

# VARIATION IN BODY SIZE OF TERRESTRIAL ISOPODS (CRUSTACEA: ONISCIDEA) AND APPLICATION OF ECOGEOGRAPHICAL RULES

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## **ABSTRACT**

Body size is the most important feature of all organisms and in this study is represented by the variables “body length” and “body width”. Bergmann’s Rule is a hypothesis concerning body size increase with latitude for homeotherms, whereas geographic version of Rensch’s Rule predicts greater body size variation with latitude for males. The trend predicted by the first rule is confirmed here for a group of ectotherms, terrestrial isopods, while that predicted by the second was not found to apply in these organisms. Several hypotheses have been proposed to explain body size variation in terms of environmental factors and interspecific interactions underlying latitudinal gradients. Thus, we used our results to test certain hypotheses proposed to account for Bergmann’s Rule. The Island Rule examines body size as it is affected by spatial parameters and reflects a complex pattern from gigantism in taxa with small sized mainland relatives, to dwarfism in taxa with large mainland relatives. Our results are not conclusive regarding this rule, but are indicative of trends that need to be examined in the future.

**Keywords:** Terrestrial isopods Body size Bergmann’s Rule Rensch’s Rule Island Rule Species Richness

## **1. INTRODUCTION**

The most important feature of all organisms through which physiological, ecological and life-history traits are reflected, is body size. Although size is treated as a fixed variable, it is continuously altered by a variety of factors, and final adult size (maximum size) is depended on interactions among time constraints, resource

allocation to growth and/or reproduction, mortality, physiological costs, ageing and food quality De Block et al. (2008). There are several variables that can represent 'body size'. Mass is regarded the best, but it varies on a seasonal or even daily basis. Body length, along with body width, is also an attractive index because it measures the whole animal Meiri (2007). Although maximum size may be sensitive to sampling and it is expected that mainland areas are more likely to include the largest individuals due to the existence of a greater number of populations there, it is used in this study because it follows maturation of terrestrial isopods and it is indicative of developmental rate, as well as to the responses of individuals to environmental thermal variation Folguera et al. (2009).

### **Latitudinal patterns with body size and species richness**

The observation of a latitudinal pattern in body size predates Darwin's evolutionary theory and is known as Bergmann's Rule. It relates temperature with body size - although latitude is often used as a proxy to temperature Ashton (2002). According to the rule, there is an increase in body size towards cold climates Bergmann (1847). Bergmann's rule was initially referring to warm-blooded vertebrate species, thus, to endotherms, at an interspecific level Watt (2010). Bergmann's rule does not make predictions for ectotherms Entling et al. (2010). Even though evidence for the dominance of Bergmann's clines in ectotherms is controversial Adams et al. (2007), similar gradients, but also their converse, have been observed in ectotherms at the interspecific level Olalla-Tarraga et al. (2007). An 80% of the ectotherms tested grow larger at lower temperatures - a trend also known as temperature-size rule Blanckenhorn et al. (2004); Ho et al. (2010)

The mechanism behind Bergmann's rule is a thermoregulatory one, on the basis that an increase in size involves a more rapid increase of body volume compared to

the increase of its surface area. Due to the fact that heat loss is related to the surface of a homeotherm, while heat production to its volume, larger animals will tend to produce more and lose less heat, an advantageous fact in cold climates. In addition, increase of body size with resource availability, rather than with decreasing temperature Rosenzweig (1968), may be another mechanism that explains Bergmann's rule. Increasing seasonality and lower predictability of environments from the tropics to the poles were thought to select for large body size, because large animals are more resistant to cold and starvation stress Olson et al. (2009).

The mechanism of heat conservation is not applicable to ectotherms, especially to those that are small, aquatic or whose body temperature largely fluctuates with ambient temperature Ho et al. (2010) or to those that do not thermoregulate behaviorally Adams et al. (2007). Many ectotherms, though, can regulate their internal temperature by modifying their behavior or by creating heat through muscular activity Watt et al. (2010). So, Heat Conservation Hypothesis, proposed by Bergmann for endotherms, could be extended to terrestrial ectotherms that can control body temperature through physiological and/or behavioral adjustments Olalla-Tarraga et al. (2007). Along with this hypothesis, there are two other interspecific mechanisms that predict increase of body size with latitude. Accelerated Maturation Hypothesis predicts a smaller adult size in warm environments Walters et al. (2006); Entling et al. (2010). Starvation Resistance Hypothesis states that an increase in body size encourages starvation resistance and this trend is regarded more important in cold, seasonal environments Entling et al. (2010). In addition, Heat Dissipation Hypothesis is based on the conviction that average body size is better described by variables reflecting both environmental parameters, temperature and moisture. Moreover, covariation of size with these variables should be stronger for large-bodied than

small-bodied species Blackburn et al. (2004). There is also another unifying physiological mechanism beyond Bergmann's rule that extends to ectotherms and tries to explain how low temperatures (the factor constraining growth) result in larger body sizes. Since the rate of growth is mainly affected by protein synthesis and secondarily by temperature, whereas development is highly dependent on temperature, organisms are expected to reach maturity more rapidly at higher temperatures while time of growth increases less rapidly, leading to smaller final size Van der Have et al. (1996). These physiological constraints apply to all parts of the body, such as eggs, sperm or single cells. Another mechanism explaining the smaller size of eggs and cells at higher temperatures is that, while oxygen diffusion depends weakly on temperature, consumption of oxygen depends strongly on it, so that large cells may suffer from hypoxia at high temperatures Woods (1999). This hypothesis provides a simple mechanism for body size clines in ectotherms, since the total size of an organism is largely the sum of its cells Van Voorhies (1996).

Another pattern that can be associated with clinal variation in body size is Rensch's rule that predicts, under the condition of the existence of geographic variation in body size for a species, geographic variation in sexual size dimorphism Pyron et al. (2007) where latitudinal clines in males are steeper than those in females Blanckenhorn et al. (2006). According to another hypothesis deriving from the positive relationship between mean and variance, whichever sex is larger should be more variable and display a steeper latitudinal slope (Larger = Steeper Hypothesis). This rule is based on the observation that male body size varies more than that of females among related species, in a way that male-biased sexual size dimorphism increases and female decreases with body size Fairbairn (1997). A possible mechanism behind this pattern may be sexual selection for large male size along with a high genetic correlation in

body size between sexes, and results in greater among-population variation in male body size Blanckenhorn et al. (2006).

