Reproduction of Neotropical isopods (Crustacea: Oniscidea) in southern Brazil: similarities and differences relative to temperate and tropical species

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Reproduction of Neotropical isopods (Crustacea: Oniscidea) in southern Brazil: similarities and differences relative to temperate and tropical species

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Abstract

Information on reproductive features, such as breeding period, fecundity, size and weight of reproductive females, and life span of temperate and tropical terrestrial isopods species are well known. As the knowledge on reproductive aspects of the Neotropical fauna is still incipient, the aim of this work is to present the available information and to provide a comparison with temperate and tropical species. The three philosciid populations studied exhibit a continuous reproduction period throughout the year, except for *Balloniscus glaber* with a breeding period that is limited to spring and summer. The reproductive peaks and fecundity are different among species and within the same species in different locations. The studied species do not achieve large body sizes, and therefore they show low fecundity; the reproductive allocation is low maybe due to a high degree of iteroparity. Our results demonstrate that Neotropical show similar reproduction features as tropical species, and differ from temperate species in terms of lower reproductive allocation, longer breeding period, and shorter time to maturity. These results constitute the basis for the determination of the first pattern on reproduction of terrestrial isopods in the Neotropics.

Keywords – breeding, Crinocheta, fecundity, Neotropics

Introduction

Reproduction is by far the best-studied aspect of terrestrial isopod biology (Warburg, 1987). Despite their worldwide distribution, most information regards species in the temperate and Mediterranean regions of the northern hemisphere (Warburg, 1987; Warburg, 1994), more specifically Europe and northern Africa. In terms of the reproduction of these isopod populations in nature, breeding period and abundance, fecundity, and size and weight of reproductive females are commonly studied and are known for a large number of species (Warburg, 1987). The study of different populations in distinct geographical locations, such as for the widespread species *Armadillidium vulgare* (Latreille 1804), allows for intraspecific comparisons (Souty-Grosset *et al.*, 1994). Most species in the northern hemisphere exhibit well-defined periods of reproduction with different durations, but usually occurring in spring and summer (Sutton *et al.*, 1984; Zimmer, 2003); during the winter, reproduction ceases. In more extreme cases, reproduction may be restricted to summer, as in the case of *Philoscia muscorum* (Scopoli 1763) in England (Sutton, 1968) and *Armadillidium opacum* (C. Koch 1841) in south-western Germany (Zimmer & Brauckmann, 1997). Most isopod species are iteroparous; only two species of the Mediterranean region are unambiguously identified as truly semelparous, namely *Schizidium tiberianum* Verhoeff 1923 and *Hemilepistus reaumurii* (Milne-Edwards 1840) (Warburg, 1994). Most species experience a period of growth (summer and autumn) and start to reproduce at the age of about one year in the subsequent spring (Warburg, 1992a,b; Farkas, 1998; Dias *et al.*, 2005). Less often, species mature at the age of two years, such as *Armadillo albomarginatus* Dollfus 1892 and *Eluma caelatum* (Miers 1877) (cited in Warburg, 1987), or even of three years, such as *Armadillo officinalis* Duméril 1816 (Warburg, 1994). Isopod lifespan ranges from one to five years (Warburg & Cohen, 1992), most commonly longevity is 2-3 years (Sutton *et al.*, 1984; Warburg & Cohen, 1992, Araujo & Bond-Buckup, 2005; Meinhardt *et al.*, 2007). The positive correlation between the size/mass of ovigerous females and their fecundity is a well-recognized reproductive pattern, and has been reported for several species. Fecundity ranges from as little as two eggs in minute species of the genus *Platyarthrus* to more than 100 in large females of the genera *Armadillidium* and *Porcellio* (reviewed in Warburg, 1987).

Knowledge on the reproduction of terrestrial isopods in the tropical region is still incipient; however, it seems to differ from the temperate regions in several aspects. As summarised by Ma *et al.* (1991a) and Dangerfield & Telford (1995), tropical isopods exhibit longer breeding periods, higher number of broods per lifetime, and lower reproductive allocation per brood as compared to temperate isopods. Also, due to breeding overlapping, the populations are usually not structured in well-defined cohorts (Vink & Sri Purwanti, 1994).

As pointed out by Warburg (1994), it is almost impossible to make generalisations on breeding patterns in isopods, owing to wide variations in latitude, season and size. Warburg (1994) also stresses the need in producing more accurate data on local, non-cosmopolitan species. As temperature and precipitation regime are important microclimatic factors that regulate isopod reproduction, a comparison of species that live in different climates may reveal interesting reproductive patterns.

The southern region of Brazil presents a combination of temperature and precipitation regimes that are different from both cold-temperate and tropical climates, and may therefore impose different pressures on isopod reproduction. The climate in this region is temperate with hot summers and absence of a dry season (former "humid subtropical" climate; type Cfa, according to Peel *et al.,* 2007). Terrestrial isopods inhabiting this region face winter temperatures that are not as severe as those in the cold-temperate regions of northern hemisphere, but that are much lower than in the tropical regions. Precipitation in southern Brazil is equally distributed among the four seasons, and thus differs from the wet-dry dichotomy of the tropical climate.

