

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Dissertação de Mestrado

Alometria entre tamanho do corpo e densidade populacional: A regra de Damuth se aplica à escala local?

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Porto Alegre, dezembro de 2018

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Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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Porto Alegre, dezembro de 2018

CIP - Catalogação na Publicação

Coriolano, Iara Reinaldo

Alometria entre tamanho do corpo e densidade populacional: A regra de Damuth se aplica à escala local? / Iara Reinaldo Coriolano. -- 2018.

33 f.

Orientador: Gonçalo Ferraz.

Dissertação (Mestrado) -- Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Programa de Pós-Graduação em Ecologia, Porto Alegre, BR-RS, 2018.

1. alometria. 2. método comparativo filogenético. 3. tamanho corporal. 4. aves amazônicas. 5. modelos SECR. I. Ferraz, Gonçalo, orient. II. Título.

Agradecimentos

Agradeço primeiramente à deusa maravilhosa que me colocou no mundo, minha mãe. Sem seu apoio e motivação eu não teria conseguido finalizar mais essa etapa acadêmica.

Ao meu companheiro e amor, Gabriel Nakamura, que apareceu inexplicavelmente na minha vida e me trouxe ânimo e esperança nos momentos mais difíceis. Sou imensamente grata por todo o apoio e paciência em ouvir minhas dúvidas e lamentações, e todo o companheirismo nessa reta final do mestrado.

À queridíssima Viviane Zulian pela amizade que construímos, pelas risadas no laboratório, dancinhas da vitória, por ter estado ao meu lado em campo quando eu mais precisava, mas também não só em campo.

Às queridas amigas, Kauane Bordin, Crisla Pott, Dirleane Ottoneli e Mariana Vieira, por todos os almoços e jantas pra descontrair a vida, pelos momentos de desabafo e empatia tão necessários nessa jornada acadêmica.

Aos meus amigos queridos Antônio Xavier, Ileyne Lopes e Naiara Martins que, mesmo à distância, me ajudaram a manter minha sanidade ao longo desses quase três anos de mestrado.

Agradeço em especial à Falla Family, que foram minha segunda família e deram todo o suporte e carinho à uma cearense em seu primeiro ano nas terras gélidas do sul.

Aos anilhadores peruanos mais sensacionais, Alexis Díaz e Gilberto Fernandez, por todo o aprendizado sobre ciclos de muda, companhia em campo e fotos toscas.

Aos meus colegas de laboratório que me ajudaram em muitos momentos, seja nos erros dos scripts no R, ou debatendo ideias, ou mesmo se lamentando.

Ao Prof. Dr. Gonçalo Ferraz por ter aceitado orientar uma cearense lá de longe, por todo o ensinamento e acompanhamento nas prévias das apresentações, nas

discussões do laboratório, na escrita da dissertação, e por ter possibilitado o contato e convívio com pesquisadores do mundo todo através dos campos em Manaus e workshops organizados por ele.

Aos professores participantes da banca examinadora Prof. Dr. Murilo Guimarães Rodrigues, Prof. Dr. Pedro Ivo Simões e Prof. Dr. Renan Maestri pelo tempo, disponibilidade, pelas valiosas contribuições e sugestões.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa de estudos de Mestrado.

Resumo

A regra de Damuth, expectativa de uma relação negativa na qual a densidade populacional diminui com o aumento da massa corporal na potência de três quartos, tem forte embasamento teórico. No entanto, estudos empíricos que sucederam os achados iniciais de Damuth, encontraram uma variedade de relações quantitativas dependendo das fontes dos dados, taxons, guildas e da escala espacial, com expoentes variando de negativos a nulos ou mesmo positivos. A divergência entre a previsão de Damuth e a literatura subsequente é evidente em estudos de escala local com amostras de número de espécies relativamente pequeno. Motivados por essas divergências, analisamos um conjunto de dados de aves em escala local, tomando os seguintes cuidados estatísticos: a) controle da não-independência filogenética entre as espécies, b) inclusão da variação intra-específica e c) estimativa da densidade populacional. Estimamos a densidade populacional usando modelos de captura-recaptura espacialmente explícitos para 44 espécies de 13 famílias. Para considerar incerteza filogenética, realizamos PGLS entre os logaritmos de densidade e massa corporal usando 1000 árvores do BirdTree. Encontramos uma consistente relação negativa entre densidade populacional e massa corporal mesmo após a inclusão de erros de medida e incerteza filogenética. O OLS entre as duas variáveis resultou uma inclinação de -0.57, mas a inclinação média obtida pelo PGLS com movimento browniano e PGLS com erros de medida para 1000 árvores foram, respectivamente, -0.73 e -0.71, muito mais próximas ao -0.75 encontrado por Damuth. Nosso trabalho demonstra que a contabilização das principais fontes de erro na inferência de uma relação alométrica influencia fortemente o resultado. Concluimos que a inclinação de $-3/4$ pode ser encontrada mesmo em escalas locais, reforçando a robustez e aplicabilidade geral da regra de Damuth.

