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Sexual size dimorphism within species increases with body size in insects

Tiit Teder and Toomas Tammaru

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Studies examining interspecific differences in sexual size dimorphism (SSD) typically assume that the degree of sexual differences in body size is invariable within species. This work was conducted to assess validity of this assumption. As a result of a systematic literature survey, datasets for 158 insect species were retrieved. Each dataset contained adult or pupal weights of males and females for two or more different subsets, typically originating from different conditions during immature development. For each species, an analysis was conducted to examine dependence of SSD on body size, the latter variable being used as a proxy of environmental quality. A considerable variation in SSD was revealed at the intraspecific level in insects. The results suggest that environmental conditions may strongly affect the degree, though not the direction of SSD within species. In most species, female size appeared to be more sensitive to environmental conditions than male size: with conditions improving, there was a larger relative increase in female than male size. As a consequence, sexual differences in size were shown to increase with increasing body size in species with female-biased SSD (females were the larger sex in more than 80% of the species examined). The results were consistent across different insect orders and ecological subdivisions. Mechanisms leading to intraspecific variation in SSD are discussed. This study underlines the need to consider intraspecific variation in SSD in comparative studies.

T. Teder, Inst. of Botany and Ecology, Univ. of Tartu, Lai 40, EE-51005 Tartu, Estonia (tiit.teder@ut.ee). T. Teder and T. Tammaru, Inst. of Zoology and Botany, Estonian Agricultural Univ., Riia 181, EE-51014 Tartu, Estonia. T. Tammaru also at: Inst. of Zoology and Hydrobiology, Univ. of Tartu, Vanemuise 46, EE-51014 Tartu, Estonia.

The direction and degree of sexual differences in body size vary greatly among different animal taxa (Andersson 1994, Nylin and Wedell 1994). This phenomenon has launched a large number of studies devoted to explaining evolutionary mechanisms underlying among-species patterns of sexual size dimorphism (hence after SSD; e.g. Hurlbutt 1987, Fairbairn 1997, Colwell 2000, Monnet and Cherry 2002). In comparative studies, it is often assumed that SSD has some narrow, species-specific degree, reflecting different selection pressures acting on male and female body sizes (Stamps 1993). Even a cursory survey of published data, however, would provide unambiguous evidence that SSD is far from being uniform at the intraspecific level. Yet, plasticity in growth patterns underlying within-species variation in SSD remains still rather poorly understood (Badyaev 2002). Insufficient knowledge of within-species level variation is unfortunate per se, but it may also confound understanding of evolutionary mechanisms behind the between-species patterns of SSD (Shine 1990, Stamps 1993, Badyaev 2002).

Sex-related differences in growth patterns form one of the major proximate determinants of SSD (Shine 1990). Hence, intraspecific variation in SSD is likely to arise when growth patterns of males and females differ in their sensitivity to environmental conditions. Sexual differences in the plasticity of growth schedules thus definitely deserve attention in the SSD context. Fortunately, there

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exist a vast number of case studies that have produced data that could be – but have only rarely been – used to assess the effect of environmental conditions on SSD. In studies on insects, it is a common practice to subject different subsets of conspecific individuals to different environmental conditions during their juvenile development. Treatments varying in food quality, juvenile density, some abiotic factors frequently form the core of experimental design in insect ecology. Body size is a common response parameter being measured in these studies, and it is frequently recorded separately for females and males.

In the present study, a systematic literature survey was undertaken to compile a database of studies reporting sex-specific body sizes for at least two different samples, typically differing in environmental conditions during juvenile development. These data were analysed to examine the effect of environmental conditions on within-species SSD in insects.

Material and methods

Database

The database used in this study was compiled on the basis of a systematic literature survey covering major entomological and ecological journals (Appendix 1). It was systematically searched for original case studies in which indices of adult size had been presented separately for males and females, and had been reported for at least two samples of the same insect species. Adult and pupal weights were accepted as indices of body size, whereas any linear measurements were ignored for reasons outlined by Gauld and Fitton (1987).

From each study included, a dataset was extracted consisting of mean weights of the two sexes for as many subsets of individuals (=samples) as presented. If data on more than one species were available in a single paper, data on each species were treated as different datasets. Analogously, datasets of the same species extracted from different studies were also treated as different datasets. The database was limited to numerical presentations of size indices, graphical presentations were not included. Data on larval size were ignored; when data on both pupal and adult weight were available, the information on pupal size was preferred. Data were ignored if body size differences of the samples were due to a factor other than different conditions during immature development (e.g. mated vs non mated individuals; large individuals vs small individuals classified as such by original author). Measurements taken from virus/bacteria-treated samples were also excluded. The database did not include social species (e.g. ants and bees) and species having a more complex size-related caste system than the ordinary male-female dichotomy (primarily aphids). A sample was ignored if either average weight of males or females was based on less than five individuals.

Most datasets were obtained from studies in which samples of juvenile insects had been assigned to different treatments varying with respect to food availability or quality, larval density, abiotic factors (e.g. temperature, photoperiod) or some other aspects. Species included in the database were sorted by taxonomic affiliation. Where possible, species were further classified according to their larval food resource (phytophages, predators, parasitoids etc.).

