

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

Type:

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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 characteristics 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

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36 36 **ABSTRACT**

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66 **INTRODUCTION**

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

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

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

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

88 In primates, both Bergmann's and Rensch's rules were explored a number of times (Gordon 2004;
89 Clauss et al 2013). Harcourt and Schreier (2009) found support for Bergmann's rule, and Smith and Cheverud
90 (2002) found Primate as a whole to obey Rensch's rule. Yet, when the model is controlled for the phylogeny, the
91 relationship disappears for both Platyrrhini and Strepsirhini.

92 Howler monkeys (genus *Alouatta*) are an ideal study model to test Bergmann's rule, Rensch's rules, and
93 their potential interaction. Howlers are highly sexually dimorphic (Ford 1994), and widely distributed in South
94 America. *Alouatta* belongs to the Atelidae family. The genus comprises 11 species, which diversified during the
95 Miocene, when their common ancestor expanded its geographical range through the Andean Cordillera (Meloro

96 et al. 2014; Lynch-Alfaro et al. 2012). Biogeographically, there are two distinct, monophyletic groups of howlers.
97 Trans-Andean *Alouatta* include species distributed over Central America and Trans-Andean Colombia and
98 Ecuador. Cis-Andean *Alouatta* include the South American species (Cortes-Ortiz et al. 2003). Although widely
99 distributed, most *Alouatta* species are restricted to a single biome and show little geographic overlap with each
100 other (i.e. they tend to be parapatric). Howler monkeys are highly-specialized leafs feeders. As with many
101 folivorous taxa, these monkeys tend to have a low activity pattern as compared to other South-American
102 primates such as capuchins (Cortes-Ortiz et al. 2003; Lynch-Alfaro et al. 2012a).

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

110 1 – *Alouatta* species follow Rensch's rule. In these primates, males tend to be larger than females and compete
111 with each other (Meloro et al. 2014). Thus, we expect a stronger relationship between sexual dimorphism and the
112 size of males rather than the size of females (i.e. male-driven increased SSD with size).

113 2 – *Alouatta* species follow Bergmann's rule at the interspecific level (Pincheira-Donoso 2010; Meiri 2011).

114 3 – Sexual size dimorphism (SSD) varies with the latitude. This hypothesis follows from hypotheses 1 and 2. If
115 Rensch's and Bergmann's rule both apply in *Alouatta*, then sexual dimorphism will also correlate with latitude
116 (as well as with the environmental variables latitude is a proxy for).

118 MATERIALS AND METHODS

120 We collected data for 227 skulls of *Alouatta*, belonging to the following six different species, *A.*

121 *belzebul*, *A. caraya*, *A. guariba*, *A. macconelli*, *A. nigerrima* and *A. seniculus* (with the exclusion of *A. sara*

122 because of the lack of specimens in the museums we visited) housed in the main Brazilian museums: Museu

123 Nacional (MNRJ), Museu Paraense Emilio Goeldi (MPEG), Museu de Zoologia da Universidade de São Paulo

124 (MZUSP), Museu de História Natural Capão da Imbuia (MHNCI), Coleção Científica de Mastozoologia da

125 UFPR (DZUP), Museu de ciências naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN/FZB). We

126 included only specimens for which collection locality geographical coordinates were available. Unfortunately,
127 body size data were not reported in most cases. We therefore relied on geometric morphometrics techniques to
128 retrieve size information from the collected specimens. In geometric morphometrics, landmarks (placed on
129 specimens' anatomically homologous points) are placed all along the structure of interest (in this case the skull).
130 The specimen centroid size (a measure of the size of the landmarks configuration) is a very good proxy for body
131 size (Zelditch et al. 2002). The data-acquisition protocol includes taking skull photographs taken at a fixed
132 distance (1 m) to the digital camera applying zoom to correct possible deformations due to lenses (Meloro et al.
133 2008). Then, digital photographs were landmarked by a single investigator (N.C.), in order to prevent inter-
134 observer error, using the software tpsDig2 2.16 (Rohlf, 2015). When taking photos, we positioned a scale bar
135 adjacent to the specimen in order to transform digital pixels into linear measurements, allowing us to compute
136 skull size directly from the configuration of landmarks. Twenty-three homologous landmarks were identified and
137 digitized in order to extract skull size information, in the form of the natural logarithm of centroid size (LnCS,
138 see configuration of landmarks used at Meloro et al. 2014). The protocol concludes with analytical and geometric
139 transformation that reduce acquisition error and scales all the measured specimens to the unity (Rohlf and Slice
140 1990).

