How coexistence may influence life history: the reproduction strategies of sympatric congeneric terrestrial isopods (Crustacea, Oniscidea)

Article *in* Canadian Journal of Zoology · July 2018

DOI: 10.1139/cjz-2018-0086

5 authors, including:


Bianca Laís Zimmermann
Instituto Federal de Educação, Ciência e Tecnologia do Rio Grande do Sul
21 PUBLICATIONS **127** CITATIONS
SEE PROFILE


Alexandre V. Palaoro
Clemson University
41 PUBLICATIONS **357** CITATIONS
SEE PROFILE


Mauricio Almerão
Centro Universitário La Salle (Unilasalle)
76 PUBLICATIONS **786** CITATIONS
SEE PROFILE


Paula Beatriz Araujo
Universidade Federal do Rio Grande do Sul
169 PUBLICATIONS **1,773** CITATIONS
SEE PROFILE

NRC Research Press

ARTICLE

How coexistence may influence life history: the reproductive strategies of sympatric congeneric terrestrial isopods (Crustacea, Oniscidea)

Bianca Laís Zimmermann, Alexandre Varaschin Palaoro, Didier Bouchon, Maurício Pereira Almerão, and Paula Beatriz Araujo

Abstract: Patterns of allocation between reproduction, survival, and maintenance are what we call life history. By investigating the life-history strategy of sympatric species, we may understand how they are able to coexist, as different strategies are expected to evolve in species that occupy similar niche space. Terrestrial isopods are a group in which multiple species frequently inhabit the same area. Notably, they are usually infected by *Wolbachia* Hertig, 1936, a notorious manipulator of the hosts' reproductive processes. Thus, the aim of this study was to analyze the investment in reproduction in three sympatric and closely related species of terrestrial isopods: *Atlantoscia floridana* (Van Name, 1940), *Atlantoscia inflata* Campos-Filho and Araujo, 2015, and *Atlantoscia petronioi* Campos-Filho, Contreira and Lopes-Leitzke, 2012, only the latter being infected with *Wolbachia*. We showed that the presence of the bacteria seems not to affect the fitness of *A. petronioi*, because there was no clear difference in the reproductive output of infected and noninfected individuals. On the other hand, we observed that the three species possess alternative life-history strategies; that is, they differ in how much they invest in maintenance (body size) and reproductive effort. Such differences probably facilitate the species coexistence, reducing the competition among them.

Key words: *Atlantoscia*, Brazil, life history, reproductive investment, *Wolbachia*, isopods.

Résumé : Les motifs d'allocation de ressources entre la reproduction, la survie et le maintien sont ce que nous appelons le cycle biologique. L'étude des stratégies de cycle biologique d'espèces sympatriques peut permettre de comprendre ce qui leur permet de coexister, puisque le développement de différentes stratégies est attendu chez des espèces qui occupent des espaces de niche semblables. Les isopodes terrestres forment un groupe dont plusieurs espèces cohabitent souvent dans la même région. Fait intéressant, ils sont habituellement infectés par *Wolbachia* Hertig, 1936, un manipulateur notoire des processus de reproduction de ses hôtes. Le but de l'étude consistait donc à analyser l'investissement dans la reproduction de trois espèces sympatriques étroitement apparentées d'isopodes terrestres : *Atlantoscia floridana* (Van Name, 1940), *Atlantoscia inflata* Campos-Filho et Araujo, 2015 et *Atlantoscia petronioi* Campos-Filho, Contreira et Lopes-Leitzke, 2012, seule cette dernière espèce étant infectée par *Wolbachia*. Nous démontrons que la présence de la bactérie ne semble pas avoir d'incidence sur l'aptitude d'*A. petronioi*, puisqu'il n'y a pas de différence claire entre les individus infectés et non infectés en ce qui concerne l'efficacité de la reproduction. En revanche, nous avons observé que les trois espèces présentent différentes stratégies de cycle biologique, c'est-à-dire qu'elles diffèrent les unes des autres en ce qui concerne l'ampleur de l'investissement dans le maintien (taille du corps) et l'effort de reproduction. De telles différences facilitent probablement la coexistence des espèces en réduisant la concurrence entre elles. [Traduit par la Rédaction]

Mots-clés : *Atlantoscia*, Brésil, cycle biologique, investissement dans la reproduction, *Wolbachia*, isopodes.

Introduction

Energy obtained from food is limited in nature, which implies a series of constrains during development. Organisms thus need to allocate their limited energy in reproduction, growth, or maintenance, and by investing in one trait, the other traits may be penalized (Lancaster et al. 2017). This decision of where and how much to invest is what we call life history (Brommer 2000). Life history impacts the individual's fitness, and thus, is prone to selection: if a given strategy increases fitness more than other strategies, then the individuals opting for that strategy will be selected (Del Giudice et al. 2015). However, the optimal life-history strategy is not fixed; as conditions change in nature, so will the optimal strategy (Bonsall and Mangel 2004). Species coexistence is one of such conditions that may alter the pay-off of the strategies adopted by the species (Moll and Brown 2008). The optimal strategy, in this case, depends on the strategies of the other species: if one

Received 28 March 2018. Accepted 29 May 2018.

B.L. Zimmermann. Programa de Pós-Graduação em Biodiversidade Animal, Centro de Ciências Naturais e Exatas, Universidade Federal de Santa Maria, Avenida Roraima 1000, Bairro Camobi, 97105-900, Santa Maria, RS, Brazil; Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, Bairro Agronomia, 91501-970, Porto Alegre, Brazil.
A.V. Palaoro. LAGE do Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão 321 - Trav. 14, Cid. Universitária, 05508-090, São Paulo, Brazil.
D. Bouchon. CNRS UMR 7267, Laboratoire Ecologie et Biologie des Interactions, équipe Ecologie Evolution Symbiose, Université de Poitiers, Batiment B8-B35, 5 rue Albert Turpain, TSA 51106, F-86073 Poitiers Cedex 9, France.
M.P. Almerão. Universidade La Salle, Avenida Victor Barreto, 2288, CEP: 92010000, Canoas, Brazil.
P.B. Araujo. Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, Bairro Agronomia, 91501-970, Porto Alegre, Brazil.
Corresponding author: Bianca Laís Zimmermann (email: bia.lais@gmail.com).

Can. J. Zool. **96**: 1214–1220 (2018) dx.doi.org/10.1139/cjz-2018-0086

species is investing in reproduction, then it may pay-off to invest in survival until conditions change (Brommer 2000). If life-history strategies and species coexistence are constantly influencing one another, then we need to investigate them simultaneously to understand the extent of this influence, which is rarely acknowledged (Lancaster et al. 2017).