Data analysis

SSD for any given sample was expressed as the ratio of mean weight of females over mean weight of males. Accordingly, females were the larger sex when this index exceeded unity, while males were larger when SSD remained below unity. In the analyses, body size was used as a proxy for describing environmental quality (food availability, food quality, photoperiod etc. depending on the particular study): a larger final (either pupal or adult) size was considered to indicate more favourable conditions during the juvenile development (a common practice in insect ecology, Awmack and Leather 2002).

To examine the dependence of SSD on environmental conditions, male size was plotted against female size separately for each species (Fig. 1). In the cases there were more than one dataset available for particular species, only the one based on the largest number of individuals was used. Mean body sizes of males and females in each sample were regarded as independent observations in these analyses. Type II regression had to be used to quantitatively describe the relations between female and male size. This is because as both female and male sizes contained random variation, type I regression would have been an inappropriate technique to estimate regression line parameters (Sokal and Rohlf 1995, Fairbairn 1997). Accordingly, reduced major axis regression was applied for parameter estimation. A freeware add-in for Microsoft Excel (Geometric mean regression add-in for Excel '97 by M. Sawada, Univ. of Ottawa) was utilised for this purpose.

The results of the regression analysis were interpreted as follows (Fig. 1). A positive slope indicated that environmental conditions affected female and male size in the same direction, i.e. male size increased with female size increasing. Such a result allowed to unambiguously rank samples according to favourability of environmental conditions. Furthermore, a zero intercept implied proportional increase of male and female sizes with conditions improving. A positive intercept indicated that female size increased relatively faster than male size, the former being then more sensitive to environmental conditions. A negative intercept indicated the opposite tendency.

These parameters allowed us to reach conclusions about the dependence of SSD on environmental conditions. In particular, it is easy to see that sex-related differences in sensitivity of body size to environmental conditions should lead to different female/male size ratios in different environments. Accordingly, with environmental quality increasing, higher sensitivity of female body size would lead to more pronounced SSD in species with female-biased SSD, whereas size ratio would decrease in species with male-biased SSD. The opposite logic would apply, if male body size appeared to be more sensitive to environmental quality.

All conclusions concerning dependence of SSD on body size, and environmental conditions, were made at the meta level. The vote counting method (Wang and Bushman 1999) was used for this purpose (positive slopes vs negative slopes; positive intercepts vs negative intercepts). The actual proportions of these votes were tested against the 1:1 ratio using chi-square test. The parameters of each within-species relationship were regarded as single observations irrespective their statistical significance. Such an approach was taken because, in most species, the number of independent samples was insufficient to draw meaningful conclusions about the statistical significance of the relationships at the intraspecific level.

To find out if there exist any significant differences in SSD between samples, standard error of female/male size ratio was estimated for each sample as based on the values of reported summary statistics (means, some statistic describing size variation and sample size) (Bevington 1969 for formula). The judgements about statistical significance of the differences in SSD among different samples were made examining the mean standard error multiplied by 1.39 (Goldstein and Healy 1995, Payton et al. 2003). Differences in SSD were regarded significant, if the intervals of female/male ratios calculated for samples with the largest and the smallest average female sizes did not overlap. Selecting the samples on the basis of values of female size (not SSD) allowed us to consider the contrasts as planned comparisons with no post-hoc adjustments necessary. Where a dataset included samples with both female- and male-biased SSD, 95% confidence intervals (SE multiplied by 1.96) were calculated to decide, if intraspecific SSD would significantly deviate from unity in one or both directions. It has to be noted that only an approximation of standard error can be calculated for a ratio when raw data are unavailable. However, as stressed above, the conclusions of this study rely on meta-level generalizations rather than statistical significance in any within-species level analysis.

Results

General patterns of SSD

As a result of the literature search, data fulfilling the selection criteria (weights of conspecific females and males for at least two samples) were found for 158 insect species (Appendix 2). The number of samples per one dataset ranged from 2 to 32 (median: 4, average: 4.8) in different species. The total number of individuals measured per one dataset varied between 28 and 2782; however, for 19% of datasets included, this parameter was unavailable.

In the majority of species, the direction of sexual differences in body size was consistent across samples, SSD being either invariably female-biased (129 species, 81.6%) or male-biased (12 species, 7.6%). Seventeen species (10.8%) showed female-biased SSD in some samples, while male-biased SSD was found in others. Of these, the datasets of 12 species were represented by samples significantly differing from unity in one, but not in the other direction. Accordingly, these 12 species were treated either as species with female-biased (7 species) or male-biased (5 species) SSD in further analyses. Three species showed no significant deviation of SSD from unity in either direction. The datasets of two species were represented by samples with both significantly male- and female-biased SSD (Ferguson et al. 1994: *Spodoptera frugiperda*, Zangger et al. 1994: *Poecilus cupreus*). Such bidirectional pattern was associated with species in which size differences between sexes were relatively limited (female/male ratio of samples ranging from 0.89 to 1.06). These two species, as well as those three species with SSD deviating from unity in neither direction, were ignored in the analyses in which species were classified by the direction of SSD.

The degree of intraspecific variation in SSD shown by different species ranged from a very subtle to more than a 1.8-fold difference between maximum and minimum SSD. Significant differences in SSD were found in 37 species out of 149 (25%) for which it was possible to calculate standard errors of female/male size ratios (Data analysis).

