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Convergent patterns of body size variation in distinct parasite taxa with convergent life cycles

Steven Ni | **Jean-François Doherty** | **Robert Poulin**

Department of Zoology, University of Otago, Dunedin, New Zealand

Correspondence
Robert Poulin, Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand.
Email: robert.poulin@otago.ac.nz

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Abstract

Aim: Interspecific variation among metazoans often follows a latitudinal pattern, with species at higher latitudes being larger bodied than related species from lower latitudes (Bergmann's rule). For parasitic species, body sizes within any higher taxon are often correlated with the body sizes of their hosts (Harrison's rule). Whether temperature-driven latitudinal effects or host-driven resource constraints act independently or additively to shape interspecific variation in parasite body sizes remains unknown. We take a comparative approach to test the effects of latitude and host body size on parasite body sizes in two taxa of parasitic worms showing convergent life cycles.

Location: Global.

Time period: Contemporary.

Major taxa studied: Hairworms (Nematomorpha) and mermithids (Nematoda) parasitic in arthropods.

Methods: With 223 records for mermithids and 258 for nematomorphs world-wide, we used linear mixed effects models to test the effects of latitude and host body size on parasite length, intraspecific length variation, parasite egg diameter and variation in egg diameter. Furthermore, we modelled parasite length with local mean annual temperature as the predictor instead of latitude, as a direct test of underlying mechanisms. All models took into account host and parasite taxonomic structure within the datasets.

Results: For both taxa, host body size was clearly the main determinant of parasite body length, with neither latitude nor local temperature (annual mean or range) having an effect. No predictor affected intraspecific length variation, whereas egg diameter was positively associated with parasite length, and variation in egg diameter was negatively associated with latitude.

Main conclusions: Our results support a strong role for host traits in shaping the evolution of parasite body sizes (Harrison's rule), but no role for latitude (Bergmann's rule), although these parasites infect ectothermic hosts. At a mechanistic level, the evolutionary driving force of external temperature on parasite physiology seems to be eclipsed by the availability of resources from the host.

KEYWORDS

Bergmann's rule, Harrison's rule, host body size, latitude, life-history traits, mermithids, nematomorphs, temperature

1 | INTRODUCTION

Body size is possibly the most fundamental life-history trait among metazoans, because it covaries strongly with many key individual-level properties, such as metabolic rate and life span (Brown et al., 2004; Peters, 1983; Speakman, 2005), in addition to population-level parameters, such as density (Currie, 1993; Damuth, 1981). The distribution of body sizes among species is usually right skewed; that is, most species within a given taxon tend to be small bodied, and only a few achieve large sizes (Blackburn & Gaston, 1994). Environmental temperature is frequently invoked as one of the key determinants of interspecific variation in body size (e.g., Atkinson, 1994; Smith et al., 2010). Consistent with the idea that temperature might be a selective force acting on body size evolution, it has often been observed that, on large spatial scales, species inhabiting higher latitudes tend to be larger bodied than closely related species from lower latitudes. This geographical pattern is referred to as Bergmann's rule (Bergmann, 1847). Originally formulated to explain spatial variation in body sizes of homeotherms, it postulates that selection favours larger sizes in cold environments to minimize heat loss through body surfaces by lowering surface area-to-volume ratios (Blackburn et al., 1999; Salewski & Watt, 2017). Although Bergmann's rule applies to some ectotherms (Atkinson, 1994), it does not hold for others (e.g., Adams & Church, 2008). In cases where ectotherms appear to follow the rule, the mechanisms usually involve temperature-dependent growth rates and ageing (Atkinson, 1994), and possibly also temperature-dependent cell sizes (Van Voorhies, 1996).

Although meant to explain patterns seen in free-living animals, Bergmann's rule can also apply to parasitic metazoans. For example, tapeworm species parasitic in pelagic sharks are larger if their hosts live at higher latitudes (Randhawa & Poulin, 2009; for other examples, see Poulin, 2021). However, the body sizes of parasitic species within any higher taxon are often correlated positively with the body sizes of their hosts (e.g., Harvey & Keymer, 1991; Maestri et al., 2020; Morand et al., 1996; Poulin, 1996), a phenomenon known as Harrison's rule (Marshall, 1981). Selection appears to have favoured parasites that can take full advantage of the available space and other resources provided by their host, leading to the evolution of larger parasites in larger hosts. This might create difficulties for tests of Bergmann's rule in parasites. If, within a higher taxon of parasites, species exploiting hosts at higher latitudes tend to be larger than those exploiting tropical hosts, is this because parasite body sizes are driven by external environmental conditions (Bergmann's rule) or simply because their hosts follow a latitudinal gradient in body size and are larger at high latitudes, and the parasites within achieve sizes that match the sizes of their hosts (Harrison's rule)? Distinguishing between these two explanations would require teasing apart the respective and independent effects of host size and latitude (see Maestri et al., 2020).