Palavras-chave: modelos SECR, aves amazônicas, alometria, método comparativo filogenético, tamanho corporal

Abstract

Damuth's rule, the expectation that population density will scale with body mass in a negative three-quarter power relationship, has strong theoretical support. However, empirical studies following up on Damuth's initial report found a variety of quantitative relationships depending on data sources, taxa, guild, and spatial scale, with exponents varying from negative to null or even positive power relationships. The discrepancy between Damuth's prediction and subsequent literature is particularly clear in local-scale studies of relatively small samples of species. Motivated by the perceived discrepancy, we analyze a local-scale avian dataset while being as careful as possible in a) controlling for phylogenetic non-independence among species, b) accounting for within-species variance, and c) estimating population density. We estimated population density using spatially explicit capture-recapture models for 44 species from 13 families and performed phylogenetic generalized least squares between the logarithms of density and body mass using 1000 trees from BirdTree to account for phylogenetic uncertainty. We found a consistently negative relationship between population density and body mass even after the inclusion of measurement errors and phylogenetic uncertainty. The OLS between the logarithm of density and body mass returned a slope of -0.57, but the mean slope obtained for PGLS with Brownian motion model and PGLS with measurement errors for 1000 trees were respectively, -0.73 and -0.71, much closer to -0.75 found by Damuth. Our study shows that accounting for the major sources of error in inferring an allometric relationship does influence the result. We conclude that the -3/4 slope can be found even at local scales adding to the robustness and general applicability of Damuth's rule.

Key-words: SECR models, Amazonian birds, allometry, size-density relationship, phylogenetic comparative method

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Introduction

The ecological implications of body mass have been widely studied (Peters 1983, Brown and West 2000), resulting in the documentation of relationships between mass and abundance (White et al. 2007), home range area (McNab 1963), metabolic rates (Russo et al. 2003) and risk of extinction (Gaston and Blackburn 1995). Such relationships are usually described as ‘allometric’ because they result from a physical or physiological trait growing with body mass, but at a ‘different measure’, or rate, that is different from the rate of body mass growth (Peters 1983). A recurrent pattern found in allometric relationships is the power ratio of $\pm 3/4$ between body mass and a given trait, that can be expressed through the following equation:

$$Y = aM^{\pm 3/4}$$

where Y is a trait, M is the organism’s body mass and a is an empirically determined proportionality constant (Peters 1983). Biologically, this equation describes a relationship where the trait Y changes in proportion to the three-quarter power of body mass.

In a crucial work, Damuth (1981) evaluated the relationship between body mass and population density for a range of herbivorous mammal species, concluding that population density decreased in proportion to increasing body mass raised to the power of $-3/4$. This relationship is presently known as Damuth’s rule. Damuth associated his finding with Kleiber’s three-quarter power relationship between body mass and basal metabolic rate, seeing in this association the possibility of a general pattern governing quarter-power relationships. The idea that metabolism scales with body mass following a three-quarter power relationship finds theoretical support in a dimensionality hypothesis that portrays organisms as acquiring energy in three dimensions but expending it in four (West et al. 1999, Ginzburg and Damuth 2008). West et al. (1999) proposed the fourth-dimension to be the fractal-like architecture of vascular system

networks, however, Ginzburg and Damuth (2008) proposed a more literal meaning for this fourth dimension, suggesting is nothing but generation time. Under the interpretation that organisms acquire energy over three dimensions (two dimensions of their surface plus time) but expend it in four (three-dimensional bodies plus time) With this interpretation, Ginzburg and Damuth (2008) explain considerable variation found in animal scaling studies. There is thus a strong theoretical footing for expecting a variety of quarter-power scaling relationships with body mass.

Despite the apparent soundness of the theoretical basis for Damuth's rule, empirical efforts to confirm the $-3/4$ power relationship between population density and body mass met with a variety of results (Brown and Maurer 1986, Cotgreave 1993, Arneberg and Andersen 2003). These divergent results arise when: (1) analyzing data of different sources, for example, studies based on data from a single area, and studies based on data compilations (Cotgreave 1993, Blackburn and Gaston 1997); (2) comparing different taxa or separating the species pool into guilds (Cotgreave 1993, Blackburn et al. 1997); (3) different spatial scales being studied, with regional or global studies with slopes similar to three-quarter-power and local studies with very different slopes (Blackburn and Gaston 1997, White et al. 2007). A review of explanations for such divergences is beyond the scope of this introduction, suffice it to say that they include reasonings based on resource allocation for local scale (White et al. 2007), competition intra-guild (Cotgreave 1993), and long-term evolutionary processes for global scale (White et al. 2007). In short, the inter-specific relationships between population density and body mass appear in the literature with a variety of slopes ranging from negative and close to $-3/4$ power relationships, as predicted by Damuth's rule, to near-zero or even positive power relationships (Blackburn and Gaston 1997, White et al. 2007).

We believe that a considerable part of the variability among empirical population density-body mass relationships—and the mismatch between empirical results and theoretical prediction—is a consequence of cumulative errors resulting from the relatively small phylogenetic samples of species studied at the local scale, the short span of body masses studied, and the difficulty in obtaining unbiased estimates of population abundance. Thus, the current study is motivated by our willingness to fit a population density-body mass relationship, while accounting for what we see as the major sources of bias in inferring this allometric relationship: phylogenetic non-independence among species, within-species variance biases, and population density estimation biases.

The first type of error that we are correcting in this study is associated with phylogenetic non-independence between the species pool. When the relationship between two traits is analyzed among several taxa, it is wrong to assume that species represent independent observations of nature. Species have a hierarchically structured phylogeny and since closely related species tend to be more similar to each other than distantly related ones, they cannot be regarded as independent points (Felsenstein 1985). Not recognizing this hierarchical structure while inferring interspecific relationships between traits would be tantamount to pseudoreplication. The use of the phylogenetic comparative method helps both to eliminate the effects of pseudoreplication caused by the non-independence of species and to obtain reliable quantifications of the association between traits (Felsenstein 1985, Harvey 1996).

