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## **Interrelations of global macroecological patterns in wing and thorax size, sexual size dimorphism, and range size of the Drosophilidae**

Rohner, Patrick T ; Pitnick, Scott ; Blanckenhorn, Wolf U ; Snook, Rhonda R ; Bächli, Gerhard ; Lüpold, Stefan

**Abstract:** Support for macroecological rules in insects is mixed, with potential confounding interrelations between patterns rarely studied. We here investigate global patterns in body and wing size, sexual size dimorphism and range size in common fruit flies (Diptera: Drosophilidae) and explore potential interrelations and the predictive power of Allen's, Bergmann's, Rensch's and Rapoport's rules. We found that thorax length ( $r^2 = 0.05$ ) and wing size ( $r^2 = 0.09$ ) increased with latitude, supporting Bergmann's rule. Contrary to patterns often found in endothermic vertebrates, relative wing size increased towards the poles ( $r^2 = 0.12$ ), a pattern against Allen's rule, which we attribute to selection for increased flight capacity in the cold. Sexual size dimorphism decreased with size, evincing Rensch's rule across the family ( $r^2 = 0.14$ ). Yet, this pattern was largely driven by the virilis – repleta radiation and only weakly in other lineages. Finally, range size did not correlate with latitude, although a positive relationship with latitude was present in a subset of the species investigated, providing no convincing evidence for Rapoport's rule. We further found little support for confounding interrelations between body size, wing loading and range size in this taxon. Nevertheless, we demonstrate that studying several traits simultaneously at minimum permits better interpretation in case of multiple, potentially conflicting trends or hypotheses concerning the macroecology of insects.

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1 **Interrelations of global macroecological patterns in wing and thorax size, sexual**  
2 **size dimorphism, and range size of the Drosophilidae**

3

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17 **ABSTRACT**

18 Support for macroecological rules in insects is mixed, with potential confounding  
19 interrelations between patterns rarely studied. We here investigate global patterns in body and  
20 wing size, sexual size dimorphism and range size in common fruit flies (Diptera:  
21 Drosophilidae) and explore potential interrelations and the predictive power of Allen's,  
22 Bergmann's, Rensch's and Rapoport's rules. We found that thorax length ( $r^2 = 0.05$ ) and wing  
23 size ( $r^2 = 0.09$ ) increased with latitude, supporting Bergmann's rule. Contrary to patterns often  
24 found in endothermic vertebrates, relative wing size increased towards the poles ( $r^2 = 0.12$ ), a  
25 pattern against Allen's rule, which we attribute to selection for increased flight capacity in the  
26 cold. Sexual size dimorphism decreased with size, evincing Rensch's rule across the family ( $r^2$   
27  $= 0.14$ ). Yet, this pattern was largely driven by the *virilis – repleta* radiation and only weakly in  
28 other lineages. Finally, range size did not correlate with latitude, although a positive  
29 relationship with latitude was present in a subset of the species investigated, providing no  
30 convincing evidence for Rapoport's rule. We further found little support for confounding  
31 interrelations between body size, wing loading and range size in this taxon. Nevertheless, we  
32 demonstrate that studying several traits simultaneously at minimum permits better  
33 interpretation in case of multiple, potentially conflicting trends or hypotheses concerning the  
34 macroecology of insects.

35        **INTRODUCTION**

36        Convergent patterns of phenotypic variation across large-scale environmental gradients  
37        have long been recognized and have given rise to several macroecological “rules” predicting  
38        such variation as putative adaptive responses to selection. These patterns are generally  
39        supported by empirical evidence and underlie theory. Until a more complete understanding  
40        of the selective mechanisms underlying the patterns is achieved, however, the predictive  
41        power of such rules must remain limited. This is particularly true for insects, in contrast to  
42        mammals and birds (Blanckenhorn and Demont 2004; Chown and Gaston 2010; Shelomi 2012).

43        As in all organisms, insect body size is inherently linked to physiology, metabolic rate,  
44        survival and reproductive success and is thus thought to evolve in predicted ways if subjected  
45        to similar selective drivers (Blanckenhorn 2000, Chown and Gaston 2010). Large size typically  
46        increases mating success in males and fecundity in females, but can entail heightened  
47        mortality risks and reproductive costs due to prolonged larval development (Blanckenhorn  
48        2000). Amongst the macroecological rules proposed to account for body size variation,  
49        Bergmann’s rule, signifying an increase in size with latitude, is well supported in  
50        homoeothermic vertebrates (Bergmann 1847; Meiri and Dayan 2003), but its absence and often  
51        its converse is prominent among invertebrates (Shelomi 2012). An increase in size with latitude  
52        has been attributed to temperature-dependent variation in growth and metabolic rates, a  
53        pattern congruent with the so-called temperature-size rule (Atkinson 1994; Atkinson & Sibly  
54        1997) that generally predicts insects to grow bigger in the cold (Kingsolver & Huey 2008).  
55        However, a shortened active season with increasing latitude can also cause adaptive negative  
56        size clines through selection for fast development if development cannot be extended across  
57        one season, both within and between species (Chown et al. 1999, Blanckenhorn and Demont  
58        2004; Zeuss et al. 2017). Small insects with rapid development are thus expected to follow

59 Bergmann clines, whereas large insects may be limited in their development by season length  
60 at high latitudes, thus emerging smaller and showing converse Bergmann clines  
61 (Blanckenhorn and Demont 2004, Zeuss et al. 2017).

62 In contrast to body size, the relative size of appendages has been found to decrease with  
63 latitude in endothermic vertebrates (e.g., Nudds and Oswald 2007, Symonds et al. 2010).  
64 Termed Allen's rule, this pattern has received considerable attention and has been attributed  
65 to selection for a reduced surface-to-volume ratio to limit heat loss in the cold. Originally  
66 documented for warm-blooded animals (Allen 1877), qualitatively similar patterns have also  
67 been described in invertebrates (e.g. Alpatov 1929, Ray 1960). In insects, most appendages,  
68 including wings and antennae, are connected to the circulatory system (Chapman et al. 2013),  
69 and the constant flow of haemolymph through these appendages can contribute to  
70 thermoregulation, as in endotherms. Patterns equivalent to Allen's rule might thus be  
71 expected. Still, particularly for small insects, body temperature is unlikely to be strongly  
72 dependent on the relative surface area as an insect's body adjusts nearly instantly to the  
73 ambient temperature (Harrison and Roberts 2000), although many insect taxa are capable of  
74 considerable thermoregulation (social Hymenoptera in particular; e.g., Stabentheiner et al.  
75 2010; Chapman et al. 2013). Consequently, small insects primarily regulate their body  
76 temperature by modifying their behavior (Clench 1966, Dillon et al. 2009), thus making best  
77 use of available microhabitats. The capacity to disperse, however, is greatly restricted at cool  
78 temperatures, which impedes take-off in winged insects (Dillon and Frazier 2006, Frazier et al.  
79 2008). As increased wing size relative to body size facilitates take-off at cooler temperatures  
80 (Frazier et al. 2008), a latitudinal increase of relative wing size (a pattern counter to Allen's  
81 rule) can be predicted. Such patterns have indeed been observed in insects (e.g. clinal  
82 population differentiation in *D. melanogaster*: Azevedo et al. 1998), but the repeatability of such

83 cines awaits further scrutiny. Whether the relative size of insect appendages increases,  
84 decreases or shows any consistent latitudinal pattern at all thus remains unclear.

85 Whereas both Bergmann's and Allen's rules describe spatial variation in body and  
86 appendage size irrespective of sex, the widely-studied Rensch's rule focuses on variation in  
87 sexual size dimorphism (SSD; Abouheif and Fairbairn 1997; Fairbairn 1997). Rensch (1950)  
88 documented that, among closely related species of many disparate taxonomic groups, SSD  
89 increases with body size in species in which males are the larger sex but decreases when  
90 females are larger than males. Unlike Bergmann's and Allen's rules, which capture size  
91 variation that likely results from natural selection, differential variation between the sexes has  
92 been attributed to a combination of sexual selection on males (e.g., via male-male contest  
93 competition) and fecundity selection on females (Fairbairn and Preziosi 1994, Fairbairn 1997,  
94 Székely et al. 2004). However, evidence for Rensch's rule is mixed, particularly in taxa with  
95 female-biased size dimorphism, such as most insects and spiders (for which SSD tends to  
96 increase with body size: Blanckenhorn et al. 2007b; Webb and Freckleton 2007; Stuart-Fox  
97 2009), undermining its predictive power.