Terrestrial isopods are currently the only group of crustaceans that managed to exploit almost the whole range of terrestrial ecosystems (Sfenthourakis and Taiti 2015), which is correlated with their high reproductive efficiency (Richardson and Araujo 2015). Thus, life-history traits related to reproduction are by far the best-studied aspects in this group (Kight 2009; Warburg 2011, 2013). Neotropical species usually exhibit longer breeding periods, higher number of broods per lifetime, and lower reproductive allocation per brood compared with temperate isopods (Quadros et al. 2008). However, we do not know how much reproductive variation can be found among Neotropical species, especially because multiple species of terrestrial isopods often inhabit the same area (Almerão et al. 2006). In fact, coexistence is thought to change life-history strategies in Palearctic species (Ando 1996), which highlights the potential of coexistence to influence life-history strategies in Neotropical species. Maybe by addressing coexistence in the Neotropics, we may be able to disentangle how much variation comes from coexistence patterns and how much comes, for example, from phylogenetic constraints (Glazier et al. 2003).

Another confounding factor regarding the life-history strategies of terrestrial isopods is the infection by the bacteria *Wolbachia* Hertig, 1936 (Bouchon et al. 2008; Zimmermann et al. 2015*a*). *Wolbachia* is notorious for the manipulations of the hosts' reproductive patterns, often causing a substantial impact to host fitness (Zug and Hammerstein, 2015). Indeed, *Wolbachia*-induced reproductive phenotypes were responsible for the reduction of fecundity and fertility, female-biased sex ratio, and other negative effects in terrestrial isopods species from palearctic region (Bouchon et al. 1998; Rigaud et al. 1999, 2001; Braquart-Varnier et al. 2008; Sicard et al. 2010). When dealing with reproductive life-history strategies of Neotropical species, the effects of *Wolbachia* are generally not considered (Quadros et al. 2009; Sokolowicz and Araujo 2013; Kenne and Araujo 2015). If its presence could affect the life-history strategies used by potential competitors sharing the same microhabitat, then it should be evaluated.

The genus *Atlantoscia* Ferrara and Taiti, 1981 comprises five species of terrestrial isopods that are found mostly in natural vegetation habitats of southeastern and southern Brazil (Quadros and Araujo 2008; Zimmermann et al. 2015*b*). Although easily distinguishable through molecular approaches, such as DNA barcoding (Zimmermann et al. 2015*b*), morphological differences among the species are quite subtle and restricted to a few characteristics. Besides being morphologically similar, all species live among leaf litter and are usually found sharing the same microhabitat, including cases in which they may or not be infected by *Wolbachia* (Zimmermann et al. 2015*a*). Since differences in life-history strategies can evolve in the presence of competitors (Bonsall et al. 2002), especially in the case of species that occupy similar niche, the aim of this study was to analyze one aspect of the life-history strategy, the investment in reproduction, in three closely related species with sympatric and syntopic distribution: *Atlantoscia floridana* (Van Name, 1940), *Atlantoscia inflata* Campos-Filho and Araujo, 2015, and *Atlantoscia petronioi* Campos-Filho, Contreira and Lopes-Leitzke, 2012, only the latter being infected with *Wolbachia*. Ultimately, we intend to provide evidence on how coexistence may modulate lifehistory strategies adopted by sympatric and syntopic species, a not fully understood but probably crucial step in the evolution of terrestrial isopods and many other organisms.

Materials and methods

Field sampling

Individuals of *A. floridana*, *A. inflata*, and *A. petronioi* were collected throughout the year in two secondary and semideciduous forest fragments in the metropolitan area of Porto Alegre, Rio Grande do Sul, Brazil. The climate in this region is humid subtropical, characterized by hot and humid summers and mild to cool winters (Cfa type of Köppen's classification; Peel et al. 2007). In the first sampled site (30°04′25″S, 51°07′19″W), the three species occur together in syntopy; in the second sampled site (30°12′30″S, 51°10′12″W), only *A. floridana* and *A. inflata* are found, also living in syntopy. Multiple leaf litter samples from each sampled site were randomly collected from January 2011 to July 2012 and taken to the laboratory where individuals were triaged and directly used in the experiments. For sex-ratio experiments, individuals were kept in containers with leaves and field soil and were under laboratory-controlled conditions (temperature of 20 °C and photoperiod of 12 h light : 12 h dark). All applicable international, national, and (or) institutional guidelines for the care and use of animals were followed.

Molecular identification of *Atlantoscia* species and detection of *Wolbachia*

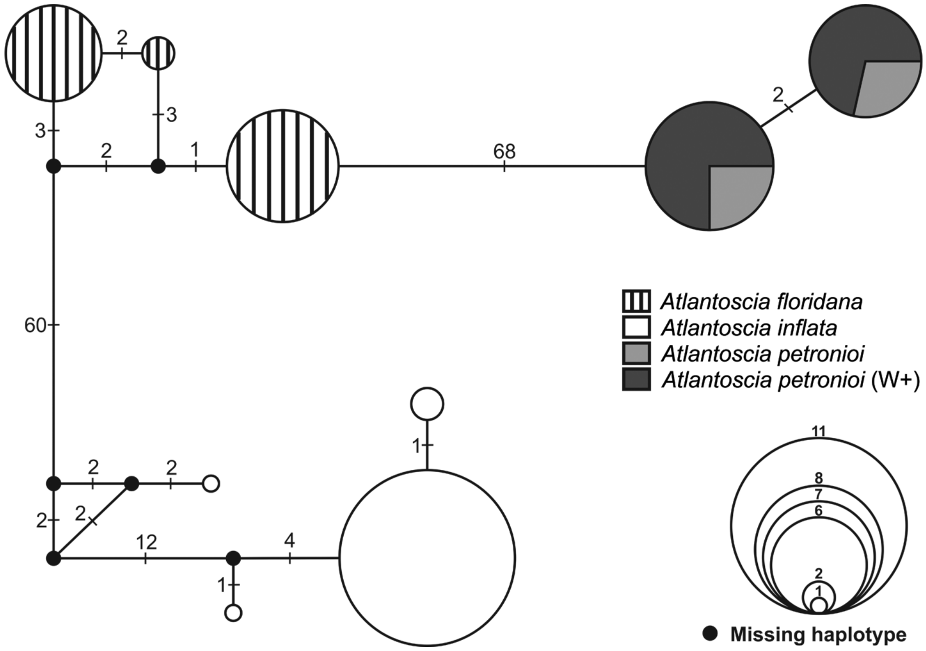
Due to the morphological similarities among *Atlantoscia* species, we selected 15 individuals of each species to confirm species identity and to verify their relationship by using the mitochondrial gene *cytochrome oxidase subunit I* (*COI*, primers LCO and HCO; Folmer et al. 1994). All individuals used in this study were also tested for the presence of *Wolbachia* with a polymerase chain reaction (PCR) assay targeting the *Wolbachia 16S rRNA* gene (primers 99F and 994R; O'Neill et al. 1992). Total DNA from adult terrestrial isopods was extracted using the Chelex protocol (BioRad). Eggs, embryos, and mancae (juvenile stage) DNA extractions were performed with the extraction kit PureLink Genomic DNA Kits (K1820-01). Standard PCR was run and the products were checked by agarose gel electrophoresis and purified. Sequences were obtained using BigDye technology by Macrogen Inc., Seoul, Korea. Consensus sequences for both strands were aligned with Muscle (Edgar 2004). The intra- and inter-specific mtDNA genetic divergences were obtained using *p*-distance model with 1000 bootstrap replicates in MEGA version 6.0 (Tamura et al. 2013). The haplotype number was estimated using DnaSP version 4.10.3 (Rozas et al. 2003) and genealogical relationships among mitochondrial sequences were determined by a haplotype network generated with the median-joining method (Bandelt et al. 1999) in NETWORK version 4.6 (http://www.fluxus-engineering.com).

