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RESEARCH ARTICLE

Rensch's rule is not verified in melanopline grasshoppers (Acrididae)

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Abstract: Sexual size dimorphism (SSD) is almost universal in animals. Rensch's rule proposes that SSD increases with increasing average body size in taxa where males are larger than females (male- biased SSD; MBSSD) and decreases when females are larger (female- biased SSD; FBSSD). Although it was proposed that both patterns are part of the same evolutionary trend, there is more evidence for Rensch's rule in the first case. We analyzed SSD in the acridid subfamily Melanoplinae in a sample of 718 species and subspecies covering all tribes and representative genera. As in all Orthopera, SSD is female-biased. Body length was used as a proxy for body size. Mean body size within the subfamily varied between 9 and 34.5 mm in males (N= 812) and 12.75 and 44.0 mm in females (N= 735). Except for five species (0.7%) all taxa (from subfamily to subspecies) showed moderate to strong FBSSD (mean= 1.27). The lowest SSD was observed in *Melanoplus chumash* (SSD= 1.01), and the highest in *Phaedrotettix aptera coquinae* (SSD= 1.83). To test Rensch's rule we performed reduced major axis (RMA) regressions between log10 (male body length) and log10 (female body length). In no case RMA slopes were significantly higher than 1.0 which would signal Rensch's rule. Thus, Melanoplinae represents a new case of FBSSD where Rensch's rule is not verified. The proximate causes of FBSSD and the non-occurrence of Rensch's rule in the Orthoptera are discussed as well as the relationship between SSD patterns at the intra- and supraspecific levels.

Key words: Body size, Melanoplinae, Model II regression, sexual size dimorphism, spur-throated grasshoppers.

Introduction

An important component of morphological variability in animal species is sexual dimorphism (SD) manifested in many traits including color, behavior and morphometry. A very frequent one is sexual size dimorphism (SSD) which can be male-biased (MBSSD) as in most mammals and birds, or female-biased (FBSSD) as in most invertebrates and some vertebrates (Ralls 1976; Andersson 1994; Fairbairn *et al.* 2007; Hochkirch & Gröning 2008). Since Darwin (1871), SSD has been considered the result of sexual selection (Dale *et al.* 2007) although other explanations may apply when natural selection favored different body sizes to suit different ecological roles or niche utilization in both sexes (Andersson 1994; Selander 1966; Mysterud 2000; Isaac 2005; Gayon 2010).

The study of proximate and ultimate causes of SSD is relevant because body size is perhaps the most important characteristic of animals being related to and influencing all aspects of natural history and biology including fecundity, reproductive success, thermal adaptation, and many others (Peters 1983; Schmidt-Nielsen 1984; LaBarbera 1989; Brown & Weste 2000; Bonner 2006; Whitman 2008a,b). As such, size affects fitness and thus is the target of natural selection. Simultaneously, body dimensions are affected by abiotic and biotic factors such as temperature, precipitation, seasonality, resource availability, predation and competition. Differences in size between sexes may have important consequences in the reproductive biology and ecological performance of species thus producing important evolutionary outcomes (LaBarbera 1989; Whitman 2008b).

Rensch's rule (Rensch 1950, 1960) proposes that the amount of SSD tends to increase with increasing average body size in taxa where males are larger than females and decreases when females are larger (Fairbairn 1997, 2005; Fairbairn *et al.* 2007; Blanckenhorn *et al.* 2007b; Bidau & Martí 2007a, 2008b,c). Although these two patterns seem to conflict, it was proposed that they may be part of the same trend (Fairbairn 1997, 2005; Fairbairn *et al.* 2007) involving greater evolutionary change in males and strong covariation of size between the sexes because of genetic correlations (Lindenfors *et al.* 2007). That trend has been relatively well documented across species in some groups where males are larger (mostly vertebrates) (Andersson 1994; Colwell 2000; Székely *et al.* 2004; Fairbairn 2005; Johannson *et al.* 2005; Webb & Freckleton 2007; Bidau & Martí 2007a, 2008b,c; Lengkeek *et al.* 2008; Stephens & Wiens 2009). However, where females are the larger sex (some vertebrates and most invertebrates), Rensch's rule has not been supported in most cases.

The Orthoptera, comprising ca. 26,000 described species (Eades *et al.* 2012) is an excellent model group for studying body size variation and SSD because it shows an impressive range of sizes from 2 mm long ant-inquiline crickets (Myrmecophilidae), to the enormous (by insect standards) *Valanga irregularis* (Burmeister, 1838) (Australian giant grasshopper), *Arachnacris corporalis* (Karny, 1924) (Malaysian giant long-legged katydid), and *Deinacrida fallai* Salmon, 1950 (New Zealand's Poor Knights giant weta) more than 100 mm long (Whitman 2008b). Within Caelifera (short-horned grasshoppers) the range of sizes in Acrididae, the largest orthopteran family, is also large (9-100mm). Thus, orthopterans constitute candidate organisms for all kind of studies relating to body size.

