CHAPTER 6

Rensch's rule in insects: patterns among and within species

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6.1 Introduction

Rensch's rule (so termed by Abouheif and Fairbairn 1997; Fairbairn 1997) describes a widespread pattern in the animal kingdom that male body size diverges faster than female body size over evolutionarily time among related species, such that male-biased sexual size dimorphism (henceforth dimorphism) increases and female-biased dimorphism decreases with body size (Rensch 1959). When first describing the phenomenon, Rensch (1950) did not offer an explanation, and its causes remain largely unclear to this day. Although it is unlikely that one single mechanism is responsible across the broad range of taxa in which it is observed (Fairbairn 1997, 2005), it has been suggested that Rensch's rule may be driven primarily by sexual selection for large male size in combination with a typically high genetic correlation in body size between the sexes (Fairbairn and Preziosi 1994; Fairbairn 1997). However, to date evidence for the general importance of sexual selection in producing Rensch's rule is equivocal at best (Fairbairn and Preziosi 1994; Fairbairn 1997, 2005; Kraushaar and Blanckenhorn 2002; Tamate and Maekawa 2005; Young 2005).

Almost 10 years ago, Abouheif and Fairbairn (1997) reviewed the evidence for Rensch's rule in animals and found support for it in a majority of taxa. However, arthropods, and especially insects, were greatly underrepresented in their survey and often displayed variation in dimorphism inconsistent with Rensch's rule (see also Chapter 7 in this volume). Since then a number of new data-sets on insects have become available, which prompted the update provided in this chapter.

The original formulation of Rensch's rule refers to a systematic pattern of variation in dimorphism among closely related species (Rensch 1950, 1959; Abouheif and Fairbairn 1997; Fairbairn 1997). Statistically, Rensch's rule is manifested in allometric slopes greater than 1 when male size is regressed on female size (described further below; Fairbairn 1997). Consequently, Rensch's rule can also be studied among populations within species. Primarily with the aim of investigating the putative mechanisms causing Rensch's rule, a number of studies have explored intraspecific variation in dimorphism in the past, but obtained mixed results (Fairbairn and Preziosi 1994; Fairbairn 1997, 2005; Kraushaar and Blanckenhorn 2002; Gustafsson and Lindenfors 2004; Tamate and Maekawa 2005; Young 2005; see also Chapters 8 and 14). Again, new intraspecific data have recently become available in connection with studies of Bergmann clines (Blanckenhorn *et al.* 2006), allowing a more comprehensive evaluation of the equivalent of Rensch's rule at this taxonomic level.

Patterns analogous to Rensch's rule can further be studied within populations of a given species, for example when animals are reared in the laboratory under different environmental conditions and several such treatments or genetic groupings (e.g. families) are compared. In such cases, body size of males and females can be affected differentially to produce allometries in dimorphism. Such phenotypic plasticity in dimorphism has recently been investigated in a comparative study of insects by Teder and Tammaru (2005), and in a more mechanistic framework by Fairbairn (2005; see also Chapter 14).

Contrary to patterns among species, where vertebrate data clearly dominate (Abouheif and Fairbairn, 1997), at this taxonomic level data are more likely to be available for smaller organisms that can be more easily reared in captivity, such as insects.

We here review the validity of Rensch's rule in insects and its extension to lower taxonomic levels: among species, among populations within species, and among families or environments within populations. We thus reduce Rensch's rule to its mere statistical manifestation: more variance in male than female body size. In so doing we ask whether allometries in dimorphism at these various taxonomic levels relate in any way, possibly in that patterns at a lower taxonomic level might uncover mechanisms generating Rensch's rule at this or higher taxonomic levels (see Fairbairn and Preziosi 1994; Kraushaar and Blanckenhorn 2002; Fairbairn 2005; Chapter 8). In this context we discuss potential proximate mechanisms producing variation in dimorphism whenever this is appropriate.

6.2 Patterns among species

Until recently, few studies of Rensch's rule in insects existed in the literature. Besides a data-set on beetles included in Rensch's (1950) original work, Abouheif and Fairbairn (1997) listed only Sivinski and Dodson's (1992) study on tephridid fruit flies, which included a parenthetical treatment of a large but unpublished data-set for stick insects (Phasmatodea; see Sivinski 1978), and work on one family of water striders (Heteroptera: Gerridae) by Fairbairn (1990, 1997) and Andersen (1994). Andersen (1997) in parallel published an extended study on additional water strider groups. Since then, data on ladybird beetles (Dixon 2000), stalk-eyed flies (Baker and Wilkinson 2001), caddisflies (Jannot and Kerans 2003), dragonflies (Johansson *et al.* 2005), and, most recently, a number of further insect groups (Blanckenhorn *et al.* 2007) have become available. As was customary, most of the earlier studies presented phylogenetically uncorrected data.