Another strong pattern is the decrease in body size with increasing richness Olson et al. (2009), a hypothesis consistent with an increase of body size with latitude Roy et al. (2001), i.e., with 'Bergmann's rule'-like trends. Species richness is related to latitude in what probably is the oldest ecological pattern observed, namely that the tropics (low latitudes) hold more species than higher latitudes Turner (2004). Although latitude cannot be a determinant of species richness *per se*, its effect is mediated through the systematic spatial variation of a variety of other factors, such as climate etc. Many explanations of this effect have been proposed, based *inter alia* on chance, historical perturbation, environmental stability, habitat heterogeneity, productivity and interspecific interactions Gaston (2000).

### **Body size and insularity**

Foster (1964) found differences in body size between different groups of terrestrial mammals inhabiting islands and their mainland congeners. He showed that rodents evolve large size on islands whereas carnivores and artiodactyls usually grow smaller. It is a pattern that describes a clear tendency for different evolutionary trends and selective pressures on islands Lomolino et al. (2006). Lomolino (1985) extended this trend by proposing that many insular forms become dwarfs or giants in comparison with their mainland relatives and predicted a trend that promotes gigantism in the smaller mainland species and dwarfism in the larger ones. The driving forces that promote gigantism are character release in response to reduced interspecific competition or predation and a force promoting dwarfism is resource limitation Meiri et al. (2005). Dwarfism can improve fitness in the case that the resources available from the reduction of size are channeled into reproduction Palmer (2002). High

population densities may promote gigantism because large individuals can more effectively deal with intraspecific competition. Different diet preferences among animals may lead to different responses to the insular environment Meiri (2007). A general factor determining the evolution of body size is the limited area of islands. Small area weakens competition and predation pressure through impoverished communities, and diminishes the abundance of resources Schillaci et al. (2009). Isolation too, can affect size evolution, because large animals have a greater chance of colonizing very isolated islands. Although the effect of phylogeny has not yet been explicitly examined, the Island Rule may hold within families or orders Meiri et al. (2009). In order to avoid effects of phylogeny as much as possible, we restricted analyses to species belonging to the same genus and/or family.

The overall aims of this study were to collate available data on morphological characteristics of terrestrial isopods in order to test: (1) whether there is a consistent trend between body size and latitude, as well as between those two parameters and species richness; (2) whether the ‘island rule’ applies to ectotherms at an interspecific level; (3) which are the main ecological factors driving body size variation; and (4) which hypotheses can explain body size variation in our study.

## **2. MATERIALS AND METHODS**

### **a) Species data**

Based on the taxonomy of the world catalog of terrestrial isopods published by Schmalfuss (2003, 2004), we collected species records from papers, books and reviews that contained information on distribution and maximum body size of males and females. Most often, authors give maximal body lengths, but in many cases maximal body widths are also reported. In cases where more than one measurement

was provided in different papers, we recorded only the largest. Maximal length and width values are believed to be a reasonable indicator of size, and according to Bertalanffy's growth function, it is the maximum attainable body size that is mostly influenced by thermal constraints Angilletta et al. (2004). Moreover, data on mass of isopod species are not available in the literature. Male length ranged from 1.5 to 32 mm, female length from 1.5 to 30 mm, male width from 0.4 to 21mm, and female width from 0.4 to 14 mm. In addition, we recorded separately species whose distribution is confined on islands and species with strictly mainland ranges. In total, we collected data on 231 island species, 265 mainland and 109 species with mixed distribution. Overall, 30 families were represented in our data set. All analyses were performed at the interspecific level.

## **b) Predictors**

We collected data on three ecological factors that are possibly linked to the size of terrestrial isopods: latitude, climate and distribution. Latitude was recorded as the mean latitude of each species overall distribution (midpoint approach), see Blackburn et al. (2004). Latitudes south of the equator were transformed to positive values. Climate records were based on the Köppen – Geiger climate classification Peel et al. (2007) that incorporates, along with temperature, data on global long-term monthly precipitation. According to this system, there are 30 climatic types, divided into 3 tropical (Af, Am and Aw), 4 arid (BWh, BWk, BSh and BSk), 9 temperate (Csa, Csb, Csc, Cfa, Cfb, Cfc, Cwa, Cwb and Cwc), 12 cold (Dsa, Dsb, Dsc, Dsd, Dfa, Dfb, Dfc, Dfd, Dwa, Dwb, Dwc and Dwd) and 2 polar (ET and EF) subtypes. The set of locations defined as having a 'B'-type climate is based on a combination of mean annual precipitation and mean annual temperature, while all other sets are mutually



exclusive and are based only on temperature criteria. We created, thus, two variables describing the climate. The first, climate1, had five levels (A=tropical, B=arid, C=temperate, D=cold and E=polar), the second, climate2, included the second characteristic of the 30 climate types given by the Köppen – Geiger classification. The variable concerning the distribution was divided into three categories: ‘mainland’, ‘island’, and ‘both’. The island surface area of all islands with ‘island’ species was recorded as found in Wikipedia (<http://wikipedia.org>).

### **c) Analyses**

We analyzed the applicability of Bergmann’s rule by using bootstrap least-squares regressions and Pearson product-moment correlations. In the first place, we examined the variation of body size with the increase of the absolute values of latitude and, next, we performed the same analysis for species belonging to the same climate, as defined by climate1. Finally, we tested body size variation in relation to latitude for isopods belonging to different climates, as defined by climate2, searching for indirect relationships of body size with precipitation and temperature. For this reason, we performed Student tests for the comparison of mean body size values for species in climates with dry summer and those living in climates having no dry season, as well as Fischer and Mann-Whitney tests to compare the variances and the medians of these samples. We compared species in deserts, rainforests and savannahs, using ANOVA and Multiple Range tests, in order to compare the means or any pair of means for any size parameter. The creation of two different groups was based on the fact that species residing in climates with dry summer and a dry season were much more numerous in relation to those belonging to the climates of the second group, therefore the

elimination of the species below and above the mean value for each size parameter would not leave the mean invariable.

We calculated the mean body length and width for species belonging to each region and plotted frequency histograms to define species numbers below and above the mean value, in order to see whether small-bodied isopods are over-represented in species-rich regions (tropics, temperate climates).

