

Sexual size dimorphism in Orthoptera (sens. str.) — a review

Authors: Hochkirch, Axel, and Gröning, Julia

Source: Journal of Orthoptera Research, 17(2) : 189-196

Published By: Orthopterists' Society

URL: <https://doi.org/10.1665/1082-6467-17.2.189>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Sexual size dimorphism in Orthoptera (*sens. str.*) — a review

AXEL HOCHKIRCH AND JULIA GRÖNING

(AH)University of Trier, Department VI, Biogeography Group, Am Wissenschaftspark 25-27, D-54296 Trier, Germany. Email: hochkirch@uni-trier.de

(JG)University of Osnabrück, Department of Biology/Chemistry, Division of Ecology, Barbarastr. 13, D-49076 Osnabrück, Germany. Email: julia.groening@gmx.de

Abstract

Sexual size dimorphism (SSD) is a common phenomenon in animal taxa. While males are the larger sex in many birds and mammals, female-biased SSD predominates among insects, including Orthoptera. We analyzed size differences of 1503 Orthoptera species, suggesting that SSD is rather uniform in Ensifera, with the females being on average 9% larger than the males (ranging from -20 to +40%). In contrast, SSD is usually much stronger in Caelifera (37%) and also more variable (ranging from -20 to +140%). Caelifera with larger females exhibit stronger size differences than smaller species, whereas in Ensifera SSD decreases with male body size, but is not related to female size. Sexual size differences in Orthoptera are usually associated with a higher number of nymphal instars in females, leading to an earlier emergence of adult males (protandry). Both growth rates and the number of instars seem to be affected by genetic and environmental cues. Two major hypotheses have been proposed to explain the ultimate causes for SSD: the intersexual competition hypothesis and the differential equilibrium hypothesis. The first suggests that sexual dimorphism is a mechanism to reduce intraspecific competition, enabling the sexes to specialize on different food items. The differential equilibrium hypothesis proposes that the different body sizes represent sex-specific fitness optima, which are caused by their specific life-history strategies. Females may maximize their reproductive success by increasing the number (or size) of eggs (fecundity selection), whereas males may maximize their reproduction by being more mobile and fertilizing many females in a short period of time. These fundamental differences in the life-history strategies of the sexes may also lead to sexual selection, which has sometimes been referred to as an additional hypothesis. There is still a need for more empirical research on the ultimate causes for SSD. At present, there is much more support for the differential equilibrium hypothesis, but the intersexual competition hypothesis has rarely been tested. We propose some experimental approaches to test both hypotheses in micro- and macroevolutionary contexts.

Key words

sexual dimorphism, Rensch's rule, fecundity selection, sexual selection, sexual conflict, intersexual competition

Introduction

The most fundamental feature of sexual reproduction is the existence of two distinct sexes with differentiation of the reproductive roles. These sexes are primarily defined by differences in their gametes and reproductive organs, but in most cases secondary differences are associated with sexuality (Andersson 1994). One intersexual difference which is widespread among animal taxa is sexual size dimorphism (SSD). While in many mammal and bird species the males are larger than the females (*e.g.*, Fairbairn 1997), female-biased SSD dominates among Orthoptera and many other invertebrates (Teder & Tammaru 2005, Blanckenhorn *et al.* 2007,

Esperk *et al.* 2007). However, there is substantial variation between and within different taxa and usually also within single species (Teder & Tammaru 2005).

The ultimate causes for SSD have been discussed controversially since Darwin (1871), who assumed that either sexual or natural selection might explain size dimorphism. Selander (1966) suggested that SSD could also be driven by intraspecific (intersexual) competition for resources. These three hypotheses (sexual selection, dimorphic niches, intersexual competition) have dominated the debate for some decades (*e.g.*, Lande 1980, Slatkin 1984, Hedrick & Temeles 1989, Shine 1989, Temeles *et al.* 2000). Recently, it has been argued that sexual selection is a consequence of sex-role specialization and therefore, it will be difficult to distinguish predictions of the sexual selection hypothesis from those of the dimorphic niches hypothesis (Fairbairn 1997, Hochkirch *et al.* 2007). Hence, male and female body size might be differently affected by opposing selective agents, which has been referred to as the "differential equilibrium model" of SSD (Blanckenhorn 2005).

The intersexual competition hypothesis states that competition between males and females leads to intersexual character displacement (Selander 1966, Slatkin 1984, Hedrick & Temeles 1989). In this case, SSD represents a mechanism to reduce intraspecific competition, such as specialization on different food items (Temeles *et al.* 2000).

In contrast, the differential equilibrium hypothesis proposes that SSD is caused by different niche optima of the sexes, as a result of sex-specific costs of reproduction (Slatkin 1984, Hedrick & Temeles 1989, Fairbairn 1997, Blanckenhorn 2000). The latter hypothesis encompasses the "fecundity selection hypothesis" (Reeve & Fairbairn 1999) which explains female body size and the "sexual selection hypothesis" which explains male body size (Blanckenhorn 2000).

As female egg production is generally believed to be more costly in terms of energetic requirements than male sperm production, females need more nutrients and time to produce offspring. They may maximize their lifetime reproductive success by increasing the number (or size) of eggs or extend their lifespan. As females are constrained by their own egg production, the benefits of multiple matings are usually lower than for males (Andersson 1994, Rowe 1994).

In contrast, males may increase their fitness by maximizing the number of matings (*i.e.*, fertilizing a high number of eggs). This sexual conflict leads ultimately to sexual selection (Hochkirch *et al.* 2007), which might act through male or female choice (*i.e.*, preferences for large or small mates) or through intrasexual combat, in which larger or smaller individuals of similar sex have an advantage (*e.g.*, protandry, territoriality). A major problem in distinguishing between the intersexual competition hypothesis and the differential

equilibrium hypothesis is that dimorphic niches might also have evolved as a consequence of competition in the past ("ghost of competition past", Connell 1980).

In this review, we synthesize evidence from studies on Orthoptera, which either support or reject the above named hypotheses. We first analyze SSD in 1503 Orthoptera species (1113 Caelifera, 390 Ensifera) and show that these two taxa follow different patterns. We then discuss the underlying proximate processes shaping SSD in Orthoptera. Afterwards, we review the published literature on the ultimate causes for sexual size dimorphism in Orthoptera. A major goal of our review is to propose important areas for future research on SSD in Orthoptera.

