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 – within each independent lineage, and for the whole dataset – employing phylogenetic generalised least-squares to control for phylogenetic inertia. The potential influence of habitat preference (lotic versus 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). By contrast, no relationship was found 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.

Key words. Aquatic insects, biogeography, habitat, inland waters, latitude, lentic, lotic, phylogeny.

Introduction

Body size is related to many physiological, life-history and ecological traits, and thus has important effects on fitness and is ultimately linked to the spatiotemporal distribution and abundance of animals (Chown & Gaston, 2010). One of the oldest and most debated ecogeographical patterns of body size is Bergmann's rule (BR) (Bergmann, 1847), which refers to size increase with decreasing temperature or increasing latitude. It has been interpreted that the rule originally referred to interspecific

patterns among closely related species in endotherm animals (Blackburn *et al.*, 1999), but the same latitudinal cline has been observed in ectotherm taxa, at both the inter- and intraspecific levels (Vinarsky, 2014), leading to an extended use of the term 'Bergmann's rule' in the literature (Meiri, 2011).

In insects, the generality and direction of body size patterns are far from consistent across taxa (Shelomi, 2012), in part because the taxonomic resolution and the phylogenetic component of size variation are not often considered, despite their known strong effects (Chown & Gaston, 2010). In aquatic insects, which remain surprisingly unexplored in comparison with terrestrial ones, the few studies of geographic variation in size are at assemblage level (Vamosi *et al.*, 2007; Zeuss *et al.*, 2017) or intraspecific, the latter showing different patterns in different

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taxa: from the typical BR (e.g. Hassal *et al.*, 2014) or U-shaped clines (e.g. Johansson, 2003) to the converse BR (i.e. decrease of size with latitude; e.g. Shama & Robinson, 2009).

Bergmann (1847) suggested that a more efficient heat conservation in large versus small organisms (because of the lower surface to volume ratio) could be the mechanism underlying the latitudinal increase of body size. However, this mechanism is not applicable to ectotherms, because large size also slows heat gain, which could be as important as decreasing heat loss. Then, a number of alternative mechanisms to explain observed clines in ectotherms have been proposed (see Blackburn *et al.*, 1999; Chown & Gaston, 2010; Vinarsky, 2014 for detailed reviews). Briefly, these are based on the influence of temperature on growth rate (temperature–size rule; Atkinson, 1994), or a positive relationship between size and dispersal ability (migration ability hypothesis; Blackburn *et al.*, 1999) or between size and starvation resistance (Calder, 1984; Lindstedt & Boyce, 1985). Concerning the converse BR, it has been suggested that shorter seasons (and the consequent shorter time available for growth and development) (Mousseau, 1997; Chown & Gaston, 2010) or lower availability of resources at high latitudes (Atkinson & Sibly, 1997) lead to a decrease in body size. Converse BR clines have been also attributed to the heat-dependent growth rates and metabolic rates of ectotherms (Makarieva *et al.*, 2005; Winterhalter & Mousseau, 2008). However, the relationship between size and latitudinal-correlated factors in insects could be influenced by voltinism, because, as the number of generations year^{-1} increases, less time per generation is available for growth (Zeuss *et al.*, 2017). Therefore, given the multiple environmental and biotic factors and individual traits directly or indirectly related with size, empirical evidence of such mechanisms is generally scarce, especially for aquatic ectotherms.

In the aquatic environment, physiological or mechanical constraints could result in patterns of body size variation that are different from those found in terrestrial animals (e.g. Zeuss *et al.*, 2017). Indeed, meta-analyses by Forster *et al.* (2012) and Horne *et al.* (2015) showed that (intraspecific) temperature–size responses (conforming to BR) were stronger in aquatic than in terrestrial species. It has been suggested that the balance between oxygen supply and demand, as an important driver of the temperature–size response, might strengthen such a response in the aquatic environment, as oxygen is less readily available in water than in air (Atkinson, 1995; Verberk *et al.*, 2011). Other indirect factors that might play a role are, however, frequently overlooked, such as species' preference for lentic or lotic waters. The contrasting stability between these habitat types (at evolutionary timescales) is known to select differentially for traits related to dispersal ability (Ribera, 2008): lentic insects are generally better dispersers than their lotic relatives and therefore have broader and more northern distribution ranges (e.g. Hof *et al.*, 2006; Abellán & Ribera, 2011; Pinkert *et al.*, 2018). If dispersal ability is positively correlated with body size in insects with a similar body structure and biology (see Rundle *et al.*, 2007), BR clines in lineages with both lotic and lentic species could actually reflect differential dispersal capacities between species specialised in each habitat. On the other hand, lotic waters may impose stronger physical constraints on body size than lentic habitats, as large insects are unable to cope with the strong drag forces produced by the water flow (Bournaud *et al.*, 1992; Ribera & Nilsson, 1995). Therefore, whereas large sizes are generally absent in lotic waters, the full variability of sizes can be found in lentic waters. Considering these physical and dispersal constraints of lotic species, we might expect that, in general, the temperature–size relationship must be clearer for lentic species. However, the annual number of generations as well as other factors at local scale could also influence such a relationship, such as, for example, the geographical and temporal variations in oxygen or temperature, which are generally higher in small, shallow lentic waters than in lotic systems (Batzer & Boix, 2016).