We applied regressions of body size parameters on latitude for both sexes, in order to conclude if the slope of the body size on latitude would be steeper for males or females, so as to test for Rensch's. This analysis was performed separately for different phylogenetic groups, namely, Ligiidae, Synocheta and Crinocheta, for which we had abundant species numbers.

To test whether the Island Rule was valid for either body length or body width, we extracted data on body size of 'island' and 'mainland' species. In order to avoid using phylogenetically non-independent data Meiri et al. (2009), we used 230 pairs of mainland-island species, ordered from smaller to bigger, belonging to either the same genus or family, and applied regressions of 'island' on 'mainland' species for body length and width of both sexes. We also applied regressions for 15 pairs belonging to the same family and 26 belonging to the same genus residing in the same climatic zone. In cases where we had more than one mainland species belonging to the same genus or family with the respective insular one, or vice versa, we calculated the mean value of the species' sizes and excluded the values above and below the mean that differed approximately the same, in order to avoid changing the initial mean value before the extraction. After that, we ranged the values for both mainland and island species from the smallest to the largest to form the pairs used in the regressions. We then tested the variation in body size of island species with island surface. Due to the

fact that large islands are ‘mainland-like’ in terms of predators and competitors, we tested size variation in a consecutive order of decreasing island size classes, namely for islands below 50,000 km<sup>2</sup>, below 10,000 km<sup>2</sup>, and below 5,000 km<sup>2</sup>. The selection of the largest threshold follows from Meiri et al. (2006), who found that similar patterns of size evolution are obtained when the area of the largest islands included is less than 50,000 km<sup>2</sup>.

Finally, we used a model-selection approach to determine the variables [distribution, climatic variables and/or taxonomic effect (Family)] that best explain geographical variation in body size among species using the log<sub>10</sub> maximum body length and width as response variables. Due to high correlation between length and width for males and females, we performed four separate modeling exercises, one for each variable. We started with a full model to arrive at an adequate one. The removal of predictor terms was based on the maximum decrease in AIC and, in the end, the overall increase in model fit for the removal of each remaining term. We stopped removing terms when no further deletion of a term produced a decrease in AIC. In each step we performed a Shapiro test to control the normality of residuals and confirm the good adjustment of the model to our data.

All numeric variables were log transformed when they weren’t normally distributed. R.2.10.1 and Statgraphics Plus 5.0 were used in all analyses.

### **3. RESULTS**

#### **Bergmann’s and Rensch’s rules**

Maximum body length and width of terrestrial isopods increases with the increase of absolute values of latitude (Table 1). So, there is an increase in body size when departing from the Equator in both the North and South hemispheres, suggesting a pattern consistent with Bergmann’s rule. Moreover, the slope of the regression of

body size on latitude is steeper for females, for all species belonging to Ligiidae, as well as for those belonging to Synocheta and Crinocheta. This results in greater among-species variation in female than male body size. So, we found no evidence in favor of Rensch's rule.

**Table 1.** Pearson product-moment correlations and linear regressions between body length/width for both sexes and absolute values of latitude.

Groups	N	Intercept ( $b_0$ )	SE	Slope ( $b_1$ )	SE	P	R <sup>2</sup> (%)	Pearson cor. coef.
<b>Regression Model Length/Width = <math>b_0 + b_1</math> (Latitude_ abs)</b>								
Length of males	605	6.371	0.495	0.067	0.015	<0.001	3.324	0.182
Length of females	605	6.572	0.498	0.082	0.015	<0.001	4.8	0.219
Width of males	605	2.768	0.286	0.039	0.009	<0.001	3.444	0.186
Width of females	605	2.882	0.261	0.043	0.008	<0.001	4.82	0.220

We then used the climatic variable 1 to test the association between body size and latitude within different climatic zones (Table 2). We found a positive correlation only for arid and temperate climates. Using the climatic variable 2, there was also a significant increase of body size with latitude in all but the dry climates ( $p < 0.05$ ) for all size parameters. Student tests and ANOVA for the comparison of the means among species belonging in different climates showed that isopods in all but the dry climates are significantly smaller than those residing in dry climates ( $P < 0.001$ ). So, there is evidence that small bodied species are favored in warm, moist climates (evidence for confirmation of Heat Conservation Hypothesis). Comparing the means and variances of the species residing in deserts, rainforests and savannahs, we found no statistically significant difference between the means of the 3 variables at the 95% confidence level. As far as climate 1 is concerned, there were statistically significant differences between the means of the four variables at the 95% confidence interval (average of maximum length and width for males and females belonging to tropical, arid, temperate and cold climates). More specifically, for all parameters tested, the

greatest average value corresponded to isopods belonging to arid climates. If we exclude the arid, there is an increase in body size from tropical to cold climates, a pattern consistent with Starvation Resistance and Accelerated Maturation hypotheses.

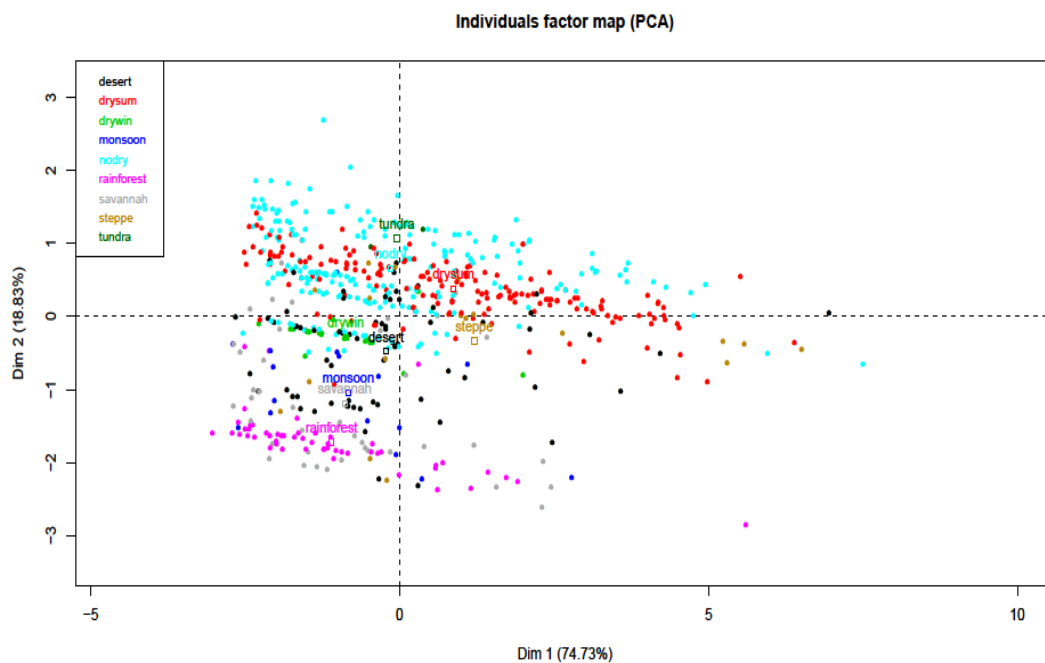
**Table 2.** Pearson product-moment correlations and linear regressions between body length/width for both sexes and absolute values of latitude for isopods belonging to the same climate type.