98 Finally, in addition to body size, populations or species have also been documented to vary  
99 in their range size. Specifically, Rapoport's rule (or "effect": Stevens 1992) predicts that species  
100 occurring close to the equator will have more restricted ranges because they exhibit limited  
101 climatic tolerance as a result of adapting to a local environment with low climatic variability.  
102 Conversely, species occurring at higher latitudes (or altitudes), which feature ample climatic  
103 variability, are predicted to be better adapted to colonize and occupy more diverse habitats.  
104 Evidence for this rule is still controversial as it might be restricted to specific latitudes and  
105 certain regions and somewhat scale dependent (Rohde 1996, Ruggiero and Werenkraut 2007).

106 The four macroecological patterns described above are often studied in isolation from each  
107 other. Nevertheless, body size, wing morphology (which relates to dispersal capacity; e.g.,  
108 Ray et al. 2016), SSD and range size are all likely to be ecologically and evolutionarily  
109 interrelated, if only because most adaptive explanations discussed above relate to climate. For  
110 example, although Rensch's rule has mostly been studied independently of environmental  
111 factors, latitudinal patterns of SSD have been observed (Blanckenhorn et al. 2006), and a  
112 relationship of Rensch's rule with the widely-observed temperature-size rule was postulated  
113 but not found after all (Hirst et al. 2015). Similarly, a large body of literature investigates  
114 relationships between range size and both dispersal capacity and body size (Gaston and  
115 Blackburn 1996, Malmqvist 2000, Lester et al. 2007, Rundle et al. 2007, Laube et al. 2013), thus  
116 raising the issue of whether clinal variation in size and dispersal might generally drive  
117 Rapoport's rule, possibly undermining its ecological relevance (Reed 2003). It is thus useful -  
118 if not imperative - to account for additional potentially confounding effects when investigating  
119 range-size variation (Laube et al. 2013).

120 Rigorous examination of macroecological patterns requires not only robust taxon sampling  
121 and coverage of a large geographic range, but also the ability to account for phylogenetic  
122 relationships among species. The Drosophilidae, a highly speciose and diverse family of fruit  
123 flies with a global distribution, should be highly suited to assess such patterns and their  
124 underlying mechanisms in insects. Many drosophilids are cosmopolitan generalists, whereas  
125 others are highly specialized and endemic to small geographic areas (e.g., see Ashburner 1981).  
126 In this taxon, Bergmann's rule has received considerable attention at the intraspecific level  
127 along both latitudinal and altitudinal gradients (e.g., *D. melanogaster*: van't Land et al. 1999,  
128 Fabian et al. 2015, Klepsatel et al. 2014; *D. buzzatii*: Karan et al. 2000; *D. subobscura*: Gilchrist et  
129 al. 2001; *Zaprionus indianus*: Karan et al. 2000), but little information is available at the



130 interspecific level. Similarly, Rensch's rule has been addressed in the *obscura* group (Huey et  
131 al. 2006), but the general pattern has not been investigated (but see Blanckenhorn et al.  
132 2007a,b). The potential relationship of range size with body and appendage size also remains  
133 largely unexplored in this group.

134 We here assessed in a comparative framework the ecogeographical patterns of thorax  
135 length and wing size, SSD, and range size in 151 drosophilid species from around the globe,  
136 including members of all three major *Drosophila* clades plus species of other genera belonging  
137 to this speciose family. Accounting for phylogenetic non-independence based on a  
138 reconstructed phylogeny, we investigated the geographical patterns described above and  
139 potential relationships between the four macroecological rules. Such relationships are  
140 expected under the prediction that they all relate (to some extent) to climate, but their  
141 covariation is poorly studied empirically. We thus aimed to better understand the causes and  
142 consequences of macroecological variation.

## 143 **MATERIALS & METHODS**

### 144 **Phylogeny reconstruction**

145 To reconstruct the drosophilid phylogeny, we obtained the sequences of six nuclear, three  
146 mitochondrial and three mitochondrial ribosome genes from GenBank (see Supplementary  
147 Table S1 for accession numbers and sequence coverage). The gene coverage per species ranged  
148 between 1 and 12 (mean  $\pm$  SD =  $7.2 \pm 2.9$  loci/species), with a total sequence length of  $6,269.2 \pm$   
149  $3,267.6$  bp (range = 337 – 14,449 bp). The nuclear sequences comprised the genes expressing  
150 the alcohol dehydrogenase (Adh),  $\alpha$ -amylase-related protein (Amyrel), aromatic-L-amino-  
151 acid decarboxylase (DOPA decarboxylase; Ddc), glycerol-3-phosphate dehydrogenase  
152 (Gpdh), and xanthine dehydrogenase (Xdh). The mitochondrial genes included the

153 cytochrome c oxidase subunits I, II, and III (COI, COII and COIII, respectively) and the NADH  
154 dehydrogenase subunit 2 (ND2). The ribosomal genes included 28S and the large and small  
155 subunits of 12S and 16S (omitting the adjacent tRNAs as they were difficult to align and  
156 represented only a small amount of data). For each locus, we aligned the sequences of all  
157 species using multiple sequence alignment (MUSCLE) as implemented in MEGA v.7.0 (Kumar  
158 et al. 2016) and determined its best nucleotide substitution model using jModelTest v.2.1.7  
159 (Darriba et al. 2012). The best substitution models were GTR+ $\Gamma$ +I for all nuclear genes and 16S,  
160 HKY+ $\Gamma$ +I for the mitochondrial genes and 12S, and HKY for 28S, respectively.

161 Subsequently, we reconstructed the phylogeny based on Bayesian inference using BEAUTi  
162 and BEAST v.1.8.3 (Drummond et al. 2012), with unlinked substitution models, a relaxed  
163 uncorrelated log-normal clock, and a Yule speciation process. Due to a lack of well-defined  
164 fossil dates in our sample of species, and because the absolute timing of speciation events was  
165 deemed less important for our analyses than the relative branch lengths, we omitted the time  
166 calibration. We ran the Markov Chain Monte Carlo (MCMC) simulation on the CIPRES Science  
167 Gateway (<http://www.phylo.org>; Miller et al. 2010) for 100 million generations, sampling  
168 every 10,000th tree. We used Tracer v.1.6 (Rambaut and Drummond 2013) to examine the  
169 convergence of the Bayesian chain and the stationary states of all parameters, considering  
170 effective sample sizes (ESSs) greater than 200 to be adequate. Finally, we generated a  
171 maximum clade credibility tree with mean node heights and a 10% burn-in using  
172 TreeAnnotator v.1.8.3 (Drummond et al. 2012).

173 In addition to the full *Drosophila* phylogeny, we separately generated a phylogeny for the  
174 *Zaprionus* dataset (for which only body lengths and no thorax lengths were available). For  
175 these species, adequate sequence coverage was restricted to the Amyrel, COI, COII, and 28S

176 genes, respectively (see Supplementary Table S2). We used the same procedures as above,  
177 except that GTR+ $\Gamma$ +I was the best substitution model for all loci and the MCMC chain was run  
178 for only 30 million generations, with a tree sampled every 3,000 generations.

### 179 **Data collection**

180 We measured sex-specific body size as thorax length of field-caught specimens (distance  
181 between the tip of the scutellum and the basis of the head, a standard measure) for 56 species  
182 of Drosophilidae stored at the Zoological Museum of the University of Zurich. Whenever  
183 available, we measured at least 10 individuals per sex per species. We further obtained thorax  
184 length data for 111 additional species and data on total body length for 20 *Zaprionus* species  
185 from the literature (see Supplementary Table S3).

186 For each of our 146 species available in the database TaxoDros  
187 (<http://www.taxodros.uzh.ch/>), we retrieved the geographic coordinates of every faunistic  
188 record. This database comprises an enormous amount of information on the taxonomy and  
189 distribution of more than 6,800 species of drosophilids. All coordinates are derived from  
190 published data or stem from museum catalogs in which the identification was verified by  
191 experts. Although these faunistic data do not stem from standardized collecting schemes but  
192 are somewhat haphazard in nature, TaxoDros represents one of the most powerful and  
193 comprehensive data sources for any insect taxon. Nonetheless, the sampling coverage might  
194 be biased towards certain regions and not be homogeneous across the globe, a common  
195 problem when handling such datasets. Thus, we concede that any inference based on these  
196 distribution data should be treated with some caution (see Conclusion).

