

REVIEW ARTICLE

Achieving high sexual size dimorphism in insects: females add instars

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Abstract. 1. In arthropods, the evolution of sexual size dimorphism (SSD) may be constrained by a physiological limit on growth within each particular larval instar. A high SSD could, however, be attained if the larvae of the larger sex pass through a higher number of larval instars.

2. Based on a survey of published case studies, the present review shows that sex-related difference in the number of instars is a widespread phenomenon among insects. In the great majority of species with a sexually dimorphic instar number, females develop through a higher number of instars than males.

3. Female-biased sexual dimorphism in final sizes in species with sexually dimorphic instar number was found to considerably exceed a previously estimated median value of SSD for insects in general. This suggests a causal connection between high female-biased SSD, and additional instars in females. Adding an extra instar to larval development allows an insect to increase its adult size at the expense of prolonged larval development.

4. As in the case of additional instars, SSD is fully formed late in ontogeny, larval growth schedules and imaginal sizes can be optimised independently. No conflict between selective pressures operating in juvenile and adult stages is therefore expected.

5. In most species considered, the number of instars also varied within the sexes. Phenotypic plasticity in instar number may thus be a precondition for a sexual difference in instar number to evolve.

Key words. Body size, evolution, instar, life history, plasticity, sex, sexual size dimorphism.

Introduction

Sexual size dimorphism (SSD), defined as the inequality of body sizes of the two sexes, is a widespread phenomenon among different groups of animals (Shine, 1989; Fairbairn, 1997; Badyaev, 2002; Blanckenhorn, 2005). Females are the larger sex in most invertebrates and poikilothermic vertebrates (e.g. Shine, 1979, 1994; Head, 1995; Teder & Tammaru, 2005) whereas male-biased SSD predominates in birds and mammals (e.g. Cabana *et al.*, 1982; Weatherhead & Teather, 1994; Isaac, 2005). SSD has typically been viewed as resulting from sexual differ-

ences in selective pressures on adult body size. Traditionally, fecundity selection (a positive correlation between female size and fecundity) has been proposed to be the major force leading to female-biased SSD, whereas sexual selection (e.g. male–male competition) has often been invoked in cases of male-biased size dimorphism (Darwin, 1871; Trivers, 1972).

While the ultimate causes of SSD have been extensively studied (reviewed, e.g. by Shine, 1989; Dunn *et al.*, 2001; Karubian & Swaddle, 2001; Blanckenhorn, 2005), proximate mechanisms leading to SSD have received considerably less attention. Moreover, most studies focus on sexual size differences in adult stage whereas aspects of juvenile development are often ignored (Badyaev *et al.*, 2001; Badyaev, 2002). However, without knowing the details of juvenile growth schedules, it may not be possible to fully understand the mechanisms underlying the evolution of SSD. This is because the different growth strategies

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leading to sexual differences in body size, rather than adult body sizes may constitute the subjects of selection (Arak, 1988; Crowley, 2000; Badyaev *et al.*, 2001; Badyaev, 2002). In particular, it is often the case that size optima do not differ between the sexes during juvenile development, even in species in which selection favours high levels of SSD among reproducing individuals (Shine, 1994; Teather & Weatherhead, 1994; Stamps & Krishnan, 1997). The combination of similar sizes early in the life, and different ones later on, may be a difficult task for natural selection to achieve. Developmental constraints may therefore play an important role in forming the patterns of SSD (Maynard Smith *et al.*, 1985; Schluter *et al.*, 1991; Badyaev, 2002).

There are three basic mechanisms that may lead to size differences between the sexes: the individuals of the ultimately larger sex could either (1) be larger already at hatching/birth, (2) grow faster (having higher instantaneous growth rates), or (3) grow for a longer time (sexual bimaturation). In the case of insects, the few studies that have focused on the role of the egg/hatching size have not revealed any difference (Mackey, 1978; Ernsting & Isaaks, 2002; Yasuda & Dixon, 2002). In contrast, both sex-specific growth rates and sex-related differences in development time have been reported repeatedly in insects. In various insect species with female-biased SSD, the larval period is longer in females with no sex-related differences in growth rates (Mackey, 1978; Lederhouse *et al.*, 1982; Nylín *et al.*, 1993; Brakefield & Mazzotta, 1995; De Block & Stoks, 2003; Mikolajewski *et al.*, 2005). In some other sexually dimorphic insects, growth rates, but not larval periods, differ between the sexes (Telang *et al.*, 2001; Yasuda & Dixon, 2002; Blanckenhorn, 2005) whereas sometimes both options are used simultaneously (Bradshaw & Holzapfel, 1996; Ernsting & Isaaks, 2002). It should then be concluded that prolonged larval period and higher growth rates of the eventually larger sex (typically females) are both available, although not universally used, options for formation of SSD among insects.

Growth curves of arthropods are discontinuous, being divided into discrete growth periods (instars) by moults. Growth slows down remarkably with moult approaching and ceases completely during the process (e.g. Sehnal, 1985; Ayres & MacLean, 1987; Esperk & Tammaru, 2004). As the maximal relative increment per instar is likely to be limited for physiological reasons (Dyar, 1890; Sehnal, 1985; Hutchinson *et al.*, 1997), evolutionary fixation of the instar number at the species level may form a severe constraint on achieving larger final sizes (Tammaru, 1998). It is therefore reasonable to assume that the option of prolonging growth periods within particular instars does not provide a sufficient basis for a response to selection favouring larger adult sizes. In contrast, going through some 'additional' instars may constitute a way enabling arthropods to continue growing, prolong the larval period and achieve a considerably larger final size.