We chose the subfamily Melanoplinae (spur-throated grasshoppers), one of the largest within the Acrididae (ca. 1,000 species) to analyze SSD (Eades *et al.* 2012). The subfamily, as most Orthoptera, shows FBSSD. Melanoplines have a vast geographic distribution in South, Central and North America, and Eurasia and are found in open habitats of herbaceous vegetation (Chintahuan-Marquier 2010; Chintahuan-Marquier *et al.* 2011). Recent molecular evidence supports a South American origin of the subfamily (Amédégnato *et al.* 2003). They show an enormous range of latitudes and elevations in their geographic distribution which is

important because it was suggested that Rensch's rule may be affected by latitudinal or altitudinal body size patterns such as Bergmann's rule (Blanckenhorn *et al.* 2006; Bidau & Martí 2008c). The objective of this paper was to assess if within the Melanoplinae, its tribes and largest genera, Rensch's rule is verified.

Material and Methods

To obtain data on male and female body size of melanopline species for calculating SSD, we elaborated a database using as guide, the Orthoptera Species File (Eades *et al.* 2012) to perform a literature search. We used body length as size estimator; this is the commonest measurement found in the literature although it was not possible to assess if all authors used the same criteria for measuring total body length (TL) (Hochkirch & Gröning 2008). This limitation is unavoidable and was not taken into consideration. However, in no case appendices were included in the calculations and only dry mounted specimens were considered. Furthermore, we used exclusively data for both males and females published by the same author(s) in the same publication that is, in no case measurements of males and females of the same species were taken from different published sources. In the case when there was a span of body size described in the source publication, we computed an average value or in a few cases, a mean of several averages. We recorded 1020 melanopline taxa (raw data is available from the corresponding author), basically species. In a few cases of species with wide geographic distributions and subspecies differing in body size, the latter were included in the database. A total of 824 species and 89 subspecies of all tribes, and genera not included in any tribe (NT), were investigated. Male and female body size were obtained for 798 and 718 taxa, respectively (many species have been described on the basis of the male or the female only). For 718 species we recorded mean male and female body lengths. Some tribes and genera are well represented (e.g. Melanoplini, Dichroplini, Jivarini). Others (Podismini, Prumnini) are not, obeying to the fact that many Asiatic species were described in obscure old journals which are difficult to find.

SSD was calculated as the ratio between the arithmetic mean of female body length, and the corresponding male mean (Smith 1999). Scaling of SSD with body size was analyzed regressing log10(male length) on log10(female length) (Fairbairn & Preziosi 1994; Abouheif & Fairbairn 1997; Fairbairn 1997, 2005). Rensch's rule is verified when the regression line slope is > 1.0, while slopes significantly < 1.0 signal its reversion (Abouheif & Fairbairn 1997; Fairbairn 1997). Ordinary least-squares regression (OLS) is inadequate for these analyses because x (here, female body length) is estimated with error; thus, the slope *b*, and its confidence interval, are estimated with error (Fairbairn 1997). Thus, model II regression is recommended (Sokal & Rohlf 1995). If the intercept *a* does not deviate from zero, the relationship between male and female size is isometric, if $a \neq 0$ the relationship is allometric, and - depending on the sign of *a* - females are on average either larger or smaller than males (Ranta *et al.* 1994). We used reduced major axis (RMA) regression to estimate slopes for the relationship between log10(male size) and log10(female size) (software: Bohonak and van der Linde (2004) (Java version)). Clarke's *T* statistic with adjusted degrees of freedom (*df*) was used for testing the null hypothesis that the RMA slope (b_{RMA}) = 1.0 (Clarke 1980). The calculations required are:

$T = |\log b - \log b'|/((1 - r^2)/(n - 2))^{1/2}$ and $df = 2 + ((n - 2)/(1 + 0.5r^2))$ (Clarke 1980; McArdle 1988). 95% confidence limits were calculated.

