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# Rensch's and Bergmann's Rules in Cis-Andean South-American Howler Monkeys (Mammalia: Alouatta)

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**Type:**

Research paper

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Howler monkeys (genus Alouatta) are large folivorous primates living in South America. We tested for the application of both Rensch’s rule and Bergmann’s rule to body size variation in Alouatta. We found that Rensch’s rule does apply in howlers. In Alouatta, males exploit dominance rank competition, and take advantage from seasonal abundance of high nutritious fruit supply in their diet. This mating system and dietary charateristics suggest positive male selection for body size is responsible for Rensch’s rule. However, since folivory favors large body size in primates (to lower mass specific metabolic rate) and it is the primary dietary habitus in howlers, larger species do occur in the Amazon basin, originating a reversed Bergmann’s rule pattern for both males and females at the interspecific level. The spatial and phylogenetic components of such body size patterns of variation are both important, implying Alouatta ecomorphological differences to occur above the species level, justifying their non-overlapping geographic distribution.

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# Manuscript Title: Rensch's and Bergmann's Rules in Cis-Andean South-American Howler Monkeys (Mammalia: *Alouatta*)

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## ABSTRACT

Howler monkeys (genus *Alouatta*) are large folivorous primates living in South America. We tested for the application of both Rensch's rule and Bergmann's rule to body size variation in *Alouatta*. We found that Rensch's rule does apply in howlers. In *Alouatta*, males exploit dominance rank competition, and take advantage from seasonal abundance of high nutritious fruit supply in their diet. This mating system and dietary charateristics suggest positive male selection for body size is responsible for Rensch's rule. However, since folivory favors large body size in primates (to lower mass specific metabolic rate) and it is the primary dietary habitus in howlers, larger species do occur in the Amazon basin, originating a reversed Bergmann's rule pattern for both males and females at the interspecific level. The spatial and phylogenetic components of such body size patterns of variation are both important, implying *Alouatta* ecomorphological differences to occur above the species level, justifying their non-overlapping geographic distribution.

**Keywords:** Howler monkeys, body size, Rensch's rule, Bergmann's rule

## INTRODUCTION

In 1847, Carl Bergmann observed that, among endothermic species, individuals living at high latidudes tend to be larger than those standing closer to the equator (Bergmann 1847). This was once explained with the higher body surface-to-volume ratio in smaller animals, which helps dissipating heat in warm habitats (Meiri et al. 2007). The heat conservation hypothesis is not a sufficient explanation for it, and further justifications regard fasting endurance (Linstedt and Boyce 1985), environmental predictability (Calder 1974), and productivity (James 1970).

Whatever the reason for Bergmann's rule is, its application is not as universal as the term 'rule' would suggest (Meiri, 2011). In small-sized animals, like rodents, there are several cases of reverse Bergmannian pattern (Maestri et al. 2015; Medina et al. 2007; Belk and Houston 2002; Gohli and Vojie 2016). In the Neotropics, Martínez et al. (2013) recorded a Bergmann's rule like pattern South to the equator for crab-eating fox *Cerdocyon*, while the reverse applies North to it. These examples suggest that, perhaps unsurprisingly, the relationship between body size and the geography is far more complicated than a simplistic rule would suggest.

While Bergmann's rule describes a latitudinal size cline, Rensch's rule predicts that sexual dimorphism (SSD) increases with body size for species whose males are larger, and the opposite if females are (Rensch 1950, Fairbairn 1997, 2007, 2013; Weckerly 1998; Fairbairn et al. 2007). Male body size is in fact expected to be the primary locus of selection for Rensch's rule, due to male-male competition for mates (Blanckenhorn 2006; Gordon 2004).

Since Bergmann's rule predicts larger body size with latitude, and Rensch's rule predicts larger SSD with males larger than females, the effect of the two patterns may conflate, provided the largest species occur farther from the equator (Eweleit et al. 2014; Werner et al. 2016). Thus, under Rensch's rule, the latitudinal trend in male body size may steepen (Blanckenhorn et al. 2006).

In primates, both Bergmann's and Rensch's rules were explored a number of times (Gordon 2004; Clauss et al 2013). Harcourt and Schreier (2009) found support for Bergmann's rule, and Smith and Cheverud (2002) found Primate as a whole to obey Rensch's rule. Yet, when the model is controlled for the phylogeny, the relationship disappears for both Platyrrhini and Strepsirhini.

Howler monkeys (genus *Alouatta*) are an ideal study model to test Bergmann's rule, Rensch's rules, and their potential interaction. Howlers are highly sexually dimorphic (Ford 1994), and widely distributed in South America. *Alouatta* belongs to the Atelidae family. The genus comprises 11 species, which diversified during the Miocene, when their common ancestor expanded its geographical range through the Andean Cordillera (Meloro et al. 2014; Lynch-Alfaro et al. 2012). Biogeographically, there are two distinct, monophiletic groups of howlers. Trans-Andean *Alouatta* include species distributed over Central America and Trans-Andean Colombia and Equador. Cis-Andean *Alouatta* include the South American species (Cortes-Ortiz et al. 2003). Although widely distributed, most *Alouatta* species are restricted to a single biome and show little geographic overlap with each other (i.e. they tend to be parapatric). Howler monkeys are highly-specialized leafs feeders. As with many folivorous taxa, these monkeys tend to have a low activity pattern as compared to other South-American primates such as capuchins (Cortes-Ortiz et al. 2003; Lynch-Alfaro et al. 2012a).

