



Contrasting latitudinal gradients of body size in helminth parasites and their hosts

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Abstract

Aim: We examined body size scaling relationships for two developmental life stages of parasitic helminths (egg and adult) separately in relationship to latitude (i.e. Bergmann's rule), temperature and temperature seasonality. Given that helminth eggs experience environmental conditions more directly, whereas adults live inside infected host individuals, we predict stronger environmentally driven gradients of body size for eggs than for adults.

Location: Global.

Time period: Present day.

Major taxa studied: Parasitic helminths.

Methods: We compiled egg size and adult body size data (both minimum and maximum) for 265 parasitic helminth species from the literature, along with species latitudinal distribution information using an extensive global helminth occurrence database. We then examined how the average helminth egg and adult body size of all helminth species present (minimum and maximum separately) scaled with latitude, temperature and temperature variability, using generalized linear models.

Results: Both the egg size and the adult body size of helminths tended to decrease towards higher latitudes, although we found the opposite body size scaling pattern for their host species. Helminth sizes were also positively correlated with temperature and negatively, but more weakly, with temperature seasonality.

Main conclusions: Instead of following the body size patterns of their hosts, helminth parasites are more similar to other ectotherms in that they follow the converse Bergmann's rule. This pattern did not differ between helminth developmental stages, suggesting that mean annual temperature and seasonality are unlikely to be related mechanistically to body size variation in this case.

KEYWORDS

Bergmann's rule, helminth size distribution, host–parasite interactions, latitude–size relationship, parasite macroecology, temperature–size relationship

1 | INTRODUCTION

How and why taxonomic and ecological diversity in regional assemblages vary across space are fundamental questions in biogeography and macroecology. A number of 'ecogeographical rules' [see Mayr (1956) for a discussion] have been proposed for describing the general spatial patterns in the variation of species features across large-scale geographical or climatic gradients (Gaston, Chown, & Evans, 2008). Bergmann's rule, which is perhaps the most studied of these rules, proposes that large bodies are favoured in colder and harsher environments at higher latitudes, resulting in a higher concentration of small-bodied species in the tropics (Bergmann, 1847). Empirical patterns of the size–latitude relationship are mixed, but some support of Bergmann's rule comes from a variety of taxa, including insects (Shelomi, 2012), freshwater fish (Belk & Houston, 2002), reptiles (Ashton, Tracy, & Queiroz, 2000) and amphibians (Ashton, 2002). Numerous mechanisms have been proposed to explain this pattern, including the original heat conservation mechanism by Bergmann (1847), and others related to primary productivity, habitat and water availability, predation, biotic interactions, evolutionary constraints, historical dispersal and human pressures (see Table 1 and associated references). Nonetheless, there is no consensus on the dominant mechanism or the relative contributions of different mechanisms that might work in concert to generate the apparent patterns.

Bergmann's rule remains a difficult subject for at least three reasons. First, the generality of the original heat conservation mechanism proposed by Bergmann (1847) remains under debate. Alternative constraints on geographical clines in body size are numerous (see Table 1), but the collinearity among many of these putative mechanisms makes parsing the real mechanism difficult. Second, the organizational scale at which Bergmann's rule has been

investigated has varied, either as the mean body size of individuals within a single species or as the mean body size of entire assemblages across ecological or spatial gradients (Blackburn et al., 1999; Morales-Castilla, Rodríguez, & Hawkins, 2012; Olalla-Tárraga, Bini, Diniz-Filho, & Rodríguez, 2010; Watt, Mitchell, & Salewski, 1999). Third, the taxonomic scope of Bergmann's rule is unclear, because many proposed mechanisms apply to endotherms only, whereas limited evidence suggests that the general pattern might be extended to ectotherms (Olalla-Tárraga et al., 2010; Olalla-Tárraga, Diniz-Filho, Bastos, & Rodríguez, 2009).