Other key life-history traits can also be influenced by host body size and/or latitude. In addition to the average body size of a parasite species, intraspecific variation in body size (i.e., the range of sizes achieved by conspecific parasites) should also be correlated with host body size. All else being equal, a relatively large host species might harbour both small and large parasites, allowing some individuals to grow larger than others, whereas a small host species can only accommodate small parasites (see Harnos et al., 2017). Empirical tests of the relationship between intraspecific variation in parasite body sizes and mean host body size are lacking. In addition, the sizes of parasite eggs might also vary with host body size and/or latitude. Trade-offs between egg size and egg numbers might be relaxed in many parasites because they live in resource-rich environments (Calow, 1983). Nevertheless, egg size might often be constrained by the body size of the female parasite (Poulin, 1996), although this does not apply to all parasite taxa (e.g., Kiefer et al., 2016). Independently of female body size, egg sizes might be expected to be larger, and variation in egg sizes to be smaller, in parasites at high latitudes, where the greater temporal variation in external conditions and resource availability might favour investment into larger offspring that can reach sexual maturity faster, given the shorter growing season. Latitudinal gradients in egg sizes are common in invertebrates, a pattern first recognized among marine invertebrates and referred to as Thorson's rule (Mileykovsky, 1971). There is some very limited evidence that it might also apply to parasites, based on interspecific relationships between latitude and both egg size and variation in egg sizes (Dallas et al., 2019; Poulin & Hamilton, 2000; see Poulin, 2021), but the relationship requires further scrutiny.

We tested the relationship between both latitude (Bergmann's rule) and host body size (Harrison's rule) as predictors, and parasite body size, variation in body size, egg size and variation in egg size as response variables in two distinct lineages of parasitic worms that have evolved very similar life cycles independently. Hairworms (phylum Nematomorpha) and roundworms of the family Mermithidae (phylum Nematoda) develop within terrestrial arthropods over several months, reaching relatively large sizes before emerging from the host (Bolek et al., 2015; Poinar, 2001). Both nematomorphs and mermithids follow a parasitoid strategy: in most cases, the host dies immediately after the parasite exits its body, although host survival is possible. The adult stage is reached either immediately before (nematomorphs) or after (mermithids) emergence from the host, with the worms undergoing no further growth post-emergence; free-living, non-feeding male and female worms find each other to mate, after which the latter lay eggs before dying. In both nematomorphs and mermithids, adults are prone to desiccation and must emerge from their host and live in water or a water-saturated substrate. Convergently, species in both lineages have evolved the ability to alter host behaviour in the late stages of infection, causing their hosts either to enter water or to spend time in areas of high humidity (Maeyama et al., 1994; Poulin & Latham, 2002a; Thomas et al., 2002). The molecular mechanisms underpinning these behavioural changes also show evidence of convergence, with similarities observed between nematomorphs and mermithids in the host protein networks they alter before emergence (Biron et al., 2005; Herbison et al., 2019). Based on the clear convergence of life histories shown at all levels by these two parasitic lineages (Poulin, 2011), we hypothesize that there should also be strong parallels between the two groups in how the evolution of their body sizes has been shaped by both latitude and the constraints imposed by host body size.

Here, using a comparative approach: (1) we test whether two broad eco-evolutionary patterns, Bergmann's and Harrison's rules, apply to nematomorphs and mermithids, by assessing the influence of latitude and host body size on parasite body size and egg size, and on the intraspecific variation in those traits; and (2) we contrast the findings from both parasite lineages to assess the extent to which the evolution of their body sizes has been shaped by the same factors. Our study provides a strong test of convergence in life-history trait evolution, by comparing patterns in two independent lineages of parasites sharing very similar life cycles and facing very similar selective pressures.

2 | MATERIALS AND METHODS

2.1 | Data assembly

Two separate datasets were compiled, one for mermithids (nematodes) and one for nematomorphs (hairworms), using searches within the Web of Science “Zoological Record” and Google Scholar databases. Search terms used for mermithids were as follows: (mermithid* OR mermis) AND (“n. sp.” OR “sp. n.” OR “new species”); for nematomorphs, they were as follows: (nematomorph* OR hairworm* OR “horsehair worm*” OR “gordian worm*” OR gordiid*) AND (“n. sp.” OR “sp. n.” OR “new species”). We identified relevant articles based on their title or abstract and obtained as many as possible through the University of Otago library system. Papers in languages other than English were translated when possible, in order to extend the geographical coverage of the datasets. Most relevant articles were original species descriptions, although other reports were included if they provided the required information. In total, 169 papers were retained for mermithids and 115 for nematomorphs (see Supporting Information Figures S1 and S2); these were published between 1893 and 2020, with the majority in the past 50 years.

From these articles, we extracted 223 data entries for mermithids and 258 for nematomorphs (many papers yielded more than one data entry). Each data entry represents a different species, except in rare cases (three mermithids and four nematomorphs) where a species was described from two distinct geographical locations; these were retained as separate entries because they represented very distinct populations using different host species. For each entry, we obtained the most recent taxonomic classification of the parasite species and the host species from the Animal Diversity Web (https://animaldiversity.org); however, the identity of the host was unknown for many nematomorphs, because they are often found as free-living adults. Also, for each entry, we recorded the variables listed below (i.e., parasite body size and egg size data, host body size, latitude and local temperature data), although in some cases information was not available for all variables (especially for nematomorphs, often described based on a single or a few specimens).