SSD and environmental conditions

Regressing (type II) male size on female size within species yielded a positive slope for 142 species (90%) and a negative slope for 14 species (9%). In two species, male size was independent of female size (female size reported as invariable across samples). Thus, in most species, environmental conditions affected female and male sizes in the same direction. The negative slopes were, most likely, occasional in the majority of cases, resulting from low among-samples variation in body size coupled with small sample sizes. The species with negative slope were ignored in further analyses, because there was no straightforward way to determine in which direction environmental conditions improved.

Of the species with a positive slope, the regression line had a positive intercept in 98 species (69%) and a negative intercept in 44 species (31%). The proportions of positive and negative intercepts differed significantly ($df = 1$, $\chi^2 = 20.5$, $p < 0.001$). These proportions were even more biased towards positive intercepts in species for which significant differences in SSD were found: positive intercepts were detected in 30 species, whereas negative ones in as few as two. This suggests that in most species, female size increased more than proportionally with male size (Fig. 1). The results were consistent both across different taxa (Fig. 2) as well as across different feeding guilds (Fig. 3). In species with female-biased SSD, a positive intercept was found in 87 species (70%), and a negative one in 37 species (30%) ($df = 1$, $\chi^2 = 20.2$, $p < 0.001$). In these species, a positive intercept indicated that SSD increased with increasing body size (Fig. 1). In species with male-biased SSD, a positive intercept was found in eight species (57%) and a negative one in six species (43%). However, it can be easily seen that in these species, a positive intercept implied a decline in SSD with increasing size. When species were classified by maximum SSD across samples, a tendency appeared for species with more female-biased SSD to be more likely exhibiting an increase in SSD in response to body size increase (Fig. 4).

Phylogenetic aspects

In the present study, species were treated as independent observations which is known to be problematic (Harvey and Pagel 1991, Martins 1996). Unfortunately, since phylogenies are available for a limited number of insect taxa, comparative methods could not be used in the present analyses. However, this shortcoming should be mitigated by a large number of species used in this study widely spread over major insect orders, and the consistency of the results across orders (Fig. 2). Moreover, high intraspecific variability compared to interspecific variability with respect to SSD allowed us to consider the use of phylogenetic approach less vital (Björklund 1997).

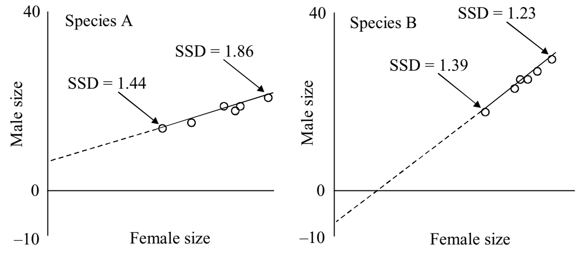

Fig. 1. Examples of reduced major axis regression models describing the relationship between female and male sizes. Both species are with female-biased SSD, each circle represents one sample. Species A has a positive intercept indicating that female size increases relatively faster, and is thus more sensitive to environmental conditions than male size. As a result, sexual differences in body size will increase with size. Species B has a negative intercept implying that male size is more sensitive to environmental conditions. As a result, SSD declines with body size increasing. A positive slope in both species suggests that female and male sizes respond to changes in environmental quality in the same direction.

Discussion

The present study revealed a considerable intraspecific variation in SSD in insects. The degree of intraspecific variation, however, greatly varied among species. For example, a hymenopterous parasitoid (Otto and Mackauer 1998) exhibited an as large as 1.8-fold difference between samples with minimum and maximum SSD while a coccinellid beetle showed virtually no variation in SSD across samples despite an 1.2-fold difference between samples in female sizes (Ueno et al. 1999). In contrast, with rare exceptions, the direction of intraspecific SSD appeared to be invariable.

In most species with female-biased SSD, female size increased more than proportionally with male size increasing. As a consequence, sexual differences in size tended to increase with increasing body size in these species. The few species with male-biased SSD showed no consistent pattern. The qualitative patterns did not vary across major insect orders and feeding guilds. The more female-biased SSD was found in a species, the higher was the probability that female size revealed higher sensitivity to environmental conditions.

The present results suggest that environmental conditions are unlikely to influence the direction of sexual differences in body size. The few exceptions showing a bidirectional pattern of size differences were associated

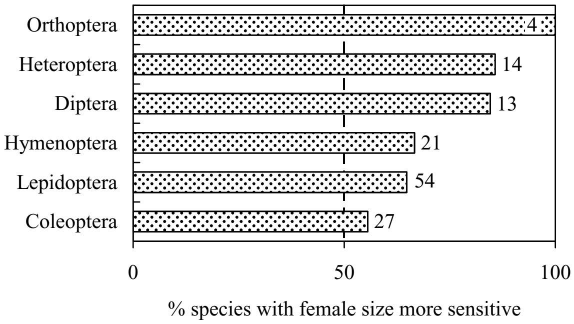

Fig. 2. Percentage of species with female size being more sensitive to environmental quality than male size. Figures next to the bars are species numbers. Species are classified according to their taxonomic affiliation.

with species with low sexual dimorphism. The qualitative conclusions of studies addressing questions about the direction of SSD at the interspecific level are thus unlikely to be influenced by intraspecific variation in SSD. In contrast, the effect of environmental conditions on the degree of sexual differences appears to be common and remarkable. Significant differences in SSD among samples were found in about 25 per cent of the species analysed. Considering the circumstantial nature of the data with respect to plasticity in SSD, this percentage is likely to underestimate rather than overestimate the commonness of differences in SSD within species. The high plasticity of SSD implies that intraspecific variation in SSD cannot be neglected in studies addressing questions about the causes of interspecific variation in SSD.

