

An interspecific test of Bergmann's rule reveals inconsistent body size patterns across several lineages of water beetles (Coleoptera: Dytiscidae)

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Abstract

1. Bergmann's rule *sensu lato*, the ecogeographic pattern relating animals' body size with environmental temperature (or latitude), has been shown to be inconsistent among insect taxa. Body size clines remain largely unexplored in aquatic insects, which may show contrasting patterns to those found in terrestrial groups because of the physiological or mechanical constraints of the aquatic environment.
2. Bergmann's rule was tested using data on body size, phylogeny and distribution for 93 species belonging to four lineages of dytiscid water beetles. The relationship between size and latitude was explored at two taxonomic resolutions: i) within each independent lineage and ii) for the whole dataset, employing phylogenetic generalized least squares to control for phylogenetic inertia. The potential influence of habitat preference (lotic vs. lentic) on body size clines was also considered.
3. Within-lineage analyses showed negative relationships (i.e., converse Bergmann's rule), but only in two lineages (specifically in those that included both lotic and lentic species). In contrast, we found no relationship between body size and latitude for the whole dataset.
4. These results suggest that there may be no universal interspecific trends in latitudinal variation of body size in aquatic insects, even among closely related groups, and show the need to account for phylogenetic inertia. Furthermore, habitat preferences should be considered when exploring latitudinal clines in body size in aquatic taxa at the interspecific level.

Keywords: inland waters, habitat, lotic, lentic, aquatic insects, latitude, biogeography, phylogeny

1 **Introduction**

2 Body size is related to many physiological, life-history and ecological traits, and thus
3 has important effects on fitness and is ultimately linked to the spatio-temporal
4 distribution and abundance of animals (Chown & Gaston, 2010). One of the oldest and
5 most debated ecogeographical patterns of body size is *Bergmann's rule* (BR hereafter)
6 (Bergmann, 1847), which refers to size increase with decreasing temperature or
7 increasing latitude. It has been interpreted that the rule originally referred to
8 interspecific patterns among closely related species in endotherm animals (Blackburn
9 *et al.*, 1999), but the same latitudinal cline has been observed in ectotherm taxa, both at
10 the inter- and intraspecific level (Vinarski, 2014), leading to an extended use of the term
11 *Bergmann's rule* in the literature (Meiri, 2011).

12 In insects, the generality and direction of body size patterns are far from being
13 consistent across taxa (Shelomi, 2012), in part because the taxonomic resolution and the
14 phylogenetic component of size variation are not often considered, despite their known
15 strong effects (Chown & Gaston, 2010). In aquatic insects, which remain surprisingly
16 unexplored in comparison with terrestrial ones, the few studies of geographic variation
17 in size are at assemblage level (Vamosi *et al.*, 2007; Zeuss *et al.*, 2017) or intraspecific,
18 the latter showing different patterns in different taxa: from the typical BR (e.g. Hassal *et*
19 *al.*, 2014) or U-shaped clines (e.g. Johansson, 2003) to the converse BR (i.e. decrease of
20 size with latitude) (e.g. Shama & Robinson, 2009).

21 Bergmann (1847) suggested that a more efficient heat conservation in large *vs* small
22 organisms (because of the lower surface to volume ratio) could be the mechanism
23 underlying the latitudinal increase of body size. However, this mechanism is not
24 applicable to ectotherms, because large size also slows heat gain, which could be as

25 important as decreasing heat loss. Then, a number of alternative mechanisms to explain
26 observed clines in ectotherms have been proposed (see Blackburn *et al.*, 1999; Chown
27 & Gaston, 2010; Vinarsky, 2014 for detailed reviews). Briefly, these are based on the
28 influence of temperature on growth rate (*temperature-size rule*; Atkinson, 1994), or a
29 positive relationship between size and dispersal ability (*migration ability hypothesis*,
30 Blackburn *et al.*, 1999) or between size and starvation resistance (Calder, 1984;
31 Lindstedt & Boyce, 1985). Concerning the converse BR, it has been suggested that
32 shorter seasons (and the consequent shorter time available for growth and development)
33 (Mousseau, 1997; Chown & Gaston, 2010) or lower availability of resources at high
34 latitudes (Atkinson & Sibly, 1997) leads to a decrease in body size. Converse BR clines
35 have been also attributed to the heat-dependent growth rates and metabolic rates of
36 ectotherms (Makarieva *et al.*, 2005; Winterhalter & Mousseau 2008). However, the
37 relationship between size and latitudinal-correlated factors in insects could be
38 influenced by voltinism, because as the number of generations per year increases, less
39 time per generation is available for growth (Zeuss *et al.*, 2017). Therefore, given the
40 multiple environmental and biotic factors and individual traits directly or indirectly
41 related with size, empirical evidence of such mechanisms is generally scarce, especially
42 for aquatic ectotherms.