This variation in support for Bergmann's rule might be a function of the taxonomic or spatial scale considered. For instance, turtles and lizards have been found to follow Bergmann's rule, whereas snakes follow a converse pattern (Ashton, Feldman, & Garland, 2003; Olalla-Tárraga, Rodríguez, & Hawkins, 2006). In *Plethodon* salamanders, a phylogenetic comparative analysis found no relationship between body size and temperature (Adams & Church, 2011). Other amphibians also have varied patterns across lineages, with anurans following Bergmann's rule and urodeles following the converse (Olalla-Tárraga & Rodríguez, 2007). This degree of mixed support among closely related groups also extends to invertebrates. For example, subclades of insects have been found following Bergmann's rule as often as following the converse rule, with a majority of studies finding no discernible latitudinal or elevational pattern (Shelomi, 2012). In sum, although empirical support for body size gradients is abundant for terrestrial endotherms distributed across the Holarctic (Morales-Castilla, Olalla-Tárraga, Purvis, Hawkins, & Rodríguez, 2012; Morales-Castilla et al., 2012; Olson et al., 2009; Rodríguez, Olalla-Tárraga, & Hawkins, 2008), the failure to detect similar body size gradients and evidence of the opposite gradient in ectotherms suggest that ectotherm body size variation is likely not to be driven by mechanisms that are frequently hypothesized, such as the heat

Hypothesis	Thermy	Indicator	Sign	References
Heat conservation	Endotherms	Temperature	-	a
Heat balance	Ectotherms	Temperature	-	b, c
Optimal body temperature	Ectotherms	Temperature	+	d
Temperature–size rule	Ectotherms	Temperature	-	e
Resource availability	Both	Net primary productivity	+	f, g
Starvation resistance	Endotherms	Net primary productivity	-	b, h, i
Water availability	Ectotherms	Precipitation	-	j, k
Habitat availability	Both	Elevation × macroclimate	+	l
Growing season length	Ectotherms	Growing degree days	-	m
Water availability	Ectotherms	Precipitation	+	n
Interspecific competition	Endotherms	Competitor richness	-	o, p, q
Past dispersal	Both	Time since colonization	-	r, s

TABLE 1 Hypotheses aimed at identifying the underlying mechanism for observed spatial variation in species body size, with both the observed sign of the relationship and the associated species groups

^aBergmann (1847). ^bCushman, Lawton, and Manly (1993). ^cOlalla-Tárraga and Rodríguez (2007). ^dAshton et al. (2003). ^eAtkinson (1995). ^fRosenzweig (1968). ^gGeist (1987). ^hCalder (1984). ⁱLindstedt and Boyce (1985). ^jNevo (1973). ^kAshton (2002). ^lRodríguez et al. (2008). ^mBidau and Martí (2007). ⁿFicetola et al. (2010). ^oBlackburn and Gaston (1996). ^pCardillo (2002). ^qOlson et al. (2009). ^rRodríguez, López-Sañudo, and Hawkins (2006). ^sMorales-Castilla et al. (2012).

conservation theory for endotherms (Olalla-Tárraga & Rodríguez, 2007). It might only become possible to estimate the underlying forces generating body size variation by gauging empirical support for ecogeographical rules in a larger variety of taxa.

Parasite species offer an interesting organismal system for exploring latitude–body size relationships. To date, latitude–body size relationships for parasitic species have focused on isolated taxonomic subsets of parasites and have found a range of relationships (Korallo-Vinarskaya, Vinarski, Khokhlova, Shenbrot, & Krasnov, 2015; Poulin, 1995, 1996, 1997, 1998). For example, monogeneans had larger adults at higher latitudes (Poulin, 1996), whereas no relationship with latitude was found for trematode species (Poulin, 1997). Contrasting latitude–body size patterns in ecto- and endoparasitic species across taxonomic subsets might provide interesting insight into the underlying mechanisms of spatial variation in body size. For instance, there is evidence that parasite latitudinal range is phylogenetically conserved (Krasnov, Shenbrot, Mescht, Warburton, & Khokhlova, 2018). Parasitic helminths are an interesting case because they often have both free-living life stages (typically during the egg and larval stages) that are exposed to the environment (Lafferty & Kuris, 1999; Pietrock & Marcogliese, 2003; Thieltges, Jensen, & Poulin, 2008) in addition to life stages in the relatively stable internal environment of the host. How helminth species body sizes vary across latitude therefore might depend on the life stage considered. However, developmental constraints on adult body sizes as a function of egg size may obscure potential differences in scaling (Benesh, Chubb, & Parker, 2013; Morand, 1996; Poulin & Latham, 2003; Poulin, Wise, & Moore, 2003). If early development constrains helminth body size, egg size and adult body size should be strongly correlated and follow the same gradients (either both following Bergmann's rule or both converse). Indeed, in Acanthocephalans and trematodes (Platyhelminthes), size at earlier developmental stages is correlated with adult helminth size, but it explains only a moderate proportion of adult size (c. 33%; Poulin & Latham, 2003; Poulin et al., 2003). Given that helminth egg size may be influenced by the environment whereas adult helminth body size may be more constrained by the within-host environment, it is also possible to see differences among life stages in their latitudinal size gradients.