We tested whether Rensch's and Bergmann's rules apply to *Alouatta* species and their interaction. We focused upon the Cis-Andean clade we have studied in the field. This is welcome because only Cis-Andean *Alouatta* occurs outside the Tropics, and occupy, as a group, a much wider latitudinal range than the Trans-Andean clade, making them better suited to study latitudinal effects on body size variation. We used latitude as the predictor variable in both cases, but since latitude is just a proxy for environmental variables (see Martinez et al. 2013; Maestri et al. 2016), such as temperature, precipitation and vegetation type, we further tested for the impact of these variables. Specifically, we stated three explicit hypotheses:

1 – *Alouatta* species follow Rensch's rule. In these primates, males tend to be larger than females and compete with each other (Meloro et al. 2014). Thus, we expect a stronger relationship between sexual dimorphism and the size of males rather than the size of females (i.e. male-driven increased SSD with size).

2 – *Alouatta* species follow Bergmann's rule at the interspecific level (Pincheira-Donoso 2010; Meiri 2011).

3 – Sexual size dimorphism (SSD) varies with the latitude. This hypothesis follows form hypotheses 1 and 2. If Rensch's and Bergmann's rule both apply in *Alouatta*, then sexual dimorphism will also correlate with latitude (as well as with the environmental variables latitude is a proxy for).

## MATERIALS AND METHODS

We collected data for 227 skulls of *Alouatta*, belonging to the following six different species, *A. belzebul*, *A. caraya*, *A. guariba*, *A. macconelli*, *A. nigerrima and A. seniculus* (with the exclusion of *A. sara* because of the lack of specimens in the museums we visited) housed in the main Brazilian museums: Museu Nacional (MNRJ), Museu Paraense Emílio Goeldi (MPEG), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu de História Natural Capão da Imbuia (MHNCI), Coleção Científica de Mastozoologia da UFPR (DZUP), Museu de ciências naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN/FZB). We included only specimens for which collection locality geographical coordinates were available. Unfortunately, body size data were not reported in most cases. We therefore relied on geometric morphometrics techniques to retrieve size information from the collected specimens. In geometric morphometrics, landmarks (placed on specimens' anatomically homologus points) are placed all along the structure of interest (in this case the skull). The specimen centroid size (a measure of the size of the landmarks configuration) is a very good proxy for body size (Zelditch et al. 2002). The data-acquisition protocol includes taking skull photographs taken at a fixed distance (1 m) to the digital camera appling zoom to correct possible deformations due to lenses (Meloro et al. 2008). Then, digital photographs were landmarked by a single investigator (N.C.), in order to prevent inter-observer error, using the software tpsDig2 2.16 (Rohlf, 2015). When taking photos, we positioned a scale bar adjacent to the specimen in order to transform digital pixels into linear measurements, allowing us to compute skull size directly from the configuration of landmarks. Twenty-three homologous landmarks were identified and digitized in order to extract skull size information, in the form of the natural logarithm of centroid size (LnCS, see configuration of landmarks used at Meloro et al. 2014). The protocol concluds with analytical and geometric transformation that reduce acquisition error and scales all the measured specimens to the unity (Rohlf and Slice 1990).

In order to study the geographical patterns of species body size and SSD, we collated geographically the specimens by performing a classic spatial sampling protocol. We overlaid the geographic dataset (sampling points) with a grid and then computed mean female body size, mean male body size, and SSD per species per each cell of the grid. This way, each body size mean and SSD datapoints acquire the geographical coordinates of the cell centroid they belong, separately for each species. We used a grid with a 250 x 250 km cell resolution in order to maximize the number of useful cells as to have at least one individual of both sexes for each species in a cell. In the end, the original dataset reduced from 227 specimens to 82 samples distributed in 38 total useful cells following the criteria explained above (Figure. 1; see also Figure S1 and Table S1).

## ENVIRONMENTAL VARIABLES

For each specimen, we recorded the geographic coordinates of its collection locality and a set of four related environmental variables: Annual Mean Temperature (BIO1), Temperature Seasonality (BIO4), Annual Precipitation (BIO12) and Precipitation Seasonality (BIO15) (Hijmans et al. 2005). These variables are provided as grogrphical raster grids at 50x50 km cell resolution (WorldClim raster database, worldclim.org). Temperature and precipitation, together with their variability, determine the dominant climate of a region. Two additional variables were taken from the Atlas of the Biosphere [net primary productivity (NPP) and evapotranspiration, https://nelson.wisc.edu/sage/data-and-models/atlas/maps.php], by using DIVA-GIS 7.5 software (http://www.divagis.org/download). These variables are informative as per the energy (biomass) available to species, which may impact on sexual dimorphism in primates (Plavcan et al. 2013).