For the infected species, we examined *Wolbachia* vertical transmission by individually testing the offspring of 30 infected females. Additionally, mancae from 15 infected females were monitored until sexual differentiation (development of male genitalia and the female genital pore, according to Araujo et al. 2004) to check offspring sex ratio. We tested if *Wolbachia* presence in the parental individual could increase the probability of females being born using a binomial test (i.e., the number of females born against the total number of offspring).

Reproductive life-history traits

To test size and offspring production, females of *A. floridana*, *A. inflata*, and *A. petronioi* were dissected and then measured (cephalothorax width (CW) as a measure for body size) with a stereomicroscope (0.01 mm of accuracy) (Araujo and Bond-Buckup 2005). We recorded the number of eggs and the number of embryos or mancae inside the marsupium of ovigerous females. We differentiated between eggs and embryos and mancae because terrestrial isopods show intramarsupial mortality, i.e., not all eggs develop into mancae (Araujo and Bond-Buckup 2005). Intramarsupial mortality was also verified in the three species. We

Fig. 1. Median-joining haplotype network for mtDNA sequences from the isopods *Atlantoscia floridana*, *Atlantoscia inflata*, *Atlantoscia petronioi*, and *Atlantoscia petronioi* infected by *Wolbachia* bacteria (W+). Area of the circles is proportional to the number of individuals sharing the same haplotype. Black circles represent missing, probably unsampled, haplotypes or extinct lineages. Lines and numbers between circles represent the number of mutational steps.



counted the eggs of 152 females of *A. floridana*, 66 of *A. inflata*, and 57 of *A. petronioi* while counting the embryos and mancae of 226 females of *A. floridana*, 51 of *A. inflata*, and 81 of *A. petronioi* (Supplementary Table S1).[1] With these data, we tested if (*i*) species differed in overall size; (*ii* and *iii*) species differed in egg and embryo and mancae investment (i.e., intercept and slope of a regression against size), and (*iv*) *Wolbachia* had any influence in the production of embryos and mancae of *A. petronioi*. Prior to testing, we evaluated if populations differed in any of these variables by visualizing histograms of the data (data not shown). This a priori analysis showed that the data from different populations were within the same range and distribution, and thus, we chose not to use "population" as a random variable, simplifying our results and interpretations. Indeed, results were similar regardless of adding the population as a random variable or not (results not shown here; the full data set used in our study is found at https://github.com/alexandrepalaoro/IsopodLifeHistory).

To test if species differ in their overall size, we used an ordinary least-squares regression (OLS) with log-transformed CW of all individuals (i.e., females used in the offspring production tests) as the response variable and species as the factor. Next, to test if species differed in the number of eggs, we used a generalized linear model (GLM) with a Poisson distribution and a log link. The number of eggs was the response variable, CW was the continuous covariable, and species was the factor. In the third analysis, we also used a GLM with a Poisson distribution and a log link, but this time we used the number of embryos and mancae as the response variable, CW as the continuous covariable, and species as the factor. Lastly, to test if *Wolbachia* infection affected fitness, we used the number of embryos and mancae of *A. petronioi* because it was the sole species that was infected (see Results). We used a GLM with a Poisson distribution and a log link with the number of embryos and mancae of *A. petronioi* as the response variable, CW as the continuous covariable, and status (i.e., infected or noninfected) as the factor.

In all tests, we scaled the continuous covariables by centering their means to zero and making their variances uniform by dividing the covariable once by their standard deviation to normalize them. Centering and scaling variables help in parameter estimation and makes parameters easily interpretable and comparable when significant interactions are present (Schielzeth 2010). We assessed differences among species by analyzing the 95% confidence intervals (95% CI) of the estimates in the analyses (i.e., if the 95% CI do not overlap, then species differ significantly). All analyses were performed using the R software (R Development Core Team 2011) and R codes used in our study are found at https://github.com/alexandrepalaoro/IsopodLifeHistory.

Results

Molecular identification of *Atlantoscia* species and detection of *Wolbachia*

The *COI* sequences produced in this study confirmed the identity of the analyzed species. In other words, the final alignment of the *COI* data set was verified against sequences of *Atlantoscia* species available from GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and they aligned unambiguously with the correct species. We found two mitochondrial haplotypes for *A. petronioi*, three for *A. floridana*, and four for *A. inflata*. The relationships among haplotypes are shown in the Fig. 1. The mean mitochondrial divergence between *A. floridana* and *A. petronioi* was 13.3%. This value was 14.9% for *A. floridana* and *A. inflata*, and 16.5% for *A. petronioi* and *A. inflata*. The intraspecific divergences were 0.7%, 0.6%, and 0.2% for *A. inflata*, *A. floridana*, and *A. petronioi*, respectively. Sequences generated in this study were deposited in GenBank under accession Nos. KY053436 to KY053444.

---

[1] Supplementary table and figure are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0086.

Table 1. Intercepts and slopes of the regression models used to test differences in the reproductive life-history traits of the isopods *Atlantoscia floridana*, *Atlantoscia inflata*, and *Atlantoscia petronioi*.

Species	Intercept (95% CI)	Slope (95% CI)
(*a*) Cephalothorax width.		
Atlantoscia floridana	**0.256 (0.248–0.265)**	—
Atlantoscia inflata	**0.030 (0.014–0.045)**	—
Atlantoscia petronioi	**0.350 (0.335–0.364)**	—
(*b*) Number of eggs.		
Atlantoscia floridana	10.838 (10.249–11.447)	1.477 (1.380–1.581)
Atlantoscia inflata	9.601 (7.541–11.918)	1.437 (1.126–1.828)
Atlantoscia petronioi	**7.905 (6.355–9.789)**	1.356 (0.995–1.842)
(*c*) Number of embryos and mancae.		
Atlantoscia floridana	10.250 (9.924–10.582)	1.527 (1.468–1.587)
Atlantoscia inflata	9.302 (7.049–12.229)	1.335 (1.084–1.647)
Atlantoscia petronioi	**7.795 (6.809–8.889)**	1.325 (1.112–1.581)
(*d*) Number of embryos and mancae infected or noninfected by *Wolbachia*.		
Infected *A. petronioi*	10.011 (9.216–10.851)	1.142 (1.053–1.238)
Noninfected *A. petronioi*	8.961 (7.714–10.332)	1.132 (0.877–1.456)

Note: 95% CI is 95% confidence interval. Values in boldface type are different (i.e., the confidence intervals do not overlap).