43 In the aquatic environment, physiological or mechanical constraints may result in
44 patterns of body size variation different to those found in terrestrial animals (e.g. Zeuss
45 *et al.*, 2017). Indeed, meta-analyses by Forster *et al.* (2012) and Horne *et al.* (2015)
46 showed that (intraspecific) temperature-size responses (conforming to BR) were
47 stronger in aquatic than terrestrial species. It has been suggested that the balance
48 between oxygen supply and demand, as an important driver of the temperature-size
49 response, might strength such response in the aquatic environment, as oxygen is less

50 readily available in water than in air (Atkinson, 1995; Verberck *et al.*, 2011). Other
51 indirect factors that may play a role are, however, frequently overlooked, such as
52 species' preference for lentic or lotic waters. The contrasting stability between these
53 habitat types (at evolutionary timescales) is known to select differentially for traits
54 related with dispersal ability (Ribera, 2008): lentic insects are generally better dispersers
55 than their lotic relatives and therefore have broader and more northern distribution
56 ranges (e.g. Hof *et al.*, 2006; Abellán & Ribera, 2011; Pinkert *et al.*, 2018). If dispersal
57 ability is positively correlated with body size in insects with a similar body structure
58 and biology (see Rundle *et al.*, 2007), BR clines in lineages with both lotic and lentic
59 species could actually reflect differential dispersal capacities between species
60 specialized in each habitat. On the other hand, lotic waters may impose stronger
61 physical constraints on body size than lentic habitats, as large insects are unable to cope
62 with the strong drag forces produced by the water flow (Bournaud, 1992; Ribera &
63 Nilsson, 1995). Therefore, while large sizes are generally absent in lotic waters, the full
64 variability of sizes can be found in lentic waters. Considering these physical and
65 dispersal constraints of lotic species, we could expect that in general, the temperature-
66 size relationship must be clearer for lentic species. However, the annual number of
67 generations as well as other factors at local scale may also influence such relationship,
68 as for example the geographical and temporal variation in oxygen or temperature, which
69 is generally higher in small, shallow lentic waters than in lotic systems (Batzer & Boix,
70 2016).

71 Among aquatic insects, diving beetles (Dytiscidae) have been proposed as good models
72 to explore body size variation along environmental gradients because of their
73 considerable variation in body and geographic range size, even among closely related
74 species (Vamosi *et al.*, 2007). The availability of well-resolved phylogenies for

75 different lineages of this group (Abellán & Ribera, 2011) provides a unique opportunity
76 to study biogeographic patterns across independent “evolutionary replicas”, controlling
77 for phylogenetic inertia. Here, we explored the relationship between body size and
78 latitude in four monophyletic lineages of diving beetles across a wide latitudinal range,
79 accounting for the potential influence of taxonomic resolution, habitat preference and
80 phylogenetic effects on body size clines.

81 **Material and methods**

82 *Study group*

83 Our dataset includes four monophyletic lineages comprising a total of 93 dytiscid
84 species (Table S1), from which morphological, distributional and phylogenetic data are
85 available from previous studies: 27 species of the *Ilybius subaeneus* group, an almost
86 exclusively lentic lineage with 33 recognized species with generally large geographical
87 ranges (Nilsson & Hájek, 2018); 20 of the western Mediterranean clade of *Deronectes*,
88 an exclusively lotic lineage with 24 known species (García-Vázquez *et al.*, 2016); 17 of
89 *Graptodytes*, a genus with 21 recognized species (Ribera & Faille, 2010) and 29 of the
90 *Hydroporus planus* group (genus *Hydroporus*; Ribera *et al.*, 2003; Nilsson & Hájek,
91 2018), which includes 51 species. The latter two groups include lentic and lotic species.
92 Most of the species studied have a Palearctic distribution, but some of them are also
93 present in the Nearctic region (Larson *et al.*, 2000) (Table S1).