## STATISTICAL ANALYSES

First, we used the cell-averaged LnCS to test for differences in sex and species (and their interaction) by using a two-way ANOVA. To test the existence of Rensch's rule, we computed the Sexual Size Dimorphism (SSD) for each species in each cell as the difference between male and female LnCS and used it as response variable versus female and male LnCS as covariates in a linear regression. Then, to test for Bergmann's rule, we used the cell-averaged female and male mean LnCS for each species against latitude of the cells centroids. Similarly, to test for a potential role of climate on these species skull size variability, we ran regression models including environmental variables as predictors and the sex-averaged LnCS for each species in each cell as response. The interaction between Rensch's and Bergmann's rule was tested by using SDD per cell as the response variable, and the latitude of the cell centroid, plus environmental variables in separate regression models (one for each predictor).

### *Controlling for the spatial autocorrelation and phylogenetic relatedness*

When dealing with geographically distributed variables, their spatial autocorrelation must be accounted for (Diniz-Filho et al. 2003). To this aim, we computed Moran's Index on both cell averaged SSD and male and female LnCS by using the software Sam v.4.0 (Rangel et al. 2010). In the case of the detection of a significant spatial autocorrelation, we took it into account in our analyses by including a new set of variables describing the spatial structure of the variables. This is done by performing the Eigenvector-based Spatial Filtering (Griffith, 2013), which is a method that uses a distance or connectivity matrix to perform a Principal Coordinate Analysis (PCOA). Then, the method selects the eigenvectors iteratively as to minimize spatial autocorrelation in the residuals (Griffith and Peres-Neto 2006). The algorithm starts by using the eigenvectors as explanatory variables in an Ordinary Least Square (OLS) regression with the trait (here cell averaged male, female LnCS, or SSD, alternatively) as the response variable. The residual autocorrelation is computed and the eigenvector in the model with smallest Moran's I coefficient is selected and becomes fixed. The algorithm proceeds iteratively by adding new eigenvectors in the (multiple) regression until the residuals autocorrelation is below a given threshold for p-values, usually 0.05 (Diniz-Filho et al. 2012; Carotenuto et al. 2015). Once the algorithm finds the most relevant eigenvectors, we can include them as additional covariates (herein named "spatial finters") in the regression modes The algorithm described above was performed by using the software SAM (Rangel et al. 2010).

Due to species shared ancestry, we also needed to take into account possible phylogenetic effects. We used as a reference the *Alouatta* tree provided by Cortes-Ortiz et al. (2003). The tree was trimmed to our dataset (i.e. by including Cis-Andean clade species only) using the Mesquite 2.75 software (Maddison and Maddison 2011) (Figure S2). We excluded *A. nigerrima* from the phylogenetic analyses because of its unstable phylogenetic positioning. Branch lengths were based on the estimated minimum ages, as reported in Cortes-Ortiz et al. (2003). The ages of undated nodes were estimated using the BLADJ algorithm (branch length adjustment; Webb et al 2008) in the Phylocom software. Since specimens were used as our sample base for the phylogeny, polytomies within each species were employed when more than one specimen per species was in the tree, conventionally setting tips within species at 0.1 Ma. The inclusion of multiple specimens per species is particularly important here, since potential within-species variation related to sex, geographical distribution and climate are the focus of the present paper. The multispecimens phylogenetic regressions were performed applying phylogenetic generalized least squares regressions (Ives et al. 2007), between environmental variables and the cell averaged values of SSD, of male LnCS, and of female LnCS, respectively, while accounting for interspecific variability, using the function pgls.SEy in 'phytools' (Revell 2012).

We performed all the regressions in four ways: by using Ordinary Least Squares (OLS); OLS with the spatial filters as additional covariates to account for spatial autocorrelation; performing PGLSs to account for phylogenetic relatedness; and drawing a more complex set of models by performing PGLS regressions including spatial filters as additional covariates to account for both phylogenetic relatedness and spatial autocorrelation at the same time.

## RESULTS

By grouping specimens using the 250 x 250 km cell resolution grid we identified 38 cells. Where a species was present with individuals of one sex only it was excluded. By this criterion, the number of cells available to testing reduced to 34.

In the two-way ANOVA model using species and sex as factors, we found size to be significantly different for both factors (Species: F = 15.626, Df = 5, P < 0.001; Sex: F = 392.251, Df = 1, P < 0.001), with no interaction between them (F = 0.801; Df = 5, P = 0.553). Males are larger than females in all species, with *A. macconnelli* and *A. seniculus* being the largest overall (Figure 2).

*Hypothesis 1. Rensch's Rule.*

We found strong evidence in favour of Rensch's rule (Table 2, Figure 3). Males skull size is significantly related to SSD, the same applies under PGLS, and when spatial filtering is applied. No significant result was found for females (Table 2, Figure 3).

*Hypothesis 2. Begmann's rule*

Against hypothesis 2, we found the reverse of Bergmann's rule to apply to both females and males in *Alouatta* when using the Ordinary Least Squares regression model (Table 3, Figure 4). The slope is positive, which means a decrease of males and females' LnCS southward. For males, the same applies when accounting for spatial and phylogenetic effects (Table 3). For females, Bergmann's rule disappeared under PGLS, and under PGLS plus spatial filter (Table 3). As regards the relationship between males LnCS and the environmental variables we found that when considering the BIO1 as covariate, all the four models were positive but significant only with the OLS and the OLS plus spatial filter (Table S3). When we considered the BIO4 as predictor, the model was always positive and significant for all the models. All the models were negative and significant when considering BIO12 as predictor, whereas no model was significant when considering BIO15. The relationships between male LnCS and evapotranspiration were all positive and significant, whereas no significant result was found when considering net primary productivity (Table S3).