Results

Body size in Melanoplinae

We obtained data of TL for males (798 taxa) and females (718 taxa). In males, the smallest mean length corresponded to *Radacris minutus* (Roberts, 1937) (NT) with 9.0 mm, and the largest, to *Oedomerus corallipes* Bruner, 1908 (Conalcaeini) with 34.5 mm. Male mean TL for the whole sample was 18.81 mm ± 4.01. The smallest female body size corresponded to *Maeacris ayasqa* Cigliano, Pocco & Lange 2011 (Jivarini) with 12.75 mm and the largest, to *Melanoplus punctulatus arboreus* Scudder, 1897 (44 mm). Female mean for the whole sample was 23.78 mm ± 5.06 (Fig. 1). The coefficients of variation of mean TL were practically identical: male CV, 21.32; female CV, 21.28. Tribes varied widely in body size (although not in their CVs) (Table 1). The distribution of mean body lengths for males and females of all taxa is shown in Fig. 1.
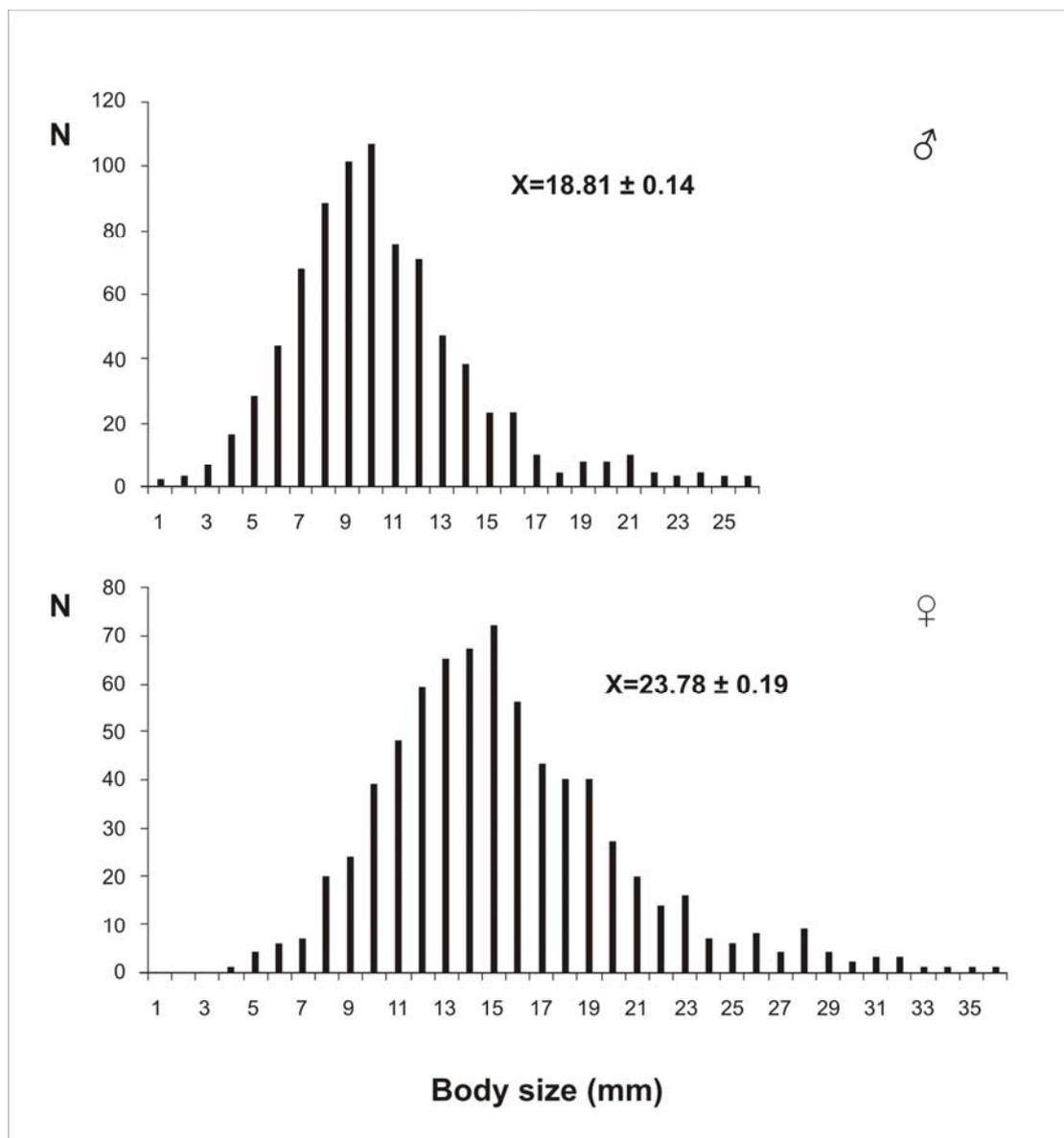
Figure 1. Distribution of mean body sizes of males and females of Melanoplinae studied in this paper. Each interval in the x axis corresponds to 1 mm starting with 1 (9-10 mm). Mean ± standard error is indicated in both plots.

Degree of SSD in Melanoplinae

The 718 taxa studied showed considerable variation in the degree of SSD. Except for five species (0.7%) all taxa showed FBSSD (Table 1; Fig. 2). The species not showing FBSSD were: *Prumna litoralis* Tarbinsky, 1832 (SSD= 0.90), *P. polaris* Miram, 1928 (SSD= 0.92) (Prumnini), *Melanoplus novato* Rentz, 1978 (SSD= 0.84), *M. ponderosus* (Scudder, 1875) (SSD= 1.0) (Melanoplini), and *Pseudoscopas nigrigena* (Rehn, 1913) (SSD= 1.0) (NT). It is probable that these species also show moderate FBSSD but possibly because of small sample size, this was obscured. The rest of taxa (99.3%) showed moderate to strong FBSSD (Fig. 2) with an average value of 1.27 (CV= 10.31). The distribution of SSD values across the sample is basically normal (Fig. 2). The lowest SSD was observed in *Melanoplus chumash* Rentz, 1978 (SSD= 1.01), and the highest in *Aptenopedes aptera coquinae* Hebard, 1936 (SSD= 1.83) (Melanoplini). Table 1 (third column) summarizes the data on SSD for the subfamily, all recognized tribes and NT. The highest variation of SSD was observed in Prumnini, about twice that of the other taxa (Table 1). However, only 12 species were available for study thus, this result must be considered cautiously.

