Interannual variability modulates Harrison's rule between cymothoid isopod and their prawn host: Insights from a long-term stream study

Alison Carlos Wunderlich[1] · **Esli Emanoel Domingues Mosna**[1,2] · **Marcelo Antonio Amaro Pinheiro**[1,2]

[1]Universidade Estadual Paulista (UNESP), Instituto de Biociências – Campus do Litoral Paulista (IB/CLP) – Departamento de Ciências Biológicas e Ambientais, Laboratório de Biologia da Conservação de Crustáceos e Ambientes Costeiros (LBS) – Grupo de Pesquisa em Biologia de Crustáceos (CRUSTA), São Vicente (SP), Brazil.

[2]Programa de Pós-Graduação em Biodiversidade de Ambientes Costeiros (PPG-BAC), UNESP IB/CLP, São Vicente (SP) – Programa de Pós-Graduação em Ecologia, Evolução e Biodiversidade (PPG-EcoEvoBio), UNESP Campus de Rio Claro (IB/RC), Rio Claro (SP), Brazil.

Correspondence

Alison C. Wunderlich

awunderlich@gmail.com

ORCID

Alison Carlos Wunderlich (*https://orcid.org/0000-0001-9222-8536*)

Esli Emanoel Domingues Mosna (*https://orcid.org/0000-0002-6330-1586*)

Marcelo Antonio Amaro Pinheiro (*https://orcid.org/0000-0003-0758-5526*)

Abstract

Host body size can influence the evolution of parasite body size in many host-parasite associations, a hypothesis called Harrison’s rule (HR). However, this pattern has not always been consistently observed, with some studies finding no association between host and parasite size. Moreover, other host-related factors (e.g., sex, immunity) and environmental changes can mediate this relationship. Here, we used a long-term dataset of cymothoid isopod-palaemonid prawn to test whether Harrison's rule applies to the relationship between host and parasite body traits (i.e., length, sex, weight), while accounting for the effect of seasons and years. Prawns were sampled seasonally over four years in a tropical stream in southeastern Brazil. We found a strong positive relationship between parasite and host body traits (i.e., length and weight), supporting Harrison’s rule. Our results further demonstrated that this relationship is independent of host sex and seasonal variation (i.e., dry and wet seasons) but is influenced by interannual variability. Host length and weight explained approximately 70% of the model variation, while interannual effects accounted for 30%. These highlight that the covariation between host and parasite body traits may be modulated by environmental changes, potentially altering Harrison's rule. Future research should consider interannual variability as a potentially critical factor driving host-parasite interactions and their evolutionary dynamics.

Keywords: Harrison’s rule · Interannual variability · *Macrobrachium brasiliense* · Seasonal effects · *Telotha henselii*

Introduction

The dynamics of host-parasite systems are influenced by host traits such as body size, sex, and mass, which can affect the host susceptibility to infection and, ultimately, drive the evolution of the parasite (Poulin, 2007; Johnson and Hoverman, 2014; Stewart Merrill *et al*. 2021; Leung, 2022). Among these traits, host body size is one of the most significant, often correlating with parasite abundance or richness (Kamiya *et al.* 2014; Esser *et al.* 2016; Harnos *et al.* 2017; Schmid-Hempel, 2021). Likewise, parasite body size increases with host body size, a Harrison's Rule (HR) pattern (Ni *et al.* 2021).

Harrison's rule has been reported across a wide range of parasite taxa, including parasitic crustaceans, fleas, ticks, mites, and parasitic worms (Johnson *et al.*, 2005; Clayton *et al.* 2016; Harnos *et al.*, 2017; Villa *et al.*, 2018; Welicky *et al.*, 2019; Rózsa *et al.* 2024). This pattern is associated with more efficient use of available niche space and resources by parasites in larger hosts (Sasal *et al.*, 1999; Lisnerová *et al.* 2022). The resources provided by larger hosts can be considered analogous to large islands in biogeographical theory (Schmid-Hempel, 2021), enhancing parasite fitness through increased body size and fecundity (e.g., larger offspring – Poulin, 2007; Ni *et al.* 2021; Rózsa *et al.* 2024). However, for some parasites, this relationship may be mediated by additional host factors such as behaviour and immunity (Johnson and Hoverman, 2014; Stewart Merrill *et al.* 2019) or environmental changes (e.g., seasonality and temperature), which can create spurious correlations in Harrison's Rule, where no intrinsic properties of the host directly affect the parasite's body size (Maestri *et al.*, 2020; Ni and Dutra, 2023).

