and 14 insect families with the location of collection and the sampling method used.

<b>Order</b>	<b>Family</b>	<b>Species</b>	<b>Location</b>	<b>Sampling method</b>
Coleoptera	Chrysomelidae	Chrysomelid sp	Plantation, Jonkershoek	Hand collection (small paint brush)
	Coccinellidae	<i>Henosepilachna vigintioctopunctata</i>	Farm outside Stellenbosch	Hand collection
	Curculionidae	<i>Gonipterus scutellatus</i>	Coetzenburg plantation, Stellenbosch	Hand collection
	Scarabaeidae	<i>Pachnoda sinuata</i>	Stellenbosch area	Hand collection & sweep net
	Apionidae	<i>Setapion provinciale</i>	Assegaaibosch, Jonkershoek	Hand collection (small paint brush)
	Apionidae	<i>Setapion quantillum</i>	Assegaaibosch, Jonkershoek	Hand collection (small paint brush)
Diptera	Tephritidae	<i>Ceratitis capitata</i>	Lab colony	N/A
Hemiptera	Lygaeidae	<i>Nysius</i> sp.	Stellenbosch area	Hand collection (small paint brush)
	Velliidae	<i>Rhagovelia maculata</i>	Garden pond, Stellenbosch	Sweep net, across water surface
Hymenoptera	Formicidae	Alates of a Formicidae sp	Vredenheim farm, outside Stellenbosch	Sweep net
	Vespidae	<i>Polistes</i> sp.	Stellenbosch area	Hand collection of nest area
	Pteromalidae	<i>Trichilogaster acacialongifoliae</i>	Jonkershoek Rd, outside Stellenbosch	Hand collection of galls, emerged in laboratory
	Pteromalidae	<i>Trichilogaster signiventris</i>	Franschoek Rd, outside Stellenbosch	Hand collection of galls, emerged in laboratory
Isoptera	Hodotermitidae	<i>Microhodotermes viator</i>	Wolseley, Tulbagh area	Hand collection (small paint brush)
Lepidoptera	Satyridae	<i>Dira clytus</i>	Jan Marais park, Stellenbosch	Sweep net
Orthoptera	Gryllidae	<i>Gryllus bimaculatus</i>	Stellenbosch University campus grounds	Hand collection

Subsequently, the normality or deviation from normality of the mass and length distributions was tested using the Shapiro-Wilks method (Zar, 1999). Furthermore, the significance of skew (sample statistic for skewness,  $g_1$ ; Sokal & Rohlf, 1995) was determined by performing student t-tests on the data (Quinn & Keough, 2002). Here a

significant, positive  $g_J$ -value indicates that the distribution is right-skewed and a significant, negative  $g_J$ -value indicates a left skew. Owing to the possibility of an increase in the occurrence of a Type I error, or false discovery rate (FDR; Benjamini & Hochberg, 1995; see García, 2003; 2004) with repeated testing of data, the  $P$ -values obtained from the two-tailed t-tests were subjected to step-up FDR tests suggested by Benjamini and Hochberg (1995; see also García, 2003; 2004). All statistical analyses for this study were performed using the modelling program Enterprise Guide version 3.0, powered by SAS version 9.1 (SAS Institute Inc., Cary, NC, USA.). Significance was set at  $P = 0.05$ .

## RESULTS

Repeatability estimates of higher than  $\tau = 0.88$  were obtained for all species and showed that the measurement process was repeatable. The number of size bins determined for each species varied from eight to ten bins depending on the sample size. Considerable variation in the degree of normality and skewness of the mass and length data were found between the different species. Out of these 16 different species, the untransformed mass frequency distributions of two of the species were bimodal, seven species had significantly right-skewed distributions, one species had a significantly left-skewed distribution, and the data of the six remaining species were normally distributed (Fig 1; Table 2a). In several cases, a log transformation of the data had no apparent effect on the distributions (e.g. the alates of the ant species and the butterfly species *Dira clytus*, Table 2a). On the other hand, as would be expected, some of the right skewed distributions were removed after log transformation of the mass data (e.g. for the fruit fly, *Ceratitis capitata*, Table 2a). The log transformation of the normally distributed data often introduced a degree of negative skew to the data, a change found to be the case for the weevil species *Setapion provinciale* and *S. quantillum*, and the parasitic wasp *Trichilogaster signiventris*, while the negative skew for the velliid species, *Rhagovelia maculata* was more pronounced (Table 2a). Here it should be noted that two of the species, i.e. *Microhodotermes viator* and the *Polistes* species, are social insects and the individual worker females are likely to be closely related. This could in turn have had some effect on the size frequency skew for these two species.

**Table 2** Statistical results for the assessment of deviation from normality (Shapiro-Wilks  $W$  statistic) and the degree of skewness ( $g_1$ ) for the (a) body mass (mg) and (b) body length (mm) frequency distributions of all 16 insect species considered. Significance was set at  $P = 0.05$ .

(a)

Species	n	Raw data			Log transformed data		
		$W$	$P$	$g_1$	$W$	$P$	$g_1$
Chrysomelid sp	175	0.929	<0.0001	1.024***	0.975	0.003	0.484**
<i>Henosepilachna vigintioctopunctata</i>	207	0.988	0.073	0.333 <sup>ns</sup>	0.991	0.263	-0.202 <sup>ns</sup>
<i>Gonipterus scutellatus</i>	138	0.979	0.032	0.229 <sup>ns</sup>	0.981	0.051	-0.291 <sup>ns</sup>
<i>Pachnoda sinuata</i>	108	0.994	0.920	0.165 <sup>ns</sup>	0.992	0.805	-0.232 <sup>ns</sup>
<i>Setapion provinciale</i>	112	0.993	0.838	-0.102 <sup>ns</sup>	0.952	0.0005	-1.00***
<i>Setapion quantillum</i>	120	0.982	0.110	-0.265 <sup>ns</sup>	0.948	0.0001	-0.851***
<i>Ceratitis capitata</i>	103	0.955	0.0015	0.559*	0.974	0.042	0.141 <sup>ns</sup>
<i>Nysius</i> sp.	120	0.989	0.477	0.227 <sup>ns</sup>	0.989	0.420	-0.274 <sup>ns</sup>
<i>Rhagovelia maculata</i>	108	0.953	0.0008	-0.694**	0.899	<0.0001	-1.226***
Formicidae sp	120	0.753	<0.0001	0.508*	0.779	<0.0001	0.412 <sup>ns</sup>
<i>Polistes</i> sp.	103	0.951	0.0007	0.693**	0.961	0.0037	-0.279 <sup>ns</sup>
<i>Trichilogaster acacialongifoliae</i>	143	0.889	<0.0001	-0.260 <sup>ns</sup>	0.859	<0.0001	-0.779***
<i>Trichilogaster signiventris</i>	107	0.976	0.051	-0.025 <sup>ns</sup>	0.955	0.001	-0.649**
<i>Microhodotermes viator</i>	102	0.923	<0.0001	0.872***	0.981	0.152	0.042 <sup>ns</sup>
<i>Dira clytus</i>	109	0.663	<0.0001	3.174***	0.860	<0.0001	1.683***
<i>Gryllus bimaculatus</i>	201	0.973	0.0006	0.537**	0.962	<0.0001	-0.607***

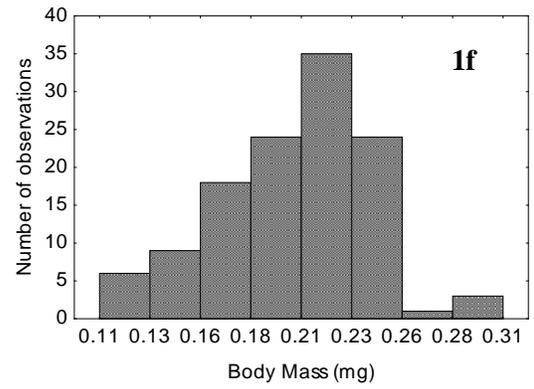
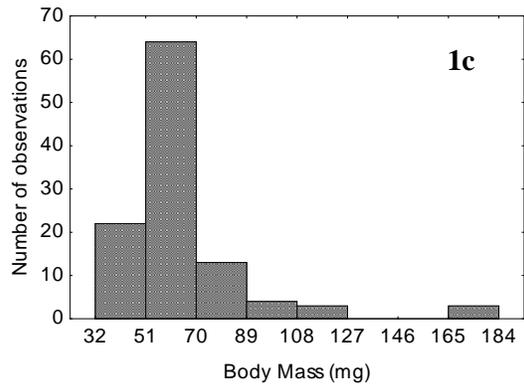
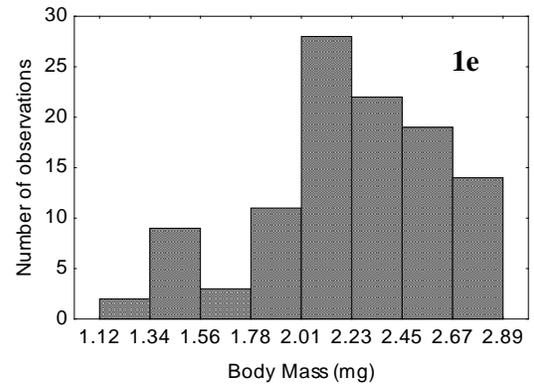
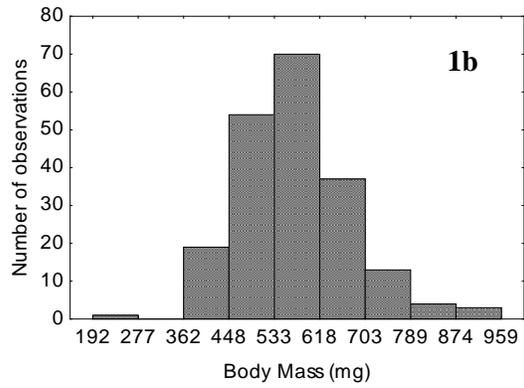
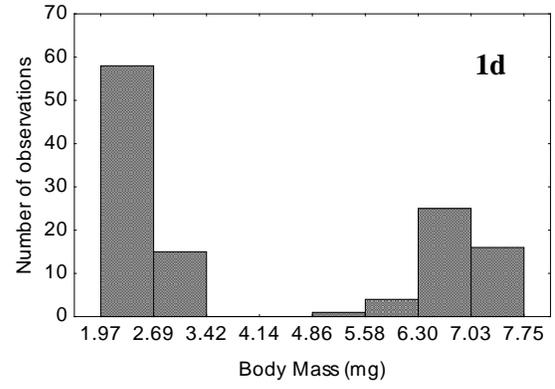
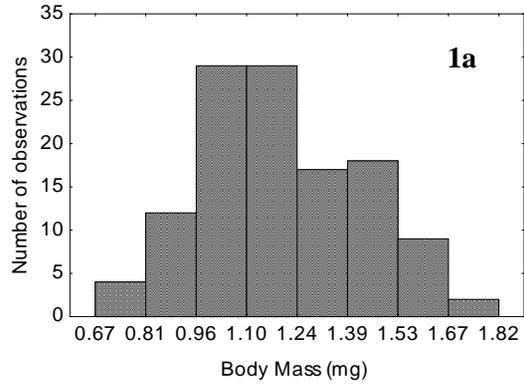
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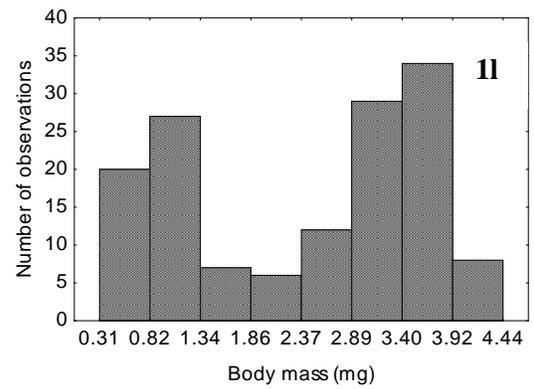
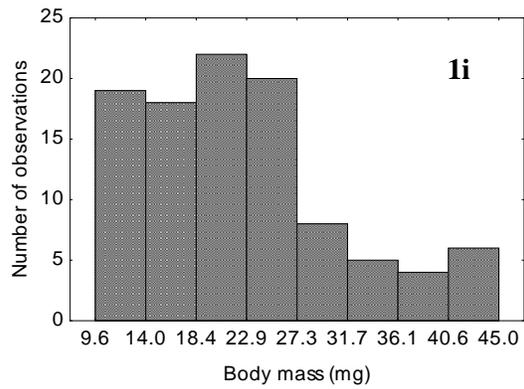
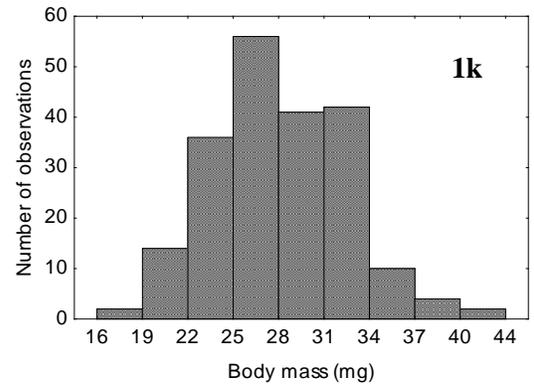
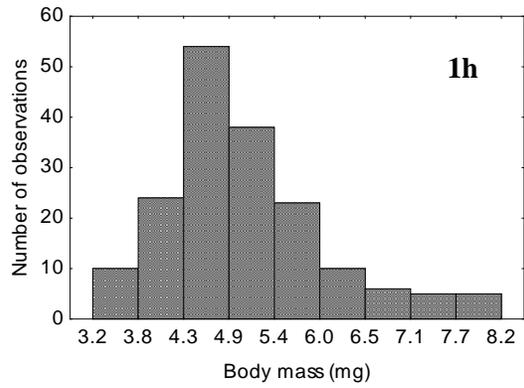
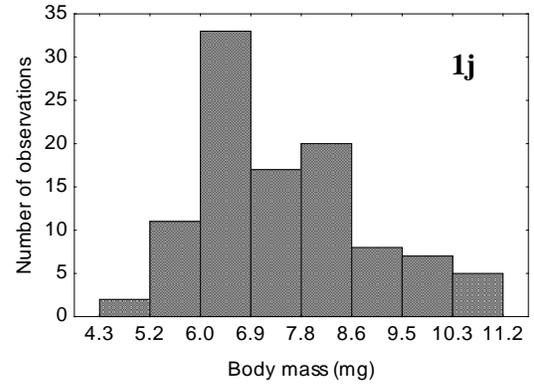
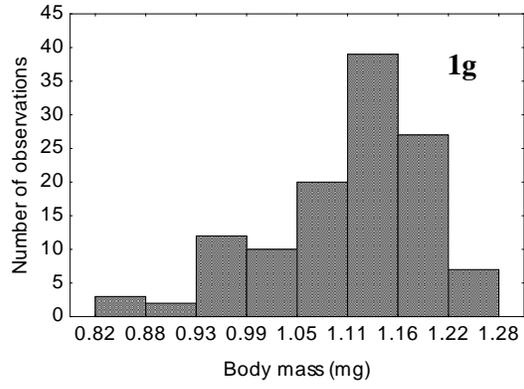
Species	n	Raw data			Log transformed data		
		$W$	$P$	$g_1$	$W$	$P$	$g_1$
Chrysomelid sp	172	0.953	<0.0001	0.046 <sup>ns</sup>	0.965	0.0002	0.444*
<i>Henosepilachna vigintioctopunctata</i>	207	0.988	0.068	-0.226 <sup>ns</sup>	0.979	0.004	-0.464**
<i>Gonipterus scutellatus</i>	138	0.965	0.0014	-0.107 <sup>ns</sup>	0.962	0.0007	-0.231 <sup>ns</sup>
<i>Pachnoda sinuata</i>	107	0.987	0.417	0.044 <sup>ns</sup>	0.987	0.0380	-0.070 <sup>ns</sup>

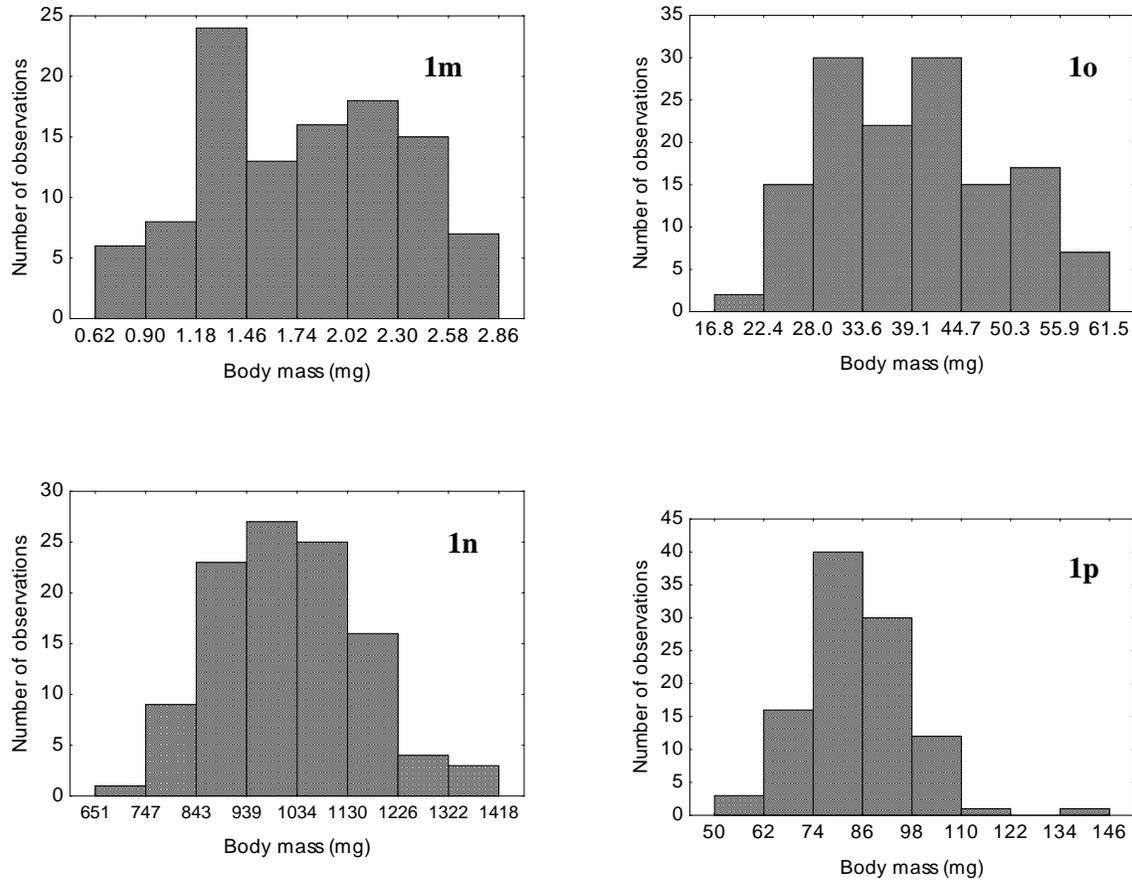
<i>Setapion provinciale</i>	112	0.975	0.035	-0.194 <sup>ns</sup>	0.972	0.016	-0.328 <sup>ns</sup>
<i>Setapion quantillum</i>	120	0.952	0.0003	-0.819***	0.928	<0.0001	-1.064***
<i>Ceratitis capitata</i>	103	0.966	0.010	0.172 <sup>ns</sup>	0.968	0.013	0.017 <sup>ns</sup>
<i>Nysius</i> sp.	120	0.980	0.071	0.094 <sup>ns</sup>	0.980	0.065	-0.119 <sup>ns</sup>
<i>Rhagovelia maculata</i>	108	0.903	<0.0001	-0.044 <sup>ns</sup>	0.903	<0.0001	-0.098 <sup>ns</sup>
Formicidae sp	119	0.766	<0.0001	0.412 <sup>ns</sup>	0.781	<0.0001	0.363 <sup>ns</sup>
<i>Polistes</i> sp.	97	0.980	0.156	0.097 <sup>ns</sup>	0.981	0.177	-0.072 <sup>ns</sup>
<i>Trichilogaster acacialongifoliae</i>	140	0.940	<0.0001	-0.608**	0.908	<0.0001	-1.002***
<i>Trichilogaster signiventris</i>	102	0.959	0.003	-0.530*	0.944	0.0003	-0.779**
<i>Microhodotermes viator</i>	98	0.894	<0.0001	0.826**	0.921	<0.0001	0.633**
<i>Dira clytus</i>	107	0.937	<0.0001	0.728**	0.953	0.0008	0.005 <sup>ns</sup>
<i>Gryllus bimaculatus</i>	199	0.971	0.0003	0.208 <sup>ns</sup>	0.973	0.0009	0.064 <sup>ns</sup>

Of the data distributions for the various measures used to represent body length of each of the 16 species, two distributions were found to be bimodal, five were right skewed, six were left skewed and three were normally distributed (Fig 2; Table 2b). The degree of the significance of skew observed for the body length distributions that displayed a skewed distribution also varied considerably between the different species (Table 2b). Log transformation of the length data often had no obvious effect on the shape of the observed distributions (e.g. the water strider species, *Rhagovelia maculata* and the southern harvester termite, *Microhodotermes viator*, Table 2b). In another case, log transformation served to increase the already present, previously non-significant left-skew in the data (e.g. the coccinellid beetle species, *Henosepilachna vigintioctopunctata*, Table 2b).