It has become standard to analyze dimorphism using allometric plots of ln(male size) on ln(female size) (or vice versa: Abouheif and Fairbairn 1997; Fairbairn 1997). Logarithmic transformations are necessary for reasons of scaling when studying such evolutionary allometries (Gould 1966; LaBarbera 1989). When (by convention) plotting female size on the x axis, Rensch's rule becomes statistically manifest in slopes $b > 1$ (i.e. hyper- or positive allometry; Fairbairn 1997). Because there is variance in both female and male size, and because the y and x variables are identical, major-axis (MA, or model II) regression should be used instead of least-squares regression (Sokal and Rohlf 1995), although this was not always done in the past (Table 6.1). In general, hypo- or negative allometry results when variance in y is less than in x, and hyper- or positive allometry results in the opposite case. Standard errors (SE) or 95% confidence intervals (CI; equal to 1.96*SE) based on error in x and y for MA slopes, or error in y only for least-squares slopes, can be calculated. Note that unless r^2 is very high, the MA slope is always greater than the least-squares slope, and the MA SE is always smaller (because in a right-angled triangle either of the two catheti, minimized in MA regression, are necessarily smaller than the hypotenuse minimized in least-squares regression).

Table 6.1 lists all allometric regression slope estimates available to date for insects, and Figure 6.1 plots the data for those groups yet unpublished (see Blanckenhorn *et al.* 2007). Phylogenetically uncorrected MA estimates based on the original data and/or corrected estimates based on independent contrasts assuming a particular phylogeny for the group are given in Table 6.1 (Felsenstein 1985; Purvis and Rambaut 1995). Because in the past least-squares estimates were often supplied, we list them for comparison. Least-squares and phylogenetically uncorrected estimates are clearly biased (Felsenstein 1985; Sokal and Rohlf 1995), so phylogenetically corrected MA estimates are preferred.

We have estimates for a total of seven insect orders, some of them featuring multiple estimates for various subtaxa. These estimates are based on different body-size traits, although this is of minor importance (but see section 6.4. below) as long as the same trait is used for both sexes and the traits are at the same scale (i.e. linear traits such as thorax or body length in contrast to volume traits

Table 6.1 Least-squares (LS) and MA allometric slopes ($\pm$95% CI) of ln(male size) on ln(female size) for various insect orders and/or some subsets (asterisks indicate slopes significantly different from 1; $^{*}P < 0.05$; $^{(*)}P < 0.1$). The RR? column indicates whether the data support (+; MA slopes >1) or are opposite to (−; MA slopes <1) Rensch's rule, or are neutral (0; MA slopes = 1).

Taxonomic group	Phylogenetically uncorrected		Phylogenetically corrected		*N*	RR?	Reference	Trait
	LS slope ($\pm$95% CI)	MA slope ($\pm$95% CI)	LS slope ($\pm$95% CI)	MA slope ($\pm$95% CI)				
Coleoptera (beetles)	0.99 ± 0.024	0.99 ± 0.017	1.02 ± 0.039	1.02 ± 0.027	35	0	Blanckenhorn *et al.* (2006)	Body mass$^{0.33}$
Carabidae	$0.97 \pm 0.024^{*}$	$0.97 \pm 0.017^{*}$	–	–	9	–	Rensch (1950)	Body length
Coccinellidae (Ladybird beetles)	1.01 ± 0.039	1.02 ± 0.026	–	–	37	0	Dixon (2000)	Body mass$^{0.33}$
Diptera (flies)								
Diopsidae (stalk-eyed flies)	1.09 ± 0.113	$1.14 \pm 0.071^{*}$	$1.13 \pm 0.110^{*}$	$1.18 \pm 0.067^{*}$	30	+	Baker and Wilkinson (2001)	Thorax length
Drosophila spp. (fruit flies)	1.09 ± 0.168	$1.18 \pm 0.104^{*}$	0.98 ± 0.210	$1.11 \pm 0.139^{(*)}$	23	+	Blanckenhorn *et al.* (2006)	Thorax length
				$1.23 \pm 0.245^{(*)}$	20		Huey *et al.* (2006)	
				$1.15 \pm 0.059^{*}$	42		Pitnick *et al.* (1995)	
Scathophagidae (dung flies)	$1.14 \pm 0.096^{*}$	$1.18 \pm 0.058^{*}$	1.06 ± 0.142	$1.14 \pm 0.090^{*}$	32	+	W.U. Blanckenhorn, R. Meier, and M. Bernasconi, unpublished work	Hind tibia length
Sepsidae (black scavenger flies)	1.00 ± 0.093	1.03 ± 0.064	$0.81 \pm 0.168^{*}$	0.91 ± 0.132	29	0	W.U. Blanckenhorn and R. Meier, unpublished work	Head width
Tephritidae (fruit flies)	1.11^{*}	1.12^{*}	–	–	27	+	Sivinski and Dodson (1992)	Thorax length
Anastrepha spp.	1.20^{*}	1.22^{*}	–	–	9	+	Sivinski and Dodson (1992)	Thorax length
Hymenoptera	0.98 ± 0.037	0.99 ± 0.025	0.95 ± 0.060	$0.96 \pm 0.044^{(*)}$	24	−	Blanckenhorn *et al.* (2006)	Body mass$^{0.33}$
Lepidoptera (butterflies)	1.03 ± 0.082	$1.07 \pm 0.055^{*}$	0.94 ± 0.106	1.00 ± 0.076	47	+	Blanckenhorn *et al.* (2006)	Body mass$^{0.33}$
Heteroptera (bugs)								
Gerrinae (water striders)	1.06 ± 0.065	$1.08 \pm 0.043^{*}$	$1.14 \pm 0.131^{*}$	$1.22 \pm 0.078^{*}$	33	+	Fairbairn (1990), (1997)	Body length
		$1.22 \pm 0.059^{*}$			65		Andersen (1997)	
Eotrechinae (water striders)	$1.22 \pm 0.059^{*}$	1.06 ± 0.133	–	–	23	+	Andersen (1997)	Body length
Halobatinae (water striders)	–	$1.72 \pm 0.125^{*}$	–	–	39	+	Andersen (1997)	Body length
Ptilomerinae (water striders)	–	$1.35 \pm 0.104^{*}$	–	–	18	+	Andersen (1997)	Body length
Rhagadotarsinae (water striders)	–	$1.12 \pm 0.098^{*}$	–	–	21	+	Andersen (1997)	Body length
Trepatobatinae (water striders)	–	$1.15 \pm 0.098^{*}$	–	–	39	+	Andersen (1997)	Body length
Odonata (dragonflies)	$1.06 \pm 0.043^{*}$	$1.07 \pm 0.028^{*}$	1.07 ± 0.170	$1.12 \pm 0.109^{*}$	21	+	Johansson *et al.* (2005)	Hind tibia length
Phasmatodea (stick insects)	0.84^{*}	–	–	–	152	−	Sivinski (1978); Sivinski and Dodson (1992)	Body length
Trichoptera (caddisflies)								
Hydropsychidae	1.05 ± 0.100	–	1.04 ± 0.120	1.09 ± 0.720	29	0	Jannot and Kerans (2003)	Body length