For females, the relationship between LnCS and BIO1 was significant and positive only when considering the spatial information. The relationships beteween females LnCS and BIO4 were negative and significant only for the OLS and the OLS + spatial filter models, and the same applied when considering BIO4 except for the sign of the slope. The relationship between BIO12 and females LnCS was positive and significant only for the OLS and OLS + spatial filter, whereas no significant relationships were found for BIO15. Evapotranspiration was positive and significant for the first two models (Table S3), whereas no model was singnificant when considering net primary productivity as predictor (see Table S3).

### *Hypothesis 3. Sexual size dimorphism and latitude*

There is no significant relationship between the degree of sexual size dimorphism and latitude, irrespective of whether spatial autocorrelation, or phylogeny are accounted for (Table 4). The same applies with environmental variables (see Table S3).

## Discussion

The body size of individuals within species can be shaped by environmental (Bergmann's rule), ethological, or ecological factors, like character displacement, or the mating system(Bubadue et al. 2016; Carotenuto et al. 2015; Lisle and Rowe 2015; Meiri et al. 2014; Schuster and Wade 2003; Lande 1980). The way individuals of both sexes within a species react to these drivers over the evolutionary time determines the degree of sexual dimorphism, and how it unfolds over space.

South American howler monkeys are folivorous primates. They are large, which helps food digestion and lowers mass specific metabolic rates (Meloro et al. 2014a; Cáceres et al. 2014) as compared to other South-American primates, such as capuchins (Cáceres et al. 2014; Canale et al. 2009; Fragaszy et al. 2004). Howler monkeys show dominance rank competition between males (Kay et al. 1988) meaning the intensity of male/male context over mates is strong, which promotes sexual dimorphism (Kelaita et al. 2011; Plavcan et al. 1997; Ford, 1994). In general terms, folivory and arboreality correlate to little sexual size dimorphism in primates (Plavcan et al. 1997), but *Alouatta* possibly makes an exception (Plavcan et al. 1997; Ford 1994). Competition takes place between *Alouatta* species (Peres 1994), meaning the scope for sexual dimorphism is potentially counterbalanced by interspecific competition pressure (so far as size overlap between species is minimized to avoid competition, Dayan and Simberloff 2005). However, dietary differences between sexes are negligible in *Alouatta* species (Pavelka et al. 2004; Glander and Tedford 1995; Bicca-Marques et al. 1994) meaning there is little competition for food between males and females. Therefore, the positive relationship between male size and sexual size dimorphism we found (in keeping with Rensch`s rule) must be driven by male/male interactions, at least to some extent. Ravosa and Ross (1994) found evidence for Rensh's rule in *Alouatta*, and similarly related their findings to the prolonged growth of males in this genus. It has been suggested that an even distribution of resources through the year decreases sexual dimorphism in polyginous species (Isaac and Johnson 2003). As *Alouatta* experience a seasonal abundance of fruit in their diet (Bicca-Marques et al. 1994; Peres 1994), it is possible that males are better in securing this occasional resource surplus than females, which would burst their growth (Weckerly 1998) and help intrasexual competition over mates. We found that Brown howler monkeys *A. guariba* follows Bergmann's rule. It is interesting noticing that the percentage of leaves in the diet of the brown howler decreases with latitude in Belize (Chaves and Bicca-Marques 2013). Assuming this to be true for other species as well, it suggests that folivory decreases body size differences with latitude within species, but increases it between species. This would help explaining why we found evidence for a reverse Bergmann's pattern for both males and females (Table 4), and why larger species do occur in the Amazon basin (Figure 1).

In summary, our results indicate that body size variation in *Alouatta* follows Rensch's rule. A possible explanation of such a pattern can be addressed to the Howler monkeys' dominance rank competition mate system (Kay et al. 1988) that, coupled with the seasonal abundance of fruits supply in the Amazon basin, favours selection for large sized males in equatorial species. We found a reverse Bergmann's rule pattern between species, although Bergmman's rule may be still valid within some individual species. This possibly depends on the relative consumption of leaves versus fruit in the diet, which is higher in the Amazon basin. Whereas larger howlers are folivorous, the occasional inclusion of fruit in the diet may increase body size within species, especially in males.

## Limitation of the study

We urge the reader to consider that the results we found are valid for some one half of the living Howler species. While this does not weaken the validity and the soundness of our findings, it would be interesting to explore, in the future, whether the same patterns accrue to Trans-Andean howlers.