There is definitely a need to find both proximate and evolutionary explanations to the revealed patterns. Why do females remain relatively smaller in poorer conditions? Why is the size of females more sensitive to environmental factors? There is hardly a common answer applicable to all cases in which this pattern emerges, but a few scenarios appear likely. If the female is the larger sex, then there are reasons to believe that the optimal size for a female adult is larger than that for a male. It is perhaps reasonable to assume that under favourable conditions, both sexes come close to achieve their optima. As the environmental quality declines, the females should attain equal relative weight surplus relative to males to keep the SSD unchanged. The costs of doing so are likely to be higher in poorer environments, just because it would take more time, and mortality risk scales with time. Since the corresponding benefit – a certain relative increase in body size – does not necessarily change, increasing costs alone should lead to a lower optimal value of size for females, relative to that of males. Alternatively, females often have different nutritional needs than males (Stockhoff 1993, Mira 2000, Telang et al. 2001, Moreau et al. 2003) being typically more dependent on nutrients of limited availability, e.g. nitrogen. Such dietary differences may imply that any equal decrease in food quality translates to more severe drawback from female's point of view.

Yet, there was a considerable proportion of species with female-biased SSD demonstrating an opposite tendency – male size being more sensitive to environmental conditions. Moreover, patterns like this have been documented also in some earlier studies (Mackauer 1996, Blanckenhorn 1997, Morin et al. 1999). In such a case, it is likely that considerations over the optimal timing of maturation enter the play. The reason for it is the frequent occurrence of strong selection for protandry, i.e. in favour of emergence of males before females (Fagerström and Wiklund 1982, Zonneveld 1996). If strong enough, development time limitations may start to constrain achieving target size more in males than in females. This, in turn would lead to a decline in SSD with increasing body size in species with female-biased SSD.

Alternatively to the plastic changes in reaction norms, intraspecific genetic differentiation or differential survival might explain intraspecific variation in SSD (Shine 1990, Madsen and Shine 1993). Yet, neither of these mechanisms is a likely cause behind the patterns of SSD observed in this study. In the majority of species analysed, different samples measured came from the same population proposing no role for intraspecific genetic differentiation. Neither can intraspecific variation in SSD be ascribed to differential survival in different environments, since in most species, samples were reared under laboratory conditions.

One might wonder if the patterns of SSD observed at the intraspecific level contradict regularities found in SSD at the among-species level. In particular, Rensch's rule states that when comparing different species, SSD tends to increase with body size in clades in which males are the larger sex, and decrease in clades in which females are the larger sex (Abouheif and Fairbairn 1997, Fairbairn 1997). The results of this work – species with female-biased SSD showing an increase in SSD

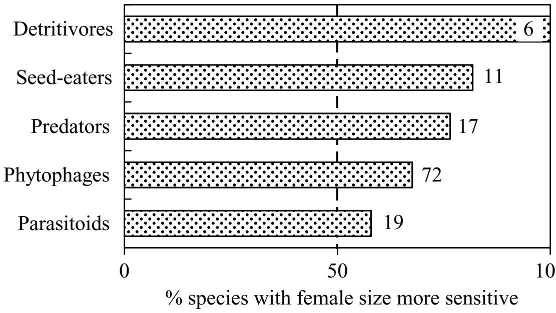

Fig. 3. Percentage of species with female size being more sensitive to environmental quality than male size. Figures next to the bars are species numbers. Species are divided into feeding guilds.

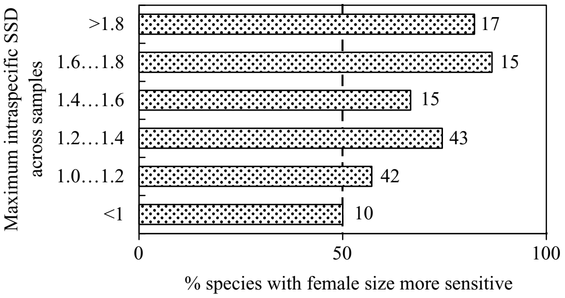

Fig. 4. Percentage of species with female size being more sensitive to environmental quality than male size. Figures next to the bars are species numbers. Species are classified according to the largest intraspecific SSD across the samples available (SSD > 1, if females are the larger sex, and SSD < 1, if males are the larger sex).

with increasing body size – seem to be inconsistent with Rensch's rule. This contradiction, however, would be only apparent. The application of Rensch's rule to explain within-species patterns of SSD (in fact, within-population patterns, above) is of questionable relevancy due to principal differences in underlying mechanisms (evolutionary vs ontogenetic).