2.2 | Parasite body dimensions

In the original publications, body sizes were reported for either adult worms emerged from their host or late juvenile stages found within their host but close to emergence based on the time of the year when sampled; therefore, the sizes of those late juveniles were taken as adult sizes. We recorded body length, body length range and maximal body diameter separately for males and females of each species, resulting in two separate data points per species wherever data on both sexes were available. For body length, we recorded the best measure of central tendency available, either the mean (in rare cases calculated manually if measurements of individual worms were supplied), the midpoint of the range or the length of the sole individual found. It was not possible to use the same measure across all entries: the median cannot be obtained when only the mean (with standard deviation) is given, nor can a mean be derived from a range. However, given that body lengths vary by more than one order of magnitude across species, slight differences between the mean and median length for a particular species are unlikely to matter. Body length range was calculated as the difference between the length of the longest and shortest worms; length range was not available if the range was not reported or if the description involved a single specimen. Maximal body diameter was recorded as the mean or midpoint of the range from all individuals measured; in the few cases where diameter was measured at different places along the bodies of the worms (e.g., mid-body and at the level of the genital pore), we used the maximal diameter observed. The above dimensions were recorded separately for males and females; in the few papers where data were not reported by sex, we still recorded body dimension measurements for the unsexed individuals, although we excluded those entries from analysis.

From the above measurements, we calculated two further variables. First, assuming that worms are approximately cylindrical, body volume was estimated as $V = \pi r^2 l$, where r is half the maximal body diameter and l is body length. However, because body width varied along the length of the body in many species (i.e., they were far from perfectly cylindrical), the body volume estimates may be unreliable. Furthermore, the relationship between body length and estimated body volume was significant but not very strong (see Supporting Information Figure S3). Therefore, we chose to use body length as a measure of parasite body size in subsequent analyses. Second, the relative intraspecific variation in length (RLV) was calculated as $\mathrm{RLV} = \mathrm{RL}/l$, where RL is the length range and l is the length. This measure provides an estimate of length variation corrected for average length.

2.3 | Parasite egg size

Egg diameter and egg diameter range were recorded, based on the longest axis of the egg when not fully spherical. Original publications reported egg measurements taken either when the eggs were still within the uterus of females or immediately after oviposition.

Egg diameter was taken as the mean or, if unavailable, the midpoint of the range from eggs measured *in situ* within female worms. Egg diameter range was calculated as the difference between the smallest and largest diameter reported. We then calculated the relative intraspecific variation in egg diameter (REV) as REV = RE/*e*, where RE and *e* are the egg diameter range and egg diameter, respectively. These egg measurements were obtained for mermithids only, because there were insufficient data to investigate egg sizes in nematomorphs.

2.4 | Host size

Host body length was recorded as a proxy of host size. Host body volume would be a better metric of host size, but the data necessary to compute it are unavailable. However, body length generally exhibits strong correlations with body volume among arthropods (Peters, 1983). Host length was rarely provided in the papers on parasite species descriptions used to assemble the dataset. Therefore, we obtained host body length from the following online resources, prioritizing them in the following order: (1) Barcode of Life Data System (BOLDSystems) v.4 (http://boldsystems.org) and BugGuide (http://bugguide.net); (2) Wikipedia (https://www.wikipedia.org); (3) Google Images (https://images.google.com); (4) taking the length of a species from the same host genus from BOLDSystems, BugGuide or Wikipedia (assuming that closely related species have similar body sizes); or (5) in rare cases, other sources (i.e., relevant scientific publications available online). BOLDSystems provides images with a scale bar for a vast number of species. In such cases, host lengths were estimated with IMAGEJ v.1.53a (https://imagej.nih.gov/ij/) from up to four images of conspecifics and then averaged; this was assumed to be adequate because intraspecific length variation of insects tends to be minimal. When BugGuide had to be used, either a single length or a length range was available; in the latter case, the midpoint was taken. If size estimates could not be obtained from either BOLDSystems or BugGuide, Wikipedia was used instead, again allowing the midpoint of the length range to be obtained. If needed, Google Images was searched for any images of the species with a scale bar and processed as described above. If all the above approaches failed or if the host species was identified to only the genus level, the length of a random congeneric host species was recorded, following the hierarchical preferences for online resources described above. As a last resort (in only two instances), in the absence of data from all the above methods, other online sources were consulted. When the host species displayed sexual size dimorphism and the source provided one measurement for each sex, the midpoint was used.

2.5 | Geographical coordinates and locality

The name of the locality and its latitude and longitude (decimal form) where the parasites were found were recorded. If needed, coordinates were derived from Google Maps, using a point as close as possible to the given sampling area when no single, precise locality was specified. Where coordinates were provided as degrees/minutes/seconds in the original papers, they were converted to decimal degrees via the World Coordinate Converter (https://twcc.fr/en/).

Our primary goal was to test Bergmann's rule in its original sense (i.e., a latitudinal gradient in body size). However, given that latitude is mainly used as a proxy for temperature, and it is temperature that underpins the processes generating latitudinal gradients, we also tested for the direct relationship between temperature and body sizes of mermithids and nematomorphs. For this, we obtained the mean annual temperature (variable BIO1, resolution 10 min, or *c.* 340 km^2) and the annual temperature range (variable BIO7) from each locality where worms were sampled, using their coordinates and extracting the temperature data from the WorldClim database (https://www.worldclim.org/).