197 We included only species with at least 20 unique sampling locations in our analyses  
198 (removing duplicate and nonsensical localities, resulting in over 25,000 unique coordinates;

199 mean number of coordinates per species: 273.3, SE: 47.9, median: 137; Fig. 1). Many  
200 drosophilids are distributed globally, but their range is often restricted within latitudinal  
201 bands such that they do not occur at the equator. We thus used the mean of the *absolute*  
202 latitudinal distribution to obtain a suitable estimate of the species-specific latitudinal  
203 distribution.

204 Although several major ecogeographic rules describe patterns of latitudinal trait variation,  
205 latitude itself remains a compound trait integrating various climatic factors. In this respect, the  
206 differential effects of temperature and seasonality are of particular interest. Using climatic  
207 data, we tried to decompose latitude into variates related to temperature or seasonality.  
208 However, due to the high collinearity among climate variables and latitude, we were unable  
209 to use multiple-regression approaches (variance inflation factor always greater than 5 and  
210 often greater than 10). When using a principal component analysis (with oblique rotation) to  
211 extract the major axes of variation, both temperature and seasonality variables loaded strongly  
212 on the first principal component (but in opposite directions, thus mirroring latitude), while all  
213 other dimensions did not explain significant proportions of variance and did not show any  
214 association to either temperature nor seasonality (Supplementary Table 1). For the sake of  
215 interpretation (as we were unable to disentangle temperature from seasonality and latitude),  
216 we decided to restrict our analyses to latitudinal patterns alone, although future studies  
217 disentangling the climate compounds of latitude are clearly desirable.

### 218 **Thorax length**

219 We analyzed the relationship between log thorax length (mean of male and female values)  
220 and median latitude, using phylogenetic generalized linear models (PGLS) as implemented in  
221 the R package *caper* (Orme et al. 2012). We used the sexual dimorphism index (SDI) as an

222 estimate of the strength and direction of SSD as proposed by Lovich and Gibbons (1992). We  
223 thus divided the thorax length of the larger sex (usually the female) by the smaller and  
224 subtracted 1 from this ratio, which arbitrarily defines the SDI positive if females are the larger  
225 sex and negative if males are larger.

## 226 **Wing size**

227 We retrieved wing-size data for 54 species from Bolstad et al. (2015). These wing sizes  
228 represent the square root of wing area derived from outline spline reconstructions. To assess  
229 clinal variation in relative wing size, we used PGLS with latitude as the predictor and thorax  
230 length as a covariate. In addition, we calculated wing loading, which is typically associated  
231 with wing-beat frequency and flight capacity (Pétavy et al. 1997; Frazier et al. 2008). Wing  
232 loading is usually defined as some ratio of body mass and wing area, where low values relate  
233 to better dispersal capacity as less weight is “loaded” onto the wing. Because body mass  
234 estimates were lacking, we used thorax length<sup>3</sup>, which scales well with mass. We analyzed its  
235 relationship with latitude using PGLS.

## 236 **Sexual size dimorphism**

237 To test whether SSD scales iso- or allometrically with body size, we applied phylogenetic  
238 reduced major-axis regressions (as implemented in the R package *phytools*: Revell 2012) of log  
239 male against log female thorax length across all species (for justification see Fairbairn 1997;  
240 Blanckenhorn et al. 2006). Rensch’s rule is evident only if the slope of this relationship exceeds  
241 one. We repeated the analysis separately for all three major clades of *Drosophila* (*Sophophora*  
242 subgenus, *immigrans-tripunctata* radiation, *virilis-repleta* radiation) and the *Zaprionus spp.* data  
243 set, for which body size was measured as total body length. To quantify the predictive strength

244 of Rensch's rule in drosophilids, we further calculated  $r^2$  from a PGLS of SDI against log mean  
245 size.

## 246 **Range size**

247 When investigating variation in range size, we considered only species with 20 or more  
248 unique records, thus reducing the number of species with sufficient data to 110 (mean number  
249 of coordinates per species: 273.3, SE: 47.9; median: 137). To approximate range sizes directly  
250 from faunistic records, we derived range-size estimates using  $\alpha$ -hulls (as in Gallagher 2016),  
251 which are more robust than simple minimum convex polygons, particularly when sampling  
252 is haphazard and not standardized (Burgman and Fox 2003). We used the Lambert azimuthal  
253 equal-area projection to generate appropriate range-size estimates in  $\text{km}^2$  across the globe and  
254 restricted these range sizes to actual land masses using the R package *rangeBuilder* (Davis  
255 Rabosky et al. 2016). A PGLS model was used to test for a relationship between log range sizes  
256 and latitude (median). In order to test for potential confounding effects of body size and  
257 relative wing length (as an estimate of short-distance dispersal), we also performed multiple  
258 PGLS regression analyses with thorax length and wing size as covariates. As wing sizes were  
259 available for only 54 species, the sample size for this analysis was drastically reduced (note,  
260 however, that the number of sampling coordinates per species was greater in this reduced data  
261 set: mean: 395.9, SE: 89.7; median: 176).

262

## 263 **RESULTS**

### 264 **Thorax length and wing size**

265 Log mean thorax length and wing size increased with median latitude (thorax length:  $r =$   
266 0.23 [95% confidence limits: 0.04, 0.39],  $\lambda = 0.97$ ,  $n = 107$ ,  $P = 0.019$ ; wing size:  $r = 0.30$  [0.04, 0.51],

267  $\lambda = 0.96$ ,  $n = 54$ ,  $P = 0.026$ ; fig. 1), although the unexplained variation in thorax and wing size  
268 was rather large (fig.1). Log wing size also showed a positive relationship with latitude when  
269 log thorax length was included as a covariate ( $r = 0.30$  [0.03, 0.50],  $\lambda = 0.55$ ,  $n = 54$ ,  $P = 0.031$ ),  
270 suggesting a disproportionate increase in wing size towards high latitudes. Accordingly, wing  
271 loading decreased with latitude ( $r = -0.35$  [-0.09, -0.54],  $\lambda = 0.00$ ,  $n = 54$ ,  $P = 0.009$ ; fig. 1).

## 272 **Sexual size dimorphism**

273 Phylogenetic signals in male thorax length ( $\lambda = 0.86$ ,  $P < 0.001$ ), female thorax length ( $\lambda =$   
274  $0.84$ ,  $P < 0.001$ ), mean body size ( $\lambda = 0.85$ ,  $P < 0.001$ ) and SSD ( $\lambda = 0.75$ ,  $P < 0.001$ , fig. 2) suggest  
275 phylogenetic inertia of body size and SSD in drosophilids (fig. 2). When testing Rensch's rule  
276 across all species, RMA slopes were significantly steeper than unity ( $\beta_{\text{phyIRMA}}$ : 1.10 [1.06, 1.15],  
277  $P < 0.001$ ,  $n = 151$ ; fig. 3), and body size explained 14% of the total variation in SDI. RMA slopes  
278 did not significantly differ between radiations (log female size x radiation interaction:  $F_{2,114} =$   
279  $2.31$ ,  $P = 0.104$ ), however, when testing Rensch's rule within the three major radiations, we did  
280 not find consistent support. Rensch's rule was evident in the *virilis - repleta* radiation ( $\beta_{\text{phyIRMA}}$ :  
281  $1.08$  [1.01, 1.14],  $P = 0.021$ ,  $n = 48$ ; fig. 3), but not in the *immigrans - tripunctata* radiation ( $\beta_{\text{phyIRMA}}$ :  
282  $1.02$  [0.92, 1.13],  $P = 0.650$ ,  $n = 22$ ; fig. 3). In the *Sophophora* subgenus, the RMA slopes were very  
283 steep ( $\beta_{\text{phyIRMA}}$ : 1.18 [1.06, 1.31],  $P = 0.002$ ,  $n = 51$ ; fig. 3), but this pattern was driven exclusively  
284 by *Drosophila prolongata*. This species is by far the largest member of this subgenus and the  
285 only one showing male-biased SSD. When excluding *D. prolongata*, Rensch's rule was no  
286 longer supported in this clade ( $\beta_{\text{phyIRMA}}$ : 0.99 [0.92, 1.08],  $P = 0.996$ ,  $n = 50$ ; fig. 3). The  
287 relationship of male and female body length also did not deviate from isometry in *Zaprionus*  
288 *spp.* ( $\beta_{\text{phyIRMA}}$  : 1.06 [0.83, 1.28],  $P = 0.577$ ,  $n = 16$ ; fig. 3). There was also no evidence for a  
289 correlation between sexual size dimorphism and latitude ( $r = 0.09$ , [-0.10, 0.27],  $\lambda = 0.67$ ,  $n =$   
290  $107$ ,  $P = 0.369$ ).