There are various species, representing several arthropod classes, in which females are known to develop through a higher number of larval instars than males (e.g. Vollrath, 1998). One of the best known examples is provided by the spiders from the genus *Nephila*, the golden orb weavers, in which females have two to six additional larval instars as compared with males

(Vollrath & Parker, 1997), although just one extra instar seems to be a more typical option for other arthropods. It is frequently assumed that in insects and spiders, the additional instars in females serve the purpose of attaining larger female size, and thereby lead to the female-biased SSD (e.g. Benson, 1950; Sephton & Hynes, 1982; Head, 1995). Surprisingly, however, empirical support for this notion is largely indirect and scattered. Moreover, the authors of the present study are not aware of any attempts to synthesise case studies in order to systematically explore the role of additional instars of female arthropods in determination of SSD.

The present review gives an overview of published case studies reporting sexual differences in instar number, in order to explore the distribution of this phenomenon among insect taxa. Synthesising the data available, the role of additional instars in the determination of SSD is then investigated. For insect species in which females have additional instars compared with males, final sizes, sizes earlier in larval life, and development times of the two sexes are compared. If the additional instars of females primarily serve the purpose of attaining large female size, one would expect sexual difference in instar number to be associated with particularly high values of SSD at the level of interspecific comparisons. Further, if the additional instar is to be the primary determinant of sexual size differences, body sizes earlier in life are not expected to differ notably between sexes. In contrast, if the additional instars are not causally related to the formation of SSD, SSD in the final size should not differ considerably between insect species in which females have additional instars, and species with no sex-related differences in instar number. Moreover, in such a case, size differences between the sexes should accumulate gradually and are thus expected to be present already earlier in the larval life. These aspects have a direct relevance for understanding adaptive evolution of SSD: the earlier the size difference between the sexes is expressed, the more weight is given to selective forces operating during the juvenile development.

In a more general context, there is certainly a need to more thoroughly consider larval instars in optimality-based insect life-history models. Giving the attention that it deserves to this key feature of insect development may lead to substantial new insights (e.g. Hutchinson *et al.*, 1997; Klingenberg & Spence, 1997), and may thereby help to distinguish between constraints and adaptations in life-history evolution.

Materials and methods

Literature used

Major ecological and entomological journals were surveyed systematically to find case studies reporting sexual differences in the number of larval instars in insects. An emphasis was given to issues from the last three decades, but a number of older works were also included. The present review was restricted to winged insects (Pterygota), which do not moult as adults. Only studies in which instar number had been determined directly by regular observations on individual larvae (e.g. based on shed cuticles) were considered. This restriction was applied because

various indirect methods of determining number of larval instars (e.g. according to distribution peaks of head capsule widths) have been shown to be unreliable in insects with intraspecific variation in instar number (Schmidt *et al.*, 1977; Fink, 1984; Daly, 1985).

In most cases in which one sex tended to go through additional instar(s) compared to the other, instar number varied also within sexes and sex-specific ranges of instar numbers often overlapped (see below, for more details). Therefore, some criteria related to the magnitude of intersexual difference in instar number, and sample sizes, had to be applied when deciding if a particular case 'qualifies' as evidence of sexual difference in instar number. Unfortunately, in most cases the original data were presented in a way that did not allow performing of proper statistical tests to confirm the difference between the sexes. As a substitute, the following set of rules was applied. First, instar number was considered to be sexually dimorphic when the difference between the sexes in the average number of instars in the sample was at least 0.2 instars. For example, females were considered to have a higher number of instars in the case when males had an invariable number of instars and at least 20% of females had one additional instar compared to males. Second, only studies based on sample sizes of at least 20 individuals were considered; in addition, at least five individuals from one sex should have passed through a different number of instars than their conspecifics from the opposite sex.

Data analysis

In the large majority of insect species with sexual difference in instar number, females had higher instar number and also achieved larger final body size compared with males (see below). To reveal the role of the additional instars of females in the formation of SSD, sizes and development times of males and females were compared in species in which females went through a higher number of larval instars than males. From the point when the sexual difference in instar number was decided to occur (see above), sex-specific means of these variables were used in further comparisons. The results of only one study were used for each species. For some species, however, several datasets were available. In these cases, the data set in which the difference in instar number between the sexes was the highest was chosen.

Data permitting, SSD was expressed as the ratio of female size over male size if females were the larger sex. However, when males were the larger sex, the index of SSD was calculated using the following equation: $2 - (\text{male size}/\text{female size})$. This method, proposed by Smith (1999), results in a continuous symmetrical SSD function, which is a desirable feature for statistical analyses. Accordingly, SSD values higher than 1 represent cases where females are larger whereas those below unity indicate that males are the larger sex. Body mass was preferred as a size measure; however the ratio of the third power of body length, or head capsule width was used in the cases when masses had not been reported (Table 2). Final sizes of the two sexes were compared, and the size difference between the sexes ear-

lier in life was estimated. Pupal size was preferred as the measure of final size in holometabolous insects while adult size was used as final size in hemimetabolous insects. However, size of the final larval instar was accepted as the measure of final size in cases when pupal and/or adult size was not reported (Table 2). Initial size of the larval instar that was last for the individuals (males) with the lowest number of instars in a particular sample was preferred as the measure of size 'earlier in life'. For example, if females developed through six instars while males had five instars, the size 'earlier in life' was that at the beginning of fifth instar. In the few cases when size at this stage was not presented, size in some earlier larval instar was considered instead (Table 2). Species-specific sexual difference in duration of larval period, referred to in the text as sexual bimaturism or SBM (Blanckenhorn *et al.*, 2007), was expressed as the ratio of the duration of female larval period to duration of male larval period.