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Appendix 1

The journals examined to compile the database used in the present study: Animal Behaviour, Annals of the Entomological Society of America, Annales Zoologici Fennici, Australian Journal of Entomology, Behavioral Ecology, Behavioral Ecology and Sociobiology, Biological Journal of the Linnean Society, Biological Reviews, Bulletin of Entomological Research, Canadian Entomologist, Canadian Journal of Zoology, Ecography, Ecological Entomology, Ecological Monographs, Ecological Research, Ecology, Ecology Letters, Ecoscience, Entomologia Experimentalis et Applicata, Environmental Entomology, European Journal of Entomology, Evolutionary Ecology Research, Evolutionary Ecology, Evolution, Florida Entomologist, Functional Ecology, Journal of Animal Ecology, Journal of Applied Entomology, Journal of Evolutionary Biology, Journal of Insect Behavior, Journal of Stored Products Research, Oecologia, Oikos, Physiological Entomology, Population Ecology, Quarterly Review of Biology, Zoological Journal of the Linnean Society. Volumes of the last few to more than forty years were inspected depending on availability.

Appendix 2

Summary statistics for each of the datasets included in the analyses with references to original sources. Min SSD and Max SSD – minimum and maximum female/male size ratios (SSD) across samples; Ratio – maximum SSD divided by minimum SSD; No. samples – number of samples, the analyses were based on; Slope and Intercept – signs of the slope and intercept of type II regression (male size regressed on female size; Data analysis). Species names are in bold if significant differences in SSD were found between samples (Data analysis).

Species	Order	Min SSD	Max SSD	Ratio	No. samples	Slope	Intercept	Reference
Acanthoscelides obtectus	Coleoptera	0.97	1.64	1.70	13	+	+	Shade et al. 1987
Acheta domesticus	Orthoptera	0.99	1.15	1.16	2	−	+	Walton 1980
Adalia bipunctata	Coleoptera	1.08	1.28	1.18	12	+	+	Rana et al. 2002
Aedes triseriatus	Diptera	1.60	1.71	1.07	2	+	+	Walker and Merritt 1988
Aelia fieberi	Heteroptera	1.04	1.15	1.11	5	+	+	Nakamura and Numata 1997
Aglais urticae	Lepidoptera	1.01	1.08	1.07	8	+	+	Bryant et al. 1999
Agrotis ipsilon	Lepidoptera	1.12	1.13	1.01	2	+	−	Sappington and Showers 1992
Amorbia cuneana	Lepidoptera	1.53	1.62	1.06	2	−	+	Honda et al. 1996
Anasa tristis	Heteroptera	1.34	1.42	1.06	3	+	−	Bonjour and Fargo 1989
Anoplophora glabripennis	Coleoptera	1.60	1.71	1.06	2	−	+	Dubois et al. 2002
Anticarsia gemmatalis	Lepidoptera	0.79	1.03	1.31	4	+	+	Anazonwu and Johnson 1986
Aphidius ervi	Hymenoptera	1.05	1.17	1.12	14	+	−	Sequeira and Mackauer 1992
Archanara sparganii	Lepidoptera	1.11	1.35	1.22	4	+	+	Teder and Tammaru 2002
Arge fuscinervis	Hymenoptera	1.64	1.71	1.04	3	+	+	Hanhimäki et al. 1994
Ascia monuste	Lepidoptera	1.10	1.20	1.09	4	+	−	Barros-Bellanda and Zucoloto 2001
Asobara tabida	Hymenoptera	1.28	1.28	1.00	2	+	+	Kraaijeveld and van der Wel 1994

Appendix 2 (*Continued*)