Considering these peculiarities, the objective of the present study was to compare the reproduction of terrestrial isopods of southern Brazil with that of species of temperate and tropical regions. Specifically, the duration of the breeding period, percent of breeding females in the populations, and reproductive allocations were compared. In order to compare the relationship between size

Table 1. Populations of the studied Neotropical isopods.

Species	Locality			Date sampled
	Name, City, State[a)]	**Coordinates**	**Environment**	
Atlantoscia floridana (Philosciidae)	Reserva Biológica do Lami, Porto Alegre, RS	30°15'S 51°05' W	Restinga Forest	April 2000 - October 2001
Atlantoscia floridana (Philosciidae)	Parque Estadual de Itapuã, Viamão, RS	30°34'S 51°05' W	Semideciduous forest	May 2004 - Apr 2005
Benthana cairensis (Philosciidae)	Taquara, RS	29°46'S 50°50'W	Secondary planted forest	March 2006 - August 2007
Balloniscus glaber (Balloniscidae)	Parque Estadual de Itapuã, Viamão, RS	30°34'S 51°05'W	Semideciduous forest	May 2004 - Apr 2005
Balloniscus glaber (Balloniscidae)	Águas Belas, Viamão, RS	30°05'S 50°47'W	Semideciduous forest	January 2006
Balloniscus sellowii (Balloniscidae)	Porto Alegre, RS	30°01'S 51°13'W	Urban environment	October 2007
Balloniscus sellowii (Balloniscidae)	São Lourenço do Oeste, SC (UFRGS 1779)[b)]	26°21'S 52°51'W	Urban environment	January 1991
Balloniscus sellowii (Balloniscidae)	Catanduvas, SC (UFRGS 1774)	27°04'S 51°39'W	Urban environment	January 1991

[a)] SC = Santa Catarina state; RS = Rio Grande do Sul state.

[b)] Populations of *Balloniscus sellowii* from São Lourenço d´Oeste and Catanduvas (SC) belong to the carcinological collection of Departamento de Zoologia (UFRGS).

Table 2. Mean weight and fecundity of breeding females of Crinocheta species as collected from literature.

Species (Location)	Mean weight (mg)[a)]	Mean fecundity	Source
"Philosciidae"			
Aphiloscia maculicornis (Victoria Falls)	16.5 lw	8.0	Dangerfield & Telford (1995)
Aphiloscia vilis (Gaborone)	20.6 lw	12.0	Dangerfield & Telford (1995)
Aphiloscia vilis (Marondera)	19.1 lw	10.0	Dangerfield & Telford (1995)
Burmoniscus ocellatus	4.64 dw	9.0	Ma *et al.* (1991b)
Philoscia muscorum (Spurn Head)	3.30 dw	14.8	Sutton *et al.* (1984)
Armadillidiidae			
Armadillidium album (Ria Formosa)	2.5 afdm	7.5	Dias *et al.* (2005)
Armadillidium nasatum (McConnellstown)	13.90 dw	54.0	Glazier *et al.* (2003)
Armadillidium nasatum (Pot Shop)	12.30 dw	49.8	Glazier *et al.* (2003)
Armadillidium vulgare (Pot Shop)	29.09 dw	107.2	Glazier *et al.* (2003)
Armadillidium vulgare (Raystown)	29.96 dw	105.6	Glazier *et al.* (2003)
Armadillidium vulgare (Spurn Head)	12.30 dw	42.0	Sutton *et al.* (1984)
Armadillidae			
Bethalus pretoriensis (Gaborone)	13.4 lw	9.0	Dangerfield & Telford (1995)
Dryadillo maculatus (Hong Kong)	7.30 dw	17.9	Ma *et al.* (1991b)
Spherillo raffaelei (Hong Kong)	14.75 dw	18.2	Ma *et al.* (1991b)
Halophilosciidae			
Halophiloscia couchii (Ria Formosa)	3.0 afdm	14.3	Dias *et al.* (2005)
Plathyarthridae			
Platyarthrus hoffmannseggi (Wytham)	0.56 dw	4.5	Sutton *et al.* (1984)
Porcellionidae			
Porcellio lamellatus (Ria Formosa)	9.6 afdm	14.2	Dias *et al.* (2005)
Porcellio scaber (McConnellstown)	7.74 dw	21.9	Glazier *et al.* (2003)
Porcellio scaber (Spurn Head)	6.10 dw	17.0	Sutton *et al.* (1984)
Porcellionides pruinosus (Gaborone)	19.5 lw	14.0	Dangerfield & Telford (1995)
Porcellionides pruinosus (Harare)	16.7 lw	16.0	Dangerfield & Telford (1995)
Trachelipodidae			
Trachelipus rathkii (McConnellstown)	12.83 dw	41.9	Glazier *et al.* (2003)
Trachelipus rathkii (Raystown)	11.84 dw	28.5	Glazier *et al.* (2003)