The second source of error that stands in the way of inferring allometric relationships is within-species variance, also described as measurement error (Ives et al. 2007). Measurement errors are all the fluctuations in a variable produced by instrument-related errors, the biological variance among individuals of a species, or even the biological variance found among populations (Garamszegi 2014). In this work we will not be correcting for measurement error between populations considering that our work

took place at only one location, *i.e.* only one population of each species was sampled. So, we will be correcting for instrument-related errors and individual variance of a species. Incorporating measurement errors in phylogenetic comparative studies can provide less biased and more accurate parameter estimates (Ives et al. 2007, Garamszegi 2014).

The third recurrent problem in inferring population density-body mass relationships is the difficulty in obtaining unbiased estimates of population density. In truth, not all studies employ estimates of population density, which measures the number of individuals per unit area, some use assessments of population size without a clear delimitation of the corresponding area, which may vary from species to species (Damuth 1987, Nee et al. 1991). However, even among studies that do relate body mass with some assessment of population density, one finds a variety of approaches to estimating density, which does not always correctly eliminate bias (Cotgreave and Harvey 1992, Blackburn et al. 1994). Before Murray Efford's work (2004), on population density estimation using spatial capture-recapture data, there was no proper solution to estimate density when distance sampling was not applicable. Efford (2004) and subsequent literature on spatial capture-recapture (Royle et al. 2014) introduced a methodological innovation that combined the modeling approaches of mark-recapture and distance sampling analysis, extending the possibility of density estimation to a whole new range of data types and field realities.

Thus, considering the relative inconsistency among published population density-body mass relationships and the availability of new statistical methods to address analytical difficulties, I revisit the allometric relationship between population density and body mass through the analysis of a particularly well-sampled bird community in Central Amazonia. My approach combines a phylogenetic comparative method for accounting for the lack of independence among species, it incorporates measurement

errors about both population density and body mass and uses spatially explicit capture-recapture models for obtaining estimates of population density that account for sampling error and animal movements. By doing so, we aim to clarify—in one carefully researched case-study—whether Damuth’s rule may apply to a local setting with a relatively small set of species and within species uncertainty in both population density and body mass.

Methods

Study site and species

Field data collection for this study took place at the camps Porto Alegre and Cabo Frio of the Biological Dynamics of Forest Fragments Project (BDFFP), 70 km north of Manaus, Amazonas, Brazil. The BDFFP region has a tropical humid climate, with annual precipitation from 1,900 to 2,500 mm and a dry season extending from June to October (Gascon and Bierregaard 2001). Both camps are situated near the boundary between patches of approximately 30-year-old secondary forest and a large expanse of old growth.

We organized our sampling in five yearly seasons, also referred to as ‘sessions’ in the Spatially Explicit Capture-Recapture (SECR) literature, which spanned the years of 2013 to 2017. Visits, also known as ‘occasions’ in the SECR literature, were periods of 8 to 12 days of fieldwork within one month and Camp. The number of visits per camp per season varied between two and five, depending on funding availability. Camp Porto Alegre was always visited in July and August of each year, while Cabo Frio visits started in June and continued up to September or October, depending on the year. Mist netting took place over approximately 21 km of trails distributed in eight grid plots, four in Cabo Frio and four in Porto Alegre, plus six transect plots in Cabo Frio (Fig. 1). Each

grid plot consisted of four 600-meter-long trails arranged as a pound-sign; Cabo Frio transect plots were linear trails that connected the Camp's four plots in a roughly triangular area. We deployed between 20 and 30 mist-nets per day depending on field team sizes and bird activity. Mist netting sites were selected randomly, with replacement between visits, so that net locations were never repeated on two consecutive days. Mist nets, 12-m long and 2.5-m high, were opened at 6 am and closed at 12 pm daily. All passerine birds captured were marked with numbered aluminum bands and their body mass measured with an electronic scale. Also, additional capture-recapture information from our colleague Cameron Rutt's mist netting works during the same period of year and sites was added to the data set. This is a very small proportion of total data corresponding to less than 0.04% of captures.

In total, the dataset consists of 8,018 captures of 130 species from 31 families, captured between 2013 and 2017. Body masses of all birds captured ranged from 2.5g to 360.2g with mean around 20,6g (sd=18.84). Because population density estimation requires a sufficient number of recaptures in space, we established two criteria to select species for our analysis: (1) species had to have at least ten recaptures, and (2) species had to be capture at least once per year throughout the study period. Whenever there was sexual dimorphism in body size, we used male body masses in our analysis. We choose males rather than females to avoid extra variability due to the weight of egg-laying females.

Estimating population density with spatially explicit capture-recapture models

SECR models use information about spatially indexed capture histories to infer the extent of individual animal movements and the population density of a target species. The SECR approach combines observation and density (state) components in a single framework, where the number N of individuals per unit area follows a Poisson

distribution (Borchers and Efford 2008). This approach provides reliable estimates of density (Efford 2004) allowing us to deal with error in the estimates, present in previous density calculations. We treated each year as one independent session in the model, with parameters density (D) and detection probability (p) modeled as constant for each species through all years. We thus treated the populations as closed within each year and at equilibrium throughout the period of this study.