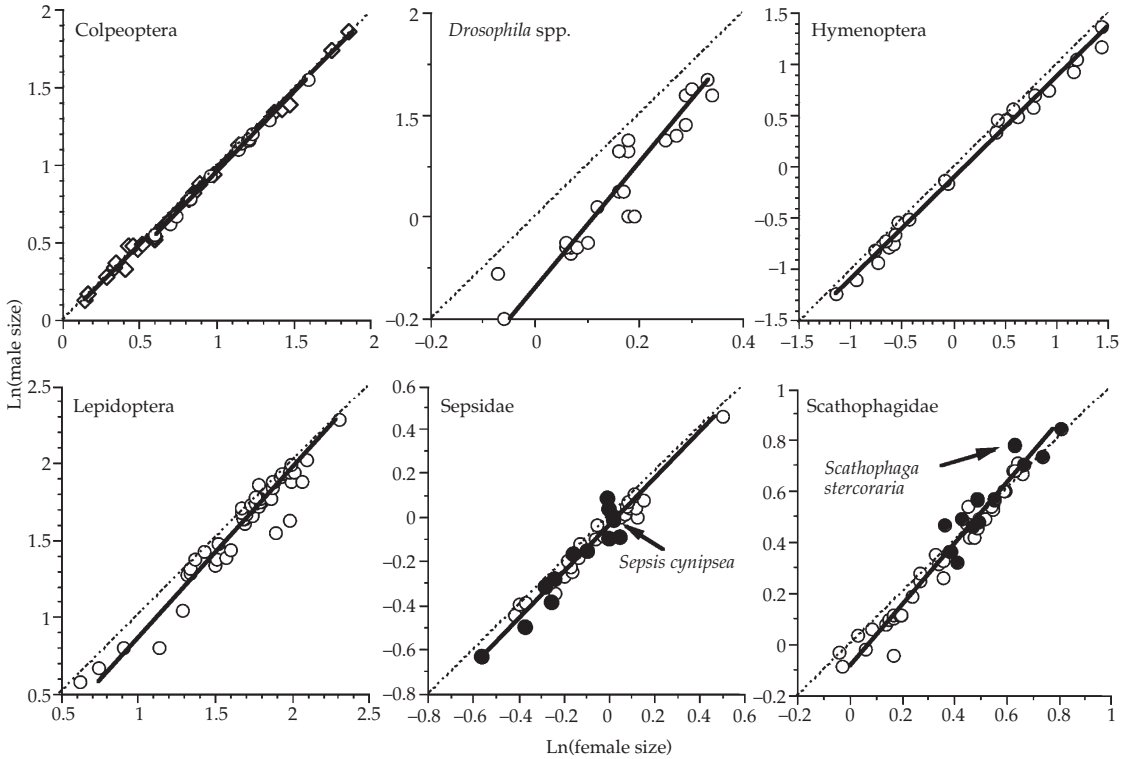

Figure 6.1 Allometric (least-squares) regression plots of mean male on mean female body size (natural-log-transformed; traits and slope estimates are given in Table 6.1) for six insect taxa (line of isometry hatched for comparison). Filled circles for the Sepsidae and Scathophagidae denote the genera *Sepsis* and *Scathophaga*, respectively.

