1 **Environmental variability influences the relationship between prawn host size**

2 **and ectoparasite body size: Insights from a long-term stream study**

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25

Abstract

Increases in host body size can, in counterpart, lead to increase in parasite body size because large individual hosts may supply energy for parasite growth. However, this correlation of matching size can also be mediated by other host and environmental factors. Here, we used a long-term dataset of cymothoid isopod-palaemonid prawn to test whether there is evidence supporting for the relationship between host and parasite body traits (i.e., length, sex, weight), while accounting for the effect of seasons (i.e., dry and wet) and years. Prawns were sampled seasonally over four years in a tropical stream in southeastern Brazil. Our analysis showed that isopod body length and weight were positively associated with host length and host weight. 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. Our models indicated that host length and weight explained approximately 70% of the variation, while environmental variability effects across time accounted for 30%. These highlight that the covariation between host and parasite body traits may be modulated by environmental changes, potentially altering this host-size versus parasite-size relationship. Future research should consider interannual variability as a potentially critical factor driving host-parasite interactions in populations from freshwater ecosystems.

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 dynamic and evolution of the parasite (Poulin 2007; Johnson and Hoverman 2014; Stewart Merrill et al. 2021; Leung 2022). In an evolutionary context, across different host and parasite taxa, we have observed a positive relationship between host body size and parasite body size, a hypothesis called Harrison´s rule (Harrison 1915; Clayton et al. 2016; Ni et al. 2021; Schmid-Hempel 2021). Evidence of this relationship 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), but within a host-parasite interaction, we expect additional variation due to ecological forces that can act to shape this pattern (Poulin 2007; Maestri et al. 2020; Patra et al. 2024; Melo et al. 2024; Sánchez‑Hernández et al. 2025).

This pattern is associated with a more efficient use of the available niche space and resources by parasites in larger hosts (Sasal et al. 1999; Lisnerová et al. 2022). It seems much more likely that parasite size and biomass within a single population increase with host body size due to host energetics (Hechinger et al. 2013). Larger host has higher resource intake and a larger pool of assimilated resources that can be used by the parasites to growth, enhancing their 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) or environmental changes (e.g., seasonality and temperature), which can create spurious correlations in this pattern, where no intrinsic properties of the host directly affect the parasite's body size (Maestri et al. 2020; Ni and Dutra 2023). Therefore, changes in this pattern can occur

75 depending on the host-parasite system and also due to ecological forces that act to shape this

76 pattern (Poulin 2007; Johnson and Hoverman 2014; Clayton et al. 2016; Lim et al. 2022).

77   Environmental variability and temperature changes can affect parasite growth rates and

78 body size, potentially altering the correlation between host and parasite body traits (Johnson et

79 al. 2005; Poulin 2007; Clayton et al. 2016; Poulin 2021; Lim et al. 2022; Lisnerová et al. 2022).

80 Furthermore, an interesting study shows that the temperature and precipitation can also disrupt

81 the relationship between hosts and parasites sizes, resulting in misleading correlations between

82 the body sizes of fleas (parasites) and their rodent hosts across assemblages (Maestri et al.

83 2020). Although this pattern has been reported in several taxa (Poulin 2007; Harnos et al. 2017;

84 Ni et al. 2021), the combined effects of host traits and seasonal variation on parasite size have

85 yet to be explored on a large temporal scale. Ni and Dutra (2023) also identified a significant

86 proportion of variance in cymothoid isopod size that cannot be attributed solely to host length,

87 suggesting a context-dependent relationship. Accordingly, we hypothesized that our long-term

88 dataset on cymothoid isopods (*Telotha henselii*) parasitizing freshwater prawn

89 (*Macrobrachium brasiliense*) could provide valuable new insights into the relationship

90 between cymothoid isopods and their host body traits.

91   Here, we used cymothoid isopods parasitizing freshwater prawns as a model system to

92 test seasonal and interannual variations in the interspecific relationship between parasite and

93 host body traits. We hypothesized that the body trait (e.g., size, mass) of cymothoid isopods

94 would correlate with the body traits (e.g., size, mass, sex) of prawns, supporting this host-size

95 versus parasite-size pattern. We also expected that this pattern would remain consistent across

96 seasons (dry vs. wet) and years (interannual scale), suggesting that the correlation of isopod

97 body size is primarily driven by host traits and is not affected by seasonal or interannual

98 variations.