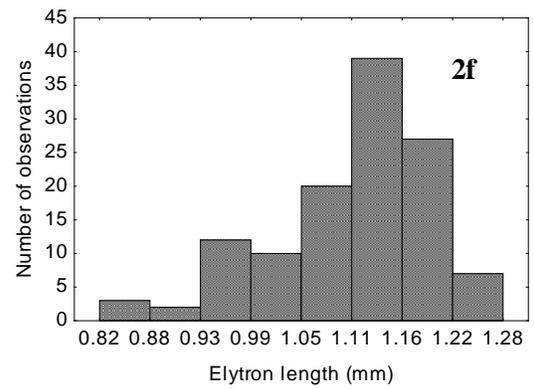
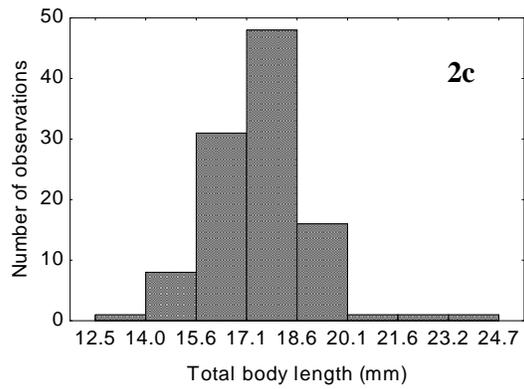
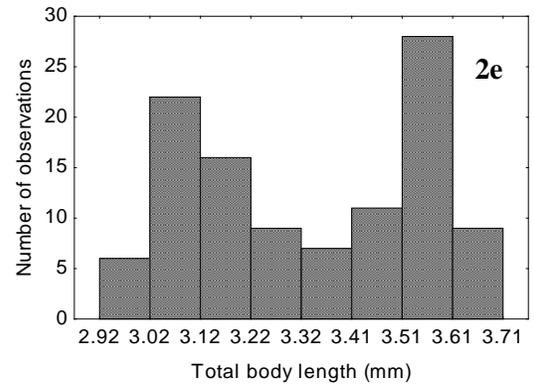
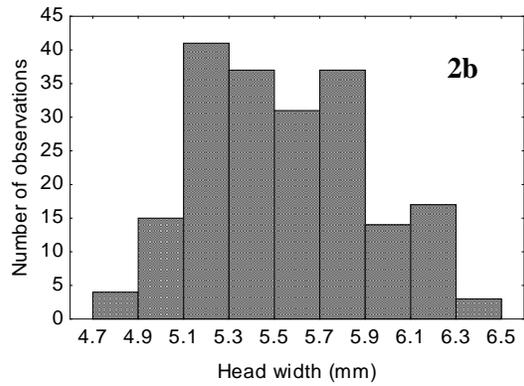
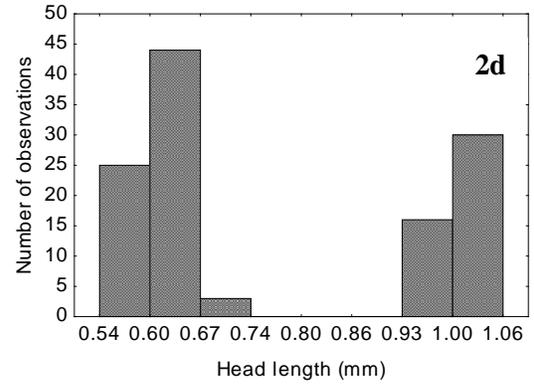
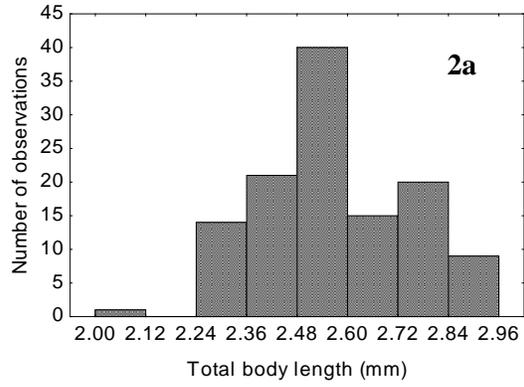
Most of the insect species considered in the present study were sexually dimorphic, where females were larger than males, with the exception of the head width length measure for the cricket species, *Gryllus bimaculatus*, where males were larger. For a few of the species, the males and the females separately did not show any significant deviations from normality in body mass or length (e.g. the alates of the ant species and *Pachnoda sinuata*; Table 3a and 4a). In some cases where only one or two weakly significant skews were found, the significance of the skew was removed after controlling for FDR (e.g. log transformed mass data for males of *Gonipterus scutelatus*; Table 3b). Most often the distributions of body mass and length for males and females respectively did not differ substantially from each other (e.g. the mass distributions for *Rhagovelia maculata*, mass and length distributions for *Setapion provinciale*, length distributions for the coccinellid species, mass and length distributions for *Trichilogaster acaciaelongifoliae* and *T. signiventris*; Table 3a and 4a). For some species however, the distributions varied greatly in the direction of the skew between males and females (Table 3a and 4a). For example, the body mass distribution of the males of the butterfly species *Dira clytus* were found to be significantly left skewed, whereas it was significantly right skewed for the females (Table 3a). In other cases where a positive skew was present in the untransformed mass and/or length data, the right skewed distributions were removed after log transformation of the data for males and females (e.g. male mass of *Ceratitis capitata* and male length of *T. acaciaelongifoliae*; Table 3b and 4b). By contrast, the log

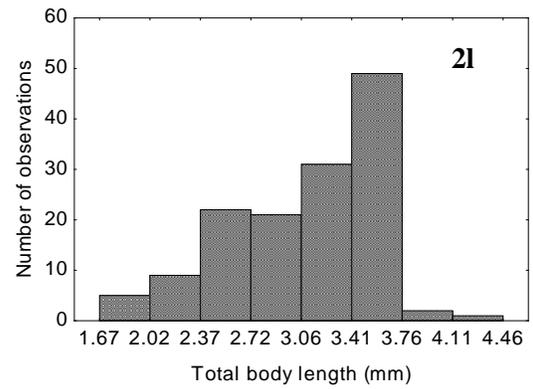
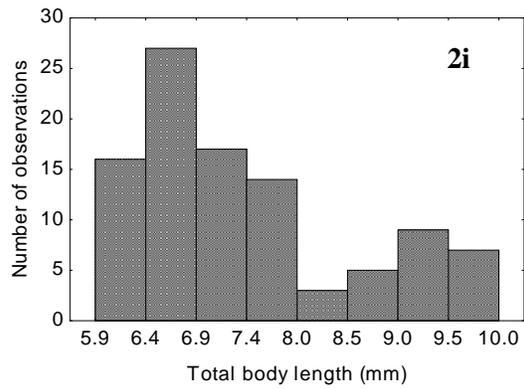
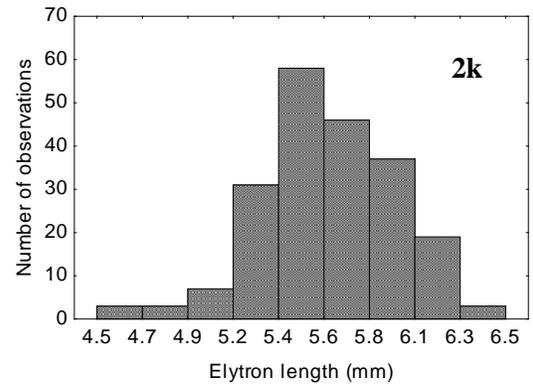
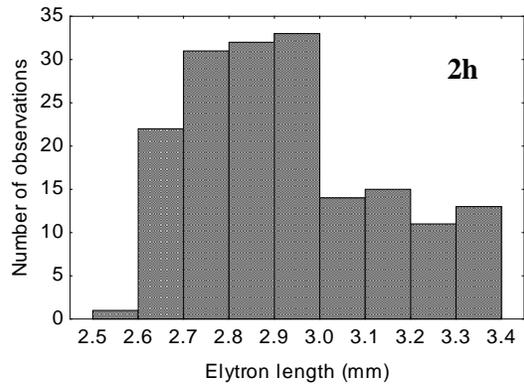
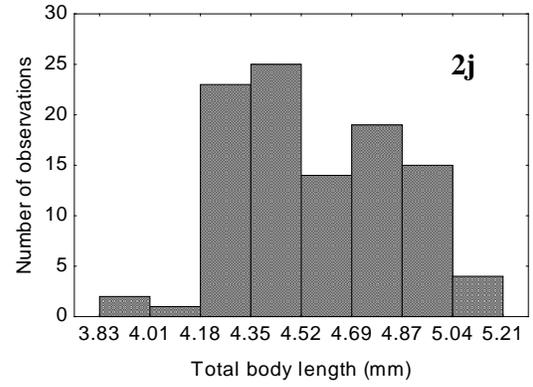
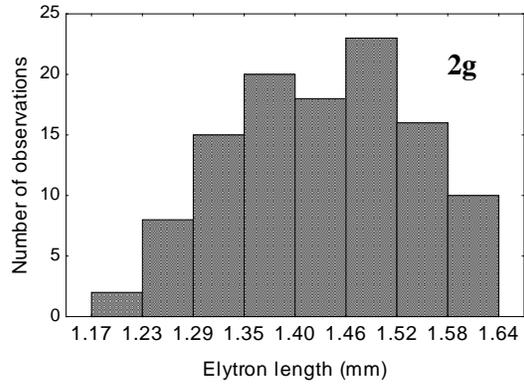


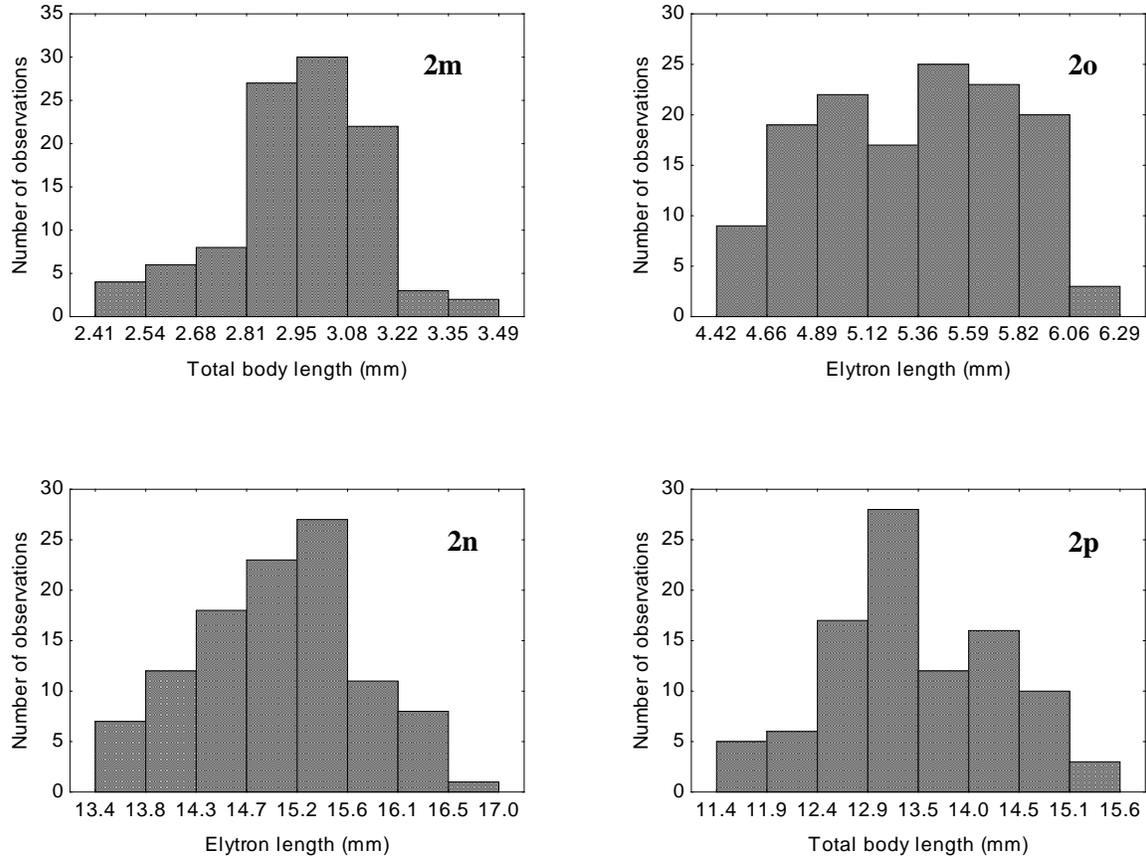




**Figure 1** Body mass frequency distributions of all 16 species considered. The number of size classes (or size bins) were calculated using Sturges rule (Equation 1; Sturges, 1926) and methods proposed by Scot (1979; Equation 2). The mass (mg) distributions are as follows; **(a)** the *Nysius* species, **(b)** *Gryllus bimaculatus*, **(c)** *Dira clytus*, **(d)** the ant species, **(e)** *Rhagovelia imaculata*, **(f)** *Setapion quantillum*, **(g)** *Setapion provinciale*, **(h)** the chrysomellid beetle species, **(i)** *Microhodotermes viator*, **(j)** *Ceratitidis capitata*, **(k)** *Henosepilachna vigintioctopunctata*, **(l)** *Trichilogaster acaciaelongifoliae*, **(m)** *Trichilogaster signiventris*, **(n)** *Pachnoda sinuata*, **(o)** *Gonipterus scutellatus* and **(p)** the *Polistes* species.







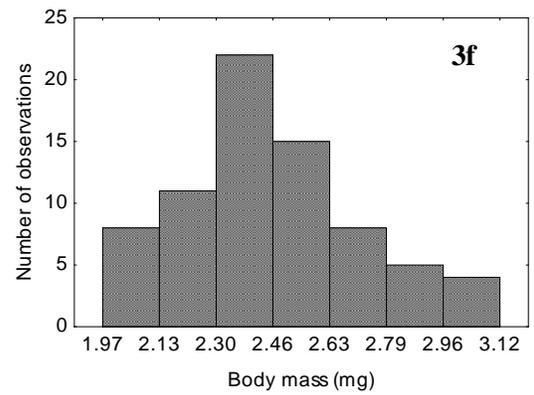
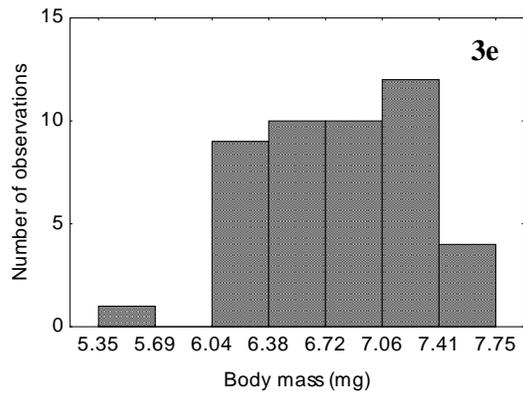
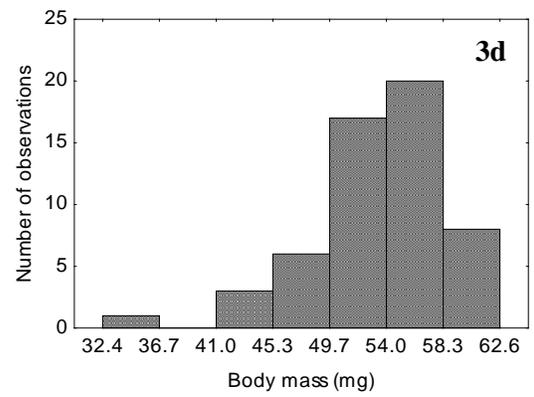
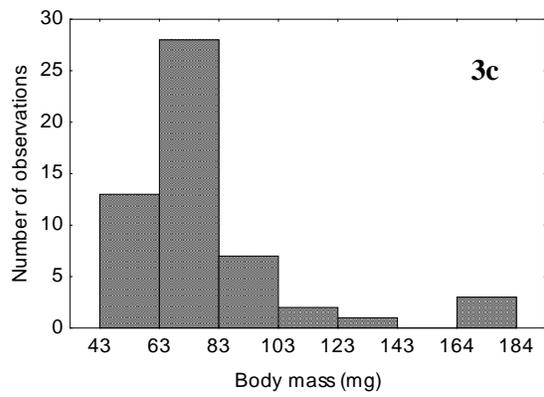
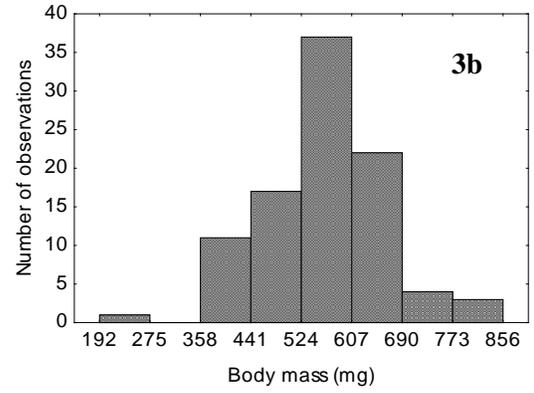
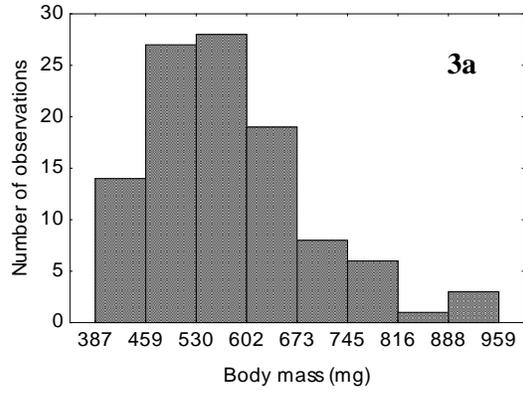
**Figure 2** Body length frequency distributions of all 16 species considered. The number of size classes (or size bins) were calculated using Sturges rule (Equation 1; Sturges, 1926) and methods proposed by Scot (1979; Equation 2). The length (mm) distributions are as follows; **(a)** the *Nysius* species, **(b)** *Gryllus bimaculatus*, **(c)** *Dira clytus*, **(d)** the ant species, **(e)** *Rhagovelia imaculata*, **(f)** *Setapion quantillum*, **(g)** *Setapion provinciale*, **(h)** the chrysomellid beetle species, **(i)** *Microhodotermes viator*, **(j)** *Ceratitis capitata*, **(k)** *Henosepilachna vigintioctopunctata*, **(l)** *Trichilogaster acaciaelongifoliae*, **(m)** *Trichilogaster signiventris*, **(n)** *Pachnoda sinuata*, **(o)** *Gonipterus scutelatus* and **(p)** the *Polistes* species.