For computational convenience, we analyzed data on a grid of 1-ha cells, aggregating captures from all the mist nets within each cell. Thus, from here on, the term ‘detector’ refers to the set of mist nets found within one 100x100 m grid cell. Depending on the number of nets per cell, particular detectors may have more or less sampling effort associated with them, resulting in a metric of sampling effort in units of nets per cell per occasion. Considering that one visit lasts up to 12 days, the number of captures per individual per visit and detector may be greater than one, so, for this reason, our model will treat detectors as proximity detectors. Proximity detectors do not hold trapped individuals beyond the moment of detection and are not limited by maximum number of captures, so the probability that one individual is registered by a detector at a given distance from the individual’s position is the same throughout the array. For this reason, we assumed that the probability of obtaining a count history followed a Poisson distribution (Efford et al. 2009). The probability of detecting an individual at a trap declines with distance (d) according to a halfnormal detection function (p_s) as recommended by Borchers & Efford (2008):

$$p_s = g_0 \exp\left(\frac{-d^2}{2\sigma^2}\right)$$

The equation above is the observation model, where d is the distance between the detector and the animal’s home range center, σ is the spatial scale parameter, and g_0 is the probability of detection when the detector is placed at the center of the home range.

In the abundance model, we estimated the density (D) for each species by maximizing the full likelihood using proximity detector (Borchers and Efford 2008) in *secr* package (Efford 2018) in R 3.4.3 (R Development Core Team 2018).

Comparative analysis

In order to investigate the relationship between mean individual body mass and population density, we need to account for the phylogeny of bird species in our sample. The main reason is that the investigation of the relationship between two traits without the phylogenetic information may lead to the inference of a spurious relationship where there is none, due to lack of phylogenetic independence between species in a sample (Felsenstein 1985). However, since we do not have perfect knowledge of the phylogenetic relationship between species in our sample, we need to base our analysis on a range of phylogenetic hypotheses. To do so, we obtained 1000 distinct but equiprobable trees from BirdTree (Jetz et al. 2012) and examine how the variation among trees influences our perception of the relationship between population density and body mass.

BirdTree is at once a database and an online tool for assembling phylogenies of user-defined bird species. It contains as yet the most complete set of phylogenies of extant birds, which combines taxonomic information for all species with molecular information for 6,663 out of nearly 10,000 known species of birds. The BirdTree assembly method uses ancestral phylogenetic relationships from previous studies—a ‘backbone’—as a foundation for its trees, and subsequently assembles fully resolved, dated trees based on genetic data, topological constraints, and fossil constraints. BirdTree uses a Bayesian approach to insert trees of bird clades that are well known onto the backbone and thus assemble a full tree for a set of user-defined species. Users of BirdTree may choose between two backbone phylogenies: Hackett et al. (2008) and

Ericson et al. (2006). We used Hackett et al.'s (2008) because it offers the most complete study in avian phylogeny to date, according to Rubolini et al. (2015).

We accounted for phylogenetic nonindependence by employing a Phylogenetic Generalized Least Squares (PGLS) analysis. Shortly, a PGLS is a form of weighted regression that uses the phylogenetic relatedness of species to estimate the slope and intercept of the statistical relationship between two traits while incorporating the knowledge that evolutionary relationship leads to non-independence of species' traits (Felsenstein 1985, Garamszegi 2014). In an ordinary least squares model, the residuals of the regression relating two traits are assumed to be independent; however, this premise is not true in an evolutionary context, because some species share more ancestry than others and thus tend to show covarying traits. The PGLS converts the phylogeny into a matrix of variance-covariance using an expected model of evolution, that describes how traits change through time, where the diagonal represents the variance of traits and the off-diagonal the covariance between species' traits. This variance-covariance matrix is used for weighing the non-independence among residuals of the regression in the PGLS model (Grafen 1989).

Our comparative analysis started with the estimation of Bloomberg's K for each trait. Bloomberg's K (or K , from here on) is a metric of phylogenetic signal (Blomberg et al. 2003) that quantifies the extent to which two species drawn from a sample resemble each other more than expected at random. Because within-species variation may result in biased phylogenetic signal estimates, we accounted for such variation by including the standard error of each species trait in the estimates of phylogenetic signal. The numeric value of K is interpreted against the expectation of interspecific similarity predicted by a Brownian motion (BM) model of trait evolution. When $K > 1$, trait values of closely related taxa are more similar than would be expected if they had evolved under BM. If K equals one, traits evolved according to the BM model. And finally, if K

< 1 , traits of closely related taxa are less similar than would be expected under the BM model. To infer whether K differs from the value expected by chance, a randomization test is usually applied, and a p-value is obtained. We estimated K separately for both variables for each tree (1000 times) using the package *phytools* (Revell 2012) and then calculated its mean, standard deviation, and associated p-value, for both body mass and population density.

After obtaining the appropriate K values, we performed three different linear regression analyses in order to compare the results from a simple regression to a more complex one with phylogenetic information: an ordinary least squares (OLS), a PGLS with BM model and a PGLS with BM model and measurement errors in both variables. We did that to see whether the inclusion of measurement errors affected the regression results. The OLS regression was fitted between the logarithm of density and body mass using the package *stats* (R Development Core Team 2018). We performed a PGLS using the BM model of evolution (PGLS Brownian) between the logarithm of density and body mass using the packages *ape* (Paradis et al. 2004) and *nlme* (Pinheiro et al. 2018). We performed the PGLS modified by Ives et al., 2007 (PGLS Ives), and implemented in R by Revell (2012) in the package *phytools*, using the same dataset. The PGLS Ives also uses a matrix of variance-covariance using a BM model like the original PGLS, but incorporate the within-species variance as measurement error for both variables including a matrix of covariance for the errors (Ives et al. 2007). This way, we can deal with measurement errors in the variables body mass and density.