Combining helminth size data compiled from published literature with a global helminth occurrence database, we investigated the spatial patterns in helminth egg size and adult body size, linking helminth parasite sizes to gradients of latitude, temperature and temperature seasonality. This was performed at the global scale and included > 260 helminth parasite species. Given that the environmental conditions experienced during early development stages (e.g. larval or egg stages) could further influence the size at later stages owing to developmental constraint, we also tested for a correlation between species egg and adult body sizes. Lastly, we examined whether positive latitude–body size relationships could be observed in helminths as a secondary property of host latitude–body size relationships, because in many cases larger helminth species tend to be found in larger host species (Morand, 1996; Poulin, 1997; Poulin & Latham, 2003). These analyses provide evidence that: (a) for helminths, both

egg size and adult size are largest in the tropics, following a converse Bergmann's rule; and (b) host species followed the opposite pattern. The similarity in body size scaling between helminth developmental stages suggests strong developmental constraints, for which we do not detect much evidence, or suggests a minimal role for temperature as the underlying mechanism for latitudinal variation in body size.

2 | METHODS

2.1 | Helminth parasite occurrence data

Helminth parasite occurrence data were obtained from the parasite database of the London Natural History Museum (LNHM), a collection of helminth [Platyhelminthes (trematodes and cestodes), Acanthocephalans and Nematodes] occurrences from published studies (Gibson, Bray, & Harris, 2005) (available at <http://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/>). These data contain > 18,000 unique host species and 27,000 unique helminth parasite species distributed across > 450 distinct terrestrial and aquatic localities. Of this complete set, we exclude localities that were overly vague (e.g. 'Western Europe'), because these localities were infeasible to georeference and were often larger localities that contained multiple nested locations. This procedure resulted in a total of 397 locations, including aquatic, terrestrial and marine environments (see Supporting Information). Together, the data consisted of 165,109 spatial occurrence records of unique host–helminth associations. For our main analyses, we also excluded locations that were difficult to georeference or were nested inside other locations, and aquatic and marine locations (e.g. 'Red Sea'). The inclusion of aquatic and marine locations does not affect our overall findings. It is possible that some of the helminth parasite species included may infect aquatic host species at some point in their life cycle. Also, it is important to note that removal of aquatic and marine locations does not entirely remove aquatic and marine host species, because inland bodies of water are georeferenced to the terrestrial locality they are contained in. However, the inclusion of these host species is unlikely to influence our findings, because restricting our analyses to only mammalian hosts provided qualitatively similar outcomes. Further discussion of these points is provided in the Supporting Information Supplemental Materials.

2.2 | Helminth morphological data

Data on helminth egg and adult body size were extracted from the species description of each parasite from five helminth taxonomy references (Anderson, 2000; Crompton & Nickol, 1985; Levine, 1980; Petrochenko & Skrjabin, 1971; Yamaguti, 1971). From these references, we compiled both minimum and maximum egg size (in micrometres) and adult body size (in millimetres). If the species description provided estimates for multiple host species, the minimum and maximum observed body sizes across hosts were used.