Rensch's rule

RMA analyses were performed for the sample covering the whole subfamily, for each recognized tribe and NT, and for genera where at least 10 species and/or subspecies were available (Tables 2, 3). In all the taxa or species groups studied, correlations between male and female body length were highly significant (Tables 2, 3) except for the Prumnini and the genera *Pseudoscopas* Hebard (significant at the 5% level), and *Phaulotettix* Scudder (non-significant).

Table 1. Body size (as estimated from body length in mm) and sexual size dimorphism (as the arithmetic mean between mean female body length/mean male body length) in the Melanoplinae tribes (and a group of South American species not assigned to any tribe, NT). CV= coefficient of variation.

TRIBE	MALE BODY SIZE			FEMALE BODY SIZE			SEXUAL SIZE DIMORPHISM		
	Range	Mean	CV	Range	Mean	CV	Range	Mean	CV
Conalcaeini	15.6-34.5	27.57	20.82	20.0-42.0	32.20	19.72	1.09-1.42	1.22	7.13
Dactylotyini	11.2-30	18.11	20.93	16.2-35.0	18.11	20.93	1.15-1.63	1.38	8.48
Dichroplini	11.75-28	18.73	16.87	11.78-28.0	23.22	18.35	1.02-1.53	1.24	7.58
Jivarini	10.26-22.7	15.92	19.41	12.75-27.3	18.49	18.66	1.06-1.37	1.18	6.52
Melanoplini	9.5-33.0	18.72	20.41	14.1-44.0	25.60	20.47	0.88-1.83	1.27	11.02
Podismini	12.5-29.0	19.20	16.30	17.5-39.0	25.7	14.86	1.07-1.67	1.34	8.81
Prumnini	15.2-29.9	22.36	20.75	20.95-36.3	28.15	18.13	0.90-1.61	1.28	17.19
NT	9.0-30.5	18.06	19.16	14.5-34.5	22.18	18.49	1.0-1.61	1.23	8.13

Table 2. Results of reduced major axis regression (RMA) of log10 (male body length) on log10 (female body length) for the Melanoplinae, all its tribes and an assemblage of genera not yet assigned to any tribe (NT). r= Pearson´s correlation coefficient; t= Student´s t statistic; b= slope of the RMA regression line; T= Clarke's T statistic; df= degrees of freedom; [1]df= Clarke's adjusted degrees of freedom for T; a= intercept of the RMA regression line; 95% CI= 95% confidence intervals; SE= standard error; P= probability.