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**Table 1**. Skull sample size for the six Alouatta species considered in this study. The data reported are referred to the whole sample of specimens and the reduced dataset after the spatial sampling by cell grid.

| **Species** | **#Specimens** | **#Females** | **#Males** | **#Specimens in cells** | **#Females in cells** | **#Males in cells** | **Average females per cell** | **Average males per cell** |
|---|---|---|---|---|---|---|---|---|
| *Alouatta belzebul* (Linnaeus, 1766) | 65 | 36 | 29 | 16 | 8 | 8 | 1 | 1 |
| *Alouatta caraya* (Humboldt, 1812) | 44 | 19 | 25 | 22 | 11 | 11 | 1.1 | 1.1 |
| *Alouatta guariba* (Humboldt, 1812) | 47 | 19 | 28 | 18 | 9 | 9 | 1 | 1 |
| *Alouatta macconelli* Elliot, 1910 | 11 | 5 | 6 | 6 | 3 | 3 | 1 | 1 |
| *Alouatta nigerrima* Lönnberg, 1941 | 10 | 5 | 5 | 2 | 1 | 1 | 1 | 1 |
| *Alouatta seniculus* (Linnaeus, 1766) | 50 | 29 | 21 | 20 | 9 | 9 | 1 | 1 |
| Total | 227 | 113 | 114 | 84 | 42 | 42 | | |

**Table 2. Results of regressions between body size and the degree of sexual dimorphism in *Alouatta*, performed separately for males and females, respectively. male LnCS = natural logarithm of males' centroid size, female LnCS = natural logarithm of females' centroid size, SSD = sexual size dimorphism. The specification 'PGLS' indicates phylogenetic generalized least squares regression results. The specification 's.filter' indicates spatial filtering was imposed on the regressor to account for spatial autocorrelation.**

| | **male LnCS vs SSD** | **male LnCS vs SSD + s.filter** | **male LnCS vs SSD in PGLS** | **male LnCS vs SSD + s.filter in PGLS** |
|---|---|---|---|---|
| **Slope** | 0.843 | 0.830 | 0.588 | 0.601 |
| **st.error** | 0.181 | 0.177 | 0.112 | 0.114 |
| **t** | 4.659 | 4.689 | 5.242 | 5.286 |
| ***p*** | 0.000 | 0.000 | 0.000 | 0.000 |
| **logLik** | 62.701 | 64.135 | 68.288 | 66.316 |

| | **female LnCS vs SSD** | **female LnCS vs SSD + s.filter** | **female LnCS vs SSD in PGLS** | **female LnCS vs SSD + s.filter in PGLS** |
|---|---|---|---|---|
| **Slope** | -0.156 | -0.169 | -0.323 | -0.331 |
| **st.error** | 0.185 | 0.181 | 0.171 | 0.176 |
| **t** | -0.845 | -0.937 | -1.893 | -1.882 |
| ***p*** | 0.403 | 0.355 | 0.066 | 0.068 |
| **logLik** | 61.873 | 63.291 | 59.911 | 57.861 |

| | **male LnCS vs female LnCS** | **male LnCS vs female LnCS + s.filter** | **male LnCS vs female LnCS in PGLS** | **male LnCS vs female LnCS + s.filter in PGLS** |
|---|---|---|---|---|
| **Slope** | 0.807 | 0.784 | 0.382 | 0.368 |
| **st.error** | 0.151 | 0.157 | 0.121 | 0.122 |
| **t** | 5.355 | 4.983 | 3.164 | 3.010 |
| ***p*** | 0.000 | 0.000 | 0.003 | 0.005 |
| **logLik** | 64.890 | 65.068 | 65.573 | 63.672 |

**Table 3. Results of regressions between body size latitude in *Alouatta*, performed separately for males and females, respectively. male LnCS = natural logarithm of males' centroid size, female LnCS = natural logarithm of females' centroid size, Latitude = latitude of the grid cell in decimal degrees. The specification 'PGLS' indicates phylogenetic generalized least squares regression results. The specification 's.filter' indicates spatial filtering was imposed on the regressor to account for spatial autocorrelation.**

| | **Latitude vs male LnCS** | **Latitude vs male LnCS + s.filter** | **Latitude vs male LnCS in PGLS** | **Latitude vs male LnCS + s.filter in PGLS** |
|---|---|---|---|---|
| **Slope** | 84.723 | 85.950 | 0.002 | 0.002 |
| **st.error** | 21.199 | 22.112 | 0.001 | 0.001 |
| **t** | 3.997 | 3.887 | 2.298 | 2.104 |
| ***p*** | 0.000 | 0.000 | 0.027 | 0.042 |
| **logLik** | -135.817 | -135.788 | 51.671 | 49.722 |

| | **Latitude vs female LnCS** | **Latitude vs female LnCS + s.filter** | **Latitude vs female LnCS in PGLS** | **Latitude vs female LnCS + s.filter in PGLS** |
|---|---|---|---|---|
| **Slope** | 88.925 | 90.029 | 0.001 | 0.001 |
| **st.error** | 27.315 | 28.637 | 0.001 | 0.001 |
| **t** | 3.256 | 3.144 | 1.423 | 1.119 |
| ***p*** | 0.002 | 0.003 | 0.163 | 0.271 |
| **logLik** | -137.903 | -137.891 | 57.165 | 55.322 |

**Table 4. The degree of sexual dimorphism (ssd) regressed against latitude in *Alouatta*. Regressions were performed separately for males and females, respectively. lat = latitude in decimal degrees. The specification 'PGLS' indicates phylogenetic generalized least squares regression results. The specification 'SF' indicates spatial filtering was imposed on the regressor to account for spatial autocorrelation.**