Environmental changes can affect parasite growth rates and body size, potentially altering the correlation between host and parasite body traits (Johnson *et al.* 2005; Poulin, 2007; Clayton *et al.* 2016; Poulin, 2021; Lim *et al.* 2022; Lisnerová *et al.* 2022). For instance, an important study demonstrated that environmental factors, such as temperature and precipitation, can disrupt the Harrison's Rule (HR) pattern, resulting in misleading correlations between the body sizes of fleas (parasites) and their rodent hosts across assemblages (Maestri *et al.* 2020). Although this rule has been reported in several taxa (Poulin, 2007; Harnos *et al.* 2017; Ni *et al.* 2021), the combined effects of host traits and seasonal variation on parasite size have yet to be explored on a large temporal scale. Ni and Dutra (2023) also identified a significant proportion of variance in cymothoid isopod size that cannot be attributed solely to host length, suggesting a context-dependent relationship. Accordingly, we hypothesized that our long-term dataset on cymothoid isopods (*Telotha henselii*) parasitizing freshwater prawn (*Macrobrachium brasiliense*) could provide valuable new insights into the relationship between parasite and host body traits.

Here, we used cymothoid isopods parasitizing freshwater prawns as a model system to test seasonal and interannual variations in the interspecific relationship between parasite and host body traits. We hypothesized that the body trait (e.g., size, mass) of cymothoids would correlate with the body traits (e.g., size, mass, sex) of prawns, supporting Harrison's Rule. We also expected that Harrison's Rule would remain consistent across seasons (dry vs. wet) and years (interannual scale), suggesting that the evolution of parasite body size is primarily driven by host size and is unaffected by seasonal or interannual variations.

Material and methods

Study area and sampling

During four years from (1995 to 1998), we collected the palaemonid prawns (*Macrobrachium brasiliense*) in a stream (Águas Claras) located in the Pardo River basin, southwest Brazil (Fig. 1a and Fig. 1b). Sampling occurred bimonthly at fixed sites for two hours during the day. At each site, prawns were manually collected using sweeping sieves (50 cm in diameter, 4 mm mesh size) near marginal aquatic vegetation. The specimens were kept in plastic thermic boxes and transported to the laboratory, where they were euthanized by thermal shock (3°C for 30 minutes), then fixed and preserved in 70% ethanol. The material was subsequently deposited in the Museum of Zoology at the University of São Paulo (MZUSP), with accession numbers for palaemonid prawns (MZUSP 47525) and cymothoid isopods (MZUSP 47526).

Measures of host-related traits

In the laboratory, prawn specimens underwent biometric analysis, including body measurements and weight. Carapace length (CL) was measured from the base of the rostral spine to the posterior margin of the carapace, and total length (TL) was determined as the distance from the base of the rostral spine to the tip of the telson). Measurements were taken using a calliper with a precision of 0.05 mm. Weight (W) was recorded in grams using a digital balance with a precision of 0.01 g. Sex was determined by checking for the presence of the appendix masculina on the endopod of the second pair of pleopods (Nogueira *et al.* 2020). Subsequently, prawns were examined externally for the presence of cymothoid isopods (Fig. 1c and Fig. 1d).

Parasitological screening and measurements

Ectoparasites found on each animal were collected and measured under a stereomicroscope (Zeiss®Stemi® SV-6), and their weight was recorded. Posteriorly, the ectoparasites were fixed in 70% ethanol and identified based on the descriptions provided by Lemos de Castro (1985), Wunderlich *et al*. (2011), and Andrade *et al.* (2020). The cymothoid isopods were identified using specific characteristics, including the second pereopod with five spines on the inner margin of the propodus and the sixth pereopod with four spines on the propodus and one on the merus.

Statistical analysis

We used generalized linear mixed models (GLMM) to examine the relationship between prawn body traits (i.e., host length and weight) and cymothoid body traits (i.e., parasite length and weight), as well as to assess whether this relationship varied with host sex (male vs. female), seasons (dry vs. wet), and years (1995, 1996, 1997, 1998). Host and parasite traits, seasons, year, and their interactions were included as fixed effects, while month and year were treated as random intercepts (random effects). Only data from the summer seasons were used to avoid bias when comparing years.