| Taxon | N | Correlation | | | | RMA slope | | | | | RMA intercept | | OLS |
		r	t	df	P	b (SE)	T	df[1]	P	95% CI	a (SE)	95% CI	b
Melanoplinae	718	0.875	48.36	716	<0.001	0.968 (0.013)	0.77	519.78	0.220	0.944, 1.014	-0.058 (0.017)	-0.092, -0.023	0.887
Conalcaeini	21	0.827	6.41	19	<0.001	1.055 (0.136)	0.18	17.65	0.427	0.770, 1.139	-0.158 (0.208)	-0.592, 0.276	0.872
Dactylotyini	29	0.924	14.72	27	<0.001	0.969 (0.071)	0.19	22.32	0.422	0.851, 1.115	-0.096 (0.099)	-0.299, 0.106	1.028
Dichroplini	117	0.892	21.16	115	<0.001	1.037 (0.044)	0.38	84.27	0.390	0.950, 1.124	-0.144 (0.060)	-0.262, -0.026	0.924
Jivarini	41	0.946	18.23	39	<0.001	1.035 (0.054)	0.30	30.32	0.383	0.934, 1.022	-0.070 (0.031)	-0.130, 0.010	0.979
Melanoplini	322	0.912	39.80	320	<0.001	0.978 (0.033)	0.44	228.01	0.309	0.972, 1.102	-0.151 (0.045)	-0.240, -0.061	0.864
Podismini	94	0.836	14.59	92	<0.001	1.046 (0.060)	0.35	70.20	0.365	0.927, 1.165	-0.189 (0.084)	-0.356, -0.022	0.874
Prumnini	12	0.595	2.35	10	<0.025	1.190 (0.302)	0.31	4.17	0.386	0.529, 1.862	-0.377 (0.436)	-1.347, 0.594	0.713
NT	85	0.915	20.65	83	<0.001	1.137 (0.050)	1.26	60.51	0.111	1.036, 1.237	-0.270 (0.068)	-0.405, -0.125	1.032
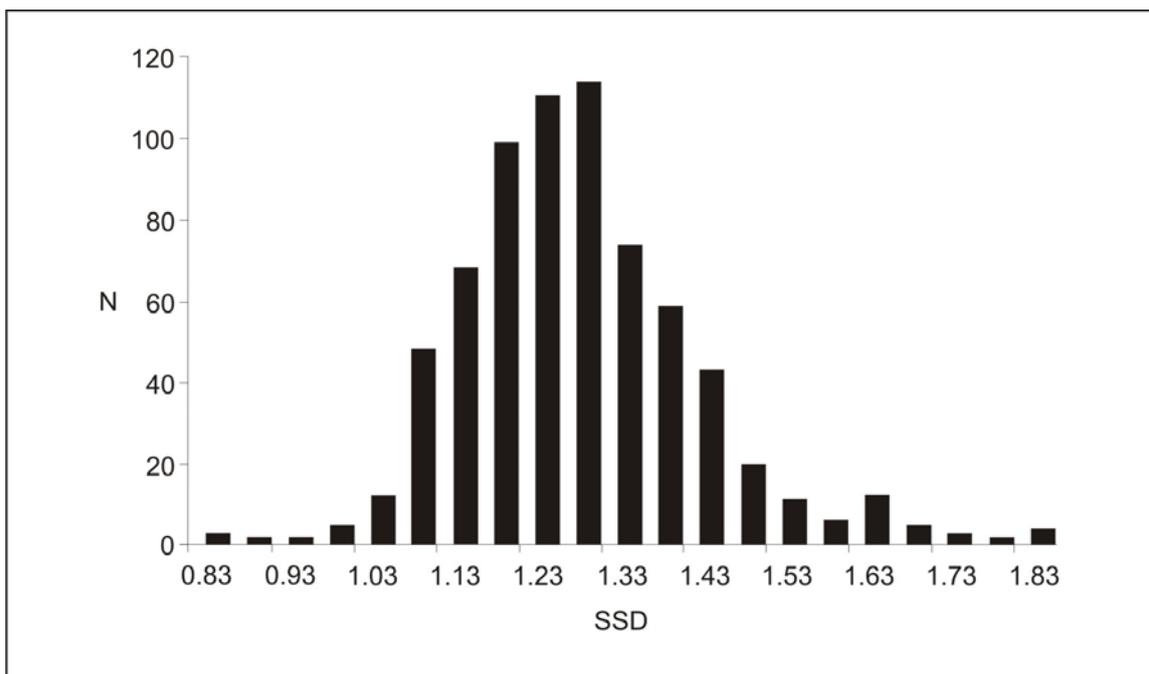
Figure 2. Distribution of SSD (the ratio between the arithmetic mean of body length of females, and the corresponding mean of males) in the Melanoplinae studied in this paper.

The right part of Tables 2 and 3 shows the results of RMA regressions for the same taxa. Values of the intercept *a* indicated that almost all relationships between log10(male length) and log10(female length) were allometric (the negative value of *a* indicates as expected that females are consistently larger than males) with four exceptions where the relationship is practically isometric: Dactylotyini, *Podisma* Berthold, *Neopedies* Hebard, and *Propedies* Hebard. In three cases, *a* was positive. Regarding Rensch's rule, in no case the RMA slopes were significantly different from *b*= 1.0 indicating that the rule is not verified within this subfamily (Tables 2, 3; Fig. 3). This is also supported by the fact that 95%CIs included 1.0 in all cases but three (Tables 2, 3). The last column of Tables 2 and 3 shows the values of the OLS regression slopes. In all but one case, they were smaller than the RMA slopes.

Table 3. Results of reduced major axis regression (RMA) of log10 (male body length) on log10 (female body length) for selected genera of Melanoplinae. *r*= Pearson´s correlation coefficient; *t*= Student´s t statistic; *b*= slope of the RMA regression line; *T*= Clarke's *T* statistic; df= degrees of freedom; [1]df= Clarke's adjusted degrees of freedom for *T*; *a*= intercept of the RMA regression line; 95% CI= 95% confidence intervals; SE= standard error; *P*= probability (1-tailed).