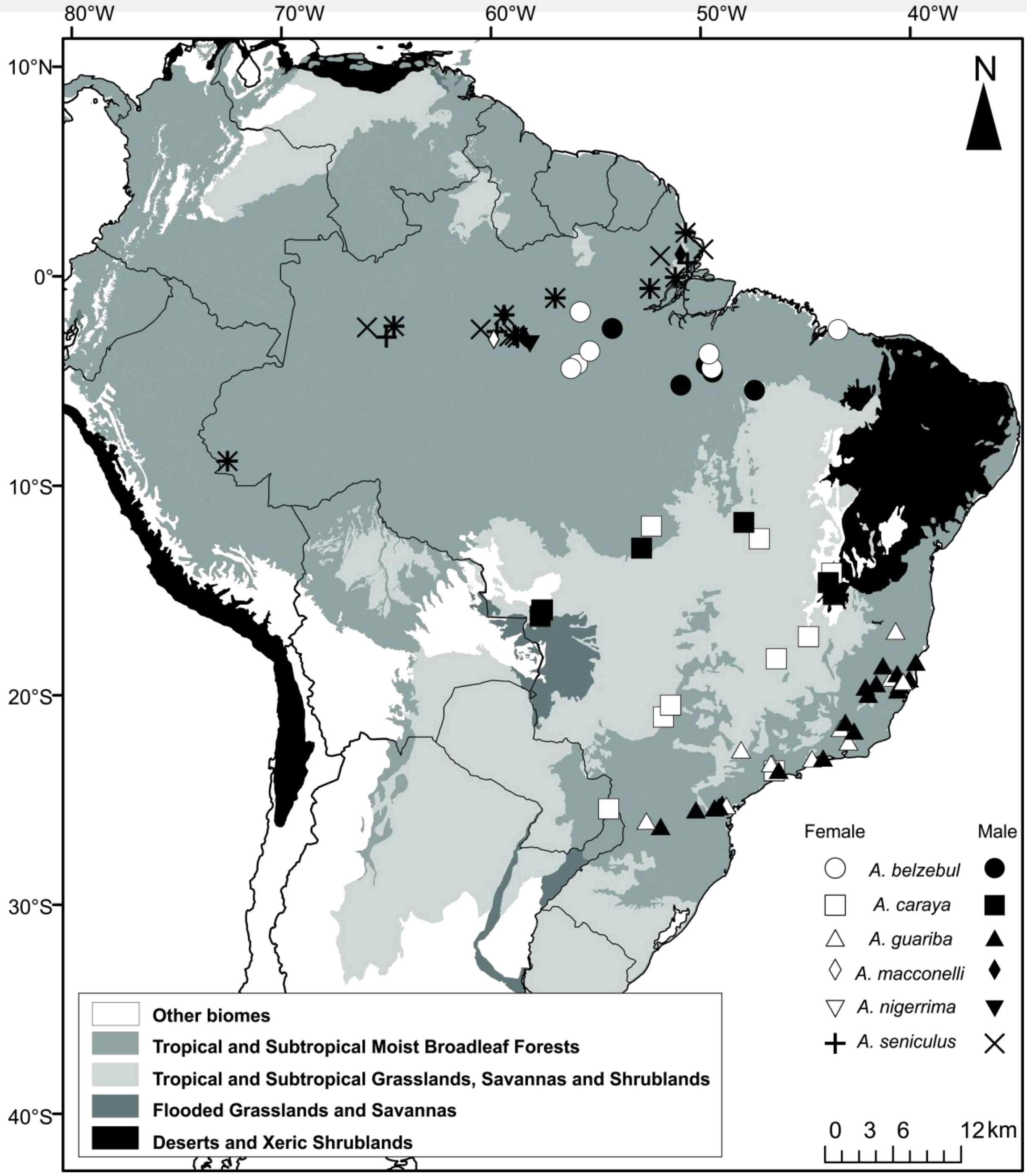
| | **Latitude vs SSD** | **Latitude vs SSD + s.filter** | **Latitude vs SSD in PGLS** | **Latitude vs SSD + s.filter in PGLS** |
|---|---|---|---|---|
| **Slope** | 47.288 | 46.432 | 0.001 | 0.001 |
| **st.error** | 34.289 | 34.649 | 0.001 | 0.001 |
| **t** | 1.379 | 1.340 | 1.125 | 1.202 |
| ***p*** | 0.176 | 0.189 | 0.268 | 0.237 |
| **logLik** | -141.838 | -141.672 | 53.671 | 51.760 |

**Figure 1.** Map of South America showing the geographic distribution of *Alouatta* specimens. Sampling localities of different species and sexes are shown by different symbols.

**Figure 2.** Box plot with standardized deviation of natural log transformed centroid size (LnCS) across sexes. Black string: median, white box: first interquartile, bar: second interquartile. Different species and sexes are shown by different symbols.

**Figure 3.** Regression plots for Rensch's sexual size dimorphism and female and male natural log transformed centroid size (LnCS). Species and sexes are labelled by different symbols.