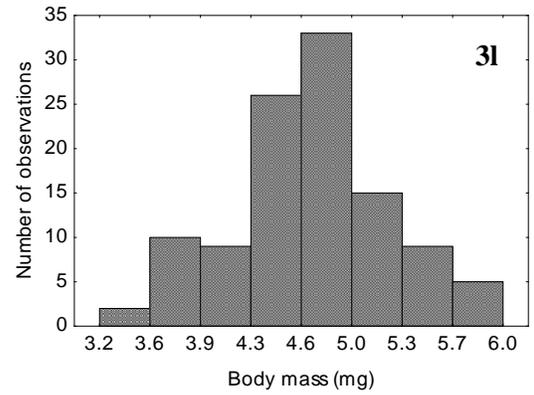
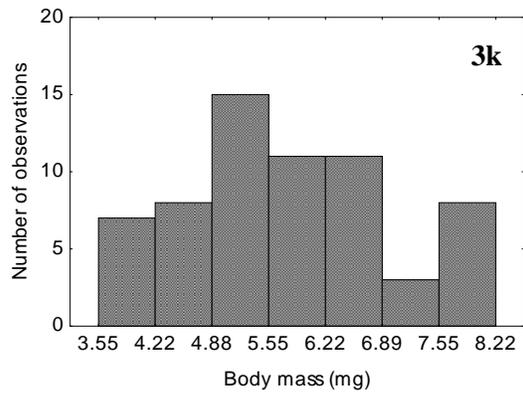
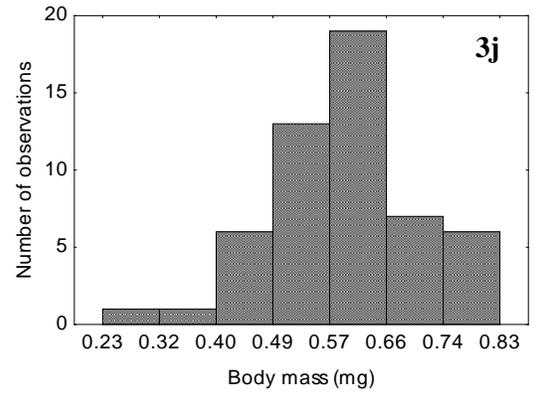
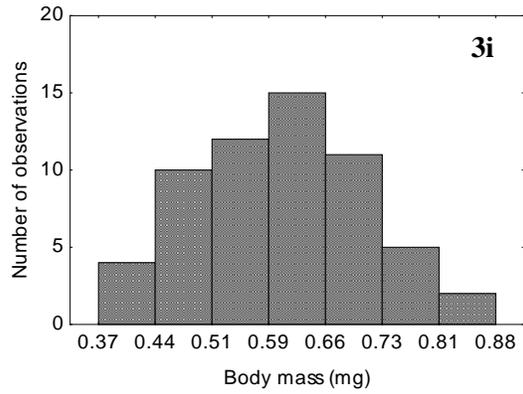
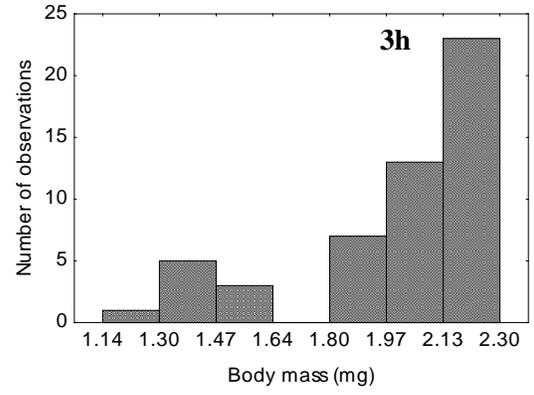
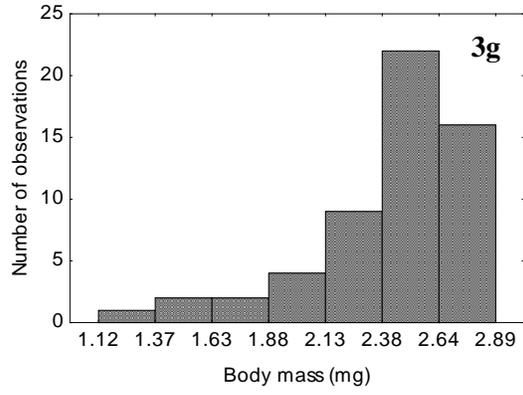
transformation of male and/or female mass and length data frequently introduced a more pronounced left skew to the data (e.g. male mass of *G. bimaculatus*, male mass of *Dira clytus*, male mass and female length of *R. maculata*, female mass and length of *Ceratitis capitata*, male and female length of the coccinellid species, female mass and length of *T. acaciaelongifoliae* and male and female mass of *T. signiventris*; Table 3b and 4b).

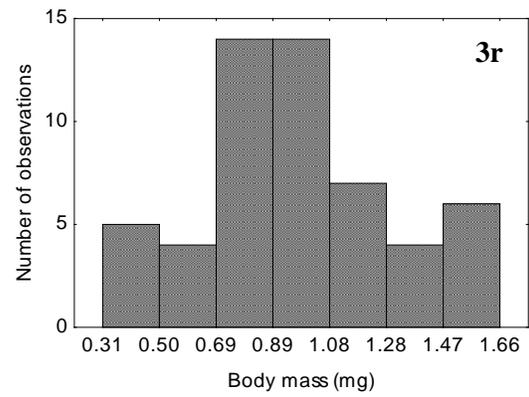
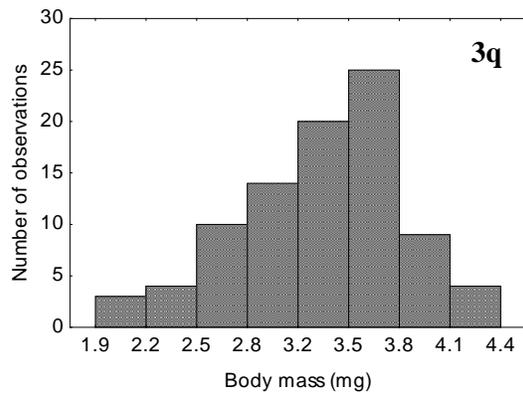
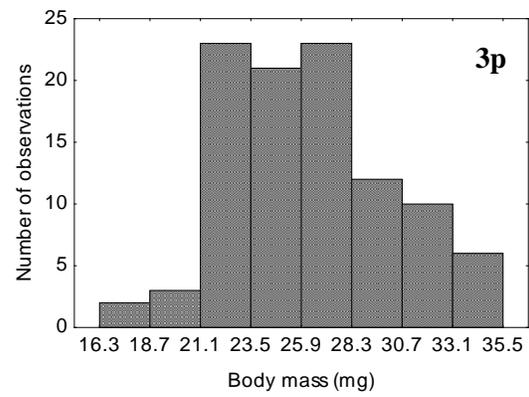
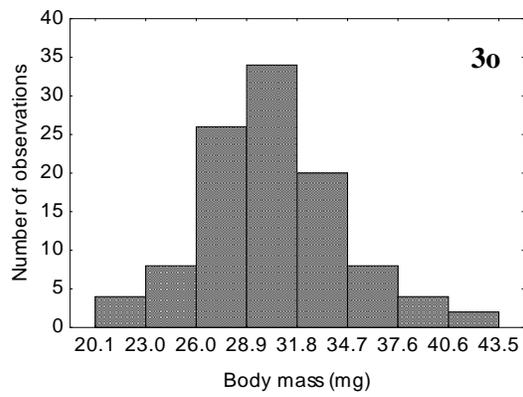
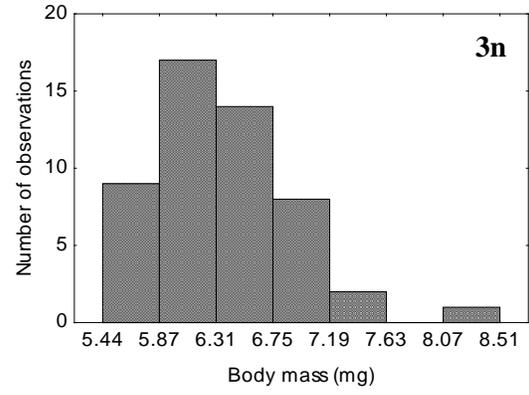
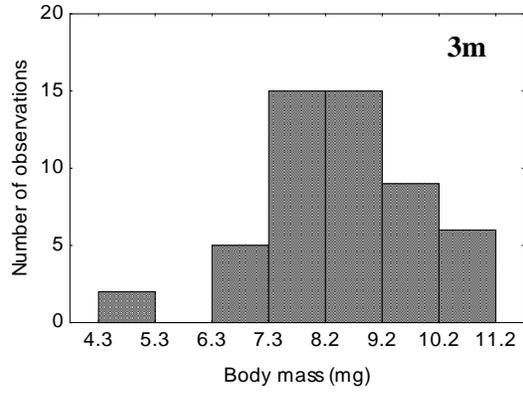
## DISCUSSION

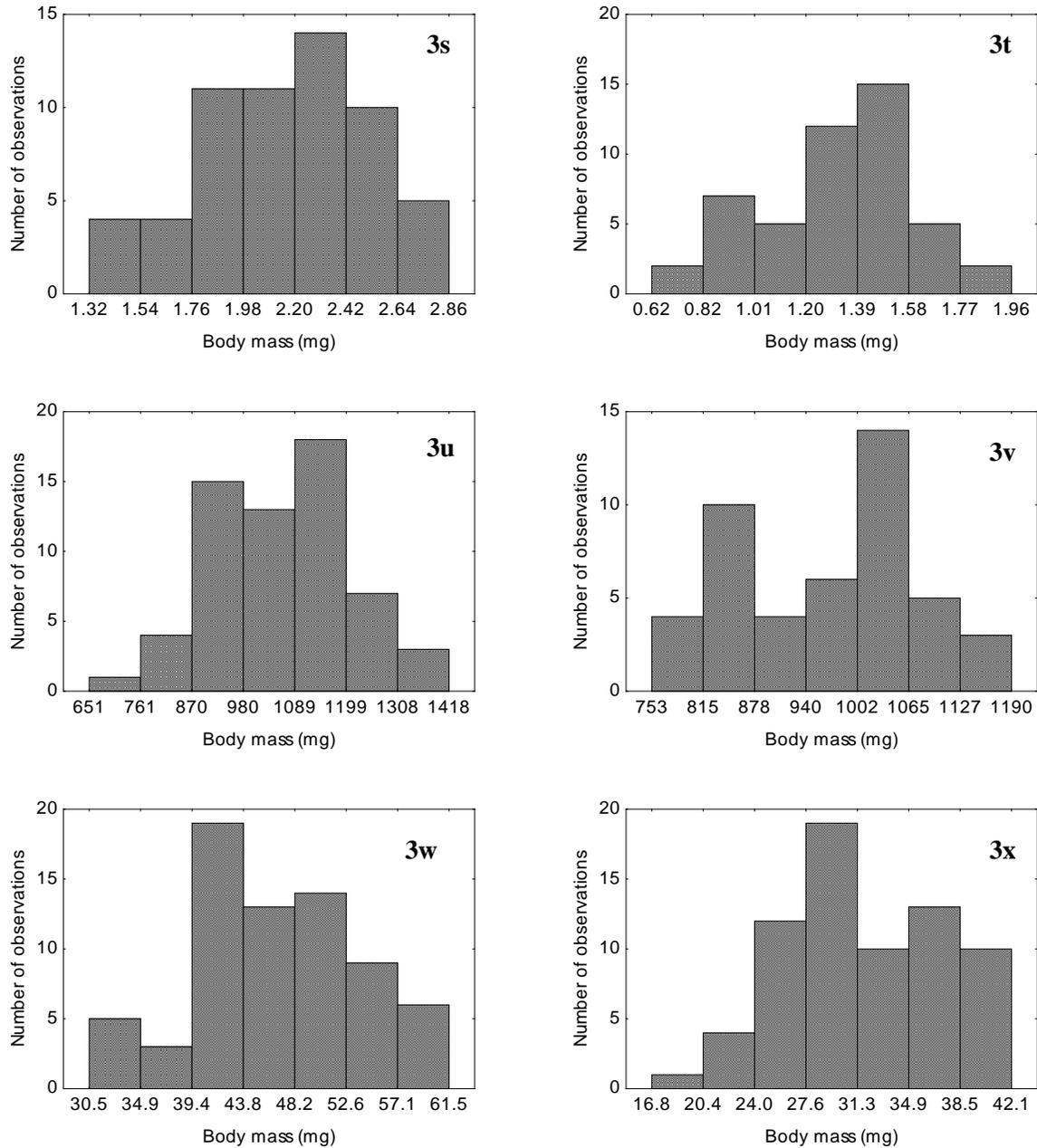
It is known that the BSFD differs at different spatial scales, and at different taxonomic levels (Gaston & Blackburn 2000). Consequently, at the interspecific level, the patterns of the BSFDs of vertebrates have been found to be predominantly right skewed (Brown & Nicoletto, 1991; Brown *et al.*, 1993; Gaston & Blackburn, 1995, 1996; Gardezi & da Silva, 1999; Bakker & Kelt, 2000; Maurer *et al.*, 2004; Smith *et al.*, 2004). However, these distributions often show a high degree of variability when the distributions are subdivided into geographic areas, different biomes (e.g. North and South American mammals, Bakker & Kelt, 2000; North American mammals, Brown & Nicoletto, 1991) or taxonomic hierarchies (e.g. aquatic and terrestrial birds, Gaston & Blackburn, 1996; mammals of the world, Smith *et al.*, 2004; Gardezi & da Silva, 1999).

A variety of patterns has also been reported for invertebrates, and the shape of the patterns has also been found to vary with geographic scale and taxonomic partition or hierarchy (Hutchinson & MacArthur, 1959; Morse *et al.*, 1985; Cambefort, 1994; Novotný & Kindlmann, 1996; Chown & Steenkamp, 1996; Gómez & Espadaler, 2000; Dixon & Hemptinne, 2001; Espadaler & Gómez, 2002; Gaston *et al.*, 2001; Ulrich, 2006). For example, in a study of the BSFDs of European Hymenoptera, Ulrich (2006) found a variety of patterns when he subdivided the data into genera, families, subfamilies and suborders. Following on what has been found for invertebrates at the interspecific level, it is therefore perhaps not surprising that a large degree of variation is present in intraspecific BSFDs of insects as shown both in this study, and in less comprehensive assessments undertaken by others (Alcock, 1984; Lounibos, 1994; David *et al.*, 1997; Evans, 2000; Gleiser *et al.*, 2000).

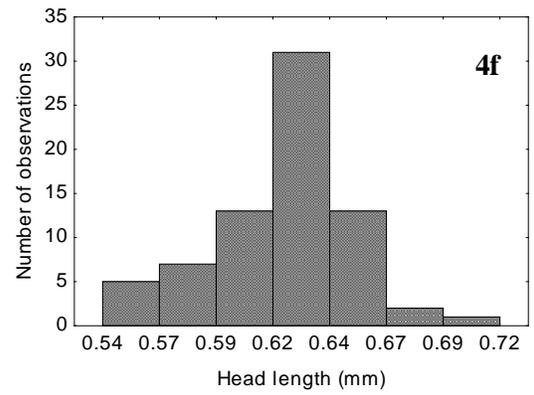
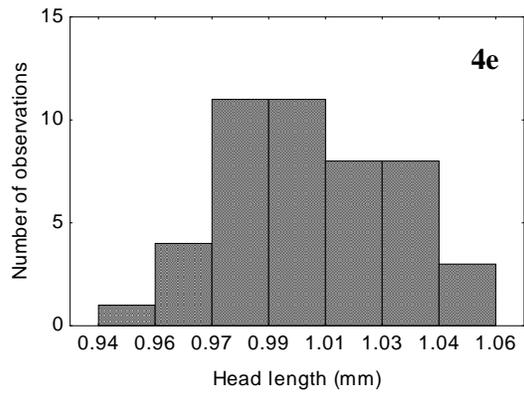
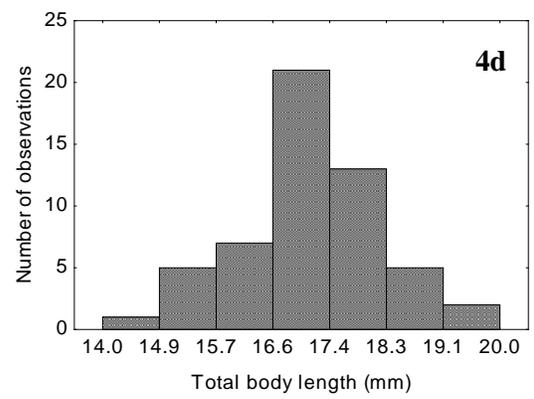
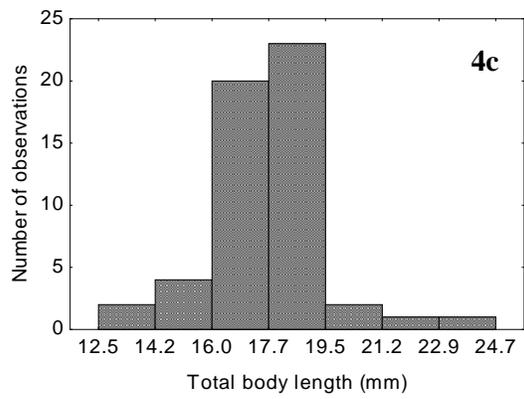
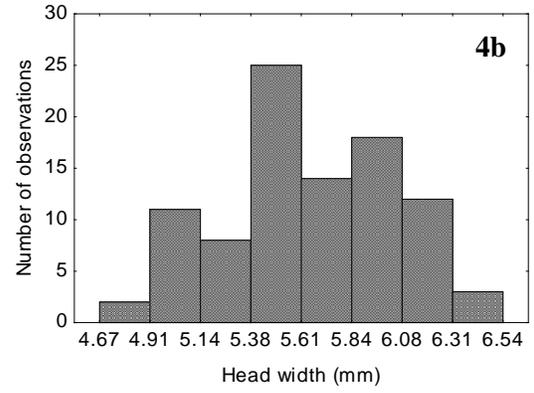
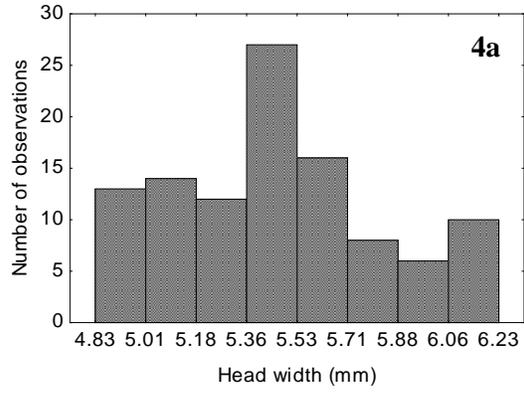


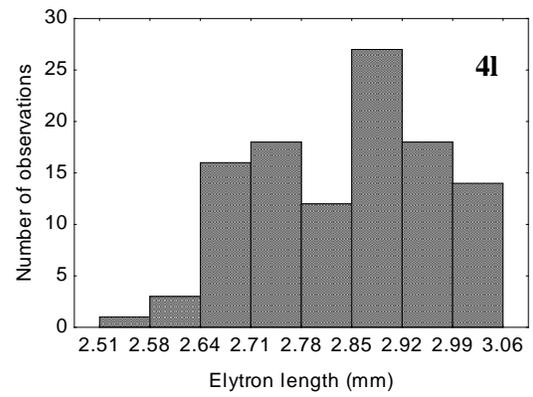
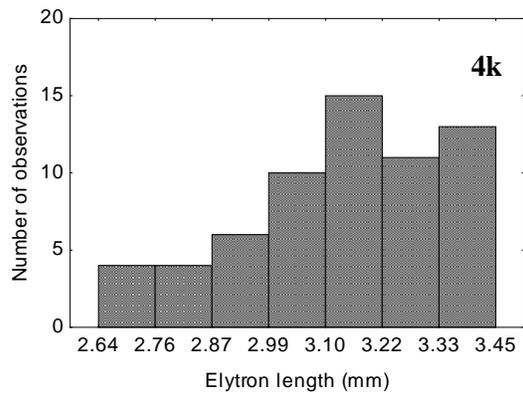
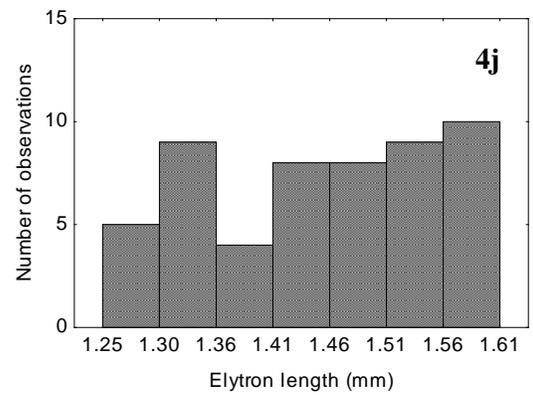
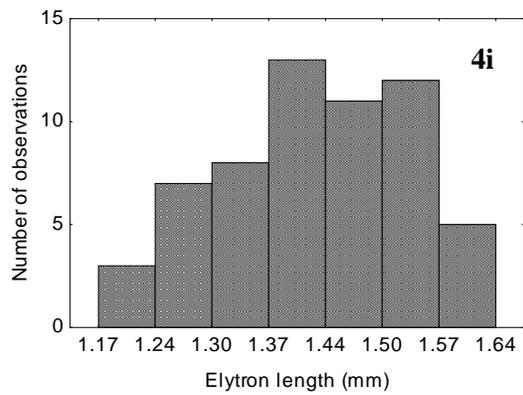
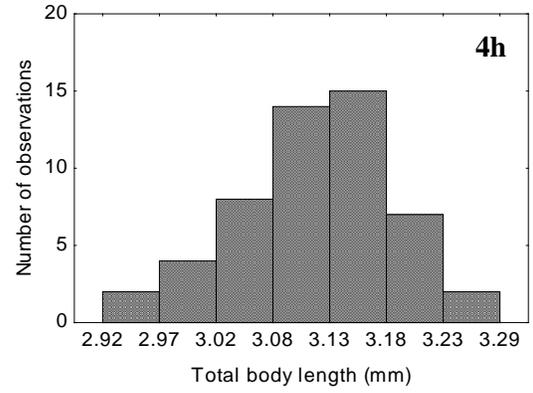
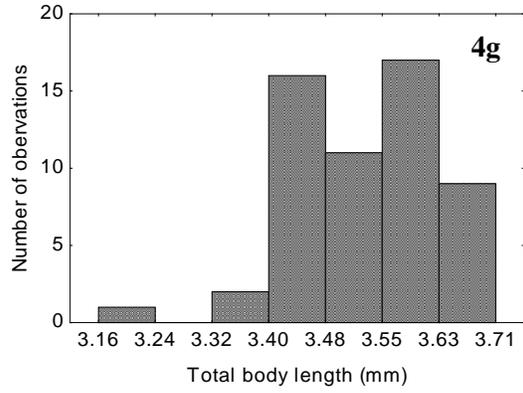