Species	Order	Min SSD	Max SSD	Ratio	No. samples	Slope	Intercept	Reference
Asphondylia spp. 11	Diptera	0.84	0.94	1.12	2	–	+	Waring and Price 1990
Attagenus unicolor	Coleoptera	1.70	1.84	1.08	2	.	.	Baker 1986
Bactra verutana	Lepidoptera	1.45	2.25	1.55	6	+	–	Frick and Wilson 1982
Baetis bicaudatus	Ephemeroptera	1.32	1.47	1.11	4	+	–	Peckarsky et al. 2002
Baetis tricaudatus	Ephemeroptera	1.21	1.41	1.17	4	+	+	Scrimgeour and Culp 1994
Bemisia tabaci	Homoptera	1.74	1.81	1.04	2	+	+	Blackmer and Byrne 1999
Bicyclus anynana	Lepidoptera	1.16	1.32	1.14	7	+	–	Brakefield and Mazzotta 1995
Blepharidopterus angulatus	Heteroptera	1.15	1.18	1.02	2	+	+	Glen 1977
Brachymeria intermedia	Hymenoptera	1.25	1.38	1.10	2	–	+	Dindo et al. 2001
Bruchidius atrolineatus	Coleoptera	1.28	1.34	1.05	3	+	+	Desroches and Huignard 1991
Busseola fusca	Lepidoptera	1.03	1.28	1.25	4	+	+	Onyango and Ochieng'-Odero 1994
Cactoblastis cactorum	Lepidoptera	2.23	3.05	1.36	2	–	+	Johnson and Stiling 1996
Calathus melanocephalus	Coleoptera	1.03	1.20	1.17	5	+	+	Van Dijk 1994
Callosobruchus maculatus	Coleoptera	1.17	1.36	1.17	6	+	–	Messina 1991
Carabus clatratus	Coleoptera	1.16	1.21	1.04	2	+	+	Huk and Kühne 1999
Carneocephala floridana	Homoptera	1.61	1.74	1.08	4	+	+	Rossi and Strong 1991
Ceratina calcarata	Hymenoptera	1.32	1.39	1.05	3	+	–	Johnson 1988
Chasmias paludator	Hymenoptera	1.03	1.03	1.01	2	+	–	Teder and Tammaru unpubl.
Choristoneura fumiferana	Lepidoptera	1.28	1.49	1.17	5	+	–	Pedersen et al. 1997
Choristoneura occidentalis	Lepidoptera	1.15	1.31	1.14	10	+	+	Campbell 1989
Choristoneura rosaceana	Lepidoptera	1.55	1.78	1.15	4	+	+	Carriere 1992
Chorthippus brunneus	Orthoptera	1.44	1.91	1.32	3	+	+	Willott and Hassall 1998
Chrysomela confluens	Coleoptera	1.28	1.32	1.03	4	+	–	Floate et al. 1993
Chrysoperla carnea	Neuroptera	1.20	1.27	1.06	4	+	–	Phoofolo and Obrycki 1998
Coccinella septempunctata	Coleoptera	1.19	1.20	1.01	3	+	–	Nielsen et al. 2002
Coenonympha pamphilus	Lepidoptera	1.58	1.83	1.16	4	+	+	Goverde et al. 2002
Coleomegilla maculata	Coleoptera	1.14	1.19	1.04	2	+	–	Phoofolo and Obrycki 1998
Cotesia glomerata	Hymenoptera	1.12	1.23	1.10	4	+	+	Geervliet et al. 2000
Cotesia rubecula	Hymenoptera	1.25	1.26	1.01	2	+	+	Brodeur et al. 1998
Crocidosema plebejana	Lepidoptera	1.22	1.36	1.12	11	+	–	Hamilton and Zalucki 1993
Culex tarsalis	Diptera	1.21	1.34	1.11	2	+	+	Garcia et al. 1992
Delia antiqua	Diptera	1.04	1.07	1.03	4	+	+	McDonald and Borden 1995
Deloyala guttata	Coleoptera	1.12	1.15	1.03	3	+	+	Rausher et al. 1993
Dendrocerus carpenteri	Hymenoptera	0.89	1.61	1.81	8	+	+	Otto and Mackauer 1998
Depressaria pastinacella	Lepidoptera	1.15	1.19	1.03	2	–	+	Nitao 1989
Diprion pini	Hymenoptera	1.88	2.00	1.06	4	+	+	Niemelä et al. 1991
Drosophila melanogaster	Diptera	1.02	1.57	1.54	11	+	+	Miller 1964
Drosophila mercatorum	Diptera	1.02	1.27	1.25	4	+	+	Gebhardt and Stearns 1988
Drosophila simulans	Diptera	1.19	1.56	1.31	11	+	+	Miller 1964
Edovum puttleri	Hymenoptera	1.11	1.20	1.08	3	+	+	Corrigan and Lashomb 1990

Appendix 2 (*Continued*)