None of the analyzed individuals of *A. floridana* and *A. inflata* was infected by *Wolbachia* (only *A. petronioi* had infected individuals) and these were more abundant than noninfected ones (111 infected versus 27 noninfected). Based on *16S rRNA* gene, all infected specimens harbour the same strain of *Wolbachia*, equal to that one observed by Zimmermann et al. (2012) (GenBank accession No. JF799948). Regarding the vertical transmission and sex ratio of infected *A. petronioi*, 273 offspring individuals were tested and 232 were positive for *Wolbachia*; that is, the rate of transmission was 84.98%. The sex ratio observed was slightly male-biased (1.108:1), and it was not more likely for females being born than males (probability of female being born = 0.474, $P = 0.734$).

Reproductive life-history traits

Overall, we collected *A. floridana* more easily than the other two species, which hints that this species is more abundant at these particular study sites. *Atlantoscia petronioi* is the largest species, followed by *A. floridana*, and *A. inflata* is the smallest species (OLS regression; $F_{[2,626]} = 467.9$, adjusted $R^2 = 0.58$, $P < 0.0001$, $n = 629$; Table 1*a*). Regarding the reproductive effort, *A. floridana* produced a higher mean number of eggs than *A. petronioi*, whereas *A. inflata* did not differ from either of the aforementioned species (Fig. 2, Table 1*b*), but the increase in the number of eggs per unit of body size did not differ among species (i.e., the slopes did not differ; Table 1*b*). Results were similar for the number of embryos and mancae: *A. floridana* produced a higher mean number of embryos and mancae than *A. petronioi*, and *A. inflata* did not differ from both species (Fig. 3, Table 1*c*). The increase in the number of embryos and mancae per unit of body size also did not differ among species (Table 1*c*). Lastly, *Wolbachia* infected and noninfected individuals of *A. petronioi* did not differ in the mean number of embryos and mancae (Fig. 4, Table 1*d*). One interesting aspect, however, is that noninfected individuals had a wider range of number of embryos and mancae and sizes (Supplementary Figs. S1*a*, S1*b*).[1] The intramarsupial mortality was 2.03% for *A. floridana*, 0.34% for *A. inflata*, and 1.77% for *A. petronioi* (1.39% and 2.79% for noninfected and infected individuals, respectively), but species did not differ between themselves (binomial GLM; $\chi^2_{[1,331]} = 5.05$, $P = 0.08$; data not shown).

Discussion

Herein, we found that sympatric congeneric *Atlantoscia* species differ in their life-history strategies; that is, they differ in how much they invest in maintenance (i.e., body size) and their reproductive effort. The largest species, *A. petronioi*, produced a lower mean number of eggs and embryos than a smaller species, *A. floridana*, suggesting that these two species adopt different strategies. On the other hand, it was hard to detect what strategy *A. inflata* adopted. It was the smallest species in our sample, but the investment in reproductive life-history traits did not differ from the other species. This suggests that either *A. inflata* has a liable reproductive strategy, or that the sample was not large enough to detect a different strategy in this species. In either case, we can discard phylogenetic constraints from our sample: all species are genetically related, so phylogeny should not play a major role on the analyzed life-history parameters. Hence, our study highlights the influence that coexistence may have on life-history strategies.

First, DNA barcoding confirmed the identity of the species analyzed. Despite the difficulty in distinguishing *Atlantoscia* species based on morphological characters, they showed high interspecific genetic divergence (Zimmermann et al. 2015*b*). Indeed, the seven valid species of the genus present a mean mtDNA *COI* genetic distance of 13.9% (Zimmermann et al. 2018). In fact, high congeneric mitochondrial divergences are usually observed for terrestrial isopod. For example, genetic distances of *COI* sequences among congeneric species of *Hawaiioscia* Schultz, 1973, *Ligidium* Brandt, 1833, *Porcellio* Latreille, 1804, and *Burmoniscus* Collinge, 1914 ranged from 14.1% to 29% (Rivera et al. 2002; Klossa-Kilia et al. 2006; Sicard et al. 2014; Karasawa 2016).

Atlantoscia petronioi was the largest species in our study; however, it exhibited one of the lowest offspring productions. Since *Wolbachia* had neutral effects on reproduction (see Results and below), it is plausible that *A. petronioi* invests more on growth and maintenance traits, decreasing the energy pool left to invest in reproduction. *Atlantoscia inflata*, on the other hand, apparently invests the same in reproduction while investing less in somatic growth. There are four main sources of variation that can explain this pattern. The first is the environment. One could argue that metal contamination (Donker et al. 1993), food quality (Hassall et al. 2002; Lardies et al. 2004), and digestive tract symbionts (Horváthová et al. 2015; Bouchon et al. 2016; Dittmer et al. 2016) could affect life-history traits. However, reproductive patterns of sympatric terrestrial isopods appear to be independent of habitat conditions. For example, in nine syntopic terrestrial isopods, species-specific female body size was the main predictor of reproductive strategy and reproductive investment (Achouri et al. 2008). In our study, all species coexist and are exposed to the same microhabitat pressures. They are also likely to feed on the same litter types, as different isopods exhibit essentially the same food preference due to the leaf palatability (Quadros et al. 2014); these factors, thus, did not affect our results significantly.

The second factor is genetics. Studies have shown that the similarity of life-history traits between species with close phylogenetic relationship is probably related to the existence of phylogenetic constraints on life-history evolution (Ma et al 1991; Glazier et al. 2003; Quadros et al. 2008). Since the species analyzed are congeneric, we can assume that genetics is not playing a major role in the observed differences in life-history strategies.

The third factor is the strategies adopted by the other species. If one species invests heavily in any given life-history trait, then the other traits will be penalized, opening up an opportunity for other strategies to thrive with different strategies. For instance, *A. floridana* is smaller than *A. petronioi*, but it is more fecund. Additionally, *A. floridana* was more abundant in our study (and is generally more abundant), being considered a habitat generalist that possess the traits attributed to a successful colonizer and pioneer species (Lemos de Castro 1985; Araujo et al. 1996; Lopes et al. 2005; Quadros et al. 2009). Thus, individuals of *A. petronioi* that exhibit an alternative strategy focusing on survival and maintenance traits may be selected in this population to avoid direct competition with *A. floridana* (Moll and Brown 2008). Since we can discard phylogenetic constraints and environmental effects, it is

Fig. 2. Number of eggs related to cephalothorax width in the congeneric isopods *Atlantoscia floridana* (black circles and black line; n = 152), *Atlantoscia inflata* (grey circles and grey line; n = 66), and *Atlantoscia petronioi* (white circles and broken line; n = 53). Lines were fitted using the parameters estimated using a generalized linear model with a Poisson distribution, which are shown in Table 1*b*. Each data point represents one female of one species.