| Taxon | N | Correlation | | | | RMA slope | | | | | RMA intercept | | OLS |
		r	*t*	df	*P*	*b* (SE)	*T*	df[1]	*P*	95% CI	*a* (SE)	95% CI	*b*
Barytettix	14	0.852	5.63	12	<0.001	0.854 (0.129)	0.46	12.27	0.317	0.573, 1.136	0.158 (0.203)	-0.284, 0.600	0.728
Hesperotettix	10	0.853	4.62	8	0.001	0.605 (0.112)	1.19	9.01	0.132	0.374, 0.863	0.406 (0.151)	0.057. 0.704	0.516
Dichroplus	21	0.840	6.74	19	<0.001	1.202 (0.150)	0.64	17.52	0.266	0.888, 1.516	-0.378 (0.206)	--0.081, 0.054	1.010
Eurotettix	12	0.894	5.97	10	<0.001	1.226 (0.173)	0.64	10.57	0.269	0.840, 1.613	-0.386 (0.236)	-0.911, 0.140	1.100
Jivarus	27	0.950	16.08	25	<0.001	1.042 (0.065)	0.28	20.60	0.391	0.908, 1.175	-0.116 (0.183)	-0.287, 0.054	0.990
Melanoplus	225	0.830	22.25	223	<0.001	1.021 (0.038)	0.24	169.28	0.406	0.946, 1.097	-0.127 (0.052)	-0.230, -0.024	0.848
Phaedrotettix	10	0.960	9.72	8	<0.001	1.443 (0.146)	1.62	8.84	0.072	1.116, 1.776	-0.675 (0.191)	-1.115, -0.235	1.388
Phaulotettix	11	0.609	1.40	9	0.100	0.822 (0.217)	0.32	11.28	0.378	0.331, 1.314	0.147 (0.304)	-0.542, 0.835	0.501
Podisma	15	0.813	5.03	13	<0.001	0.926 (0.150)	0.20	13.27	0.423	0.603, 1.250	-0.023 (0.211)	-0.478, 0.432	0.753
Neopedies	10	0.795	3.70	8	0.0035	0.971 (0.208)	0.06	9.60	0.477	0.491, 1.450	-0.032 (0.264)	-0.640, 0.575	0.771
Parascopas	13	0.897	6.73	11	<0.001	1.118 (0.149)	0.38	11.27	0.356	0.790, 1.445	'-0.235 (0.217)	-0.713, 0,243	1.003
Propedies	34	0.851	9.16	32	<0.001	0.965 (0.090)	0.17	26.96	0.433	0.782, 1.148	-0.049 (0.120)	-0.294, 0.196	0.821
Pseudoscopas	11	0.639	2.49	9	0.017	1.562 (0.400)	0.74	11.14	0.238	0.666, 2.468	-0.810 (0.522)	-1.991, 0.371	0.998
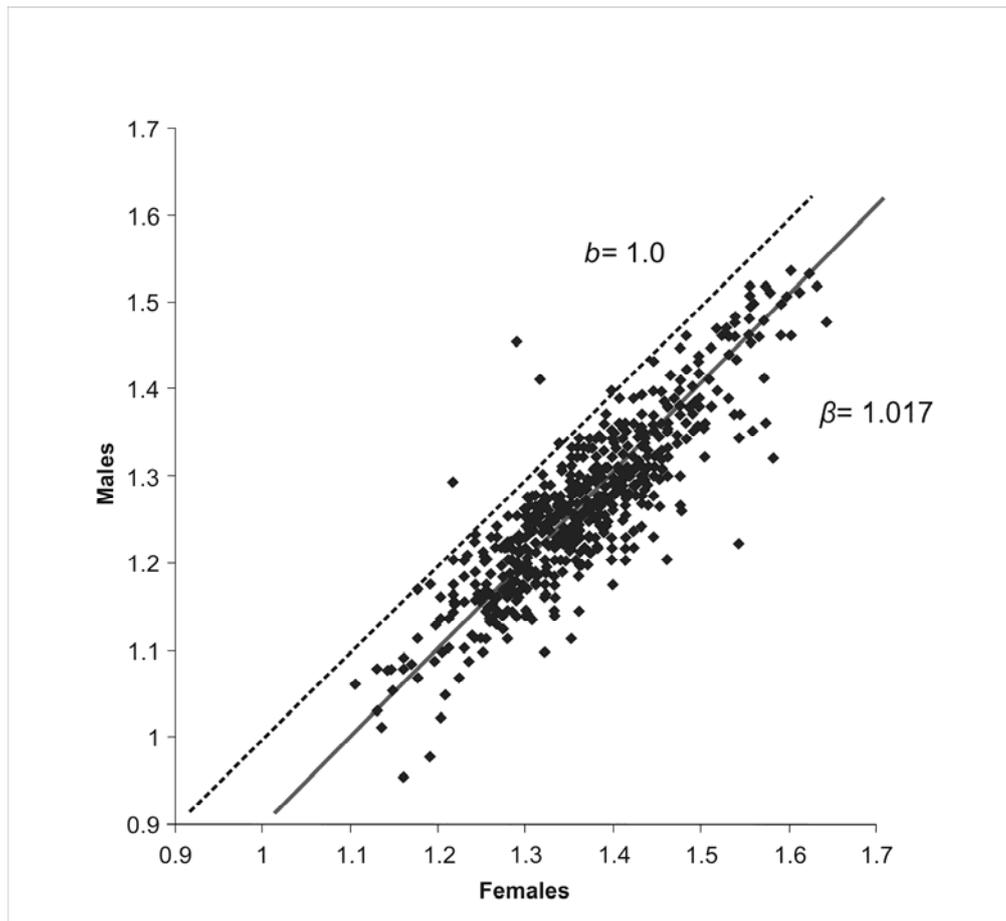
Figure 3. Model II (RMA) regression for estimating allometry of SSD following the method of Abouheif & Fairbairn (1997).