[a)] lw: live weight, dw: dry weight, afdm: ash-free dry mass

and fecundity among species, we used the approach of Kaplan & Salthe (1979) for allometrically scaling reproduction components. Although we are aware of information on the reproduction of Tylida, Diplocheta, and Synocheta species (Standen, 1973; Warburg, 1987; Dias *et al.,* 2005), we restricted our comparison to Crinocheta, because this section includes the most frequently studied isopods (Warburg, 1987). Information on the ecology of terrestrial isopods of southern of Brazil is scarce in spite of the considerable body of knowledge on the isopod fauna (Araujo & Zardo, 1995; Araujo *et al.,* 1996; Araujo & Quadros, 2005; Lopes *et al.*, 2005; Almerão *et al.,* 2006; Araujo & Almerão, 2007). The only studies concerning the ecology of native Neotropical species are those by Araujo & Bond-Buckup (2005) on *Atlantoscia floridana* (van Name 1940) (Philosciidae), by Quadros & Araujo (2007) on *A. floridana* and *Balloniscus glaber* Araujo & Zardo 1995 (Balloniscidae) and by Quadros & Araujo (2008) considering six species of woodlice.

Material and methods

A list of the species studied and sampling data is presented in Tab. 1. Due to differences in sampling effort and methods, not all populations were included in all analyses.

The populations of *A. floridana* from Lami and Itapuã, *B. glaber* from Itapuã, and *Benthana cairensis* Sokolowicz, Araujo & Boelter 2008 (Philosciidae) from Taquara were sampled according to standard procedure (Araujo & Bond-Buckup, 2005) with the aid of a circular bottomless frame with a 30-cm diameter. Standard sampling allows comparison of these data, despite the different durations: samplings were carried out monthly for one year in Itapuã, and for 18 months in Taquara and in Lami. Based on these samplings, the length of the breeding period and percent of breeding females were determined. Isopods were classified as males, ovigerous, non-ovigerous or post-ovigerous females, or undifferentiated juveniles or mancae in the laboratory. Both ovigerous and post-ovigerous females were considered breeding females. The proportion of breeding females was calculated relative to a) the total number of females, and b) the total number of individuals in the population in the month with highest reproductive peak. Ovigerous females were measured (cephalothorax width) and dissected for fecundity determination (number of eggs or mancae inside the marsupium).

Balloniscus glaber population from Águas Belas and all *Balloniscus sellowii* (Brandt, 1833) populations were obtained by manually searching the leaf litter in single-occasion samplings. The fecundity and size of ovigerous females were determined in these populations. Mean fecundity and size were compared considering 95% confidence intervals.

The reproductive allocation of *A. floridana* and *B. glaber* in Itapuã was obtained by capturing ovigerous females in late stage of marsupial development in the field. In the laboratory, females were individualised in Petri dishes and observed until hatching. After hatching, mancae and their mothers were dried and weighed. Reproductive allocation (RA) was then calculated as: RA = ((mean weight of mancae upon release x number of mancae in the brood)/female weight) (Sutton *et al.*, 1984; Ma *et al.*, 1991a), and compared using one-way ANOVA.

In order to compare traits influenced by size, such as fecundity, effects due to allometry alone must be removed. One method is to determine the existing relationship within a group by fitting mean values of the traits of the species to a regression analysis (Kaplan & Salthe, 1979). This relationship is then used as a null hypothesis and to make predictions on other sample populations. Statistically significant deviation of the sample means may suggest interesting ecological specializations (Kaplan & Salthe, 1979). Therefore, we attempted to compare the relationship between weight and fecundity of *A. floridana* and *B. glaber* with a general relationship within Crinocheta. This general regression was obtained by collecting mean female weight and fecundity data of several species from literature. Although these data are heterogeneous as to number of observations and precision of measurements and counts, a statistically significant strong positive correlation indicates there is a true relationship (Kaplan & Salthe, 1979). The original values used for building the regression analysis are shown in Tab. 2. When only female live weight was mentioned, the equivalent dry-weight was estimated by multiplying live weight per 0.3, based on observations that an isopod looses approximately 70% of its live weight after drying (Standen, 1973; pers. obs.). After these corrections, all values were log transformed and fitted to a regression analysis. The slopes and intercepts obtained for *A. floridana* and *B. glaber* were then compared to the general regression using