Generalized linear mixed models (GLMMs) using a gamma distribution with a log link function were used for continuous response variables (Zuur *et al.* 2013), and we also calculated the R^2 values (i.e., marginal R^2_{m}, which represents only the fixed effects, and conditional R^2_{c}, which is associated with the fixed and the random effects) for each model (Nakagawa and Schielzeth, 2013). Multicollinearity among predictors was assessed using a variance inflation factor (VIF) from the R package *performance* (Lüdecke *et al.* 2021) and predictors with VIFs > 5 were excluded (Zuur *et al.* 2013). Diagnostic plots from the R package *DHARMA* (Hartig 2022) were used to verify normality and homoscedasticity of residuals. Last, model selection was performed using the Akaike Information Criterion (AIC) with the *performance* package (Lüdecke *et al.* 2021), while the relative importance of each fixed predictor was evaluated using the R package *glmm.hp* (Lai *et al.* 2022).

All GLMM analyses were conducted in R version 4.4.1 (R Development Core Team 2024) using the *lme4* (Bates *et al.* 2015) and *glmmTMB* (Magnusson *et al.* 2020) packages. Maps were created using QGIS version 3.34.3 (QGIS Development Team, 2024), and the graphics were performed with *ggplot2* package (Wickham 2011).

Results

Overall, we observed a slight difference in average length and weight between male and female prawns across seasons and years (i.e., males were approximately 2–3 mm longer on average than females; Table 1), except in 1998, where males were significantly larger than females (i.e., males were ~6 mm longer on average than females; Table 1). Similar differences were also observed in weight, with males consistently heavier than females (Table 1). Parasite length and weight varied in association with the corresponding measures in prawns across seasons and years (Table 1).

Our models indicated isopod body length (Length model) and weight (Weight model) were positively associated with host length ($R^2_c = 0.79$; and $R^2_m = 0.72$; Table 2, Fig. 2a) and host weight ($R^2_c = 0.82$; $R^2_m = 0.74$; Table 2, Fig. 3a). However, no significant associations were found for host sex (Table 2, Figs. 2b and 3b) or seasons (Table 2, Figs. 2c and 3c). Our models also show a significant effect of the year on parasite length (Table 2, Fig. 2d) and weight (Table 2, Fig. 3d). Finally, the predictors with the highest individual contribution percentages were host length (I. perc = 67.4%) and year (I. perc = 25.4%) for the length model, and host weight (I. perc = 60.6%) and year (I. perc = 29.1%), for the weight model, respectively (Table 2).

Discussion

We found strong evidence supporting Harrison's rule (HR) through the positive relationship between parasite length and host length, as well as parasite weight and host weight. However, we did not detect any influence of the host sex or seasons on this relationship. Contrary to our prediction, we observed interannual differences in HR over the years. These findings highlight demonstrated the importance of size and mass in this ectoparasite-host system, demonstrating that both body length and weight (of parasite and host) tend to be positively and significantly correlated (Harrison 1915; Clayton *et al.* 2016; Ni *et al*. 2021; Poulin 2021; Leung 2022; Ni and Dutra, 2023).

Although this pattern has often been corroborated across various parasite taxa (Morand *et al*. 1996; Nagler *et al.* 2017; Harnos *et al.* 2017; Maestri *et al.* 2020; Lisnerová *et al.* 2022; Rózsa *et al.* 2024), evidence for HR in cymothoid isopods parasitizing arthropod hosts has been scarce, with most studies focusing on fish hosts (Welicky *et al.* 2019; Ni and Dutra 2023). Our results provide strong support to HR, aligning with findings by Welicky *et al.* (2019) and Kottarathil *et al.* (2019), who also reported positive and significant correlations between the length of cymothoid isopods and the length of their fish hosts. In arthropods, few studies have confirmed Harrison's rule (Ni *et al.* 2021; Lim *et al.* 2022). For instance, Lim *et al.* (2022) identified a positive correlation between cleptoparasitic bees and their host bees, while Ni *et al.* (2021) also found evidence supporting HR for hairworms (Nematomorpha) and mermithids (Nematoda) parasitizing arthropods.