99

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

124 Ectoparasites found on each animal were collected and measured under a stereomicroscope

125 (Zeiss®Stemi® SV-6), and their weight was recorded. Posteriorly, the ectoparasites were fixed

126 in 70% ethanol and identified based on the descriptions provided by Lemos de Castro (1985),

127 Wunderlich et al. (2011), and Andrade et al. (2020). The cymothoid isopods were identified

128 using specific characteristics, including the second pereopod with five spines on the inner

129 margin of the propodus and the sixth pereopod with four spines on the propodus and one on

130 the merus.

131

132 **Statistical analysis**

133 We used generalized linear mixed models (GLMM) to examine the relationship between prawn

134 body traits (i.e., host length and weight) and cymothoid body traits (i.e., parasite length and

135 weight), as well as to assess whether this relationship varied with host sex (male vs. female),

136 seasons (dry vs. wet), and years (1995, 1996, 1997, 1998). Host and parasite traits, seasons,

137 year, and their interactions were included as fixed effects, while month and year were treated

138 as random intercepts (random effects). To avoid the effect of parasite competition on hosts (i.e.,

139 host resources are shared among parasitic isopods), we use individual hosts parasitized with

140 one cymothoid isopod only in our analyses. Only data from the summer seasons were also used

141 to avoid bias when comparing years.

142   Generalized linear mixed models (GLMMs) using a gamma distribution with a log link

143 function were used for continuous response variables (Zuur et al. 2013), and we also calculated

144 the R^2 values (i.e., marginal R^2_m, which represents only the fixed effects, and conditional R^2_c,

145 which is associated with the fixed and the random effects) for each model (Nakagawa and

146 Schielzeth 2013). Multicollinearity among predictors was assessed using a variance inflation

147 factor (VIF) from the R package *performance* (Lüdecke et al. 2021) and predictors with VIFs

148 > 5 were excluded (Zuur et al. 2013). Diagnostic plots from the R package *DHARMA* (Hartig

149 2022) were used to verify normality and homoscedasticity of residuals. Last, model selection

150 was performed using the Akaike Information Criterion (AIC) with the *performance* package

151 (Lüdecke et al. 2021), while the relative importance of each fixed predictor was evaluated using

152 the R package *glmm.hp* (Lai et al. 2022). All GLMM analyses were conducted in R version

153 4.4.1 (R Development Core Team 2024) using the *lme4* (Bates et al. 2015) and *glmmTMB*

154 (Magnusson et al. 2020) packages. Maps were created using QGIS version 3.34.3 (QGIS

155 Development Team 2024), and the graphics were performed with *ggplot2* package (Wickham

156 2011).

157

158 **Results**

159 Overall, we observed a slight difference in average length and weight between male and female

160 prawns across seasons and years (i.e., males were approximately 2–3 mm longer on average

161 than females; Table 1), except in 1998, where males were significantly larger than females (i.e.,

162 males were ~6 mm longer on average than females; Table 1). Similar differences were also

163 observed in weight, with males consistently heavier than females (Table 1). Parasite length and

164 weight varied in association with the corresponding measures in prawns across seasons and

165 years (Table 1).

166   Our models indicated isopod body length (Length model) and weight (Weight model)

167 were positively associated with host length ($R^2_c = 0.79$; and $R^2_m = 0.72$; Table 2, Fig. 2a) and

168 host weight ($R^2_c = 0.82$; $R^2_m = 0.74$; Table 2, Fig. 3a). However, no significant associations

169 were found for host sex (Table 2, Figs. 2b and 3b) or seasons (Table 2, Figs. 2c and 3c). Our

170 models also show a significant effect of the year on parasite length (Table 2, Fig. 2d) and weight

171 (Table 2, Fig. 3d). Finally, the predictors with the highest individual contribution percentages

172 were host length (I. perc = 67.4%) and year (I. perc = 25.4%) for the length model, and host

173　weight (I. perc = 60.6%) and year (I. perc = 29.1%), for the weight model, respectively (Table

174　2).