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

151 ENVIRONMENTAL VARIABLES

152 For each specimen, we recorded the geographic coordinates of its collection locality and a set of four related
153 environmental variables: Annual Mean Temperature (BIO1), Temperature Seasonality (BIO4), Annual
154 Precipitation (BIO12) and Precipitation Seasonality (BIO15) (Hijmans et al. 2005). These variables are provided
155 as geographical raster grids at 50x50 km cell resolution (WorldClim raster database, worldclim.org). Temperature

156 and precipitation, together with their variability, determine the dominant climate of a region. Two additional
157 variables were taken from the Atlas of the Biosphere [net primary productivity (NPP) and evapotranspiration,
158 <https://nelson.wisc.edu/sage/data-and-models/atlas/maps.php>], by using DIVA-GIS 7.5 software
159 (<http://www.divagis.org/download>). These variables are informative as per the energy (biomass) available to
160 species, which may impact on sexual dimorphism in primates (Plavcan et al. 2013).

162 STATISTICAL ANALYSES

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

174 *Controlling for the spatial autocorrelation and phylogenetic relatedness*

175 When dealing with geographically distributed variables, their spatial autocorrelation must be accounted for
176 (Diniz-Filho et al. 2003). To this aim, we computed Moran's Index on both cell averaged SSD and male and
177 female LnCS by using the software Sam v.4.0 (Rangel et al. 2010). In the case of the detection of a significant
178 spatial autocorrelation, we took it into account in our analyses by including a new set of variables describing the
179 spatial structure of the variables. This is done by performing the Eigenvector-based Spatial Filtering (Griffith,
180 2013), which is a method that uses a distance or connectivity matrix to perform a Principal Coordinate Analysis
181 (PCOA). Then, the method selects the eigenvectors iteratively as to minimize spatial autocorrelation in the
182 residuals (Griffith and Peres-Neto 2006). The algorithm starts by using the eigenvectors as explanatory variables
183 in an Ordinary Least Square (OLS) regression with the trait (here cell averaged male, female LnCS, or SSD,
184 alternatively) as the response variable. The residual autocorrelation is computed and the eigenvector in the model
185 with smallest Moran's I coefficient is selected and becomes fixed. The algorithm proceeds iteratively by adding

186 new eigenvectors in the (multiple) regression until the residuals autocorrelation is below a given threshold for p-
187 values, usually 0.05 (Diniz-Filho et al. 2012; Carotenuto et al. 2015). Once the algorithm finds the most relevant
188 eigenvectors, we can include them as additional covariates (herein named “spatial filters”) in the regression
189 modes. The algorithm described above was performed by using the software SAM (Rangel et al. 2010).

190 Due to species shared ancestry, we also needed to take into account possible phylogenetic effects. We
191 used as a reference the *Alouatta* tree provided by Cortes-Ortiz et al. (2003). The tree was trimmed to our dataset
192 (i.e. by including Cis-Andean clade species only) using the Mesquite 2.75 software (Maddison and Maddison
193 2011) (Figure S2). We excluded *A. nigerrima* from the phylogenetic analyses because of its unstable
194 phylogenetic positioning. Branch lengths were based on the estimated minimum ages, as reported in Cortes-Ortiz
195 et al. (2003). The ages of undated nodes were estimated using the BLADJ algorithm (branch length adjustment;
196 Webb et al. 2008) in the Phylocom software. Since specimens were used as our sample base for the phylogeny,
197 polytomies within each species were employed when more than one specimen per species was in the tree,
198 conventionally setting tips within species at 0.1 Ma. The inclusion of multiple specimens per species is
199 particularly important here, since potential within-species variation related to sex, geographical distribution and
200 climate are the focus of the present paper. The multispecimens phylogenetic regressions were performed
201 applying phylogenetic generalized least squares regressions (Ives et al. 2007), between environmental variables
202 and the cell averaged values of SSD, of male LnCS, and of female LnCS, respectively, while accounting for
203 interspecific variability, using the function `pgls.SEy` in ‘phytools’ (Revell 2012).