such as body mass). At the order level, Coleoptera, Hymenoptera, and Phasmatodea show allometry that is inconsistent with Rensch's rule, with the latter two even revealing an opposite trend, whereas Diptera, Heteroptera, and (potentially) the Lepidoptera conform to Rensch's rule. Ironically, Rensch's (1950) original carabid beetle example does not follow Rensch's rule, although admittedly he had mentioned that this is not a particularly good example. This limited data-set suggests that Rensch's rule occurs in only about half of insect orders and may consequently not be the norm in insects. Note that the number of estimates within the different orders, as well as their quality (phylogenetic correction or not), varies considerably: for Diptera and Heteroptera several families have been investigated, whereas for most other orders species from all families were combined or only a single family (e.g. Trichoptera) were investigated. However, the various sub-estimates for Diptera and Heteroptera are rather consistent in supporting Rensch's rule. Nevertheless, as shall be shown further below for the Sepsidae (see Figure 6.2 below), within any group Rensch's rule might hold at one taxonomic level (e.g. the family) but not at another (e.g. the genus). Thus overall support for Rensch's rule in the insects remains rather mixed and probably does not deserve the attribute "rule", a pattern also true for spiders (see Chapter 7).

6.3 Patterns among populations within species

A long-standing hypothesis for the evolution of allometry consistent with Rensch's rule is that it is driven by sexual selection for large male size in combination with a generally very high genetic

correlation in body size between the sexes (reviewed in Fairbairn 1997). Fairbairn and Preziosi (1994) investigated this hypothesis by comparing dimorphism together with the intensity of sexual selection on male size among isolated populations of the water strider *Aquarius remigis* (see also Chapter 9). Their reasoning was that if sexual selection on male body size is consistently stronger in one population compared to another living in a different environment (with viability and fecundity selection assumed to be equal), male size should increase, and hence dimorphism change, faster over evolutionary time in that population. Such divergent selection should eventually result in more variation in male than female size among populations, thus generating Rensch's rule (Fairbairn and Preziosi 1994). In so doing, they extended Rensch's rule to the within-species taxonomic level, following a major tenet of evolutionary biology in trying to explain a macroevolutionary pattern among species by studying the putative underlying selective mechanisms operating at the microevolutionary level.

The approach of Fairbairn and Preziosi (1994) was replicated in two species of dung fly by Kraushaar and Blanckenhorn (2002), and intraspecific variation in dimorphism was further studied in two vertebrates (humans and salmon) by Gustafsson and Lindenfors (2004) and Young (2005), yielding overall mixed results. Recently, Blanckenhorn *et al.* (2006) took advantage of sex-specific studies of latitudinal clines to investigate intraspecific patterns of Rensch's rule. Except for the studies by Fairbairn and Preziosi (1994) on Gerridae and Kraushaar and Blanckenhorn (2002) on Sepsidae and Scathophagidae, all estimates presented here stem from studies of sex-specific latitudinal clines (Blanckenhorn *et al.* 2006). Only few individual estimates differ significantly from a MA slope of 1 (shown in italics in Table 6.2) and the data reveal no overall pattern, as only 20 of 37 species have allometric slopes >1 that are consistent with Rensch's rule (mean slope $\pm$ 95% CI, 0.970 ± 0.078). That is, as for the interspecific pattern, there is no evidence for the prevalence of an intraspecific pattern analogous to Rensch's rule in insects. As is well known for insects, dimorphism is female-biased overall (only five of 37 species have larger males), as evidenced by a positive mean size dimorphism index (SDI) of 0.036 ± 0.035 ($\pm$ 95% CI).

Note that when investigating the relationship between male and female body size (as in Figure 6.1), it is actually sufficient to know body-size means and standard deviations. This is because the reduced MA slope of a regression of ln(male size) on ln(female size), which closely approximates the MA slope, can conveniently be calculated as the ratio of the standard deviations of ln(male size) and ln(female size) (Sokal and Rohlf 1995). This should facilitate further studies of Rensch's rule within species as undertaken here.

6.4 Patterns within populations of a given species

In studies examining Rensch's rule, dimorphism has been commonly assumed to have some narrow, species-specific range. In an extensive re-analysis of insect case studies, Teder and Tammaru (2005) demonstrated that this assumption is not necessarily correct. Instead, dimorphism can strongly vary as a function of developmental conditions. Typically, differences between female and male size increased as conditions improved and body size increased. The phenomenon was attributable to a disproportional increase in the size of the larger sex, which was the females in most species analyzed. As a result, female body size was usually more variable than male size at the intra-population level—a pattern of body-size plasticity opposite to that predicted by Rensch's rule. As a plausible explanation, Teder and Tammaru (2005) suggested that the two sexes may be differently constrained by growth conditions when attaining their optimal body sizes: the larger sex responds more strongly to a reduction in environmental quality, thus deviating more from its optimal size than the smaller sex.