Parameters	Climate1	N	Intercept (b <sub>0</sub> )	SE	Slope (b <sub>1</sub> )	SE	P	R <sup>2</sup> (%)	Pearson cor. coef.
Length of males	Tropical	111					n.s.		-0.1
Length of females	Tropical	111					n.s.		-0.034
Width of males	Tropical	111					n.s.		-0.162
Width of females	Tropical	111					n.s.		-0.124
Length of males	Arid	87	4.995	1.332	0.161	0.049	0.001	11.21	0.335
Length of females	Arid	87	5.864	1.239	0.141	0.046	0.003	10.00	0.316
Width of males	Arid	87	1.246	0.903	0.125	0.033	0.000	14.08	0.375
Width of females	Arid	87	2.012	0.675	0.089	0.025	0.001	13.02	0.361
Length of males	Temperate	319	3.758	1.668	0.139	0.046	0.002	2.86	0.169
Length of females	Temperate	319	3.961	1.701	0.158	0.046	0.001	3.50	0.188
Width of males	Temperate	319	1.866	0.924	0.063	0.025	0.013	1.90	0.138
Width of females	Temperate	319	2.273	0.886	0.061	0.024	0.012	1.96	0.140
Length of males	Cold	85					n.s.		-0.060
Length of females	Cold	85					n.s.		-0.030
Width of males	Cold	85					n.s.		-0.098
Width of females	Cold	85					n.s.		-0.050

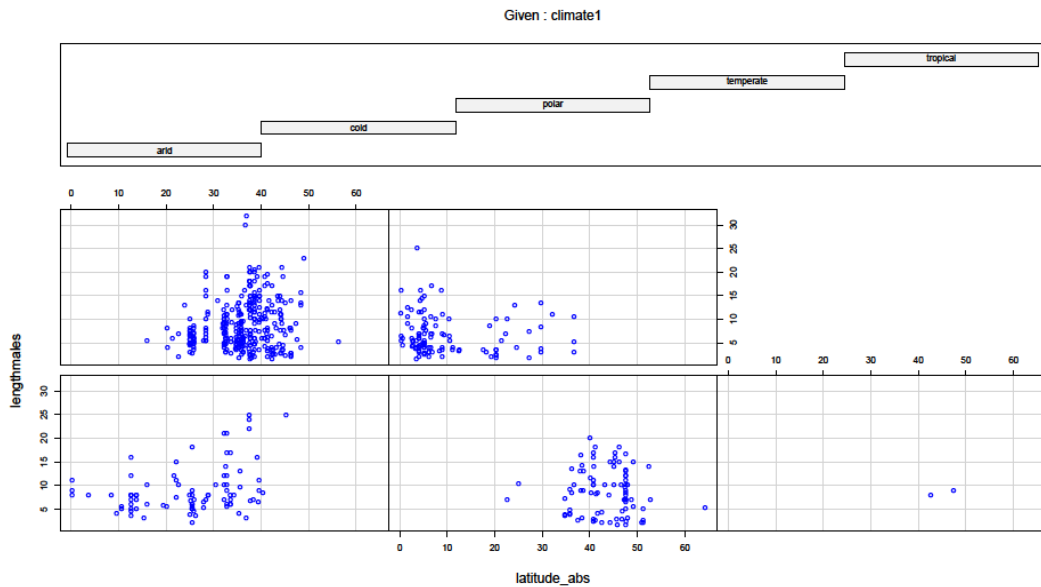
There was a greater response of small-bodied species to climate1 ( $P < 0.05$ ) in relation to the large-bodied. For climate2, there was a larger response for small-bodied males and females as far as the length was concerned ( $P < 0.001$  length small males;  $P < 0.005$  length small females), but the opposite trend was found for width ( $P < 0.001$  width large males;  $P < 0.005$  width of large females). So, Heat Conservation Hypothesis may be more likely to explain body size trends found in this study in relation to Heat Dissipation Hypothesis.

## Body size and species richness

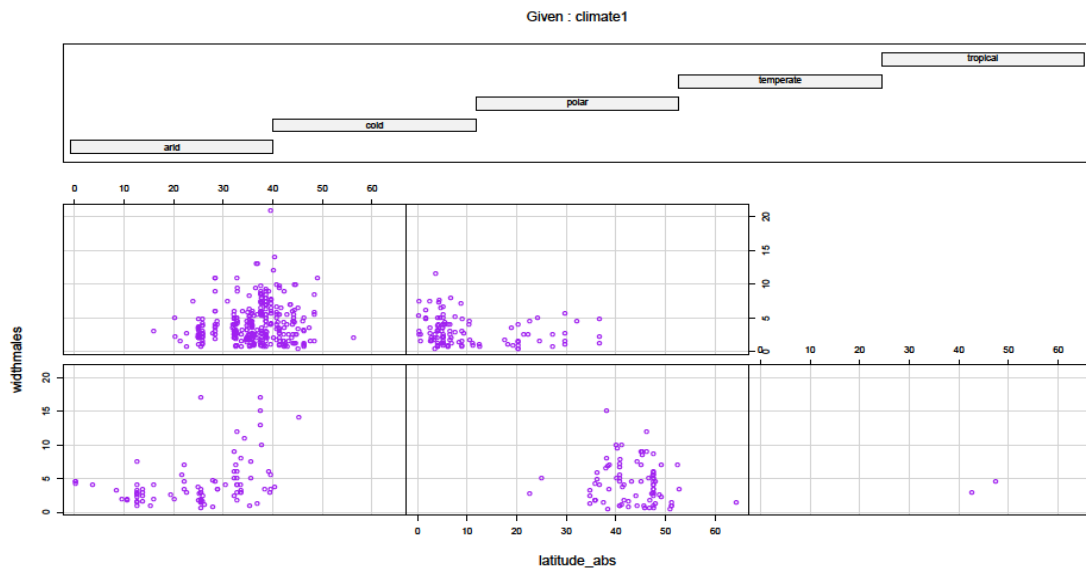
The number of isopod species decreases above and below 50 degrees of latitude. The greatest number of species is recorded in temperate climates. This observation may be a result of recording bias, because species in temperate areas are more thoroughly examined and more easily accessible in comparison to those existing in deserts and Polar Regions. In any case, though, in our case there is no general pattern of increase in species richness with decreasing latitude. Species richness increases with latitude from the tropics to temperate climates and so does body size. We found no inverse pattern between species-poor and species-rich regions, as small-bodied species were always more abundant. Nevertheless, there was a tendency towards equalization of small and large-bodied species from the tropics to cold climates, where the numbers of small- and large-bodied species were almost equal.