94 Total length of these species (excluding head) was obtained from Scheffer *et al.* (2015)
95 and distributional data (latitudinal centroids and maximum latitude) from Abellán &
96 Ribera (2011).

97 *Data analyses: Bergmann’s rule tests*

98 We tested the relationship between body size and latitude at two different taxonomic
99 resolutions: i) within each lineage, and ii) for the whole dataset, pooling the four
100 lineages. Phylogenetic generalized least squares (PGLS) were used to control for
101 phylogenetic inertia. For the analyses within lineages, the phylogenetic trees from
102 Abellán & Ribera (2011) were used. For the pooled dataset, we combined the
103 phylogenies of the four lineages in a global tree using the most recent family-level
104 phylogeny for Dytiscidae (Désamoré *et al.*, 2018) as a base tree representing the
105 evolutionary relationships among lineages (see Figure S1). The depth of each clade tree
106 in the global tree was set from the age of each lineage as provided in Abellán & Ribera
107 (2011). While this meta-tree approach has a number of limitations, it provides an
108 operational phylogenetic hypothesis based on the currently available data suitable for
109 comparative analysis (Funk & Specht, 2007). The phylogenetic signal of the
110 regressions' residuals was assessed by maximum-likelihood estimated values of Pagel's
111 lambda (λ ; Pagel, 1999) and likelihood ratio tests to determine whether it significantly
112 differed from zero (i.e. from a model assuming that patterns of body size variation are
113 independent of phylogeny).

114 To account for the potential influence of habitat, we included it and the interaction with
115 latitude as predictors for those analyses including species with different habitat
116 preferences (i.e., the whole dataset, *Graptodytes* and *Hydroporus*). For simplicity, and
117 because the main size constraints are presumably expected in lotic species (Ribera &
118 Nilsson, 1995), we considered two habitat categories: lotic specialists and the rest
119 (including both lentic specialists and non-specialists). Additionally, when habitat was
120 significant, we fitted separate PGLS models for each habitat category.

121 All analyses were performed for both average size and central latitude, and maximum
122 size and maximum latitude, in R v. 3.3.3 (R Core Team, 2017). We used a single

123 datapoint for each species, as intraspecific variation of size in diving beetles is relatively
124 low in relation to interspecific variation (see Larson et al. 2000 and Table S1).

125 **Results**

126 Average and maximum body size and central and maximum latitude were strongly
127 correlated for all the lineages (Table S2), so we report only the relationships between
128 average body size and central latitude (but see Table S3 for results for maximum size
129 and maximum latitude).

130 PGLS for the whole dataset showed no significant relationships between size and
131 neither latitude, habitat or their interaction (Tables 1 and S3). The different lineages
132 were clearly clustered by (mainly) size and latitude, especially for *Ilybius*, the largest
133 and most northerly distributed group (Fig. 1A). Within-lineage analyses revealed no
134 consistent patterns across the different groups. No significant relationships were found
135 in *Ilybius* or *Deronectes*, while average size and central latitude showed a significant
136 relationship in *Hydroporus* as well as maximum size and maximum latitude in
137 *Graptodytes* (Tables 1 and S3), negative in both cases (i.e. following a converse BR)
138 (Figs. 1B and C). This pattern showed a strong significant phylogenetic signal in
139 *Hydroporus* (Table 1).

140 In *Graptodytes* and *Hydroporus* species, the two lineages that include both lentic and
141 lotic species, body size was also significantly related with habitat (Tables 1 and S3).
142 When the relationship between body size and latitude was tested separately for species
143 grouped by habitat, the converse BR cline only held for non-lotic specialist species of
144 *Hydroporus*, with a significant phylogenetic signal (Tables 1 and S3).