Species	Order	Min SSD	Max SSD	Ratio	No. samples	Slope	Intercept	Reference
Ephedrus californicus	Hymenoptera	1.30	1.46	1.12	5	+	–	Sequeira and Mackauer 1993
Ephestia kuehniella	Lepidoptera	1.17	1.25	1.07	2	+	+	Anderson and Löfqvist 1996
Epilachna varivestis	Coleoptera	1.05	1.07	1.02	2	+	+	Hughes and Chiment 1988
Epilachna vigintioctomaculata	Coleoptera	1.09	1.09	1.00	2	+	+	Ueno et al. 1999
Epirrita autumnata	Lepidoptera	1.07	1.12	1.05	2	+	–	Hanhimäki and Senn 1992
Eucelatoria bryani	Diptera	0.95	1.15	1.21	7	+	–	Reitz 1996
Eucelatoria rubentis	Diptera	0.92	0.98	1.06	6	+	+	Reitz 1996
Eucosma womonana	Lepidoptera	1.25	1.31	1.05	2	+	–	Rogers 1985
Euschistus heros	Heteroptera	1.06	1.09	1.03	2	+	–	Panizzi and Oliveira 1998
Galerucella sagittariae	Coleoptera	1.09	1.12	1.03	2	+	–	Nokkala and Nokkala 1998
Geocoris punctipes	Heteroptera	1.31	1.62	1.23	12	+	+	Naranjo and Stimac 1985
Glaucopsyche lygdamus	Lepidoptera	1.02	1.10	1.08	5	+	+	Fraser et al. 2001
Harmonia axyridis	Coleoptera	1.05	1.12	1.07	3	+	–	Ueno 2003
Helicoverpa zea	Lepidoptera	0.96	0.98	1.02	2	+	–	Ellsbury et al. 1989
Hemiargus isola	Lepidoptera	1.04	1.14	1.09	2	+	–	Wagner and Martinez del Rio 1997
Hemileuca lucina	Lepidoptera	1.37	1.49	1.08	3	+	+	Stamp and Bowers 1990
Hylobius pales	Coleoptera	1.10	1.13	1.04	7	+	–	Hunt et al. 1993
Hylobius radicis	Coleoptera	1.17	1.26	1.08	7	+	+	Hunt et al. 1993
Hyposoter exiguae	Hymenoptera	1.07	1.11	1.03	2	+	+	Jowyk and Smilowitz 1978
Ibalia leucospoides	Hymenoptera	1.47	1.70	1.16	2	+	–	Fukuda and Hijii 1996
Inachis io	Lepidoptera	1.07	1.19	1.11	8	+	–	Bryant et al. 1999
Ips sexdentatus	Coleoptera	0.87	0.98	1.13	4	+	+	Colineau and Lieutier 1994
Ips typographus	Coleoptera	0.92	0.96	1.04	5	+	–	Anderbrant et al. 1985
Junonia coenia	Lepidoptera	1.12	1.23	1.10	4	+	+	Fajer et al. 1991
Lasiommata megera	Lepidoptera	1.13	1.29	1.14	2	+	+	Karlsson and Wiklund 1984
Lasiommata petropolitana	Lepidoptera	1.03	1.15	1.12	6	+	+	Gotthard 1998
Leptinotarsa decemlineata	Coleoptera	1.20	1.22	1.02	3	+	–	Franca et al. 1994
Lobesia botrana	Lepidoptera	1.21	1.38	1.14	12	+	+	Savopoulou-Soultani and Tzanakakis 1988
Lycaena tityrus	Lepidoptera	1.04	1.15	1.11	3	+	–	Fischer and Fiedler 2000
Lygaeus kalmii	Heteroptera	1.21	1.25	1.03	2	+	+	Chaplin and Chaplin 1981
Lymantria dispar	Lepidoptera	2.65	3.00	1.13	4	+	+	Lazarević et al. 2002
Malacosoma californicum	Lepidoptera	1.54	2.03	1.32	9	+	+	Myers and Williams 1987
Malacosoma disstria	Lepidoptera	1.36	1.41	1.04	2	+	+	Fortin and Mauffette 2001
Megachile rotundata	Hymenoptera	1.07	1.26	1.17	4	+	+	Peach et al. 1995
Megarcys signata	Plecoptera	2.10	2.29	1.09	2	+	+	Taylor et al. 1998
Melanoplus differentialis	Orthoptera	1.30	1.36	1.05	2	+	+	Lewis 1984
Monoctonus paulensis	Hymenoptera	1.17	1.33	1.14	12	+	–	Mackauer and Chau 2001
Musca autumnalis	Diptera	1.46	1.68	1.15	11	+	+	Gaaboub and Hayes 1984
Myrmeleotettix maculatus	Orthoptera	1.36	1.42	1.04	2	+	+	Willott and Hassall 1998
Neodiprion lecontei	Hymenoptera	2.03	2.32	1.14	2	+	+	Codella Jr. and Raffa 1995

Appendix 2 (*Continued*)