**Figure 1:** Principal Component Analysis showing a clear tendency of the species residing in climates with dry summers and in steppes to be larger compared to those residing in warm and moist climates (rainforests, monsoon and savannah). Body size increases towards the positive values on the X axis.



**Figure 2.** Coplot: length of males in relation to absolute values of latitude given the climate1. Note that although in arid and temperate climates (down left and upper left diagrams) there is a clear pattern of increase in body length for males with latitude, for cold and tropical climates (middle down and upper right diagram), there is a small tendency of reduction of body length with latitude.



**Figure 3.** Coplot: Width of males in relation to absolute values of latitude given the climate1. Note that although in arid and temperate climates (down left and upper left diagrams) there is a clear pattern of increase in body width for males with latitude, for cold and tropical climates (middle down and upper right diagrams), there is a small tendency of reduction of body width with latitude.

### Body size and insularity

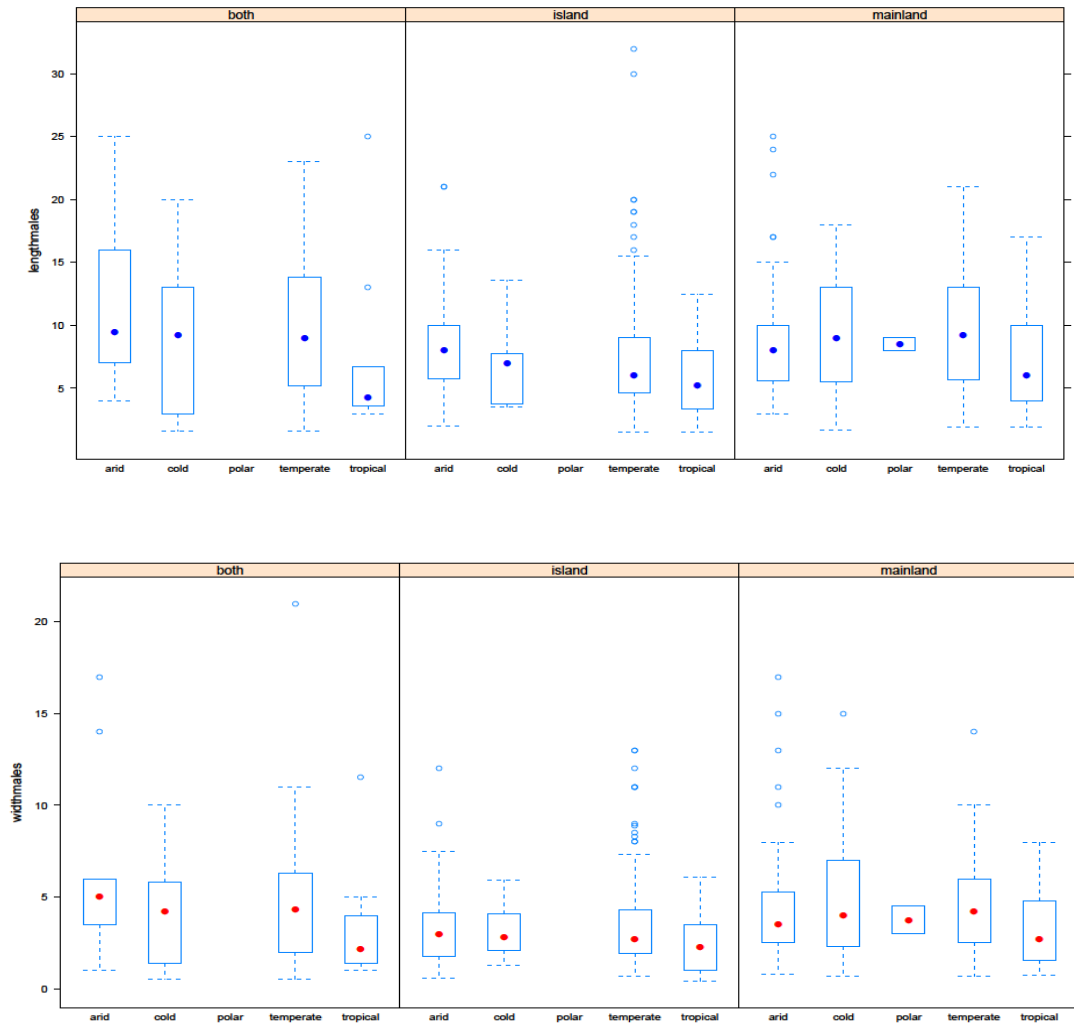
As far as the island rule is concerned, the slope of insular on mainland length and width is always smaller than one. Even when we control for phylogenetic signal, the

slope is again smaller for pairs within the same genus (Table 3). The effect is not present for species belonging to the same family, but this is probably due to the small number of pairs tested. Thus, the null hypothesis of no consistent differences between insular and mainland body size can be rejected for the cases referred before. More specifically, maximum length and width seems to evolve in the direction predicted by the Island Rule for large mainland species, which evolve smaller on islands for all isopods tested, as well as for those belonging to the same genus. Small mainland species evolve larger, following the Island Rule only among species belonging to the same genus. Pairs of mainland-island species belonging to the same climatic zone were examined. No significant difference in mean body length and width was found for 44 species pairs belonging to the tropics. The same was true for 35 pairs belonging to arid and 7 pairs belonging to cold climates. Only the 109 pairs that reside in temperate climates showed a significant difference in mean body length and width between insular and mainland species for both sexes. Mainland species are always larger (Table 4 and Figures 4-5).