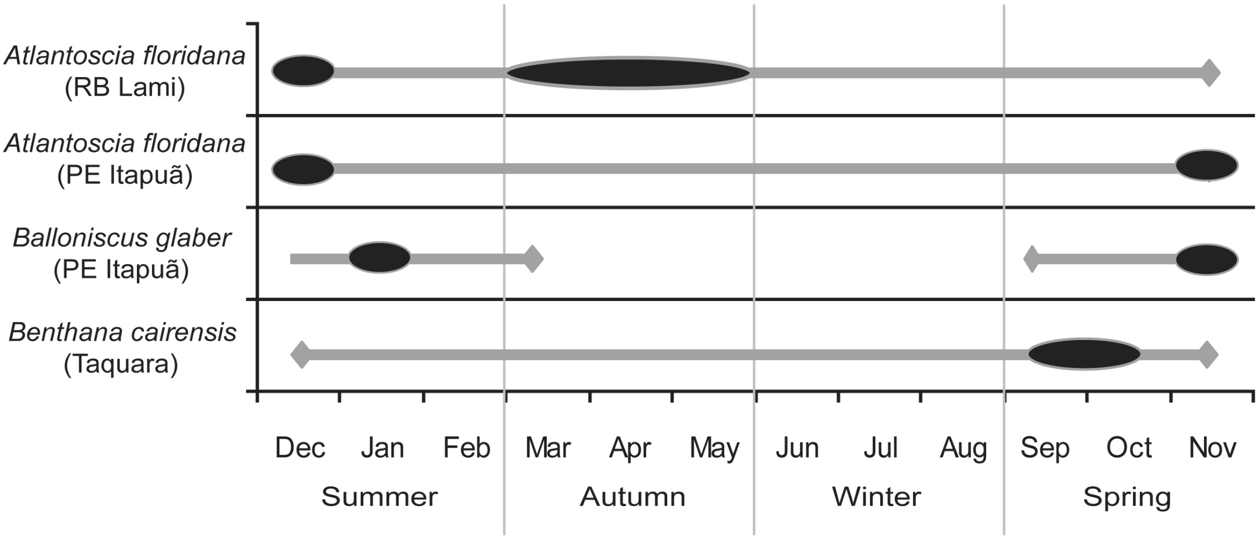

Figure 1. Breeding period of *Atlantoscia floridana*, *Balloniscus glaber* and *Benthana cairensis* in different locations in southern Brazil. The grey line indicates the presence of ovigerous females. The dark marks indicate the month(s) with the highest abundance of ovigerous female.

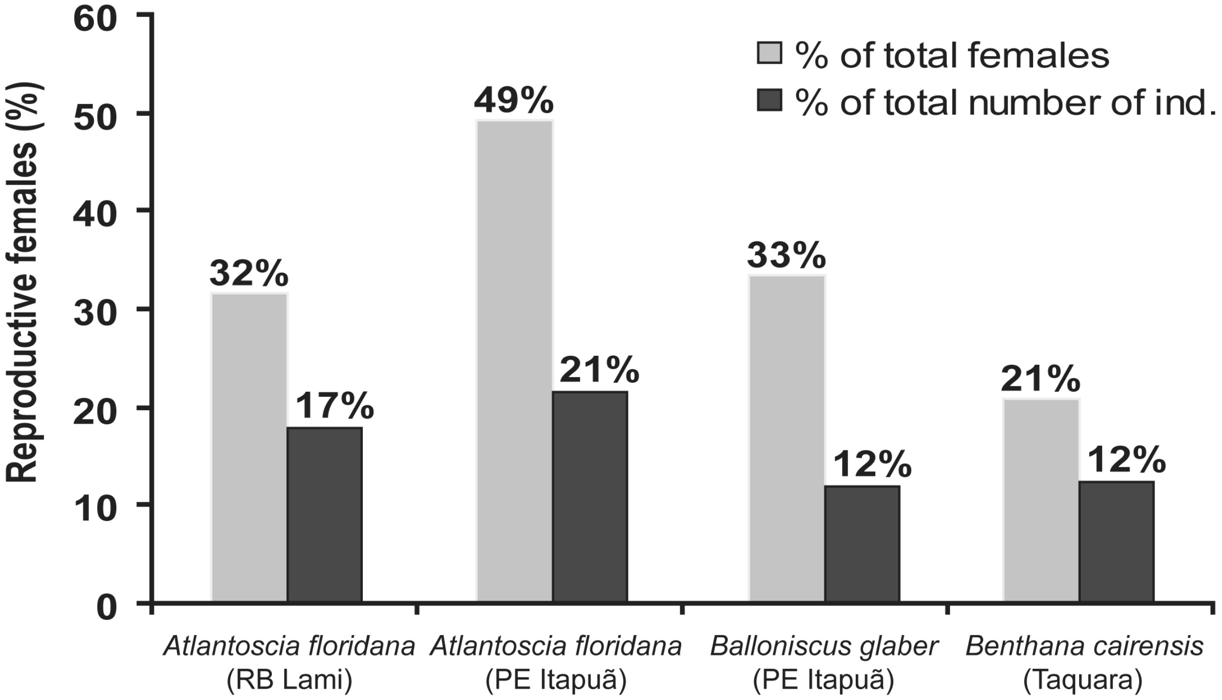

Figure 2. Proportion of breeding females relative to total number of females (grey) and total number of individuals (black) in the month with the highest abundance of ovigerous females (see Fig. 1).

ANCOVA. All these procedures were performed using Bioestat 4.0 software (Ayres *et al.*, 2006).