Discussion

As common in animals and because body size influences the abundance and distribution of species, the Orthoptera show a right-skewed distribution between species richness and size implying few very small, many medium-sized, and few very large species (Kozlowski & Gawelczyc 2002; Whitman 2008b). The Melanoplinae, ubiquitous in most terrestrial communities, are usually medium-sized. However, in species with large geographic distributions, body size may vary widely in relation to abiotic and biotic factors at large scales (Bidau & Martí 2007a,b, 2008a) but also at smaller scales (Miño *et al.* 2011; Bidau *et al.* 2012).

FBSSD is the rule within Orthoptera with few Ensifera species where males are larger than females (Hochkirch & Gröning 2008). The range of FBSSD in Caelifera is higher than in Ensifera: mean SSD varies between 1.0 and 2.4 (mean= 1.37), while the Ensifera vary between 0.8 and 1.4 (mean= 1.09) (Hochkirch & Gröning 2008). Melanoplinae showed FBSSD in all analysed taxa independently of tribe or genus. An important question is why males are invariably smaller than females. This is a problem already discussed by Darwin (1871) in "*The Descent of Man and Selection in relation to Sex*". For example: "*With insects of all kinds the males are commonly smaller than the females; and this difference can often be detected even in the larval state.*" (p.345). Then Darwin presents an hypothesis proposed by the lepidopterologist A.I. Wallace: "*He finds* [Wallace], [...] *that in proportion as the individual moth is finer, so is the time required for its metamorphosis longer; and for this*

reason the female, which is the larger and heavier insect, from having to carry her numerous eggs, will be preceded by the male, which is smaller and has less to mature." (p. 346), and continues suggesting that since insects are short-lived, it would be advantageous if males mature first in large numbers ready to fecundate females as soon as the latter are ready to mate. This situation would favour selection of small male size. Darwin anticipated this hypothesis in page 260: "*Throughout the great class of insects the males almost always emerge from the pupal state before the other sex, so that they generally swarm for a time before any females can be seen. […]Those males which annually first migrated into any country, or which in the spring were first ready to breed, or were the most eager, would leave the largest number of offspring; and these would tend to inherit similar instincts and constitutions.*" (Darwin 1871).

Darwin was referring to the phenomenon called "protandry" (Wiklund & Fagerström 1977; Bulmer 1983; Wiklund 1995; Morbey & Ydenberg 2001)". Protandry is defined as "[…] *the more common form of sex-biased arrival timing, occurs when males arrive at breeding areas earlier in the season on average than females.*" (Morbey & Ydenberg 2001). Protandry is common in insects with discrete, nonoverlapping generations in which females mate once only soon after emergence (Bulmer 1983), and has been suggested as a cause of the smaller male size in insects owing to the males' shorter developmental time (Bidau & Martí 2007a; Jarošík & Honek 2007; Whitman 2008b). There are at least seven different models proposed to explain protandry (Morbey & Ydenberg 2001). In some cases, females increase the number of instars with respect to males (Esperk *et al.* 2007; Bidau & Martí 2008c). It is worth noting that although Darwin considered protandry a product of sexual selection, natural selection could also be effective in producing this pattern. However, if protandry caused by differential developmental time (sexual bimaturism) is not adaptive within a group and both sexes mature at the same time, the proximate cause of SSD should be differences in growth rate between the sexes (Blanckenhorn *et al.* 2007a).

Smaller males could result from other causes not involving protandry and protandry may occur without being the cause of FBSSD. Also, a small size in males could imply lower predation intensity or a decrease in food requirements (Nylin *et. al.* 1993; Blanckenhorn 2000). Natural selection could also favor differences in body size to avoid competition for resources between sexes, or select smaller body size for increased mobility (Kelly *et al.* 2008). However, plasticity of growth patterns that may affect within-species variation are far from being understood (Badyaev 2002; Stillwell *et al.* 2010).

SSD is almost universal in animals being female-biased in most invertebrates and usually but not exclusively, male-biased in vertebrates (Teder & Tammaru 2005; Fairbairn *et al.* 2007). Regarding SSD, there is an unresolved problem posed by Rensch's rule that proposes that SSD increases with body size in groups were males are larger than females and decreases when females are larger (Rensch 1950, 1960; Andersson 1994; Abouheif & Fairbairn 1997; Fairbairn 1997, 2005; Székely *et al.* 2004; Bidau & Martí 2008b). Fairbairn (1997) proposed that both instances are part of the same trend (see Introduction). However, Rensch's rule has been verified more frequently where MBSSD occurs than in cases of FBSSD (Jannot & Kerans 2003; Tubaro & Bertelli 2003; Blanckenhorn *et al.* 2007b; Lindenfors *et al.* 2007; Webb & Freckleton 2007; Hochkirch & Gröning 2008; Stephens & Wiens 2009; Stuart-Fox 2009; Hálamková *et al.* 2013; Liao *et al.* 2013). The Melanoplinae represent a new case where Rensch's rule is not verified in presence of FBSSD. The trend was observed independently of taxonomic level: RMA slopes were not significantly different from 1.0 and 95% confidence intervals almost always included the 1.0 value, reinforcing the previous results. There were only three exceptions: the group of NT species and the genera *Hesperotettix* Scudder and *Phaedrotettix* (Tables 2, 3). NT is an artificial assemblage of