Methods

In order to achieve data on SSD in Orthoptera, we created a database using the taxonomic literature of three large geographic areas (Bei-Bienko & Mishchenko 1963 for the former USSR, Harz 1969, 1975 for Europe, Dirsh 1970 for the Congo), comprising a total of 1503 species. A problem with the existing data on body sizes in Orthoptera is that taxonomists often do not clearly define their measures, such as "body length" or "total length" which is also true for the literature analyzed. It is reasonable to assume that a single author has been consistent in his measures, but this is not necessarily true among authors. As most authors present ranges of body sizes rather than means and variances, we calculated averages for each sex from the minima and maxima given. For practical reasons it was not possible to include all known species, genera or even families of Orthoptera, but the database covers large parts of the Palearctic fauna and some Oriental and African taxa. If data for more than one subspecies were available, only the first subspecies mentioned was included. The database was afterwards corrected with

the current online version of the Orthoptera Species File (Eades *et al.* 2007). We removed synonymized taxa from the database and assigned valid taxa to their current systematic position. If data for one species were included in more than one of the publications analyzed, the minimum and maximum values were chosen. We are aware that even the current systematic status might not reflect the real phylogenetic history and the status of some species might still be disputed. However, we had to compromise on these qualities to obtain a comprehensive database. It should be noted that averages and standard deviations for SSD did change only negligibly after correcting the database for double entries and synonymies, which led to a deletion of 172 entries.

Although at a first glance measuring SSD seems to be a simple task, there are some fundamental problems associated with size measurements. One might choose to measure body length, weight, dimensions of a single part of the body (pronotum, leg *etc.*) or calculate surface areas (Uvarov 1966). As museum material shrinks on drying, body lengths might not be well suited for such analyses, but shrinking might affect both sexes in a similar way. On the other hand, even the length of living Orthoptera females varies substantially with the oviposition cycle. A similar problem arises when weight is used as measure. Daily variation of weight might be even more pronounced due to the uptake of water and food. In females, substantial loss of weight is associated with oviposition and this daily variation has even been used to reconstruct the oviposition cycle of individuals in the field (Kriegbaum 1988). Some authors try to deal with the problem of shrinkage by measuring less variable parts of the body, such as the length of a hind femur (*e.g.*, del Castillo *et al.* 1999, Nosil 2002). However, measuring single parts of the body might just illustrate sexual dimorphism in this particular trait (Kelly 2005) and some characters (*e.g.*, the shape of the pronotum) are known to differ even between wing morphs (Uvarov 1966). Hence,

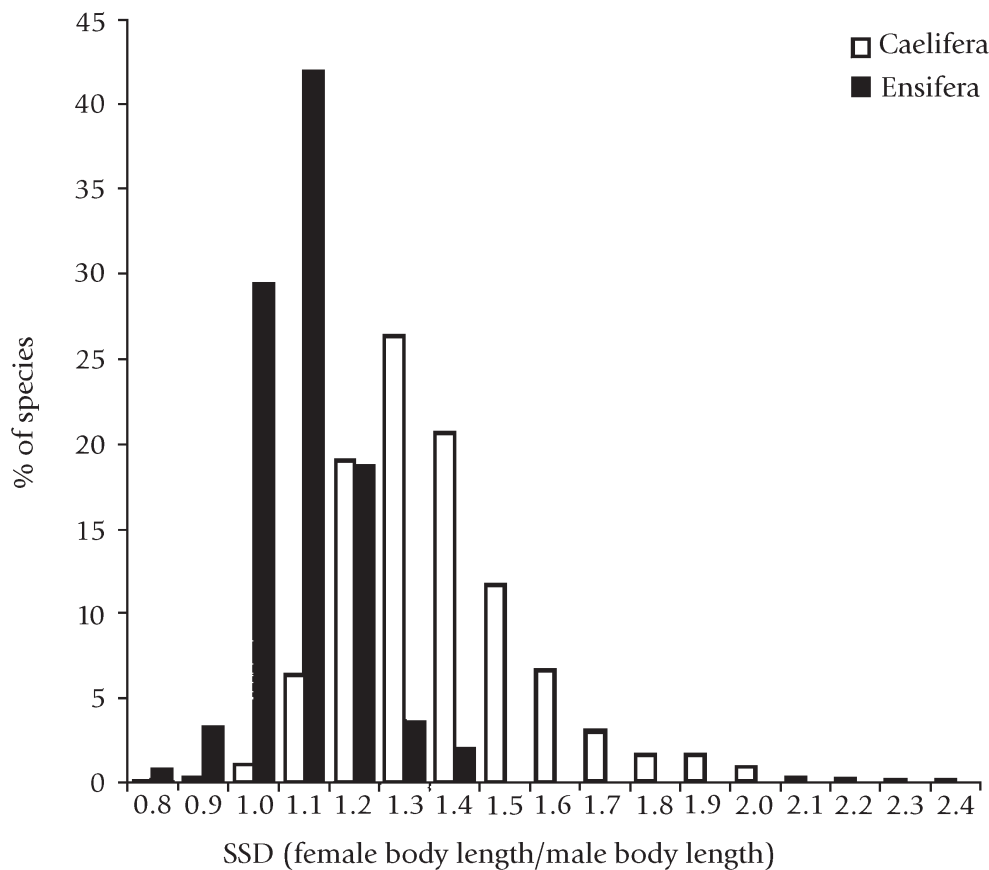


Fig. 1. Comparison of sexual size dimorphism (SSD) in Caelifera and Ensifera. While in Caelifera the females are often much larger than the males (average 1.37), SSD is less pronounced in Ensifera (average 1.09). Moreover, the degree of variation is much higher in Caelifera than in Ensifera, ranging from 0.83 to 2.45 in the former group and from 0.77 to 1.44 in the latter. Note that the original values have been rounded to one decimal place.