Because of the limited amount of information on insect phylogenies available, and the unsystematic circumstantial nature of the data retrieved, comparative methods based on explicit phylogenies could not be applied. Moreover, pairwise comparative methods, proposed for the cases of poorly known phylogenies (e.g. Møller & Birkhead, 1992), could not be used for comparing species that have a sexually dimorphic instar number with their sister groups lacking such a sexual difference. This is because studies that explicitly report lack of sexual difference in instar number are notably scarce. However, as in most insect species male and female larvae are likely to develop through an equal number of instars, the following method in comparing SSD in final size could be applied. Species with a known sexual difference in instar number (Table 1) were excluded from a data set containing SSD values for a high number of insect species (used in Teder & Tammaru, 2005). Then, based on the subsample remaining, i.e. including species for which the instar number was not known to vary, medians of final SSD were calculated separately for families (if data for at least three species were available for a family), and for the orders (excluding species already represented in family-wise analyses). The medians of the families and orders were then compared with respective values for the species with a proven sexual difference in instar number, using paired *t*-test (Table 3).

As there were not enough comparable data available for the SSD in earlier larval life, and for durations of larval periods of male and female larvae, the method described could not be used for these variables. However, as the primary goal of this study was to detect general qualitative patterns that are invariable across insect taxa, the possible bias resulting from disregarding phylogenetical relationships is not expected to be critical. Moreover, the results are based on a number of species, widely distributed over the major insect orders. Due to high variation in compared life-history parameters within the major taxa, as compared with the variation between the taxa, possible pitfalls resulting from ignoring phylogenetic relationships should have been further reduced (Björklund, 1997). Nevertheless, to evaluate the potential bias resulting from ignoring phylogenetic aspects, all analyses were alternatively performed using both species- and family-specific means as individual data points.

Table 1. The insect species in which females are known to develop through a higher number of larval instars than males. The number of instars is presented as a total range, as well as the range of the mean values across treatments/case studies. The classification is based on the Tree of Life Web Project (<http://tolweb.org>).

Taxa	Range of the number of larval instars				References
	Males		Females		
	Total	Treatments	Total	Treatments	
O. Diptera					
F. Blaberidae					
<i>Diploptera punctata</i>	3–5	3.1–3.8	3–5	3.9–4.2	Willis <i>et al.</i> (1958), Woodhead & Paulson (1983), Holbrook & Schal (1998)
<i>Leucophaea maderae</i>	7–8	7.0–7.4	7–8	7.8–8.0	Willis <i>et al.</i> (1958)
<i>Nauphoeta cinerea</i>	7–8	7.6	7–8	7.8	Willis <i>et al.</i> (1958)
<i>Opisthoptalia orientalis</i>	5–6	5.7–6.0	6–7	6.2–7.0	Zhu & Tanaka (2004)
F. Blattellidae					
<i>Blattella germanica</i>	5–8	5.0–7.1	5–9	5.5–7.5	Willis <i>et al.</i> (1958), Tanaka & Hasegawa (1979), Tanaka (1981, 1982), Tanaka <i>et al.</i> (1987)
<i>B. vaga</i>	5–7	6.0	5–7	6.3	Willis <i>et al.</i> (1958)
F. Blattidae					
<i>Blatta orientalis</i>	7–8	7.8	9–10	9.3	Willis <i>et al.</i> (1958)
O. Orthoptera					
F. Acrididae					
<i>Bryophlyma debilis</i>	5	5.0	6	6.0	Luong-Skovmand & Balanço (1999), Luong-Skovmand (2001)
<i>Chorthippus brumeus</i> ^{abc}	4	4.0	4–5	4.0–5.0	Hassall & Grayson (1987), Willott & Hassall (1998)
<i>Locusta migratoria</i> ^c	5	5.0	5–6	5.0–6.0	Key (1936)
<i>Melanoplus differentialis</i> ^d	6–7	6.0–6.1	6–7	6.0–6.6	Dingle & Haskell (1967)
<i>M. femurrubrum</i>	6–8	6.0–6.8	6–8	6.2–7.1	Bellinger & Pienkowski (1987, 1989)
<i>Omocestus viridulus</i> ^c	4	4.0	4–5	4.0–4.3	Berner & Blanckenhorn (2006)
<i>Ornithacris turbida</i>	6–7	6.1–6.4	6–7	6.7–7.0	Antoniu (1973)
<i>Schistocerca gregaria</i> ^d	5–6	5.0–5.8	5–6	5.0–6.0	Injayan & Tobe (1981)
F. Pyrgomorphidae					
<i>Zonocerus variegatus</i>	5–6	5.7	5–6	5.9	Iheagwam (1981)
O. Phasmida					
F. Heteronemiidae					
<i>Diapheromera femorata</i>	4–5	4.7	4–6	4.9	Severin & Severin (1911)
F. Phyllidae					
<i>Necroscia sparaxes</i>	5	5.0	6	6.0	Gangrade (1963)
O. Plecoptera					
F. Nemouridae					
<i>Nemurella pictetii</i>	15	15.0	17	17.0	Elliott (1984)
O. Coleoptera					
F. Dermestidae					
<i>Anthrenus sarnicus</i>	5–?	5.6–12.1	5–?	5.9–13.1	Armes (1990)
<i>Trogoderma glabrum</i>	5–8	5.0–6.7	6–9	6.1–7.3	Beck (1971), Archer & Strong (1975)
<i>T. inclusum</i>	4–7	5.2–5.3	5–9	5.8–6.5	Strong (1975)
<i>T. simplex</i>	6–9	6.2–7.0	6–10	7.2–7.8	Strong & Mead (1975)
<i>T. variabile</i>	5–9	5.8–7.2	5–10	6.4–8.2	Partida & Strong (1975)

Table 1. Continued.