Likewise, adult worm lengths span both male and female sizes (if both were reported). This captures the morphological variation in helminth parasite size as a function of host species and sex. For length measurements of adult Acanthocephalans and Nematodes, the reported sizes correspond to the final larval moult, and therefore, do not correspond to maximum potential size but provide a conservative estimate of adult size standardized to a known developmental stage of the adult life cycle. Thus, maximum size is not necessarily the largest size found in that species, which is largely variable and potentially dependent on the host species infected, but the maximum size at a specific life stage. For the Platyhelminthes, we used reported adult worm size. A final concern is that helminth body sizes could be host specific, and such variation in helminth minimum and maximum sizes could be host specific. However, using the minimum and maximum size across all potential host species, we fully capture the range of body sizes potentially attained by each helminth species. In total, we obtained data on helminth egg and adult sizes for 265 helminth parasite species (see www.doi.org/10.6084/m9.figshare.6406823).

The number of helminth parasite species used in analyses was dependent on the available body size data and the occurrence of these helminth species in the helminth occurrence database. Thus, we obtained helminth body size data for 265 species, but complete information for minimum and maximum egg and adult size was available for only 145 helminth species (17 Acanthocephalans, 46 Nematodes and 57 Platyhelminthes). Complete data on all morphological measures was not necessary, however, and for each analysis we used all available species for analyses of helminth adult body size ($n = 202$) and egg size ($n = 182$).

2.3 | Helminth range approximation

Helminth occurrences provided in this database were georeferenced at the country scale. Although this is coarse, the data contain the most complete record of helminth parasites compared with any other existing database in terms of both the quantity of data and the number of unique helminth species recorded (Dallas et al., 2018). Using country-level occurrence data, we calculated the latitudinal range for the 265 helminth species for which size information was available. Thus, we estimated the latitudinal range of parasites using the minimum and maximum latitudes of countries in which the parasite was recorded, using the latitude of each country's centre as an approximation. Given the size of the dataset and the large range of a majority of the helminth species examined, we believe this approximation is justified.

2.4 | Helminth body size and temperature

Latitude in Bergmann's rule may be a surrogate for temperature (Riener, Guralnick, & White, 2018). To explore this relationship, we determined the thermal range of each helminth species in the same way as we estimated latitudinal range. Annual mean temperature was estimated from the BioClim data (Hijmans, Cameron, Parra,

Jones, & Jarvis, 2005), based on 1970–2000. We consider helminth thermal range to be the range of temperatures potentially occupied by the parasite, estimated from the temperature at country centre. To examine the role of temperature seasonality on body size distributions, we also obtained temperature seasonality estimates from the BioClim data, which capture the variation in mean monthly temperatures (Hijmans et al., 2005). Although these are coarse estimates of thermal range, the lack of georeferenced data below the country level requires operational assumptions. However, these data currently represent the most species-rich and spatially comprehensive data available with which to test macroecological and ecogeographical patterns.

2.5 | Statistical analysis

Given that we are interested in how regional environment influences the morphological (and thus ecological) diversity of parasitic helminths, we adopted the assemblage-based approach to test whether helminth species body size generally increases with latitude (Bergmann's rule; McNab, 1971; Blackburn et al., 1999). Along gradients of both latitude and temperature, we extracted the average value for minimum/maximum helminth body length and egg size for the entire helminth parasite assemblage, defined by all species whose latitudinal or thermal ranges contain a given point. Bergmann's rule was assessed using generalized linear models (log link; Gaussian error), relating latitude, temperature or seasonality to average minimum and maximum helminth parasite egg size or body length, resulting in 12 linear models (Table 2).

3 | RESULTS

3.1 | Latitude–size patterns

We found support for a converse Bergmann's rule for both helminth developmental stages; helminth egg size (Figure 1a) and adult body length (Figure 1d). The community of helminth parasite species tended to be composed of smaller-bodied species at higher absolute latitudes and larger-bodied species at lower absolute latitudes. In addition, we found evidence in support of Bergmann's rule for the host species associated with helminth parasite occurrences (see Supporting Information), suggesting opposing latitude–size patterns for host communities and their resident parasite communities.