2.6 | Statistical analyses

All statistical analyses were conducted in R v.3.6.1 (R Core Team, 2019). Linear mixed effects regression models (LMMs) from the *lme4* package (Bates et al., 2015) were fitted to analyse the following response variables, separately for each dataset: parasite length, relative length variation, parasite egg diameter, and relative egg diameter variation; the last two variables were analysed only for the mermithid dataset. The exact number of entries used in each model varies owing to data availability (see Table 1). Log$_e$-transformations were applied to all response variables, with the exception of relative egg diameter variation and relative length variation for nematomorphs, where square root transformations were applied in order to correct for non-normality of the data. For nematomorphs, data on species of the single-genus order Nectonematoidea (the marine hairworms *Nectonema*) were excluded from analyses. This order represents a basal divergence from the order Gordiacea (which includes all other hairworms) (Bleidorn et al., 2002), making nectonematid hairworms phylogenetically and ecologically very distant from all others. Furthermore, we excluded the few data entries on fossilized amber specimens or entries in which the nematomorph host was not an insect (e.g., a spider), in addition to those from extant species in which sex was unspecified. Given that all other entries included data for both males and females, these were treated as separate data points.

No comprehensive phylogeny is available for either parasite group. Therefore, in all models, parasite taxonomy was included as a random factor to account for phylogenetic non-independence and trait similarity among related species. For all mermithid models, only genus was included as a random factor, whereas for nematomorph models, genus was nested within family (all species in the final dataset belong to the same order). Additionally, host order was also included as a random factor in all models (except in the model analysing nematomorph length without host length as a predictor;

TABLE 1 Results of all linear mixed effects models tested on all analysed response variables, with the corresponding effects of all main predictors included in the model (significant ones are in bold); sample sizes and random factors are also shown

Parasite taxa	Response variable	Fixed factors*	Coefficient estimate	*t*-Value	*p*-Value	95% Confidence interval	Random factors	Marginal r^2	Conditional r^2	Cohen's f^2
Mermithidae	Log length (*n* = 319)	Intercept	3.3462	12.441	< .0001	2.8112 to 3.8875	Parasite taxonomy, host order	0.1545	0.8075	0.1827
		Latitude	0.0024	0.923	.357	−0.0027 to 0.0075				
		Host length	**0.0592**	**7.814**	**< .0001**	**0.0441 to 0.0741**				
		Sex	**−0.2200**	**−2.660**	**.008**	**−0.3818 to −0.0576**				
		Host length*sex	**−0.0359**	**−5.053**	**< .0001**	**−0.0499 to −0.0219**				
	Log relative length variation (*n* = 301)	Intercept	−0.7955	−4.863	< .0001	−1.1132 to −0.4782	Parasite taxonomy, host order	0.0151	0.1458	0.0153
		Latitude	0.0043	1.324	.187	−0.0022 to 0.0106				
		Host length	−0.0064	−1.297	.196	−0.0161 to 0.0041				
		Sex	−0.0271	−0.371	.711	−0.1697 to 0.1163				
	Log maximal egg diameter (*n* = 87)	Intercept	3.9935	38.496	< .0001	3.7885 to 4.2167	Parasite taxonomy, host order	0.1585	0.7304	0.1884
		Latitude	−0.0013	−0.608	.545	−0.0053 to 0.0028				
		Female length	**0.0028**	**4.156**	**< .0001**	**0.0015 to 0.0042**				
	Square root of relative maximal egg diameter variation (*n* = 58)	Intercept	0.5894	7.908	< .0001	0.4433 to 0.7354	Parasite taxonomy, host order	0.0790	0.4059	0.0858
		Latitude	**−0.0033**	**−2.435**	**.0192**	**−0.0060 to −0.0006**				
		Female length	−0.0005	−1.073	.2881	−0.0014 to 0.0004				
Nematomorpha	Log length (*n* = 339)	Intercept	5.2766	24.733	.014	4.7861 to 5.7823	Parasite taxonomy	0.0220	0.3092	0.0225
		Latitude	−0.0004	−0.221	.825	−0.0042 to 0.0034				
		Sex	**−0.1639**	**−3.190**	**.002**	**−0.2644 to −0.0626**				
	Log length (*n* = 81)	Intercept	5.0944	26.950	.000	4.7481 to 5.4631	Parasite taxonomy, host order	0.1634	0.3273	0.1953
		Latitude	−0.0027	−0.989	.3556	−0.0078 to 0.0027				
		Host length	**0.0057**	**2.993**	**.004**	**0.0021 to 0.0095**				
		Sex	0.0356	0.255	.799	−0.2371 to 0.3040				
		Host length*sex	−0.0050	−1.932	.058	−0.0100 to 0.000				
	Square root of relative length variation (*n* = 168)	Intercept	0.6781	11.923	< .0001	0.5667 to 0.7896	Parasite taxonomy	0.0215	0.0215	0.0220
		Latitude	0.0023	1.599	.112	−0.0005 to 0.0052				
		Sex	−0.0530	−1.123	.263	−0.1455 to 0.0395				
	Square root of relative length variation (*n* = 52)	Intercept	0.9112	4.565	.0461	0.5200 to 1.3025	Parasite taxonomy, host order	0.0509	0.6131	0.0536
		Latitude	0.0014	0.526	.6013	−0.0038 to 0.0066				
		Host length	−0.002405	−1.943	.0582	−0.0048 to 0.0000				
		Sex	0.007678	0.111	.9118	−0.1273 to 0.1427				

Note: Sex effects are relative to females. Marginal and conditional r^2 indicate the proportion of variation attributed to the main predictors or all factors, respectively, whereas Cohen's f^2 represents the effect size.

see next paragraph), to account for taxon-dependent host effects. In the models, only random intercepts were fitted.