Taxa	Range of the number of larval instars				References
	Males		Females		
	Total	Treatments	Total	Treatments	
O. Diptera					
F. Tabanidae					
<i>Tabanus lineola</i>	8–10	8.7	8–10	9.2	Orminati & Hansens (1974)
O. Hymenoptera^e					
F. Argidae					
<i>Arge nigrimodosa</i>	5–6	5.3–6.0	6–7	6.5–7.0	Adachi (1981)
<i>A. nipponensis</i>	5–7	5.2–5.8	6–7	6.2–6.8	Adachi (1981)
F. Diprionidae					
<i>Neodiprion gillettei</i>	4	4.0	5	5.0	Dunbar & Wagner (1992)
<i>N. sertifer</i>	4	4.0	5	5.0	Larsson <i>et al.</i> (1986)
F. Pergidae					
<i>Phylacteophaga froggatti</i>	4	4.0	5	5.0	Farrell & New (1980)
F. Tenthredinidae					
<i>Athalia rosae</i>	4	4.0	5	5.0	Sawa <i>et al.</i> (1989)
<i>Caliroa quercuscoccineae</i>	5	5.0	6	6.0	Nordin & Johnson (1984)
<i>Pachymenatus cliellatus</i>	5	5.0	6	6.0	Barker & Maczka (1996)
O. Lepidoptera					
F. Arctiidae					
<i>Apantesis vittata</i> (A. radians) ^f	6–7	6.1	6–8	6.5	Bachelier & Habeck (1974)
<i>Hyphantria cunea^c</i>	6–7	6.0–6.1	6–7	6.0–6.8	Gomi <i>et al.</i> (2003)
F. Cossidae					
<i>Pritoxystus robiniae</i>	8–13 ^g	9.9 ^g	9–15 ^g	10.5 ^g	Solomon (1973)
	14–30 ^h	19.1 ^h	17–31 ^h	21.7 ^h	
F. Crambidae					
<i>Chilo partellus^b</i>	6–7	6.0–6.1	6–7	6.0–6.5	Ochieng'-Odero <i>et al.</i> (1994)
<i>Diatraea grandiosella</i>	5–6	5.1	5–6	5.7	Jacob & Chippendale (1971)
<i>D. lineolata^a</i>	5–7	5.8–6.1	5–7	6.0–6.2	Rodríguez-del-Bosque <i>et al.</i> (1989)
<i>D. saccharalis</i>	5–7	5.5	5–7	6.0	Roe <i>et al.</i> (1982)
F. Lasiocampidae					
<i>Sireblote panda</i>	?	5.9	?	6.5	Calvo & Molina (2004)
F. Lymantriidae					
<i>Dasychira horsfieldi</i>	6	6.0	7	7.0	Gupta <i>et al.</i> (1989)
<i>Lymantria dispar</i> (<i>Porthetria dispar</i>)	4–7	5.0–5.5	5–8	5.9–6.4	Leonard (1966, 1968, 1970), Nagasawa (1988), Schopf & Steinberger (1996), Esperk & Tammaru (2006)
<i>Orgyia antiqua</i>	4–6	4.4–4.8	4–7	5.2–5.6	Esperk & Tammaru (2006)
<i>O. postica</i>	4	4.0	5	5.0	Gu <i>et al.</i> (1992)
F. Noctuidae					
<i>Xestia c-nigrum</i> (<i>Amathes c-nigrum</i>)	5–7	5.8	5–7	6.0	Honěk (1979)
F. Nymphalidae					
<i>Pararge aegeria</i>	4–5	4.0–4.6	4–5	4.7–5.0	Shreeve (1986)

Table 1. Continued.

Taxa	Range of the number of larval instars				References
	Males		Females		
	Total	Treatments	Total	Treatments	
F. Pyralidae					
<i>Corcyra cephalonica</i>	6–12	6.5–10.0	7–15	7.0–11.4	Russell <i>et al.</i> (1980)
F. Tineidae					
<i>Tineola bisselliella</i>	5–10	5.9–7.7	6–16	6.3–8.0	Titschack (1926)
F. Tortricidae					
<i>Bombyx crataegidis</i> ^b	5–7	5.0–6.1	5–7	5.0–6.9	Bentancourt <i>et al.</i> (2004)
<i>Choristoneura occidentalis</i> ^b	5–8	6.1–6.4	6–7	6.3–6.5	Schmidt & Lauer (1977)
<i>C. retiniana</i> (<i>C. viridis</i>) ^f	6–8	6.5–6.8	6–8	6.7–7.0	Schmidt & Lauer (1977), Schmidt <i>et al.</i> (1977)
<i>Ctenopseustis obliquana</i>	5–6	5.5	5–6	5.9	Clare & Singh (1988)
<i>Platynota stultana</i>	5	5.0	5–6	5.2–6.0	Zenner-Polania & Helgesen (1973)

^{a–d}Instar number between sexes differ only in certain: ^arearing temperatures, ^bfood treatments, ^cgenetic lines, ^drearing densities.