3.2 | Temperature–size patterns

Helminth egg size and adult body length increased at higher mean temperatures (Figure 1). We demonstrate a link between latitudinal and temperature range of helminth parasites in the Supporting Information (see Supporting Information). Interestingly, helminth egg size was only weakly related to helminth adult body length across species, suggesting that the existence of a converse Bergmann's rule is not driven by one developmental stage,

TABLE 2 Bergmann's rule in helminth parasites along gradients of both latitude and temperature

	Parasite trait	Estimate	SE	t	p	R ²
Latitude	Minimum length	-.08	.01	-13.64	<.0001	.69
	Maximum length	-.16	.01	-13.67	<.0001	.69
Minimum egg size		-.03	.02	-1.59	.115	.02
	Maximum egg size	-.09	.02	-4.55	<.0001	.19
Temperature	Minimum length	2.03	.10	20.49	<.0001	.82
	Maximum length	.45	.03	14.05	<.0001	.72
	Minimum egg size	-.03	.06	-.46	.648	<.01
	Maximum egg size	.20	.08	2.59	.012	.07
Temperature seasonality	Minimum length	-.02	.00	-14.30	<.0001	.77
	Maximum length	-.08	.01	-7.40	<.0001	.46
	Minimum egg size	-.00	.01	-.35	.727	<.01
	Maximum egg size	-.02	.01	-2.63	.011	.09

Note. Bergmann's rule was supported for helminth egg size (in micrometres), but this relationship was not driven by temperature, because egg sizes were larger at higher temperatures. Likewise, adult parasite body length (in millimetres) followed a converse Bergmann's rule in terms of both latitude and temperature.