In addition to the positive relationship between parasite length and host length, we also found a positive association between parasite weight and host weight; however, no such relationship was observed for host sex. Behavioural and spatial aggregation between males and females (Nogueira *et al.*, 2019) can influence parasite exposure and, consequently, the HR pattern. Although male prawns (*Macrobrachium brasiliense*) are generally larger and heavier than females, exhibiting sexual dimorphism (Mantelatto and Barbosa 2005; Taddei *et al.* 2017; Nogueira *et al.* 2019; Nogueira *et al.* 2022), we did not find a significant difference in the HR pattern between sexes. This lack of effect can be attributed to several factors. Firstly, males and females may share similar habitats and behaviours, resulting in comparable exposure rates to the parasite across sexes (see Wunderlich *et al.* 2024). Additionally, *Telotha henselii* may have evolved to exploit both sexes proportionally to the host's size, thereby minimising differences associated with sexual dimorphism. Another factor to consider is the representativeness of the sampling across time and seasons, which could have influenced the detection of potential sex-related differences. Finally, more dominant factors, such as overall host size or interannual variability, may have masked any effect of sex on the HR pattern. These findings suggest that, in the system analysed, sexual dimorphism, although pronounced, does not play a significant role in determining the relationship between parasite and host body traits.

The evolution of parasite body size typically depends on host traits (e.g., length and weight), but morphological similarities and divergences between parasites and host traits can occur depending on the host-parasite system (Poulin 2007; Johnson and Hoverman, 2014; Clayton *et al*. 2016; Lim *et al.* 2022). Consequently, Harrison's Rule (HR) does not apply universally across all parasite groups, even when controlling for confounding phylogenetic effects (Morand and Poulin 2002; Poulin, 2007). This covariation of host and parasite body traits may fluctuate (Johnson *et al.* 2005; Poulin 2007; Lisnerová *et al.* 2022) and be influenced by temporal (Maestri *et al.* 2020) and environmental changes (Poulin, 2021), which can affect HR.

Recent studies have shown that some environmental factors, such as temperature and precipitation, can disrupt the HR pattern, resulting in misleading correlations between the body sizes of fleas and their rodent hosts across assemblages (Maestri *et al.* 2020). Our study observed significant interannual variation in HR over the four-year period, with a marked difference in the final year (1998). This variation may be explained by environmental changes, such as precipitation and dry periods, during that year, which could have influenced the population structure of prawns. Such changes likely resulted in differences in the average length and weight of males and females. Precipitation and/or dry periods are known to affect benthic macroinvertebrates in streams (Herbst *et al.*, 2019; Bae and Park, 2019), potentially altering hydrological regime that can affect the parasitism in freshwater prawns (Wunderlich *et al.* 2024). Temperature has also been suggested affect the parasitism in freshwater systems, but a recent study revealed that the change in temperature may has a weak effect in prevalence of infection in first intermediate hosts, suggesting that the seasonal variation in infection can be species- or system-specific (Paterson *et al*. 2024). Thus, our findings suggest that host traits primarily drive HR but may also be influenced by significant interannual variability.

In summary, we observed an unexpected interannual variation in Harrison’s Rule, along with the expected positive relationship between isopod and prawn traits, except for host sex and across dry and wet seasons. Future studies should investigate interannual variability in other host-parasite systems to determine whether Harrison’s Rule is affected by environmental and temporal changes.

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Author´s contributions

ACW and MAAP conceived and designed study. ACW analyzed the data and wrote the first draft of the manuscript. EEDM and MAAP provided critical input and made substantial contribution to improve the map (Fig. 1) and manuscript editing. All authors read and approved the final manuscript.

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Data availability

Data supporting the findings of this study are available upon request from the corresponding author.

Code availability

R code will be made available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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Table 1. Total length (mm) and weight (g) of *Macrobrachium brasiliense* prawns and *Telotha henselii* cymothoid isopods across seasons and years. Values are presented as mean ± standard deviation (Mean±SD).