We fitted the PGLS Brownian and the PGLS Ives for the same subset of 1000 trees in order to account for uncertainty about the phylogenetic hypotheses presented by BirdTree. Both PGLS analyses generated a distribution of coefficients from which we calculated the mean and standard deviation (SD) for intercepts, slopes and, in the case of PGLS Brownian, for p-values. The PGLS Ives implemented in the *phytools* package

does not provide straight away a null hypothesis test with a p-value to check whether the regression slope is significantly different from zero. Therefore, in order to perform a null hypothesis test, we fitted the model once more for 1000 trees, but now with the slope forced to zero, and then compared the two models for each tree with the likelihood ratio (LR) test using the package *lmtest* (Zeileis and Hothorn 2002). With this approach, we could obtain a statistic of significance for the slope estimates from PGLS Ives, and then, calculate the mean and standard deviation (sd) for those p-values resulted from the 1000 LR tests.

Results

Data

A total of 46 species from 13 families fulfilled our selection criteria totaling 6,844 captures of 4,971 individuals. *Pithys albifrons* was the species with the highest number of recaptures (560), while *Conopophaga aurita* had the lowest (11). *Pipra pipra* was the species with the highest total number of captures (879) and *Lanio fulvus* had the lowest, with only 20 total captures. Two families comprised the majority of species analyzed: *Thamnophilidae* representing 29.5% of the total species with mean body mass of 16.21g (sd = 13.05, n = 13) and *Furnariidae* with 22.7% of all species with a mean body mass of 28.97g (sd = 7.93, n = 10). Mean body masses of species ranged from 7.6g (sd = 0.6, n = 247) for *Myrmotherula axillaris* to 53g (sd = 4.3, n = 462) for *Dendrocincla merula* (Supplemental Material Table S1).

Population density estimates

We estimated population density for 44 species because *Ceratopipra erythrocephala* and *Thamnophilus murinus* were dropped from analysis. *C. erythrocephala* had a density of 107.86 with a 95% confidence limit of 35.43 to 328.33 making the estimate

very uncertain and was therefore dropped from the regression analysis. The density estimate for *T. murinus* was also discarded because the parameter σ was not estimated by the model, consequently making the density estimate unreliable. *P. pipra* was the species with the highest estimate of density with 102.83 individuals per km² (CL 80.73-130.99). The lowest density was estimated for *Onychorhynchus coronatus* with 0.54 ind/km² (CL 0.24-1.2). Four species had very uncertain density estimates, with confidence limits ranging over more than forty individuals per square km (*Mionectes macconnelli*, *P. pipra*, *Platyrrhinus coronatus*, and *Tachyphonus surinamus*; Supplemental Material Table S1).

Regressions of abundance on body mass

The mean estimate of Blomberg's *K* for mass was 0.36 (sd = 0.13) with a mean p-value of 0.14 (sd = 0.18) meaning that with a p-value not significant as we have, even with a $K < 1$, our data did not show evidence that the evolutionary process for body mass is non-random. For density, the mean *K* was 1.06 (sd = 0.13) with a p-value of 0.03 (sd = 0.01) meaning that this trait evolved under a BM model which based our choice in using BM model in the variance-covariance matrix. The OLS between the logarithm of density and body mass returned a slope of -0.57 with a p-value of 0.051 (Table 1). When correcting for phylogeny across 1,000 trees using PGLS Brownian (without measurement error in the model) we found a mean slope of -0.73 (sd = 0.15). The phylogenetic regressions including measurement error, PGLS Ives, also showed a negative tendency with a mean slope of -0.71 (sd = 0.06) as shown in Figure 2. The likelihood ratio test with PGLS Ives resulted in 598 out of 1000 comparisons with p-values > 0.050 , with a mean of 0.054 (sd = 0.014; Table 1). We could observe that although the slope estimates from PGLS Brownian and PGLS Ives are not so different, the uncertainty around the estimates in the later is much narrower than in the former.

Discussion

Our results showed a clear negative relationship between population density and body mass, meaning that at each unit of increase in the logarithm of body mass, the logarithm of density decreases in approximately 0.75 units. Although the mean p-value of the PGLS Ives is slightly out of a 95% confidence limit, we consider our result consistent with the general hypothesis of size-density relationship in which density scales with body size at $-3/4$ exponent (Damuth 2007, Ginzburg and Damuth 2008). Also, the mean slope obtained by PGLS Ives was -0.71 with confidence intervals that include the value of -0.75 slope obtained by Damuth (1981) in a sample of 307 species of mammal primary consumers. The negative relationship remained consistent even after the inclusion of measurement errors and phylogenetic uncertainty. Moreover, we achieved a more precise estimate of slope in PGLS Ives than PGLS Brownian including within-species variance in the analysis. We accomplished that by taking statistical care in three levels: density estimates, phylogenetic non-independence, and the inclusion of measurement errors. Here we explain the implications of these three types of statistical care.

One frequent problem reported in macroecological studies is the lack of information about data quality in datasets (Gaston and Blackburn 1999, Beck et al. 2012), for example, the data used is often a compilation of abundances from secondary sources with different methods to achieve the numbers. In this work, we addressed the methodological inaccuracies related to data collection by using a capture-recapture dataset originated from a sample design that was carefully delineated aiming for accuracy in population parameters estimates. The SECR model, on the other hand, generally provides density estimates with minor bias (Efford 2004), allowing

consideration of sampling error in the analysis to include estimates uncertainty associated with the sampling processes.

At the beginning of the 1990s, comparative studies that used phylogenetic information were still only a few. Nee et al. (1991) were the first to try to correct for phylogenetic non-independence in abundance-size relationships. They performed regressions on different taxonomic levels and found positive, negative and no significant relationship depending on the group of birds analyzed. Overall, no relation between abundance and body mass was found. However, what Nee et al. (1991) did was to reduce the amount of phylogenetic variance between species by progressively splitting the species pool into different taxonomic levels. Therefore, in each taxonomic group, there is still shared evolutionary history and the species are still not independent of each other. So, the apparent divergence between Nee's and Damuth's work could be the result of variance decrease inside groups. Nowadays, PGLS is a widespread tool used in phylogenetic comparative studies. The PGLS Ives used in our work, however, is until the present moment not very used although it corrects more properly the slope estimates by using both phylogenetic information and measurement errors giving more strength to the Damuth's $-3/4$ rule.