^eInstar number is given without prepupal stage.

^fIf the name used in the original paper differs from the current usage, it is given in parentheses.

^gUnivoltine development.

^hSemivoltine development.

Results

Sexual differences in instar number

As a result of the literature survey, 64 case studies reporting sexual differences in the number of larval instars were found. Data were obtained for 56 insect species, representing nine orders and 26 families (Table 1). In 54 species, females developed through a higher number of instars than males. Males tended to have additional instars compared to females only in two species, *Labidura riparia* (Dermaptera, Labiduridae) and *Lycaena hippothoe* (Lepidoptera, Lycaenidae) (Shepard *et al.*, 1973; Fischer & Fiedler, 2001). Moreover, in the latter species, the average instar number in males exceeded that of females only under particular rearing conditions (Fischer & Fiedler, 2001).

In most species, instar number varied also within sexes, and typically, some overlap occurred between the sexes (Table 1). Sawflies (Hymenoptera: Argidae, Diprionidae, Pergidae, Tenthredinidae) formed an exception, as in six species out of eight the number of instars was invariable within sexes and thus no overlap in instar number existed between males and females. The same was true also for the single species representing the orders Plecoptera and Phasmida (Table 1). At least for two *Neodiprion* sawflies and the plecopteran *Nemurella pictetii*, the sample sizes of around 100 or higher allow this result to be viewed with reasonable confidence. In several species of Orthoptera and Lepidoptera, instar number differed between the sexes only in some populations and/or under particular environmental conditions (Table 1).

Sexual dimorphism in size and in development time

In the following comparisons only those species were considered in which females had additional instars compared to males (54 species). Some data necessary to calculate SSD in final sizes had been reported for 27 species, while data to estimate SSD earlier in life were available for 18 species (Table 2). Sexual dimorphism in final sizes ranged from 1.1 to 4.2 across species, with 1.97 as the among-species mean (SD = 0.73) and 1.8 as the median (Fig. 1a, Table 2). The mean value differed significantly from 1 (one-sample *t*-test: $T = 6.92$, d.f. = 26, $P < 0.0001$). These results indicate strong female-biased dimorphism in final size in general, although there was a considerable quantitative variation among species. Moreover, the phylogenetically corrected analysis showed that the medians for the order-specific and family specific final SSD were significantly higher in insects in which females had a higher instar number than males, as compared to phylogenetically related species in which such a difference was not known to occur (Table 3).

In turn, mean SSD earlier in life ranged from 0.6 to 1.2 with 0.95 (SD = 0.19) as the among-species mean and 1.0 as the median (Fig. 1b, Table 2). The among-species mean did not differ significantly from 1 ($T = 1.12$, d.f. = 17, $P = 0.28$). These results thus suggest no directional size differences between sexes among younger larvae. Corresponding means and medians were also calculated using family-specific means of SSD as individual data points. The patterns remained largely unchanged

both qualitatively and quantitatively: the median for final SSD was 1.7 (family medians differed significantly from 1; $T = 6.23$, d.f. = 14, $P < 0.0001$) and the median for SSD earlier in life was 1.0 (family medians did not differ significantly from 1; $T = 0.17$, d.f. = 11, $P = 0.87$).

Development times of both sexes had been reported for 29 species. Sexual bimaturism (SBM) ranged from 0.9 to 1.3, while in 26 species values were equal or higher than 1.1, indicating longer larval periods for females (Table 2). SBM differed significantly from 1 both in an analysis using species as data points ($T = 9.38$, d.f. = 28, $P < 0.0001$), as well as in an analysis at the level of family medians ($T = 7.58$, d.f. = 12, $P < 0.0001$). Only in one species, the roach *Blatella vaga*, males developed longer, on average, than females, despite their lower instar number (Willis *et al.*, 1958; Table 2).

Discussion

The available evidence demonstrates that a sex-related difference in the number of larval instars is not a rare phenomenon among insects. Such differences have been recorded both in hemimetabolous and holometabolous taxa, and in most of the major insect orders (Table 1). In all but two species, females were the sex with a higher number of instars. This bias towards the female sex *per se* can perhaps be interpreted as indirect evidence showing that the adaptive function of the additional instars is, indeed, the attaining of higher adult body mass. This is most likely an effect of strong positive correlation between female body mass and fecundity in insects (Honěk, 1993): higher final body mass is likely to be more important and, in fact, is often achieved by females as compared to males (e.g. Teder & Tammaru, 2005). For the sake of completeness, it has to be mentioned that in addition to the two species included in our data set, males of most scale insects (Hemiptera, Coccoidea) have typically an additional larval instar, as compared to females. However, these insects were not considered in the present study because penultimate and ultimate instar male larvae of scale insects do not feed; therefore, if one counts only active larval instars, females have one more instar than males (Miller, 1991; Gullan & Kosztarab, 1997).