Season/Year	*Macrobrachium brasiliense*						*Telotha henselii*		
		Male length	Male weight		Female length	Female weight		Parasite length	Parasite weight
	n	Mean±SD	Mean±SD	n	Mean±SD	Mean±SD	n	Mean±SD	Mean±SD
1995									
Winter	13	24.2±4.6	0.176±0.067	34	20.6±3.7	0.117±0.054	49	4.4±1.1	0.005±0.003
Spring	10	26.3±4.8	0.214±0.091	14	23.6±3.5	0.169±0.053	24	5.3±1.5	0.007±0.004
Summer	7	20.6±7.6	0.130±0.102	9	17.2±3.2	0.079±0.037	13	3.2±1.1	0.002±0.002
Autumn	9	21.3±5.5	0.126±0.077	24	20.3±3.1	0.102±0.046	37	3.8±0.8	0.003±0.002
Total	39	23.7±5.6	0.170±0.087	81	20.7±3.9	0.117±0.056	123	4.3±1.3	0.004±0.003
1996									
Winter	-	-	-	-	-	-	-	-	-
Spring	-	-	-	-	-	-	-	-	-
Summer	10	21.2±4.2	0.143±0.082	13	19.1±3.7	0.102±0.067	29	3.4±1.5	0.003±0.004
Autumn	-	-	-	-	-	-	-	-	-
Total	10	21.2±4.2	0.143±0.082	13	19.1±3.7	0.102±0.067	29	3.4±1.5	0.003±0.004
1997									
Winter	11	27.6±3.1	0.222±0.074	16	25.4±2.8	0.188±0.056	32	5.2±0.9	0.005±0.003
Spring	-	-	-	-	-	-	-	-	-
Summer	11	20.7±4.2	0.129±0.079	14	18.9±3.2	0.098±0.049	27	3.3±1.5	0.003±0.004
Autumn	-	-	-	-	-	-	-	-	-
Total	22	24.1±5.1	0.176±0.089	30	22.4±4.4	0.146±0.069	59	4.3±1.5	0.004±0.003
1998									
Winter	-	-	-		-	-		-	-
Spring	-	-	-		-	-		-	-
Summer	6	24.8±1.1	0.184±0.015	21	17.5±3.1	0.081±0.051	36	2.8±0.7	0.001±0.001
Autumn	12	25.5±2.6	0.245±0.075	24	20.1±2.5	0.137±0.041	52	3.4±0.7	0.002±0.002
Total	18	25.4±2.3	0.236±0.072	45	19.3±3.3	0.111±0.053	88	3.2±0.8	0.002±0.001
TOTAL	89	23.7±5.2	0.175±0.088	169	20.4±3.9	0.119±0.061	299	3.9±1.4	0.003±0.003

Table 2 Results of generalized linear mixed models describing the relationship between parasite length (Length model) and parasite weight (Weight model) as a function of host length, host weight, host sex (male vs. female), seasons (i.e. wet vs. dry), and years (i.e. 1995, 1996, 1997, 1998). Parameter estimates, standard error (SE), Wald z-values, *P*-value, 95% confidence interval, total marginal (R^2_m), conditional (R^2_c), and individual contribution percentage (I. perc %) are provided for each predictor and model. Bold values and the confidence intervals (CI) that exclude zero indicate significant variables.

Model	Parameter estimate	SE	Wald *z*-value	*P*-value	95% CI		R^2_c	R^2_m	I. perc (%)
					Lower	Upper			
Length model							0.79	0.72	
Intercept	0.384	0.082	4.674	**0.001**	**0.212**	**0.554**			
Host length	0.048	0.002	18.752	**0.001**	**0.043**	**0.053**			67.4
Host sex (male)	-0.0004	0.021	-0.022	0.982	-0.042	0.043			2.4
Season (wet)	-0.048	0.068	-0.707	0.479	-0.183	0.086			4.8
Year (1996)	-0.139	0.114	-1.218	0.223	-0.363	0.084			25.4
Year (1997)	-0.042	0.100	-0.426	0.670	-0.239	0.153			
Year (1998)	-0.245	0.075	-3.267	**0.001**	**-0.392**	**-0.098**			
Weight model							0.82	0.74	
Intercept	-6.590	0.193	-33.991	**0.001**	**-7.042**	**-6.253**			
Host weight	8.193	0.456	17.958	**0.001**	**7.300**	**9.089**			60.6
Host sex (male)	-0.057	0.058	-0.976	0.329	-0.057	0.172			3.2
Season (wet)	-0.354	0.217	-1.629	0.103	-0.777	0.069			7.1
Year (1996)	-0.438	0.368	-1.190	0.234	-1.162	0.268			29.1
Year (1997)	-0.233	0.313	-0.745	0.456	-0.859	0.357			
Year (1998)	-1.072	0.239	-4.479	**0.001**	**-1.538**	**-0.607**			