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

213 RESULTS

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

217 217 In the two-way ANOVA model using species and sex as factors, we found size to be significantly
218 218 different for both factors (Species: $F = 15.626$, $Df = 5$, $P < 0.001$; Sex: $F = 392.251$, $Df = 1$, $P < 0.001$), with no
219 219 interaction between them ($F = 0.801$; $Df = 5$, $P = 0.553$). Males are larger than females in all species, with *A.*
220 220 *macconnelli* and *A. seniculus* being the largest overall (Figure 2).

221 221
222 222 *Hypothesis 1. Rensch's Rule.*

223 223 We found strong evidence in favour of Rensch's rule (Table 2, Figure 3). Males skull size is significantly related
224 224 to SSD, the same applies under PGLS, and when spatial filtering is applied. No significant result was found for
225 225 females (Table 2, Figure 3).

226 226
227 227 *Hypothesis 2. Bergmann's rule*

228 228 Against hypothesis 2, we found the reverse of Bergmann's rule to apply to both females and males in *Alouatta*
229 229 when using the Ordinary Least Squares regression model (Table 3, Figure 4). The slope is positive, which means
230 230 a decrease of males and females' LnCS southward. For males, the same applies when accounting for spatial and
231 231 phylogenetic effects (Table 3). For females, Bergmann's rule disappeared under PGLS, and under PGLS plus
232 232 spatial filter (Table 3). As regards the relationship between males LnCS and the environmental variables we
233 233 found that when considering the BIO1 as covariate, all the four models were positive but significant only with
234 234 the OLS and the OLS plus spatial filter (Table S3). When we considered the BIO4 as predictor, the model was
235 235 always positive and significant for all the models. All the models were negative and significant when considering
236 236 BIO12 as predictor, whereas no model was significant when considering BIO15. The relationships between male
237 237 LnCS and evapotranspiration were all positive and significant, whereas no significant result was found when
238 238 considering net primary productivity (Table S3).

239 239 For females, the relationship between LnCS and BIO1 was significant and positive only when considering the
240 240 spatial information. The relationships between females LnCS and BIO4 were negative and significant only for
241 241 the OLS and the OLS + spatial filter models, and the same applied when considering BIO4 except for the sign of
242 242 the slope. The relationship between BIO12 and females LnCS was positive and significant only for the OLS and
243 243 OLS + spatial filter, whereas no significant relationships were found for BIO15. Evapotranspiration was positive
244 244 and significant for the first two models (Table S3), whereas no model was significant when considering net
245 245 primary productivity as predictor (see Table S3).

247 247 *Hypothesis 3. Sexual size dimorphism and latitude*

248 248 There is no significant relationship between the degree of sexual size dimorphism and latitude, irrespective of
249 249 whether spatial autocorrelation, or phylogeny are accounted for (Table 4). The same applies with environmental
250 250 variables (see Table S3).

251 251

252 252 **Discussion**

253 253 The body size of individuals within species can be shaped by environmental (Bergmann's rule),
254 254 ethological, or ecological factors, like character displacement, or the mating system (Bubadue et al. 2016;
255 255 Carotenuto et al. 2015; Lisle and Rowe 2015; Meiri et al. 2014; Schuster and Wade 2003; Lande 1980). The way
256 256 individuals of both sexes within a species react to these drivers over the evolutionary time determines the degree
257 257 of sexual dimorphism, and how it unfolds over space.

258 258 South American howler monkeys are folivorous primates. They are large, which helps food digestion
259 259 and lowers mass specific metabolic rates (Meloro et al. 2014a; Cáceres et al. 2014) as compared to other South-
260 260 American primates, such as capuchins (Cáceres et al. 2014; Canale et al. 2009; Fragaszy et al. 2004). Howler
261 261 monkeys show dominance rank competition between males (Kay et al. 1988) meaning the intensity of male/male
262 262 context over mates is strong, which promotes sexual dimorphism (Kelaita et al. 2011; Plavcan et al. 1997; Ford,
263 263 1994). In general terms, folivory and arboreality correlate to little sexual size dimorphism in primates (Plavcan et
264 264 al. 1997), but *Alouatta* possibly makes an exception (Plavcan et al. 1997; Ford 1994). Competition takes place
265 265 between *Alouatta* species (Peres 1994), meaning the scope for sexual dimorphism is potentially counterbalanced
266 266 by interspecific competition pressure (so far as size overlap between species is minimized to avoid competition,
267 267 Dayan and Simberloff 2005). However, dietary differences between sexes are negligible in *Alouatta* species
268 268 (Pavelka et al. 2004; Glander and Tedford 1995; Bicca-Marques et al. 1994) meaning there is little competition
269 269 for food between males and females. Therefore, the positive relationship between male size and sexual size
270 270 dimorphism we found (in keeping with Rensch's rule) must be driven by male/male interactions, at least to some
271 271 extent. Ravosa and Ross (1994) found evidence for Rensch's rule in *Alouatta*, and similarly related their findings
272 272 to the prolonged growth of males in this genus. It has been suggested that an even distribution of resources
273 273 through the year decreases sexual dimorphism in polyginous species (Isaac and Johnson 2003). As *Alouatta*
274 274 experience a seasonal abundance of fruit in their diet (Bicca-Marques et al. 1994; Peres 1994), it is possible that
275 275 males are better in securing this occasional resource surplus than females, which would burst their growth
276 276 (Weckerly 1998) and help intrasexual competition over mates. We found that Brown howler monkeys *A. guariba*