Models on mermithids and nematomorphs with the same response variable share the same set of predictors, in order to test for evidence of convergent forces shaping the evolution of body sizes. For parasite length and relative length variation, the predictors were latitude (absolute value, regardless of north or south), host length, parasite sex, and the interaction between host length and sex. We tested for collinearity between our two main predictors, latitude and host length, and found none ($p > .8$ for both datasets); in other words, there was no latitudinal gradient in host body sizes. In analyses of the nematomorph dataset, the inclusion of host length dramatically reduced the number of data points that could be included (because host data are missing in many cases); therefore, the models for nematomorphs were also run without including host length as a predictor. For parasite egg diameter and relative egg diameter variation (mermithids only), the predictors were latitude and female worm length. All models are presented in Table 1. In addition, models for parasite length were repeated as above, in both mermithids and nematomorphs, but including annual mean temperature or annual temperature range (in separate analyses) instead of latitude as a predictor; results for these models are presented in the Supporting Information Table S1.

For parasite length and relative length variation in mermithids, model selection was conducted via the Akaike information criterion corrected for small sample size (AICc); this led to the interaction between host length and parasite sex not being included in the final models for relative length variation. The p-values were obtained via the *lmerTest* package (Kuznetsova et al., 2017) and r^2 values via the *MuMin* package (Barton, 2020). Residual plots were inspected visually for model fit. Data were visualized using *ggplot2* (Wickham, 2016).

3 | RESULTS

The mermithid dataset comprised 50 distinct genera (including a few excluded from analysis), whereas the nematomorph dataset included species of 17 different genera, three families and two orders (including the nectonematid worms excluded from analysis) (see full datasets in the Dryad Digital Repository: https://doi.org/10.5061/dryad.f7m0cfxwx). Latitudinal coverage spanned > 70° (irrespective of north or south), although large clusters of data points came from localities in Europe and in North and South America (Figure 1). Mermithids had a diverse range of hosts, comprising taxa belonging to 17 different arthropod orders. In contrast, nematomorphs were found parasitizing only eight arthropod host orders (including host taxa excluded from analysis). Body size distributions were right skewed in both mermithids and nematomorphs, with more small-bodied species than large ones (Figure 2). Mermithids (typically 10–50 mm long) were generally smaller than nematomorphs (typically, 100–300 mm long), with females being larger than conspecific males in both taxa.

3.1 | Parasite length

The LMMs were formulated to test for the effects of latitude, host length, parasite sex, and the interaction between host length and sex. In mermithids, the analysis revealed that length was positively associated with host length and that males were smaller than females (Table 1; Figure 3). There was also a weak interaction between host length and parasite sex, indicating that the positive relationship between host length and body length was weaker in males. However, no association was found between latitude and parasite length (Supporting Information Figure S4).

In nematomorphs, the model that included only the predictors latitude and parasite sex revealed no influence of latitude on parasite length (Supporting Information Figure S4) but showed that male nematomorphs were smaller than females. However, when host length was added as an additional predictor, it emerged as the only significant correlate of parasite length, with the difference between sexes disappearing (most certainly owing to a much-reduced sample size); as for mermithids, host length was positively associated with parasite length (Table 1; Figure 3). Although no statistically significant interaction was found between parasite sex and host length, the trend was the same as with mermithids; again, limited statistical power owing to a smaller sample size might have influenced this finding. Overall, the patterns observed were similar across both groups of parasites. In addition, the random factors consisting of host and parasite taxonomy also accounted for a large proportion of unexplained variance in both worm taxa.

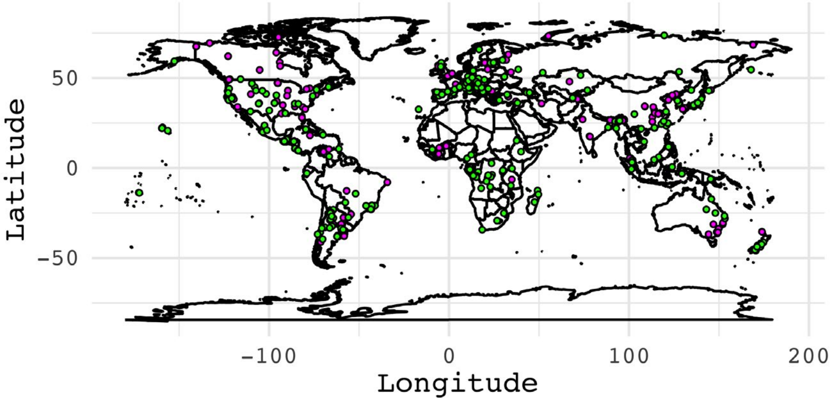

FIGURE 1 Geographical distribution of data points in both the mermithid (pink dots) and nematomorph (green dots) datasets