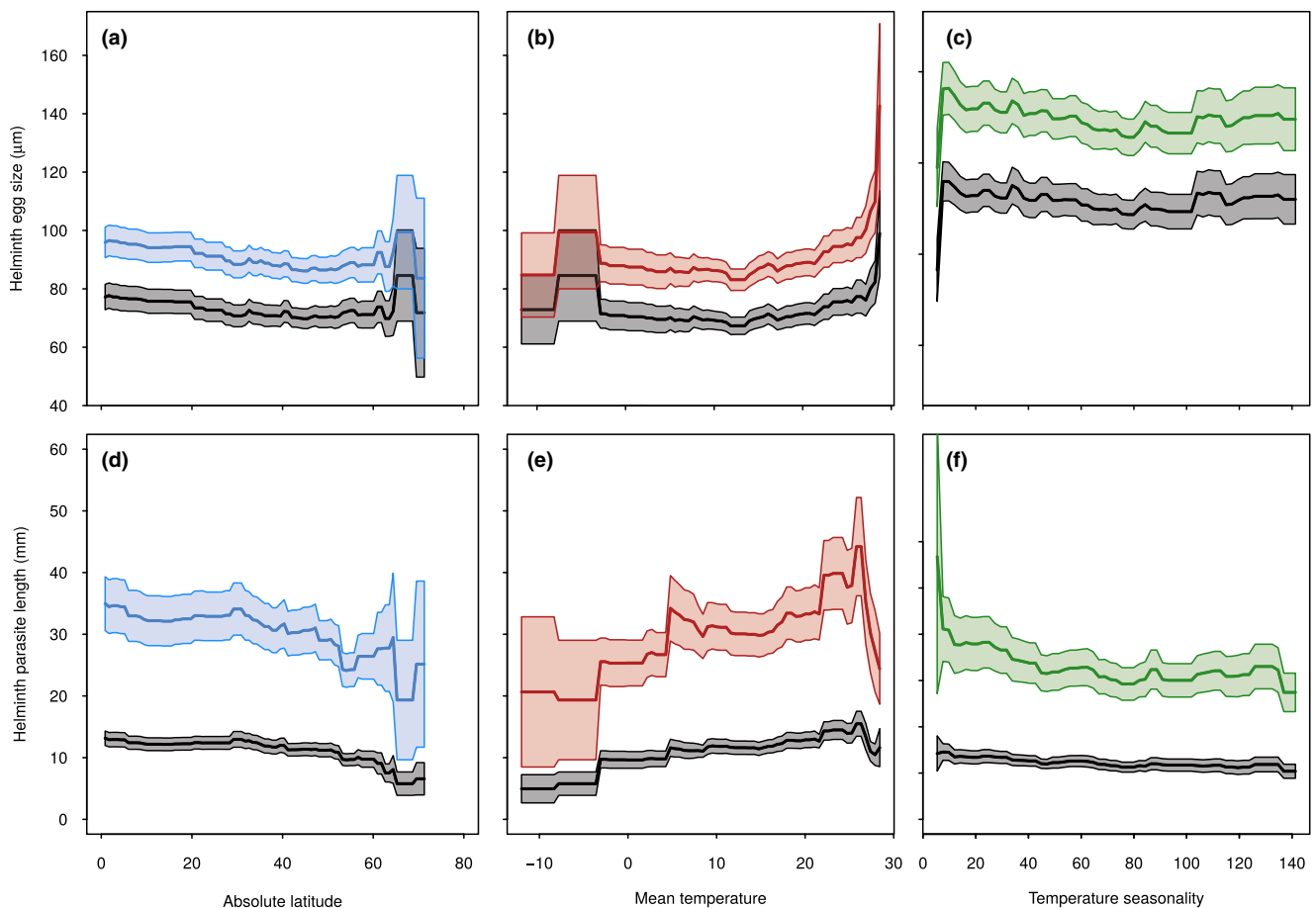


FIGURE 1 Body size patterns were observed for maximum (grey line) and minimum (black line) helminth egg size (top row) and adult body length (bottom row) for latitude (degrees) (a and d), temperature (b and e) and temperature seasonality ($100 \times \text{SD}$) (c and f), providing evidence for a converse Bergmann's rule in helminth parasites at the global scale for both latitude and temperature. Mean temperature ($10 \times \text{C}^\circ$) was estimate as mean annual temperature times 10, and temperature seasonality was calculated as the standard deviation of monthly temperature values times 100

but that both stages respond to variation in latitude or temperature. Lastly, higher temperature seasonality was weakly related to smaller helminth eggs and adults (Figure 1), and larger helminth parasites tended to occupy thermally stable environments (Table 2). These results were consistent, albeit greatly weakened, when aquatic and marine locations were included in the analyses (see Supporting Information). In the Supporting Information Supplemental Materials, we explore the relationship between helminth developmental stages (Figure S6) and the potential influence of shifting helminth communities across latitudes (see Supporting Information).

3.3 | Data biases and limitations

There are a number of potential biases that exist inherently in global databases based on museum specimens and published literature (Gibson et al., 2005). It is possible that some biases may be reduced with a larger quantity of data. If this is the case, the LNHM data represent the largest host–parasite database to date, containing > 215,000 host–helminth occurrence records, which is > 23 times what the U.S. National Parasite Collection (Lichtenfels, Pilit, & Hoberg, 1992) contains (c. 9,000 host–parasite records) and more than seven times the contents of the Global Mammal Parasite Database (c. 30,000 records; Nunn & Altizer, 2005). However, sampling biases probably still exist in the database, either in the thoroughness of sampling host–parasite interactions across geographical space or in the differential sampling of certain host or parasite species. It is impossible to account fully for these sources of bias, but we have attempted to address them in the Supporting Information (see Supporting Information) by: (a) examining differential spatial representation of certain helminth taxa; (b) testing whether Bergmann's rule existed for host species in the LNHM database; and (c) removing aquatic, coastal or ambiguous geographical locations. In short, we found no systematic variation in helminth taxa as a function of latitude, provided clear evidence for Bergmann's rule in host species using the same data and approach used to examine helminth body size gradients, and observed qualitatively similar findings when removing aquatic, coastal or ambiguously defined geographical locations from the analysis.

4 | DISCUSSION

At the global scale, helminth egg and adult body sizes were both negatively correlated with latitude and positively correlated with temperature, following the converse of Bergmann's rule. This supports previous findings in ectothermic organisms (Shelomi, 2012), where one key mechanism is based on the trade-off between body size and growth rate; the more limited resources and shorter growing season at higher latitudes might select for faster growth rate and thus smaller sizes (Mousseau, 1997). This theory could explain the similarity in response between the two helminth life stages, even

though the adults and eggs typically live inside host bodies and outside, exposed to the external environment, respectively. Our findings of a converse Bergmann's rule in helminths regardless of life stage but of little correlation between the sizes of the two stages across species (except for Platyhelminthes) also suggest that helminth parasite size does not exhibit strong developmental constraint (but see Benesh et al., 2013; Poulin & Latham, 2003; Poulin et al., 2003), so that scaling of adult helminth body size is not merely a secondary property of the scaling of helminth egg sizes. It is more likely that both stages are affected by latitudinal gradients in their respective environment. Lastly, we found that host body sizes scaled in a manner opposite to their helminth parasites. Overall, we suggest that helminth parasite body size does scale with latitude, seemingly opposing host body size gradients and relatively independent of the thermal environment, because helminth parasite eggs and adults followed the same pattern.