## 291      **Range size**

292      Log range size did not correlate with latitude in the simple linear model using the full data  
293 set ( $r = 0.03$  [-0.16, 0.22],  $\lambda = 0.03$ ,  $n = 105$ ,  $P = 0.777$ , fig. 4). However, in a phylogenetic multiple  
294 regression including thorax and wing size as additional explanatory variables, range size  
295 increased towards the poles ( $r = 0.37$  [0.11, 0.56],  $P = 0.007$ ,  $\lambda = 0.98$ ) whereas thorax and wing  
296 length had no effect on range size (thorax:  $r = 0.10$  [-0.17, 0.36],  $P = 0.469$ ,  $\lambda = 0.98$ ; wing size:  $r$   
297  $= 0.04$  [-0.23, 0.30],  $P = 0.770$ ,  $\lambda = 0.98$ ). Note that the data underlying this multiple regression  
298 represent only a subset of the data because wing size, thorax length and range extent data were  
299 available for only 54 species.

300

## 301      **DISCUSSION**

302      Our study of the morphology and global distribution patterns of Drosophilidae lends  
303 support to several macroecological phenomena. In accordance with Bergmann's rule, thorax  
304 length and wing size increased with latitude, and the same was true for relative wing size  
305 (contrary to Allen's rule). Our data on SSD also support Rensch's rule overall, but this pattern  
306 was mostly driven by the *virilis - repleta* radiation, with weak support in three other major  
307 clades. We found no further evidence for a latitudinal cline in SSD. Range size did not vary  
308 with latitude across all species of our study, not generally supporting Rapoport's rule.  
309 However, when controlling for the potentially confounding effects of body size and shape  
310 (and thus reducing our dataset), we found a significant increase in range size with latitude. In  
311 the following, we link our results to the ecology and physiology of drosophilids and discuss  
312 potential causes and consequences of these macroecological patterns and their apparent  
313 idiosyncrasy depending on which species are analyzed.



## 314 **Latitudinal effects on body size, shape and range size evolution**

315 Bergmann's rule is thought to be driven by variation in temperature (Atkinson and Sibly  
316 1997, Shelomi 2012), whereas its converse represents an adaptive response to season length  
317 (Blanckenhorn and Demont 2004). Drosophilids generally follow a weak positive Bergmann  
318 cline, thus at best suggesting only minor effects of temperature and no role of season length in  
319 this family. As most drosophilids are small, fast-developing and therefore strongly  
320 multivoltine (although some univoltine species and populations exist; e.g., Lakovaara et al.  
321 2009), this could be expected (Blanckenhorn and Demont 2004). Compared to the strength of  
322 interspecific clinal variation in other insects, the variation explained by latitude in wing ( $r^2 =$   
323  $0.09$ ) and thorax length ( $r^2 = 0.05$ ) is below average, though not particularly low (cf.  $r^2$  for  
324 similar interspecific comparisons from Shelomi (2012): mean = 0.22, median = 0.10, SD = 0.25,  
325  $n = 18$ ). Given that most individuals measured for this study were collected in the field and  
326 not raised under controlled environments, a considerable amount of body size variation must  
327 be attributable to phenotypic plasticity. Although this typically also applies to other studies of  
328 various taxa, it is possible that we underestimate the strength of the latitudinal pattern.

329 Even though processes acting within species (sometimes termed neo-Bergmannian rule or  
330 James's rule) do not necessarily coincide with among-species patterns (Blackburn et al. 1999),  
331 the interspecific clinal variation observed here is consistent with analogous intraspecific  
332 variation in drosophilids (e.g., Chown and Gaston 2010). Due to this qualitative consistency,  
333 it is reasonable to assume a common underlying mechanism. However, following the  
334 temperature-size rule (Atkinson 1994), drosophilids tend to grow larger in cool environments  
335 in general (e.g. Ray 1960), and experimental laboratory rearing would be required to test  
336 whether this between-species pattern is driven by evolutionary or purely plastic (i.e.

337 physiological) responses. Note, however, that intra-specific common-garden experiments  
338 suggest a strong genetic component (e.g., James et al. 1995).

339 Along with thorax length, wing size increased with absolute latitude, though its steeper  
340 increase resulted in disproportionately larger wings at higher latitudes and consequently  
341 lower wing loading. Because log wing length showed an isometric relationship with log thorax  
342 length across species (evolutionary allometric coefficient derived from a phylogenetic reduced  
343 major axis regression:  $\beta = 0.94$ ,  $P = 0.528$ ), allometric scaling relationships cannot explain the  
344 relative increase in wing size with latitude. In contrast to warm-blooded animals, in which  
345 latitudinal variation in appendage size has been attributed to selection for thermoregulatory  
346 efficiency (e.g. reduced bill size in birds: Symonds et al. 2010), such mechanisms seem unlikely  
347 to act in insects. Yet, thermoregulation may still be involved in shaping the observed pattern.  
348 Being unable to control body temperature endogenously, small insects such as drosophilids  
349 regulate body temperature mostly by modifying their behavior (Dillon et al. 2009, Kjærsgaard  
350 et al. 2010). Since flight is hampered in the cold and larger wings lower the temperature  
351 threshold for take-off (Dillon and Frazier 2006, Frazier et al. 2008), relatively larger wings near  
352 the poles could represent an adaptation to large climatic variability or low temperatures  
353 (Angelo and Frank 1984, Pivnick and McNeil 1986, Azevedo et al. 1998, Dillon et al. 2009). Such  
354 correlations between dispersal capacity and latitude or altitude have been documented in  
355 several species (Hassall 2015, Kjærsgaard et al. 2015, Rohner et al. 2015), including latitudinal  
356 clines for wing loading in *D. melanogaster* (Azevedo et al. 1998, Klepsatel et al. 2014), and again  
357 suggest a common underlying mechanism of intra- and interspecific clines. Yet, greater  
358 dispersal capacity may be an essential prerequisite for colonizing habitats at high latitudes in  
359 the first place (e.g., following colonization after the last glacial period). Invading less  
360 predictable habitats may then in turn promote the evolution of physiological adaptations that

361 are linked to the climate experienced. This alternative explanation seems unlikely, however,  
362 given that wing loading did not correlate with range size (see below), and therefore a direct  
363 link between colonization success and short-range dispersal ability appears questionable.  
364 Increased relative wing size could thus indeed be associated with cold temperature or  
365 increased climatic variability *per se* and, consequently, a common pattern in small pterygote  
366 insects. Whether this pattern constitutes evidence against Allen's rule as originally formulated  
367 or whether such patterns should be discussed in this context at all is certainly debatable, but  
368 also not the main point here.

369 When considering all data, we found no significant correlation between range size and  
370 absolute latitude, suggesting no support for Rapoport's rule overall. Our multivariate analysis  
371 further suggests that wing size (a proxy for short-range dispersal potential) and thorax length  
372 do not confound this relationship, even though both traits have been shown to play major roles  
373 in range-size evolution (Malmqvist 2000, Lester et al. 2007, Rundle et al. 2007, Gaston 2009,  
374 Swaegers et al. 2014). Surprisingly, the subset of species for which both wing and thorax data  
375 were available showed a significant increase of range size with latitude. This discrepancy is  
376 unlikely explained by phylogeny, as the species used in the multivariate analysis are well  
377 distributed across all major clades (see fig. S1). At the same time, there was more faunistic  
378 information available for these 54 species (based on the number of coordinates), thus likely  
379 increasing the precision of our range-size estimation. Alternatively, this deviating pattern  
380 could also be caused by the ecology of these particular species. Unlike many other drosophilids  
381 (Markow and O'Grady 2006), these species can be cultured easily in the laboratory, so they  
382 may be particularly flexible and undemanding in their ecological preferences. If so, their range  
383 size might be less affected by ecological barriers such as the distribution of substrate host

384 species. Given this non-random subset and the non-standardized sampling scheme used to  
385 derive range size, future research should test these patterns at the global scale.

### 386 **Sexual size dimorphism and Rensch's rule**

387 Females were the larger sex in nearly all species investigated. There is, however, one  
388 particularly conspicuous exception to this trend: *Drosophila prolongata*. This species is not only  
389 the largest-bodied species in the *Sophophora* subgenus, but also the only species exhibiting  
390 pronounced male-biased sexual size dimorphism (also see Rohner et al. 2017). This species  
391 adds further evidence to the notion that there is great potential for rapid evolution of reversed  
392 SSD in Diptera, and its apparent association with increased male–male contests (Rohner et al.  
393 2016), which are also common in *D. prolongata* (Kudo et al. 2015). Given its large size and male-  
394 biased SSD, *D. prolongata* strongly affected the statistical appraisal of Rensch's rule here (Fig.  
395 3), reemphasizing potential issues with the classic assessment of Rensch's rule when male- and  
396 female-biased taxa differ in size (see Webb and Freckleton 2007). Nevertheless, the mating  
397 system, including the evolutionary drivers of SSD and body size, of *D. prolongata* is likely to  
398 be derived, such that this single extraordinary species may obscure rather than testify to  
399 Rensch's rule in *Sophophora*.