The quantitative analyses of the present study further support the idea that passing through additional larval instars is a specific mechanism that has evolved to enable females to attain larger sizes, and thus also leads to sexual divergence in size as an expected by-product. In particular, almost all species in which females passed through a higher number of instars exhibited an unusually high sexual dimorphism in final size, with females being, as an among-species average, almost twice the size of the males (Fig. 1a, Table 2). Even though females are the larger sex in the majority of insects, SSD typically remains much lower, with an estimate of the mean around 1.3 and median around 1.2, calculated over a large set of species (Teder & Tammaru, 2005). Moreover, a simple phylogenetically corrected analysis revealed higher SSD values in species with females developing through a higher instar number than males as compared to their relatives (Table 3).

In contrast, earlier in life, there were no systematic size differences between the sexes (Fig. 1b, Table 2); the large differences in final sizes thus arose solely due to the extra instars. This finding further emphasises the crucial role of the additional instar of females in the determination of SSD. Moreover, the absence of SSD earlier in the immature development contrasts intriguingly with the developmental patterns in sexually dimorphic species with no sex-related difference in instar number. In the latter, SSD tends to 'accumulate' in the course of larval development: sexual differences in body size appear already in early instars, and progress with time (Lederhouse *et al.*, 1982; Tammaru, 1998; Mikolajewski *et al.*, 2005; Esperk & Tammaru, 2006). This pattern of accumulation of the difference may imply that any considerable level of SSD cannot solely arise by means of a sexually dimorphic growth schedule within *one* (e.g. last) immature instar (Esperk & Tammaru, 2006). In turn, the absence of early sexual growth divergence in the case of additional instars in females may indicate that the higher instar-specific increments in females, potentially leading to SSD, are always avoided when not 'needed'. In concert, these observations suggest that there exists a rather narrow optimum for the relative within-instar growth increment. Constraints appear to preclude insects from exceeding this value considerably, whereas minor alternations are possible but entail certain costs. The physiological basis of these costs is not known for certain, although the recently demonstrated reduction of aerobic capacity associated with the growth within an instar may provide a promising explanation (Greenlee & Harrison, 2004, 2005).

In species with a higher number of instars in females, larval period in females was also significantly longer than in males. This allows one to view the additional instars of females as a special case of attaining large size via a prolonged growing period. Female-biased sexual bimaturism has been reported for numerous insect species exhibiting female-biased SSD (e.g. Mackey, 1978; Nylin *et al.*, 1993; Mikolajewski *et al.*, 2005). However, as most of the studies do not consider the question of a possible sexual difference in instar number, a sexually dimorphic instar number may actually constitute a far more common mechanism leading to SSD in insects than previously appreciated.

Due to the unsystematic nature of the data available, and indisputable differences in popularity of different insect groups as study objects, it is not possible to reach any definitive conclusions about the possible predisposition of certain insect taxa to display a sexual difference in instar number. It may, however, still be noteworthy that this phenomenon tended to occur more frequently in some orders, as compared to others. In particular, species representing Lepidoptera and Hymenoptera were especially numerous among those with a sexual difference in instar number. These are the orders in which selection for large female size and short development time in males (protandry) frequently occurs simultaneously (Blanckenhorn *et al.*, 2007). In contrast, the orders in which protandry generally does not occur (Blanckenhorn *et al.*, 2007), were not represented (Hemiptera), or were clearly underrepresented (Diptera). These results lead to the suggestion that, beside the scenario in which females have evolved to add an instar to attain a large body size, female-biased sexual difference in instar number might, at least

Table 2. Sexual size dimorphism (SSD) and sexual bimaturism (SBM) of the insect species in which females go through more larval instars than males. SSD is expressed as 'female mass/male mass' if females were larger and as ' $2 - \text{male mass/female mass}$ ' if males were larger. Third power of linear measurements is used when masses were not reported. SBM is calculated as 'duration of larval period of females/duration of larval period of males'.

Taxa	SSD		Size measurement			SBM	References
	EL ^a	Final	EL	Final	Final		
O. Dictyoptera							
F. Blaberidae							
<i>Diploptera punctata</i>	1.1	1.5	3rd instar weight	Adult weight	1.2	Woodhead & Paulson (1983)	
<i>Leucophaea maderae</i>	– _b	–	–	–	1.2	Willis <i>et al.</i> (1958)	
<i>Nauphoeta cinerea</i>	–	–	–	–	1.2	Willis <i>et al.</i> (1958)	
<i>Opisthoplattia orientalis</i>	–	–	–	–	1.1	Zhu & Tanaka (2004)	
F. Blattellidae							
<i>Blattella germanica</i>	1.0	1.4	5th instar HCW ^c	Adult HCW	1.0	Tanaka (1982), Tanaka & Hasegawa (1979)	
<i>B. vaga</i>	–	–	–	–	0.9	Willis <i>et al.</i> (1958)	
O. Orthoptera							
F. Acrididae							
<i>Bryophyma debilis</i>	0.9	1.2	5th instar weight	Last instar weight	1.3	Luong-Skovmand & Balanca (1999), Luong-Skovmand (2001)	
<i>Chorthippus brunneus</i>	0.6	1.8	3rd instar weight	Adult weight	1.1	Hassall & Grayson (1987), Willott & Hassall (1998)	
<i>Melanoplus differentialis</i>	–	2.0	–	Adult HCW	–	Dingle & Haskell (1967)	
<i>Ornithacris turbida</i>	–	1.6	–	Adult weight	1.2	Antoniou (1973)	
O. Phasmida							
F. Heteronemidae							
<i>Diapheromera femorata</i>	–	–	–	–	1.1	Severin & Severin (1911)	
O. Plecoptera							
F. Nemouridae							
<i>Nemurella picteti</i>	–	2.2	–	Last instar body length	1.1	Elliott (1984)	
O. Coleoptera							
F. Dermestidae							
<i>Anthrenus sarinicus</i>	–	–	–	–	1.1	Armes (1990)	
<i>Trogoderma glabrum</i>	1.0	>2.0	5th instar HCW	Last instar HCW	1.1	Beck (1971)	
<i>T. inclusum</i>	–	–	–	–	1.1	Strong (1975)	
<i>T. simplex</i>	–	–	–	–	1.1	Strong & Mead (1975)	
<i>T. variabile</i>	–	–	–	–	1.1	Partida & Strong (1975)	
O. Hymenoptera							
F. Diprionidae							
<i>Neodiprion gillettei</i>	1.0	1.8	4th instar HCW	Last instar HCW	1.2	Dunbar & Wagner (1992)	
<i>N. sertifer</i>	–	2.2	–	Pupal (dry) weight	1.2	Larsson <i>et al.</i> (1986)	
F. Pergidae							
<i>Phylacteophaga froggatti</i>	1.2	1.8	4th instar HCW	Last instar HCW	–	Farrell & New (1980)	
F. Tenthredinidae							
<i>Athalia rosae</i>	–	2.4	–	Adult body length	1.2	Sawa <i>et al.</i> (1989)	
<i>Caliroa quercusoccineae</i>	0.6	1.7	5th instar HCW	HCW of prepupa	1.1	Nordin & Johnson (1984)	
<i>Pachymenatus clitellatus</i>	–	2.5	–	Adult (dry) weight	–	Barker & Maczka (1996)	