We also compared the relationship between size and fecundity among the Neotropical species by fitting the mean values obtained in each population to a regression analysis. *Balloniscus sellowii* was significantly different from the other species, and therefore was analysed separately. After the significance of each regression equation was analysed, they were compared using ANCOVA. All values were log-transformed prior to these procedures (Kaplan & Salthe, 1979).

Results

Reproduction was continuous throughout the year in the three philosciid species, whereas *B. glaber* showed a well-defined breeding period during the austral spring and summer (Fig. 1). Reproductive peaks were different between and within populations in time (Fig. 1) and intensity (Fig. 2). In Itapuã, both *A. floridana* and *B. glaber* showed a peak in the summer (Dec-Jan) and in the spring (Nov) (Fig. 1). In Lami, however, *A. floridana* population showed a long peak of reproduction over the entire autumn (Fig. 1). *Benthana cairensis* was different from the others as its highest peaks occurred in the beginning of spring (Fig. 1). During their highest reproductive peak, ovigerous females accounted for 49 % of the females of *A. floridana* in Itapuã (Fig. 2). In Lami, the proportion of ovigerous females was 32 % (Fig. 2). *Benthana cairensis* showed the least intense peak of reproduction, with ovigerous females accounting for only 21 % of the females (Fig. 2).

Reproductive allocation ranged from 9 % to 29 % for *A. floridana* (n = 50), and from 6 % to 42 % for *B. glaber* (n = 24). ANOVA results indicate the mean reproductive allocation of *A. floridana* (16 %) was significantly lower than *B. glaber*'s (20 %) (ANOVA $F_{1,72} = 6.955$; p = 0.01).

Mean size and fecundity of the ovigerous females were different among both populations of the same species and different species (Fig. 3). The population of *B. glaber* in Águas Belas was significantly larger and more fecund than the Itapuã population (Fig 3). *Atlantoscia floridana* in Lami and Itapuã presented differences in size, but not in fecundity (Fig. 3). Interestingly, ovigerous females of *B. sellowii* were intermediate in size between *B. cairensis* and *B. glaber* (Itapuã population), but showed much higher fecundity (Fig. 3). As indicated by ANCOVA (Tab. 3), these results are indeed different from the expected relationship between size and fecundity in Neotropical isopods (Fig. 4).

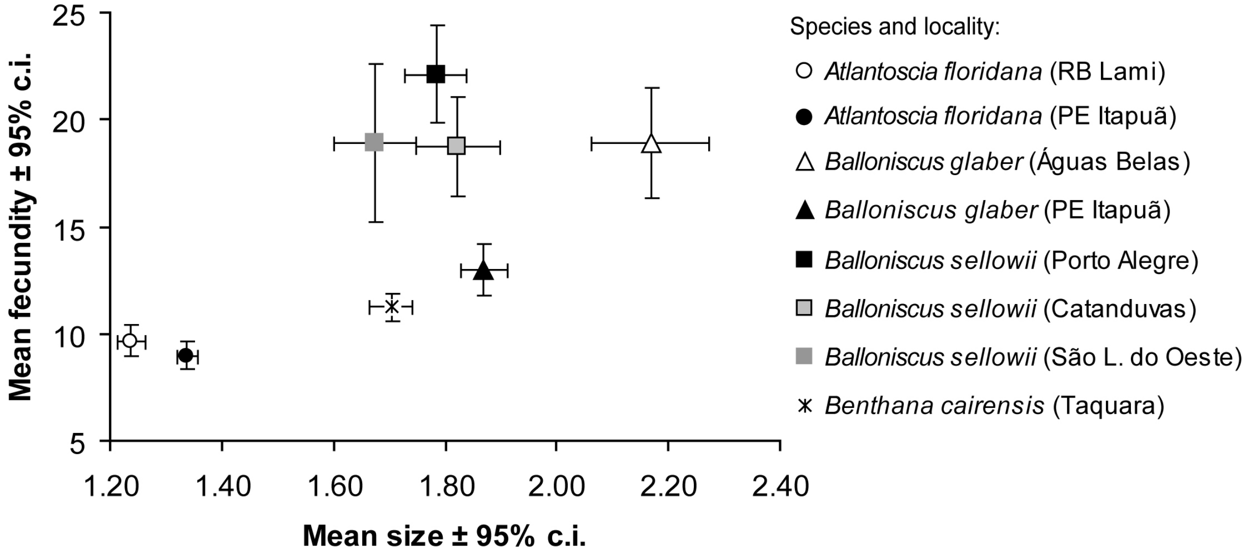

Figure 3. Mean size (mm cephalothorax width) and fecundity (number of marsupial eggs) of eight different populations of four Neotropical isopod species.

Before these data were pooled, no differences among the fitted regression equations of each population were detected (Porto Alegre, São Lourenço do Oeste and Catanduvas) (ANCOVA; slope: $F_{2,42} = 0.6692$; $p = 0.5222$; intercept: $F_{2,44} = 2.8575$; $p = 0.0670$).