277 follows Bergmann's rule. It is interesting noticing that the percentage of leaves in the diet of the brown howler
278 decreases with latitude in Belize (Chaves and Bicca-Marques 2013). Assuming this to be true for other species as
279 well, it suggests that folivory decreases body size differences with latitude within species, but increases it
280 between species. This would help explaining why we found evidence for a reverse Bergmann's pattern for both
281 males and females (Table 4), and why larger species do occur in the Amazon basin (Figure 1).

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

291 **Limitation of the study**

292 We urge the reader to consider that the results we found are valid for some one half of the living Howler
293 species. While this does not weaken the validity and the soundness of our findings, it would be interesting to
294 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	
<i>Alouatta belzebul</i> (Linnaeus, 1766)				65	36	29	16	8	8	1	1
<i>Alouatta caraya</i> (Humboldt, 1812)				44	19	25	22	11	11	1.1	1.1
<i>Alouatta guariba</i> (Humboldt, 1812)				47	19	28	18	9	9	1	1
<i>Alouatta macconelli</i> Elliot, 1910				11	5	6	6	3	3	1	1
<i>Alouatta nigerrima</i> Lönnerberg, 1941				10	5	5	2	1	1	1	1
<i>Alouatta seniculus</i> (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

494 **Table 3. Results of regressions between body size latitude in *Alouatta*, performed separately for males and**
 495 **females, respectively. male LnCS = natural logarithm of males' centroid size, female LnCS = natural**
 496 **logarithm of females' centroid size, Latitude = latitude of the grid cell in decimal degrees. The**
 497 **specification 'PGLS' indicates phylogenetic generalized least squares regression results. The specification**
 498 **'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.