Teder and Tammaru (2005) focused their analyses on body mass, the size trait most commonly available. However, some evidence exists that different size traits can show different sex-related patterns of variance. For example, van Alphen and Thunnissen (1983) showed in a parasitoid wasp that an equal increase in head width in the two

Table 6.2 Among-population MA allometric slopes (reduced MA in case of most butterfly data) of ln(male size) on ln(female size) and overall size dimorphism (SDI = (female size/male size − 1) when females are larger; SDI = −(male size/female size − 1) when males are larger; after Lovich and Gibbons 1992) for various insect species. All sizes are in millimeters except *Papilio canadensis* (mg); italic MA values are significantly different from 1; Asterisks indicate multiple estimates; see Blanckenhorn *et al.* (2006a) for references.

Order	Family	Species	Trait	*N*(populations)	Male size	Female size	SDI	MA slope
Coleoptera	Carabidae	*Carabus nemoralis*	Elytron length	26	14.15	14.98	0.059	1.039
Coleoptera	Chrysomelidae	*Phyllotreta striolata*	Elytron length	9	76.62	81.13	0.059	*1.176*
Coleoptera	Chrysomelidae	*Stator limbatus*	Elytron length	92	1.55	1.52	−0.020	*0.879*
Diptera	Drosophilidae	*Drosophila alduchi*	Wing length	5	1.94	2.08	0.072	0.674
Diptera	Drosophilidae	*Drosophila buzzanti*	Wing length	5	1.98	2.15	0.086	1.355
Diptera	Drosophilidae	*Drosophila melanogaster*	Thorax length	18	0.77	0.86	0.117	0.943
Diptera	Drosophilidae	*Drosophila serrata*	Wing length	20	1.19	1.30	0.092	1.047
Diptera	Drosophilidae	*Drosophila simulans*	Wing length	5	1.88	2.16	0.149	*0.609*
Diptera	Drosophilidae	*Drosophila subobscura*	Wing length	10	1.20	1.35	0.125	1.001
Diptera	Drosophilidae	*Zaprionus indianus*	Wing length	10	2.67	2.73	0.022	*1.267*
Diptera*	Scathophagidae	*Scathophaga stercoraria*	Hind tibia length	6	3.56	2.79	−0.276	1.074
				30	3.69	2.94	−0.255	0.931
				30	3.42	2.45	−0.396	1.197
Diptera*	Sepsidae	*Sepsis cynipsea*	Hind tibia length	25	1.36	1.42	0.044	1.002
				25	1.21	1.27	0.050	0.855
Hemiptera*	Gerridae	*Aquarius remigis*	Body length	8	12.83	14.33	0.117	*1.459*
				31				*1.250*
Lepidoptera	Lycaenidae	*Heodes virgaureae*	Wing length	16	15.60	14.80	−0.054	0.919
Lepidoptera	Lycaenidae	*Lycaena helle*	Wing length	12	13.20	13.30	0.008	1.215
Lepidoptera	Lycaenidae	*Palaeocrysophanus hippothoei*	Wing length	15	15.80	16.50	0.044	0.816
Lepidoptera	Lycaenidae	*Polyommatus icarus*	Wing length	10	15.60	14.84	−0.051	0.154
Lepidoptera	Lymantriidae	*Lymantrea dispar*	Wing length	36	24.25	30.27	0.248	*1.274*
Lepidoptera	Papilionidae	*Papilio canadensis*	Body mass$^{0.33}$	2	9.19	9.41	0.024	0.652
Lepidoptera	Satyridae	*Aphantopus hyperantus*	Wing length	15	20.10	21.90	0.090	0.921
Lepidoptera	Satyridae	*Coenonympha arcania*	Wing length	7	16.20	17.00	0.049	1.127
Lepidoptera	Satyridae	*Coenonympha hero*	Wing length	5	15.70	16.20	0.032	1.135
Lepidoptera	Satyridae	*Coenonympha pamphilus*	Wing length	20	14.40	15.80	0.097	0.907
Lepidoptera	Satyridae	*Coenonympha tullia*	Wing length	8	17.50	18.30	0.046	0.950
Lepidoptera	Satyridae	*Erebia ligea*	Wing length	14	22.30	22.50	0.009	1.050
Lepidoptera	Satyridae	*Hipparchia semel*	Wing length	6	24.60	26.70	0.085	0.880
Lepidoptera	Satyridae	*Lasiommata maera*	Wing length	10	24.30	25.20	0.037	0.541
Lepidoptera	Satyridae	*Lasiommata megera*	Wing length	5	21.10	22.70	0.076	1.189
Lepidoptera	Satyridae	*Lasiommata petropolis*	Wing length	8	20.30	20.90	0.030	1.234
Lepidoptera	Satyridae	*Lycaena phlaeas*	Wing length	10	14.00	14.60	0.043	0.790
Lepidoptera	Satyridae	*Maniola jurtina*	Wing length	12	20.90	23.20	0.110	0.767
Lepidoptera	Satyridae	*Pararge aegeria*	Wing length	7	21.20	21.80	0.028	1.012
Odonata	Coenagrionidae	*Enallagma cyathigerum*	Thorax length	7	4.05	4.08	0.007	0.792
Orthoptera	Acridinae	*Caledia captiva*	Pronotum length	8	3.84	4.96	0.292	1.284
Orthoptera	Gryllidae	*Allonemobius socius*	Femur length	21	6.51	7.06	0.084	*0.718*
Orthoptera	Gryllidae	*Pteronemobius fascipes*	Head width	10	1.72	1.86	0.081	1.023
Orthoptera	Gryllidae	*Telogryllus emma*	Head width	19	6.23	6.20	−0.005	*1.028*