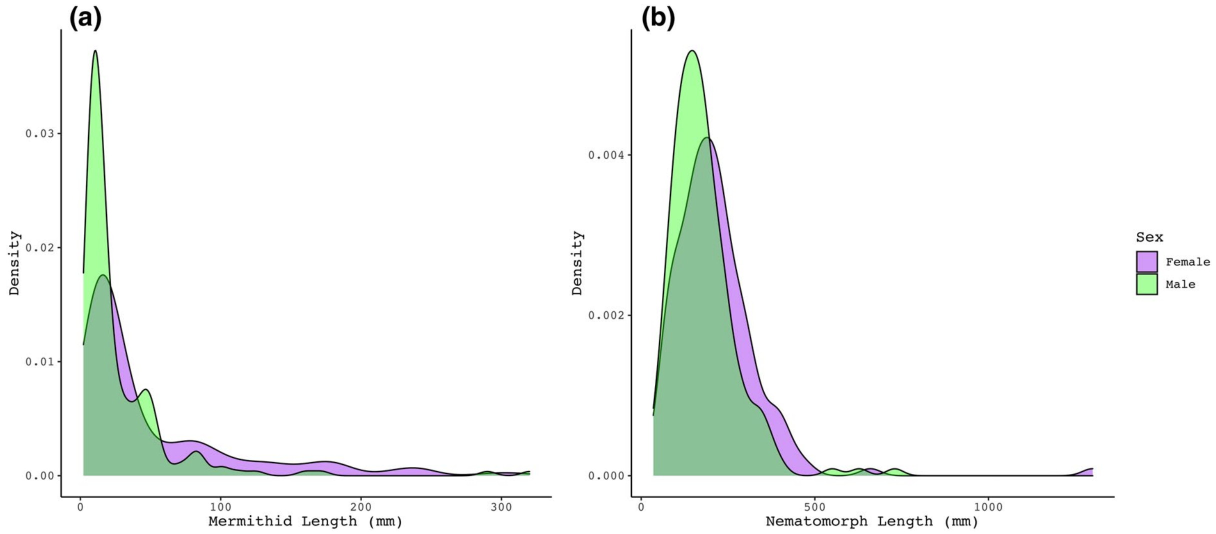

FIGURE 2 Density distributions (relative number of species) of body sizes for species in both the (a) mermithid and (b) nematomorph datasets. Data are shown separately for males and females. Note the different size scales for the two parasite taxa

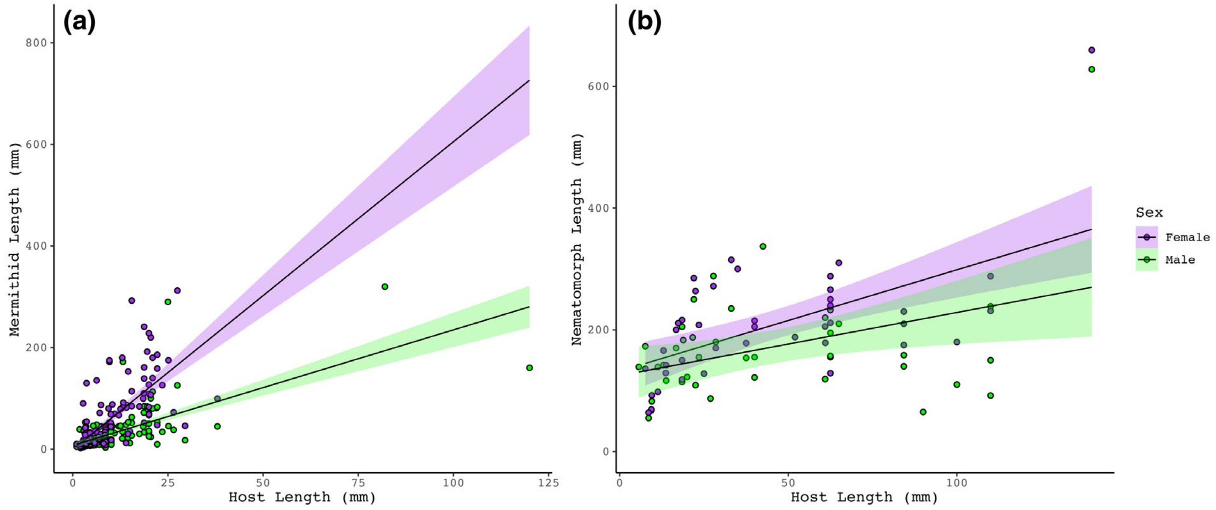

FIGURE 3 Interspecific relationship (with 95% confidence intervals; shaded area) between parasite body length and host body length, for both (a) mermithids and (b) nematomorphs. Data are plotted separately for male and female parasites

In the additional models using temperature as a predictor instead of latitude, we found that mean annual temperature was significantly and negatively associated with mermithid body length, whereas annual temperature range showed a positive relationship with mermithid body length, but both these effects were extremely weak (Supporting Information Table S1). In contrast, neither measure of temperature was related to nematomorph body length. For both worm taxa, host length and parasite sex again emerged as the main determinants of parasite length.

3.2 | Parasite relative length variation

For both mermithids and nematomorphs, there was no evidence that relative length variation was associated with latitude, host length or parasite sex (Table 1; Supporting Information Figures S5 and S6). Host and parasite taxonomy, as random factors, explained a greater proportion of variance than the main predictors in both parasite taxa (Table 1).