Among aquatic insects, diving beetles (Dytiscidae) have been proposed as good models to explore body size variation along environmental gradients because of their considerable variation in body and geographic range size, even among closely related species (Vamosi *et al.*, 2007). The availability of well-resolved phylogenies for different lineages of this group (Abellán & Ribera, 2011) provides a unique opportunity to study biogeographic patterns across independent 'evolutionary replicas', controlling for phylogenetic inertia. Here, we explored the relationship between body size and latitude in four monophyletic lineages of diving beetles across a wide latitudinal range, accounting for the potential influence of taxonomic resolution, habitat preference and phylogenetic effects on body size clines.

Material and methods

Study group

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

The total length of these species was obtained from Scheffer *et al.* (2015) and distributional data (latitudinal centroids and maximum latitude) were obtained from Abellán and Ribera (2011).

Data analyses: Bergmann's rule tests

We tested the relationship between body size and latitude at two different taxonomic resolutions: (i) within each lineage; and (ii) for the whole dataset, pooling the four lineages. Phylogenetic generalised least squares (PGLS) were used

Table 1. Results of phylogenetic generalised least squares (PGLS) testing the relationship between average size and central latitude for the whole dataset and each lineage, respectively.

Group	Predictor	Slope ± SD	d.f.	F	P-value	R²	λ†
All species	Latitude	−0.015 ± 0.020	1	1.412	0.238		
	Habitat type	0.571 ± 0.944	1	2.983	0.088		
	Latitude × habitat type	−0.004 ± 0.023	1	0.035	0.853		
	Full model				0.227	0.049	0.969 (*P* < 0.001)
Ilybius	Latitude	−0.016 ± 0.041	1	0.145	0.707	0.007	0.670 (*P* = 0.004)
Deronectes	Latitude	0.004 ± 0.010	1	0.203	0.658	0.011	0.977 (*P* = 0.003)
Hydroporus (all)	Latitude	−0.029 ± 0.015	1	7.540	0.011		
	Habitat type	0.800 ± 0.687	1	19.619	<0.001		
	Latitude × habitat type	−0.004 ± 0.018	1	0.056	0.814		
	Full model				<0.001	0.537	0.988 (*P* = 0.028)
Hydroporus (lotic)	Latitude	−0.025 ± 0.018	1	2.011	0.194	0.200	0.920 (*P* = 0.162)
Hydroporus (non-lotic)	Latitude	−0.034 ± 0.008	1	17.142	<0.001	0.502	1 (*P* = 0.002)
Graptodytes (all)	Latitude	−0.064 ± 0.018	1	3.061	0.104		
	habitat	−1.844 ± 0.763	1	3.751	0.075		
	Latitude × habitat type	0.056 ± 0.021	1	7.600	0.016		
	Full model				0.018	0.526	0 (*P* = 1)
Graptodytes (lotic)	Latitude	−0.064 ± 0.027	1	5.769	0.074	0.591	0 (*P* = 1)
Graptodytes (non-lotic)	Latitude	−0.004 ± 0.006	1	0.506	0.495	0.053	1 (*P* = 0.035)

†Maximum likelihood-estimated Pagel's λ; in parentheses, *P*-values of the test assessing whether it differed from zero (i.e. no phylogenetic signal).