Figure legends

Fig. 1 Geographic location of the Rio Pardo basin (a), highlighting the Águas Claras stream (b), where the palaemonid prawns (*Macrobrachium brasiliense*) (c) and the cymothoid isopods (*Telotha henselii*) (d) were collected. Scale bar: c = 4 mm and d = 1 mm

Fig. 2 Relationships between host length and parasite length modelled using a generalised linear mixed model (a) and comparisons based on sex (b), seasons (c), and year (d). Rug marks represent the distribution of the data along the y and x axes. R^2 and significance values are given in the text

Fig. 3 Relationships between host weight and parasite weight modelled using a generalised linear mixed model (a) and comparisons based on sex (b), seasons (c), and year (d). Rug marks represent the distribution of the data along the y and x axes. R^2 and significance values are given in the text

Fig.1

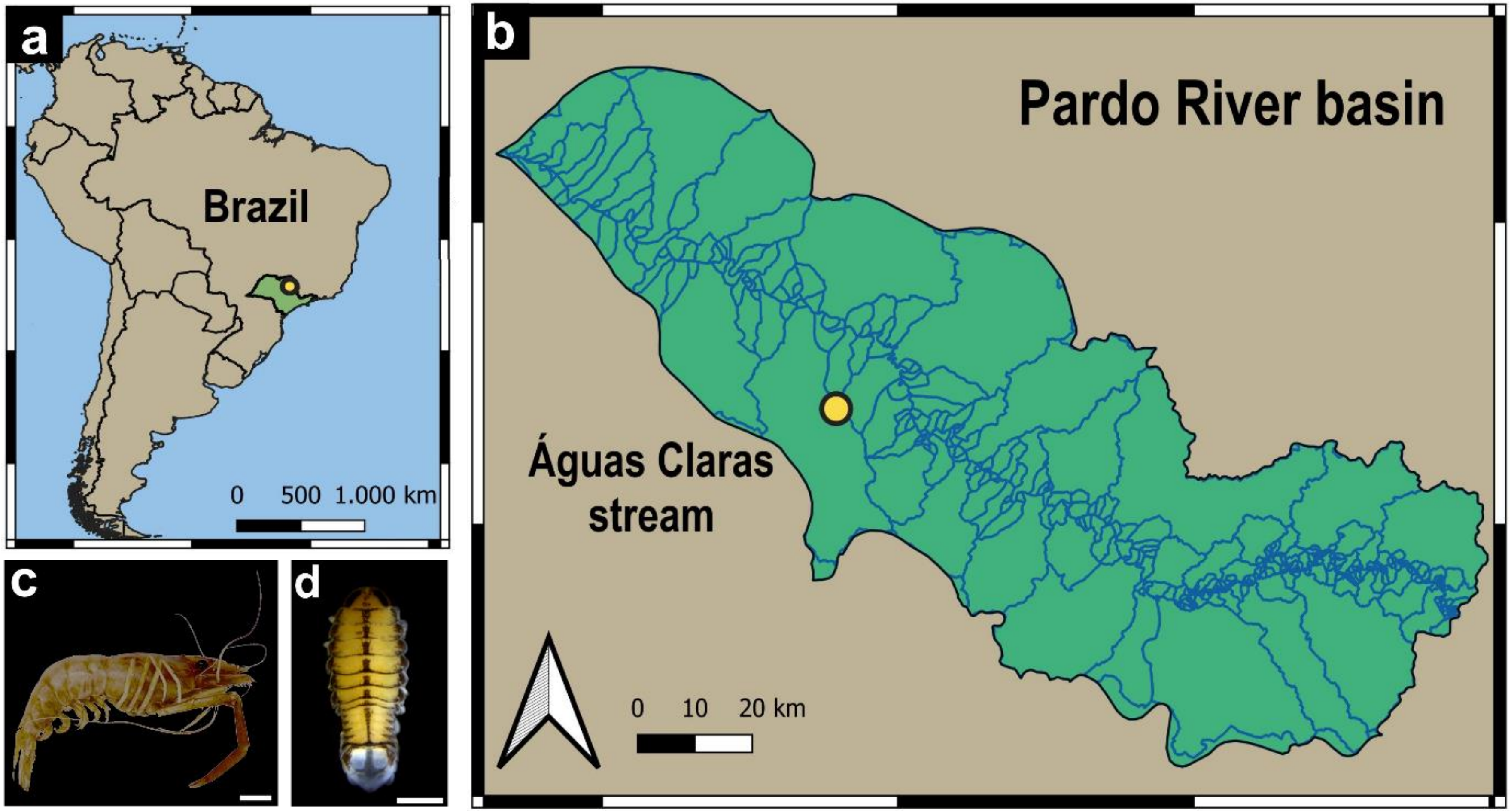