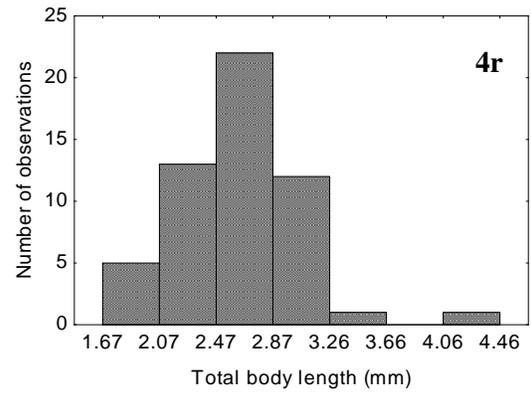
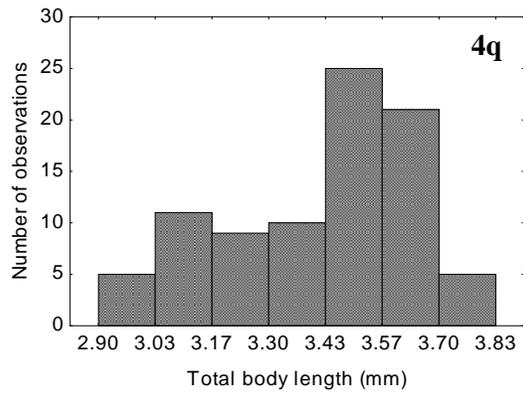
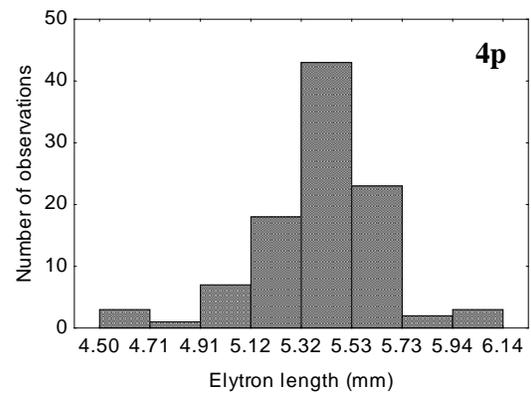
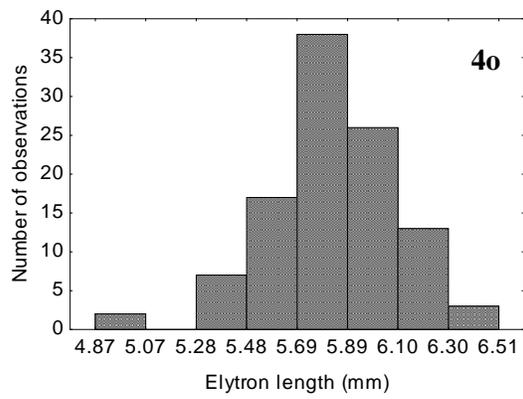
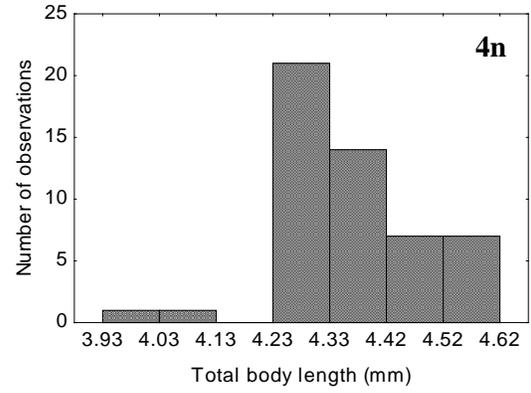
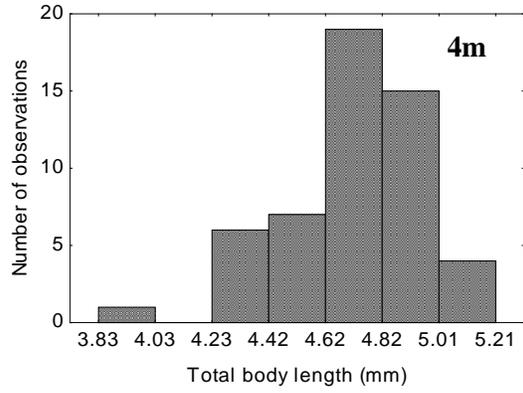


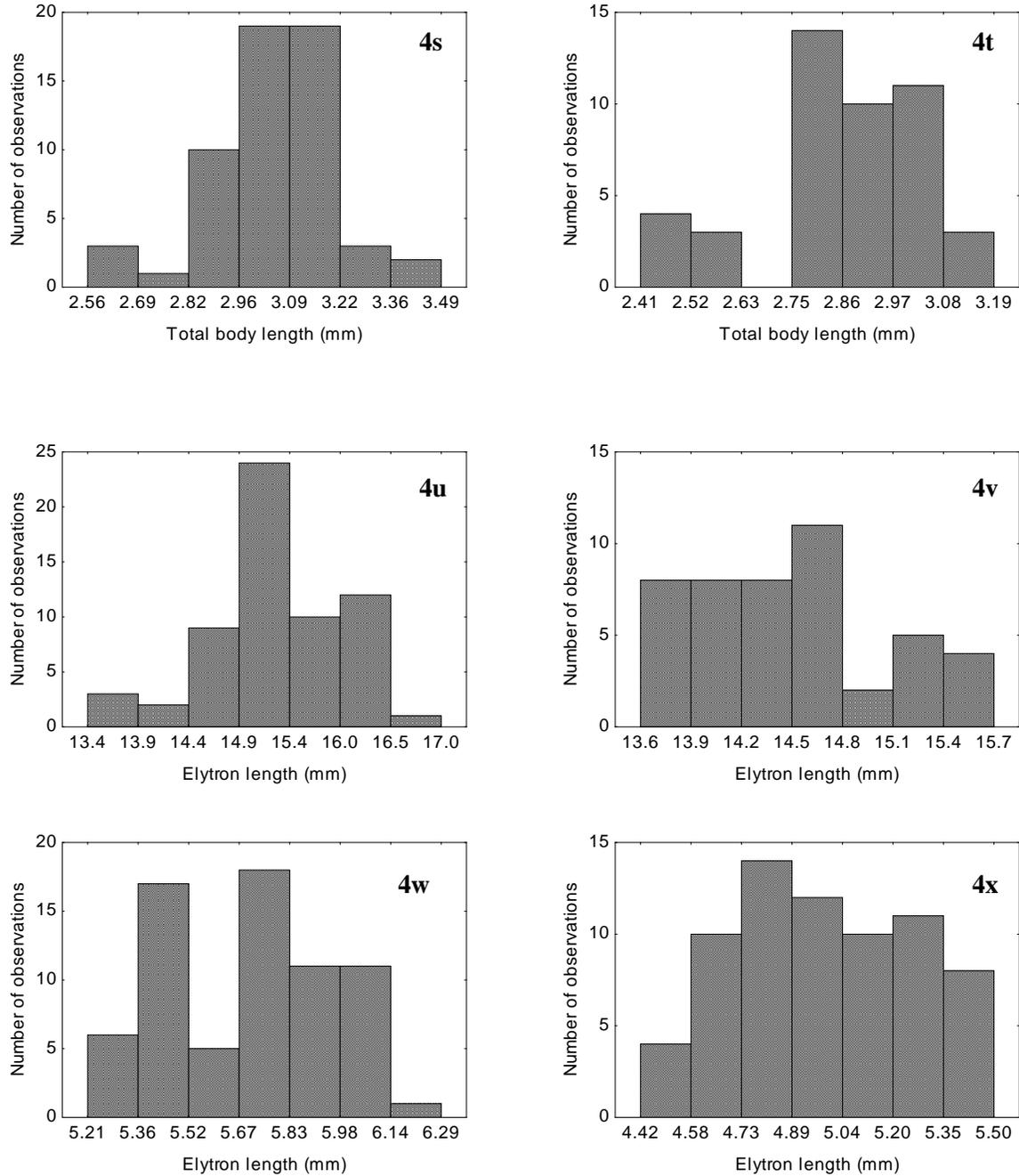


**Figure 3** Body mass (mg) frequency distributions of males and females separately for 12 of the insect species considered. The distributions for the females are presented on the left and the male distributions are on the right. The distributions are as follows; **(a)** *Gryllus bimaculatus* females and **(b)** males, **(c)** *Dira clytus* females and **(d)** males, **(e)** the ant species females and **(f)** males, **(g)** *Rhagovelia imaculata* females and **(h)** males, **(i)** *Setapion provinciale* females and **(j)** males, **(k)** the chrysmellid species females and **(l)** males, **(m)** *Ceratitis capitata* females and **(n)** males, **(o)** *Henosepilachna vigintioctopunctata* females and **(p)** males, **(q)** *Trichilogaster acaciaelongifoliae* females and **(r)** males, **(s)** *Trichilogaster signiventris* females and **(t)** males, **(u)** *Pachnoda sinuata* females and **(v)** males, and **(w)** *Gonipterus scutelatus* females and **(x)** males.









**Figure 4** Body length (mm) frequency distributions of males and females separately for 12 of the insect species considered. The distributions for the females are presented on the left and the male distributions are on the right. The distributions are as follows; **(a)** *Gryllus bimaculatus* females and **(b)** males, **(c)** *Dira clytus* females and **(d)** males, **(e)** the ant species females and **(f)** males, **(g)** *Rhagovelia imaculata* females and **(h)** males, **(i)** *Setapion provinciale* females and **(j)** males, **(k)** the chrysmellid species females and **(l)** males, **(m)** *Ceratitis capitata* females and **(n)** males, **(o)** *Henosepilachna vigintioctopunctata* females and **(p)** males, **(q)** *Trichilogaster acaciaelongifoliae* females and **(r)** males, **(s)** *Trichilogaster signiventris* females and **(t)** males, **(u)** *Pachnoda sinuata* females and **(v)** males, and **(w)** *Gonipterus scutelatus* females and **(x)** males.

**Table 3a** Statistical results for the deviation from normality (Shapiro-Wilks  $W$  statistic) and the degree of skewness ( $g_1$ ) for the **(a)** untransformed body mass (mg) and **(b)** log transformed body mass frequency distributions of the males and females of 12 of the insect species considered. Table 3a also includes the Type III chi-squared model results testing for sexual size dimorphism between the sexes.

**(a)**

Species	Males					Females			
	$\chi^2$	n	$W$	$P$	$g_1$	n	$W$	$P$	$g_1$
Chrysomelid sp	56.48****	109	0.991	0.680	-0.031 <sup>ns</sup>	63	0.975	0.238	0.192 <sup>ns</sup>
<i>Henosepilachna vigintioctopunctata</i>	47.98****	100	0.983	0.206	0.213 <sup>ns</sup>	106	0.975	0.044	0.500*
<i>Gonipterus scutellatus</i>	118.28****	69	0.983	0.447	-0.106 <sup>ns</sup>	69	0.982	0.399	-0.111 <sup>ns</sup>
<i>Pachnoda sinuata</i>	13.04***	46	0.954	0.068	-0.143 <sup>ns</sup>	61	0.993	0.980	-0.078 <sup>ns</sup>
<i>Setapion provinciale</i>	0.06 <sup>ns</sup>	53	0.971	0.224	-0.420 <sup>ns</sup>	59	0.988	0.803	0.184 <sup>ns</sup>
<i>Ceratitis capitata</i>	74.86****	51	0.930	0.005	1.209***	52	0.946	0.020	-0.589 <sup>ns</sup>
<i>Rhagovelia maculata</i>	35.92****	52	0.832	<0.0001	-1.311***	56	0.845	<0.0001	-1.630***
Formicidae sp	420.45****	73	0.977	0.200	0.436 <sup>ns</sup>	46	0.979	0.557	-0.314 <sup>ns</sup>
<i>Trichilogaster acacialongifoliae</i>	274.64****	54	0.984	0.676	0.121 <sup>ns</sup>	89	0.973	0.061	-0.537*
<i>Trichilogaster signiventris</i>	107.68****	48	0.977	0.468	-0.343 <sup>ns</sup>	59	0.981	0.479	-0.366 <sup>ns</sup>
<i>Dira clytus</i>	34.03****	55	0.937	0.006	-1.069**	54	0.682	<0.0001	2.523***
<i>Gryllus bimaculatus</i>	1.81 <sup>ns</sup>	94	0.983	0.254	-0.086 <sup>ns</sup>	107	0.943	0.0002	0.981***

**(b)**

Species	Males				Females			
	n	$W$	$P$	$g_1$	n	$W$	$P$	$g_1$
Chrysomelid sp	109	0.983	0.167	-0.395 <sup>ns</sup>	63	0.978	0.306	-0.219 <sup>ns</sup>
<i>Henosepilachna vigintioctopunctata</i>	100	0.983	0.235	-0.202 <sup>ns</sup>	106	0.987	0.364	-0.045 <sup>ns</sup>
<i>Gonipterus scutellatus</i>	69	0.965	0.049	-0.644*	69	0.966	0.057	-0.514 <sup>ns</sup>
<i>Pachnoda sinuata</i>	46	0.947	0.035	-0.319 <sup>ns</sup>	61	0.978	0.334	-0.543 <sup>ns</sup>
<i>Setapion provinciale</i>	53	0.892	0.0002	-1.583***	59	0.986	0.741	-0.261 <sup>ns</sup>

<i>Ceratitis capitata</i>	51	0.960	0.082	0.797*	52	0.871	<0.0001	-1.561***
<i>Rhagovelia maculata</i>	52	0.788	<0.0001	-1.578***	56	0.761	<0.0001	-2.214***
Formicidae sp	73	0.987	0.643	0.171 <sup>ns</sup>	46	0.968	0.228	-0.567 <sup>ns</sup>
<i>Trichilogaster acacialongifoliae</i>	54	0.951	0.027	-0.803*	89	0.927	<0.0001	-1.085***
<i>Trichilogaster signiventris</i>	48	0.934	0.010	-0.924*	59	0.949	0.015	-0.833*
<i>Dira clytus</i>	55	0.880	<0.0001	-1.733***	54	0.833	<0.0001	1.595***
<i>Gryllus bimaculatus</i>	94	0.916	<0.0001	-1.404***	107	0.984	0.214	0.439 <sup>ns</sup>

**Table 4a** Statistical results for the deviation from normality (Shapiro-Wilks  $W$  statistic) and the degree of skewness ( $g_1$ ) for the (a) untransformed body length (mm) and (b) log transformed body length frequency distributions of the males and females of 12 of the insect species considered. Table 4a also includes the Type III chi-squared model results testing for sexual size dimorphism between the sexes.

(a)

Species	Length Measure	$\chi^2$	n	Males			Females			
				$W$	$P$	$g_1$	n	$W$	$P$	$g_1$
Chrysomelid sp	Elytron length	106.85****	109	0.975	0.975	-0.218 <sup>ns</sup>	63	0.950	0.012	-0.612 <sup>ns</sup>
<i>Henosepilachna vigintioctopunctata</i>	Elytron length	100.44****	100	0.934	<0.0001	-0.676*	106	0.969	0.013	-0.509**
<i>Gonipterus scutellatus</i>	Elytron length	144.64****	69	0.965	0.050	0.111 <sup>ns</sup>	69	0.962	0.036	-0.170 <sup>ns</sup>
<i>Pachmoda sinuata</i>	Elytron length	33.96****	46	0.964	0.165	0.291 <sup>ns</sup>	61	0.978	0.334	-0.340 <sup>ns</sup>
<i>Setapion provinciale</i>	Elytron length	2.12 <sup>ns</sup>	53	0.950	0.027	-0.219 <sup>ns</sup>	59	0.986	0.729	-0.148 <sup>ns</sup>
<i>Ceratitis capitata</i>	Total body length	61.96****	51	0.929	0.004	-0.441 <sup>ns</sup>	52	0.925	0.003	-1.014*
<i>Rhagovelia maculata</i>	Total body length	196.10****	52	0.947	0.021	-0.327 <sup>ns</sup>	56	0.910	0.0005	-1.058**
Formicidae sp	Head length	421.68****	72	0.960	0.021	0.059 <sup>ns</sup>	46	0.947	0.037	0.072 <sup>ns</sup>
<i>Trichilogaster acacialongifoliae</i>	Total body length	124.94****	54	0.920	0.001	1.135**	86	0.947	0.001	-0.626*
<i>Trichilogaster signiventris</i>	Total body length	22.48****	45	0.937	0.016	-0.729 <sup>ns</sup>	57	0.949	0.018	-0.358 <sup>ns</sup>
<i>Dira clytus</i>	Total body length	2.17 <sup>ns</sup>	54	0.968	0.163	-0.126 <sup>ns</sup>	53	0.941	0.011	0.609 <sup>ns</sup>
<i>Gryllus bimaculatus</i>	Head width	-15.52****	92	0.976	0.083	-0.126 <sup>ns</sup>	107	0.955	0.001	0.380 <sup>ns</sup>

(b)

Species	Males				Females			
	n	W	P	$g_1$	n	W	P	$g_1$
Chrysomelid sp	109	0.972	0.023	-0.310 <sup>ns</sup>	63	0.938	0.004	-0.758*
<i>Henosepilachna vigintioctopunctata</i>	100	0.918	<0.0001	-0.983***	106	0.956	0.001	-0.756**
<i>Gonipterus scutellatus</i>	69	0.967	0.062	0.007 <sup>ns</sup>	69	0.960	0.025	-0.257 <sup>ns</sup>
<i>Pachnoda sinuata</i>	46	0.967	0.210	0.220 <sup>ns</sup>	61	0.971	0.157	-0.505 <sup>ns</sup>
<i>Setapion provinciale</i>	53	0.946	0.019	-0.312 <sup>ns</sup>	59	0.982	0.517	-0.307 <sup>ns</sup>
<i>Ceratitis capitata</i>	51	0.924	0.003	-0.574 <sup>ns</sup>	52	0.903	0.0005	-1.291***
<i>Rhagovelia maculata</i>	52	0.944	0.016	-0.397 <sup>ns</sup>	56	0.900	0.0002	-1.190***
Formicidae sp	72	0.960	0.021	-0.111 <sup>ns</sup>	46	0.948	0.039	0.015 <sup>ns</sup>
<i>Trichilogaster acacialongifoliae</i>	54	0.962	0.084	0.095 <sup>ns</sup>	86	0.934	0.0003	-0.748**
<i>Trichilogaster signiventris</i>	45	0.921	0.005	-0.894*	57	0.940	0.007	-0.634 <sup>ns</sup>
<i>Dira clytus</i>	54	0.963	0.091	-0.417 <sup>ns</sup>	53	0.953	0.038	-0.107 <sup>ns</sup>
<i>Gryllus bimaculatus</i>	92	0.973	0.049	-0.284 <sup>ns</sup>	107	0.960	0.003	0.243 <sup>ns</sup>

Of the species considered in this study, 37.5% had right-skewed body mass frequency distributions, 6.25% were left skewed, 6.25% were bimodal and 50% were relatively normally distributed, or did not have a significantly skewed pattern. After log transformation of the mass data, 12.5% of the distributions were right-skewed, 37.5% were left-skewed, 6.25% were bimodal and 43.75% were relatively normally distributed. A variety of patterns were also apparent in the body length frequency distributions of the sixteen insect species considered in this study. Clearly this shows a large degree of variation in the patterns found for insects at the intraspecific level, contrary to what would be expected from May's (1981) arguments regarding multiplicative processes and growth. Nevertheless, when a right-skewed distribution was present, log transformation often resulted in lognormally distributed mass or length data. Moreover, it is unlikely that individuals within a species would respond in exactly the same way to identical conditions for growth. Indeed, individuals within a population are unlikely to switch resources from growth to reproduction in response to environmental conditions at the same times (see Kozłowski *et al.*, 2004). Therefore, the assumption that growth is a multiplicative process, which differs little between individuals, and which would consequently lead to a lognormal distribution (see Gaston & Chown, in press) is flawed. Much as this idea, based on the central limit theorem, is attractive, it is unlikely to be operating in practise. Consequently, if May's (1981) assumptions are not met at the intraspecific level, it is unlikely that it would apply at the interspecific level. This is clearly shown by the variation in interspecific BSFD patterns found in the literature. Of course, this begs the question of what does generate patterns in the intraspecific BSFD.