Table 2. Continued.

Taxa	SSD		Size measurement		SBM	References
	EL ^a	Final	EL	Final		
O. Lepidoptera						
F. Arctiidae						
<i>Apantesis vittata</i>	–	–	–	–	1.2	Bacheler & Habeck (1974)
<i>Hyphantria cunea</i>	–	1.5	–	Pupal weight	1.1	Gomi <i>et al.</i> (2003)
F. Cossidae						
<i>Prionoxystus robiniae</i>	1.2	–	8th instar HCW ^d 14th instar HCW ^e	–	–	Solomon (1973)
F. Crambidae						
<i>Diatraea lineolata</i>	–	–	–	–	1.0	Rodriguez-del-Bosque <i>et al.</i> (1989)
<i>D. saccharalis</i>	1.0	1.7	4th instar HCW	Pupal weight	1.1	Roe <i>et al.</i> (1982)
F. Lymantriidae						
<i>Dasychira horsfieldi</i>	–	3.4	–	Pupal length	–	Gupta <i>et al.</i> (1989)
<i>Lymantria dispar</i>	1.1	2.8	4th instar weight	Pupal weight	1.3	Esperk & Tammaru (2006)
<i>Orgyia antiqua</i>	0.8	3.2	4th instar weight	Pupal weight	1.3	Esperk & Tammaru (2006)
<i>O. postica</i>	1.1	4.2	4th instar weight	Last instar weight	1.2	Gu <i>et al.</i> (1992)
F. Nymphalidae						
<i>Pararge aegeria</i>	–	1.1	–	Pupal weight	1.2	Shreeve (1986)
F. Pyralidae						
<i>Corcyra cephalonica</i>	–	1.7	–	Adult weight	–	Russell <i>et al.</i> (1980)
F. Tineidae						
<i>Tineola biselliella</i>	<1.0	2.0	5th instar HCW	Adult weight	–	Titschack (1926)
F. Tortricidae						
<i>Bonagota cranaodes</i>	1.0	1.5	5th instar HCW	Pupal weight	1.2	Bentancourt <i>et al.</i> (2004)
<i>Choristoneura retiniana</i>	1.0	1.3	6th instar HCW	Last instar HCW	–	Schmidt <i>et al.</i> (1977)
<i>Ctenopseustis obliquana</i>	0.6	1.3	5th instar HCW	Pupal weight	1.2	Clare & Singh (1988)
<i>Platynota stultana</i>	1.0	1.4	5th instar HCW	Last instar HCW	–	Zenner-Polania & Helgesen (1973)

^aEL, earlier in larval life (i.e. typically, initial weight of the final instar for males).^bNot presented.^cHCW, head capsule width.^dUnivoltine development.^eSemivoltine development.