a
Brazil
0 500 1.000 km
b
Pardo River basin
Águas Claras stream
0 10 20 km
c
d

Fig.2

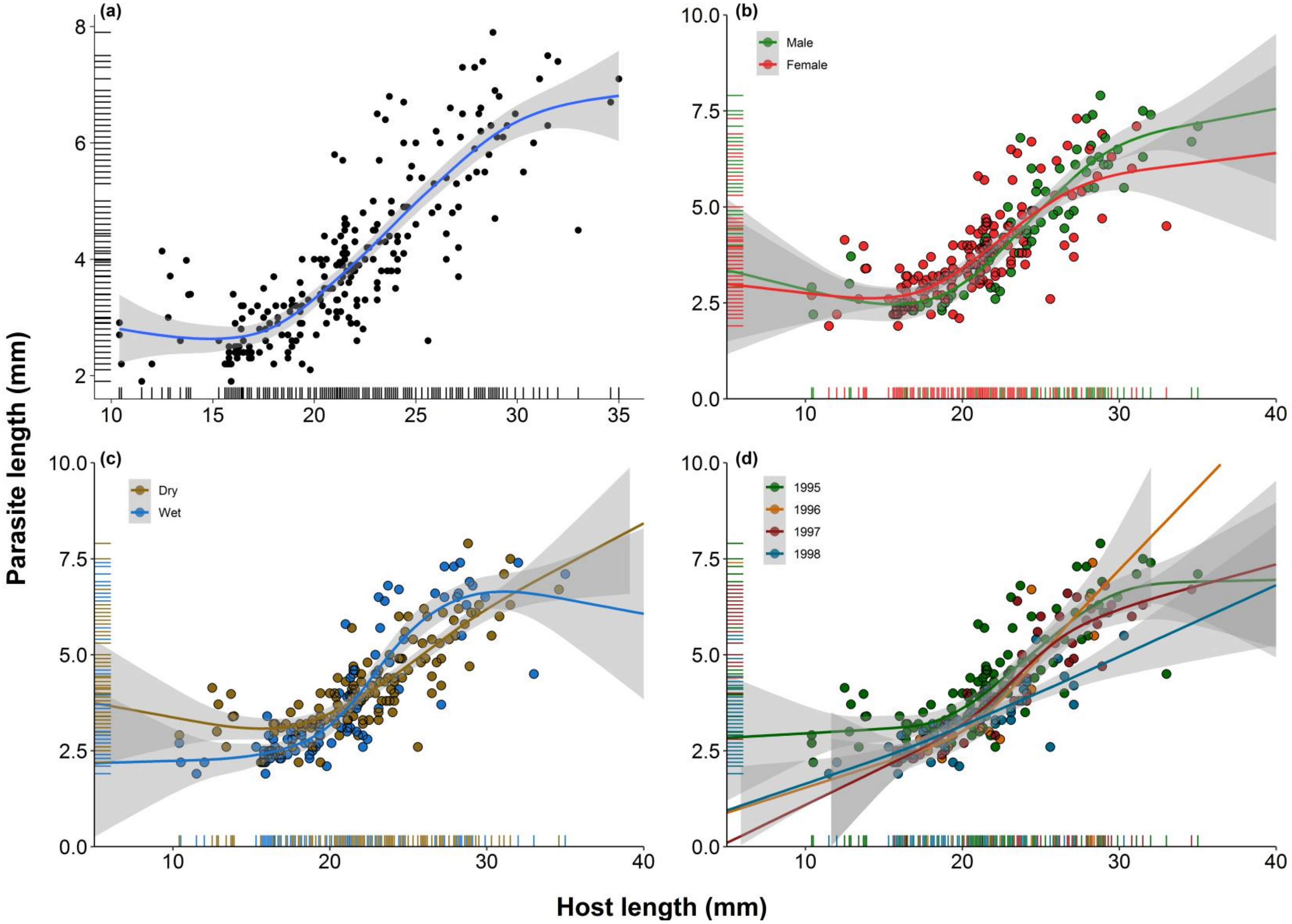
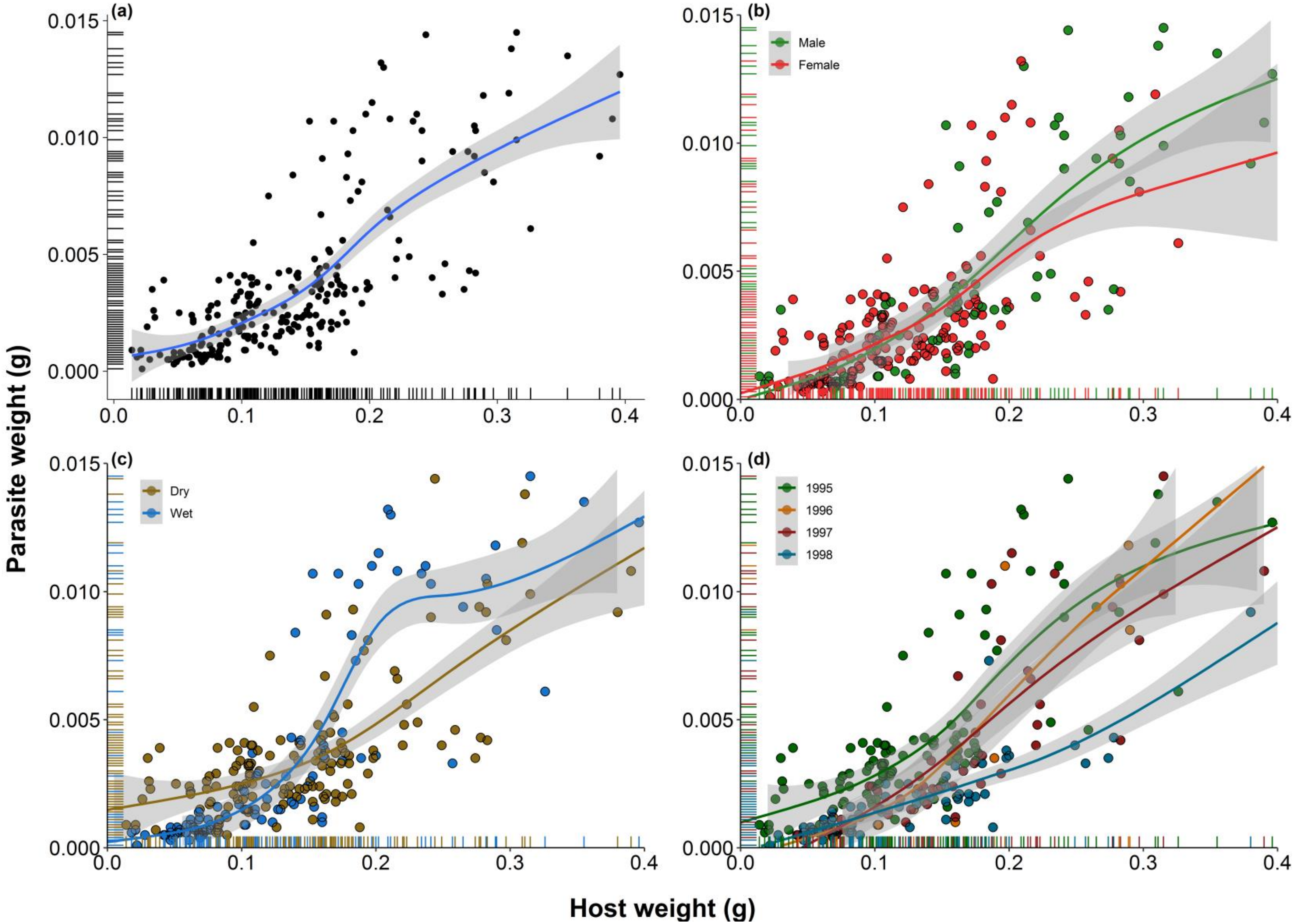

(a)
(b)
(c)
(d)
Male
Female
Dry
Wet
1995
1996
1997
1998
Parasite length (mm)
Host length (mm)
2
4
6
8
0.0
2.5
5.0
7.5
10.0
10
15
20
25
30
35
40

Fig.3


(a)
(b)
(c)
(d)
Male
Female
Dry
Wet
1995
1996
1997
1998
0.000
0.005
0.010
0.015
0.0
0.1
0.2
0.3
0.4
Parasite weight (g)
Host weight (g)