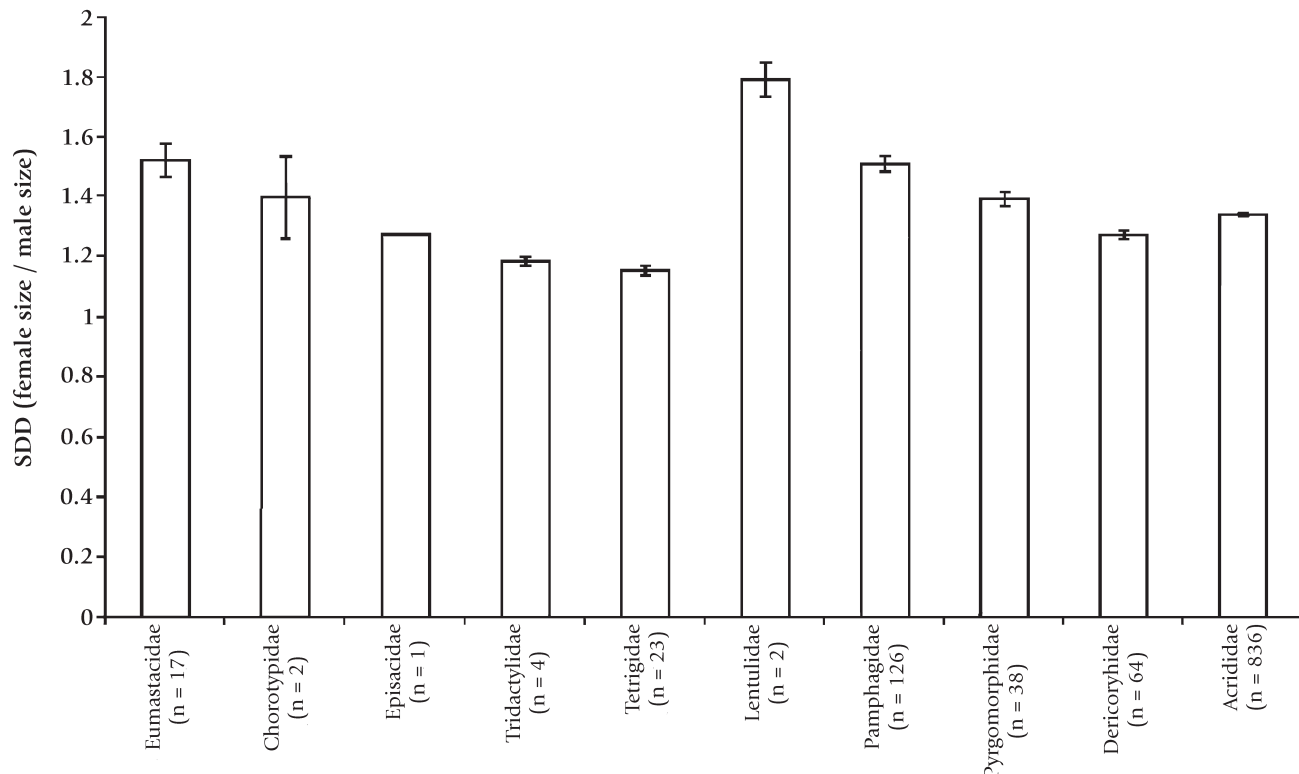


Fig. 2. Comparison of sexual size dimorphism (SSD) across different Caeliferan families. Note that some values (particularly Lentulidae) might be affected by a low number of species included in the database.

the best method to measure SSD would probably be multivariate morphometrics, the first function of which usually uncovers general size differences (Hockkirch 2005). However, in this review we tried to maximize the number of species included and therefore, we had to rely on the data presented in the taxonomic literature. As body length was the measure presented by all authors, we calculated an index of sexual size dimorphism as the ratio of female body size/male body size. We examined the allometric relationships of SSD following Fairbairn (1997) as the slope (β) of a model-II regression of \log (male size) on \log (female size). All statistical analyses were carried out with "R 2.5.1" (R Development Core Team 2007).

The pattern: SSD in Orthoptera

The analysis of our database revealed that female-biased SSD dominates among Orthoptera (Fig. 1). This is particularly true for Caelifera species, in 99% of which females are larger than males (1106 species). We only found five Caelifera species (0.4%), in which average male size was greater than average female size, but this might also be due to typing errors or to insufficiently long series being examined.

Nevertheless, there was substantial intraspecific variation. In 207 species the largest male size was greater than the smallest female size (19%) and in a further 45 species, the largest males were of similar size as the smallest females (4%). This remarkable intraspecific variation might be caused by environmental factors (Teder & Tammaru 2005). Understanding these microevolutionary patterns of SSD might also be fundamental to understanding the general pattern. Female Caelifera were on average $1.37 (\pm 0.006 \text{ s.e.})$ times larger than males, but there were substantial differences between families (Fig. 2, see also below). In Ensifera, females were on average only $1.09 (\pm 0.005 \text{ s.e.})$ times larger than the males and in 49

species (13%) the males were larger than the females. Moreover, in 21 species (6%) the sexes were of similar size and in 295 species the largest males were bigger than the smallest females (76%). These general differences between Caelifera and Ensifera suggest that the selective forces differ substantially between the two orders.

The degree of interspecific variability was much lower in Ensifera than in Caelifera, ranging in Ensifera from 0.77 to 1.44, in Caelifera, 0.83 to 2.45 (Fig. 1). This low degree of variation was also apparent when families were compared. Although in Mogoplistidae SSD seemed to be higher than in other families (average: 1.23, ANOVA, $F_{5,384} = 2.96$, $p = 0.012$), only four species of this family had been included in the database. In Caelifera, SSD increased with female body size (linear model, $R^2 = 0.11$, $p < 0.0001$), but was independent of male size. In contrast, SSD decreased with male body size in Ensifera (linear model, $R^2 = 0.05$, $p < 0.0001$), but was independent of female size.

These results indicate that in Caelifera, SSD is mainly caused by changes in female body size, while in Ensifera, SSD is mainly affected by changes in male size. These differences are likely to be caused by different life history strategies of the two orders, particularly the differences in mate acquisition (see below). An examination for allometric relationships using a Model II regression as proposed by Fairbairn (1997) revealed a more or less isometric pattern for Ensifera ($\beta = 1.02$, Fig. 3a) and an allometric pattern for Caelifera ($\beta = 0.94$, Fig. 3b). Hence, both taxa do not exhibit Rensch's rule, which proposes that SSD decreases with increasing female size (Blanckenhorn 2000).

The higher variability in Caelifera might be affected by the higher number of these species included in the database (comprising three continents). However, the averages and data distributions were rather similar among the three sources (averages: Bei-Bienko & Mishchenko 1963: 1.38, Dirsh 1970: 1.35, Harz 1975: 1.36; Fig. 4). Although we