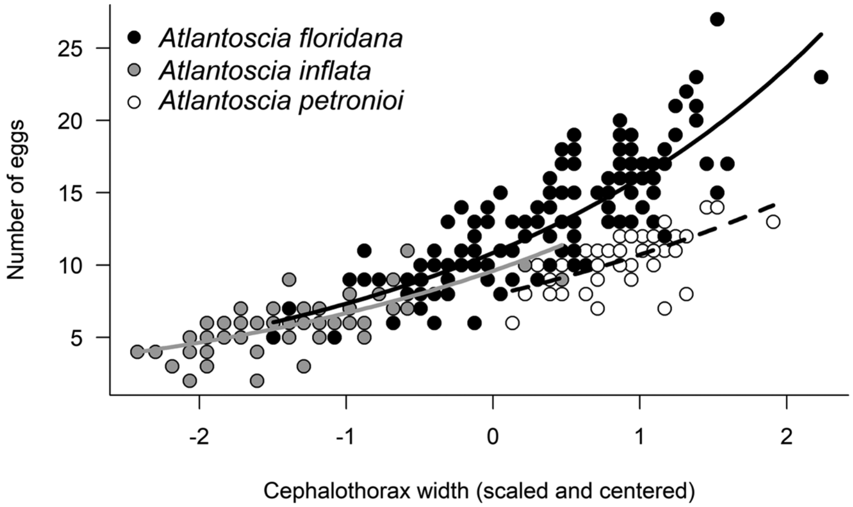
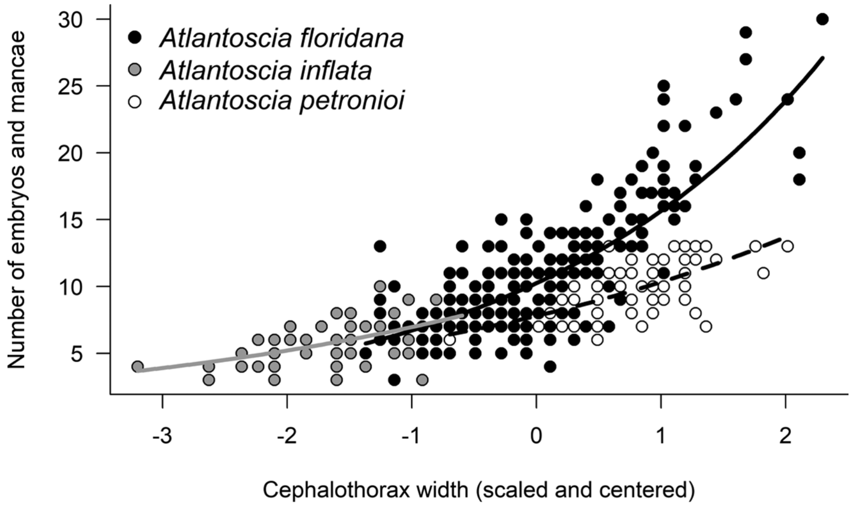


Fig. 3. Number of embryos and mancae related to cephalothorax width in the congeneric isopods *Atlantoscia floridana* (black circles and black line; n = 226), *Atlantoscia inflata* (grey circles and grey line; n = 51), and *Atlantoscia petronioi* (white circles and broken line; n = 81). Lines were fitted using the parameters estimated using a generalized linear model with a Poisson distribution, which are shown in Table 1*c*. Each data point represents one female of one species.



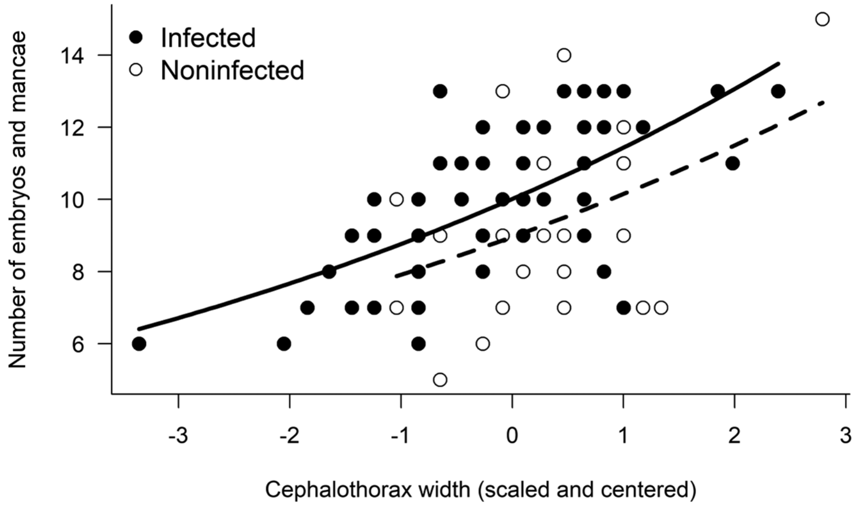
likely that coexistence acts on the selection of *A. petronioi* life-history strategy; the same pattern being applied for *A. inflata*.

The last factor is the *Wolbachia* infection. We have shown that only *A. petronioi* is infected and that the presence of *Wolbachia* does not affect reproductive fitness, although considerable evidence shows contrary scenarios (generally related to fitness decrease) in terrestrial isopods (e.g., Rigaud et al. 1999, 2001; Rigaud and Moreau 2004; Braquart-Varnier et al. 2008; Sicard et al. 2010). Up to 80% of individuals were infected, and the vertical transmission rate was also high (~85%). Despite its high prevalence, the effect of *Wolbachia* on reproductive output was apparently neutral, because there was no difference in the reproductive output of infected and noninfected individuals of this species. Besides, the offspring of infected individuals were not female-biased, discarding a feminizing effect of the infection, commonly observed in terrestrial isopods (Bouchon et al. 1998, 2008). The combined observations of (*i*) unbiased sex ratio, (*ii*) high but not fixed prevalence, and (*iii*) high but imperfect vertical transmission rate may suggest that *Wolbachia* induces cytoplasmic incompatibility in this species (for a review see Werren et al. 2008). Cytoplasmic incompatibility is a conditional embryonic lethality that occurs when males infected with *Wolbachia* strains inducing cytoplasmic incompatibility are crossed with uninfected females or with females carrying other incompatible *Wolbachia* strains (Moret et al. 2001; Sicard et al. 2014). Some questions, on the other hand, remain to be investigated, as only the *Wolbachia* effects on reproduction were examined, and not on other traits (such as survival, immunity, etc.).

It is intriguing that only one of the studied species is infected despite the phylogenetic proximity and microhabitat sharing among them. In fact, the large number of species that carry *Wolbachia* is a product of its high capacity to infect new host species; but although it spreads fast, *Wolbachia* is also commonly lost in some species. Furthermore, host species vary in their ability to support *Wolbachia* infection, which, when combined with the rapid spread and loss of infection, may explain why only one species in our sample is infected (for a review see Siozios et al. 2018).

In summary, much attention has been given to the reproductive life-history evolution of terrestrial isopods (Hassall et al. 2003;

Fig. 4. Number of embryos and mancae related to cephalothorax width in *Atlantoscia petronioi* infected by *Wolbachia* bacteria (black circles and solid line; $n = 111$) and females that are noninfected (white circles and broken line; $n = 27$). Lines were fitted using the parameters estimated using a generalized linear model with a Poisson distribution, which are shown in Table 1*d*. Each data point represents one female.