3.3 | Egg diameter and relative egg diameter variation

Analyses of these variables were conducted only for mermithids because there were insufficient data for nematomorphs. These LMMs tested for the effect of latitude and female length. Female length was found to be positively associated with egg diameter, whereas latitude showed no relationship with egg diameter (Table 1; Figure 4a; Supporting Information Figure S7). On

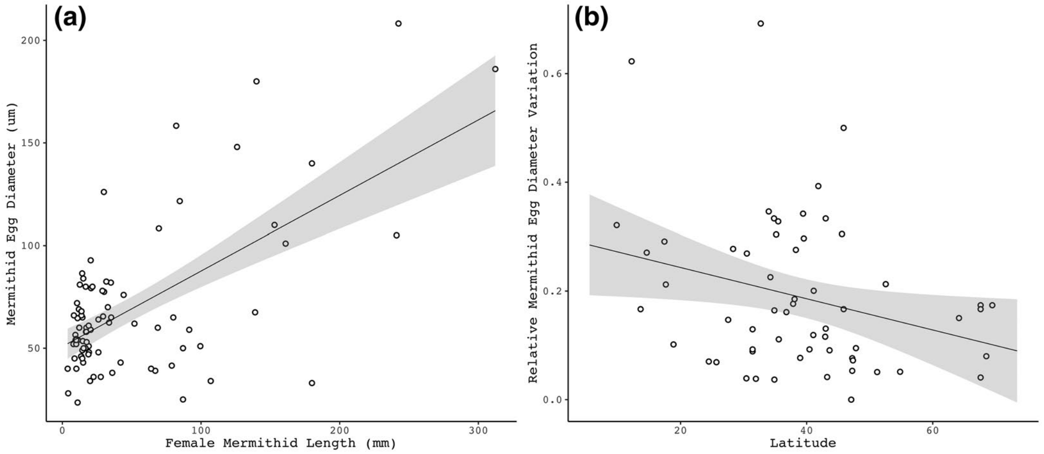

FIGURE 4 Interspecific relationship (with 95% confidence intervals; shaded area) between (a) mermithid egg diameter and female body length, and (b) the relative variation in mermithid egg diameter and latitude

the contrary, latitude was found to be negatively associated with relative egg diameter variation, whereas female length was not (Table 1; Figure 4b; Supporting Information Figure S7). Additionally, host and mermithid taxonomy explained a large proportion of variance in both response variables.

4 | DISCUSSION

Given the central importance of body size for all aspects of metazoan biology (Brown et al., 2004; Peters, 1983), much attention has been paid to the determinants of interspecific variation in body size among related species. Most research to date has focused on free-living organisms. However, the patterns observed for free-living organisms might not necessarily apply to parasitic organisms (Dallas et al., 2018). Here, we examined the determinants of interspecific variation in body length within two taxa of parasitic worms that have evolved very similar life cycles convergently. Specifically, we tested whether two commonly reported patterns applied, independently of each other, to both parasite taxa: a latitudinal gradient in body sizes (Bergmann's rule) and a positive relationship between host body size and parasite body size (Harrison's rule). Our results provide no support for the former, but clear support for the latter.

Given that our a priori goal was to test Bergmann's rule, we used latitude as a predictor in our models; however, latitude is merely a rough proxy for local environmental conditions. Therefore, we used average annual temperature as a predictor in additional models, and still found no association with parasite body length in one case (nematomorphs) and a very weak relationship running in the opposite direction to what would be anticipated in the other case (mermithids). We also repeated the analyses with annual temperature range, instead of mean annual temperature, as the main predictor; again, this variable showed no relationship with nematomorph body length and only a very weak positive association with mermithid body length. These findings suggest that temperature-driven effects on metabolic processes are not important determinants of parasite growth.

Comparative analyses, such as the present one, are only as reliable as the data they use. Our datasets do not include all known species from both parasite groups, but nevertheless comprise large and representative samples. The geographical distribution of data points is slightly uneven, possibly owing to spatial heterogeneity in the allocation of parasitological research efforts; nonetheless, the data points span a wide latitudinal range and come from all major biogeographical zones. In several cases, we had to obtain estimates of host body sizes from a conspecific host species, owing to a lack of data. This undoubtedly created some error, especially for nematomorphs, which often parasitize insect orders with greater size differences among congeneric species (e.g., Mantodea, Orthoptera). Nevertheless, given the > 10-fold variation in host lengths in our datasets, it is unlikely that such small errors had any influence on the findings. Also, some species of mermithids and (especially) nematomorphs can use two or more insect host species (Schmidt-Rhaesa, 2013). Although these hosts almost invariably belong to the same order, they may vary in body size. Selection might have optimized typical body length (and its variation) of a parasite species for its most common or ancestral host species. Without knowing which host this is, there might be a few mismatches between parasite body sizes and the host sizes we entered in our databases. Finally, both mermithids and nematomorphs show intraspecific phenotypic plasticity in their final body sizes. In particular, the average body size achieved by individuals within a species decreases with the intensity of infection (i.e., with the number of individual parasites per host), for both mermithids (Maure & Poulin, 2016; Poulin & Latham, 2002b) and nematomorphs (Hanelt, 2009; Schmidt-Rhaesa et al., 2005). The average intensity of infection may vary across species, and it represents another selective force acting on body size evolution; unfortunately, no comprehensive data are available on this variable.