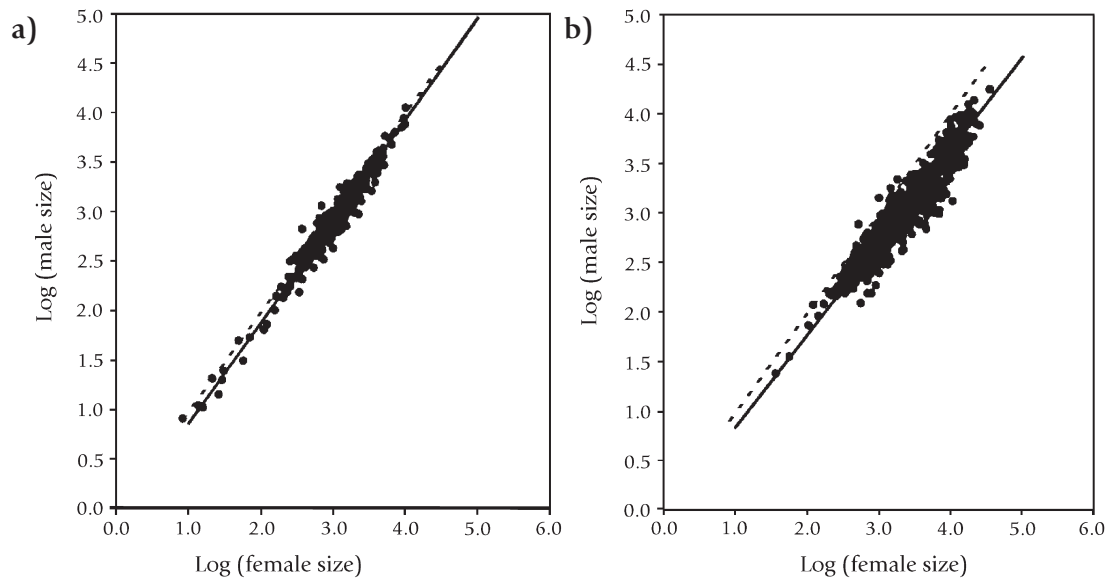


Fig. 3. Model II regressions for estimating allometry of SSD following the method proposed by Fairbairn (1997). The dashed line represents similar body sizes of both sexes. Note that in (a) Ensifera the SSD is generally weak and the ratio remains constant across the body sizes ($\beta = 1$), whereas in (b) Caelifera SSD increases with female body size ($\beta = 0.94$).

found significant differences in SSD between the species treated by Bei-Bienko & Mishchenko (1963) and Dirsh (1970) (ANOVA, $F_{2,1095} = 4.21$, $p = 0.02$), these differences were probably caused mainly by the different representation of families on the different continents. SSD was particularly pronounced among Pamphagidae (1.53, $n = 126$), whereas it was rather low in Tetrigidae (1.16, $n = 23$; Fig. 2). As different size dimorphisms among families might also be caused by over-representation of large or small species in particular families, we included female average size as a covariate, which did not change the results (ANCOVA, $F_{9,1094} = 18.9$, $p < 0.0001$).

Although the Lentulidae had an even stronger SSD (average: 1.8, $n = 2$) than Pamphagidae, this was probably affected by the low number of species included. A later inclusion of the revision

of the genus *Usambilla* (Jago 1981) resulted in a strong decline of SSD for the Lentulidae (average: 1.33, $n = 20$).

Among species, the strongest female-biased SSD was found in *Bufo nigriventris* (2.45, Pamphagidae: Nocarodesinae) and eight of the nine species with values > 2 were either Nocarodesinae or Tropidaucheninae (genera *Paranocarodes*, *Paranothotes*, *Nocarodes*, *Bufo nigriventris*). Despite the strong SSD in Pamphagidae, there was substantial variation among the subfamilies within this family, ranging from 1.12 (Porthetinae, $n = 2$) to 1.90 (Nocarodesinae, $n = 20$), suggesting that phylogenetic relationships alone could not explain these values. In fact, high intersexual size differences were found in ancient taxa (Eumastacidae, Pamphagidae, Pyrgomorphidae) as well as in very young groups (e.g., the genera *Acrida*, *Chorthippus*,

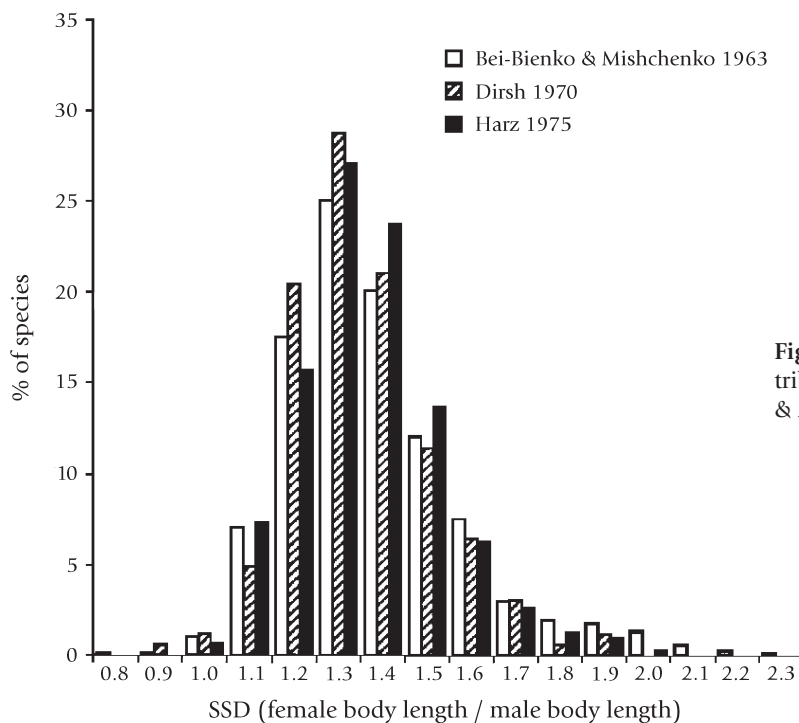


Fig. 4. Comparison of sexual size dimorphism (SSD) distributions of Caelifera from different sources (Bei-Bienko & Mishchenko 1963, Dirsh 1970, Harz 1975).

Acrotylus). The strongest male-biased SSD (0.77) was found in *Dolichopoda araneiformis* (Raphidophoridae), but in this case only one measure was available for each sex.

Proximate causes for SSD

In insects, SSD is often associated with intersexual differences in growth rates (Blanckenhorn *et al.* 2007) and developmental time, leading to differences in the number of nymphal or larval instars (Uvarov 1966, Esperk *et al.* 2007). Indeed, female Caelifera usually pass an additional instar during development compared to males, whereas in Ensifera the number of instars is often equal between the sexes (Ingrisch & Köhler 1998). In some taxa the number of instars seems to be genetically fixed (*e.g.*, Tetrigidae), whereas many species show a phenotypic plasticity in this regard with strong effects of the environmental conditions (Adis & Junk 2003, Adis *et al.* 2004, Berner & Blanckenhorn 2006). The lower number of instars in males has often been used as argument for a strong selection in favor of an advanced emergence, *i.e.*, protandry (Fagerström & Wiklund 1982, Zonneveld 1996, Teder & Tammaru 2005, Berner & Blanckenhorn 2006). However, whether females have evolved an additional instar or males have lost one instar, cannot easily be distinguished.