At least in the case of minimum adult size, temperature and seasonality both explain more variance than latitude per se, indicating that the spatial pattern of average adult body size in helminth species assemblages might be mainly driven by variation in environmental factors. Temperature was also more explanatory than latitude for helminth egg sizes, further suggesting a role for temperature in driving patterns of helminth parasite body sizes. Perhaps given the similar relationship across parasite developmental stages that have different exposure to temperature gradients, the role of temperature observed here is simply through collinearity with another, more relevant, ecological gradient. This explanation could reconcile the lack of difference observed between helminth developmental stages, where both adult and egg size appeared to be correlated with temperature, although only eggs are directly exposed to the external environmental conditions. Indeed, previous work on trematodes (Poulin & Latham, 2003), Acanthocephalans (Poulin et al., 2003) and cestodes (Benesh et al., 2013) has suggested that parasite sizes at different developmental stages are correlated. Likewise, the lack of adult size differences between endothermic and ectothermic definitive hosts further suggests that temperature is not a strong determinant of adult body size (Poulin & Latham, 2003; Poulin et al., 2003). Annual mean temperature, besides imposing pressure on species thermal tolerance, is often an indicator of resource availability in the environment (e.g. primary productivity), which could affect parasite growth and persistence both directly and indirectly through driving host abundance and diversity (Benesh, 2016; Brown, 2014). Although differences in size measures (i.e. surface area, biovolume or length) might explain some of the variation in findings, further research on the scaling relationships between sizes of developmental stages might provide more information on the trait and phylogenetic correlates of body size scaling. That is, intraspecific variation in body size and climatic constraints on parasitic body sizes might alter parasite body size relationships at different developmental stages.

The shorter growing seasons at higher latitudes could further restrict resource availability and time for growth and development (Blanckenhorn & Demont, 2004; Mousseau, 1997). Both adult body size and egg mass in helminths are typically associated with age at

maturity (Peters, 1983); therefore, faster maturation would allow advancement in onset of egg production, whereas larger body sizes and increased egg production require delayed maturation, thus longer growing seasons. Directly exposed to the physical environment in a region, eggs that hatch and develop as free-living larvae may suffer high larval mortality outside their optimal thermal and moisture ranges. The variation (e.g. seasonality) in temperature and moisture can thus strongly restrict the growth of free-living stages and determine the seasonality in development of different species (Rossanigo & Gruner, 1995). In addition, highly seasonal environments allow only restricted windows for transmission (reviewed by Altizer et al., 2006; Grassly & Fraser, 2006), which might further enforce selection for smaller-bodied species with faster maturation. Surprisingly, we also found decreasing adult length with high temperature seasonality, suggesting the possibility that seasonality influences host physiology to promote smaller adult helminth body sizes. Additional indirect effects on adult helminth size could come from variation in egg viability or seasonal opportunities for transmission (Altizer et al., 2006).

Many free-living species experience consistent environmental gradients throughout their lifetimes. The variability in life cycle and the fact that helminths infect both endo- and ectothermic hosts enable us to explore at what life stage body size could be determined among species. Our finding that both egg and adult helminth body sizes were related to temperature and temperature variability has at least two potential explanations. First, developmental constraints on adult body size imposed by eggs might force a consistent gradient of body size. That is, helminths might reach larger sizes within lower latitudes in their adult stages simply owing to their eggs being larger, analogous to what is observed in non-thermoregulating ectothermic organisms Olalla-Tárraga et al. (2006)). However, we found only a single (rather weak) correlation between egg and adult sizes out of the three helminth clades examined (see Supporting Information), suggesting that developmental constraint might not be the main mechanism underlying the patterns we found. We acknowledge that many helminth species have additional life stages that were not examined in the present study owing to data limitation, and we propose a further investigation on the complete life cycles of those species as an important next step towards complete understanding of the current patterns. Second, temperature and temperature variability might simply be related to the fundamental driver of the size patterns. For example, environmental temperature interacts with precipitation (Frenne et al., 2013) to produce gradients in primary productivity, which is a key factor in shaping biodiversity patterns in general (Fritz et al., 2016). Temperature gradients also tend to correspond to variation in dispersal ability and interspecific competition in hosts (Hillebrand, 2004), both of which might affect transmission dynamics of parasites, and more directly, to variation of community composition in parasites (Dallas & Poisot, 2018; Krasnov, Mouillot, Shenbrot, Khokhlova, & Poulin, 2010; Krasnov et al., 2015).