Lardies et al. 2004; Lardies and Bozinovic 2008; Warburg 2012; Medini-Bouaziz et al. 2015, 2017), but studies regarding strategies used by sympatric and syntopic species generally consider those that are distantly related (e.g., Ma et al. 1991; Achouri et al. 2008; Quadros et al. 2009; Tanaka and Karasawa 2018). In one of the exceptions, Ando (1996) suggested that two sympatric and congeneric species (*Ligidium japonicum* Verhoeff, 1918 and *Ligidium koreanum* Flasarova, 1972) have different life histories and that such differences facilitate their coexistence. Additionally, studies generally do not account for the effect of *Wolbachia*. In our case, we showed that the effect is apparently neutral in the reproductive aspects analyzed, as well as in many coevolved associations involving these bacteria (Zug and Hammerstein 2015). But, *Wolbachia* may play a large role in life-history strategies in species in which it has negative effects on reproduction. Here, differences in reproductive effort among the three *Atlantoscia* species appear to be linked with the alternative life-history strategies, which resulted from microevolutionary changes that occurred in the balance of resource allocation between survivorship, growth, and reproduction (Hassall et al. 2005). Such differences could prevent or reduce competition between species, allowing their coexistence. In fact, life-history variation has proven to be a critical coexistence mechanism, and variation in life-history strategies is also likely to be an important driver of local diversity (Lancaster et al. 2017).

Acknowledgements

We are grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for productivity fellowship granted to P.B.A.; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for regular and abroad scholarship (Programa de Doutorado Sanduíche no Exterior (PDSE)) to B.L.Z.; and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for the postdoctoral grant for A.V.P. (process no: 2016/22679-3). This work was supported by CNPq (grant number Universal 470286/2011-3).

References

Achouri, M.S., Charfi-Cheikhrouha, F., and Zimmer, M. 2008. Reproductive patterns in syntopic terrestrial isopod species (Crustacea, Isopoda, Oniscidea) from Morocco. Pedobiologia, **52**(2): 127–137. doi:10.1016/j.pedobi.2008.05.002.

Almerão, M.P., Mendonça, M.D.S., Jr., Quadros, A.F., Pedó, E., Silva, L.G., and Araujo, P.B. 2006. Terrestrial isopod diversity in the subtropical Neotropics: Itapuã State Park, southern Brazil. Iheringia Ser. Zool. **96**(4): 473–477. doi:10.1590/S0073-47212006000400012.

Ando, Y. 1996. Life history patterns of two coexisting isopods (*Ligidium japonicum* and *Ligidium koreanum*) in a *Cryptomeria japonica* plantation of southwestern Japan. Edaphologia, **56**: 31–46.

Araujo, P.B., and Bond-Buckup, G. 2005. Population structure and reproductive biology of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscidea) in southern Brazil. Acta Oecol. **28**: 289–298. doi:10.1016/j.actao.2005.05.005.

Araujo, P.B., Buckup, L., and Bond-Buckup, G. 1996. Isópodos terrestres (Isopoda, Oniscidea) de Santa Catarina e Rio Grande do Sul. Iheringia Ser. Zool. **81**: 111–138.

Araujo, P.B., Augusto, M.M., and Bond-Buckup, G. 2004. Postmarsupial development of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscidea): the manca stages. J. Nat. Hist. **38**: 951–965. doi:10.1080/0022293031000068428.

Bandelt, H.J., Forster, P., and Röhl, A. 1999. Median-joining networks for inferring intraspecific phylogenies. Mol. Biol. Evol. **16**: 37–48. doi:10.1093/oxfordjournals.molbev.a026036. PMID:10331250.

Bonsall, M.B., and Mangel, M. 2004. Life-history trade-offs and ecological dynamics in the evolution of longevity. Proc. R. Soc. B Biol. Sci. **271**(1544): 1143. doi:10.1098/rspb.2004.2722.

Bonsall, M.B., Hassell, M.P., and Asefa, G. 2002. Ecological trade-offs, resource partitioning, and coexistence in a host–parasitoid assemblage. Ecology, **83**(4): 925–934. doi:10.1890/0012-9658(2002)083[0925:ETORPA]2.0.CO;2.

Bouchon, D., Rigaud, T., and Juchault, P. 1998. Evidence for widespread *Wolbachia* infection in isopod crustaceans: molecular identification and host feminization. Proc. R. Soc. B Biol. Sci. **265**(1401): 1081–1090. doi:10.1098/rspb.1998.0402.

Bouchon, D., Cordaux, R., and Grève, P. 2008. Feminizing *Wolbachia* and the evolution of sex determination in isopods. *In* Insect symbiosis. *Edited by* K. Bourtzis and T. Miller. CRC Press, Boca Raton, Fla. pp. 273–294.

Bouchon, D., Zimmer, M., and Dittmer, J. 2016. The terrestrial isopod microbiome: an all-in-one toolbox for animal–microbe interactions of ecological relevance. Front. Microbiol. **7**: 1472. doi:10.3389/fmicb.2016.01472. PMID:27721806.

Braquart-Varnier, C., Lachat, M., Herbiniere, J., Johnson, M., Caubet, Y., Bouchon, D., and Sicard, M. 2008. *Wolbachia* mediate variation of host immunocompetence. PLoS ONE, **3**: e3286. doi:10.1371/journal.pone.0003286. PMID:18818770.

Brommer, J.E. 2000. The evolution of fitness in life-history theory. Biol. Rev. Camb. Philos. Soc. **75**(3): 377–404. doi:10.1017/S000632310000551X. PMID:11034016.

Del Giudice, M., Gangestad, S.W., and Kaplan, H.S. 2015. Life history theory and evolutionary psychology. *In* The handbook of evolutionary psychology. Vol. 1. *Edited by* D.M. Buss. Psychology Press, London. pp. 88–114. doi:10.1002/9781119125563.evpsych102.

Dittmer, J., Lesobre, J., Moumen, B., and Bouchon, D. 2016. Host origin and tissue microhabitat shaping the microbiota of the terrestrial isopod *Armadillidium vulgare*. FEMS Microbiol. Ecol. **92**(5): fiw063. doi:10.1093/femsec/fiw063. PMID:27004796.

Donker, M.H., Zonneveld, C., and Van Straalen, N.M. 1993. Early reproduction and increased reproductive allocation in metal-adapted populations of the terrestrial isopod *Porcellio scaber*. Oecologia, **96**: 316–323. doi:10.1007/BF00317500. PMID:28313645.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. **32**: 1792–1797. doi:10.1093/nar/gkh340. PMID:15034147.

Folmer, O., Black, M., Hoeh, W., Lutz, R., and Vrijenhoek, R. 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotechnol. **3**: 294–299. PMID:7881515.

Glazier, D.S., Wolf, J.F., and Kelly, C.J. 2003. Reproductive investment of aquatic and terrestrial isopods in central Pennsylvania (U.S.A.). *In* Biology of terrestrial isopods, V (Crustaceana Monographs, 2). *Edited by* S. Sfenthourakis, P.B. Araujo, E. Hornung, H. Schmalfuss, S. Taiti, and K. Szlávecz. Brill, Leiden, the Netherlands. pp. 151–179.