175

176　**Discussion**

177　We found strong evidence that the larger individual of prawns also support larger individual

178　isopod cymothoids, through the positive relationship between parasite length and host length,

179　as well as parasite weight and host weight. However, we did not detect any influence of host

180　sex or seasons on this relationship. Contrary to our prediction, we observed interannual

181　differences in the relationship between parasite and host sizes over the years. These findings

182　highlight demonstrated the importance of size and mass in this ectoparasite-host system,

183　demonstrating that both body length and weight (of parasite and host) tend to be positively and

184　significantly correlated (Clayton et al. 2016; Ni et al. 2021; Poulin 2021; Leung 2022; Ni and

185　Dutra 2023).

186　　　　Although this pattern has often been corroborated in various host and parasite taxa

187　(Morand et al. 1996; Nagler et al. 2017; Harnos et al. 2017; Maestri et al. 2020; Lisnerová et

188　al. 2022; Rózsa et al. 2024), evidence for this pattern in cymothoid isopods parasitizing

189　arthropod hosts has been scarce, with most studies focusing on fish hosts (Welicky et al. 2019;

190　Ni and Dutra 2023). Our results provide strong support for this relationship, aligning with the

191　findings of Welicky et al. (2019) and Kottarathil et al. (2019), who also reported positive and

192　significant correlations between the length of cymothoid isopods and the length of their fish

193　hosts. In arthropods, few studies have confirmed this relationship between hosts and parasite

194　sizes (Ni et al. 2021; Lim et al. 2022). For example, Lim et al. (2022) identified a positive

195　correlation between cleptoparasitic bees and their host bees, while Ni et al. (2021) also found

196　evidence supporting this relationship for hairworms (Nematomorpha) and mermithids

197　(Nematoda) parasitizing arthropods.

198   In addition to the positive relationship between parasite length and host length, we also

199   found a positive association between parasite weight and host weight; however, no such

200   relationship was observed for host sex. Behavioral and spatial aggregation between males and

201   females (Nogueira et al. 2019) can influence parasite exposure and, consequently, the outcome

202   of relationship. Although male prawns (*Macrobrachium brasiliense*) are generally larger and

203   heavier than females, exhibiting sexual dimorphism (Mantelatto and Barbosa 2005; Taddei et

204   al. 2017; Nogueira et al. 2019; Nogueira et al. 2022), we did not find a significant difference

205   in the pattern between sexes. This lack of effect can be attributed to several factors. First, males

206   and females may share similar habitats and behaviors, resulting in comparable exposure rates

207   to the parasite across sexes (see Wunderlich et al. 2024). Additionally, *Telotha henselii* may

208   have evolved to exploit both sexes proportionally to the host's size, thereby minimizing

209   differences associated with sexual dimorphism (Beck 1979; Rasch and Bauer 2015). Another

210   factor to consider is the representativeness of the sampling across time and seasons, which

211   could have influenced the detection of potential sex-related differences. Finally, more dominant

212   factors, such as overall host size or interannual variability, may have masked any effect of sex

213   on this pattern. These findings suggest that in the system examined, sexual dimorphism,

214   although pronounced, does not play a significant role in determining the relationship between

215   parasite and host body traits.

216   In an evolutionary context, the evolution of parasite body size typically depends on host

217   traits (e.g., length and weight), but in ecological context, some works have provided a

218   mechanistic explanation for the relationship between parasites and host traits (Morand et al.

219   2000; Johnson et al. 2005; Poulin 2007). They have shown that the relationship between host

220   size and parasite size is simply the by-product of the need for the parasite to be larger to enhance

221   their attachment and locomotion on the host (Clayton et al. 2016). It makes sense in our prawn-

222   isopod system, because while the prawn grows, we expect that the cymothoid isopod also

223   would adjust to the host size to keep attach on their carapace. However, this relationship

224   between host and parasites sizes does not apply universally to all parasite groups, even when

225   controlling confounding phylogenetic effects (Morand and Poulin 2002; Poulin 2007). This

226   covariation of host and parasite body traits may fluctuate (Johnson et al. 2005; Poulin 2007;

227   Lisnerová et al. 2022) and be influenced by temporal (Maestri et al. 2020) and environmental

228   changes (Poulin 2021), which can affect this relationship, particularly within a simple host

229   population.