We note that there may be limitations in our ability to detect patterns based on the amount or quality of data. However, we provide three lines of evidence that suggest data biases probably did not

have a strong influence on our findings. First, helminth community composition was fairly consistent across latitudes (see Supporting Information), suggesting that compositional shifts in helminth parasite taxa were unlikely to influence the detection of a latitude–body size relationship. Second, we examined our ability to detect Bergmann's rule among the helminth host species included in our dataset by extracting host body size data from PanTHERIA (Jones et al., 2009). We found evidence for Bergmann's rule in host species, in which host body mass increased greatly over gradients of both latitude and temperature, suggesting that host species were sufficiently well sampled in the LNHM data to produce the expected latitude–body size relationship. This provides evidence of the completeness of host sampling data and supports our findings of latitude–size patterns in helminth parasites (see Supporting Information). This also suggests the possibility that larger host species might be infected by smaller parasite species, although we do not find evidence for this (Supporting Information Figure S7). This might relate to the coarseness of the available data or lack of data on intraspecific body size variation, because host–parasite body size scaling relationships have been found previously, sometimes referred to as Harrison's rule (Johnson, Bush, & Clayton, 2005). We found qualitatively similar relationships between helminth parasite size and latitude or temperature when we included aquatic and coastal sites, suggesting that our results are robust to the inclusion of aquatic host and parasite species (see Supporting Information). Third, we found similar findings for helminth body size patterns when we considered only mammalian host species (see Supporting Information).

4.1 | Conclusion

Taken together, these results provide evidence that a relationship exists between parasite body size and latitude, at least partly attributable to the gradients in temperature and seasonality, but it is not the customary Bergmann's rule. Furthermore, we find opposing latitude–body size relationships for host and parasite species, suggesting that spatial gradients seemingly decouple the relationship between host and parasite body size previously observed in parasitic helminth species (Morand, 1996; Poulin, 1997; Poulin & Latham, 2003). That is, if larger parasite species are found in larger host species, then the average body size of host and parasitic species should scale along latitudinal gradients. The presence of the opposite relationship could be the result of differential responses to spatial gradients between host and parasite species, changes in community composition over latitude, or differential selective forces on the host (e.g. species physiology and metabolic demands) and parasite (e.g. potential scaling between body size and transmission potential) body sizes. We offer suggestions for why these patterns may persist, but we cannot provide a definitive mechanistic explanation. However, our study highlights the utility of using parasitic organisms to disentangle different explanations for macroecological patterns that are posited to apply broadly across taxonomic scales and opens new questions; for instance, do the inverse body size patterns among hosts and parasites hold in other taxa? Within the field

of macroecology, datasets on parasites and pathogens have become considerably richer in recent years (Stephens et al., 2016). With a larger quantity and more complete data, we hope that this study encourages further research on the mechanistic underpinnings of body size allometry in parasitic species.

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CONFLICT OF INTEREST

We declare we have no competing interests.

AUTHOR CONTRIBUTIONS

T.A.D. and A.G. performed the analyses and plotting. All authors contributed to study design and manuscript writing.

DATA ACCESSIBILITY

Data used in the present study are available from Gibson et al. (2005) and accessible through R using the helminthR package (Dallas, 2016). R code to reproduce the analyses is provided at <https://doi.org/10.6084/m9.figshare.6406823.v1>. A table summarizing all the data sources used can be found in Supporting Information Appendix A1 (Table A1).

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BIOSKETCH

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SUPPORTING INFORMATION

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

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