to control for phylogenetic inertia. For the analyses within lineages, the phylogenetic trees from Abellán and Ribera (2011) were used. For the pooled dataset, we combined the phylogenies of the four lineages in a global tree, using the most recent family-level phylogeny for Dytiscidae (Désamoré *et al.*, 2018) as a base tree representing the evolutionary relationships among lineages (see Fig. S1). The depth of each clade tree in the global tree was set from the age of each lineage, as provided in Abellán and Ribera (2011). While this meta-tree approach has a number of limitations, it provides an operational phylogenetic hypothesis based on the currently available data suitable for comparative analysis (Funk & Specht, 2007). The phylogenetic signal of the regressions' residuals was assessed by maximum-likelihood estimated values of Pagel's lambda (λ; Pagel, 1999) and likelihood ratio tests to determine whether it differed significantly from zero (i.e. from a model assuming that patterns of body size variation are independent of phylogeny).

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

All analyses were performed for both average size and central latitude, and maximum size and maximum latitude, in R v. 3.3.3 (R Core Team, 2017). We used a single datapoint for each species, as intraspecific variation of size in diving beetles is relatively low in relation to interspecific variation (see Larson *et al.*, 2000 and Table S1).

Results

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

Phylogenetic generalised least-squares for the whole dataset showed no significant relationships between size and either latitude or habitat, or their interaction (Tables 1 and S3). The different lineages were clearly clustered by (mainly) size and latitude, especially for *Ilybius*, the largest and most northerly distributed group (Fig. 1a). Within-lineage analyses revealed no consistent patterns across the different groups. No significant relationships were found in *Ilybius* or *Deronectes*, whereas average size and central latitude showed a significant relationship in *Hydroporus* as well as maximum size and maximum latitude in *Graptodytes* (Tables 1 and S3), negative in both cases (i.e. following a converse BR) (Fig. 1b,c). This pattern showed a strong significant phylogenetic signal in *Hydroporus* (Table 1).

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

Discussion

The currently available data show that latitudinal clines in body size are much less consistent across insects (and ectotherms in general) than endothermic taxa (Shelomi, 2012; Vinarsky, 2014). Here, we found no support for BR in the studied lineages,
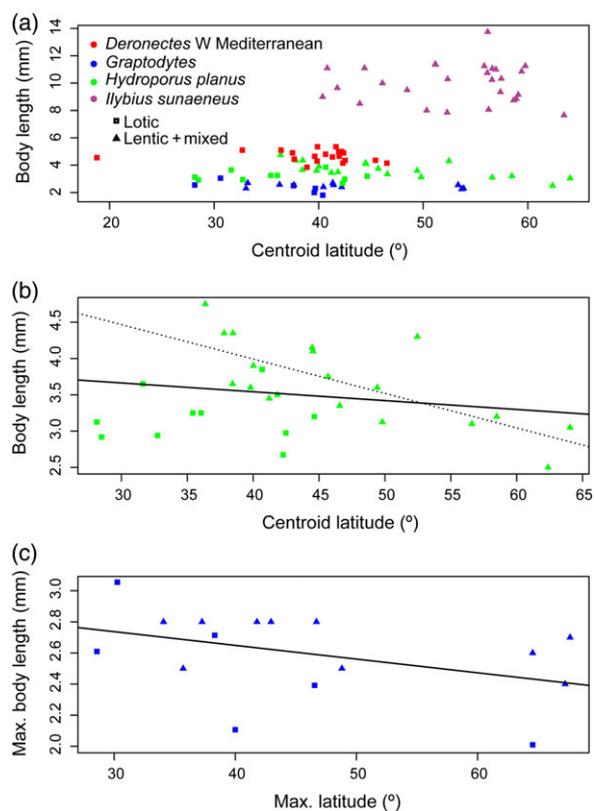
Fig. 1. Relationships between average body length and central latitude for the whole dataset (a), average body length and central latitude for *Hydroporus* species (b), and maximum body length and maximum latitude for *Graptodytes* species (c). Regression lines of significant relationships are shown (continuous for all species; dashed for lentic and mixed-habitat species). [Colour figure can be viewed at wileyonlinelibrary.com].

and inconsistent latitudinal patterns of body size at the two taxonomic resolutions explored, as well as among the different lineages.