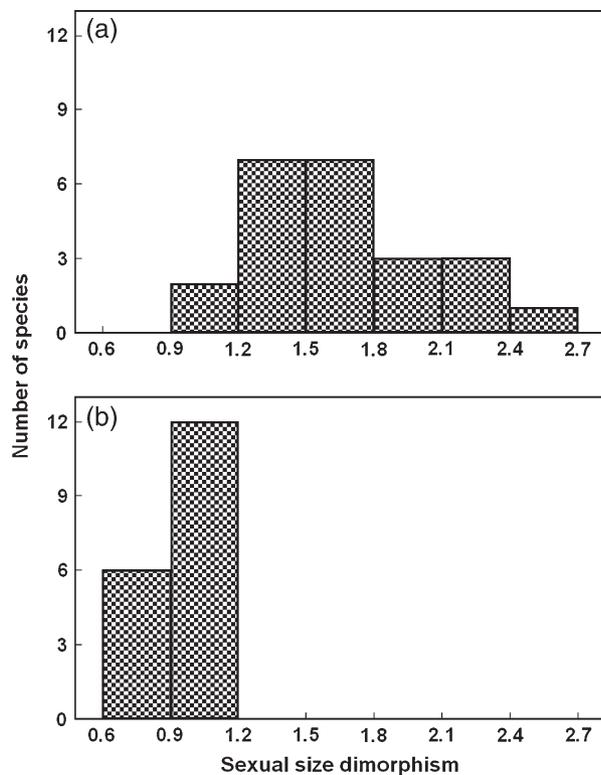


Fig. 1. Sexual size dimorphism (SSD) in insect species in which females develop through a higher number of larval instars than males. SSD is expressed as female/male size ratio when females were the larger sex, but calculated as '2 - (male size/female size)' when males were larger (see Materials and methods for details). (a) SSD in final size; (b) SSD earlier in life (i.e. typically, the initial weight of the instar which was final for males). Four species of Lymantriid moths (Lepidoptera, Lymantriidae) with exceptionally high SSD values (2.8–4.2) were omitted from (a).

sometimes, also arise by means of males omitting an instar, which allows them to achieve short development times.

Table 3. Comparison of medians of final sexual size dimorphism (SSD) between insects in which females go through a higher number of larval instars than males and the rest of species in the taxon (with sexual difference in instar number not known). Final SSD of the former group was significantly higher than that of the latter group (paired *t*-test: $t = 2.91$, d.f. = 7, $P = 0.02$).

Taxa	Females with a higher instar number		Other species ^a	
	Median of SSD	Number of species	Median of SSD	Number of species
O. Orthoptera	1.7	4	1.2	2
O. Plecoptera	2.2	1	1.8	2
O. Coleoptera	2.0	1	1.1	29
O. Hymenoptera	2.0	6	1.3	20
O. Lepidoptera ^b	2.8	7	1.1	33
F. Nymphalidae	1.1	1	1.1	9
F. Pyralidae	1.7	1	1.3	4
F. Tortricidae	1.4	4	1.4	8

^aData from Teder and Tammaru (2005), the species included in Table 1, and their congenics, were removed from this data set.

^bData on the families of Lepidoptera presented separately are not included in the overall figures for Lepidoptera.

At a more general level, our analysis demonstrates that, in arthropods, there is an easy way available to reconcile the controversy between the 'needs' of juveniles and adults, as it comes to stage-specific optimal body sizes. Having a sex-related difference in instar number implies that the abrupt change producing sexually dimorphic adults occurs late in individual ontogeny. This enables the juveniles of both sexes to follow exactly the same growth patterns early in their lives. The latter is presumably adaptive in the typical case because it is hard to see why the optima should differ between the sexes in the early growing stage. For the same reason it seems likely that, in insects with a sexual difference in instar number, selective pressures operating early in ontogeny have no influence on the evolutionarily stable values of adult SSD. This is in contrast with various other animal species, in which growing apart of the sexes starts much earlier in life. Such an early divergence, driven by sexually dimorphic optima for adults, is likely to be selected against in the juvenile stage, and actual values of SSD must be seen as a compromise of selective pressures acting at different stages of individual ontogeny (Schluter *et al.*, 1991; Teather & Weatherhead, 1994; Badyaev, 2002).

Interestingly, with sawflies (and, possibly, stoneflies and stick insects) forming the exceptions, insects with a sexual difference in the number of instars showed also intrasexual variation in instar number. This indicates that intrasexual variation in instar number may be a prerequisite for sexual differences in instar number to evolve. In particular, plasticity in the number of instars may indicate that the species has overcome the proposed constraint of species-specific constant instar number (Tammaru, 1998). Moreover, the fact that in some species the instar number differs also between populations/genetic lines (Table 1) further suggests that when the constraint of invariable instar number has once been broken, high levels of genetic variability may persist in this trait. This, in turn, may allow a sexual difference in the number of instars to evolve.

While additional instars of females serve as a mechanism leading to notably larger size when compared with males, the function of extra instars appears to be different within each of the sexes. In particular, within sexes, passing through additional instars is often known to be characteristic of small,

slow-growing larvae and/or larvae reared under suboptimal conditions (e.g. Wigglesworth, 1972; Nijhout, 1994; Corbet, 1999). While development times of the larvae with additional instars are usually considerably longer than that of the 'normal' ones, final sizes of the groups often do not differ considerably (e.g. Liquido & Nishida, 1985; Strand, 1990). Interestingly, similar within-sexes patterns occur also at least for some insect species with sexually dimorphic instar number (e.g. Schmidt *et al.*, 1977; Shreeve, 1986; Esperk & Tammaru, 2006). The additional instar may thus simultaneously permit large body size to be attained in females, as well as being a 'compensatory' mechanism for slow-growing larvae within the sexes to achieve a certain species-specific 'threshold' size for pupation. The threshold, however, may be different for males and females (Nijhout, 1975, 1994).

In summary, the results of the present study demonstrate the importance of considering taxon-specific ontogenetic features when trying to understand adaptive evolution of SSD, and body size in general. In the particular case of insects, one should not ignore variation in instar number, especially because of the complex nature of the phenomenon, and its strong influence on fitness-related traits. Adding a larval instar allows an insect to increase its body size considerably at the expense of prolonging growth period, which may otherwise well be a (plastic or evolutionary) change associated with severe constraints. At a more practical level, it is thus definitely desirable that case studies on insect development pay more attention to recording, and reporting, instar numbers. In fact, the number of studies from which this type of information can be extracted is still notably low, when viewed against the background of the vast number of papers on various aspects of insect development.

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