sexes lead to a disproportional increase in female body mass, implying differences in body shape. Consequently, any index of dimorphism may strongly differ within species depending on the size trait used for its calculation. For example, a study on four parasitoid wasps revealed that dimorphism based on linear (hind tibia length) and volume (adult mass) measurements may differ even qualitatively: females were typically heavier, whereas males were the larger sex with regard to hind tibia length (Teder 2005). Similarly, Väisänen and Heliövaara (1990) measured a number of different linear size indices in a heteropteran bug, and showed that the corresponding SDI varied between 0 and 0.5 (see also Chapter 9).

To test whether the patterns of sex-related variance in linear structural traits coincide with patterns of variance in body mass found by Teder and Tammaru (2005), we here performed analogous analyses using linear size indices instead of body mass. We extracted relevant data for 58 insect species from the literature. A data-set for any particular species consisted of means of some linear measure of adult size, presented separately for males and females, and reported for at least two different population samples (e.g. in different environments). For each species, ln (male size) was plotted against ln (female size). A reduced MA regression slope $b > 1$ indicates greater variance in male size, whereas $b < 1$ indicates greater variance in female size.

The proportion of species in which linear traits of females responded more strongly to a reduction in environmental quality than those of males was nearly equal to the proportion of species with an opposite trend: $b < 1$ in 29 species (52%); $b > 1$ in 27 species (48%). In contrast, Teder and Tammaru (2005), analyzing an analogous data-set using body mass instead of structural traits, found female body mass to be more sensitive to environmental conditions in nearly 70% of species ($b < 1$ in 98 species; $b > 1$ in 44 species). The two distributions of linear structural and body-mass traits differed significantly (Fisher's exact probability test, $P = 0.03$). A similar tendency was found when comparing the allometric slopes based on body masses with those based on some linear size measure for a paired subset of 16 species for which both types of trait were available (Table 6.3). Within this set of species, the slope of the log–log regression of the structural trait of males on that of females was typically greater than the corresponding slope for male on female body mass (12 higher compared with four lower; binomial test, $P = 0.08$; Table 6.3). In other words, the tendency of female size to be more plastic was stronger when size was expressed in terms of body mass than when linear size traits were used. This is not merely a statistical artifact due to a common mean–variance correlation, which can be largely removed by proper (logarithmic) transformation of the data (Gould 1966; LaBarbera 1989).

Why then do the sex-related patterns of variance depend on the size measure used? A likely explanation is associated with the relative nature of dimorphism based on body mass and linear measures. It is well known in insects that sexual differences in body mass are to a considerable degree attributable to sexual differences in abdomen size. For example, Wickman and Karlsson (1989) demonstrated in seven butterfly species and a calliphorid fly that the proportion of abdomen mass relative to the total body mass is higher in females than in males. The relatively larger abdomens of females have been commonly interpreted as resulting from fecundity selection: a larger abdomen can hold more eggs (Karlsson and Wickman 1990; Preziosi *et al.* 1996; Chapter 9). In the extreme, there may be no optimum for female size as larger (abdomen) size may always be better (e.g. Tammaru *et al.* 2002). In line with this, Wickman and Karlsson (1989) showed that the proportion of abdomen mass relative to total body mass increases with total mass. Male fitness, however, is often determined by his ability to find mating partners, and selection on larger abdomen mass (sperm production) may therefore be counterbalanced by selection on better locomotory abilities (Ghiselin 1974; e.g. Blanckenhorn *et al.* 1995). In contrast, sex-related differences in selection pressure on the sizes of structural traits associated with head and thorax (including wings and legs) are expected to be generally less striking. It follows that, with environmental conditions improving (and body size increasing), females and males should diverge in body mass more than in linear traits.

Table 6.3 Paired comparison of reduced MA regression slopes of ln(male size) on ln(female size) and minimum and maximum size dimorphism across samples (SDI = (female size/male size − 1) when females are larger, and SDI = −(male size/female size−1) when males are larger) for body mass and linear traits.