400 Although we found support for Rensch's rule across the entire family, this pattern did not  
401 hold within some of the major (sub)radiations. Nevertheless, in most cases the reduced major-  
402 axis slope between males and females was steeper than one. In fact, empirical research  
403 demonstrates frequently that support for Rensch's rule depends strongly on the taxonomic  
404 level with considerable variation among closely related clades (e.g., Webb and Freckleton  
405 2007). Even if supported in interspecific comparisons, Rensch's rule does not necessarily hold  
406 among or within populations of these species (Blanckenhorn et al. 2007a). Within-population

407 variation in SSD is likely driven, at least in part, by ontogenetic processes and thus not  
408 necessarily linked to selective forces driving Rensch's rule across species (Teder and Tammaru  
409 2005). In theory, Rensch's rule should nonetheless hold across populations *and* species. Sexual  
410 selection on male size tends to be the strongest and most consistent evolutionary driver of  
411 large male size (e.g.: Székely et al. 2004, Rohner et al. 2016), and Rensch's rule is arguably more  
412 prominently supported in taxa with male-biased SSD due to this selective homogeneity (e.g.,  
413 Stuart-Fox 2009). In contrast, fecundity selection mediates female-biased SSD to a much lesser  
414 extent than expected, as selection for small male size or other evolutionary scenarios are also  
415 common (Pincheira-Donoso and Hunt 2015). Blanckenhorn et al. (2007b) and Huey et al. (2006)  
416 found evidence for Rensch's rule in *Drosophila* based on 23 and 42 species, respectively. Our  
417 data suggest that this result is robust, but driven mostly by the *virilis - repleta* radiation, while  
418 tests in other clades do not support deviations from isometry.

## 419 **Conclusions**

420 Macroecological rules are sometimes considered to be weak and idiosyncratic, partly  
421 because their predictive strength and manifestation varies across taxa, but possibly also  
422 because they might be interrelated or confounded. While our comparative analyses largely  
423 corroborate previously reported intraspecific patterns for thorax length and wing size, support  
424 for Rensch's rule was inconsistent among clades (although slopes did not significantly differ  
425 between clades). Moreover, we found no support for Rapoport's rule overall and showed that  
426 this pattern is not necessarily associated with thorax length or wing size of high-latitude  
427 species. Although entirely correlational, we further suggest that increased relative wing size  
428 at higher latitudes may be driven by selection for more efficient flight and thermoregulatory  
429 behavior.

430 We conclude that studying the relationships between several prominent macroecological  
431 patterns can shed more light on broad ecogeographic patterns. However, we here found only  
432 little evidence for confounding effects. Nevertheless, given that their putative underlying  
433 causes are often linked to climatic factors, considering several macroecological patterns  
434 simultaneously at minimum permits better interpretation in case of multiple, potentially  
435 conflicting trends or hypotheses, as was the case here for wing size and its potential  
436 relationship with Allen's rule. Future research should focus on the underlying physiological  
437 mechanisms to definitively discern the causes and consequences of various macroecological  
438 patterns in Drosophilidae and other taxa.

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#### 445 **REFERENCES**

- 446 Abouheif, E. and Fairbairn, D. J. 1997. A comparative analysis of allometry for sexual  
447 size dimorphism: assessing Rensch's rule. - *Am. Nat.* 149: 540–562.
- 448 Allen, J. . 1877. The influence of physical conditions in the genesis of species. - *Radic.*  
449 *Reveiw* 1: 108–140.
- 450 Alpatov, W. 1929. Biometrical studies on variation and races of the honey bee (*Apis*  
451 *mellifera* L.). - *Q. Rev. Bioi.* 4: 1–58.
- 452 Angelo, M. J. and Frank, S. J. . 1984. Body building by insects: trade-offs in resource

453 allocation with particular reference to migratory species. - Florida Entomol. 67:  
454 22–41.

455 Ashburner, M. 1981. Entomophagous and other bizarre Drosophilidae. - In:  
456 Ashburner, M. et al. (eds), The Genetics and Biology of *Drosophila*. 3a ed.n.  
457 Academic press inc., pp. 395–429.

458 Atkinson, D. 1994. Temperature and organism size - a biological law for ectotherms? -  
459 Adv. Ecol. Res. 25: 1–58.

460 Atkinson, D. and Sibly, R. M. 1997. Why are organisms usually bigger in colder  
461 environments? Making sense of a life history puzzle. - Trends Ecol. Evol. 12: 235–  
462 239.

463 Azevedo, R. B. R. et al. 1998. Latitudinal variation of wing: thorax size ratio and wing-  
464 aspect ratio in *Drosophila*. - Evolution. 52: 1353–1362.

465 Blackburn, T. M. et al. 1999. Geographic gradients in body size: A clarification of  
466 Bergmann's rule. - Divers. Distrib. 5: 165–174.

467 Blanckenhorn, W. U. 2000. The evolution of body size: What keeps organisms small? -  
468 Q. Rev. Biol. 75: 385–407.

469 Blanckenhorn, W. U. and Demont, M. 2004. Bergmann and converse Bergmann  
470 latitudinal clines in arthropods: two ends of a continuum? - Integr. Comp. Biol.  
471 44: 413–424.

472 Blanckenhorn, W. U. et al. 2006. When Rensch meets Bergmann: does sexual size  
473 dimorphism change systematically with latitude? - Evolution. 60: 2004–2011.

474 Blanckenhorn, W. U. et al. 2007a. Rensch's rule in insects: patterns among and within  
475 species. - In: Fairbairn, D. J. et al. (eds), Sex, Size and Gender Roles. pp. 60–70.

476 Blanckenhorn, W. U. et al. 2007b. Proximate causes of Rensch's rule: does sexual size

477 dimorphism in arthropods result from sex differences in development time? - Am.  
478 Nat. 169: 245–257.

479 Bolstad, G. H. et al. 2015. Complex constraints on allometry revealed by artificial  
480 selection on the wing of *Drosophila melanogaster*. - Proc. Natl. Acad. Sci. U. S. A.  
481 112: 13284–9.

482 Burgman, M. A. and Fox, J. C. 2003. Bias in species range estimates from minimum  
483 convex polygons: implications for conservation and options for improved  
484 planning. - Anim. Conserv. 6: 19–28.

485 Chapman, R. F. et al. 2013. The insects: Structure and function (RF Chapman, SJ  
486 Simpson, and AE Douglas, Eds.). - Cambridge University Press.

487 Chown, S. L. and Gaston, K. J. 2010. Body size variation in insects: A macroecological  
488 perspective. - Biol. Rev. 85: 139–169.

489 Chown, S. L. et al. 1999. Exploring links between physiology and ecology at macro-  
490 scales : the role of respiratory metabolism in insects. - Biol. Rev 74: 87–120.

491 Clench, H. 1966. Behavioral thermoregulation in butterflies. - Ecology 47: 1021–1034.

492 Darriba, D. et al. 2012. jModelTest 2: more models, new heuristics and parallel  
493 computing. - Nat. Methods 9: 772–772.

494 Davis Rabosky, A. R. et al. 2016. Coral snakes predict the evolution of mimicry across  
495 New World snakes. - Nat. Commun. 7: 11484.

496 Dillon, M. E. and Frazier, M. R. 2006. *Drosophila melanogaster* locomotion in cold thin  
497 air. - J. Exp. Biol. 209: 364–371.