Studies on the proximate causes of SSD are relatively sparse and there is little knowledge of the factors determining the number of instars in Orthoptera. They might include innate sex differences in energy intake, expenditure and allocation, which might be influenced by physiology or endocrinology (*e.g.*, Cox *et al.* 2005). As outlined above, environmental cues seem to influence the number of instars in addition to genetic factors. Regional differences in the numbers of instars have been reported by Ismail & Fuzeau-Braesch (1972) for the field cricket, *Gryllus campestris*. Hassall & Grayson (1987) have shown that the number of instars in *Chorthippus brunneus* is related to different grazing regimes on pastures. Ahnesjö & Forsman (2003) found that different color morphs of the ground-hopper *Tetrix undulata* differ in body size. Although the latter authors suggest a genetic correlation of these traits, it should be noted that color-morph determination is also often environmentally cued in Orthoptera (Dearn 1990), including Tetrigidae (Hockkirch *et al.* 2008). It is, therefore, possible that body size is influenced by the differing thermal capacities of these color morphs.

Climatic effects on body size seem to be common in Orthoptera (*e.g.*, Willott & Hassall 1998). Berner & Blanckenhorn (2006) found that females of *Omocestus viridulus* in the Alps possess an additional nymphal instar at low, but not at high, altitudes. Interestingly, large individuals of this species developed faster than small ones, suggesting genetic variation in growth rates (Berner & Blanckenhorn 2006).

In most Caelifera species the females are more variable in body size than males, indicating that under unfavorable conditions females might compromise on body size (Teder & Tammaru 2005) in order to become adult and maximize the number of eggs laid during their lifespan. One might easily test this hypothesis by rearing Orthoptera under different degrees of food limitation (as has been done for spiders by Fernández-Montraveta & Moya-Laraño 2007) or under different climatic conditions (as has been done for beetles by Stillwell & Fox 2007). Telenga (1930) showed that *Schistocerca* nymphs skip one instar when reared on a poor diet, but the opposite was reported for *Melanoplus sanguinipes* (Uvarov 1966).

Ultimate causes for SSD

Studies supporting the differential equilibrium hypothesis

The differential equilibrium hypothesis proposes that SSD is a consequence of sex-specific fitness optima due to the sexes' different reproductive roles (Slatkin 1984, Blanckenhorn 2000). Females may maximize their fitness by achieving a higher adult body size, allowing them to produce more eggs, whereas males may maximize their lifetime reproductive success by multiple matings during a relatively short period of time (Shine 1989). Indeed, one of the most striking consequences of larger female body size in insects is a higher number of produced eggs per oviposition (Honek 1993). However, larger body size is also associated with substantial costs (Blanckenhorn 2000, Gotthard *et al.* 2007). These costs involve a shorter time for reproduction due to the longer time of development (which might be particularly important for species from regions with strong seasonality), or a lower viability of large insects due to a higher cumulative mortality, a greater detectability, a reduced agility and higher energetic requirements in order to attain and maintain a large body size (Roff 1980, Blanckenhorn 2000, Gotthard *et al.* 2007).

In Orthoptera, a positive relationship between body size and the number of eggs per pod has been documented by del Castillo *et al.* (1999) for the pyrgomorphid *Sphenarium purpurascens*. Females of larger species generally seem to produce larger egg pods (Honek 1993), but there is substantial variation depending on the life history strategy of the species involved (Hockkirch 1998). The lifetime reproductive success is not only affected by the number of eggs per pod, but also by egg size or by the number of egg pods produced during a lifetime. Thus, smaller females might produce smaller egg pods, but maximize their fitness by being reproductive for a longer time. Lewis (1984) has shown that larger females of *Melanoplus differentialis* produce more eggs per pod, more pods per female and also larger eggs. In addition to the number and size of eggs, larger females might also profit from larger auditory organs, allowing them to locate males over a greater distance (Bailey 1998). Indeed, Gwynne & Bailey (1999) found that females of the bush-cricket *Kawanaphila nartee* profit from larger auditory spiracles, but this advantage was independent of body size. On the other hand, Bailey & Kamien (2001) have shown that female auditory traits in *Requena verticalis* are positively allometrically related to body size, whereas this was not the case for males.

While fecundity selection for females is well supported in many taxa (Fairbairn 1997), it has been shown that males may also profit from larger body size in terms of higher fertility. Wedell (1997) found a strong relationship between body size and ejaculate size in males of twenty bushcricket species, whereas the size of the nuptial gifts was not related to body size. However, a positive correlation between body size and the size of nuptial gifts has been found in *Allonemobius socius* (Fedorka & Mousseau 2002). Simmons (1988) showed that larger males of *Gryllus bimaculatus* had lower costs of spermatophore production and, subsequently, a shorter refractory period. Moreover, small males had a lower ability to attach spermatophores to females (but see Weissman *et al.*, this issue). Large male size might also be advantageous if, as expected, larger males produce louder songs: increased intermale spacing of competing singers could result (Thiele & Bailey 1980). Hence, the relatively low degree of SSD in Ensifera compared to Caelifera might be a result of the different mating postures and life history strategies of these taxa (Gwynne 2004). Males of many Ensifera are territorial and produce nuptial gifts, which might favor larger males producing louder songs, larger nuptial gifts and stronger competition against rivals.

Males of Caelifera are usually mobile and actively search for potential mates, which might favor smaller males. Blanckenhorn (2005) points out that the evidence for advantages of large body size is overwhelming for both sexes, whereas the potential disadvantages have rarely been studied. Several authors suggest that mobility might be a key advantage of smaller body size in male insects (*e.g.*, Neems *et al.* 1990, Blanckenhorn 2005). Another (possibly even more important) advantage of smaller body size could be protandry (sooner emergence of adult males, Morbey & Ydenberg 2001, Teder & Tammaru 2005, Berner & Blanckenhorn 2006, Blanckenhorn *et al.* 2007). If males become adult before females do, they are able to secure high quality territories or fertilize virgins (Wang *et al.* 1990). This will be particularly important for species in which females lose receptivity rapidly after their first copulation as being able to store sperm. Females of *Chorthippus biguttulus* are known to be highly receptive during one week at the beginning of their adult life (starting four to five days after the final molt). During this time, they usually mate only once and rarely mate afterwards (Kriegbaum 1988).

While the above-mentioned mechanisms might maximize lifetime reproductive success by increasing the individuals' capacity of egg production or egg fertilization, sexual selection might also influence SSD. Sexual selection includes intersexual selection (mate choice) and intrasexual selection (combat). One simple kind of sexual selection acting on SSD is a male preference for large females or a female preference for small males. A preference for larger females is widespread in many insects (Thornhill & Alcock 2000, Bonduriansky 2001) and has also been found in Orthoptera (*pers. data unpub.*). Interestingly, females of many Orthoptera also prefer larger mates (Gwynne 1982, 1984; Simmons 1988; De Luca & Morris 1998), which is in conflict with the hypothesis that sexual selection alone can account for female-biased SSD.