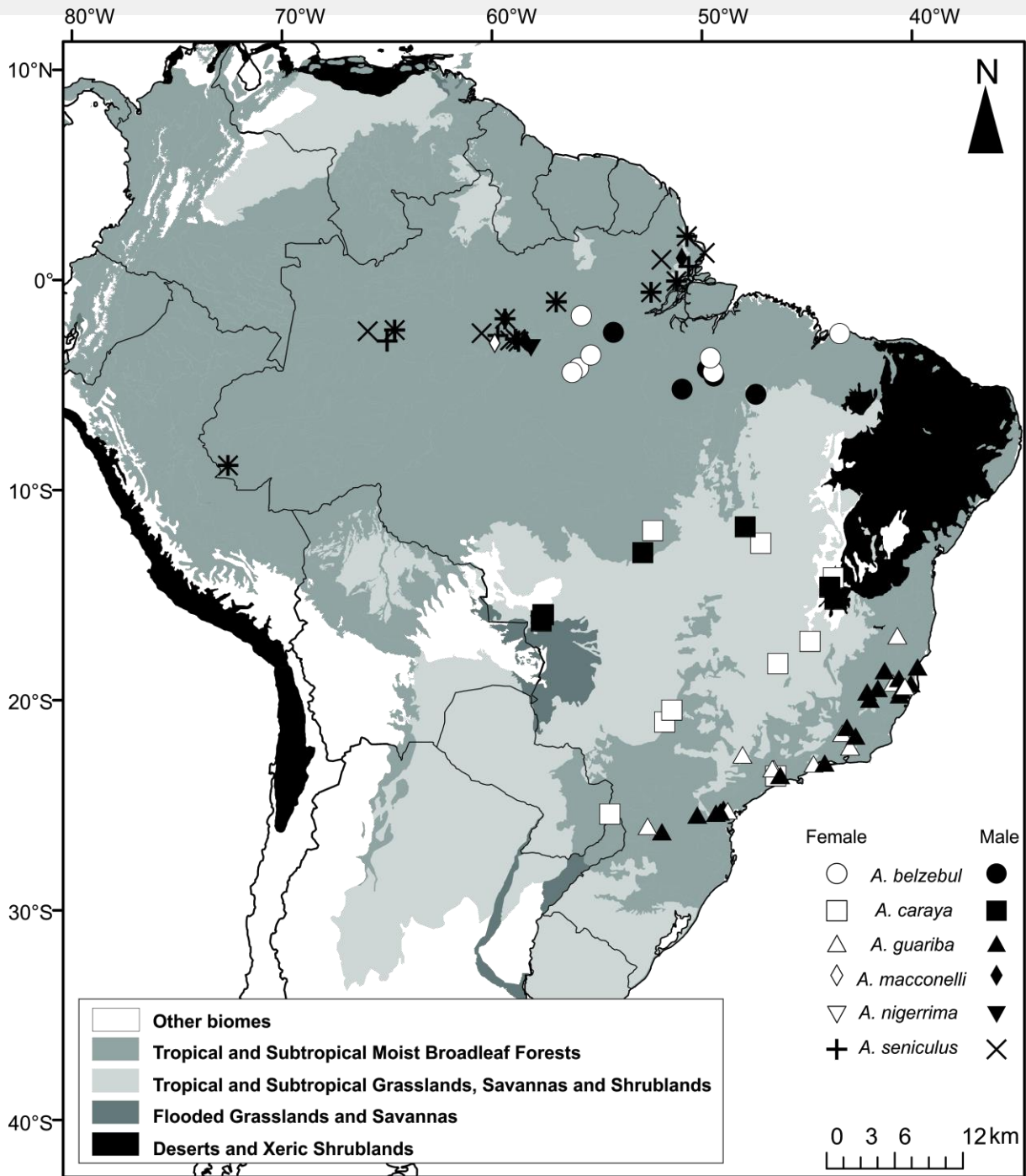
	Latitude vs SSD	Latitude vs SSD + s.filter	Latitude vs SSD in PGLS	Latitude vs SSD + s.filter in PGLS
Slope	47.288	46.432	0.001	0.001
st.error	34.289	34.649	0.001	0.001
t	1.379	1.340	1.125	1.202
p	0.176	0.189	0.268	0.237
logLik	-141.838	-141.672	53.671	51.760