498 Dillon, M. E. et al. 2009. Review: Thermal preference in *Drosophila*. - J. Therm. Biol. 34:  
499 109–119.



- 500 Drummond, A. J. et al. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7.  
501 - Mol. Biol. Evol. 29: 1969–1973.
- 502 Fabian, D. K. et al. 2015. Spatially varying selection shapes life history clines among  
503 populations of *Drosophila melanogaster* from sub-Saharan Africa. - J. Evol. Biol. 28:  
504 826–840.
- 505 Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: Pattern and process in the  
506 coevolution of body size in males and females. - Annu. Rev. Ecol. Syst. 28: 659–  
507 687.
- 508 Fairbairn, D. J. and Preziosi, R. F. 1994. Sexual selection and the evolution of allometry  
509 for sexual size dimorphism in the water strider, *Aquarius remigis*. - Am. Nat. 144:  
510 101–108.
- 511 Frazier, M. et al. 2008. Cold rearing improves cold-flight performance in *Drosophila* via  
512 changes in wing morphology. - J. Exp. Biol. 211: 2116–2122.
- 513 Gallagher, R. V. 2016. Correlates of range size variation in the Australian seed-plant  
514 flora. - J. Biogeogr. 43: 1287–1298.
- 515 Gaston, K. J. 2009. Geographic range limits: achieving synthesis. - Proc. R. Soc. B 276:  
516 1395-1406.
- 517 Gaston, K. J. and Blackburn, T. M. 1996. Range size-body size relationships: Evidence  
518 of scale dependence. - OIKOS 75: 479–485.
- 519 Ghosh, S. M. et al. 2013. Temperature-size rule is mediated by thermal plasticity of  
520 critical size in *Drosophila melanogaster*. - Proc. R. Soc. B 280: 20130174.
- 521 Gilchrist, G. W. et al. 2001. Rapid evolution of wing size clines in *Drosophila subobscura*.  
522 - Genetica 112–113: 273–286.
- 523 Harrison, J. F. and Roberts, S. P. 2000. Flight respiration and energetics. - Annu. Rev.

- 524       Physiol. 62: 179–205.
- 525       Hassall, C. 2015. Strong geographical variation in wing aspect ratio of a damselfly,  
526       *Calopteryx maculata* (Odonata: Zygoptera). - PeerJ 3: e1219.
- 527       Hirst, A. G. et al., 2015. Equal temperature-size responses of the sexes re widespread  
528       within arthropod species. - Proc. R. Soc. B 282: 20152475.
- 529       Huey, R. B. et al. 2006. Sexual size dimorphism in a *Drosophila* clade, the *D. obscura*  
530       group. - Zoology 109: 318–330.
- 531       James, A. C. et al. 1995. Cellular basis and developmental timing in a size cline of  
532       *Drosophila melanogaster*. - Genetics 140: 659–666.
- 533       Karan, D. et al. 2000. Geographical clines for quantitative traits in natural populations  
534       of a tropical drosophilid: *Zaprionus indianus*. - Genetica 108: 91–100.
- 535       Kingsolver, J.G. & Huey, R.B. (2008) Size, temperature, and fitness: three rules.  
536       *Evolutionary Ecology Research*, **10**, 251-268.
- 537       Kjærsgaard, A. et al. 2010. Locomotor activity of *Drosophila melanogaster* in high  
538       temperature environments: plastic and evolutionary responses. - Clim. Res. 43:  
539       127–134.
- 540       Kjærsgaard, A. et al. 2015. Plasticity in behavioural responses and resistance to  
541       temperature stress in *Musca domestica*. - Anim. Behav. 99: 123–130.
- 542       Klepsatel, P. et al. 2014. Similarities and differences in altitudinal versus latitudinal  
543       variation for morphological traits in *Drosophila melanogaster*. - Evolution. 68: 1385–  
544       1398.
- 545       Kudo, A. et al. 2015. Variation in morphological and behavioral traits among isofemale  
546       strains of *Drosophila prolongata* (Diptera: Drosophilidae). - Entomol. Sci. 18: 221–  
547       229.
- 548       Kumar, S. et al. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0

549 for bigger datasets. - Mol. Biol. Evol. 33: msw054.

550 Lakovaara, S. et al. 2009. Aspects of diapause and its genetics in northern drosophilids.  
551 - Hereditas 70: 89–96.

552 Laube, I. et al. 2013. Towards a more mechanistic understanding of traits and range  
553 sizes. - Glob. Ecol. Biogeogr. 22: 233–241.

554 Lester, S. E. et al. 2007. The relationship between dispersal ability and geographic  
555 range size. - Ecol. Lett. 10: 745–758.

556 Lovich, J. E. and Gibbons, J. W. 1992. A review of techniques for quantifying sexual  
557 size dimorphism. - Growth, Dev. aging 56: 269–81.

558 Makarieva, A. M. et al. 2005. Temperature-associated upper limits to body size in  
559 terrestrial poikilotherms. - Oikos 111: 425–436.

560 Malmqvist, B. 2000. How does wing length relate to distribution patterns of stoneflies  
561 (Plecoptera) and mayflies (Ephemeroptera)? - Biol. Conserv. 93: 271–276.

562 Markow, T. a. and O’Grady, P. 2006. *Drosophila*: A guide to species identification and  
563 use. - Elsevier: 259.

564 Meiri, S. and Dayan, T. 2003. On the validity of Bergmann’s rule. - J. Biogeogr. 30: 331–  
565 351.

566 Miller, M. A. et al. 2010. Creating the CIPRES science gateway for inference of large  
567 phylogenetic trees. - 2010 Gatew. Comput. Environ. Work. GCE 2010

568 Nudds, R. L. and Oswald, S. A. 2007. An interspecific test of Allen’s rule: Evolutionary  
569 implications for endothermic species. - Evolution. 61: 2839–2848.

570 Orme, C. D. L. et al. 2012. CAPER: Comparative analyses of phylogenetics and  
571 evolution in R. - Methods Ecol. Evol. 3: 145–151.

572 Pétavy, G. et al. 1997. Growth temperature and phenotypic plasticity in two *Drosophila*  
573 sibling species: probable adaptive changes in flight capacities. - J. Evol. Biol. 10:  
574 875–887.

575 Pincheira-Donoso, D. and Hunt, J. 2015. Fecundity selection theory: concepts and  
576 evidence. - Biol. Rev.: 10.1111/brv.12232.

577 Pivnick, K. A. and McNeil, J. N. 1986. Sexual differences in the thermoregulation of  
578 *Thymelicus lineola* adults (Lepidoptera: Hesperiiidae). - Ecology 67: 1024–1035.

579 Rambaut, A. and Drummond, A. J. 2013. Tracer v1.6. - Available from  
580 <http://tree.bio.ed.ac.uk/software/tracer/>.

581 Ray, C. 1960. The application of Bergmann's and Allen's Rules to the poikilotherms. -  
582 J. Morphol. 106: 85–108.

583 Ray, R. P. et al. 2016. Enhanced flight performance by genetic manipulation of wing  
584 shape in *Drosophila*. - Nat. Commun. 7: 10851.

585 Reed, R. N. 2003. Interspecific patterns of species richness, geographic range size, and  
586 body size among New World venomous snakes. - Ecography. 26: 107–117.

587 Rensch, B. 1950. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße.  
588 - Bonner Zool. Beiträge 1: 58–69.

589 Revell, L. J. 2012. phytools: An R package for phylogenetic comparative biology (and  
590 other things). - Methods Ecol. Evol. 3: 217–223.

591 Rohde, K. 1996. Rapoport's rule is a local phenomenon and cannot explain latitudinal  
592 gradients in species diversity. - Biodivers. Lett. 3: 10–13.

593 Rohner, P. T. et al. 2015. Distribution, diversity gradients and Rapoport's elevational  
594 rule in the black scavenger flies of the Swiss Alps (Diptera: Sepsidae). - Insect  
595 Conserv. Divers. 8: 367–376.

596 Rohner, P. T. et al. 2016. Sexual selection on male size drives the evolution of male-  
597 biased sexual size dimorphism via the prolongation of male development. -  
598 Evolution. 70: 1–11.

599 Ruggiero, A. and Werenkraut, V. 2007. One-dimensional analyses of Rapoport's rule  
600 reviewed through meta-analysis. - Glob. Ecol. Biogeogr. 16: 401–414.

601 Rundle, S. D. et al. 2007. Range size in North American *Enallagma* damselflies  
602 correlates with wing size. - Freshw. Biol. 52: 471–477.

603 Shelomi, M. 2012. Where are we now? Bergmann's rule sensu lato in insects. - Am. Nat.  
604 180: 511–519.

605 Stabentheiner, A. et al. (2010) Honeybee colony thermoregulation - regulatory  
606 mechanisms and contribution of individuals in dependence on age, location  
607 and thermal stress. *PLoS One*, 5.

608 Stevens, G. C. 1992. The elevational gradient in altitude range: an extension of  
609 Rapoport's latitudinal rule to altitude. - Am. Nat. 140: 893–911.

610 Stuart-Fox, D. 2009. A test of Rensch's rule in dwarf chameleons (*Bradypodion spp.*), a  
611 group with female-biased sexual size dimorphism. - *Evol Ecol* 23: 425–433.