145 **Discussion**

146 The currently available data show that latitudinal clines in body size are much less
147 consistent across insects (and ectotherms in general) than endothermic taxa (Shelomi,
148 2012; Vinarsky, 2014). Here, we found no support for Bergmann's rule in the studied
149 lineages, and inconsistent latitudinal patterns of body size at the two taxonomic
150 resolutions explored and also among the different lineages.

151 No significant relationship between body size and latitude was detected when data from
152 the four lineages were pooled; however, two of the studied lineages (*Hydroporus* and
153 *Graptodytes*) showed a converse BR cline when assessed independently. The first
154 important point to be drawn from these results is the importance of considering well-
155 defined, complete taxonomic units when examining biogeographic patterns in body
156 size. It was not our goal to examine body size trends at the family level, given the
157 limited extent of our size and distribution dataset and the lack of a comprehensive
158 phylogeny at such level. However, our analyses show that body size patterns (or the
159 absence of them) observed when different taxonomic groups are pooled arbitrarily may
160 be confounded by inconsistent patterns among lower taxonomic groups. Other studies
161 have found similar inconsistencies, as those on latitudinal body size clines in bees
162 (Gérard *et al.*, 2018) or size variation in Lepidoptera along elevational gradients (e.g.
163 Hawkins & DeVries, 1996; Brehm & Fielder, 2004). However, Brehm *et al.* (2018)
164 found a consistent pattern of body size increase along an extensive altitudinal gradient
165 working with a large dataset of tropical moths. We furthermore found a strong
166 phylogenetic signal in body size variation, which is common in insects, highlighting the
167 importance of accounting for phylogenetic relatedness (Chown & Gaston, 2010).

168 Few interspecific studies of Bergmann's rule in aquatic insects are available to compare
169 with the patterns found here, but the closest one, by Vamosi *et al.* (2007) (also on
170 dytiscids), found a positive relationship between the proportion of large species with

171 latitude, contrary to the trends (or lack of them) observed here within specific lineages.
172 However, that study was done at the assemblage level (i.e. the body sizes of all dytiscid
173 species were pooled within each grid cell) and restricted to a geographic political region
174 (southern Alberta, Canada). Thus, because of the different taxonomic and spatial
175 resolutions, and for the reasons outlined above, these results are not directly
176 comparable.

177 One of the physiological mechanisms proposed to explain size patterns in aquatic
178 ectotherms is based on the fact that aerobic performance in the aquatic environment is
179 worse in warmer habitats, because oxygen demand exceeds supply, constraining size at
180 lower latitudes (Verberck *et al.*, 2011). Makarieva *et al.* (2005) proposed that the
181 interactions between metabolic rates, growth and temperature are behind the size
182 decrease with temperature (BR) in aquatic organisms (e.g. Chapelle & Peck, 1999) and
183 the opposite pattern (i.e. converse BR) in terrestrial ones (e.g. Ashton & Feldman,
184 2003), as oxygen concentrations in aquatic environments are lower than the atmosphere.
185 However, we found the converse Bergmann's rule in two of the studied aquatic groups.
186 Because of the respiratory mode of dytiscids, both adults and larvae, by a physical
187 compressible gill that needs to be renewed on surface, they are highly dependent on
188 atmospheric air, while O₂ exchange with surrounding water is supposed to be minimal
189 (Calosi *et al.*, 2007). Thus, body size patterns in aquatic insects with this respiratory
190 mode may be driven by similar metabolic constraints than those on terrestrial rather
191 than aquatic ectotherms. However, no empirical evidence supports this idea.