**Table 3.** Results from least squares regression of insular body length and width on mainland body length and width for all isopods and within species belonging to the same genus and family.

Groups	N (pairs)	Intercept (bo)	SE	Slope (b1)	SE	P	R <sup>2</sup>
<b>Regression model: Length/ Width island = bo + b1 (length/ width mainland)</b>							
<b>All species</b>							
Length of males	230	-0.181	0.199	0.845	0.019	<0.001	89.29
Length of females	230	0.350	0.210	0.817	0.019	<0.001	88.56
Width of males	230	0.067	0.058	0.752	0.011	<0.001	95.40
Width of females	230	-0.114	0.079	0.840	0.015	<0.001	93.06
<b>Species within family</b>							
Length of males	15					n.s.	
Length of females	15					n.s.	
Width of males	15					n.s.	
Width of females	15					n.s.	
<b>Species within genus</b>							
Length of males	26	1.150	1.186	0.792	0.148	<0.001	54.27
Length of females	26	1.822	1.335	0.780	0.154	<0.001	49.60
Width of males	26	0.143	0.406	0.880	0.105	<0.001	74.54
Width of females	26	0.460	0.522	0.875	0.128	<0.001	65.97





**Figures 4 and 5.** Bwplot: length and width of males determined by the distribution of species given the climate

### Island area

In general, there was no consistent trait that indicates a significant correlation between body size and island area. A significant correlation was found only for small isopods concerning the length of females for islands below 5,000 km<sup>2</sup> ( $r = 0.172$ ,  $P = 0.031$ ), so in this case a decreasing island surface did not promote gigantism. Only the width of small females that reside on islands smaller than 50,000 km<sup>2</sup> ( $r = -0.206$ ,  $P = 0.024$ ), as well as the width of large males residing on the same islands ( $r = -0.261$ ,  $P =$

= 0.014), show consistency with the Island Rule. Therefore, we cannot deduct general consistency with the Island Rule using island area as a predictor variable.

**Table 4.** Results from regressions of island species against mainland species belonging to the same climatic zone.

Climate		N (pairs)	Mean $\pm$ SE	T	P
Tropical	Length of males	44	Main: 7.256 +/-1.437	1.752	0.083
	Length of females	44	Main: 7.423 +/- 1.415	1.586	0.116
			Isl: 6.089 +/- 0.936		
	Width of males	44	Main: 3.251 +/- 0.721	1.876	0.064
			Isl: 2.451 +/- 0.467		
	Width of females	44	Main: 3.444 +/- 0.704	2.052	0.043
		Isl: 2.581 +/- 0.471			
Arid	Length of males	35	Main: 8.888 +/- 2.00	0.447	0.656
			Isl: 8.343 +/- 1.461		
	Length of females	35	Main: 9.528 +/- 1.845	0.656	0.514
			Isl: 8.774 +/- 1.435		
	Width of males	35	Main: 4.516 +/- 1.396	1.345	0.183
			Isl: 3.450 +/- 0.800		
Temperate	Width of females	35	Main: 4.410 +/- 0.970	1.194	0.236
			Isl: 3.673 +/- 0.795		
	Length of males	109	Main: 9.628 +/- 0.890	2.83	0.005
			Isl: 7.641 +/- 1.069		
	Length of females	109	Main: 10.523 +/- 0.966	2.726	0.007
			Isl: 8.551 +/- 1.059		
Cold	Width of males	109	Main: 4.575 +/- 0.492	2.669	0.008
			Isl: 3.578 +/- 0.553		
	Width of females	109	Main: 4.908 +/- 0.493	2.657	0.008
			Isl: 3.919 +/- 0.549		
	Length of males	7	Main: 9.086 +/- 6.241	0.815	0.431
			Isl: 6.728 +/- 3.338		
Cold	Length of females	7	Main: 9.300 +/- 6.469	0.419	0.682
			Isl: 8.028 +/- 3.639		
	Width of males	7	Main: 4.714 +/- 5.244	0.678	0.511
			Isl: 3.200 +/- 1.543		
	Width of females	7	Main: 5.043 +/- 4.043	0.573	0.577
		Isl: 4.000 +/- 1.863			

### Multiple regression models for maximum body size

Pearson correlation tests showed a strong correlation between the length and width of males ( $r= 0.902$ ) and between the length and width of females ( $r= 0.898$ ). So, we built separate models to describe these size parameters, in order to avoid using them in the same model. The best multiple regression model for the length of males

included climate1, climate2, distribution, family and the interaction between climate1 and family, and explained 51.22% of variance. The best model for the length of females included the same predictors, and explained 45.86% of variance. The best model for the width of males did not include the interaction between climate1 and family neither the climatic variable 2, and explained 47.73% of variance. Finally, for the width of females the model did not include the interaction between climate1 and family, plus the climatic variable 1 this time, and explained 45.03% of variance.

Using ANCOVA, we tested for effects of temperature and precipitation, as expressed through climatic variables, distribution and phylogenetic signal (family). After analyzing length and width, there were effects (model for male length) of family (d.f.=27, F=18.897, P<0.001), climate2 (d.f.=5, F=11.466, P<0.001), climate1 (d.f.=4, F=10.032, P<0.001), distribution (d.f.=2, F=15.457, P<0.001) and interaction between climate1:family (d.f.=36, F=1.959, P<0.001), ranked from the most to the least important. For female length, there were effects of family (d.f.=27, F=14.998, P<0.001), climate2 (d.f.=5, F=10.979, P<0.001), climate1 (d.f.=4, F=12.305, P<0.001), distribution (d.f.=2, F=11.078, P<0.001), climate1:family (d.f.=36, F=1.943, P<0.002). For male width, there were effects of family (d.f.=27, F=18.998, P<0.001), distribution (d.f.= 2, F=18.858, P<0.001) and climate1 (d.f.= 4, F= 9.382, P<0.001), and for females width, the effects, ranked from the most to the least important, were: family (d.f.=27, F=15.508, P<0.001), climate2 (d.f.=8, F=12.101, P<0.001) and distribution (d.f.=2, F=16.142, P<0.001). The standardized coefficient for family indicates that this variable is the main driver of variation for all the parameters tested. It seems that for the length and width of females, as long as for the length of males, the second most important driver of variation is climatic variable 2, while for the width of males the second most important driver is distribution. Latitude

is not included into the models because it is not a primary factor by itself, but a parameter through which other factors of variation are expressed.