612 Swaegers, J. et al. 2014. Ecological and evolutionary drivers of range size in *Coenagrion*  
613 damselflies. - *J. Evol. Biol.* 27: 2386–95.

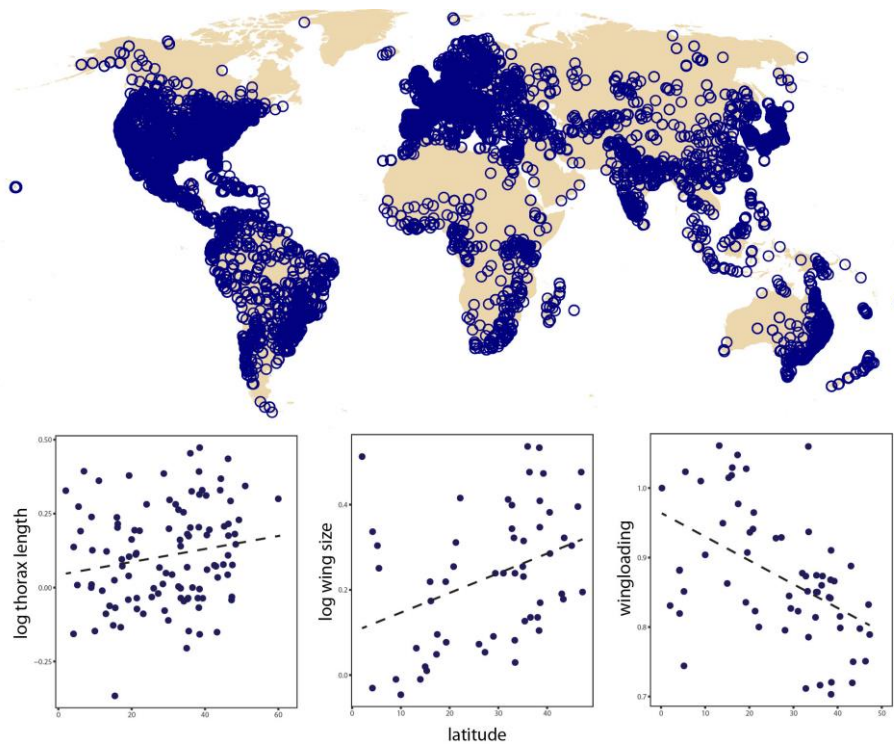
614 Symonds, M. R. E. et al. 2010. Geographical variation in bill size across bird species  
615 provides evidence for Allen's rule. - *Am. Nat.* 176: 188–197.

616 Székely, T. et al. 2004. Sexual selection explains Rensch's rule of size dimorphism in  
617 shorebirds. - *Proc. Natl. Acad. Sci. U. S. A.* 101: 12224–12227.

618 Teder, T. and Tammaru, T. 2005. Sexual size dimorphism within species increases with  
619 body size in insects. - *Oikos* 108: 321–334.

620 van't Land, J. et al. 1999. Latitudinal variation in wild populations of *Drosophila*

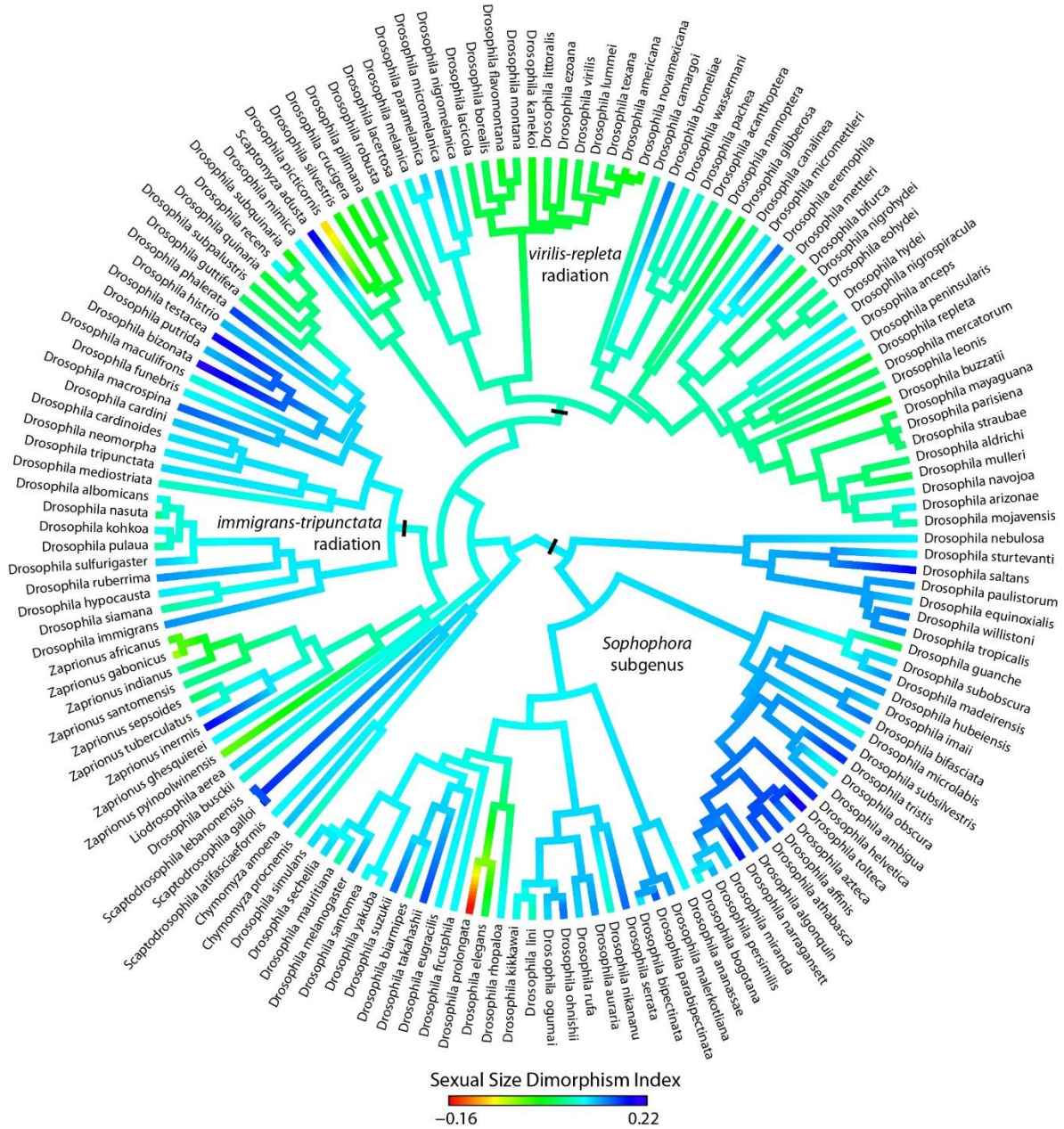
- 621 *melanogaster*: heritabilities and reaction norms. - J. Evol. Biol. 12: 222–232.
- 622 Webb, T. J. and Freckleton, R. P. 2007. Only half right: Species with female-biased  
623 sexual size dimorphism consistently break Rensch's rule. - PLoS One 2: e897.
- 624 Zeuss, D. et al. 2017. Environmental drivers of voltinism and body size in insect  
625 assemblages across Europe. - Glob. Ecol. Biogeogr. 26(2): 154-165.  
626 doi:10.1111/geb.12525.
- 627



629

630 Figure 1: Top: Species specific range size estimates and mean latitudinal distributions were  
 631 derived from over 25,000 unique sampling locations depicted here. This global dataset was  
 632 retrieved from TaxoDros, a large and detailed database on taxonomy and diversity of  
 633 drosophilids (<http://www.taxodros.uzh.ch/>). Bottom: thorax length and wing size increases  
 634 with mean absolute latitude, demonstrating a weak interspecific Bergmann cline in  
 635 drosophilids. Wing size increased more strongly with latitude than thorax length, resulting in  
 636 lower wing loading (thorax length<sup>3</sup>/wing area) towards the poles. These plots showing simple  
 637 linear regressions are for illustrative purposes only. All analyses were done using PGLS  
 638 (phylogenetically corrected correlation coefficients are given in the text).