230   Recent studies have shown that some environmental factors, such as precipitation and

231   temperature, can disrupt this relationship, resulting in misleading correlations between the body

232   sizes of fleas and their rodent hosts across assemblages (Maestri et al. 2020). Our study

233   observed significant interannual variation in this relationship between host and parasite sizes

234   over the four-year period, with a marked difference in the final year (1998). This variation may

235   be explained by environmental changes, such as precipitation and dry periods, during that year,

236   which could have influenced the population structure of prawns. Such changes likely resulted

237   in differences in the average length and weight of males and females. Precipitation and/or dry

238   periods are known to affect benthic macroinvertebrates in streams (Herbst et al. 2019; Bae and

239   Park 2019), potentially altering the hydrological regime that can affect the parasitism in

240   freshwater prawns (Wunderlich et al. 2024). Temperature has also been suggested to affect the

241   outcome of interactions between parasite and host through altering metabolic process in host

242   traits, that improves parasite feeding rates at the level of host individual (Hechinger et al. 2013;

243   Byers 2021) and can also scale allometrically in hosts across ecosystem level (Grunberg and

244   Anderson 2022). However, a recent study revealed that the change in temperature may have a

245   weak effect in outcomes of infection in first intermediate hosts, suggesting that the seasonal

246   variation in infection may be species- or system-specific (Paterson et al. 2024). Thus, our

247   findings suggest that the relationship between host and parasite sizes can be driven by host

248   energetic that supplies individual parasite but may also be influenced by significant interannual

249   variability.

250   In summary, we observed an unexpected interannual variation in this relationship, along

251   with the expected positive relationship between isopod and prawn traits, except for host sex

252   and across dry and wet seasons. Future studies should investigate environmental variability

253   throughout time and space in estimating the relationship between the size of prawn host and

254   the body size of the ectoparasite and if our findings are proven to be valid for other host-parasite

255   systems.

256

261

262 **Author´s contributions**

263 ACW and MAAP conceived and designed study. ACW analyzed the data and wrote the first

264 draft of the manuscript. EEDM and MAAP provided critical input and made substantial

265 contribution to improve the map and manuscript editing. All authors read and approved the

266 final manuscript.

267

273   fellowships to ACW (UNESP/PROPE - Editais #13/2022 and #05/2024: Programa Unesp de

274   Pós-Doutorado) and indirectly to FAPESP (ACW #2017/16650–5).

275

276   **Data availability**

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

278   author.

279

280   **Code availability**

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

282

283   # Declarations

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

285   **Ethics approval** Not applicable.

286   **Consent to participate** Not applicable.

287   **Consent for publication** Not applicable.