Hassall, M., Tuck, J.M., Smith, D.W., Gilroy, J.J., and Addinson, R.K. 2002. Effects of spatial heterogeneity on feeding behaviour of *Porcellio scaber* (Isopoda: Oniscidea). Eur. J. Soil Biol. **28**: 53–57. doi:10.1016/S1164-5563(01)01124-4.

Hassall, M., Helden, A., and Benton, T. 2003. Phenotypic plasticity and interpopulation differences in life history traits of *Armadillidium vulgare* (Isopoda: Oniscidae). Oecologia, **137**(1): 85–89. doi:10.1007/s00442-003-1325-1. PMID: 12827489.

Hassall, M., Helden, A., Goldson, A., and Grant, A. 2005. Ecotypic differentiation and phenotypic plasticity in reproductive traits of *Armadillidium vulgare* (Isopoda: Oniscidea). Oecologia, **143**: 51–60. doi:10.1007/s00442-004-1772-3. PMID: 15599769.

Horváthová, T., Kozłowski, J., and Bauchinger, U. 2015. Growth rate and survival of terrestrial isopods is related to possibility to acquire symbionts. Eur. J. Soil Biol. **69**: 52–56. doi:10.1016/j.ejsobi.2015.05.003.

Karasawa, S. 2016. Eleven nominal species of *Burmoniscus* are junior synonyms of *B. kathmandius* (Schmalfuss, 1983) (Crustacea, Isopoda, Oniscidea). ZooKeys, **607**: 1–24. doi:10.3897/zookeys.607.8253.

Kenne, D.C., and Araujo, P.B. 2015. *Balloniscus glaber* (Crustacea, Isopoda, Balloniscidae), a habitat specialist species in a disturbed area of Brazil. Iheringia Ser. Zool. **105**: 430–438. doi:10.1590/1678-476620151054430438.

Kight, S.L. 2009. Reproductive ecology of terrestrial isopods (Crustacea: Oniscidea). Terr. Arthropod. Rev. **1**(2): 95–110. doi:10.1163/187498308X414724.

Klossa-Kilia, E., Kilias, G., Tryfonopoulos, G., Koukou, K., Sfenthourakis, S., and Parmakelis, A. 2006. Molecular phylogeny of the Greek populations of the genus *Ligidium* (Isopoda, Oniscidea) using three mtDNA gene segments. Zool. Scripta, **35**(5): 459–472. doi:10.1111/j.1463-6409.2006.00243.x.

Lancaster, L.T., Morrison, G., and Fitt, R.N. 2017. Life history trade-offs, the intensity of competition, and coexistence in novel and evolving communities under climate change. Philos. Trans. R. Soc. B Biol. Sci. **372**(1712): 20160046. doi:10.1098/rstb.2016.0046.

Lardies, M.A., and Bozinovic, F. 2008. Genetic variation for plasticity in physiological and life-history traits among populations of an invasive species, the terrestrial isopod *Porcellio laevis*. Evol. Ecol. Res. **10**(5): 747–762. Available from http://www.evolutionary-ecology.com/abstracts/v10/2330.html [accessed 3 March 2018].

Lardies, M.A., Carter, M.J., and Bozinovic, F. 2004. Dietary effects on life history traits in a terrestrial isopod: the importance of evaluating maternal effects and trade-offs. Oecologia, **138**: 387–395. doi:10.1007/s00442-003-1447-5. PMID: 14685846.

Lemos de Castro, A. 1985. Considerações sobre *Atlantoscia alceui* Ferrara & Taiti, 1981 (Isopoda, Oniscoidea, Philosciidae). Rev. Bras. Biol. **45**(4): 417–442.

Lopes, E.R.C., Mendonça, M.S., Jr., Bond-Buckup, G., and Araujo, P.B. 2005. Oniscidea diversity across three environments in an altitudinal gradient in northeastern Rio Grande do Sul, Brazil. Eur. J. Soil Biol. **41**(3–4): 99–107. doi:10.1016/j.ejsobi.2005.11.002.

Ma, H.H.T., Lam, P.K.S., and Dudgeon, D. 1991. Inter- and intraspecific variation in the life histories of three sympatric isopods in a Hong Kong forest. J. Zool. (Lond.), **224**(4): 677–687. doi:10.1111/j.1469-7998.1991.tb03795.x.

Medini-Bouaziz, L., El-Gtari, M., and Charfi-Cheikhrouha, F. 2015. Reproductive traits of *Porcellio variabilis* Lucas, 1946 (Isopoda, Oniscidea) from Tunisia. Open Life Sci. **10**(1): 505–513. doi:10.1515/biol-2015-0052.

Medini-Bouaziz, L., El Gtari, M., Hamaied, S., and Charfi-Cheikhrouha, F. 2017. Population dynamics and reproductive aspects of *Porcellio albinus* (Isopoda, Oniscidea) of Zarat (Gabes, Tunisia). Int. J. Invertebr. Reprod. Dev. **61**(1): 18–26. doi:10.1080/07924259.2016.1263242.

Moll, J.D., and Brown, J.S. 2008. Competition and coexistence with multiple life-history stages. Am. Nat. **171**(6): 839–843. doi:10.1086/587517. PMID: 18462131.

Moret, Y., Juchault, P., and Rigaud, T. 2001. *Wolbachia* endosymbiont responsible for cytoplasmic incompatibility in a terrestrial crustacean: effects in natural and foreign hosts. Heredity, **86**(3): 325. doi:10.1046/j.1365-2540.2001.00831.x. PMID:11488969.

O'Neill, S.L., Giordano, R., Colbert, A.M.E., Karr, T.L., and Robertson, H.M. 1992. 16S rDNA phylogenetic analysis of the bacterial endosymbionts associated with cytoplasmic incompatibility in insects. Proc. Natl. Acad. Sci. U.S.A. **94**: 2699–2702. doi:10.1073/pnas.89.7.2699. PMID:9122259.

Peel, M.C., Finlayson, B.L., and McMahon, T.A. 2007. Updated world map of the Köppen–Geiger climate classification. Hydrol. Earth Sys. Sci. **11**: 1633–1644. doi:10.5194/hess-11-1633-2007.

Quadros, A.F., and Araujo, P.B. 2007. Ecological traits of two neotropical oniscideans (Crustacea: Isopoda). Acta Zool. Sin. **53**: 241–249.

Quadros, A.F., and Araujo, P.B. 2008. An assemblage of terrestrial isopods (Crustacea) in southern Brazil and its contribution to leaf litter processing. Rev. Bras. Zool. **25**(1): 58–66. doi:10.1590/S0101-81752008000100009.

Quadros, A.F., Araujo, P.B., and Sokolowicz, C.C. 2008. Reproduction of neotropical isopods (Crustacea: Oniscidea) in southern Brazil: similarities and differences relative to temperate and tropical species. *In* Proceedings of the International Symposium of Terrestrial Isopod Biology, ISTIB-07. *Edited by* M. Zimmer, F. Charfi-Cheikhrouha, and S. Taiti. Shaker Verlag GmbH, Aachen, Germany. pp. 81–90.