Still, regarding the contradictory results found in literature, we stress two types of relationships that arise in LSDR: polygonal and linear relationships. Polygonal (nonlinear or triangular) relationships are characterized by maximum abundance peaks at intermediate body masses and minimum abundance present across all sizes (Marquet et al. 1995, White et al. 2007). Polygonal relationships have been frequently found in LSDR studies and hypothesized to be the result of a short range in variance, so the pool of species in these studies would be a slice of a global negative relationship (Blackburn and Gaston 1997, White et al. 2007). Despite our work be characterized as LSDR the relationship between body mass and density was similar to Damuth's results,

reinforcing the need to address the three types of errors that we stress in order to reach to an accurate and precise estimate relating body mass and density.

Another conflicting results present in the literature is the difference in slopes from studies with mammals and birds, with mammal studies tending to result in steeper slopes than bird studies (Gaston and Blackburn 2000). However, Cotgreave and Harvey (1992) found no evidence to support this finding when reviewing studies from 90 bird communities. Also, Blackburn and Gaston (1997) found no differences between the regression slopes of assemblages considered to use the space in two (e.g. mammals) or three dimensions (birds). Our OLS results could be seen as supporting a shallower regression slope for birds because the estimated slope is somewhat distant from the -0.75 exponent found for mammals, however, after the inclusion of the phylogeny in the analysis the results became much more consistent with Damuth's rule.

Furthermore, when accounting for measurement error and phylogenetic non-independence, Damuth's rule is apparent even at the local scale. Both PGLS analyses showed to be sensitive to the phylogenetic hypotheses being used, returning slopes varying from -0.43 to -1.02 depending on the tree, showing the importance of using multiple trees in comparative studies. In many cases, because there is only one phylogeny available, and there is little information of uncertainty about the relationship, one may end up with erroneous conclusions. Also, the importance of statistical care becomes much more crucial in the context of local scale studies. As previously shown, the negative relationship is frequently not found, or regressions have shallower slopes at a local scale. A variety of hypotheses have been invoked to explain these inconsistencies with Damuth's rule. We believe that a considerable part of these inconsistencies may be due to a combination of errors that we addressed in this paper at the local scale. We demonstrated that, when accounting for phylogeny, intra-specific

variability and sampling error, the $-3/4$ slope can be found even at a local scale. Our result adds to the robustness and general applicability of Damuth's rule.

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Tables and figures

Table 1. Regression slopes for OLS, PGLS without measurement errors (PGLS Brownian) and PGLS with measurement errors (PGLS Ives).

Regression	Slope \pm sd [95% c.i.]	p-value \pm sd [95% c.i.]
OLS	-0.57	0.051
PGLS Brownian	-0.73 \pm 0.15 [-0.43, -1.02]	0.041 \pm 0.029 [-0.015, 0.098]
PGLS Ives	-0.71 \pm 0.06 [-0.59, -0.83]	0.054 \pm 0.014 [0.027, 0.081]

Figure 1. Study area with circles highlighting the camps Porto Alegre and Cabo Frio at Biological Dynamics of Forest Fragments Project (BDFFP), Brazil. Primary forest is represented in dark grey, secondary forest in light grey and pasture in white. Each pound-sign in black is a grid plot, and lines, also in black, are transect plots where mist-netting took place.

Figure 2. Scatterplot and phylogenetic regression between the logarithm of population density (ind/km²) and the logarithm of body mass (g) for the forty-four species analyzed in this study. The values displayed at the axis refer to the original values, but the plot is in logarithm scale. The dotted line plots the OLS regression. The continuous line plots the mean estimates from PGLS with Brownian motion model of evolution (PGLS Brownian) without measurement errors in the variables for 1,000 distinct trees. The dashed line plots the PGLS with measurement errors (PGLS Ives) according to the mean slope and mean intercept from the 1,000 regressions. Each light gray line corresponds to one regression fit with PGLS Ives for each of 1,000 phylogenetic hypotheses downloaded from BirdTree. The vertical and horizontal dark gray lines in each point represent the standard error for density estimates and the standard deviation for body mass. Mean parameter values are displayed at the top of the graph. The different symbols in the graph indicate bird families: ●: *Thamnophilidae*; ■: *Furnariidae* and ○: all other families with less than seven species.