Most earlier tests of Bergmann's rule in parasites have not controlled either for phylogenetic non-independence among species (e.g., Dallas et al., 2019; Seeman & Nahrung, 2018) or for the potential effect of host body size (e.g., Dallas et al., 2019; Traynor & Mayhew, 2005), making it difficult to distinguish a mere host size–parasite size correlation from other processes directly associated with Bergmann's rule. This is important, because host size and latitudinal distribution are not necessarily independent of each other. For example, hairworms of the genus *Chordodes* infect predominantly praying mantids, which are both large and mostly found in the tropics and subtropics (Schmidt-Rhaesa, 2013). Furthermore, mechanisms other than temperature that have been proposed to underpin Bergmann's rule include larger bodies providing an insurance against the more frequent periods of starvation at high latitudes or larger body sizes merely reflecting the random ancestral colonization and subsequent diversification of high latitudes by large-bodied lineages (Blackburn et al., 1999). Our study incorporated both phylogenetic influences and host body size as confounding variables in testing for Bergmann's rule, ruling out these alternative mechanisms. Our analyses did not merely contrast latitude versus host body size as drivers of parasite body size evolution. At a mechanistic level, the analyses compared the relative effects of environmental temperature on metabolism and associated physiological processes versus constraints on growth imposed by resources (space and nutrients) available from the host. Our analyses were also replicated across two independent parasite lineages, with the findings consistent between the two. In both parasite groups, worms grow from a microscopic size to a relatively large size over several months, within the haemocoel of the arthropod host. Our results suggest that the volume within the haemocoel that can be occupied by the parasite without causing the host to die prematurely places an upper limit on parasite size. In contrast, once controlling for the effect of host size, latitude/temperature has no measurable or meaningful effect. From an evolutionary perspective, body size is directly proportional to lifetime egg output in nematomorphs (Hanelt, 2009) and most nematodes (Morand & Sorci, 1998). Thus, our findings point toward a fitness-maximizing strategy common to both mermithids and nematomorphs, whereby natural selection has consistently favoured the maximal parasite body size that can be accommodated and tolerated by the host, regardless of external conditions.

Relationships between host body size and parasite body size have been reported for oxyurid nematodes (Harvey & Keymer, 1991; Morand et al., 1996) and for other taxa of parasitic helminths (Poulin, 1996; Poulin et al., 2003). In fact, host features such as body size have been proposed as key determinants of life-history evolution in parasitic nematodes (Morand & Sorci, 1998). The co-evolutionary process between hosts and parasites, involving reciprocal adaptations, can be expected to result in covariation between parasite and host life-history traits (Clayton et al., 2016). Thus, evolutionary changes in host size or life span translate into changes in resource abundance and persistence for parasites, which select for evolutionary adjustments in their own size and life span. The role of co-evolution might explain why, in our models, the random factors consisting of host and parasite taxonomy accounted for much of the unexplained variance in both worm taxa.

Our analyses addressed other response variables. First, our results indicate that neither latitude nor host body size has any effect on intraspecific variation in parasite body sizes. There is thus no support for the idea that larger-bodied hosts allow for greater phenotypic plasticity in body sizes (Harnos et al., 2017). It must be pointed out that our estimates of variation in body sizes within species were probably inaccurate in many cases, owing to a low number of individuals measured in the original studies. Second, we confirmed that, among mermithid species, egg diameter is positively correlated with female parasite body size. Not only is this a common pattern among parasitic helminths (Poulin, 1996), but this finding indicates that larger body sizes, when host body size allows it, can translate into fitness benefits for the parasite in terms of larger offspring. Indeed, comparative data from other nematodes suggest that there is no measurable trade-off between egg size and egg numbers, suggesting that production of larger offspring does not come at the cost of lowered fecundity (Skorping et al., 1991). In contrast, intraspecific variation in egg diameter was not associated with female body size, but instead covaried negatively with latitude. In other words, mermithid species at high latitudes produced eggs of more consistent sizes than those in the tropics. This result supports the idea that selection might favour more equitable investments into each offspring in environments with greater temporal variation in external conditions and resource availability, allowing only a short optimal growth period (Poulin & Hamilton, 2000). Finally, our data reveal a very similar female-biased sexual size dimorphism in both mermithids and nematomorphs, a common pattern in dioecious helminths including nematodes (e.g., Morand & Hugot, 1998) and free-living animals (Shine, 1989) that is driven by the relationship between size and fecundity.

The main finding of our study is that host body size is a more important driver of body size evolution than latitude, in both nematomorphs and mermithids. These parasites infect ectothermic hosts and are therefore subject to external thermal conditions; nevertheless, resource availability seems to trump temperature-driven metabolic and growth rates and might be the limiting factor for parasite size. If a Bergmann-type latitudinal trend were to be observed in these parasites, it might simply be an epiphenomenon emerging from a similar pattern among their hosts (Poulin, 2021). In other words, any geographical trend in host body size should inevitably be reflected in the body sizes of their parasites. Our findings support Harrison's rule for a body size correlation between hosts and parasites, pointing to host-mediated constraints as the main drivers of parasite life-history evolution.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

R.P. and J.-F.D. conceived and designed the study; S.N. compiled the data; S.N. and J.-F.D. analysed the data; and R.P. and S.N. led the writing of the manuscript, with critical input from J.F.D. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Full datasets are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.f7m0cfxwx

ORCID

Robert Poulin https://orcid.org/0000-0003-1390-1206

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BIOSKETCHES

Steven Ni is a student at Otago University, New Zealand, whose interests include all aspects of evolutionary biology and animal behaviour.

Jean-François Doherty is a doctoral student at Otago University, New Zealand, whose research interests encompass entomology and parasitology.

Robert Poulin is a Professor of Zoology at Otago University, New Zealand, whose research extends to all ecological and evolutionary aspects of host–parasite interactions, across all taxa and biomes.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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