**Figure 4.** Regression plots for Bergmann's rule on its original form, latitude, and female and male natural log transformed centroid size (LnCS). Species and sexes are labelled by different symbols.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40°S
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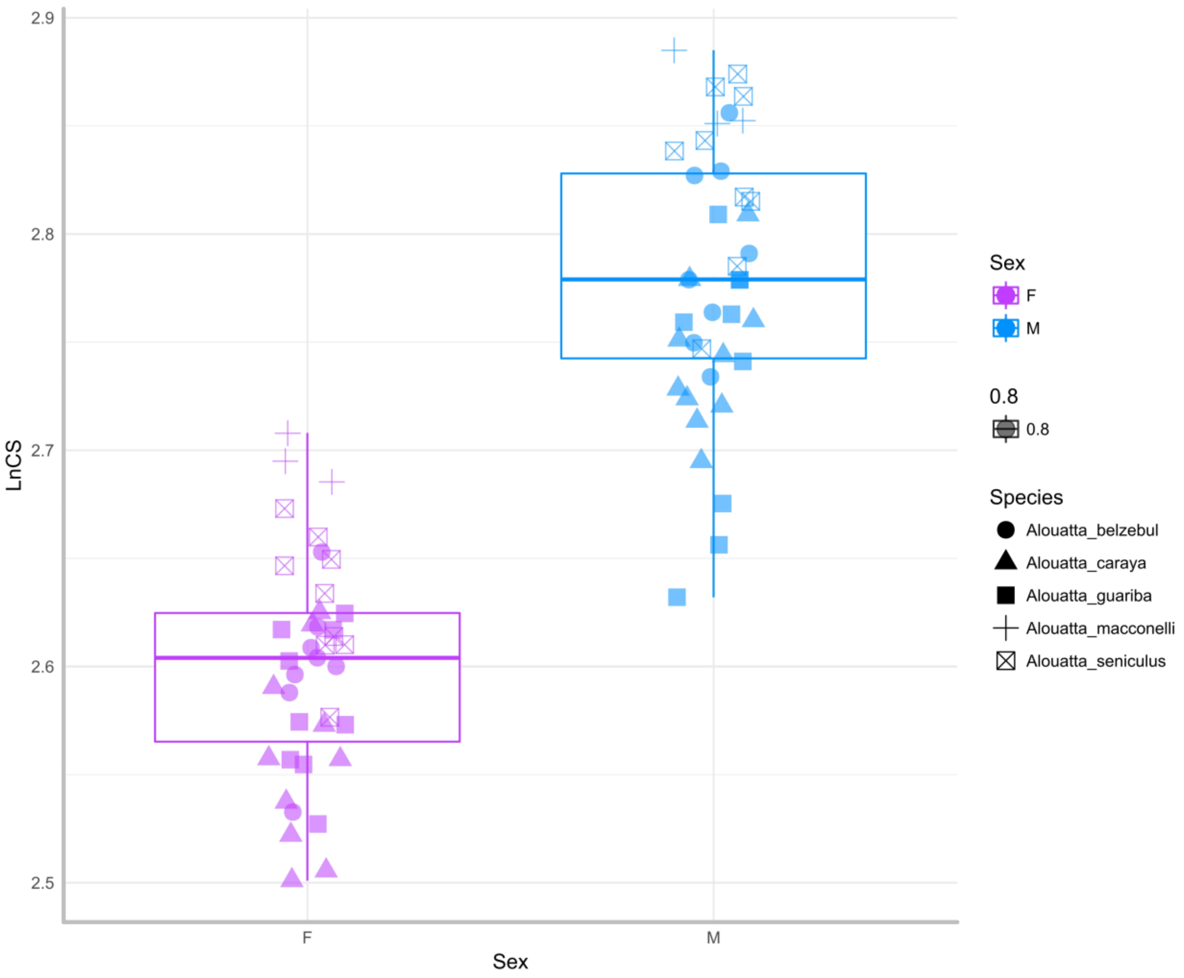
Female
Male
A. belzebul
A. caraya
A. guariba
A. macconelli
A. nigerrima
A. seniculus
Other biomes
Tropical and Subtropical Moist Broadleaf Forests
Tropical and Subtropical Grasslands, Savannas and Shrublands
Flooded Grasslands and Savannas
Deserts and Xeric Shrublands
0 3 6 12 km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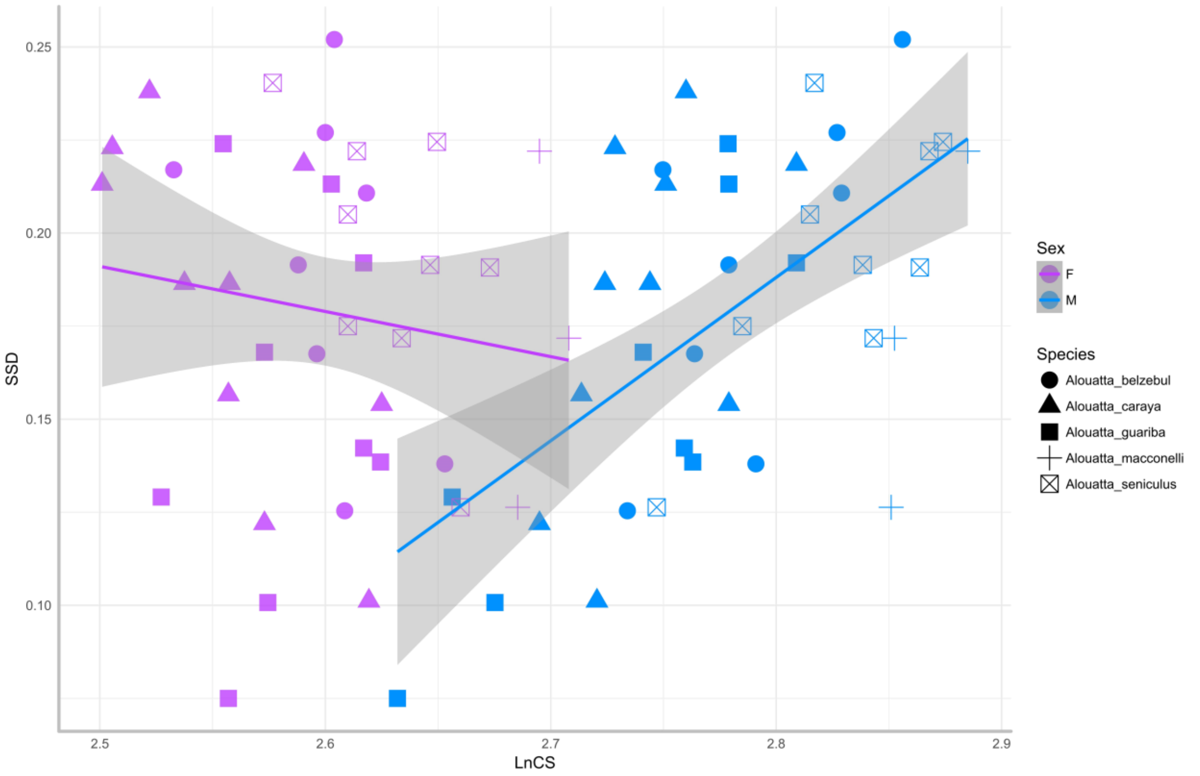
Alouatta_macconelli
Alouatta_seniculus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Alouatta_seniculus