Intrasexual selection has mainly been used to explain large male body size, as larger males might be more competitive in polygynous species (Owens & Hartley 1998). In the weta *Hemideina maori*, larger males are able to defend harems under rock cavities, but they take longer to become adult (Koning & Jamieson 2001, Leisnham & Jamieson 2004). Large males of the grasshopper *Sphearnium purpurascens* (Pyrgomorphidae) are able to perform mate guarding longer than smaller males (del Castillo 2003). However intrasexual combat could not explain an advantage of small males (as long as protandry is not regarded as a kind of intrasexual sexual selection). Intrasexual combat is rarely discussed for females, but in some cases courtship role reversal seems to occur in Orthoptera and females fight for access to mates (Gwynne 1984, Simmons & Bailey 1990). Another possible mechanism of intrasexual selection in females is a competitive advantage during habitat choice (*e.g.*, for oviposition sites).

The third aspect of the differential equilibrium hypothesis is sexual conflict, which arises due to sex-specific fitness optima. Female fitness is determined by their lifetime capacity of egg production, which is influenced by the trade-off between body size and longevity (Blanckenhorn 2005). In males, fitness mainly results from their chance to fertilize as many eggs as possible, which might be realized only during the short time of females' maximum receptivity. Hence, females will be affected by male harassment and a large body size might increase their ability to reject male mating attempts. On the other hand, this argument could also be reversed: mating attempts of larger males might be more successful due to their better ability to resist female defense.

Studies supporting the intersexual competition hypothesis

The intersexual competition hypothesis predicts that competition between males and females leads to intersexual character displacement (Selander 1966, Slatkin 1984, Hedrick & Temeles 1989, Fairbairn 1997). Indeed, intersexual food partitioning has been found to be related to SSD in some taxa (Carothers 1984, Shine 1991, Temeles *et al.* 2000), including Orthoptera (Hochkirch *et al.* 2000, Vincent 2006). However early on, Selander (1966) realized the problem of disentangling cause and consequences.

SSD might be a means to reduce competition, but reduced competition might also be a simple byproduct of SSD. Moreover, competition might have acted in the past and might, therefore, be difficult to prove at present ("ghost of competition past", Connell 1980).

Due to the extensive evidence for the differential equilibrium hypothesis, Fairbairn (1997) proposed that intersexual competition may, at most, play a subsidiary role in the evolution of SSD. Other authors argue that intersexual competition for food is unlikely in small herbivorous organisms (Merilaita & Jormalainen 1997). Although Nosil (2002) found that larger individuals of *Acheta domesticus* are stronger competitors for food, it has to be kept in mind that most Orthoptera species are food generalists (Chapman 1990) and food is rarely limited for these insects (Reinhardt *et al.* 2005, Hochkirch *et al.* 2007). Another argument against intersexual character displacement is that both sexes should be equally likely to become the larger sex if competition was the cause, but female-biased SSD predominates in Orthoptera.

The intersexual competition hypothesis is difficult to test experimentally. The best method would probably be to breed Orthoptera over some generations with different degrees of food limitation of two discrete (differently sized) food items, and measure whether changes in SSD occur in the expected direction. An observational approach could be to measure SSD in different populations of one species, which occur in different species assemblages. Under these circumstances, one would expect that SSD increases if interspecific competition decreases. However, different populations might also be subject to different microclimatic conditions — a factor which could be better controlled under experimental conditions. Butler *et al.* (2007) proposed that the degree of SSD should be negatively related to the extent of adaptive radiation, as both might be alternative means of ecological diversification. However, our data do not support this hypothesis, as the most species-rich grasshopper genera do not exhibit significantly lower degrees of SSD than their relatives (*Chorthippus*: 1.32, *Conophyma*: 1.28, *Sphingonotus*: 1.39).

Future research directions

Although the ultimate causes for SSD have been discussed since Darwin (1871), the prevailing hypotheses have rarely been tested explicitly in Orthoptera. Our results show that these insects are particularly suitable for studies on SSD, as they exhibit a strong degree of intra- and interspecific variation. The major differences between Caelifera and Ensifera suggest that SSD is strongly related to differences in life-history strategies, which could be easily tested. A comparison of different species with different life histories would be one interesting approach and seems to be feasible, as even within single genera the variability of SSD seems to be high. Moreover, a microevolutionary approach is useful to test the above named hypotheses.

Such studies might include a comparison of different populations of one species, or of individuals within one population. In

any case, it would be advantageous to conduct comprehensive studies, including the complete sex-specific fitness costs and benefits of body size (Blanckenhorn 2005), such as mortality (also predation and parasites) and reproductive success. Although there is not much evidence for the intersexual competition hypothesis (Fairbairn 1997), this hypothesis should also be tested thoroughly (as outlined above).

Another reason for the high suitability of Orthoptera for studies on SSD is the existence of extreme cases within this group. In the Canarian endemic genus *Purpuraria* (Pamphagidae), two sister species exist in similar habitat types, one with a miniature male and one with a larger male (López *et al.* 2007). These species are closely related sister species and ideal study objects for future research on SSD. The weta *Hemideina crassidens* is another very interesting research object, as it represents one of only a few animal species, which exhibit trimorphism with large territorial males and small males, which seem to follow a sneak strategy (Kelly 2005). Taxa, in which the variability of female size is exceptionally high (*e.g.*, the genera *Calliptamus* or *Acrida*) might also represent useful study objects. The questions to be answered do not only involve the ultimate or proximate causes for SSD, but also the reasons for the general difference between the two Orthopteran suborders. Why do Ensifera have such a low degree of SSD and why are they so constant in this regard? And why do Caelifera have such a strong degree of SSD and why are they so variable?

Acknowledgments

We are grateful to the Division of Ecology at the University of Osnabrück for providing research facilities and financial support. K. Witzemberger gave valuable comments on a previous version of the manuscript.