Quadros, A.F., Caubet, Y., and Araujo, P.B.A. 2009. Life history comparison of two terrestrial isopods in relation to habitat specialization. Acta Oecol. **35**: 243–249. doi:10.1016/j.actao.2008.10.007.

Quadros, A.F., Zimmer, M., Araujo, P.B., and Kray, J.G. 2014. Litter traits and palatability to detritivores: a case study across bio-geographical boundaries. Nauplius, **22**(2): 103–111. doi:10.1590/S0104-64972014000200004.

R Development Core Team. 2011. R: a language and environment for statistical computing. Version 3.2.4 [computer program]. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Richardson, A., and Araujo, P.B. 2015. Lifestyles of terrestrial crustaceans. *In* The natural history of the Crustacea. Lifestyles and feeding biology. *Edited by* M. Thiel and L. Watling. Oxford University Press, Oxford. pp. 299–336.

Rigaud, T., and Moreau, J. 2004. A cost of *Wolbachia*-induced sex reversal and female-biased sex ratios: decrease in female fertility after sperm depletion in a terrestrial isopod. Proc. R. Soc. B Biol. Sci. **271**: 1941–1946. doi:10.1098/rspb.2004.2804.

Rigaud, T., Moreau, J., and Juchault, P. 1999. *Wolbachia* infection in the terrestrial isopod *Oniscus asellus*: sex ratio distortion and effect on fecundity. Heredity, **83**: 469–475. doi:10.1038/sj.hdy.6885990. PMID:10583549.

Rigaud, T., Pennings, P., and Juchault, P. 2001. *Wolbachia* bacteria effects after experimental interspecific transfers in terrestrial isopods. J. Invertebr. Pathol. **77**: 251–257. doi:10.1006/jipa.2001.5026. PMID:11437528.

Rivera, M.A.J., Howarth, F.G., Taiti, S., and Roderick, G.K. 2002. Evolution in Hawaiian cave-adapted isopods (Oniscidea: Philosciidae): vicariant speciation or adaptive shifts? Mol. Phylogenet. Evol. **25**: 1–9. doi:10.1016/S1055-7903(02)00353-6. PMID:12383746.

Rozas, J., Sánchez-DelBarrio, J.C., Messeguer, X., and Rozas, R. 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics, **19**: 2496–2497. doi:10.1093/bioinformatics/btg359. PMID:14668244.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol. Evol. **1**: 103–113. doi:10.1111/j.2041-210X.2010.00012.x.

Sfenthourakis, S., and Taiti, S. 2015. Patterns of taxonomic diversity among terrestrial isopods. ZooKeys, **515**: 13–25. doi:10.3897/zookeys.515.9332.

Sicard, M., Chevalier, F., De Vlechouver, M., Bouchon, D., Grève, P., and Braquart-Varnier, C. 2010. Variations of immune parameters in terrestrial isopods: a matter of gender, aging and *Wolbachia*. Naturwissenschaften, **97**: 819–826. doi:10.1007/s00114-010-0699-2. PMID:20676599.

Sicard, M., Bouchon, D., Ceyrac, L., Raimond, R., Thierry, M., Le Clec'h, W., Marcadé, I., Caubet, Y., and Grève, P. 2014. Bidirectional cytoplasmic incompatibility caused by *Wolbachia* in the terrestrial isopod *Porcellio dilatatus*. J. Invertebr. Pathol. **121**: 28–36. doi:10.1016/j.jip.2014.06.007. PMID:24984056.

Siozios, S., Gerth, M., Griffin, J.S., and Hurst, G.D. 2018. Symbiosis: *Wolbachia* host shifts in the fast lane. Curr. Biol. **28**: R269–R271. doi:10.1016/j.cub.2018.02.008. PMID:29558644.

Sokolowicz, C.C., and Araujo, P.B. 2013. Reproductive pattern of the neotropical terrestrial isopod *Benthana cairensis* (Isopoda: Philosciidae). J. Crustac. Biol. **33**: 210–217. doi:10.1163/1937240X-00002126.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., and Kumar, S. 2013. MEGA6: molecular evolutionary genetics analysis. Version 6.0. Mol. Biol. Evol. **30**: 2725–2729. doi:10.1093/molbev/mst197. PMID:24132122.

Tanaka, R., and Karasawa, S. 2018. Life histories and soil water content preferences of sympatric exotic and native terrestrial isopods. Entomol. Sci. **21**(1): 1–12. doi:10.1111/ens.12301.

Warburg, M.R. 2011. Cost of breeding in oniscid isopods: a partial review. Crustaceana, **84**(12–13): 1561–1580. doi:10.1163/156854011X607006.

Warburg, M.R. 2012. The oniscid isopod female reproductive system and gestation, with a partial review. Invertebr. Reprod. Dev. **56**(2): 87–110. doi:10.1080/07924259.2011.573812.

Warburg, M.R. 2013. Post-parturial reproduction in terrestrial isopods: a partial review. Invertebr. Reprod. Dev. **57**(1): 10–26. doi:10.1080/07924259.2011.633620.

Werren, J.H., Baldo, L., and Clark, M.E. 2008. *Wolbachia*: master manipulators of invertebrate biology. Nat. Rev. Microbiol. **6**: 741–751. doi:10.1038/nrmicro1969. PMID: 18794912.

Zimmermann, B.L., Almerão, M.P., Bouchon, D., and Araujo, P.B. 2012. Detection of *Wolbachia* (Alphaproteobacteria: Rickettsiales) in three species of terrestrial isopods (Crustacea: Isopoda: Oniscidea) in Brazil. Braz. J. Microbiol. **43**: 711–715. doi:10.1590/S1517-83822012000200036. PMID:24031883.

Zimmermann, B.L., Bouchon, D., Almerão, M.P., and Araujo, P.B. 2015*a*. *Wolbachia* in Neotropical terrestrial isopods. FEMS Microbiol. Ecol. **91**: fiv025. doi:10.1093/femsec/fiv025. PMID:25764472.

Zimmermann, B.L., Campos-Filho, I.S., Deprá, M., and Araujo, P.B. 2015*b*. Taxonomy and molecular phylogeny of the Neotropical genus *Atlantoscia* (Oniscidea, Philosciidae): DNA barcoding and description of two new species. Zool. J. Linn. Soc. **174**: 702–717. doi:10.1111/zoj.12256.

Zimmermann, B.L., Campos-Filho, I.S., Cardoso, G.M., Santos, S., Aguiar, J.O., and Araujo, P.B. 2018. Two new species of *Atlantoscia* Ferrara Taiti, 1981 (Isopoda: Oniscidea: Philosciidae) from southern Brazil described in the light of integrative taxonomy. Zootaxa, **4482**(3): 551–565. doi:10.11646/zootaxa.4482.3.7. PMID:30313814.

Zug, R., and Hammerstein, P. 2015. Bad guys turned nice? A critical assessment of *Wolbachia* mutualisms in arthropod hosts. Biol. Rev. Camb. Philos. Soc. **90**: 89–111. doi:10.1111/brv.12098. PMID:24618033.