HYSTRIX
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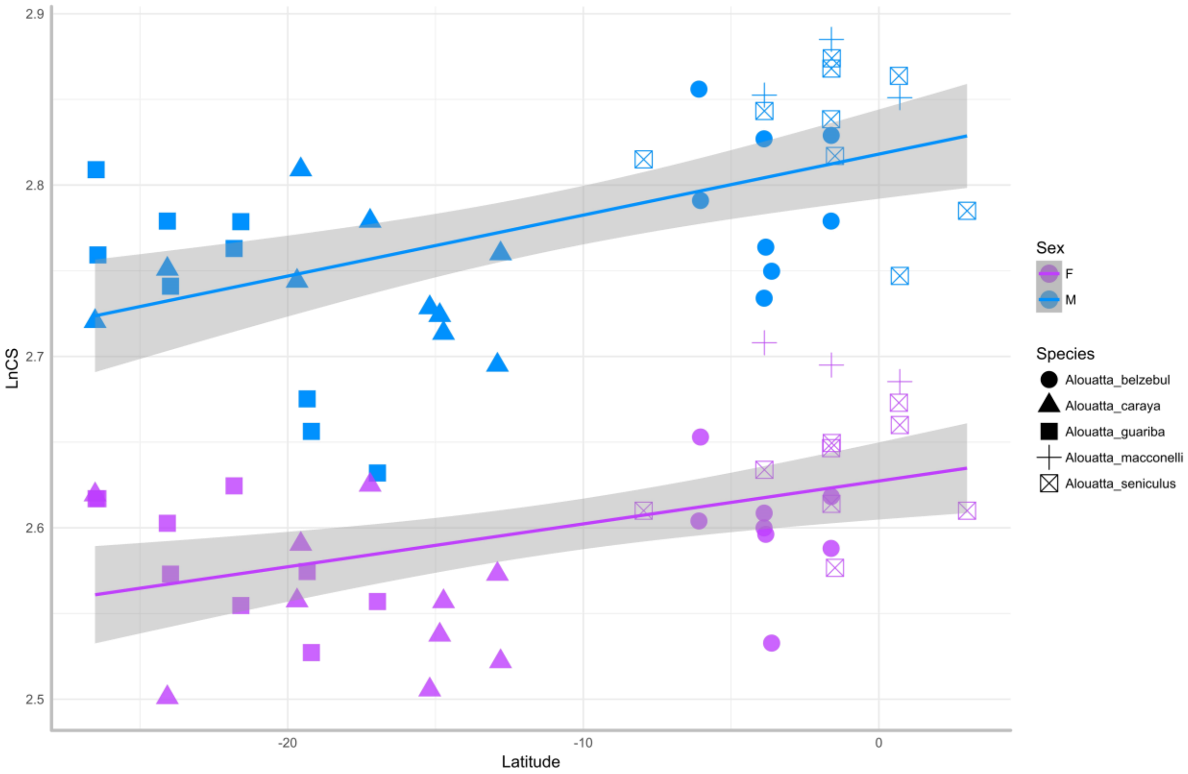

**Supplemental information**

**Figure S1.** The 250x250 cell resolution geographical grid used to average morphological and environmental variables related to the recorded specimens. Red points indicate sampling localities, blue points indicate centres of the related cells.

**Figure S2.** Phylogenetic tree used in all the phylogenetic informed analyses. The colour of the branches represents the mapped Sexual Size Dimorhism (SSD). States of internal nodes are reconstructed via Maximum Likelihood Estimation.

**Table S1.** The dataset used in this study.

**Table S2.** Spatial autocorrelation results.

**Table S3**. Results of the regressions between males and females'LnCS and the environmental variables.

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