References

- Adis J., Junk W.J. 2003. Feeding impact and bionomics of the grasshopper *Cornops aquaticum* on the water hyacinth *Eichhornia crassipes* in Central Amazonian floodplains. *Studies on Neotropical Fauna and Environment* 38: 245-249.
- Adis J., Lhano M., Hill M., Junk W.J., Marques M.I., Oberholzer H. 2004. What determines the number of juvenile instars in the tropical grasshopper *Cornops aquaticum* (Leptysminae: Acrididae: Orthoptera)? *Studies on Neotropical Fauna and Environment* 39: 127-132.
- Ahnesjö J., Forsman A. 2003. Correlated evolution of colour pattern and body size in polymorphic pygmy grasshoppers, *Tetrix undulata*. *Journal of Evolutionary Biology* 16: 1308-1318.
- Andersson M. 1994. *Sexual Selection*. University Press, Princeton.
- Bailey W.J. 1998. Do large bushcrickets have more sensitive ears? Natural variation in hearing thresholds within populations of the bushcricket *Requena verticalis* (Listroselidinae: Tettigoniidae). *Physiological Entomology* 23: 105-112.
- Bailey W.J., Kamien D. 2001. Hearing dimorphism, trait variation and conflicts over space in the thorax of the bushcricket *Requena verticalis* (Listroselidinae: Tettigoniidae: Orthoptera). *Journal of Comparative Physiology A* 187: 647-652.
- Bei-Bienko G.Y., Mishchenko L.L. 1963. *Locusts and grasshoppers of the U.S.S.R. and adjacent countries. Part I & II*. Israel Program for Scientific Translations, Jerusalem.
- Berner D., Blanckenhorn W.U. 2006. Grasshopper ontogeny in relation to time constraints: adaptive divergence and stasis. *Journal of Animal Ecology* 75: 130-139.
- Blanckenhorn W.U. 2000. The evolution of body size: what keeps organisms small? *Quarterly Review of Biology* 75: 385-407.
- Blanckenhorn W.U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology* 111: 977-1016.
- Blanckenhorn W.U., Dixon A.F.G., Fairbairn D.J., Foellmer M.W., Gibert P., van der Linde K., Meier R., Nylin S., Pitnick S., Schoff C., Signorelli M., Teder T., Wiklund C. 2007. Proximate causes of Rensch's rule: does sexual size dimorphism in arthropods result from sex differences in development time? *American Naturalist* 169: 245-257.
- Bonduriansky R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biological Reviews* 76: 305-339.
- Butler M.A., Sawyer S.A., Losos J.B. 2007. Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature* 447: 202-205.
- Carothers J.H. 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. *American Naturalist* 124: 244-254.
- Chapman R.F. 1990. Food selection, pp. 39-72. In: Chapman R.F., Joern A. (Eds) *Biology of Grasshoppers*. John Wiley and Sons, New York.
- Connell J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35: 131-138.
- Cox R.M., Skelly S.L., John-Adler H.B. 2005. Testosterone inhibits growth in juvenile male eastern fence lizards (*Sceloporus undulatus*): implications for energy allocation and sexual size dimorphism. *Physiological and Biochemical Zoology* 78: 531-545.
- Darwin C. 1871. *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.
- De Luca P.A., Morris G.K. 1998. Courtship communication in meadow katydids: female preference for large male vibrations. *Behaviour* 135: 777-794.
- Dearn J.M. 1990. Color pattern polymorphism, pp. 517-549. In: Chapman R.F., Joern A. (Eds) *Biology of Grasshoppers*. John Wiley & Sons, New York.
- del Castillo R.C. 2003. Body size and multiple copulations in a neotropical grasshopper with an extraordinary mate-guarding duration. *Journal of Insect Behavior* 16: 503-522.
- del Castillo R.C., Nunez-Farfan J., Cano-Santana Z. 1999. The role of body size in mating success of *Sphenarium purpurascens* in Central Mexico. *Ecological Entomology* 24: 146-155.
- Dirsh V.M. 1970. Acridoidea of the Congo. *Annales Musée Royal de l'Afrique Centrale*; ser. 8° 182: 1-605.
- Eades D.C., Otte D., Naskrecki P. 2007. Orthoptera Species File Online. <http://osf2x.orthoptera.org/HomePage.aspx>
- Esperk T., Tammaru T., Nylin S., Teder T. 2007. Achieving high sexual size dimorphism in insects: females add instars. *Ecological Entomology* 32: 243-256.
- Fagerström T., Wiklund C. 1982. Why do males emerge before females - protandry as a mating strategy in male and female butterflies. *Oecologia* 52: 164-166.
- Fairbairn D.J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* 28: 659-687.
- Fedorka K.M., Mousseau T.A. 2002. Tibial spur feeding in ground crickets: larger males contribute larger gifts (Orthoptera: Gryllidae). *Florida Entomologist* 85: 317-323.
- Fernández-Montraveta C., Moya-Laraño J. 2007. Sex-specific plasticity of growth and maturation size in a spider: implications for sexual size dimorphism. *Journal of Evolutionary Biology* 20: 1689-1699.
- Gotthard K., Berger D., Walters R. 2007. What keeps insects small? Time limitation during oviposition reduces the fecundity benefit of female size in a butterfly. *American Naturalist* 169: 768-779.
- Gwynne D.T. 1982. Mate selection by female katydids (Orthoptera, Tettigoniidae, *Conocephalus nigropleurum*). *Animal Behaviour* 30: 734-738.
- Gwynne D.T. 1984. Sexual selection and sexual differences in mormon crickets (Orthoptera, Tettigoniidae, *Anabrus simplex*). *Evolution* 38: 1011-1022.
- Gwynne D.T. 2004. Sexual differences in response to larval food stress in two nuptial feeding orthopterans — implications for sexual selection. *Oikos* 105: 619-625.
- Gwynne D.T., Bailey W.J. 1999. Female-female competition in katydids: sexual selection for increased sensitivity to a male signal? *Evolution* 53: 546-551.
- Harz K. 1969. *Die Heuschrecken Europas, Volume I*. Dr. W. Junk N. V., The Hague.