This question of the skewness of BSFDs has recently been addressed by Kozłowski and Gawelczyk (2002). Their body size optimisation models showed that a right-skewed size frequency distribution should be most common at the intraspecific level, compared to a diversity of other patterns. In the present study, however, most of the mass and length distributions were relatively normally distributed and not right-skewed. Alternatively, it was initially suggested by Fish (1985; see Lounibos, 1994) that a right, or positive skew in the body sizes of mosquitoes, is probably strongly associated with ephemeral habitats, where food availability is limited and/or larval growth is strongly affected by high density. A left, or negative skew, was suggested to be associated to more stable habitats

for larval growth, where population composition and density effects are controlled by predation (Lounibos, 1994, and references therein). For most populations of the four *Anopheles* species studied by Lounibos (1994) the BSFDs were left-skewed, with only two of the species being significantly skewed. Based on the suggestions made by Fish (1985; see Lounibos, 1994), one could therefore argue that these species endure less negative effects of larval density and food availability. Subsequently, Lounibos (1994) did find some effect of larval density and food availability to different degrees in each species, although no distinction could be made between these two factors. How these arguments apply to the present data is difficult to tell, but they seem unlikely given the preponderance of normal distributions.

Food availability and larval density could also indirectly affect the success of establishment of a species in a new environment. Several insect species have been introduced to South Africa for various reasons. For example, the two *Trichilogaster* parasitoid wasp species were introduced into South Africa as bio-control agents for two invasive *Acacia* tree species from Australia (see Henderson, 2001; Zimmerman *et al.*, 2004), while the weevil species, *Gonipterus scutellatus*, which is a pest of certain *Eucalyptus* trees also from Australia, was accidentally introduced (Annecke & Moran, 1982). Evans (2000) investigated the establishment and success of an introduced alien coccinellid species, *Coccinella septumpunctata* in North America. Similar to what was found by Lounibos (1994) for the mosquito species *Anopheles aquasalis*, *C. septumpunctata* showed a high variability in body size relative to the indigenous species (Evans, 2000). This could be an indication of a high degree of genetic variation being present in the sample populations, therefore allowing for the development and survival under a variety of environmental conditions (Evans, 2000). Thus, for the species in the present study, a large range of body sizes could indicate the ability of a particular species to be able to survive in various environments. Additionally, it could also be an indication of a high density and increased genetic variation of individuals within a population of a species (Lounibos, 1994; Evans, 2000). However, evidence for these ideas is quite limited, and at least some of the variation is more likely a consequence of sexual size dimorphism, than environmental conditions, recency of introduction, or genetic variability. The latter case seems especially unlikely for *Trichilogaster acaciaelongifoliae*

because recent work has shown a small number of haplotypes in this species (T. Lado, personal communication).

Males and females were distinguishable for most species, with the exception of two, i.e. the *Nysius* species and *Setapion quantillum*, which was mainly due to their small size. The termite *Microhodotermes viator* and the *Polistes* species, are both social insects and individual collected from these colonies were therefore all female workers. Nonetheless, in the remaining species, the females were larger than males, with one exception, i.e. the cricket species *Gryllus bimaculatus*. This pattern of larger females than males is common to most insect species (see Helms, 1994; Fairbairn, 1997; Teder & Tammaru, 2005), although exceptions, such as the yellow dung fly have been well documented (Kraushaar & Blanckenhorn 2002). Furthermore, it was noted by Teder and Tammura (2005) that variation in sexual size dimorphism at the intraspecific level is likely to occur when males and females differ in their response and sensitivity in growth to varying environmental conditions. Sexual selection effects on the BSFD of males and females of a population of a species would also affect how the size of the different sexes will be distributed (Tatsuta *et al.*, 2004). The presence of a negative skew in males could, for example, be a result of the reproductive advantages of larger size in males, resulting in more intermediate- to larger-sized individuals being present in a population. However, although Alcock (1984) found copulating males of the bee species *Centris pallida* to have a pronounced reproductive advantage over smaller 'patrolling' males, the range of head widths of the populations from 1974-1982 remained similar, i.e. right skewed. Therefore, the presence of more, smaller-sized individuals was maintained within the population over time (Alcock, 1984). The author suggested that the great range in size present in the males is largely controlled by the females and the smaller size classes are maintained in the population because they are able to cope in the highly competitive 'reproductive' environments within which they find themselves (Alcock, 1984). Perhaps unsurprisingly then, despite the size differences between males and females within each species in this study, sex-related variation in the shape of the frequency distributions was often negligible or small.

In this study, both mass and some measure of length were used to assess size variation within a population. The outcomes of the analyses of skew differed between

these variables in more than half of the cases (Table 2). This clearly indicates that linear and volumetric estimates of size and size variation within a population cannot simply be considered surrogates for each other. Rather, it must be realized that both kinds of variables are likely to be subject to different constraints depending on the life-history of the organism, its taxonomic affiliations, and constraints placed on morphological evolution by relationships between character complexes (see for e.g. LaBarbera, 1989; Kaspari & Weiser 1999; Strobbe & Stoks, 2004; Weiser & Kaspari, 2006). Therefore, it seems best to recommend that for consistency in assessments of body size frequency distributions, mass is used as a standard variable, despite the limitations thereon (see also Gaston & Blackburn, 2000).

Although the findings of this study provide a basic set of information for body size variation of insects, much information is still needed to understand why there is such substantial variation. Therefore, investigations regarding the life history and especially the voltinism of the species considered in this study, and how voltinism varies over space (see for example Roff, 1980) and time, would be highly informative and worth the effort. Lastly, much more work is needed considering this subject in order to get a more thorough representation of BSFDs of all the insect orders, especially in the southern hemisphere.

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## **Chapter 3**

### **Intraspecific altitudinal variation in the body size of beetles: testing the major hypotheses**

## INTRODUCTION

Body size is one of the most characteristic variables of any individual or species. In consequence, understanding the patterns in, and causes and consequences of body size variation is a major goal of ecology (e.g. Roff, 1981; Nylin *et al.*, 1996; Nylin & Gotthard 1998; Brown *et al.*, 2004; Makarieva *et al.*, 2005). At the interspecific level in arthropods, mean body size of assemblages may show an increase, decline, or little change over space (reviewed in Chown & Gaston, 1999; see also Gómez & Espadaler, 2000; Brehm & Fiedler, 2004). Several adaptive explanations for spatial changes in the mean size or in the form of the size frequency distribution of an assemblage have been proposed, with starvation resistance being the most widely accepted (Cushman *et al.*, 1993; Blackburn *et al.*, 1999). However, variation in the interspecific body size frequency distribution may have a variety of other causes, including variation in patterns of alpha and beta diversity, variation in the form of intraspecific size clines among species (Gaston & Chown, in press), and variation in the form of regional species pools from which local assemblages may represent little more than a random sample (Blackburn & Gaston, 2001). In consequence, understanding intraspecific size clines, patterns in alpha and beta diversity, and the determinants of regional species pools are essential for understanding spatial variation in species body size frequency distributions.

At the intraspecific level, in insects, mean size may increase (David & Bocquet, 1975; Bryant, 1977; Nylin & Svård, 1991; James *et al.*, 1995; Karan & Parkash, 1998; Arnett & Gotelli, 1999; Marcondes *et al.*, 1999; Huey *et al.*, 2000; Karan *et al.*, 2000; Loeschcke *et al.*, 2000; Chown & Klok, 2003; Heinze *et al.*, 2003; Gilchrist *et al.*, 2004; Peat *et al.*, 2005), decline (Park, 1949; Masaki, 1967, 1978, 1996; Mosseau & Roff, 1989; Nylin & Svård, 1991; Brennan & Fairbairn, 1995; Chown & Klok, 2003; Johansson, 2003) show a saw-tooth pattern (Masaki, 1978, 1996; Roff, 1980) or show no variation with an increase in latitude or altitude (see reviews in Chown & Gaston, 1999; Blanckenhorn & Demont, 2004). Several mechanistic hypotheses have been proposed to explain these patterns of variation in ectotherms. They can be classified as those that attribute body size variation either solely or predominantly to natural selection, those that consider this variation an epiphenomenon of the differential effects of temperature on growth and development, or those that explore some interaction of the two. Adaptive hypotheses have a long history,

beginning with the explanations based on von Bertalanffy's (1957) growth equation. The latter have largely been rejected owing to the absence of empirical evidence in their favour and logical problems associated with them (Berrigan & Charnov, 1994; Day & Taylor, 1997; Angilletta & Dunham, 2003; Kozłowski *et al.*, 2004). Currently, the most widely accepted of the adaptive explanations are those proposed by Kozłowski and colleagues building on earlier work by Roff (1980) and others (reviewed in Kozłowski *et al.*, 2004; Gaston & Chown, in press). The resource allocation switching curve models proposed by Kozłowski *et al.* (2004) are able to effectively account for both increases and declines in size across spatial gradients in season length and temperature. However, Makarieva *et al.* (2005) have proposed an alternative explanation based on a temperature independent minimum value of mass specific metabolic rate, which also accounts for both increases and declines in size with increasing temperature.

By contrast, a proximate biophysical model for the temperature size rule (Atkinson, 1994) was presented by van der Have and de Jong (1996). They suggested that an increase in size with declining temperature can generally be explained by differential effects of temperature on growth rate and differentiation rate within the thermal tolerance boundaries of development in ectotherms. Because the differentiation rate coefficient is higher than the growth rate coefficient, it is expected that at higher temperatures size at maturity will be smaller than at lower temperatures (van der Have & de Jongh, 1996). Unfortunately, the model cannot account for declines in size with temperature (or with latitude or altitude – with which temperature usually covaries) and is therefore not general. However, Chown and Gaston (1999) recently incorporated this mechanism into a broader explanation in which growing season length and temperature are considered separately, and suggested that differential effects of temperature on growth and development might only be found where growing season length is long relative to development time. Although evidence exists to suggest that this explanation has merit (Blanckenhorn & Demont, 2004), Kozłowski *et al.* (2004) have subsequently shown that the differential temperature effects mechanism is flawed. Gaston and Chown (in press) have consequently revised their earlier explanation and cast it within the adaptive and life history framework of the resource allocation switching models proposed by Kozłowski *et al.* (2004).

More recently, the epiphenomenon approach has been revisited by Walters and Hassal (2006). They suggested that the temperature-size rule can be explained by the relationship between the minimum threshold temperature for development ( $TT_D$ ) and the minimum threshold temperature for growth ( $TT_G$ ) (temperature threshold hypothesis). If  $TT_G < TT_D$ , an ectotherm should obey the temperature-size rule, whereas if  $TT_G > TT_D$ , an ectotherm should be an exception to the temperature-size rule, which was the case for their study species. The mechanistic underpinning of the explanation for the relationship between size and temperature proposed by Walters and Hassal (2006) is similar to that of van der Have and de Jongh (1996), although they suggested that selection acts on  $TT_G$  and  $TT_D$  specifically, optimizing the relationship between the two depending on whether or not large size at a high temperature is favoured. However, voltinism apparently affects the efficacy of selection depending on the actual voltinism of the population, with an increase in size with temperature ( $TT_G > TT_D$ ) being more likely in univoltine populations.

The final hypothesis for clinal size variation is that of starvation resistance, or resistance to unfavourable conditions more generally. It was originally proposed to explain size clinal variation at the interspecific level (e.g. Cushman *et al.*, 1993), although Chown and Gaston (1999) argued that resistance to starvation and/or desiccation should apply at the intraspecific level too. A major prediction of the hypothesis is that size should increase in areas with high intra-annual seasonality because larger-sized animals are capable of greater resource storage, especially if the size-storage relationship is allometric with a slope exceeding 1 (Chown & Gaston, 1999).

At present, no consensus on the mechanisms underlying intraspecific spatial variation in arthropod size has yet emerged (see also Angilletta & Dunham, 2003). Moreover, distinguishing between the various mechanisms is likely to be difficult because their predictions with regard to temperature (or altitude or latitude) and size are not mutually exclusive. Hence, the most appropriate way of addressing the current lack of consensus is to jointly examine the predictions of all of the mechanisms within a strong inference, model-building framework (see Huey *et al.*, 1999; Johnson & Omland, 2004), and to test them on an appropriate model system.

**Table 1.** Predictions of the hypotheses proposed to date to explain spatial size variation in insects

Hypothesis Description	I Proximate biophysical model <sup>1</sup>	II Temperature threshold hypothesis <sup>2</sup>	III Resource allocation switching curves <sup>3</sup>	IV Minimum metabolic rate <sup>4</sup>	V Starvation resistance <sup>5</sup>
Size change with temperature	-	-/+	-/+	-/+	-
Interspecific differences	No	Yes	Yes	Yes	Yes
Larval mortality factors	No	No	Yes	No	No
Size ratio prediction	No	No	No	Yes	No
Extent of seasonal differences	No	No	No	No	Yes
Significance of season length	No	Yes	Yes	No	Yes
Cell size and number	No	No	No	Yes	No

1 Van der Have & de Jongh 1996

2 Walters & Hassal 2006

3 Kozłowski *et al.* 2004

4 Makarieva *et al.* 2005

5 Chown & Gaston 1999

The four major hypotheses make a range of predictions for variation in size with temperature, the extent to which interspecific differences in the form of the size-temperature should vary, the existence of specific size ratios between different temperature environments (see equation 4 of Makarieva *et al.*, 2005), the significance of temperature only as a significant predictor of size variation rather than temperature and other extrinsic factors that influence larval mortality, whether cell size and number should vary in different ways depending on the direction of change in body size, and the extent to which the relationship between season length and life cycle length should affect the form of the size variation (Table 1). The starvation resistance hypothesis, which to date has not been formulated mathematically, nonetheless also makes several predictions regarding the relationship between size and the extent of environmental variability and season length.

Here we test the majority of these predictions by investigating altitudinal variation in size and the environmental correlates thereof in three beetle species, i.e. the univoltine carabid *Thermophilum decemguttatum*, and the univoltine tenebrionids *Stenocara dentata* and *Zophosis gracilicornis* (Fig. 1) across a 2000 m, east-west altitudinal gradient in the Cederberg district of South Africa, over a period of four years. Sampling over several years was undertaken to verify the consistency of the spatial variation in size.

## **MATERIALS AND METHODS**

### **Study animals, sites and sampling procedure**

The three beetle species are widespread and commonly found across south-western South Africa (Penrith, 1982; Picker *et al.*, 2002), and represent two different trophic groups: the carabid is carnivorous (Scholtz & Holm, 1985; Picker *et al.*, 2002), and the two tenebrionids are detritivores (Scholtz & Holm, 1985; Picker *et al.*, 2002).

Sampling was undertaken in October each year from 2002 to 2005 (as part of a larger study, see Botes *et al.*, 2006) along an altitudinal transect stretching from Lamberts Bay (sea level) over the Cederberg mountains (Sneeukop, 1926 m above sea level), down to Wupperthal (500 m above sea level) in the Western Cape, South Africa (Fig. 2). Seventeen altitudinal sites were sampled along this transect at approximately every 200 m

in altitude (Fig. 2 and Table 2). The field sampling procedures are described in detail in Botes *et al.* (2006). Briefly, at each of the 17 sites, forty, 62 mm diameter (150 ml) pitfall traps, divided into four groups of ten, were placed at each altitudinal site and GPS readings were taken of their positions for spatial analysis. At each site, the four groups of ten pitfalls were randomly placed at least 300 m apart from each other. In each of these groups, the pitfalls were placed in two rows of five traps, spaced at 10 m intervals. Each trap contained 50% propylene glycol and water solution as preservative and was left open in the field for five days. The traps were collected and returned to the laboratory. Here, the beetles were removed from the traps, sorted, labelled and pinned or preserved in ethanol. This material forms the subject of the present study. Voucher specimens of the three beetle species in question are housed at the Department of Botany and Zoology, Stellenbosch University, Western Cape Province, South Africa.

### **Morphometrics**

The body lengths of five to fifteen males and five to fifteen females (Appendix A) of each species from each altitudinal sampling site were determined by measuring the elytron length of each individual. Where no or only a few individuals of each species were sampled at a particular altitudinal site, these sites were excluded (see Farrel-Gray & Gotelli, 2005 for rationale). Krasnov *et al.* (1996) showed that elytron length is significantly related to total body length and it has also been used as a measure of body size in other investigations of beetles (e.g. Clayton, 1991; Chown & Stamhuis, 1992; Ward & Seely, 1996; Chown *et al.*, 1998; Janse van Rensburg *et al.*, 2003). Moreover, pilot morphometric analyses of the species examined here showed that elytron length was strongly related to several size measures. Individuals were measured using a StereoLEICA MZ 7.5 (Leica Microsystems, Wetzlar, Germany) microscope fitted with an ocular micrometer. To account for sexual size dimorphism, the sex of each individual beetle was determined by dissection.

(a)



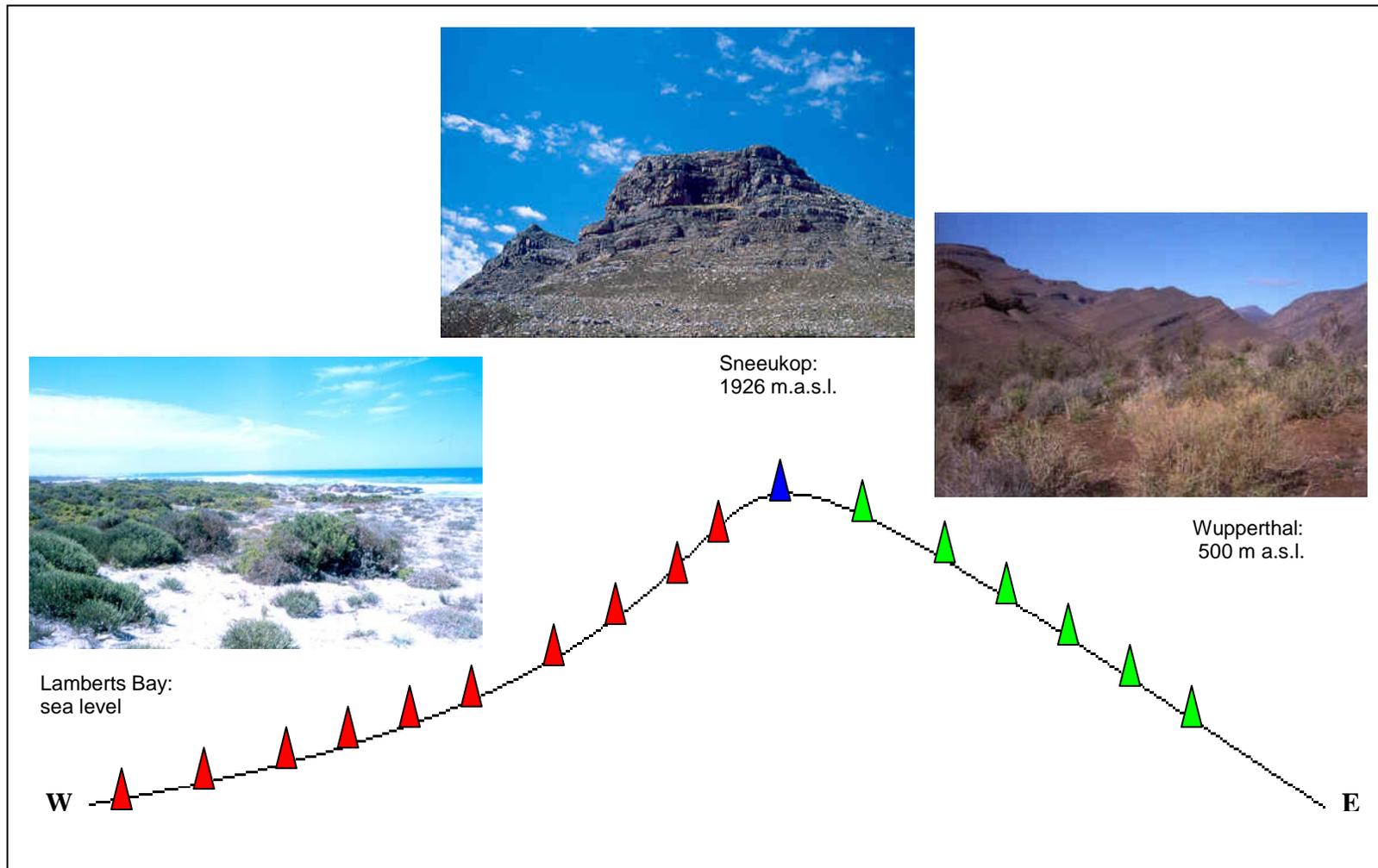
(b)



(c)



**Figure 1** Photographs of each of the three beetle species, **a)** *Thermophilum decemguttatum*, **b)** *Stenocara dentata* (photo by Brent Sinclair) and **c)** *Zophosis gracilicornis*. Photographs not according to scale.



**Figure 2** Schematic of the study transect, with sites placed approximately every 200m in altitude, starting at Lambert's Bay (sea level) in the west and ending at Wupperthal (500 meters above sea level) in the east.

**Table 2** Sampling area and vegetation types along the altitudinal transect stretching from Lamberts Bay over the Cederberg Mountains down to Wupperthal in the Greater Cederberg Biodiversity Corridor.