288

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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		47	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		16	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		33	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		120	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		23	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		23	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		27	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		25	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		52	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		27	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		36	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		63	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		258	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 Lower	95% CI Upper	R^2_c	R^2_m	I. perc (%)
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
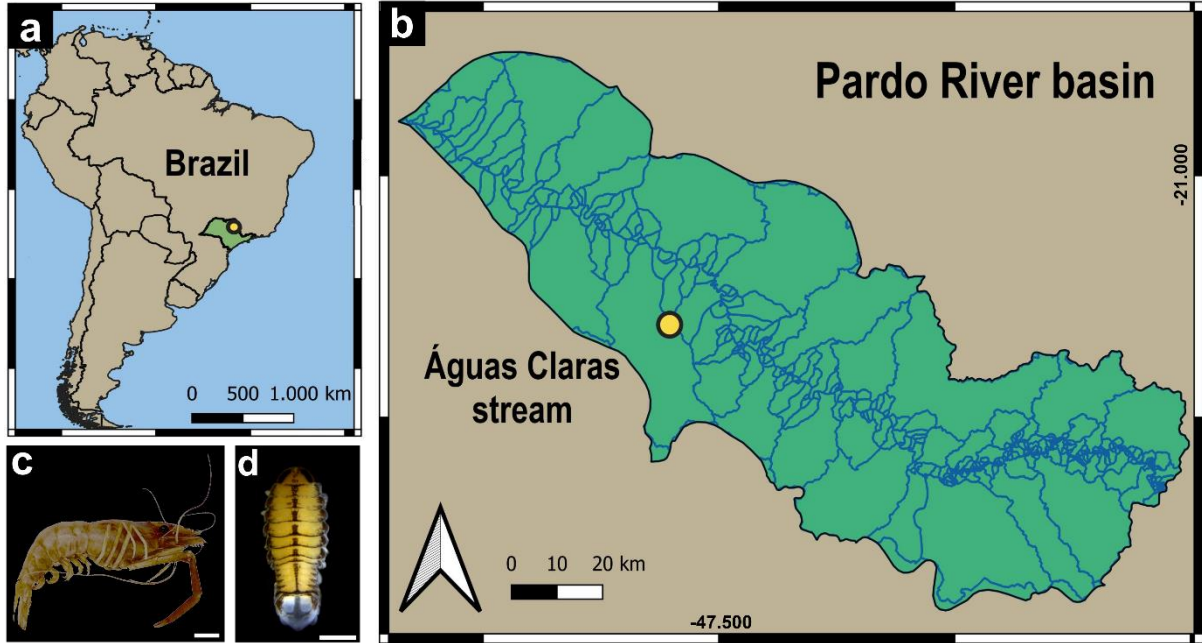
Fig. 2 Relationships between host length and parasite length modelled using a generalised linear mixed model (a) and comparisons based on sex (b), seasons (c), and year (d). Rug marks represent the distribution of the data along the y and x axes. R^2 and significance values are given in the text
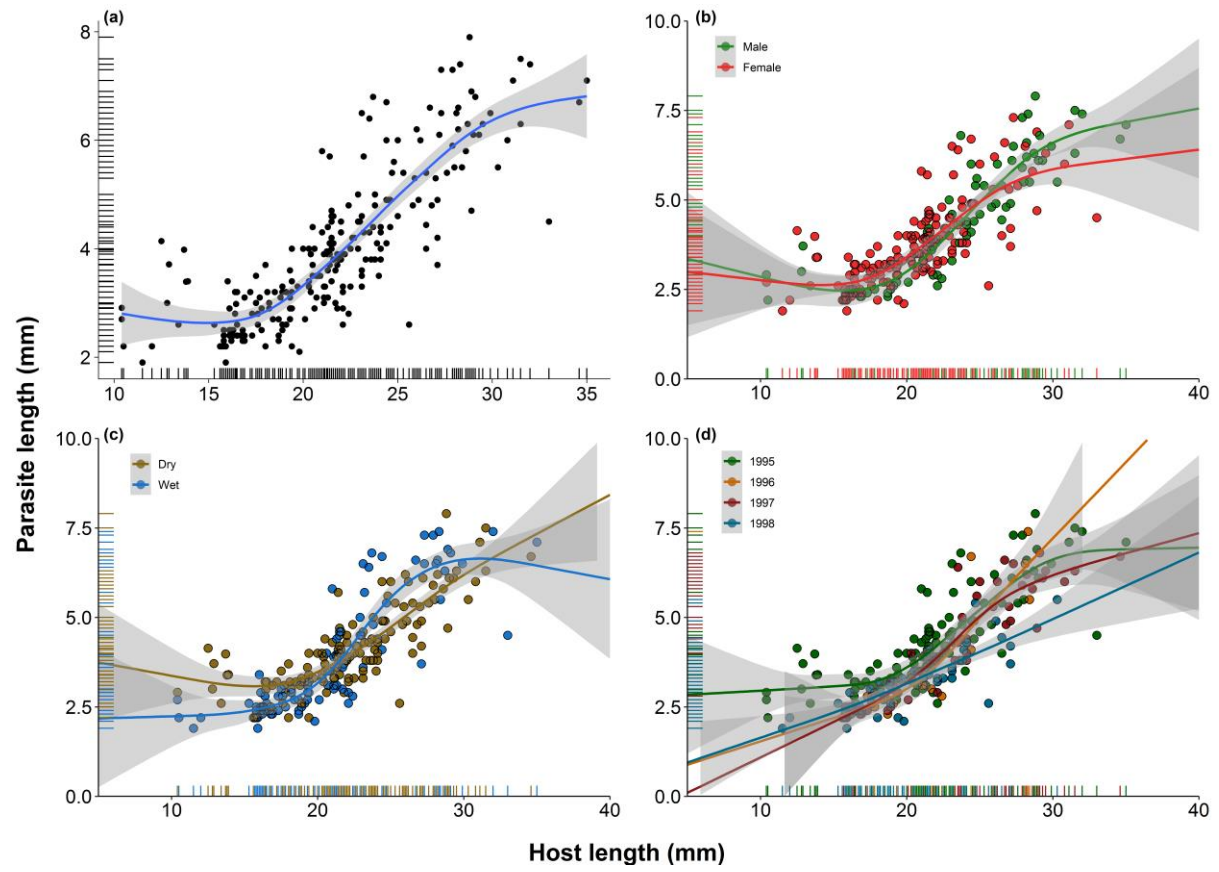
Fig. 3 Relationships between host weight and parasite weight modelled using a generalised linear mixed model (a) and comparisons based on sex (b), seasons (c), and year (d). Rug marks represent the distribution of the data along the y and x axes. R^2 and significance values are given in the text

Fig.1

Fig.2

Fig.3