The fitted regression of mean weight and fecundity data of Crinocheta species collected from literature showed a strong relationship between these traits (R^2 = 76 %) (Fig. 5). While significant, *A. floridana* and *B. glaber* regression coefficients were lower as compared to literature data (Tab. 4). ANCOVA indicated that *B. glaber* fecundity was significantly lower than that expected for a Crinocheta species, while *A. floridana* fitted well the expected relationship for this group (Tab. 4).

Discussion

Intraspecific differences were observed among the studied populations, despite the small geographic distance between them. It seems that some traits, such as reproductive peak, proportion of breeding females, and size and fecundity, are more likely a response to small-scale environmental variables rather than a species-specific trait. *Balloniscus sellowii* was different from the other species in terms of presenting much higher fecundity than expected considering mean female size and ANCOVA results. Although we do not have further information on its ecology, we do know that this species is widespread in southern Brazil, and colonises many different environments, both in rural and urban areas. Moreover, it is able to colonise plantations of exotic tree species, such as *Eucalyptus* spp. (Araujo *et al.*, 1996). Based on this preliminary information, we suggest that *B. sellowii* is a generalist isopod, and its elevated fecundity is perhaps a life-history trait, providing good colonisation ability. On the other hand, *B. glaber* shows opposite

Table 3. Results of regression analysis and ANCOVA within and between *Balloniscus sellowii* and Neotropical isopods.

Group	Regression equations of fecundity against female size	R^2	ANOVA	n
Balloniscus sellowii	y= 2.1167x + 0.7751	43%	$F_{1,44}$ = 33.4923; p<0.0001	46
Neotropical isopods	y= 1.1709x + 0.828	86%	$F_{1,3=}$ 18.0175; p=0.02	5

Comparison of slopes and intercepts (ANCOVA)		
	Slope	**Intercept**
B. sellowii vs. Neotropical isopods	$F_{1,47=}$ 2.8433; p= 0.0949	$F_{1,48=}$ 13.972; **p< 0.001**

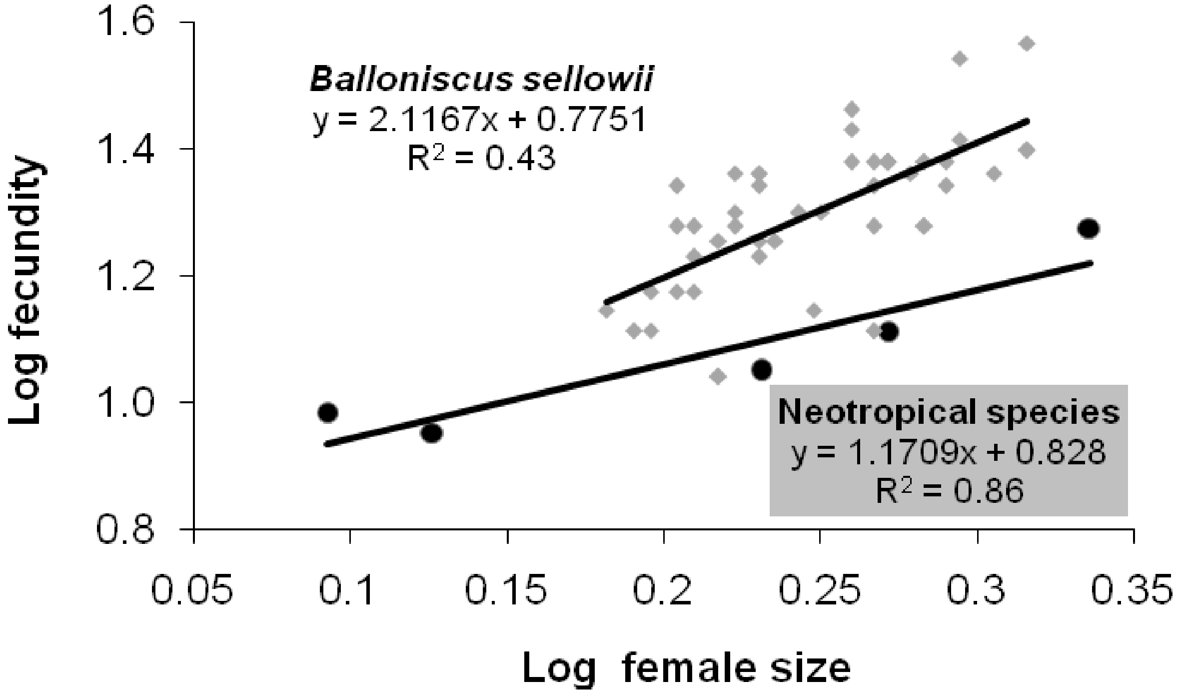

Figure 4. Relationship between female mean size (cephalotorax width) and mean fecundity. Black circles indicate the overall relationship of 5 populations of Neotropical terrestrial isopods (3 species) using one mean value per species. Grey marks indicate the relationship for *Balloniscus sellowii* (three populations pooled; n = 46). Refer to Table 3 for regression and ANCOVA results.

characteristics: much lower fecundity in relation to size and a very restricted distribution and habitat use (pers. comm.). The Neotropical philosciids *A. floridana* and *B. cairensis* share continuous breeding throughout the year and similar fecundity ranges. Although the Philosciidae are considered paraphyletic, the genera *Atlantoscia* and *Benthana* are sister groups (Leistikow, 2001) and their mode of reproduction may be connected to their phylogenetic proximity.