Altitudinal site	GPS	Altitude	Vegetation type	Geology
1 Lamberts Bay	32° 10,682'S 18° 18,858'E	5 m	Strandveld Succulent Karoo	Dunesand, in areas highly calcareous
2	32° 16,598'S 18° 31,799'E	256 m	Restioid Mountain Fynbos	Quartzitic sandstone with
3	32° 20,518'S 18° 59,491'E	370 m	Ecotonal, Succulent Karoo and Proteoid Mountain Fynbos	minor shale and conglomerate lenses
4	32° 21,067'S 19° 00,417'E	537 m	Proteoid Mountain Fynbos	
5	32° 24,471'S 19° 05,079'E	766 m	Proteoid Mountain Fynbos	
6	32° 25,445'S 19° 09,970'E	922 m	Restioid Mountain Fynbos	
7	32° 27,581'S 19° 14,459'E	1133 m	Ericoid Mountain Fynbos	
8	32° 26,100'S 19° 13,969'E	1337 m	Ericoid Mountain Fynbos	
9	32° 21,435'S 19° 08,753'E	1543 m	Ericoid Mountain Fynbos	
10	32° 21,310'S 19° 08,938'E	1687 m	Ericoid Mountain Fynbos	Quartzitic sandstone with
11	32° 21,305'S 19° 09,695'E	1926 m	Restioid Mountain Fynbos	thin shale and conglomerate lenses

**Table 1** Continued

<b>Eastern slope of altitudinal gradient:</b>				
12	32° 21,241'S 19° 10,018'E	1740 m	Ericoid Mountain Fynbos	Quartzitic sandstone with thin shale and conglomerate lenses
13	32° 20,888'S 19° 10,213'E	1543 m	Ericoid Mountain Fynbos	Quartzitic sandstone with minor shale and conglomerate lenses
14	32° 20,340'S 19° 10,899'E	1365 m	Ericoid Mountain Fynbos	
15	32° 20,140'S 19° 11,623'E	1158 m	Ericoid Mountain Fynbos	
16	32° 19,637'S 19° 12,086'E	965 m	Restioid Mountain Fynbos	
17 Wupperthal	32° 16,674'S 19° 13,161'E	520 m	Lowland Succulent Karoo	Siltstone, shale

To test for repeatability of the measurement process, and therefore measurement precision (see Walther & Moore, 2005), the same ten specimens from each species were measured repeatedly when 33%, 50%, 66% and 100% of all the beetles had been measured. Repeatability was determined using the intraclass correlation coefficient ( $\tau$ , Krebs, 1999), obtained from an analysis of variance (ANOVA) and the equation for repeatability provided by Lessels & Boag (1987, see also Krebs, 1999).

### **Environmental variables**

Based on the mechanisms predicted to underlie spatial variation in body size, and on the likely factors influencing larval growth and survival, several environmental variables were chosen for inclusion in models of spatial variation in body size. First, temperature variation is a component of all of the explanations proposed for intraspecific body size clines. Therefore, temperature data were acquired from iButton (Semiconductor Corporation, Dallas/Maxim) loggers, two of which were buried 10 mm underneath the soil surface at each altitudinal site and were set to take temperature readings at hourly intervals (see Botes *et al.*, 2006). The hourly recording of soil temperature commenced in June 2002 and is ongoing. Soil temperature data obtained during June 2002 to October 2005 were used to calculate mean annual temperature at each altitudinal site per year, as well as mean daily minimum. Years were taken to run from November of each year to October of the following year, presuming that this represents a more biologically realistic year for these species than the calendar year given high adult abundances in spring, but their virtual absence in autumn (Botes *et al.*, 2007).

Although the majority of the hypotheses proposed to explain clinal size variation make no predictions for the influence of larval mortality on the clines, this is the case for the resource allocation switching curves hypothesis. Therefore, several major environmental factors that are likely to influence larval mortality were included in the analyses. These included the proportion of sand in the soil, the proportion of vegetation cover per site, and the vegetation height complexity per site. Soil texture is known to influence larval mortality directly (Thiele, 1977; Rushton *et al.*, 1991; Sanderson *et al.*, 1995), whilst vegetation cover and complexity can affect mortality either indirectly through their influences on predation and parasitism (Connor, 1991; Gunnarsson, 1996;

Hawkins *et al.*, 1997; Larsson *et al.*, 1997; Tschanz *et al.*, 2005) or directly via resource availability and acquisition (Huk & Kühne, 1999; Messina & Fry, 2003; Jones & Widemo, 2005). In the latter case, annual productivity is also a significant measure of resource availability. By contrast, the starvation resistance hypothesis predicts that annual variability in productivity will account for much variation in size and the sign of this relationship should be positive. With little variability starvation is likely to be much less of a problem than with pronounced variability, and therefore in the former case individuals should be smaller (Chown & Gaston, 1999).

Vegetation structure at each of the sampling grids was assessed in each year to determine cover and density as described in Botes *et al.* (2006). Briefly, percentage ground cover was estimated by placing a 1 m<sup>2</sup> quadrat over each pitfall trap and estimating the percentage cover of each of the above mentioned categories. The vertical vegetation complexity ('foliage height profiles', Bestelmeyer & Wiens, 1996) of the vegetation at each sampling grid was estimated at four points situated at 90° angles from each other on a 1.5 m radius. These points were centered on each trap and a 1.5 m pole was placed vertically at each sampling point. Maximum height of vegetation was accepted as the highest 25 cm interval where vegetation made contact with the pole (Rotenberry & Wiens, 1980). The average total number of hits per sample point was determined and used as a measure of the change in the vertical distribution of vegetation (Rotenberry & Wiens, 1980).

A 20 cm<sup>3</sup> soil sample was taken at each sampling grid in October 2002 for the determination of soil properties. The 20 cm<sup>3</sup> was taken from twenty sub-samples that were taken randomly at each grid and then mixed. These soil samples were then air-dried in the laboratory for approximately 10 days and then analysed for composition (rock, sand, clay and silt) by BemLab (Pty Ltd.), South Africa (Botes *et al.*, 2006 provide details).

To assess the mean and variation in productivity the mean monthly Normalized Difference Vegetation Index (NDVI, see Kerr and Ostrovsky 2003), and the difference between mean January and mean July NDVI (NDVI difference), respectively were calculated. NDVI data were obtained at a 30 m x 30 m resolution from the Satellite

Application Centre of the CSIR (Council for Scientific and Industrial Research) in Pretoria (South Africa) for October 2002 to October 2004 for each site.

### **Data analyses**

Normality of data was tested using the Shapiro-Wilks method (Zar, 1999), and where data were not normally distributed, appropriate transformations or analytical methods were used. Patterns of collinearity amongst the original set of environmental variables were investigated using multiple regression methods to determine which, if any, variables were highly correlated with each other. The tolerance values for each of the variables were calculated and used to determine collinearity among the environmental variables. (Quinn & Keough, 2002). Most of the variables had tolerance values approaching or lower than 0.1. Although mean annual temperature and proportion of sand in the soil were not found to be highly collinear (tolerance of 1.000), these variables significantly covaried along the altitudinal transect ( $r = 0.492$ ;  $\chi^2 = 44.88$ ;  $P < 0.0001$ ).

Given the predictions of each of the models, several sets of analyses were undertaken, in each case using generalized linear models (GENMOD procedure, SAS Institute Inc., Cary, NC, USA: GLZ, Type III models, assuming a normal distribution and a log link function; McCullagh & Nelder, 1989; Quinn & Keough, 2002). The Akaike Information Criterion (AIC) and Akaike weights (Burnham & Anderson, 1998; Quinn & Keough, 2002) were used to select the best fit models throughout.

In the first analysis, differences in elytron length were examined using altitude, species, sex and sampling year as the predictor variables. The proximate biophysical model predicts no differences in the form of the relationship among species (Table 1), therefore this analysis provides a conclusive test of that hypothesis. The second analysis used the same set of predictors, but here each species was analyzed separately owing to significance of the species term in the previous model. The main aim of this analysis was to determine the extent of variation associated with year and sex. *Stenocara dentata* was omitted from further analyses because its elytron length did not vary with altitude, and the other species were always analyzed separately. In the third set of analyses models exploring the relationship between elytron length and sex, mean annual temperature (MAT), proportion of sand in the soil, vegetation complexity, vegetation cover, mean

annual NDVI, and NDVI difference were built. The first set of models included all length data from the study, but excluded NDVI and NDVI difference as predictors because an annual set of data for these variables were available for the 2003 and 2004 years only. These analyses were also repeated excluding proportion of sand because of its collinearity with temperature. Thereafter, identical models were built but for 2003 and 2004 only, including the NDVI data. In all cases, models were run using mean elytron length for each of the sexes for each of the sites (environmental variables were site rather than individual specific). Although spatial autocorrelation can influence the estimates from and significance of models (e.g. Lennon 2000), initial analyses indicated that insufficient degrees of freedom were available in the models using mean elytron length to include spatial autocorrelation in the form of a third-order polynomial model (Legendre & Legendre, 1998). The use of individual length measurements might have circumvented this problem, but would have caused another because environmental variables were site specific. However, to determine the likely effect of spatial autocorrelation, the residuals from the best fit environmental models (2003 and 2004 data only) were examined for spatial autocorrelation as recommended by Diniz-Filho *et al.* (2003). The Spatial Analysis in Macroecology v1.1 (SAM) package (Rangel *et al.*, 2006) was used to calculate Moran's I values for the residuals from the best-fit models for both *Z. gracilicornis* and *T. decemguttatum*. The default options of the software were adopted (equal numbers of point pairs) and significance was determined by permutation. Although the inclusion of environmental predictors in the above models provided an opportunity to test the predictions of most of the hypotheses for size change with altitude, they did not provide a test of the size ratio prediction of Makarieva *et al.*'s (2005) minimum metabolic rate model. To do this, their equation 4 was used:

$$\frac{L_{\max}(T_1)}{L_{\max}(T_2)} = Q_{10}^{\Delta T / 10^{\circ}C} \quad (1)$$

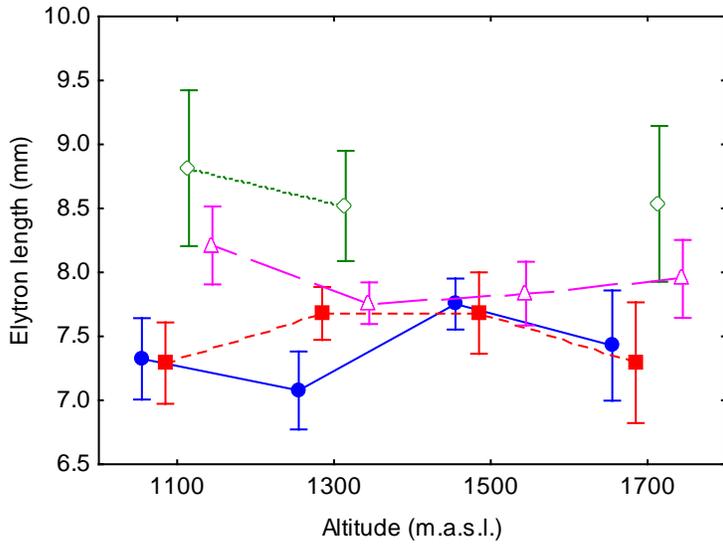
where the left-hand term of the equation is the ratio of the maximum body size of species living at one temperature and the maximum body size of species living at a different temperature, and the right-hand term is  $Q_{10}$  to the power of the difference in temperature

at which metabolic rate of active adults is at a minimum divided by 10. However, because differences among populations are involved here mean size of each of the populations was used. Moreover, because larvae are likely to be active year round, because it is growth conditions of the larvae that affect final adult size (see Atkinson, 1994), and because the species are univoltine, mean daily minimum temperature was used to approximate the temperature at which metabolic rate is likely to be lowest. Additionally, it was assumed that  $Q_{10} = 2$ , owing to the frequency with which such a  $Q_{10}$  value is found in insects (Chown & Nicolson, 2004). The way in which the minimum metabolic rate hypothesis was tested was to calculate the expected ratio for a given set of altitudinal pairs based on their mean daily minimum temperature using the right-hand term of the equation and then to calculate the size-ratio for the same pair of altitudes using mean body size and the left-hand term in the equation. The relationship between the ratios for the altitudinal pairs was then investigated using ordinary least squares regression assuming that for identity of the two ratios the slope would be 0 and the intercept 1. Clearly, the use of all altitudinal pairs would artificially elevate the degrees of freedom in the models owing to non-independence of adjacent pairs of sites. Therefore, the procedure was repeated excluding every second set of sites in two ways (effectively, odds and evens) and the slopes and intercepts re-assessed. In each case, outliers that lay beyond  $2 * S.E.$  were removed and the analyses redone. Reduced major axis regression was not used because temperature was measured with much greater precision than length, and even so, length measurements showed substantial precision (McArdle, 1988). Clearly, several other assumptions could have been made about the environmental temperatures and sizes to be assessed in this test of the minimum metabolic rate model, but those made here appeared most appropriate based on the biology of the species.

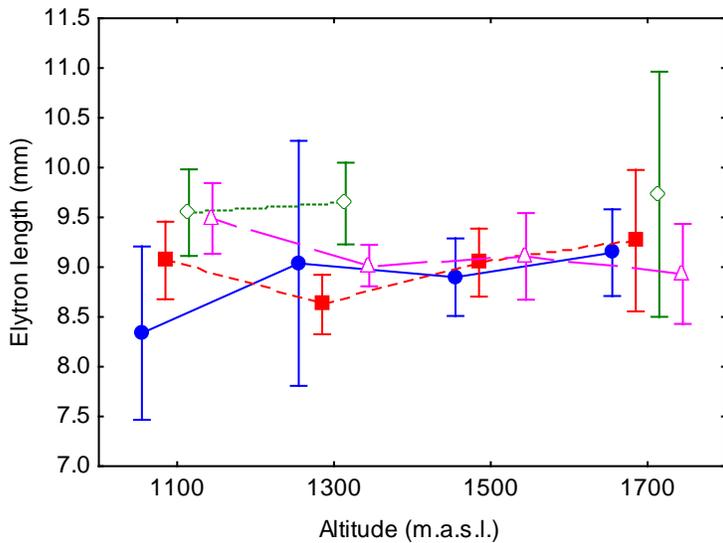
**Table 3** Results for the best-fit generalised linear models examining the relationship between elytron length and altitude, sex, year and species, including their interactions, and for the former variables per species.

	Parameter Estimate $\pm$ SE	$\chi^2$	P
<b>Species pooled</b>			
<i>(r<sup>2</sup> = 0.994, df = 137)</i>			
Altitude	-0.022 $\pm$ 0.002	130.31	< 0.0001
Sex	0.111 $\pm$ 0.031	67.97	< 0.0001
Species		716.95	< 0.0001
Year		12.50	0.0059
Species*Sex		9.28	0.0096
<b><i>Thermophilum decemguttatum</i></b>			
<i>(r<sup>2</sup> = 0.860, df = 34)</i>			
Altitude	-0.039 $\pm$ 0.003	64.57	< 0.0001
Sex	0.076 $\pm$ 0.009	43.03	< 0.0001
Year		9.50	0.0233
<b><i>Stenocara dentata</i></b>			
<i>(r<sup>2</sup> = 0.926, df = 22)</i>			
Sex	0.141 $\pm$ 0.019	69.98	< 0.0001
Year		40.55	< 0.0001
Sex*Year		7.97	0.0467
<b><i>Zophosis gracilicornis</i></b>			
<i>(r<sup>2</sup> = 0.789, df = 63)</i>			
Altitude	-0.021 $\pm$ 0.002	56.01	< 0.0001
Sex	0.110 $\pm$ 0.011	60.27	< 0.0001
Year		53.33	< 0.0001

**3 (a)**

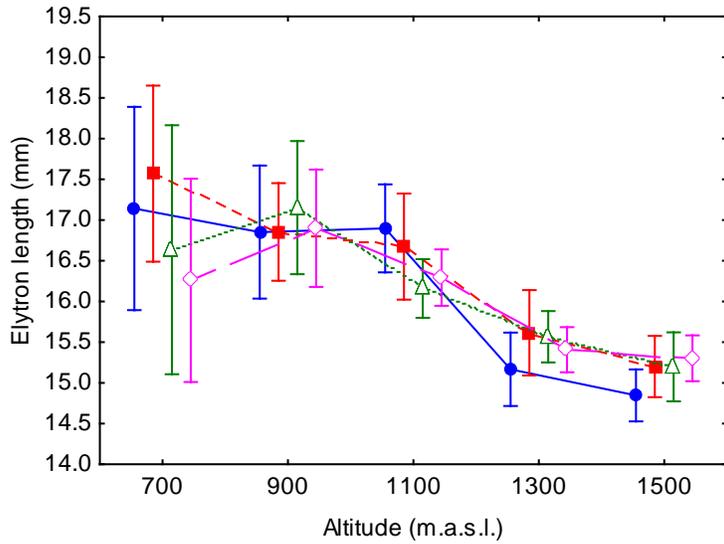


**3 (b)**

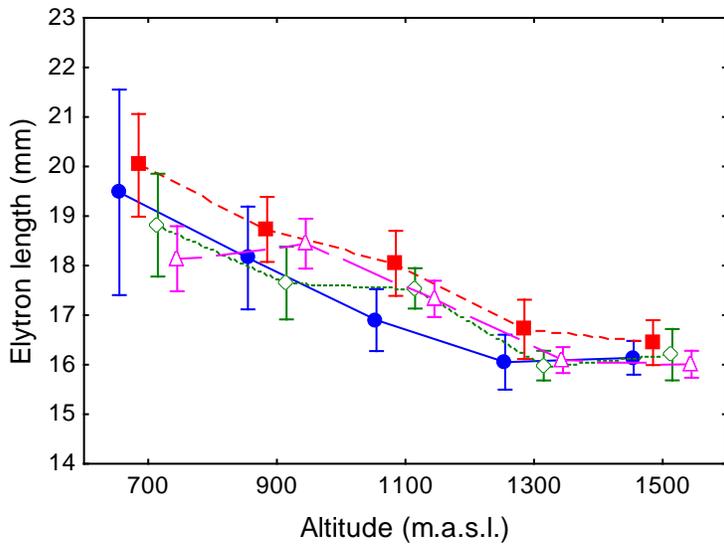


**Figure 3** Elytron length variation along the western slope of the altitudinal gradient in the Cederberg district transect for **(a)** *Stenocara dentata* males and **(b)** females. The solid blue line and closed circles denote variation in October 2002, the broken red line and solid squares denote variation in October 2003, the dashed green line and open triangles denote variation in October 2004 and the broken pink line and open diamonds denote variation in October 2005. Data are presented as least squares means and 95% confidence limits.

4 (a)

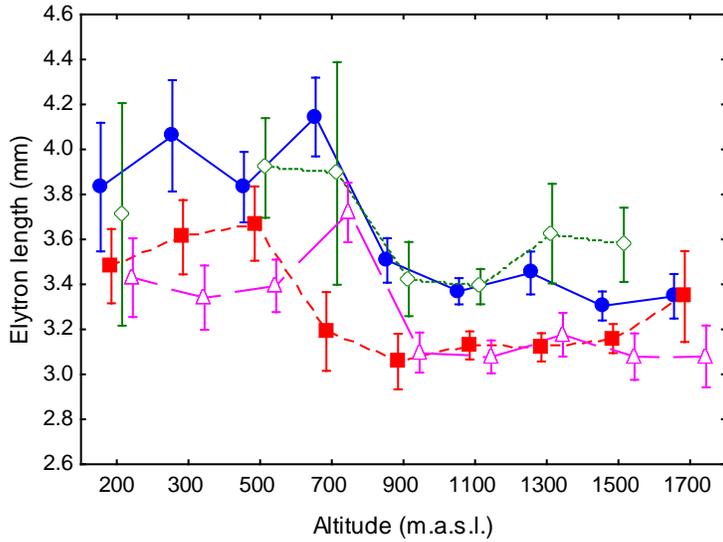


4 (b)

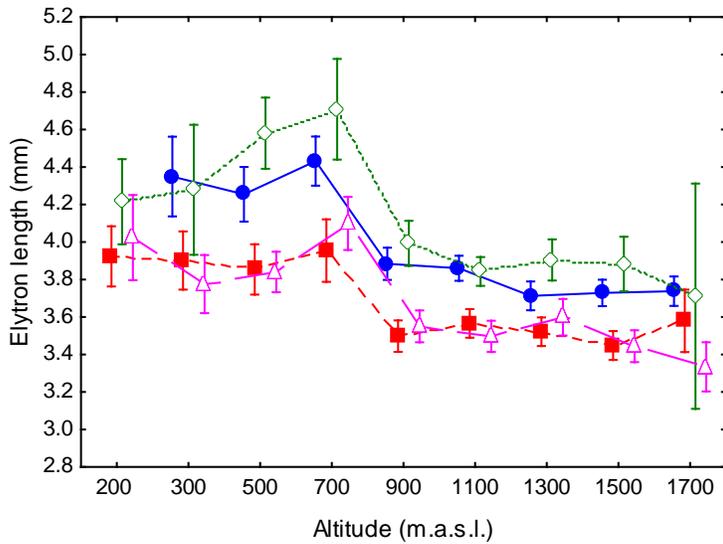


**Figure 4** Elytron length variation along the western slope of the altitudinal gradient in the Cederberg district transect for (a) *Thermophilum decemguttatum* males and (b) females. The solid blue line and closed circles denote variation in October 2002, the broken red line and solid squares denote variation in October 2003, the dashed green line and open triangles denote variation in October 2004 and the broken pink line and open diamonds denote variation in October 2005. Data are presented as least squares means and 95% confidence limits.