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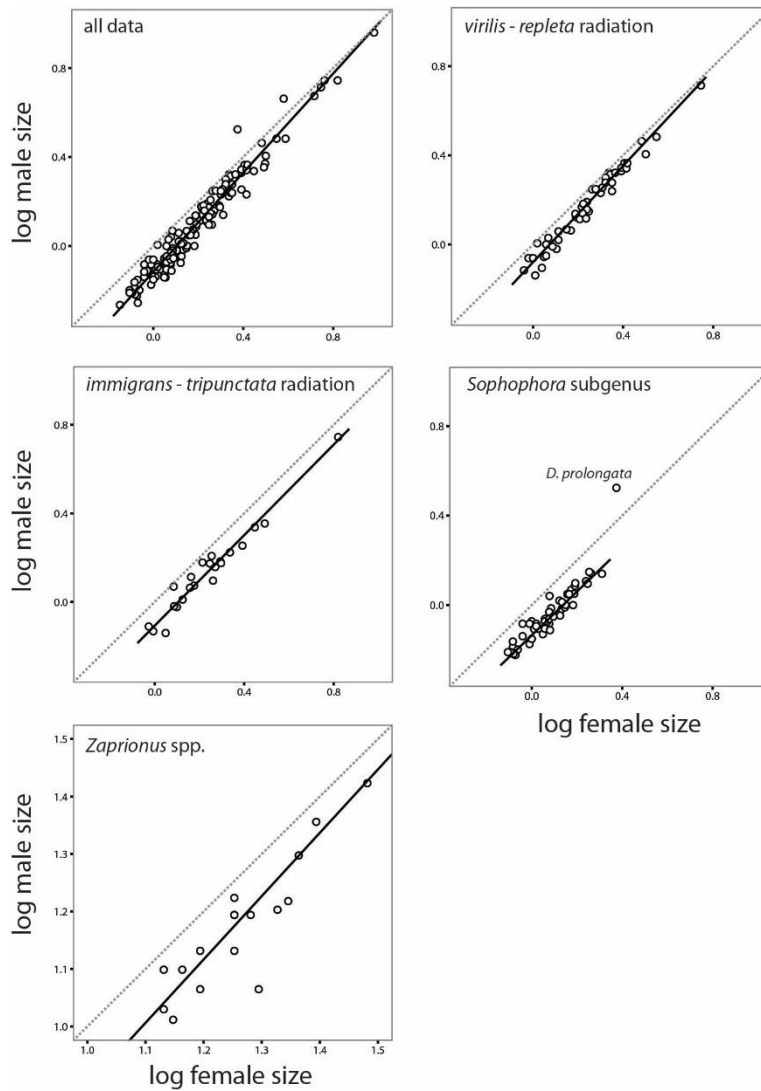


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641 Figure 2: Ancestral state reconstruction of sexual size dimorphism (SDI = (thorax length of  
 642 larger sex / thorax length of smaller sex) -1; arbitrarily defined negative if males are the larger  
 643 sex), for illustration purposes only. SSD shows strong phylogenetic signal and in most species  
 644 females are the larger sex (positive SDI values). The conspicuous exception is *Drosophila*  
 645 *prolongata*, which shows pronounced male-biased SSD.

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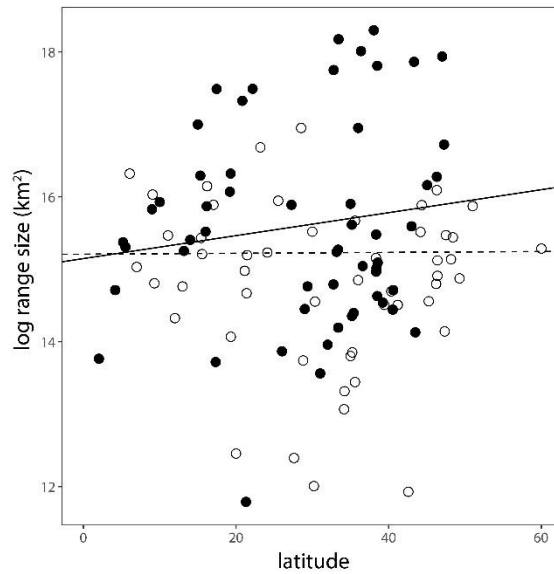


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649 Figure 3: Male size increases more with body size than female size, supporting Rensch's rule  
 650 for drosophilids. This pattern is however mostly driven by the *virilis-repleta* radiation and  
 651 absent in all other major clades. For *Zaprionus spp.*, only total body length was available while  
 652 for all other species thorax length was used. Note that regression lines are derived from non-  
 653 phylogenetic major axis regressions for illustrative purposes only.

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656 Figure 4: Alpha-hull derived range sizes did not correlate with latitude when all species were  
 657 analyzed (broken regression line). However, when applying a multiple PGLS regression  
 658 controlling for thorax length and wing size, range size increased with latitude (solid regression  
 659 line). Based on merely a limited number of species, this does not seem to be a general pattern  
 660 across the family, although species for which wing size data were available are dispersed well  
 661 across the family . The plot shows simple linear regressions for illustrative purposes only. All  
 662 analyses were done using PGLS (phylogenetically corrected correlation coefficients are given  
 663 in the text).

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670 Supplementary files:

671 Table S1: Principal component analysis of four bioclimatic variables did result in one  
672 significant axis of variation. Given that the variables related to temperature load opposite to  
673 climate variation variables, the first principal component essentially represents latitude and  
674 the effects of temperature and variation cannot be disentangled.

Proportion of variance explained				
	PC1	PC2	PC3	PC4
Eigenvalue	3.29	0.68	0.03	0.00
Proportion of variance explained	0.82	0.17	0.01	0.00
Cumulative variance	0.82	0.99	1.00	1.00

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PC loadings	
	PC1
Annual Mean Temperature	-0.98
Temperature Seasonality	0.95
Temperature Annual Range	0.91
Mean Temperature of Warmest Quarter	-0.78

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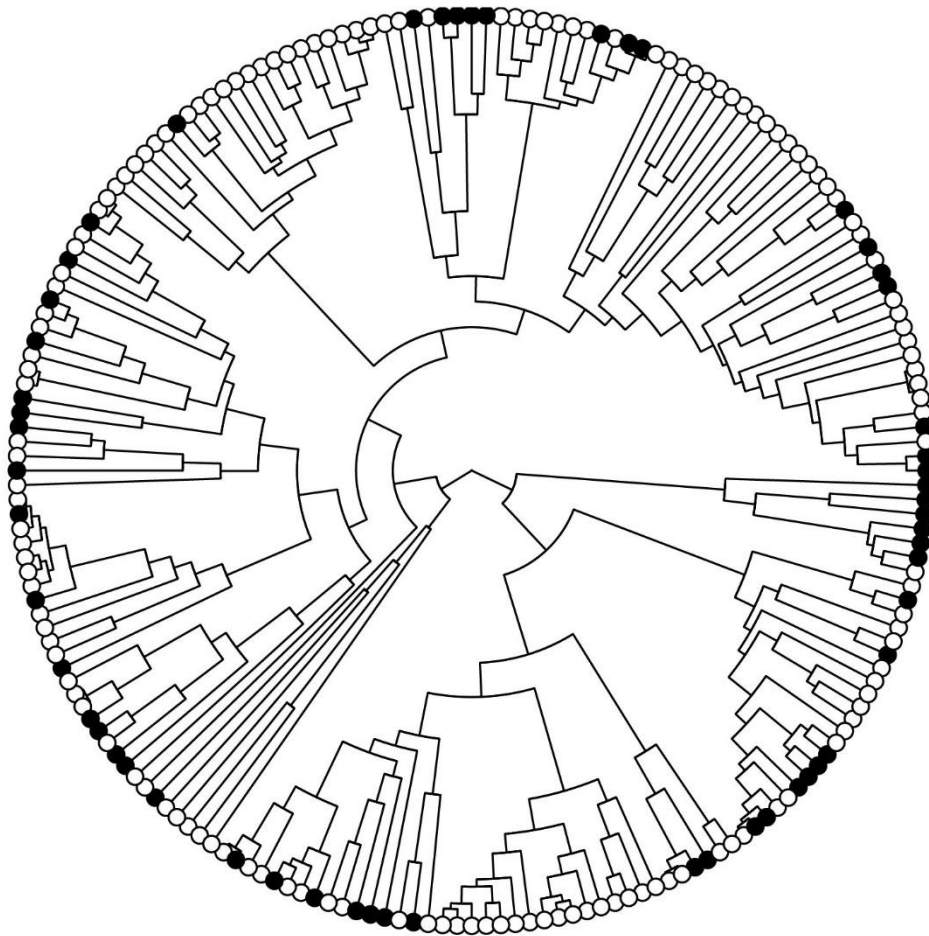
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687 Figure S1: Taxa for which distribution data were available are well dispersed across the  
688 phylogeny.



- only distribution data
- distribution and wing size data

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