The reproductive patterns of the studied Neotropical species present higher similarity to those of tropical species than to those temperate species. While terrestrial isopods in temperate regions usually reproduce by means of seasonal iteroparity associated with a short summer and rigorous winter (Sutton *et al.*, 1984), reproduction in tropical regions takes place almost continuously and it is mainly constrained by the dry season (Vink & Sri Purwanti, 1994; Vink & Kurniawati, 1996). Ma *et al.* (1991a; 1991b) observed breeding periods ranging from 7 to 10 months with interruption during winter (dry season) in three species inhabiting a tropical forest of Hong Kong. Vink & Sri Purwanti (1994) studied two sympatric species of the genus *Burmoniscus* in Central Java (Indonesia), and verified that reproduction occurs mainly during the wet season (Oct-Mar), with a duration of 6 and 10 months. In southern Brazil, the absence of weather extremes (severe winter/dry season)

Table 4. Results of regression analysis and ANCOVA within and between *Atlantoscia floridana*, *Balloniscus glaber* and Crinocheta species.

Group	Regression equations of fecundity against female weight	R^2	ANOVA	n
Atlantoscia floridana	y= 0.8568x + 0.5506	31%	$F_{1,48}$=21.3815; p=0.0001	50
Balloniscus glaber	y= 0.834x + 0.260	39%	$F_{1,20}$=12.5759; p=0.002	22
Crinocheta isopods	y= 0.8457x + 0.5752	76%	$F_{1,21}$= 65.7032; p<0.0001	23

Comparison of slopes and intercepts (ANCOVA)

	Slope	Intercept
A. floridana vs. Crinocheta isopods	$F_{1,69}$= 0.002; p=0.9602	$F_{1,70}$= 0.1569; p=0.6956
B. glaber vs. Crinocheta isopods	$F_{1,39}$= 1.6647; p=0.2051	$F_{1,40}$= 50.9787; **p<0.0001**

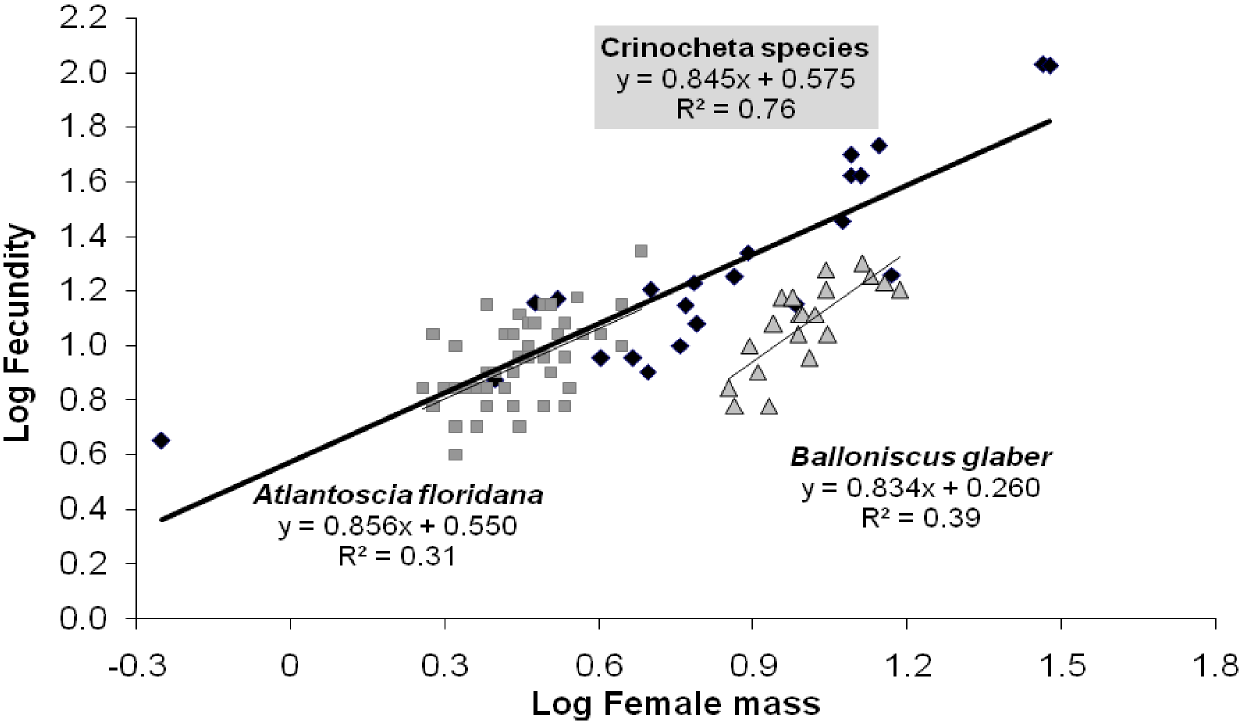

Figure 5. Relationship between female mean weight and mean fecundity across 23 populations of Crinocheta (16 species) (black) and of *Atlantoscia floridana* (n = 50; grey squares) and *Balloniscus glaber* (n = 22; grey triangles), both from Itapuã. Refer to Table 4 for regression and ANCOVA results.