5 (a)



5 (b)



**Figure 5** Elytron length variation along the western slope of the altitudinal gradient in the Cederberg district transect for (a) *Zophosis gracilicornis* males and (b) females. The solid blue line and closed circles denote variation in October 2002, the broken red line and solid squares denote variation in October 2003, the dashed green line and open triangles denote variation in October 2004 and the broken pink line and open diamonds denote variation in October 2005. Data are presented as least squares means and 95% confidence limits.

**Table 4** Best-fit generalized linear models examining the effects of the environmental variables (excluding NDVI and NDVI difference) on elytron length in the two beetle species which showed significant elytron length variation with altitude. df = degrees of freedom,  $r^2$  = coefficient of determination, AIC value = Akaike Information Criterion value,  $w_i$  = Akaike weight.

Model	df	$r^2$	Predictors	AIC value	$w_i$
<i>Thermophilum decemguttatum</i>					
I	36	0.579	+0.600 Proportion of sand**** +0.006 Vegetation complexity - 0.224* Vegetation cover <sup>ns</sup>	103.393	0.249
II	37	0.556	+0.687 Proportion of sand**** +0.005 Vegetation complexity *	103.569	0.228
III	35	0.593	+0.003 MAT <sup>ns</sup> +0.544 Proportion of sand**** +0.004 Vegetation complexity <sup>ns</sup> -0.134 Vegetation cover <sup>ns</sup>	104.065	0.178
<i>Zophosis gracilicornis</i>					
I	65	0.299	-0.005 MAT <sup>ns</sup> +0.271 Proportion of sand* +0.016 Vegetation complexity***	42.898	0.196
II	66	0.277	+0.194 Proportion of sand <sup>ns</sup> +0.013 Vegetation complexity***	43.066	0.180
III	64	0.317	-0.006 MAT <sup>ns</sup> +0.236 Proportion of sand <sup>ns</sup> +0.016 Vegetation complexity**** +0.003 Vegetation cover <sup>ns</sup>	43.101	0.177

$P < 0.05$  \*

$P < 0.01$  \*\*

$P < 0.001$  \*\*\*

$P < 0.0001$  \*\*\*\*

## RESULTS

Although individuals of all three species were found at sites on both the eastern and western slopes of the transect, occurrence was sporadic on the eastern slopes. Therefore, data from the western slopes of the transect only were used (Appendix A). The measurement process was found to be highly repeatable ( $\tau > 0.80$  for all species for all years) and therefore the length data were considered sound and relatively free of measurement inaccuracy. Elytron length measurements were generally right-skewed when data from all populations and years were pooled for each species (*T. decemguttatum*, Shapiro-Wilk W-statistic = 0.989,  $P < 0.0001$ , skew = 0.393,  $P < 0.001$ ; *S. dentata*, Shapiro-Wilk W-statistic = 0.982,  $P = 0.0003$ , skew = 0.411,  $P = 0.002$ ; *Z. gracilicornis*, Shapiro-Wilk W-statistic = 0.980,  $P < 0.0001$ , skew = 0.542,  $P < 0.001$ ). Log-transformation typically removed this skew.

Outcomes of the models used in the first and second analyses revealed significant effects of altitude, species, sex, and year as well as significant interactions between the latter, categorical predictors (Table 3). Species-specific models showed that the species term was largely significant owing to little consistent change in elytron length with altitude in *Sternocara dentata* (Fig. 3; Table 3). In the two remaining species, elytron length declined with altitude, males were smaller than females and some variation in these patterns was found among years (Table 3, Figs 4 and 5).

The best-fit models for the full period, excluding NDVI and NDVI differences revealed substantial effects of proportion of sand and vegetation complexity and cover, with little role for mean annual temperature (Table 4). However, this may have been a consequence of strong covariation between proportion of sand in the soil and mean annual temperature (see Materials and Methods), and exclusion of the former variable certainly led to an increase in the importance of mean annual temperature, at least for *T. decemguttatum* (Table 5). Analysis of the sexes separately resulted in largely the same outcomes (Appendix B). Best-fit models including NDVI and NDVI difference over the two year period differed substantially from the previous ones (Table 6). Here, mean annual temperature was always included in the models, together with vegetation cover or complexity in the case of *T. decemguttatum* and NDVI or NDVI difference in *Z. gracilicornis*. Separate analyses of the sexes revealed that the importance of mean annual

**Table 5** Best-fit generalized linear models examining the effects of the environmental variables (excluding NDVI, NDVI difference and proportion of sand in the soil) on elytron length in the two beetle species which showed significant elytron length variation with altitude. df = degrees of freedom,  $r^2$  = coefficient of determination, AIC value = Akaike Information Criterion value,  $w_i$  = Akaike weight.

Model	df	$r^2$	Predictors	AIC value	$w_i$
<i>Thermophilum decemguttatum</i>					
I	37	0.383	+0.009 MAT*** -0.305 Vegetation cover***	116.738	0.533
II	36	0.404	+0.007 MAT* 0.004 Vegetation density <sup>ns</sup> -0.316 Vegetation cover***	117.340	0.395
<i>Zophosis gracilicornis</i>					
I	66	0.275	+0.015 Vegetation density***** +0.004 Vegetation cover <sup>ns</sup>	43.184	0.403
II	67	0.246	+0.015 Vegetation density*****	43.922	0.278
III	65	0.281	-0.003 MAT <sup>ns</sup> -0.017 Vegetation density***** +0.004 Vegetation cover <sup>ns</sup>	44.608	0.197

$P < 0.05$  \*

$P < 0.01$  \*\*

$P < 0.001$  \*\*\*

$P < 0.0001$  \*\*\*\*

**Table 6** Best-fit generalized linear models examining the effects of the environmental variables on elytron length in the two beetle species which showed significant elytron length variation with altitude over the 2003-2004 period. df = degrees of freedom,  $r^2$  = coefficient of determination, AIC value = Akaike Information Criterion value,  $w_i$  = Akaike weight, MAT = mean annual temperature.

Model	df	$r^2$	Predictors	AIC value	$w_i$
<i>Thermophilum decemguttatum</i>					
I	17	0.592	+0.021 MAT*** -0.224 Vegetation cover*	54.755	0.204
II	16	0.631	+0.029 MAT*** -0.008 Vegetation density <sup>ns</sup> -0.150 Vegetation cover <sup>ns</sup>	54.784	0.201
III	17	0.591	+0.034 MAT**** -0.012 Vegetation density*	54.817	0.198
<i>Zophosis gracilicornis</i>					
I	31	0.507	+0.014 MAT* -0.0001 NDVI difference***	13.291	0.290
II	30	0.520	+0.016 MAT** -0.0001 NDVI difference*** +0.000 Mean annual NDVI <sup>ns</sup>	14.427	0.164
III	30	0.518	+0.018 MAT* -0.0001 NDVI difference*** -0.161 Proportion of sand <sup>ns</sup>	14.562	0.154

$P < 0.05$  \*

$P < 0.01$  \*\*

$P < 0.001$  \*\*\*

$P < 0.0001$  \*\*\*\*

**Table 7** Best-fit generalized linear models examining the effects of the environmental variables on elytron length in males and in females, respectively, of **(a)** *Thermophilum decemguttatum* males and females and **(b)** *Zophosis gracilicornis*, over the 2003-2004 period. df = degrees of freedom,  $r^2$  = coefficient of determination, AIC value = Akaike Information Criterion value,  $w_i$  = Akaike weight, MAT = mean annual temperature.

**(a)**

Model	df	$r^2$	Predictors	AIC value	$w_i$
<b>Males</b>					
I	4	0.993	+0.013 MAT***** -0.000 NDVI variation* +0.000 Mean annual NDVI*** +0.211 Proportion of sand***** -0.190 Vegetation cover*****	-13.823	0.518
II	3	0.994	+0.013 MAT***** -0.000 NDVI variation <sup>ns</sup> +0.000 Mean annual NDVI** +0.206 Proportion of sand***** -0.0004 Vegetation density <sup>ns</sup> -0.192 Vegetation cover*****	-11.920	0.200
III	5	0.990	+0.014 MAT***** +0.000 Mean annual NDVI** +0.201 Proportion of sand**** -0.177 Vegetation cover*****	-11.278	0.145
<b>Females</b>					
I	7	0.875	+0.038 MAT***** -0.014 Vegetation density**	18.320	0.299
II	6	0.889	+0.040 MAT***** +0.000 Mean annual NDVI <sup>ns</sup> -0.015 Vegetation density**	19.126	0.200
III	6	0.883	+0.038 MAT***** +0.000 NDVI variation -0.012 Vegetation density*	19.671	0.152

(b)

Model	df	$r^2$	Predictors	AIC value	$w_i$
<b>Males</b>					
I	13	0.767	-0.0001 NDVI variation**** +0.008 Vegetation density*	-12.044	0.255
II	13	0.763	+0.010 MAT* -0.0001 NDVI variation****	-11.790	0.225
III	12	0.779	+0.006 MAT <sup>ns</sup> -0.0001 NDVI variation**** +0.005 Vegetation density <sup>ns</sup>	-10.939	0.147
<b>Females</b>					
I	13	0.777	+0.033 MAT*** -0.0001 NDVI variation** -0.431 Proportion of sand* +0.162 Vegetation cover <sup>ns</sup>	-4.485	0.235
II	14	0.749	+0.026 MAT*** -0.0001 NDVI variation** -0.253 Proportion of sand <sup>ns</sup>	-4.352	0.220
III	15	0.716	+0.019 MAT*** -0.0001 NDVI variation**	-4.086	0.193

$P < 0.05$  \*

$P < 0.01$  \*\*

$P < 0.001$  \*\*\*

$P < 0.0001$  \*\*\*\*

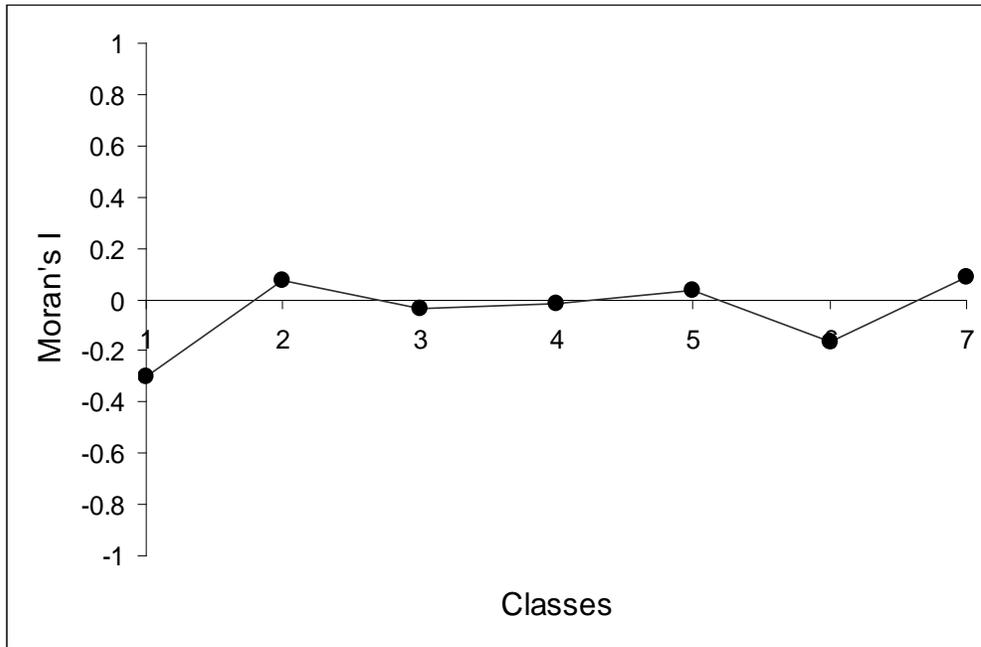
temperature varied among the sexes especially in *Z. gracilicornis* (Table 7), as did the extent of the influence of the other environmental variables. Spatial autocorrelation analyses revealed no spatially structured residual variation in the data (Fig. 6), perhaps unsurprising given the high explanatory value of the models.

Investigation of the suitability of the minimum metabolic rate models gave different results for *T. decemguttatum* and *Z. gracilicornis*. In *T. decemguttatum*, the relationships between the length ratios and the temperature ratio ( $Q_{10}^{\Delta T/10}$ ) were almost always significant, although the variation around them was typically high ( $R^2$  values were never higher than 0.6 even when outliers were removed). Moreover, the slopes and intercepts were not significantly different from 1 and 0, respectively (Table 8). By contrast, in *Z. gracilicornis* the relationships were typically not significant, and where this was the case the slope differed from 1 and the intercept from 0 (Table 8).

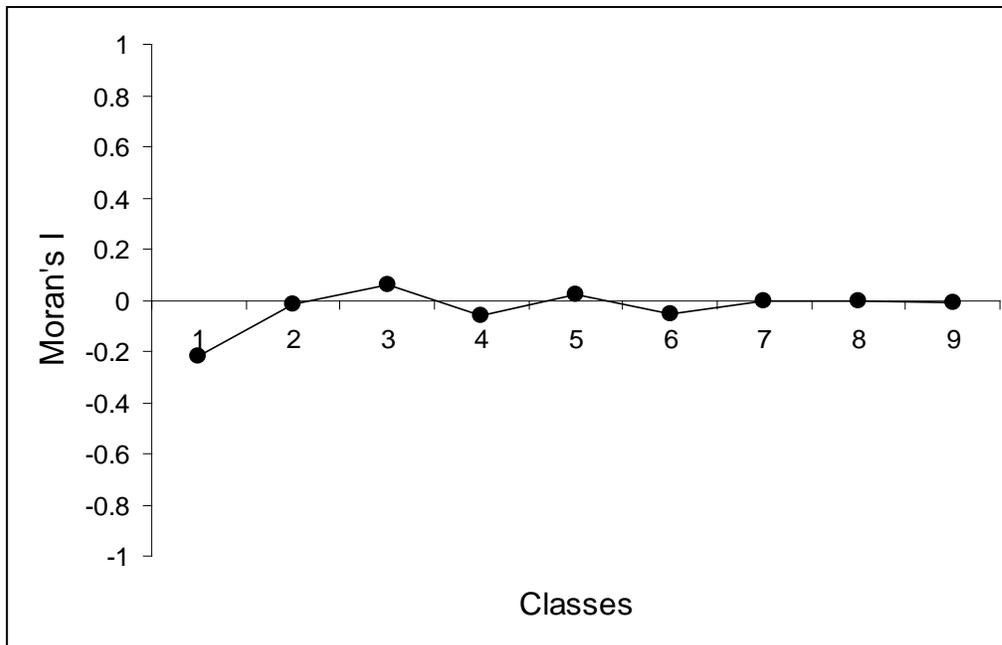
**Table 8** Outcomes of the ordinary least squares regression analyses of length ratios on  $Q_{10}^{\Delta T/10}$  for *T. decemguttatum* and *Z. gracilicornis*. Where outliers (2\*S.E.) affected the regressions, the outcomes following removal of the outliers are also shown. Full analyses are compromised by inflated degrees of freedom, but this is not the case for the partial analyses. The two partial analyses are alternative sets of alternating altitudinal pairs. \*\*p <0.01.

	Slope ± S.E.	t <sub>(df)</sub>	Intercept ± S.E.	t <sub>(df)</sub>	Regression p =
<b><i>Thermophilum decemguttatum</i></b>					
Full	1.29 ± 0.44	0.667 <sub>(32)</sub> <sup>ns</sup>	-0.33 ± 0.45	-0.737 <sub>(32)</sub> <sup>ns</sup>	0.0057
Partial 1	2.13 ± 0.65	1.729 <sub>(15)</sub> <sup>ns</sup>	-1.13 ± 0.66	-1.715 <sub>(15)</sub> <sup>ns</sup>	0.0052
Partial 2	1.53 ± 0.62	0.850 <sub>(15)</sub> <sup>ns</sup>	-0.63 ± 0.65	-0.958 <sub>(15)</sub> <sup>ns</sup>	0.027
Outliers removed					
Full	1.09 ± 0.30	0.337 <sub>(29)</sub> <sup>ns</sup>	-0.13 ± 0.31	-0.412 <sub>(29)</sub> <sup>ns</sup>	0.0009
Partial 1	2.13 ± 0.65	1.729 <sub>(15)</sub> <sup>ns</sup>	-1.13 ± 0.66	-1.715 <sub>(15)</sub> <sup>ns</sup>	0.0052
Partial 2	1.56 ± 0.33	1.706 <sub>(12)</sub> <sup>ns</sup>	-0.66 ± 0.35	-1.881 <sub>(12)</sub> <sup>ns</sup>	0.0047
<b><i>Zophosis gracilicornis</i></b>					
Full					0.43
Partial 1					0.69
Partial 2					0.26
Outliers removed					
Full	0.38 ± 0.16	-3.7 <sub>(35)</sub> **	0.59 ± 0.17	3.5 <sub>(35)</sub> **	0.0267
Partial 1					0.45
Partial 2					0.27

6 (a)



6 (b)



**Figure 6** Moran's I values for the residuals of the best-fit models for **a)** *Thermophilum decemguttatum*, and **b)** *Zophosis gracilicornis*, calculated using SAM v1.1. None of the values were significant in either of the cases and the overall form of the relationships indicates little spatial structure to the residuals.

## DISCUSSION

The beetles investigated in this study were similar to other insects in several respects. Males were smaller than females as is the case in most other species (Helms, 1994; Fairbairn, 1997; Teder & Tammaru, 2005), and their body size frequency distributions had a right skew, as has been found for many species (Gaston & Chown, in press, but see Pielou, 1977 for the dangers of pooling data for frequency distributions). In at least two of the species, elytron length, used here as a surrogate for overall body size, declined with altitude. Such declines of body size with altitude have been recorded in a variety of species including field crickets (Masaki, 1967), tenebrionid beetles (Krasnov *et al.*, 1996), grasshoppers (Orr, 1996), ant lions (Arnett & Gotelli, 1999a) and weevils (Chown & Klok, 2003). However, *Sternocara dentata* showed no change in size with altitude. Although such altitudinal size-invariance seems unusual, lack of variation with altitude or latitude has been recorded previously in insects (see e.g. Krasnov *et al.*, 1996; see also Chown & Gaston, 1999; Blanckenhorn & Demont, 2004).

The differences in the response of the three species to altitude, with which mean annual temperature strongly covaries ( $r = 0.619$ ) in the Cederberg, and the decline in size with declining temperature, indicate that the proximate biophysical model proposed by van der Have & de Jong (1996) can be rejected as a hypothesis accounting fully for size change in the species investigated here. This is perhaps not surprising since the model has also been rejected on theoretical grounds (Kozłowski *et al.*, 2004). Likewise, the decline in size with declining temperature in *Thermophilum decemgutattum* and *Zophosis gracilicornis* also suggests that the starvation resistance hypothesis is inappropriate for these species. Although NDVI difference, a measure in annual variation of productivity, was included in the models, its sign was typically negative. The starvation resistance hypothesis proposes that size should be larger where resource availability is more variable (Cushman *et al.*, 1993; Chown & Gaston, 1999; Arnett & Gotelli, 2003), whereas the converse was found here. Of course, it might be argued that NDVI and its variability are poor proxies for resource availability for a carnivore and a detritivore, especially given the several trophic levels lying between producer and consumer in these cases (see also discussion in Gaston, 2000). However, the combination of a decline in size with declining temperature, a decline in size with increasing environmental

variability, and the importance of other environmental predictors, likely associated with larval mortality, suggest that this hypothesis can be rejected for both species.