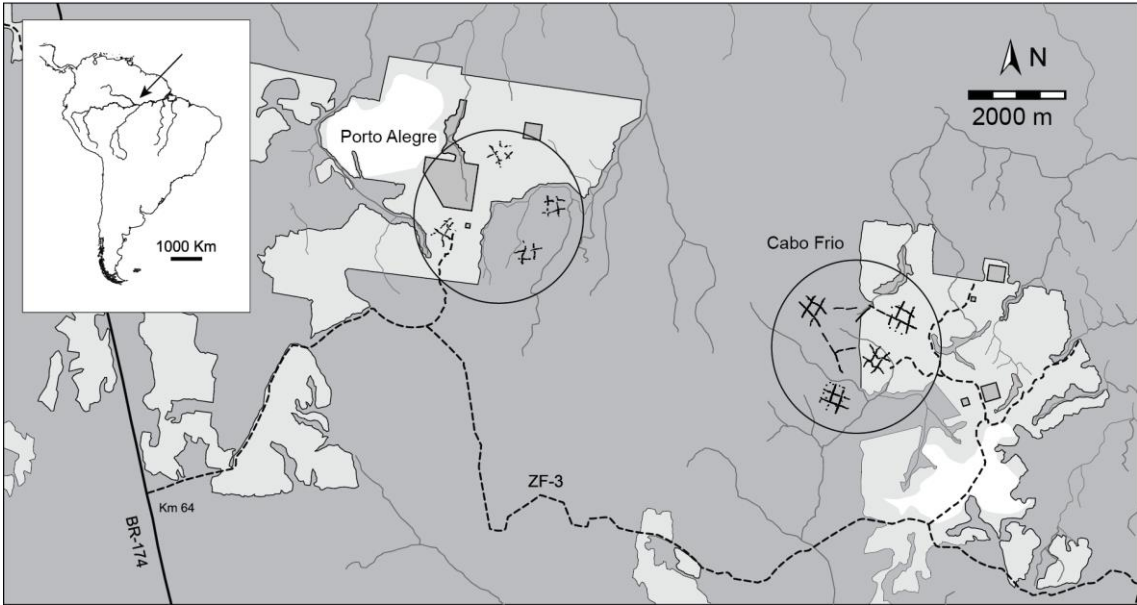


Figure 1

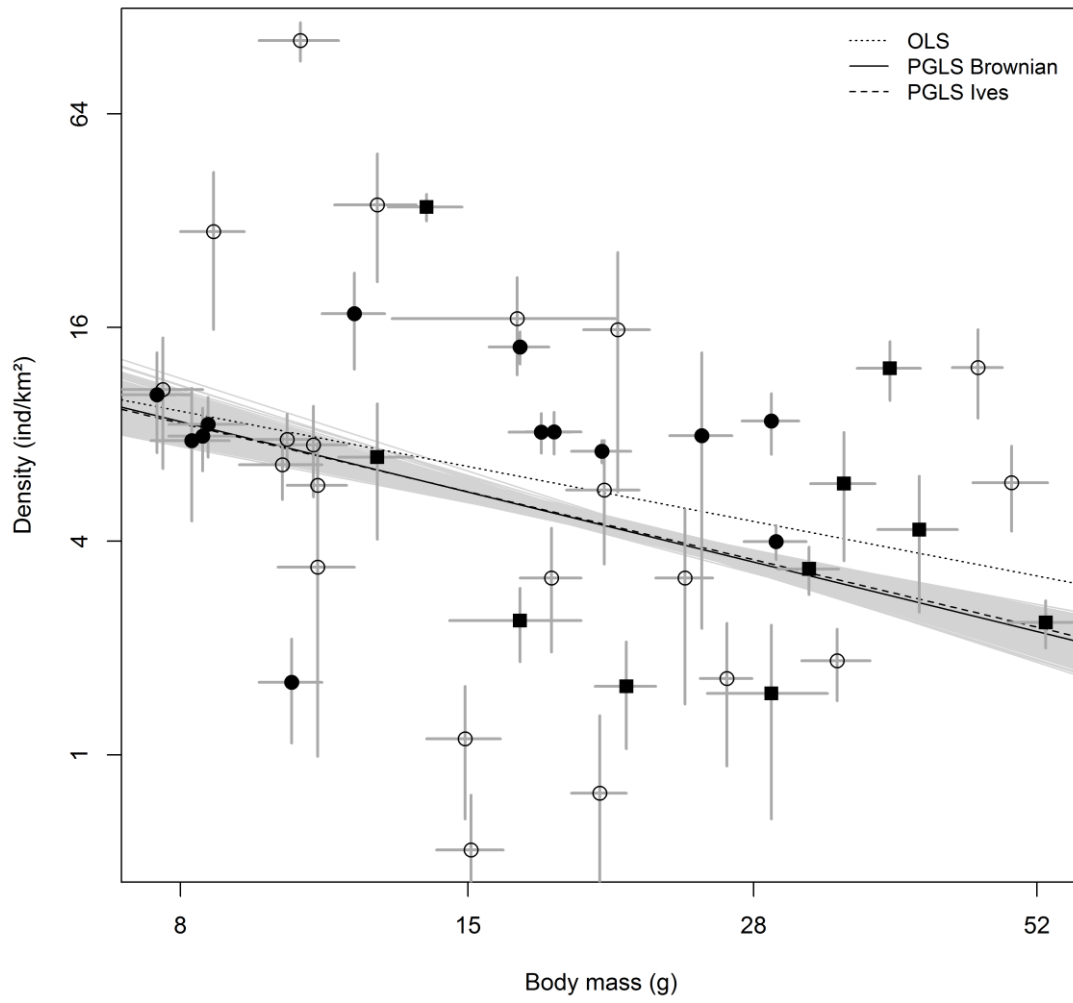


Figure 2

Supplemental Information

Table S1. Density estimate and body masses for forty four species of birds of Amazônia, standard error (se) and 95% confidence limit (c.l.) for density; and standard deviation (sd) and number of individuals measured (N) for body mass.