seems to offer the conditions required for continuous reproduction throughout the year. In the present study, *A. floridana* and *B. cairensis* showed a continuous reproduction, although the number of *A. floridana* reproductive females during winter was reduced, both in Lami (Araujo & Bond-Buckup, 2005) and in Itapuã (Quadros & Araujo, 2007). The breeding period seems, then, to be continuous rather than seasonal, except for *B. glaber* that shows the temperate mode of reproduction restricted to spring and summer.

The proportion of breeding females verified in the month of highest ovigerous abundance in the present study was much lower than that recorded in temperate species. For instance, breeding females accounted for 71 % of the total in *Trachelipus nodulosus* (C. Koch, 1838) (Hornung, 1989) and approx. 75 % of *P. muscorum* (Zimmer, 2003) during their highest breeding peak. The lower proportion of breeding females observed each month may be a result of the constant recruitment in these populations.

Reproductive allocation is predicted to be lower in tropical than in temperate species, due to a higher degree of iteroparity, which in turn is favoured by higher juvenile mortality and higher risk of total brood failure (Ma *et al.*, 1991b; Dangerfield & Telford, 1995). The reproductive allocation of *A. floridana* and *B. glaber* was in the range recorded for tropical species: 13-18 % (Ma *et al.*, 1991a) and 16-27 % (Dangerfield & Telford, 1995). However, it must be taken into account that this range is much more variable in temperate species (27-47 % in Sutton *et al.*, 1984; 7-53 % in Warburg, 1994), probably due to the high number of species and reproductive strategies studied.

The studied Neotropical species also presented higher similarity to tropical species in terms of time needed to mature as compared to temperate species. Age at maturity of *A. floridana* was 4 months in Lami (Araujo *et al.*, 2004) and 4.4 months in Itapuã, whereas *B. glaber* matured at 7.5 months of age (pers. comm.). Similarly, the tropical philosciid isopod *Burmoniscus ocellatus* (Verhoeff, 1928) takes four months to reach maturity (Ma *et al.*, 1991a). These time intervals are significantly shorter than those observed for temperate species, which usually begin to reproduce only at one year of age (Sutton *et al.,* 1984).

In studies on reproductive strategies, two frequently assessed components are number and size of produced offspring, and it is well known that these vary according to female size interspecifically as well as within and among populations (Kaplan & Salthe, 1979). This is clearly the case in terrestrial isopods with their fecundity constrained by female size. The general regression equation obtained for Crinocheta was interesting, as it revealed a strong determination coefficient, despite the noise that could have been generated by data collected from literature and the corresponding differences in sampling methods and times, geographic regions, and habitats of the studied species. This finding indicates that the relationship between fecundity and body size is a consistent trait among Crinocheta. In the future, the use of other dependent variables in relation to body size may help to identify other life-history traits that deviate from a common pattern. In the present study, for instance, *B. glaber* showed lower fecundity than expected for Crinocheta considering its average size. However, we do not know yet under which selective pressure this difference has evolved, or what are, if any, the trade-offs involved. A known trade-off is between size and number of offspring, i.e., the partitioning of the energy available for reproduction among reproductive events (Stearns, 1992).

Finally, based on the species studied so far, we conclude that reproduction in Neotropical species is usually continuous, with peaks during spring and summer. Females begin to reproduce within less than one year after hatching, and a very low percent of the population is thought to reach two years of age. These species do not reach very large body sizes, and therefore their mean fecundity is low (10 to 20 eggs). Maybe due to a higher degree of iteroparity, the reproductive allocation in each reproductive event is also low (16-20 %). This could be considered the general reproductive pattern of Neotropical terrestrial isopods living in the leaf litter of forests. We do not know yet if the reproductive pattern of *B. glaber* verified in the present study is more likely to be the rule or the exception. One possible explanation for fecundity differences between *B. glaber* and *A. floridana* and *B. cairensis* and other Crinocheta is habitat specialization: *B. glaber* has burrowing abilities, whereas *A. floridana, B. cairensis,* and *B. sellowii* are typically surface litter-dwelling species. Before a more comprehensive pattern is established, further information is required on more exclusive species that show different lifestyles, such as endogean species of the genera *Trichorhina* (Platyarthridae) and *Alboscia* (Philoscidae), or bark inhabitants associated with bromeliads, e.g. *Neotroponiscus daguerrii* (Giambiagi de Calabrese, 1939) (Bathytropidae).

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