mainly Neotropical genera some closely related and some, not. This heterogeneity could be the cause of the observed result. *Phaedrotettix* showed the maximum RMA slope observed (*b*RMA= 1.443; p= 0.07) thus it is possible that Rensch's rule occurs in this genus. In contrast, *Phaulotettix Scudder* showed a very low albeit non-significant RMA slope (*b*RMA= 0.605) thus reversing Rensch's rule; in both cases sample size was N= 10. McArdle (1988) cautions that Clarke's (1980) statistics perform better at larger sample sizes; if sample size is small, results must be considered carefully. Nevertheless, the consensus is that in Melanoplinae, Rensch's rule is not verified.

The only other large scale metanalysis of SSD and Rensch's rule in Orthoptera is that of Hochkirch & Gröning (2008). For Caelifera, they plotted log10(male size) on log10(female size) for 1113 species from ten families (75% corresponded to Acrididae and 11% to Pamphagidae). They obtained a slope of *b*RMA= 0.94 thus, less than 1.0 and, although no statistical analysis was presented, the authors state that Caelifera do not exhibit Rensch's rule. In this case, if the slope were significantly different from 1.0, Rensch's rule would be inverted.

Another problem regarding Rensch's rule is the existence of the pattern at the intraspecific level. Little evidence for Rensch's rule in insects was observed in a comprehensive analysis by Blanckenhorn *et al.* (2007b) even in cases where Rensch's rule occurred at the supraspecific level suggesting that patterns of SSD within species cannot be extrapolated to higher taxonomic levels as proposed by Fairbairn and Preziosi (1994) and Kraushaar and Blanckenhorn (2002). The only three studies of Rensch's rule performed to date within Melanoplinae species support this view. Bidau & Martí (2008c) studied two species of the Neotropical genus *Dichroplus* Stål, *D. pratensis* Bruner, 1900 (25 populations) and *D. vittatus* Bruner, 1900 (19 populations). Both species are very closely related (Cigliano & Otte 2003), have vast geographic distributions overlapping over a wide area in Argentina, and similar habits. However, both species show opposite patterns of SSD: *D. pratensis* exhibited Rensch's rule, SSD decreasing with increasing body size in six linear body size estimators while *D. vittatus* showed an inversion of Rensch's rule for the same six traits (Bidau & Martí 2008c). In *D. pratensis* protandry is probably the main proximate cause of the pattern; in *D. vittatus*, differential responses of males and females to environmental conditions probably affect SSD. It is worth noting that both species show highly significant converse Bergmannian patterns related to seasonality and developmental time (Bidau & Martí 2007a, b, 2008a). In this respect, Blanckenhorn *et al.* (2006) studying the relationship between Bergmann's and Rensch's rules in 98 species at the intraspecific level concluded that latitudinal body size variation between populations is possibly a mediator, or at least a correlate of Rensch's rule within species although causes remain obscure. This consideration can be applied to the melanoplines just described. A third case, is *Ronderosia bergi* Stål, 1875 belonging to the same tribe as *Dichroplus*. We studied SSD and Rensch's rule in 17 populations (unpublished results) using four linear traits as estimators of body size. Rensch's rule was not verified for any trait: no slope was significantly different from 1.0. This species also does not show a Bergmannian or converse Bergmannian pattern.

Thus, three species of the same tribe show three different SSD patterns: Rensch's rule in *D. pratensis*, converse Rensch's rule in *D. vittatus*, and no Rensch's rule in *R. bergi*, while the tribe as a whole and the respective genera do not exhibit Rensch's rule (see Table 1). These results confirm the lack of predictive power about SSD of the intraspecific situation with respect to the interspecific taxonomic level (Blanckenhorn *et al.* 2007b).

Why is Rensch's rule so infrequent in cases of FBSSD? While in MBSSD sexual selection is the most plausible explanation for the larger size of males due to male-male

competition for females (Szekély *et al.* 2004), the opposite situation is not so easily explained except perhaps in few cases of FBSSD where females compete actively for males. Fecundity selection and/or selection for smaller more mobile or agile males that fertilize more females in a shorter period of time, could be involved (Hochkirch & Gröning 2008; Stuart-Fox 2009). It is thus relevant to perform analyses of SSD and Rensch's rule at both large interspecific and small intraspecific scales, to gain insight on this puzzling problem and disentangle the proximate and ultimate causes of these phenomena.

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