Species	Order	Min SSD	Max SSD	Ratio	No. samples	Slope	Intercept	Reference
Neodiprion sertifer	Hymenoptera	1.70	2.19	1.29	4	+	+	Codella Jr. and Raffa 1995
Neomegalotomus parvus	Heteroptera	1.03	1.24	1.20	5	+	+	Santos and Panizzi 1998
Nephotettix virescens	Homoptera	1.13	1.61	1.42	5	+	+	Rapusas and Heinrichs 1987
Nezara viridula	Heteroptera	1.23	1.29	1.04	4	+	+	Kester et al. 1984
Nonagria typhae	Lepidoptera	1.30	1.39	1.07	4	+	+	Teder and Tammaru 2002
Notiophilus biguttatus	Coleoptera	1.03	1.12	1.08	4	+	+	Ernsting et al. 1992
Ochlerotatus triseriatus	Diptera	1.56	2.16	1.38	3	+	+	Daugherty and Juliano 2002
Omocestus viridulus	Orthoptera	1.66	1.72	1.04	2	+	+	Willott and Hassall 1998
Oncopeltus fasciatus	Heteroptera	1.29	1.34	1.04	2	+	+	Chaplin and Chaplin 1981
Operophtera brumata	Lepidoptera	1.00	1.17	1.17	8	+	+	Tikkanen et al. 2000
Orgyia leucostigma	Lepidoptera	2.64	3.26	1.23	4	+	–	Agrell et al. 2000
Orgyia pseudotsugata	Lepidoptera	3.02	3.89	1.29	3	+	+	Beckwith 1982
Orgyia vetusta	Lepidoptera	4.17	4.19	1.01	2	+	–	Harrison 1995
Orius sauteri	Heteroptera	1.13	1.44	1.27	4	+	+	Yano et al. 2002
Ostrinia nubilalis	Lepidoptera	0.70	0.86	1.23	20	+	–	Ewete et al. 1996
Panolis flammea	Lepidoptera	0.88	1.05	1.19	3	–	+	Leather et al. 1998
Papilio polyxenes	Lepidoptera	1.12	1.37	1.22	3	+	–	Lederhouse et al. 1982
Pararge aegeria	Lepidoptera	1.00	1.22	1.22	5	–	+	Nylin et al. 1993
Paropsis atomaria	Coleoptera	1.38	1.68	1.22	6	+	+	Morrow and Fox 1980
Perillus bioculatus	Heteroptera	1.26	1.33	1.06	3	+	+	Yocum and Evenson 2002
Phyllonorycter salicifoliella	Lepidoptera	0.90	1.00	1.12	3	+	+	Auerbach and Alberts 1992
Phyllotreta nemorum	Coleoptera	0.95	1.07	1.13	8	+	–	Nielsen 1999
Physocephala rufipes	Diptera	1.12	1.25	1.11	3	+	+	Schmid-Hempel and Schmid-Hempel 1996
Pieris brassicae	Lepidoptera	0.97	1.25	1.29	4	+	+	Karowe and Schoonhoven 1992
Pieris melete	Lepidoptera	0.77	1.00	1.30	10	+	–	Ohsaki and Sato 1994
Pieris napi	Lepidoptera	0.90	0.99	1.10	11	+	+	Wiklund et al. 1991
Pieris rapae	Lepidoptera	0.86	0.98	1.13	8	+	+	Ohsaki and Sato 1994
Piezodorus guildinii	Heteroptera	1.07	1.10	1.03	4	+	+	Panizzi 1992
Pimpla turionellae	Hymenoptera	1.29	2.11	1.64	6	+	+	Arthur and Wylie 1959
Platynota idaeusalis	Lepidoptera	1.42	1.52	1.07	3	+	+	Hunter et al. 1994
Plodia interpunctella	Lepidoptera	1.22	1.36	1.11	5	+	+	Sait et al. 1994
Plutella xylostella	Lepidoptera	1.09	1.26	1.15	6	+	+	Raps and Vidal 1998
Podisus maculiventris	Heteroptera	1.31	1.83	1.39	5	+	+	Legaspi et al. 1996
Podisus nigrispinus	Heteroptera	1.36	1.43	1.05	3	+	+	Mohaghegh et al. 1999
Poecilus cupreus	Coleoptera	0.99	1.06	1.07	3	+	+	Zangger et al. 1994
Polygonia c-album	Lepidoptera	0.97	1.07	1.10	9	+	+	Bryant et al. 1999
Polyommatus icarus	Lepidoptera	0.86	0.94	1.10	2	+	–	Fiedler and Hölldobler 1992
Potamophylax cingulatus	Trichoptera	1.20	1.47	1.22	3	+	+	Svensson 1975
Psacothea hilaris	Coleoptera	1.01	1.15	1.15	8	+	–	Shintani and Ishikawa 1998
Pterostichus versicolor	Coleoptera	0.92	1.18	1.29	4	+	+	Van Dijk 1994
Rhopobota naevana	Lepidoptera	1.21	1.24	1.02	2	–	+	Fitzpatrick and Troubridge 1993
Rhyacionia frustrana	Lepidoptera	1.22	1.64	1.34	20	+	+	Asaro and Berisford 2001
Rhynchophorus cruentatus	Coleoptera	1.00	1.04	1.04	3	+	–	Giblin-Davis et al. 1989
Sabulodes aegrotata	Lepidoptera	1.23	1.25	1.02	2	+	+	Honda et al. 1996
Schistocerca shoshone	Orthoptera	1.41	1.67	1.18	2	–	+	Sword and Chapman 1994

Appendix 2 (*Continued*)

Species	Order	Min SSD	Max SSD	Ratio	No. samples	Slope	Intercept	Reference
Sicus ferrugineus	Diptera	1.09	1.10	1.01	2	+	+	Schmid-Hempel and Schmid-Hempel 1996
Sirex nitobei	Hymenoptera	2.10	2.17	1.03	2	+	+	Fukuda and Hijii 1996
Soyedina carolinensis	Plecoptera	1.33	1.65	1.25	32	+	+	Sweeney and Vannote 1986
Spalangia cameroni	Hymenoptera	1.23	1.29	1.05	2	.	.	King 1990
Spalangia endius	Hymenoptera	1.59	1.73	1.09	2	+	−	King 2000
Spilichneumon limnophilus	Hymenoptera	0.67	0.76	1.14	2	+	+	Teder and Tammaru unpubl.
Spodoptera eridania	Lepidoptera	1.31	1.32	1.01	2	+	+	Gunderson et al. 1985
Spodoptera exempta	Lepidoptera	0.98	1.14	1.17	12	+	+	Parker and Gatehouse 1985
Spodoptera frugiperda	Lepidoptera	0.89	1.04	1.17	11	+	+	Ferguson et al. 1994
Spodoptera pectinicornis	Lepidoptera	1.34	1.54	1.15	2	+	−	Wheeler et al. 1998
Tortrix viridana	Lepidoptera	1.02	1.61	1.58	8	−	+	Hunter and Willmer 1989
Trichoplusia ni	Lepidoptera	0.87	0.94	1.08	2	−	+	Honda et al. 1996
Vanessa atalanta	Lepidoptera	0.95	1.02	1.07	9	+	+	Bryant et al. 1999
Winthemia fumiferanae	Diptera	0.88	0.95	1.08	2	+	−	Hébert and Cloutier 1990
Xanthogaleruca luteola	Coleoptera	1.05	1.15	1.10	8	+	+	Young and Hall 1986
Yponomeuta evonymellus	Lepidoptera	1.26	1.33	1.05	2	+	+	Kooi et al. 1991
Yponomeuta padellus	Lepidoptera	1.08	1.19	1.10	2	−	+	Kooi et al. 1991