

Hierarchical effects on body size evolution and the macroecology of South American rainforest mammals

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Abstract. *The relationship between geographic range size and body size analyzed at the continental scale for many species has been described recently by an envelope region defined in bivariate space and limited by ecological and physical constraints. These constraints can be explained by stochastic extinction related to minimum population density and energetic theories for an optimal body size. However, since data are obtained for different species in a large taxonomic group, it is possible that these variables may be strongly affected by phylogenetic autocorrelation. In this paper, we analyzed data on geographic range size and body size for 87 species of Neotropical rainforest mammals from South America, searching for phylogenetic effects changing the shape of constraint space. We used a nested ANOVA design to evaluate and remove large scale hierarchical (phylogenetic) trends in the two variables. Body size was more affected by phylogenetic effects than geographic range size. After removing these effects, we noted that the two macroecological variables analyzed support the shape of constraint space previously observed in North American species. The most important aspect of our analyses is that a model for optimal body size related to life-history variations provides an useful theoretical framework to understand how processes of species dynamics can lead to the observed macroecological patterns.*

Introduction

The relationship between body size and geographic range size for multiple species, as many other macroecological relationships, has been described by a polygonal region in a bivariate space enclosing combinations of both variables (the constraint envelope, Brown and Maurer 1987), in such a way that lines fitted to the borders of this polygon can be interpreted as different ecological and evolutionary constraints (Brown and Maurer 1987, Brown 1995, Marquet et al. 1995). At least theoretically, species can exhibit different combinations of the two characters that fall within the constraint space. For the relationship between body size and geographic range size, four constraint lines are usually described. The minimum body size for any group is determined by functional and structural morphological constraints, and the maximum geographic range is determined by a spatial constraint (available habitat or continental area) limiting colonization capacity. The two other constraints, relating minimum geographic ranges for different body size classes, are much more interesting, because they may be determined by a combination of ecological and evolutionary processes, as described below (Brown and Maurer 1987, Brown 1995, Grantham 1995).

The relationship between body size and minimum geographic range is not constant across all body size classes, as occurs with other ecological traits, such as population density, home range, clutch size and dispersion rates (Brown 1995). This change in the slope of minimum geographic range size may be interpreted as a trade-off between different size-related ecological processes, i.e., the relatively lower capacity of extracting energy from local resources combined with increasing liability to explore resources in different patches. This combination permits then to minimize the probability of stochastic extinction related to low local population densities (Brown 1995). Large species require more energy and should use a large area of the environment, in such a way that small geographic range implies

higher intraspecific competition and low local population density and, therefore, higher probability of extinction. Below some critical body size, the relationship between minimum geographic range and body size inverts, because density constraints are inoperative and colonization capacity becomes determinant, because the necessity of foraging on distant patches of highly specific resources, increasing then geographic range size (Gaston and Lawton 1988a,b, Brown 1995). Thus, a species with body size near the optimal may live in small geographic ranges and still survive, or colonize entire continental areas, depending on its colonization capacity. At species levels, speciation rates may be also higher, and combined with low extinction, may explain why species richness is high at optimal body size (Maurer et al, 1992).

In mammals, this critical body size value seems to be around 102 g (Peters 1983, Brown and Maurer 1989, Brown 1995). This value has been recognized as the optimum body size for the group, and modeled in terms of maximizing the rate of conversion of energy from environment into useful work for reproduction (reproductive power) (Brown et al. 1993). These two capacities (acquisition and conversion) (K_0 and K_1) are allometrically related to body size, $K_0=C_0M^{b_0}$ and $K_1=C_1M^{b_1}$. The allometric coefficients b_0 and b_1 remain constant across different kinds of organisms, whereas C_0 and C_1 are taxon-specific parameters. Optimal body size (M^*) is then obtained by maximizing reproductive power, and it is given by the expression

$$M^* = [(-C_1b_0)/(C_0b_1)]^{1/(b_0-b_1)}$$

Thus, optimal body size depends on the way that phylogenetic constraints in each lineage limit variation in body size, fitting organisms to the environment (expressed by C_0 and C_1 in the above equations).

However, since there are phylogenetic patterns in body size, it is important to remove inertial phylogenetic trends before inferring that life history traits and optimum body size are responsible for the overall shape of macroecological constraint space. Gaston and Blackburn (1996) recently pointed out that the positive relationship between geographic range size and body size would be simply an artifact related to the fact that older and larger species would occupy a greater proportion of the potential range size, since all barriers for dispersion were already overcome. Also, optimum body size may vary because of the changes in life history traits in different groups (Brown et al. 1993, Blackburn and Gaston, 1996). This phylogenetic structure in data is a common problem in comparative data analysis (closely related species share variation due to common ancestry), in such a way that treating them as independent points in statistical analyses overestimates the actual adaptive correlation among traits or between traits and environmental components (Felsenstein 1985, Harvey and Pagel 1992, Blackburn et al. 1996).