Family and species name	Density (individuals/km ²)	Body mass (g)	
	$\mu \pm se$ [95% c.l.]	$\mu \pm sd$	N
Galbulidae			
<i>Galbula albirostris</i>	3.15 ± 1.2 [1.53, 6.48]	18 ± 1.2	199
Thamnophilidae			
<i>Myrmotherula gutturalis</i>	8.53 ± 1.63 [5.88, 12.36]	8.5 ± 0.7	299
<i>Gymnopithys rufigula</i>	3.99 ± 0.44 [3.21, 4.95]	29.4 ± 2	564
<i>Hypocnemis cantator</i>	17.49 ± 5.29 [9.79, 31.23]	11.7 ± 0.8	328
<i>Myrmotherula guttata</i>	1.6 ± 0.52 [0.86, 2.97]	10.2 ± 0.7	142
<i>Myrmeciza ferruginea</i>	7.93 ± 5.66 [2.26, 27.87]	25 ± 1.7	147
<i>Myrmotherula axillaris</i>	10.34 ± 3.24 [5.67, 18.84]	7.6 ± 0.6	247
<i>Myrmotherula longipennis</i>	7.9 ± 1.59 [5.35, 11.68]	8.4 ± 0.6	324
<i>Myrmotherula menetriesii</i>	7.68 ± 3.12 [3.57, 16.52]	8.2 ± 0.7	202
<i>Percnostola rufifrons</i>	8.72 ± 1.7 [5.97, 12.72]	29.1 ± 1.8	343
<i>Pithys albifrons</i>	7.17 ± 0.52 [6.22, 8.26]	20.1 ± 1.3	1798
<i>Thamnomanes ardesiacus</i>	8.13 ± 1.1 [6.24, 10.58]	18.1 ± 1.1	700
<i>Thamnomanes caesi</i>	8.12 ± 1.04 [6.33, 10.41]	17.6 ± 1.2	489
<i>Willisornis poecilinotus</i>	14.09 ± 1.47 [11.49, 17.29]	16.8 ± 1.1	700
Conopophagidae			
<i>Conopophaga aurita</i>	3.15 ± 1.76 [1.13, 8.73]	24.1 ± 1.5	83
Formicariidae			
<i>Formicarius colma</i>	12.33 ± 3.45 [7.21, 21.11]	45.7 ± 2.5	253
Furnariidae			
<i>Automolus infuscatus</i>	3.34 ± 0.51 [2.48, 4.49]	31.6 ± 2.1	470
<i>Automolus ochrolaemus</i>	5.81 ± 2.29 [2.76, 12.23]	34.1 ± 2.4	130
<i>Deconychura stictolaema</i>	2.39 ± 0.56 [1.52, 3.77]	16.8 ± 2.4	454
<i>Deconychura longicauda</i>	1.49 ± 0.83 [0.54, 4.14]	29.1 ± 3.8	127
<i>Dendrocicla fuliginosa</i>	4.31 ± 1.79 [1.97, 9.41]	40.2 ± 3.5	293
<i>Dendrocicla merula</i>	2.36 ± 0.36 [1.75, 3.19]	53 ± 4.3	462
<i>Glyphorhynchus spirurus</i>	34.95 ± 3.04 [29.49, 41.42]	13.7 ± 1.1	1876
<i>Sclerurus rufigularis</i>	1.56 ± 0.52 [0.82, 2.96]	21.2 ± 1.4	268
<i>Xenops minutus</i>	6.9 ± 2.85 [3.18, 15.01]	12.3 ± 1	292
<i>Xiphorhynchus pardalotus</i>	12.28 ± 2.31 [8.51, 17.7]	37.7 ± 2.6	821
Tyrannidae			
<i>Corythopsis torquatus</i>	1.11 ± 0.45 [0.52, 2.37]	14.9 ± 1.2	318
<i>Mionectes macconnelli</i>	35.45 ± 13.93 [16.86, 74.51]	12.3 ± 1.1	1320
<i>Myiobius barbatus</i>	5.75 ± 1.81 [3.15, 10.5]	10.8 ± 0.7	378
<i>Onychorhynchus coronatus</i>	0.54 ± 0.23 [0.24, 1.2]	15.1 ± 1.1	59
<i>Platyrrhynchus coronatus</i>	29.8 ± 14 [12.41, 71.52]	8.6 ± 0.6	20
<i>Platyrrhynchus saturatus</i>	3.38 ± 2.39 [0.97, 11.75]	10.8 ± 0.9	192
<i>Rhynchocyclus olivaceus</i>	0.78 ± 0.51 [0.24, 2.5]	20 ± 1.2	114
Pipridae			
<i>Corapipo gutturalis</i>	10.69 ± 4.28 [5.02, 22.76]	7.7 ± 0.7	91
<i>Pipra pipra</i>	102.83 ± 12.75 [80.73, 130.99]	10.4 ± 0.9	273
<i>Lepidothrix serena</i>	7.74 ± 1.38 [5.47, 10.95]	10.1 ± 0.7	211

<i>Manacus manacus</i>	16.95 ± 5.19 [9.42, 30.48]	16.7 ± 4	2
Tityridae			
<i>Schiffornis turdina</i>	1.84 ± 0.42 [1.18, 2.85]	33.6 ± 2.5	441
Vireonidae			
<i>Hylophilus ochraceiceps</i>	6.57 ± 1.33 [4.43, 9.74]	10 ± 0.9	399
Troglodytidae			
<i>Cyphorhinus arada</i>	5.57 ± 2.12 [2.71, 11.47]	20.2 ± 1.6	280
Poliophtilidae			
<i>Microbates collaris</i>	7.47 ± 2.14 [4.31, 12.95]	10.7 ± 0.8	489
Turdidae			
<i>Turdus albicollis</i>	5.84 ± 1.57 [3.48, 9.8]	49.2 ± 4	677
Thraupidae			
<i>Lanio fulvus</i>	1.64 ± 0.71 [0.72, 3.7]	26.4 ± 1.5	17
<i>Tachyphonus surinamus</i>	15.76 ± 10.26 [4.91, 50.55]	20.8 ± 1.5	168