Order	Family	Species	Linear trait	Slope (body mass)	Slope (linear trait)	Min; max SDI (body mass)	Min; max SDI (linear traits)	Reference
Coleoptera	Carabidae	*Notiophilus biguttatus*	Pronotum width	0.884	1.027	0.032; 0.119	0.032; 0.039	Emsting *et al.* (1992)
Coleoptera	Carabidae	*Poecilus cupreus*	Elytra length	0.333	0.658	−0.010; 0.058	0.004; 0.007	Zangger *et al.* (1994)
Coleoptera	Scolytidae	*Ips sexdentatus*	Pronotum width	0.721	1.245	−0.149; −0.020	−0.061; −0.026	Colineau and Lieutier (1994)
Diptera	Muscidae	*Musca autumnalis*	Wing length	0.610	1.068	0.462; 0.679	0.080; 0.104	Gaaboub and Hayes (1984)
Diptera	Tachinidae	*Eucelatoria rubentis*	Tibia length	2.671	2.758	−0.214; −0.005	−0.120; −0.056	Reitz (1996)
Hymenoptera	Cephidae	*Cephus cinctus*	Forewing length	0.923	1.125	0.821; 1.087	0.039; 0.162	Cárcamo *et al.* (2005)
Hymenoptera	Encyrtidae	*Syrphophagus aphidivorus*	Wing length	0.550	0.001	0.000; 0.200	0.039; 0.117	Buitenhuis *et al.* (2004)
Hymenoptera	Megaspilidae	*Dendrocerus carpenteri*	Hind tibia length	0.963	0.970	−0.124; 0.612	−0.025; 0.156	Otto and Mackauer (1998)
Orthoptera	Acrididae	*Chorthippus brunneus*	Hind femur length	0.515	0.527	0.443; 0.910	0.161; 0.281	Willott and Hassall (1998)
Orthoptera	Acrididae	*Myrmeleotettix maculatus*	Hind femur length	0.784	0.915	0.360; 0.419	0.154; 0.157	Willott and Hassall (1998)
Orthoptera	Acrididae	*Omocestus viridulus*	Hind femur length	0.676	0.910	0.660; 0.721	0.246; 0.250	Willott and Hassall (1998)
Lepidoptera	Lycaenidae	*Hemiargus isola*	Forewing length	2.409	2.059	0.041; 0.139	−0.001; 0.022	Wagner and Martinez del Rio (1997)
Lepidoptera	Noctuidae	*Agrotis ipsilon*	Forewing length	1.048	1.172	0.122; 0.132	0.044; 0.052	Sappington and Showers (1992)
Lepidoptera	Noctuidae	*Spodoptera frugiperda*	Forewing width	0.823	0.389	−0.085; 0.038	−0.036; 0.035	Ferguson *et al.* (1994)
Lepidoptera	Tortricidae	*Bactra verutana*	Wing length	1.067	0.935	0.451; 1.250	0.121; 0.183	Frick and Wilson (1982)
Trichoptera	Limnephilidae	*Potamophylax cingulatus*	Wing length	0.763	1.123	0.204; 0.475	0.017; 0.060	Svensson (1975)

6.5 Relationships among the various taxonomic levels

After investigating the evidence for Rensch's rule at three taxonomic levels (among species, among populations within species, and within populations), we now ask whether the patterns correlate. As outlined in the Introduction, plots of male on female size (Figure 6.1), indicating sexual differences in body-size variance, and hence Rensch's rule, can formally be generated at all these levels by plotting species means, population means, or family or group means in various environments, respectively, as done here. Direct comparisons are possible if such estimates are available for a given group of species, and we here present two such examples for the sepsid and scathophagid flies (Figure 6.2). Data for the higher taxonomic levels (species, genera) stem from field-caught, pinned specimens at the Zoological Museum, Copenhagen, Denmark, whereas laboratory and field estimates at lower taxonomic levels were gathered at the Zoological Museum, Zurich, Switzerland. The species estimates refer to the genera *Sepsis* spp. and *Scathophaga* spp., and the population and family estimates refer to *Sepsis cynipsea* and *Scathophaga stercoraria* (data from Blanckenhorn 1997b, 1998a, unpublished work; Kraushaar and Blanckenhorn 2002). In most sepsids, as is the case for *S. cynipsea,* females are larger than males, and in many scathophagids, as is the case for *S. stercoraria,* males are larger than females (Figure 6.1).

Four observations can be gathered from this admittedly limited comparison of allometric body-size slopes at various taxonomic levels in these two species groups (Figure 6.2). First, in the scathophagids all estimates are congruent in that males show greater variance than females at all taxonomic levels, with slopes generally >1, consistent with Rensch's rule. In the sepsids, in contrast, the estimates are incongruent: only the interspecific estimates tend to conform to Rensch's rule (slope >1), males thus exhibiting more variance, whereas the intraspecific estimates show slopes ≤1, indicating greater variance among females (or equal variances for both sexes). In the sepsids, therefore, intraspecific patterns do not predict interspecific patterns, whereas in the scathophagids they do (see Kraushaar and Blanckenhorn 2002). Second, in both families intraspecific body-size variance tends to be greater in the larger sex (females in *S. cynipsea,* males in *S. stercoraria*; Figure 6.2; see section 6.4). This is consistent with a correlation between mean and variance that is frequently observed in metric data: often a data-set with a greater mean also displays greater variance, which is one of the prime reasons for statistical data transformation (Sokal and Rohlf 1995). It also suggests that intraspecific patterns largely reflect mechanisms generated by phenotypic plasticity, whereas interspecific patterns should rather reflect