No significant relationship between body size and latitude was detected when data from the four lineages were pooled; however, two of the studied lineages (*Hydroporus* and *Graptodytes*) showed a converse BR cline when assessed independently. The first important point to be drawn from these results is the importance of considering well-defined, complete taxonomic units when examining biogeographic patterns in body size. It was not our goal to examine body size trends at the family level, given the limited extent of our size and distribution dataset and the lack of a comprehensive phylogeny at such level. However, our analyses show that body size patterns (or the absence of them) observed when different taxonomic groups are pooled arbitrarily may be confounded by inconsistent patterns among lower taxonomic groups. Other studies have found similar inconsistencies, such as those on latitudinal body size clines in bees (Gérard *et al.*, 2018) or size variation in Lepidoptera along elevational gradients (e.g. Hawkins & DeVries, 1996; Brehm & Fiedler, 2004). However, Brehm *et al.* (2018) found a consistent pattern of body size increase along an extensive

altitudinal gradient working with a large dataset of tropical moths. We furthermore found a strong phylogenetic signal in body size variation, which is common in insects, highlighting the importance of accounting for phylogenetic relatedness (Chown & Gaston, 2010).

Few interspecific studies of BR in aquatic insects are available for comparison with the patterns found here, but the closest one, by Vamosi *et al.* (2007) (also on dytiscids), found a positive relationship between the proportion of large species with latitude, contrary to the trends (or lack of them) observed here within specific lineages. However, that study was done at the assemblage level (i.e. the body sizes of all dytiscid species were pooled within each grid cell) and was restricted to a geographic political region (southern Alberta, Canada). Thus, because of the different taxonomic and spatial resolutions, and for the reasons outlined earlier, these results are not directly comparable.

One of the physiological mechanisms proposed to explain size patterns in aquatic ectotherms is based on the fact that aerobic performance in the aquatic environment is worse in warmer habitats, because oxygen demand exceeds supply, constraining size at lower latitudes (Verberk *et al.*, 2011). Makarieva *et al.* (2005) proposed that the interactions between metabolic rates, growth and temperature are behind the size decrease with temperature (BR) in aquatic organisms (e.g. Chapelle & Peck, 1999) and the opposite pattern (i.e. converse BR) in terrestrial ones (e.g. Ashton & Feldman, 2003), as oxygen concentrations in aquatic environments are lower than the atmosphere. However, we found the converse BR in two of the studied aquatic groups. Because of the respiratory mode of dytiscids (both adults and larvae) by a physical compressible gill that needs to be renewed at the surface, they are highly dependent on atmospheric air, whereas O_2 exchange with surrounding water is supposed to be minimal (Calosi *et al.*, 2007). Thus, body size patterns in aquatic insects with this respiratory mode could be driven by similar metabolic constraints to those on terrestrial rather than aquatic ectotherms. However, no empirical evidence supports this idea.

In part, the inconsistent patterns among the studied lineages could reflect different constraints imposed by habitat type on both size and distribution, which have typically been ignored when studying body size patterns in the aquatic environment. Here, significant relationships between size and latitude were only found in lineages that include lentic and lotic species (i.e. *Hydroporus* and *Graptodytes*) and, among these, the relationship was only significant for species with lentic or indistinct habitat preference. Lotic species in our dataset were mostly restricted to lower latitudes, a pattern that has previously been attributed to the well-supported hypothesis that they have lower propensity for dispersal than lentic ones (Abellán & Ribera, 2011). On the other hand, size variability was higher between lentic than between lotic species. The largest species in our dataset were lentic or with indistinct habitat preference (Fig. 1), which might be related to the physical constraint on size imposed by the currents in running water (Ribera & Nilsson, 1995). Therefore, it is likely that, because size and dispersal are constrained in lotic species, the latitudinal body size clines we found in *Hydroporus* and *Graptodytes* species actually reflect the size gradient of lentic (or mixed-habitat) species.

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

Our results suggest that there may be no universal interspecific trends in latitudinal variation of body size across aquatic insect groups and, therefore, these cannot be explained by a single universal mechanism, but are instead driven by complex interactions among competing traits (Angilletta & Dunham, 2003). We suggest that, in addition to being analysed and interpreted within a clear taxonomic and phylogenetic context, examination of body size patterns in aquatic animals should also consider the potential constraints on size and dispersal imposed by the habitat.

Acknowledgements

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Data on body size, habitat and geographic range of all studied taxa.

Figure S1. Combined phylogenetic tree of the four studied lineages.

Table S2. PGLS testing the relationship between average and maximum sizes and central and maximum latitudes.

Table S3. PGLS testing the relationship between maximum size and maximum latitude.