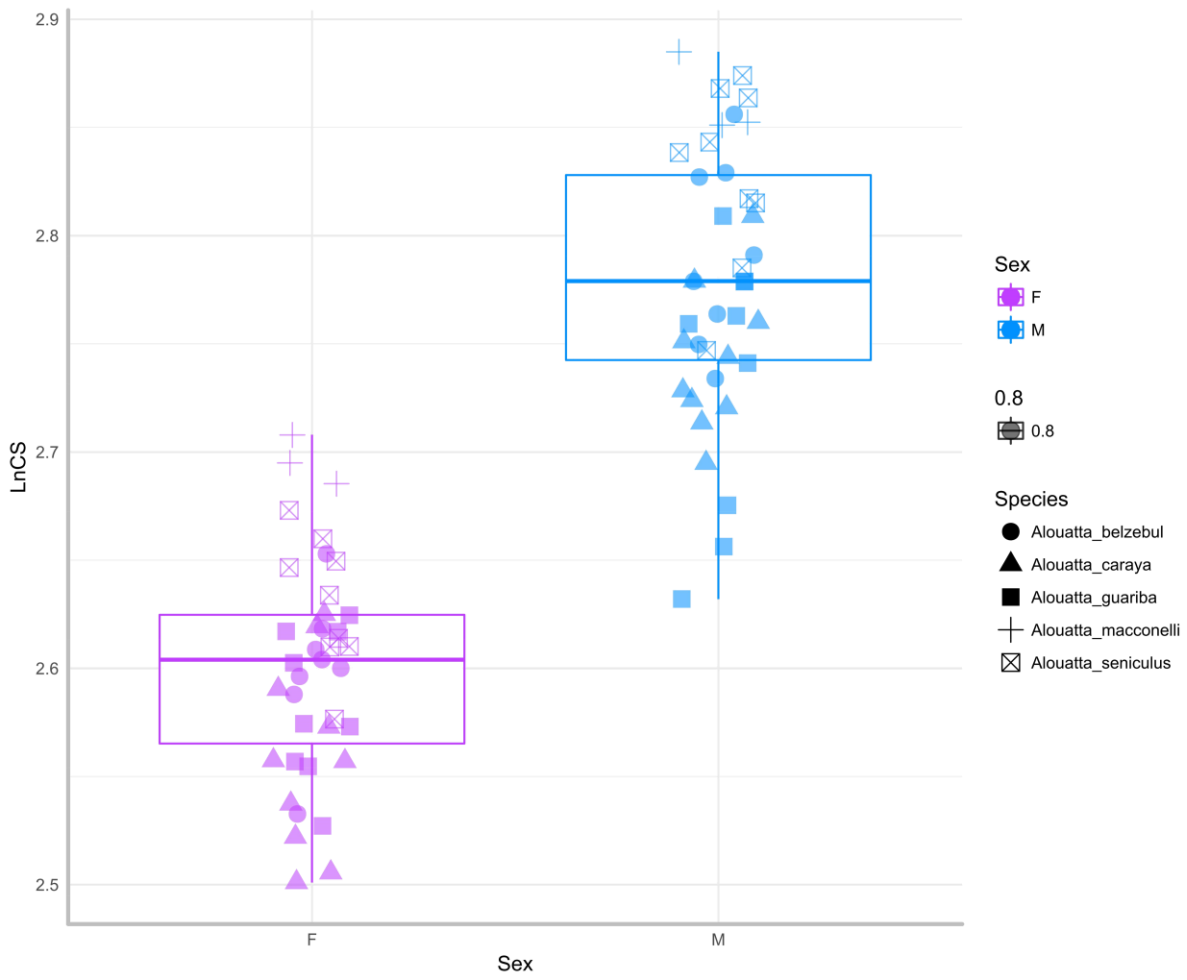
524 **Figure 1.** Map of South America showing the geographic distribution of *Alouatta* specimens. Sampling localities
525 of different species and sexes are shown by different symbols.

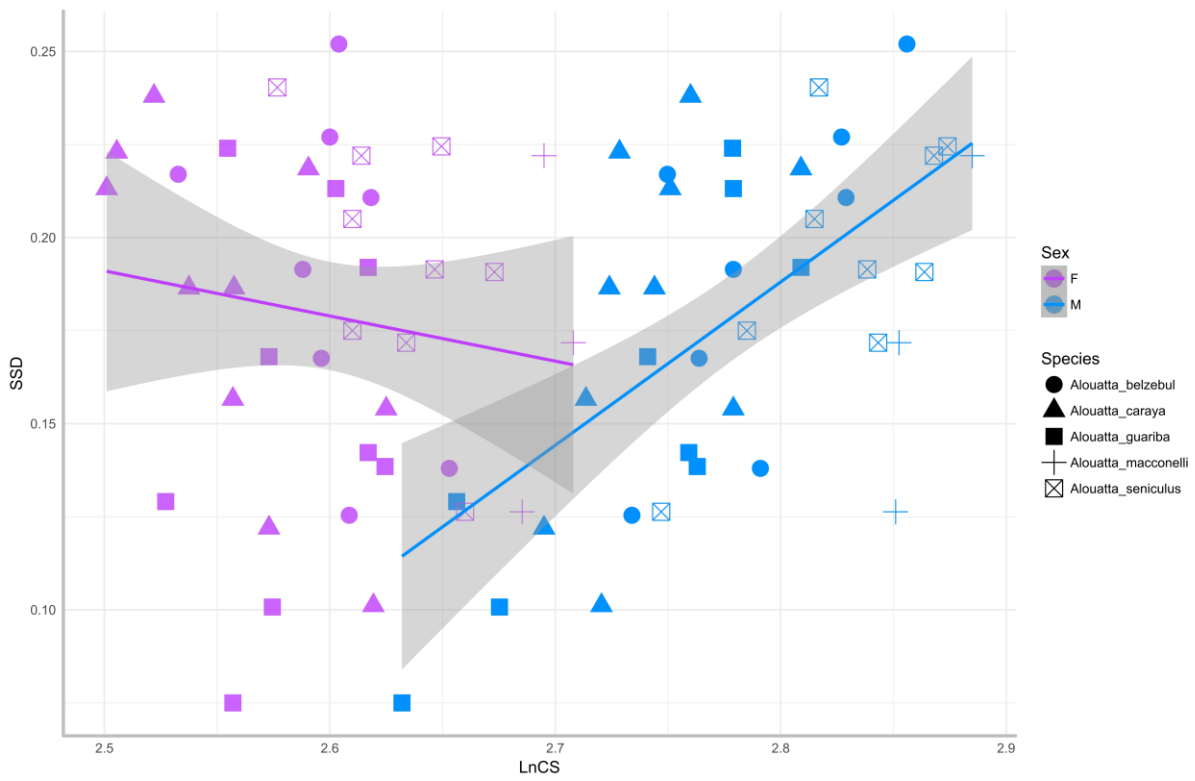
526 **Figure 2.** Box plot with standardized deviation of natural log transformed centroid size (LnCS) across sexes.
527 Black string: median, white box: first interquartile, bar: second interquartile. Different species and sexes are
528 shown by different symbols.