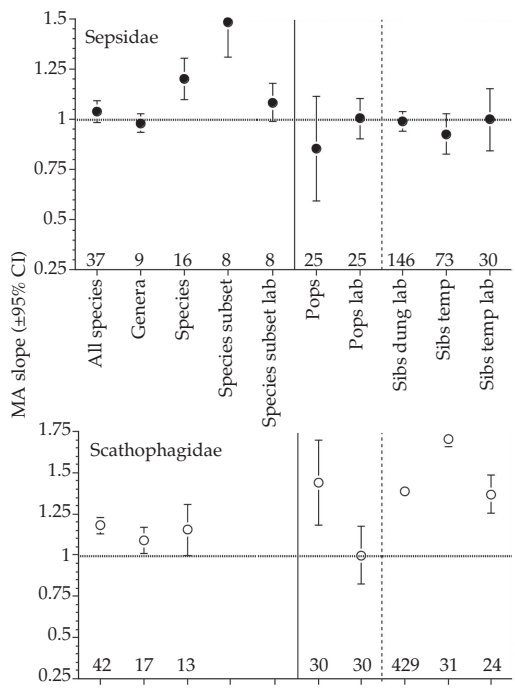

Figure 6.2 MA regression slopes (± 95% CI) at various taxonomic levels (from left to right: among species, among populations, and among families of *Sepsis cynipsea* and *Scathophaga stercoraria*), for field-caught and laboratory-reared specimens of the Dipteran groups Sepsidae and Scathophagidae (sample sizes given underneath). The species subset for the Sepsidae refers to eight species of *Sepsis* for which field and laboratory data were available. Sibs dung lab: full-sib offspring (families) of one population, reared in the lab at various dung (= food) conditions; Sibs temp: full-sib offspring (families) of one population, reared in the field throughout the season at various temperatures; Sibs temp lab: full-sib offspring (families) of one population, reared in the lab at various temperatures.

mechanisms related to the speciation process, with possibly little correspondence between the two (see Fairbairn 2005). Thus interspecific patterns are unlikely to be generally predictable from intraspecific (among-population) studies, as originally envisioned by Fairbairn and Preziosi (1994) and Kraushaar and Blanckenhorn (2002). Third, at least in the sepsids (Figure 6.2) even the interspecific estimates are quite variable: allometric slopes among *Sepsis* species are clearly >1, following Rensch's rule, whereas among genera (averaging various species within a given genus) and overall the slopes are equal to 1. Thus interspecific patterns at various taxonomic levels (species, genus, family, etc.) are not necessarily consistent, and it would be interesting to systematically investigate this pattern in other groups. Such variation in interspecific dimorphism at various taxonomic levels, typically revealed by nested analysis of variance, is known from other taxa (e.g. Kappeler *et al.* 1996; Jannot and Kerans 2003). Fourth, again in the sepsids, allometric slopes generated from field-caught specimens were substantially steeper than those obtained when the same eight species were reared in the laboratory (Figure 6.2). This suggests that standardized and rather benign rearing procedures in the laboratory, which typically reduce the degree of phenotypic plasticity and hence produce adults of maximal body size, can affect even interspecific allometric slopes and ultimately the extent of Rensch's rule (see section 6.4). More data-sets of this kind are clearly needed to evaluate the generality of these findings.

6.6 Summary and conclusions

Abouheif and Fairbairn (1997) found Rensch's rule to be a common pattern among animal species, a result largely dominated by vertebrates, with data on invertebrates being rare in their sample. We here re-evaluated the evidence for insects with new data-sets and found Rensch's rule consistently in Diptera (flies) and Heteroptera (Gerridae; water striders), but not in other insect groups (except perhaps in Lepidoptera; Table 6.1), suggesting that the mechanisms causing the pattern are unevenly distributed among taxa. Extending our investigation to the level among populations within species also revealed no consistent evidence for Rensch's rule (Table 6.2), although when populations are ordered by latitude a pattern consistent with Rensch's rule was found more commonly than expected by chance (Blanckenhorn *et al.* 2006). In contrast, at the level within populations of a given species at different environmental conditions, reflecting phenotypic plasticity, the majority of insects show more variation in female (typically the larger sex) than male body size, opposite to Rensch's rule (Teder and Tammaru 2005), a result that weakened when linear structural traits were used as a size measures instead of body mass. A specific comparison of these three taxonomic levels revealed congruence in scathophagid flies, typically featuring male-biased dimorphism and allometry consistent with Rensch's rule at all levels, but no congruence in sepsid flies, in which female-biased dimorphism dominates (the common pattern in insects). Patterns of body size allometry at the three taxonomic levels consequently generally do not correspond well. Whether patterns at lower levels can reveal the (selective) mechanisms causing Rensch's rule at higher levels therefore remains questionable and should be scrutinized further. To extend or correct the patterns found here, we strongly encourage researchers to gather more data on female and male body size variation at multiple taxonomic levels for a given species group, taking both linear structural and body mass traits for direct comparison and analyzing the data using the standardized methods exemplified here.

6.7 Acknowledgments

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6.8 Suggested readings

Abouheif, E. and Fairbairn, D.J. (1997) A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *American Naturalist* **149**, 540–562.

Blanckenhorn, W.U., Stillwell, R.C., Young, K.A., Fox, C.W., and Ashton, K.G. (2006) When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude? *Evolution* **60**, 2004–2011.

Teder, T. and Tammaru, T. (2005) Sexual size dimorphism within species increases with body size in insects. *Oikos* **108**, 321–334.