References

Abellán, P. & Ribera, I. (2011) Geographic location and phylogeny are the main determinants of the size of the geographical range in aquatic beetles. *BMC Evolutionary Biology*, **11**, 344.

Angilletta, M.J. & Dunham, A.E. (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *American Naturalist*, **162**, 332–342.

Ashton, K.G. & Feldman, C.R. (2003) Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution*, **57**, 1151–1163.

Atkinson, D. (1994) Temperature and organism size – a biological law for ectotherms? *Advances in Ecological Research*, **25**, 1–54.

Atkinson, D. (1995) Effects of temperature on the size of aquatic ectotherms: exceptions to the general rule. *Journal of Thermal Biology*, **20**, 61–74.

Atkinson, D. & Sibly, R.M. (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution*, **12**, 235–239.

Batzer, D. & Boix, D. (2016) *Invertebrates in Freshwater Wetlands*. Springer, Cham, Switzerland.

Bergmann, K.G.L.C. (1847) Über die Verhältnisse der wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, **3**, 595–708.

Blackburn, T., Gaston, K.J. & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, **5**, 165–174.

Bournaud, M., Richoux, P. & Usseglio-Polatera, P. (1992) An approach to the synthesis of qualitative ecological information from aquatic coleoptera communities. *Regulated Rivers: Research & Management*, **7**, 165–180.

Brehm, G. & Fiedler, K. (2004) Bergmann's rule does not apply to geometrid moths along an elevational gradient in an Andean montane rain forest. *Global Ecology and Biogeography*, **13**, 7–14.

Brehm, G., Zeuss, D. & Robert, C. (2018) Moth body size increases with elevation along a complete tropical elevational gradient for two hyperdiverse clades. *Ecography*. https://doi.org/10.1111/ecog.03917.

Calder, W.A. III (1984) *Size, Function and Life History*. Harvard University Press, Cambridge, Massachusetts.

Calosi, P., Bilton, D.T. & Spicer, J.I. (2007) The diving response of a diving beetle: effects of temperature and acidification. *Journal of Zoology*, **273**, 289–297.

Chapelle, G. & Peck, L. (1999) Polar gigantism dictated by oxygen availability. *Nature*, **399**, 114–115.

Chown, S. & Gaston, K. (2010) Body size variation in insects: a macroecological perspective. *Biological Reviews*, **85**, 139–169.

Désamoré, A., Laenen, B., Miller, K.B. & Bergsten, J. (2018) Early burst in body size evolution is uncoupled from species diversification in diving beetles (Dytiscidae). *Molecular Ecology*, **27**, 979–993.

Forster, J., Hirst, A.G. & Atkinson, D. (2012) Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 19310–19314.

Funk, V.A. & Specht, C.D. (2007) Meta-trees: grafting for a global perspective. *Proceedings of the Biological Society of Washington*, **120**, 232–240.

García-Vázquez, D., Bilton, D.T., Alonso, R., Benetti, C., Garrido, J., Valladares, L.F. *et al.* (2016) Reconstructing ancient Mediterranean crossroads in *Deronectes* diving beetles. *Journal of Biogeography*, **43**, 1533–1545.

Gérard, M., Vanderplanck, M., Franzen, M., Kuhlmann, M., Potts, S.G., Rasmont, P. *et al.* (2018) Patterns of size variation in bees at a continental scale: does Bergmann's rule apply? *Oikos*, **00**, 1–9.

Hassal, C., Keat, S., Thompson, D.J. & Watts, P.C. (2014) Bergmann's rule is maintained during a rapid range expansion in a damselfly. *Global Change Biology*, **20**, 475–482.

Hawkins, B.A. & DeVries, P. (1996) Altitudinal gradients in the body sizes of Costa Rican butterflies. *Acta Oecologica*, **17**, 185–194.

Hof, C., Brändle, M. & Brandl, R. (2006) Lentic odonates have larger and more northern ranges than lotic species. *Journal of Biogeography*, **33**, 63–70.

Horne, C.R., Hirst, A.G. & Atkinson, D. (2015) Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. *Ecology Letters*, **18**, 327–335.

Johansson, F. (2003) Latitudinal shifts in body size of *Enallagma cyathigerum* (Odonata). *Journal of Biogeography*, **30**, 29–34.

Larson, D.J., Alarie, Y. & Roughley, R.E. (2000) *Predaceous Diving Beetles (Coleoptera: Dytiscidae) of the Nearctic Region, with emphasis on the fauna of Canada and Alaska*. NRC Research Press, Ottawa, Canada.