- Harz K. 1975. Die Heuschrecken Europas, Volume II. Dr. W. Junk N. V., The Hague.
- Hassall M., Grayson F.W.L. 1987. The occurrence of an additional instar in the development of *Chorthippus brunneus* (Orthoptera, Gomphocerinae). *Journal of Natural History* 21: 329-337.
- Hedrick A.V., Temeles E.J. 1989. The evolution of sexual dimorphism in animals - hypotheses and tests. *Trends in Ecology & Evolution* 4: 136-138.
- Hockkirch A. 1998. A comparison of the grasshopper fauna (Orthoptera: Acridoidea & Eumastacoidea) of the Uluguru Mountains and the East Usambara Mountains, Tanzania. *Journal of East African Natural History* 87: 221-232.
- Hockkirch A. 2005. Morphometric differentiation in the East African grasshopper genus *Afrophlaeoba* Jago, 1983 (Orthoptera: Acrididae), pp. 109-118. In: Huber B.A., Sinclair B.J., Lampe K.-H. (Eds) *African Biodiversity: Molecules, Organisms, Ecosystems*: Springer Verlag, Berlin.
- Hockkirch A., Deppermann J., Gröning J. 2008. Phenotypic plasticity in insects: the effects of substrate colour on the coloration of two ground-hopper species. *Evolution and Development* 10: 350-359.
- Hockkirch A., Gröning J., Krause S. 2007. Intersexual niche segregation in Cepero's Ground-hopper, *Tetrix ceperoi*. *Evolutionary Ecology* 21: 727-738.
- Hockkirch A., Gröning J., Loos T., Metzger C., Reichelt M. 2000. Specialized diet and feeding habits as key factors for the habitat requirements of the grasshopper species *Tetrix subulata* (Orthoptera: Tettigidae). *Entomologia Generalis* 25: 39-51.
- Honek A. 1993. Intraspecific variation in body size and fecundity in insects — a general relationship. *Oikos* 66: 483-492.
- Ingrisch S., Köhler G. 1998. Die Heuschrecken Mitteleuropas. Westarp Wissenschaften, Magdeburg.
- Ismail S., Fuzeau-Braesch S. 1972. Action du photopériodisme sur le nombre des stades larvaire, la diapause et la morphogèse chez *Gryllus campstris* (Orthoptère). *Comptes Rendus de l'Académie des Sciences Paris Series D* 275: 2535-2538.
- Jago N.D. 1981. A revision of the genus *Usambilla* Sjöstedt (Orthoptera: Acridoidea) and its allies. *Bulletin British Museum of Natural History (Entomology)* 43: 1-38.
- Kelly C.D. 2005. Allometry and sexual selection of male weaponry in Wellington tree weta, *Hemideina crassidens*. *Behavioral Ecology* 16: 145-152.
- Koning J.W., Jamieson I.G. 2001. Variation in size of male weaponry in a harem-defence polygynous insect, the mountain stone weta *Hemideina maori* (Orthoptera: Anostomatidae). *New Zealand Journal of Zoology* 28: 109-117.
- Kriegbaum H. 1988. Untersuchungen zur „Lebensgeschichte“ von Feldheuschrecken (Acrididae, Gomphocerinae): Fortpflanzungsstrategie und akustisches Verhalten im natürlichen Habitat. PhD Thesis, University of Erlangen.
- Lande R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34: 292-305.
- Leisnham P.T., Jamieson I.G. 2004. Relationship between male head size and mating opportunity in the harem-defence, polygynous tree weta *Hemideina maori* (Orthoptera: Anostomatidae). *New Zealand Journal of Ecology* 28: 49-54.
- Lewis A.C. 1984. Plant quality and grasshopper feeding — effects of sunflower condition on preference and performance in *Melanoplus differentialis*. *Ecology* 65: 836-843.
- López H., Contreras-Díaz H.G., Oromí P., Juan C. 2007. Delimiting species boundaries for endangered Canary Island grasshoppers based on DNA sequence data. *Conservation Genetics* 8: 587-598.
- Merilaita S., Jormalainen V. 1997. Evolution of sex differences in microhabitat choice and colour polymorphism in *Idotea baltica*. *Animal Behaviour* 54: 769-778.
- Morbey Y.E., Ydenberg R.C. 2001. Protandrous arrival timing to breeding areas: a review. *Ecology Letters* 4: 663-673.
- Neems R.M., McLachlan A.J., Chambers R. 1990. Body size and lifetime mating success of male midges (Diptera, Chironomidae). *Animal Behaviour* 40: 648-652.
- Nosil P. 2002. Food fights in house crickets, *Acheta domesticus*, and the effects of body size and hunger level. *Canadian Journal of Zoology* 80: 409-417.
- Owens I.P.F., Hartley I.R. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proceedings Royal Society of London, Series B* 265: 397-407.
- RDevelopment Core Team. 2007. R: a language and environment for statistical computing. <http://www.R-project.org>
- Reeve J.P., Fairbairn D.J. 1999. Change in sexual size dimorphism as a correlated response to selection on fecundity. *Heredity* 83: 697-706.
- Reinhardt K., Köhler G., Maas S., Detzel P. 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. *Ecography* 28: 593-602.
- Roff D. 1980. Optimizing development time in a seasonal environment - the ups and downs of clinal variation. *Oecologia* 45: 202-208.
- Rowe L. 1994. The costs of mating and mate choice in water striders. *Animal Behaviour* 48: 1049-1056.
- Selander R.K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68: 113-151.
- Shine R. 1989. Ecological causes for the evolution of sexual dimorphism — a review of the evidence. *Quarterly Review of Biology* 64: 419-461.
- Shine R. 1991. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* 138: 103-122.
- Simmons L.W. 1988. Male size, mating potential and lifetime reproductive success in the field cricket, *Gryllus bimaculatus* (De Geer). *Animal Behaviour* 36: 372-379.
- Simmons L.W., Bailey W.J. 1990. Resource influenced sex roles of Zaprochiline tettigoniids (Orthoptera, Tettigoniidae). *Evolution* 44: 1853-1868.
- Slatkin M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38: 622-630.
- Stillwell R.C., Fox C.W. 2007. Environmental effects on sexual size dimorphism of a seed-feeding beetle. *Oecologia* 153: 273-280.
- Teder T., Tammaru T. 2005. Sexual size dimorphism within species increases with body size in insects. *Oikos* 108: 321-334.
- Telenga N.A. 1930. Biological observations on *Schistocerca gregaria* Forsk. In Khoresm in 1929 [in Russian]. *Izvestiya Khorezmskoï Selskokhozyaistvennoï Opytnoi Stantsyi* 6: 1-27.
- Temeles E.J., Pan I.L., Brennan J.L., Horwitt J.N. 2000. Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science* 289: 441-443.
- Thiele D., Bailey W.J. 1980. The function of sound in male spacing behaviour in bush-cricket (Tettigoniidae, Orthoptera). *Australian Journal of Ecology* 5: 275-286.
- Thornhill R., Alcock J. 1983. *The Evolution of Insect Mating Systems*. Harvard Univ. Press, Cambridge.
- Uvarov B.P. 1966. Grasshoppers and Locusts: a Handbook of General Acridology. Vol. 1. Cambridge University Press, Cambridge.
- Vincent S.E. 2006. Sex-based divergence in head shape and diet in the Eastern lubber grasshopper (*Romalea microptera*). *Zoology* 109: 331-338.
- Wang G.Y., Greenfield M.D., Shelly T.E. 1990. Intermale competition for high-quality host-plants — the evolution of protandry in a territorial grasshopper. *Behavioral Ecology and Sociobiology* 27: 191-198.
- Wedell N. 1997. Ejaculate size in bushcrickets: the importance of being large. *Journal of Evolutionary Biology* 10: 315-325.
- Willott S.J., Hassall M. 1998. Life-history responses of British grasshoppers (Orthoptera: Acrididae) to temperature change. *Functional Ecology* 12: 232-241.
- Zonneveld C. 1996. Being big or emerging early? Polyandry and the trade-off between size and emergence in male butterflies. *American Naturalist* 147: 946-965.