**Table 5.** Multiple regression models for maximum body length and width. Models are ranked in each case by AIC from worst to best-fitting model. Codes for interactions between predictor variables are: F\*C1: family and climate1, D\*C1: distribution and climate1, C1\*C2: climate1 and climate2, C2\*F: climate2 and family, D\*F\*C2: distribution and family and climate2.

Parameters	Climate1	Distribution	Family	Climate2	F*C1	D*C1	C1*C2	C2*F	D*F*C2	AIC
<b>Length of males</b>	7.24	5.57	92.0	10.3	12.83	1.65	0.004			-963.5
	7.24	5.57	92.0	10.3	12.82	1.65				-965.3
	7.24	5.57	92.0	10.3	12.72					-966.2
<b>Length of females</b>	9.02	4.06	74.2	10.0	12.88		0.51	7.606		-948.0
	9.02	4.06	74.2	10.0	12.88		0.51			-958.4
	9.02	4.06	74.2	10.0	12.82					-959.4
<b>Width of males</b>	10.55	8.96	132.7	15.2			0.23			-731.9
	10.55	8.96	132.7	15.2						-733.0
	10.55	10.59	144.1							-734.9
<b>Width of females</b>		8.11	105.2	24.3				20.763	19.388	-919.9
		8.11	105.2	24.3				20.763		-930.6
		8.11	105.2	24.3						-947.6

#### 4. DISCUSSION

Isopods are peracaridan crustaceans with representatives in almost all kinds of environments. Members of the suborder Oniscidea (about 3,600 species) are by far the most successful group of crustaceans on land. They are the better adapted among crustaceans, but much worse adapted to land than other terrestrial arthropods. Given that, in general, they exhibit behavioral regulation of body temperature, they could be considered as a proper group of ectotherms for testing Bergmann's and other related ecogeographical rules. In this study, we found that body size in terrestrial isopods follows trends that are consistent with Bergmann's Rule, namely an increase in body size with latitude, but not with the geographic version of Rensch's Rule, since we

found greater variation in female body size with latitude, the opposite of what is expected by the latter rule. After testing the response of body size in relation to two climatic variables, we found a positive correlation for arid and temperate climates and a significant increase of body size with latitude in all but the dry climates. Moreover, those species residing in these climates were significantly smaller than the ones found in dry climates. We came to the conclusion that small-bodied species show a greater response to climatic variable one than large-bodied but, as far as the climatic variable two was concerned, there was a larger response for small-bodied males and females in length and an opposite trend in width. In addition, we tested body size variation with species richness and found that the number of isopod species decreases above and below 50 degrees of latitude, with the greatest species number being recorded in temperate regions. In addition, small-bodied species were over-represented in both species-poor and species-rich regions but, with the increase of latitude, there was a tendency for equal representation of small and large-bodied species, in a way that in cold climates the number of small- and large-bodied animals was almost equal. Finally, we found some consistent differences between insular and mainland species that were in agreement with the Island Rule, such as that large mainland species tend to evolve smaller on islands, and vice versa. Nevertheless, when using related species pairs, differences in size were found only for species residing in temperate climates, with mainland species always being larger. Moreover, decreasing island surface does not seem to promote gigantism in smaller insular species or dwarfism in larger ones. The major factor affecting size, besides phylogenetic relationship (documented by variable 'family'), was 'climatic variable two', which incorporates information on both temperature and precipitation.

The fact that isopod species residing in rainforests and in other permanently humid areas are significantly smaller compared to species in areas with dry summers (either in tropical, temperate or cold climates) suggests that body size may be associated with desiccation avoidance. Generally, species that have developed pleopodal lungs as a means for respiration are more resistant to drought and can attain larger body size (e.g., Armadillidae, Armadillidiidae, Eubelidae, Porcellionidae). Terrestrial isopods display a generally low resistance to desiccation Crawford (1992), so that moisture is a very important limiting factor for these animals. To minimize water evaporation, they frequent cool and humid sites, seek shelter under stones, and exhibit nocturnal lifestyles Horiguchi et al. (2007). The differences in activity of woodlice are due to the continuous alteration in their water content, and there is a reduction in activity with increasing relative humidity to the point of becoming totally akinetic Waloff (1941). The decreased activity of isopods in areas with high humidity (e.g., rainforests) suggests low metabolism and small body size towards the tropics, a trend consistent with our results. At the same time, small body size creates problems of desiccation in hot and dry environments that is why dry environments may select for individuals that are larger, in order to resist dehydration Stillwell et al. (2007), something that is also in consistency with our results, since isopods residing in deserts are larger in comparison to those residing in humid areas and this reduces surface-to-volume ratio and increases absolute water content Chown & Gaston (1999). The relative roles of temperature and humidity in temperate and cold climates are probably different, and large body size is promoted.