192 In part, the inconsistent patterns among the studied lineages may reflect different
193 constraints imposed by habitat type on both size and distribution, which have been
194 typically ignored when studying body size patterns in the aquatic environment. Here,
195 significant relationships between size and latitude were only found in lineages that

196 include lentic and lotic species (i.e. *Hydroporus* and *Graptodytes*) and among these, the
197 relationship was only significant for species with lentic or indistinct habitat preference.
198 Lotic species in our dataset were mostly restricted to lower latitudes, a pattern which
199 has been previously attributed to the well-supported hypothesis that they have lower
200 propensity for dispersal than lentic ones (Abellán & Ribera, 2011). On the other hand,
201 size variability was higher between lentic than between lotic species. The largest species
202 in our dataset were lentic or with indistinct habitat preference (Fig. 1), which might be
203 related with the physical constraint on size imposed by the currents in running waters
204 (Ribera & Nilsson, 1995). Therefore, it is likely that because size and dispersal are
205 constrained in lotic species, the latitudinal body size clines we found in *Hydroporus* and
206 *Graptodytes* species actually reflect the size gradient of lentic (or mixed habitat)
207 species.

208 Voltinism has also been shown to be an important constrain on body size on
209 macroecological scales. For example, a positive size-latitude relationship was reported
210 in univoltine Odonata at the assemblage level, but this was negative for multivoltine
211 species (Zeus *et al.*, 2017). These authors suggested that because multivoltine species
212 (or populations) have less time per generation available for growth than univoltine ones,
213 multivoltine species should be smaller than univoltine species, and among the latter,
214 larger sizes can be reached in cold areas. Unluckily, the lack of life-cycle data for most
215 of the studied species does not allow testing this hypothesis.

216 Our results suggest that there may be no universal interspecific trends in latitudinal
217 variation of body size across aquatic insect groups and therefore, these cannot be
218 explained by a single universal mechanism, but are instead driven by complex
219 interactions among competing traits (Angilletta & Dunham, 2003). We suggest that, in
220 addition to be analysed and interpreted within a clear taxonomic and phylogenetic

221 context, examination of body size patterns in aquatic animals should also consider the
222 potential constraints on size and dispersal imposed by the habitat.

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354

355 **Tables**

356 Table 1. Results of PGLS testing the relationship between average size and central
 357 latitude for the whole dataset and each lineage, respectively.

Group	Predictor	slope±sd	df	F	p-value	R ²	λ ^a
All species	lat	-0.015±0.020	1	1.412	0.238		
	hab	0.571±0.944	1	2.983	0.088		
	lat*hab	-0.004±0.023	1	0.035	0.853		
	full model				0.227	0.049	0.969 (p<0.001)
<i>Ilybius</i>	lat	-0.016±0.041	1	0.145	0.707	0.007	0.670 (p=0.004)
<i>Deronectes</i>	lat	0.004±0.010	1	0.203	0.658	0.011	0.977 (p=0.003)
<i>Hydroporus</i> (all)	lat	-0.029±0.015	1	7.540	0.011		
	hab	0.800±0.687	1	19.619	<0.001		
	lat*hab	-0.004±0.018	1	0.056	0.814		
	full model				<0.001	0.537	0.988 (p=0.028)
<i>Hydroporus</i> (lotic)	lat	-0.025±0.018	1	2.011	0.194	0.200	0.920 (p=0.162)
<i>Hydroporus</i> (non-lotic)	lat	-0.034±0.008	1	17.142	<0.001	0.502	1 (p=0.002)
<i>Graptodytes</i> (all)	lat	-0.064±0.018	1	3.061	0.104		
	hab	-1.844±0.763	1	3.751	0.075		
	lat*hab	0.056±0.021	1	7.600	0.016		
	full model				0.018	0.526	0 (p=1)
<i>Graptodytes</i> (lotic)	lat	-0.064±0.027	1	5.769	0.074	0.591	0 (p=1)
<i>Graptodytes</i> (non-lotic)	lat	-0.004±0.006	1	0.506	0.495	0.053	1 (p=0.035)

358 ^a Maximum-likelihood estimated Pagel's lambda with p-values of the test assessing
 359 whether it differs from zero (i.e. no phylogenetic signal) in parentheses.

360 lat: latitude, hab: habitat type

361

362 **Figure legends**

363 Figure 1. Relationships between A) average body length and central latitude for the
364 whole dataset, B) average body length and central latitude for *Hydroporus* species and
365 C) maximum body length and maximum latitude for *Graptodytes* species. Regression
366 lines of significant relationships are shown (continuous for all species; dashed for lentic
367 and mixed-habitat species).

368