As is the case with the starvation resistance hypothesis, neither the proximate biophysical model, nor the temperature threshold and minimum metabolic rate hypotheses place any emphasis on the role of larval mortality factors in influencing body size variation (van der Have & de Jong 1996; Makarieva *et al.*, 2005; Walters & Hassall 2006). The retention and significance of soil type, vegetation cover and complexity, and NDVI in the best-fit models for both species suggest that mortality factors, and presumably larval as well as adult mortality factors, are playing a significant role in determining adult body size. Although this study provided no direct evidence of the significance of these environmental factors for larval and adult mortality, several other studies have shown how vegetation density and cover, resource availability, and soil type affect mortality rates. For example, in the case of vegetation cover and complexity, the abundance and therefore indirectly the mortality rates of arthropods were shown to be affected by the vegetation structure and density in their habitat. Soil type and/or soil moisture has been shown to affect survival in carabid beetles (Thiele, 1977; Rushton *et al.*, 1991) and several other insect taxa (Sanderson *et al.*, 1995). Finally, resource availability is a well-known factor influencing larval and adult survival in insects (Connor, 1991; Huk & Kühne, 1999; Messina & Fry, 2003; Jones & Widemo, 2005) and is typically included in life history models both as a direct influence on mortality and as a factor altering foraging bout number and duration, which in turn increases exposure to predators (Kozłowski, 1992, 1996; Kozłowski *et al.*, 2004; Gaston & Chown, in press).

Therefore, it seems likely that the temperature threshold and minimum metabolic rate models can also be rejected as explanations for altitudinal size variation in *T. decemguttatum* and *Z. gracilicornis*. However, it is notable that the minimum metabolic rate hypothesis could not be rejected for *T. decemguttatum*.

This hypothesis was originally developed to account for size variation in groups of species from areas differing substantially in temperature, and more specifically the tendency for large terrestrial ectotherms to be found in the tropics, but larger marine ectotherms to be found in Polar regions (Makarieva *et al.*, 2005). The intraspecific version of the hypothesis is somewhat more complex than has been suggested here,

especially because the direction of size change with temperature is dependent on whether cell number or mass-specific metabolic rate are constrained. It is well-known that in some species metabolic rate varies only slightly with environmental temperature (often termed metabolic cold adaptation, see Chown & Gaston, 1999), and that size increases may be mediated either by changes in cell size or by changes in cell number or by both (Chown & Gaston, 1999; Kozłowski *et al.*, 2003; Blanckenhorn & Llaurens, 2005). Therefore, the hypothesis proposed by Makarieva *et al.* (2005) remains plausible, but unfortunately the data available for this study could not test it as carefully as its intraspecific version requires.

Having said this, the most plausible hypothesis to account for size variation (or lack thereof) with altitude in the species examined here is the resource allocation switching curves model of Kozłowski *et al.* (2004). These models suggest that temperature, resource availability, and other factors that are likely to influence juvenile and adult mortality will determine the form of the relationship between environmental temperature and adult size, or when resources accumulated by an organism should be switched from growth to reproduction. Their models explicitly predict that temperature as well as other variables such as resource availability, and those that might influence survivorship, should play a role in determining adult size (see also Gaston & Chown, in press). Here, the best-fit models for the years for which a full range of data were available, not only included mean annual temperature, but also a surrogate for resource availability (NDVI) and variables likely to influence larval and/or adult survivorship (see above). Moreover, the best-fit models varied substantially between species and between genders. This is exactly what would be expected for optimality models that take into account physiological variation in resource acquisition and utilization among the sexes (see e.g. Chown & Nicolson, 2004; Terblanche *et al.*, 2004, 2005), and varying life histories associated both with sex (reproductive strategies differ) and species (predators, apparency, foraging behaviour also differ). Therefore, the present data show that of the five models proposed to explain intraspecific, temperature-related variation in adult body size, only the model proposed by Kozłowski *et al.* (2004) cannot be rejected, because its predictions are supported. Clearly, some ground exists for examining the relationships between the resource allocation switching curve models and the minimum metabolic rate

models, especially because they both are concerned with size relationships of resource allocation and utilization. However, such a theoretical analysis is beyond the scope of this work. Nonetheless, further investigations of the life histories and physiologies of the species examined here could go some way in resolving the relationships between these hypotheses, especially because this study remains mensural, making use of correlations which still do not provide a final assessment of causation.

Although a wide variety of studies has investigated intraspecific body size variation in insects (see Introduction), few of these works have sought to assess all of the current hypotheses for such spatial variation. Indeed, many of them fail to distinguish pattern from mechanism (a first step in investigations of size clines – see review in Blackburn *et al.*, 1999; James, 1970), and even when this is done, most studies either conclude with investigations of covariation with altitude or latitude (which incorporate variation not only in temperature but many other environmental variables too), or with investigations of covariation with temperature. As this study has demonstrated, most of the mechanistic hypotheses proposed to explain spatial body size variation predict covariation with temperature, and therefore temperature covariation alone is insufficient to distinguish between them. Rather, covariation of factors thought to influence resource availability and survivorship also need to be investigated. Such an approach is likely also to reconcile the somewhat divergent fields of life history investigations of age and size at maturity (e.g. Roff, 1980; Kozłowski *et al.*, 2004), and macroecological investigations of clinal size variation, which tend to be done almost exclusively under the rubric of Bergmann's rule (e.g. Ashton & Feldman, 2003; Freckleton *et al.*, 2003; Blackburn & Hawkins, 2004; Millien *et al.*, 2006). Indeed, investigations of ectotherms appear to be leading the way forward in this synthesis (Angilletta *et al.*, 2004; Blanckenhorn *et al.*, 2006).

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## **Chapter 4**

### **General Conclusion**

Through this study, my main aims were to add a sound data base to the few studies available on intraspecific body size frequency distributions, and to contribute a strong inference approach (Huey *et al.*, 1999) to the analysis of clinal size variation. By starting at the basic form of body size variation, i.e. the body size frequency distribution, one can gain some insight into how individuals of a species would differ in body size in response presumably both to each other and to their environment. A variety of size frequency distribution patterns were found for the 16 different insect species considered in this study. These patterns ranged from right-skewed, to normal, to left-skewed and to bimodal. Contrary to what was expected, most of the distributions were not right-skewed, neither for body mass nor body length, although log transformation often removed the skew for those distributions that were right-skewed. Furthermore, males and females of the different species most often showed similar patterns and therefore the effects of sexual size dimorphism on variation in the shape of the frequency distributions was often negligible or small.

When considering altitudinal variation in body size of insects it is relatively simple to identify the pattern of how the body sizes of individuals vary over space and time. Why they do so is more complicated a matter. Several hypotheses have been proposed to explain the variation of body size of ectotherms. In particular, five have been found to be central in identifying mechanisms underlying size variation (Cushman *et al.*, 1993; van der Have & de Jong, 1996; Chown & Gaston, 1999; Kozłowski *et al.* 2004; Makarieva *et al.*, 2005; Walters & Hassal, 2006). By collection of appropriate environmental data and by careful consideration of each of these hypotheses I was able to distinguish them and to identify those whose predictions were supported. The outcome was reasonably clear. It seems most plausible that the resource allocation switching curve model (Kozłowski *et al.* 2004) explains the patterns found here, although minimum metabolic rate might also play a role (Makarieva *et al.*, 2005).

The results presented in both chapters of this study clearly show that the patterns in insect body size distributions vary considerably for different insect species. Furthermore, there is also some variation in the mechanisms underlying variation in body size within populations of a species, over a geographical gradient and over time. Depending on habitat use and trophic level, different species respond in differing ways to a set of

conditions and sometimes such differences are also apparent between males and females of a species

Despite what might be expected (see May, 1981), insect species differ in how their body sizes are distributed. Therefore, at the intraspecific level, the BSFDs of insect populations are not necessarily log-normally distributed, as was shown by this study. It has also become clear that when considering how body size is distributed within populations of a species, several factors that influence distribution patterns should be taken into account. These factors include sample size, the presence of sexual size dimorphism, the size measure used, season and time of sampling and the number of size class groupings (Loder *et al.*, 1997; Gaston & Blackburn, 2000; Gleiser *et al.*, 2000; Teder & Tammaru, 2005).

Furthermore, although the findings presented here provide the basic background of information for how insects vary in body size, much information is still needed to understand the degree of variation. A great deal can be added to our general knowledge on body size variation within insect populations if other factors influencing the functioning of populations are considered. Consequently, investigations regarding several aspects of the life history of a species, especially the voltinism and variation in voltinism of the populations of a species over space (see for example Roff, 1980) and time would be of great importance.

One theme that emerges repeatedly in both chapters of this study is that individuals within populations of a species, and different species within an assemblage, would not necessarily respond in exactly the same way to a set of abiotic and biotic conditions. It would therefore be highly informative and crucial to further, more causal tests of the hypotheses proposed to explain clinal variation, to investigate such variation in body size in conjunction with life history and physiological traits to gain a clear indication as to how these factors are influenced by covariation of factors that have been identified to influence resource availability and survival of individuals of different species.

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**Appendix A** Elytron length means (mm) and standard errors at each of the altitudinal sites (western and eastern slopes) along the study transect where individuals of the three species were collected. Sample size is given in parenthesis.

	Sex	2002	2003	2004	2005
<i>Thermophilum</i>					
<i>decemguttatum</i>					
200 m.a.s.l. W	M	18.232 ± 0.391 (5)	16.362 ± 0.825 (3)	15.895 (1)	
	F	18.855 (1)			
300 m.a.s.l. W	M	16.986 ± 0.312 (2)			16.674 ± 0.562 (3)
	F			18.934 ± 1.481 (2)	20.803 ± 0.078 (2)
500 m.a.s.l. W	M				
	F				16.986 (1)
700 m.a.s.l. W	M	17.141 ± 0.784 (3)	17.570 ± 0.801 (4)	16.635 ± 0.273 (2)	16.258 ± 0.888 (3)
	F	19.479 (1)	20.024 ± 0.234 (4)	18.817 ± 0.265 (4)	18.139 ± 0.380 (10)
900 m.a.s.l. W	M	16.852 ± 0.367 (7)	16.853 ± 0.349 (13)	17.152 ± 0.450 (7)	16.899 ± 0.187 (9)
	F	18.154 ± 0.588 (4)	18.731 ± 0.440 (10)	17.648 ± 0.418 (8)	18.443 ± 0.244 (17)
1100 m.a.s.l. W	M	16.898 ± 0.369 (16)	16.674 ± 0.416 (11)	16.159 ± 0.228 (36)	16.292 ± 0.187 (39)
	F	16.900 ± 0.443 (11)	18.045 ± 0.258 (10)	17.540 ± 0.256 (26)	17.328 ± 0.234 (32)
1300 m.a.s.l. W	M	15.166 ± 0.219 (23)	15.615 ± 0.239 (17)	15.566 ± 0.152 (47)	15.387 ± 0.141 (62)
	F	16.050 ± 0.322 (14)	16.713 ± 0.258 (12)	15.981 ± 0.126 (48)	16.123 ± 0.115 (62)
1500 m.a.s.l. W	M	14.846 ± 0.137 (46)	15.201 ± 0.185 (33)	15.197 ± 0.222 (26)	15.301 ± 0.110 (59)
	F	16.139 ± 0.185 (37)	16.445 ± 0.210 (21)	16.202 ± 0.248 (16)	16.008 ± 0.121 (58)
1700 m.a.s.l. W	M				15.427 ± 0.489 (4)
	F				16.051 (1)
1700 m.a.s.l. E	M	14.804 (1)	15.271 (1)	15.739 (1)	
	F			15.583 ± 0.156 (2)	
1500 m.a.s.l. E	M	14.414 ± 0.857 (2)			15.038 ± 0.702 (2)
	F	17.063 ± 0.078 (2)			15.479 ± 0.138 (3)
1300 m.a.s.l. E	M				
	F				16.362 (1)
1100 m.a.s.l. E	M			16.518 ± 0.769 (3)	16.635 ± 0.263 (16)
	F	17.765 (1)	19.790 (1)		17.196 ± 0.276 (19)
900 m.a.s.l. E	M			17.298 ± 0.624 (2)	16.986 (1)

	F			19.011 ± 0.935 (2)	19.167 (1)
<b><i>Stenocara dentata</i></b>					
Lamberts Bay	M				
	F	9.389 (1)			
1100 m.a.s.l. W	M	7.324 ± 0.151 (11)	7.291 ± 0.102 (11)	8.814 ± 0.476 (3)	8.211 ± 0.107 (12)
	F	8.337 ± 0.078 (2)	9.069 ± 0.178 (10)	9.928 ± 0.299 (10)	9.489 ± 0.163 (12)
1300 m.a.s.l. W	M	7.077 ± 0.223 (12)	7.679 ± 0.095 (26)	8.519 ± 0.411 (6)	7.759 ± 0.070 (42)
	F	9.038 (1)	8.624 ± 0.134 (17)	9.639 ± 0.254 (9)	9.016 ± 0.096 (35)
1500 m.a.s.l. W	M	7.754 ± 0.123 (29)	7.657 ± 0.107 (12)		7.834 ± 0.103 (18)
	F	9.027 ± 0.306 (9)	9.045 ± 0.152 (13)		9.108 ± 0.236 (8)
1700 m.a.s.l. W	M	7.428 ± 0.158 (6)	7.294 ± 0.256 (5)	8.536 ± 0.377 (3)	7.949 ± 0.128 (12)
	F	9.145 ± 0.241 (8)	9.266 ± 0.483 (3)	9.732 (1)	8.932 ± 0.216 (6)
1700 m.a.s.l. E	M	7.462 ± 0.066 (48)	7.589 ± 0.125 (15)	8.255 ± 0.081 (16)	7.676 ± 0.075 (46)
	F	8.859 ± 0.082 (34)	9.136 ± 0.199 (11)	9.411 ± 0.271 (7)	9.055 ± 0.082 (24)
1500 m.a.s.l. E	M	7.611 ± 0.132 (15)	7.123 ± 0.194 (11)	8.429 ± 0.249 (4)	7.854 ± 0.159 (15)
	F	8.571 ± 0.186 (7)	8.635 ± 0.251 (5)	9.265 ± 0.615 (2)	9.000 ± 0.159 (19)
500 m.a.s.l. E	M		7.657 ± 0.191 (8)	8.814 ± 0.110 (6)	7.793 ± 0.425 (4)
	F	9.194 (1)	10.271 ± 0.185 (2)	10.272 ± 0.141 (11)	9.412 ± 0.255 (7)
<b><i>Zophosis gracilicornis</i></b>					
200 m.a.s.l. W	M	3.827 ± 0.061 (3)	3.481 ± 0.103 (9)	3.711 (1)	3.430 ± 0.091(8)
	F		3.924 ± 0.104 (14)	4.215 ± 0.202 (7)	4.023 ± 0.143 (7)
300 m.a.s.l. W	M	4.061 ± 0.132 (4)	3.609 ± 0.103 (9)		3.341 ± 0.095 (12)
	F	4.349 ± 0.085 (8)	3.901 ± 0.106 (15)	4.279 ± 0.512 (3)	3.776 ± 0.791 (15)
500 m.a.s.l. W	M	3.832 ± 0.061 (10)	3.670 ± 0.169 (9)	3.918 ± 0.083 (5)	3.393 ± 0.080 (18)
	F	4.254 ± 0.091 (17)	3.854 ± 0.076 (20)	4.580 ± 0.094 (10)	3.840 ± 0.071 (31)
700 m.a.s.l. W	M	4.144 ± 0.169 (8)	3.190 ± 0.938 (8)	3.893 (1)	3.719 ± 0.080 (14)
	F	4.431 ± 0.085 (21)	3.954 ± 0.092 (13)	4.708 ± 0.168 (5)	4.099 ± 0.089 (18)
900 m.a.s.l. W	M	3.506 ± 0.066 (25)	3.057 ± 0.048 (16)	3.423 ± 0.071 (9)	3.097 ± 0.047 (31)
	F	3.884 ± 0.047 (49)	3.498 ± 0.033 (51)	3.993 ± 0.065 (25)	3.550 ± 0.044 (50)
1100 m.a.s.l. W	M	3.369 ± 0.029 (72)	3.129 ± 0.027 (63)	3.390 ± 0.034 (40)	3.077 ± 0.032 (46)
	F	3.860 ± 0.033 (81)	3.566 ± 0.036 (62)	3.843 ± 0.040 (62)	3.497 ± 0.033 (52)

1300 m.a.s.l. W	M	$3.451 \pm 0.064$ (27)	$3.120 \pm 0.027$ (62)	$3.625 \pm 0.165$ (5)	$3.176 \pm 0.049$ (26)
	F	$3.713 \pm 0.040$ (61)	$3.521 \pm 0.035$ (62)	$3.904 \pm 0.056$ (30)	$3.599 \pm 0.048$ (38)
1500 m.a.s.l. W	M	$3.304 \pm 0.028$ (59)	$3.153 \pm 0.026$ (58)	$3.576 \pm 0.093$ (9)	$3.078 \pm 0.047$ (23)
	F	$3.728 \pm 0.038$ (73)	$3.448 \pm 0.032$ (61)	$3.882 \pm 0.066$ (17)	$3.444 \pm 0.038$ (50)
1700 m.a.s.l. W	M	$3.347 \pm 0.047$ (25)	$3.346 \pm 0.070$ (6)		$3.079 \pm 0.056$ (13)
	F	$3.738 \pm 0.033$ (59)	$3.580 \pm 0.086$ (13)	3.711 (1)	$3.334 \pm 0.039$ (21)
1700 m.a.s.l. E	M	$3.329 \pm 0.088$ (9)	$3.226 \pm 0.060$ (17)	$3.508 \pm 0.113$ (3)	$3.085 \pm 0.072$ (7)
	F	$3.682 \pm 0.035$ (43)	$3.646 \pm 0.042$ (33)	$4.015 \pm 0.183$ (2)	$3.489 \pm 0.044$ (26)
1500 m.a.s.l. E	M	$3.341 \pm 0.048$ (26)	$3.115 \pm 0.059$ (20)		$3.440 \pm 0.037$ (47)
	F	$3.727 \pm 0.040$ (48)	$3.526 \pm 0.032$ (51)	$3.954 \pm 0.188$ (4)	$3.031 \pm 0.043$ (18)
1100 m.a.s.l. E	M			$4.276 \pm 0.098$ (9)	
	F			$4.628 \pm 0.064$ (18)	
900 m.a.s.l. E	M	$3.624 \pm 0.080$ (12)	$3.485 \pm 0.119$ (7)	$3.659 \pm 0.060$ (26)	$3.184 \pm 0.047$ (23)
	F	$3.765 \pm 0.053$ (26)	$3.704 \pm 0.045$ (27)	$4.107 \pm 0.046$ (37)	$3.642 \pm 0.036$ (32)
500 m.a.s.l. E	M	$3.406 \pm 0.161$ (3)	$3.178 \pm 0.125$ (4)	$3.183 \pm 0.284$ (3)	$3.148 \pm 0.233$ (4)
	F	$3.528 \pm 0.061$ (3)	$3.411 \pm 0.087$ (15)	$3.919 \pm 0.171$ (7)	3.711 (1)

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**Appendix B** Best-fit generalized linear models examining the effects of the environmental variables on elytron length in males and in females, respectively, of **(a)** *Thermophilum decemguttatum* males and females and **(b)** *Zophosis gracilicornis*, over the 2002-2005 period. df = degrees of freedom,  $r^2$  = coefficient of determination, AIC value = Akaike Information Criterion value,  $w_i$  = Akaike weight, MAT = mean annual temperature. In these analyses the proportion of sand was excluded from the models due to its significant covariation with mean annual temperature.

**(a)**

Model	df	$r^2$	Predictors	AIC value	$w_i$
<b>Males</b>					
I	16	0.560	+0.005 MAT <sup>ns</sup> +0.005 Vegetation density <sup>ns</sup> -0.295 Vegetation cover <sup>***</sup>	41.510	0.405
II	17	0.504	+0.007 MAT <sup>**</sup> -0.286 Vegetation cover <sup>**</sup>	41.936	0.327
III	17	0.487	+0.007 Vegetation density <sup>**</sup> -0.290 Vegetation cover <sup>**</sup>	42.586	0.237
<b>Females</b>					
I	17	0.534	+0.011 MAT <sup>***</sup> -0.294 Vegetation cover <sup>**</sup>	55.863	0.581
II	16	0.552	+0.009 MAT <sup>*</sup> +0.003 Vegetation density <sup>ns</sup> -0.306 Vegetation cover <sup>**</sup>	57.067	0.319

(b)

Model	df	$r^2$	Predictors	AIC value	$w_i$
<b>Males</b>					
I	30	0.463	-0.006 MAT <sup>ns</sup> +0.019 Vegetation density**** -0.197 Vegetation cover <sup>ns</sup>	2.836	0.331
II	31	0.420	-0.006 MAT <sup>ns</sup> +0.020 Vegetation density****	3.466	0.242
III	31	0.418	+0.015 Vegetation density -0.192 Vegetation cover <sup>ns</sup>	3.568	0.230
<b>Females</b>					
I	33	0.334	+0.015 Vegetation density***	9.728	0.393
II	32	0.365	+0.015 Vegetation density**** +0.002 Vegetation cover <sup>ns</sup>	10.062	0.332
III	32	0.334	+0.001 MAT <sup>ns</sup> +0.014 Vegetation density**	11.699	0.147

$P < 0.05$  \*

$P < 0.01$  \*\*

$P < 0.001$  \*\*\*

$P < 0.0001$  \*\*\*\*