The increase of body size from the equator to the poles shows a trend consistent with Bergmann's Rule which is confined to endotherms. Nevertheless, there is a set of mechanisms applicable to ectotherms that can explain such a pattern. The only

mechanism actually tested on ectotherms, though, particularly on ants, is the Seasonality Hypothesis Lindstedt (1985) according to which the limiting factor for growth is the seasonality of resources. Since terrestrial isopods are not food limited Warburg (1984), the Seasonality Hypothesis, but also the Starvation Resistance Hypothesis that explains the positive body size correlation with latitude in ectotherms through a greater capacity for larger organisms to store food (Nekola et al. in press), are unlikely to hold for terrestrial isopods. Water may be a more important limiting resource than food, and can lead to an increase in body size with frequency and severity of moisture stress (Nekola et al. in press). Herein, we used precipitation through the variable climate2 as a proxy of the influence of water on body size, even though moisture is not a linear function of precipitation. Our results support the view that latitudinal variation of body proportions is largely dependent on a combination of water availability and temperature, since the variable climate2 (effects of temperature and precipitation) is by far more important than climate1 (effect of temperature alone). There are two conflicting mechanisms that differ in whether body size varies in response to the demands of keeping cool (Heat Dissipation Hypothesis) or keeping warm (Heat Conservation Hypothesis) Cushman (1993). According to the first hypothesis, variables related to temperature and moisture describe better average body size, because large-bodied animals need to respond to the challenge of dissipating heat and keeping cool, whereas smaller species do not Blackburn (2004). In contrary, Heat Conservation Hypothesis predicts greater response to temperature amongst small-bodied animals, because they face more challenges in keeping warm. Since the application of the latter hypothesis demands a thermoregulatory mechanism Watt et al. (2010), and due to the fact that terrestrial isopods do show behavioral, physiological and morphological regulatory mechanisms for temperature control

Caubet et al. (1998), we can assume that this hypothesis could be extended also to such ectotherms. We found that covariation with climate2 (temperature and precipitation) was larger for small-bodied species, as far as length was concerned, but the trend was reversed for width. On the other hand, the greater response to temperature (climate1) found in small-bodied species for both sexes and for both parameters of body size, indicates that the Heat Conservation Hypothesis is more likely to explain the body size trends found herein.

'Bergmann's Rule'-like patterns may in fact be causally linked to the latitudinal gradient of decreasing species diversity towards the poles. Low alpha-diversity means reduced interspecific interactions, including competition. In the absence of larger competitors, smaller members of the same guild often exhibit ecological release, increasing in size in species-poor environments, such as those at high latitudes McNab (1971); Dayan (1990); Iriarte et al. (1990). Besides the fact that there is a general tendency for richness to be greater in the tropics Orme et al. (2006), such a pattern is not reflected in our study. There is strong evidence for a broadly positive monotonic relationship between species richness and energy availability Gaston (2000). The increment of energy is thought to enable a greater biomass to be supported in an area Kerr et al. (1997). So, species richness may represent a trade-off between body size and abundance in a way that limiting resources can increase body size and decrease abundance Olson et al. (2009). Lack of energy, expressed through shortage of resources towards higher latitudes, may be an explanation of the increase in body size of terrestrial isopods towards the poles, and may account for latitudinal trends in species diversity (Energy Availability Hypothesis) Roy et al. (2001). According to the Habitat Heterogeneity Hypothesis, species richness depends on water availability, heat and light Davies et al. (2007), and due to the trade-off between



body size and abundance, these abiotic factors are very likely to affect body size trends

Any latitudinal change in environmental factors that affects one sex more than the other can generate variation in male and female body size clines and induce dimorphism Blanckenhorn et al. (2006). In our study, the slope of body size increase with latitude is steeper for females than males (inverse of geographic version of Rensch's Rule), which also means a larger body size for females (larger = steeper hypothesis) Blanckenhorn et al. (2006) and that sexual size dimorphism declines with increasing latitude Chown et al. (2010). In order to identify the mechanisms that produce steeper female clines requires studies quantifying latitudinal variation in sex-specific natural and sexual selection on body size. A mechanism that induces smaller size in males is their early emergence and maturation Bidau et al. (2008). Also, the bias in sex ratio towards females, very common in Oniscidea, might give a greater probability to females to include larger body sizes, in relation to the fewer males in the population. A possible link between Bergmann's Rule (clinal size variation) and differential size variability among sexes (Rensch's Rule) has not yet been explicitly explored.

The Island Rule Clegg (2002) is a complex pattern not reflecting only gigantism or dwarfism towards islands, but also a graded trend towards gigantism in smaller mainland species and dwarfism in larger. This reflects the relative importance of selective forces on islands and among species of different body size Lomolino, (2005). According to Meiri et al. (2009), the Island Rule may hold within taxonomic groups, such as family or order, therefore we compared mainland and island pairs of species belonging to the same genus and to the same family. For species belonging to the same genus we found the tendency, predicted by Lomolino et al. (2006), of insular

species to become dwarfs or giants according to the size of their mainland relatives. More specifically, large mainland species become smaller on islands and small mainland species become larger, given that they belong to the same genus. The same results arose when all isopod species were tested. Because climatic conditions that affect available resources and primary productivity differ on islands Lomolino (2005), affecting, in turn, the intensity and the type of intra- and interspecific relationships among species, we tried to see if the Island Rule applies in islands belonging to the same climatic zone. Only pairs belonging to the temperate zone showed a significant difference in body size, with island species always being smaller than mainland ones. The fact that there are a great number of different possible climatic conditions that confine with the general temperate and cold climate, may give a wider variability of climatic conditions within the temperate and the cold zone. So, selective forces on islands may be more vigorous and they may swift more often, driving to dwarf forms on islands Lomolino (2005). Another reason that can promote dwarfism is resource limitation that can lead to an increase of intraspecific competition Lomolino (2005). Differences on body size between mainland and island species could not be evaluated for species residing in cold climates because the number of pairs tested was very limited.

Size evolution is not only affected by latitude, but also by isolation and island area Meiri (2007). There is a conviction that decreasing island area promotes gigantism in smaller insular species and dwarfism in larger ones. Area did not seem to be important in determining changes in size of island species. Beside the fact that Island Rule should be manifest mostly on small islands Meiri et al. (2009), neither of the three island categories based on area exhibited a change in size of insular species. As a consequence, we found little evidence for an effect of area on body size evolution of

isopods. This is consistent with the fact that most studies found area not to affect size (Lawlor (1982); Angerbjörn (1986); Yom-Tov et al. (1999); Anderson & Handley (2002); Boback (2003); Meiri et al. (2005)). Of course, our study used an interspecific approach and was not restricted to land-bridge islands. Moreover, we had no available data to quantify the selective forces associated with interspecific pressures (predation, parasitism, interspecific competition) and those associated with intraspecific competition for limited resources. In addition, the calculation of the mean value of body length and width for the formation of pairs and the extraction of values (species), even though it did not change the initial mean value, induces a bias for the real body size of some mainland-island pairs. As a consequence, we cannot claim our results to be conclusive at any rate regarding the Island Rule, but only that they are indicative of trends to be explored further in the future.

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