Lindstedt, S.L. & Boyce, M.L. (1985) Seasonality, fasting endurance, and body size in mammals. *American Naturalist*, **125**, 873–878.

Makarieva, A.M., Gorshkov, V.G. & Li, B.-L. (2005) Temperature-associated upper limits to body size in terrestrial poikilotherms. *Oikos*, **111**, 425–436.

Meiri, S. (2011) Bergmann's rule – what's in a name? *Global Ecology and Biogeography*, **20**, 203–207.

Mousseau, T.A. (1997) Ectotherms follow the converse to Bergmann's rule. *Evolution*, **51**, 630–632.

Nilsson, A.N. & Hájek, J. (2018) *A world catalogue of the family Dytiscidae (Coleoptera, Adephaga)*, 304 pp. Internet version 31.I.2018. [WWW document]. URL www.waterbeetles.eu [accessed on April 2018].

Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

Pinkert, S., Dijkstra, K.-D.B., Zeuss, D., Reudenbach, C., Brandl, R. & Hof, C. (2018) Evolutionary processes, dispersal limitation and climatic history shape current diversity patterns of European dragonflies. *Ecography*, **41**, 795–804.

R Core Team (2017) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ribera, I. (2008) Habitat constraints and the generation of diversity in freshwater macroinvertebrates. *Aquatic Insects: Challenges to Populations* (ed. by J. Lancaster and R. A. Briers), pp. 289–311. CAB International Publishing, Wallingford, U.K.

Ribera, I. & Faille, A. (2010) A new microphthalmic stygobitic Graptodytes Seidlitz from Morocco, with a molecular phylogeny of the genus (Coleoptera, Dytiscidae). *Zootaxa*, **2641**, 1–14.

Ribera, I. & Nilsson, A.N. (1995) Morphometric patterns among diving beetles (Coleoptera: Noteridae, Hygrobiidae, and Dytiscidae). *Canadian Journal of Zoology*, **73**, 2343–2360.

Ribera, I., Bilton, D.T., Balke, M. & Hendrich, L. (2003) Evolution, mitochondrial DNA phylogeny and systematic position of the Macaronesian endemic Hydrotarsus Falkenstrom (Coleoptera: Dytiscidae). *Systematic Entomology*, **28**, 493–508.

Rundle, S., Bilton, D.T. & Foggo, A. (2007) By wind, wings or water: Body size, dispersal and range size in aquatic invertebrates. *Body Size: The Structure and Function of Aquatic Ecosystems* (ed. by A. G. Hildrew, D. G. Raffaelli and R. Edmonds-Brown), pp. 186–209. Cambridge University Press, New York, New York.

Scheffer, M., Vergnon, R., van Nes, E.H., Cuppen, J.G.M., Peeters, E.T.H.M., Leijs, R. *et al.* (2015) The evolution of functionally redundant species; evidence from beetles. *PLoS One*, **10**, e0137974.

Shama, L.N.S. & Robinson, C.T. (2009) Microgeographic life history variation in an alpine caddisfly: plasticity in response to seasonal time constraints. *Freshwater Biology*, **54**, 150–164.

Shelomi, M. (2012) Where are we now? Bergmann's rule sensu lato in insects. *American Naturalist*, **180**, 511–519.

Vamosi, S.M., Naydani, C.J. & Vamosi, J.C. (2007) Body size and species richness along geographical gradients in Albertan diving beetle (Coleoptera: Dytiscidae) communities. *Canadian Journal of Zoology*, **85**, 443–449.

Verberk, W.C., Bilton, D.T., Calosi, P. & Spicer, J.I. (2011) Oxygen supply in aquatic ectotherms: partial pressure and solubility together explain biodiversity and size patterns. *Ecology*, **92**, 1565–1572.

Vinarsky, M.V. (2014) On the applicability of Bergmann's rule to ectotherms: the state of the art. *Biology Bulletin Reviews*, **4**, 232–242.

Winterhalter, W.E. & Mousseau, T.A. (2008) The strength of temperature-mediated selection on body size in a wild insect population. *Journal of Orthoptera Research*, **17**, 347–351.

Zeuss, D., Brunzel, S. & Brandl, R. (2017) Environmental drivers of voltinism and body size in insect assemblages across Europe. *Global Ecology and Biogeography*, **26**, 154–165.