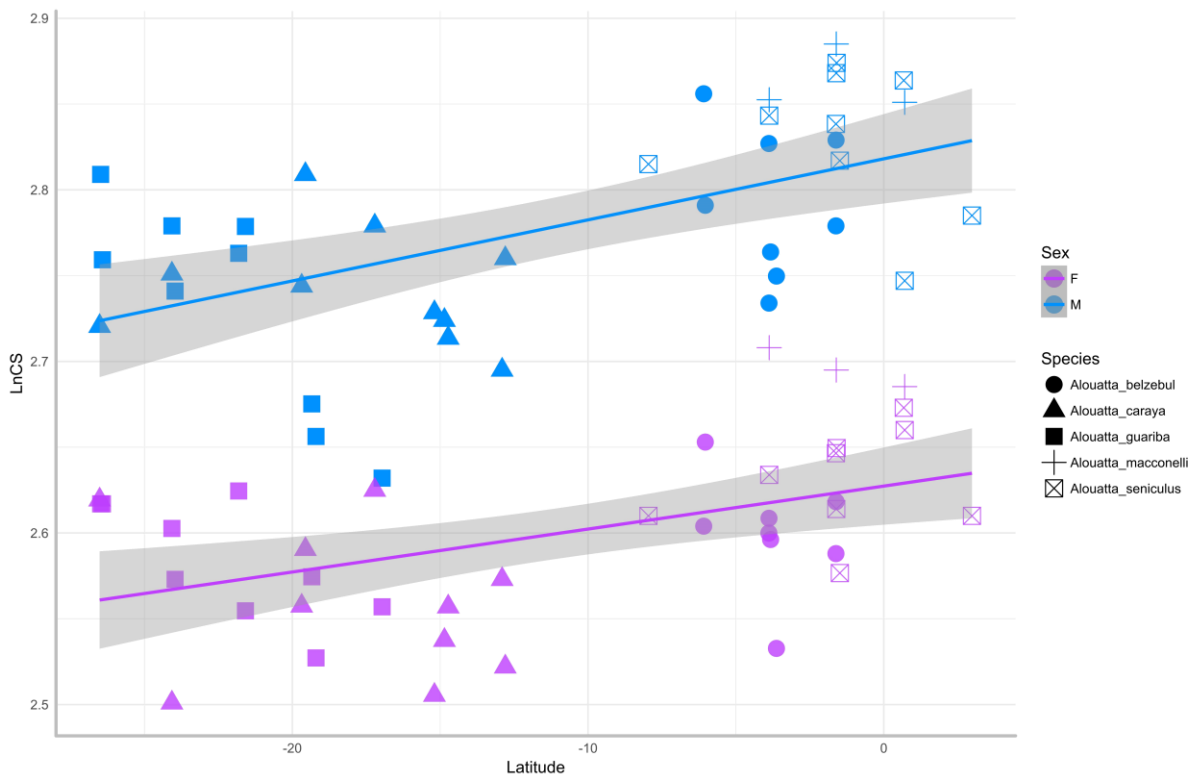
529 **Figure 3.** Regression plots for Rensch's sexual size dimorphism and female and male natural log transformed
530 centroid size (LnCS). Species and sexes are labelled by different symbols.

531 **Figure 4.** Regression plots for Bergmann's rule on its original form, latitude, and female and male natural log
532 transformed centroid size (LnCS). Species and sexes are labelled by different symbols.









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 Dimorphism (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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