Mammals have been a common subject for macroecological analyses worldwide (Wilson 1974, Brown and Maurer 1989, Pagel et al. 1991, Brown and Nicolleto 1991, Letcher and Harvey 1994), not only because of their relatively well-known taxonomy and geographic distribution, but also because of the importance of macroecological interpretations for biological conservation and preservation of endangered species (Pagel et al. 1991, Brown 1995, Lomolino and Channell 1995). In the Neotropical region, some macroecological patterns in mammals have been investigated by Arita et al. (1990), to explain rarity among species and establish better conservation strategies for them, and by Ruggiero (1994), who established the adherence of some taxonomic groups (Carnivora, Primates and Chiroptera) to Rapoport's rule and analyzed the effect of continental shape in determining geographic ranges and latitudinal gradients in species diversity.

The purpose of this paper is to test the following hypotheses: 1) the relationship between geographic range size and body size for Neotropical rainforest mammals follows the patterns found in other taxonomic groups, expressed by a polygonal constraint space; 2) the macroecological constraint space is not an artifact resulting from inertial phylogenetic patterns on body size and geographic range size; 3) if evolution of optimal body size is determined in each lineage according to constraints related to its ecological and life-history traits, optimizing the ratio speciation/extinction, then the maximum variation in geographic range size should occur at a modal size, even after removing phylogenetic trends.

Materials and Methods

Data Set

Data for this study were extracted from Emmons (1990) survey of Neotropical rainforest mammals. We restricted our analysis to a sample of 87 mammal species that are exclusively found in South America (to standardize effects of spatial constraints at continental scale), and for which body weight was given. These species are distributed among 6 orders, 13 families and 42 genera. Non-terrestrial mammals (Chiroptera and aquatic mammals, including Sirenia and Cetacea) were not analyzed here because of their particular ecological and evolutionary characteristics affecting body size and geographic range (Brown 1995). As in previous analyses, the number of rodent species is clearly underestimated in our sample (see also Arita et al. 1990). However, these sampling problems may be eliminated by removing phylogenetic-taxonomic hierarchy prior to the analyses.

Geographic range size (GRS) for each species was defined as the extent of occurrence (Gaston 1991, 1996) and measured from the maps provided by Emmons (1990). These distribution maps were redrawn in a standardized grid map with 858 quadrats, 150 km on a side, using polyconic projection (scale=1:7,530,000). GRS were expressed as a percentage of continental area and transformed to natural logarithms prior to the analysis (Brown and Maurer 1987, 1989, Gaston 1996). To check the accuracy of geographic range size in our data set, the values obtained in our analyses were correlated with those from Arita et al. (1990), using 40 species that are common to both studies. Since the correlation coefficient was high and very significant ($r=0.950$; $P<0.01$), our estimates seem to be accurate enough for macroecological analyses. Body size (BS) was defined by the adult non-pregnant body weight, and was also transformed to natural logarithms.

Statistical Analyses

The shape of macroecological constraint space was tested using the method of Blackburn et al. (1992), which consists of fitting different least square regressions to maximum and minimum values of the response variable (in this case, the geographic range size) on the averages of class intervals in the predictor variable (body size, in this case). According to Brown and Maurer (1987, 1989) and Brown (1995), minimum geographic ranges must increase or decrease with body size, for values higher or lower than optimal body size, respectively. Maximum GRS is determined by continental constraint, and would be independent of body size.

The phylogenetic effects in GRS and BS were evaluated using comparative methods (Harvey and Pagel 1992). It is difficult to find a common taxonomic level to establish ecologically constrained optimal body size, as predicted by Brown's et al. (1993) model, because of the common strong phylogenetic gradients on body size (Cheverud et al. 1985, Gittleman and Kot 1990, Geffen et al. 1996). If C_0 and C_1 the allometric constants in Brown's et al. (1993) model, express relative constraints on body size due to ecological and life-history characteristics, these aspects may be relevant to establish at which critical level data should be analyzed. We followed Stearns (1983) and used the family as a cutoff level in terms of relative homogeneity in ecological and life-history characteristics. Also, in this work, using this level maximizes the number of replicates within each group.

We then used a nested analysis of variance (ANOVA) (Sokal and Rohlf 1995), using orders and families as factors, to remove large-scale hierarchical taxonomic or phylogenetic effects on BS and GRS (Stearns 1983, Bell 1989, Harvey and Pagel 1992). The residuals of this ANOVA model are, by definition, independent of the hierarchical structure, and measure the standardized within-family variation. Despite the more sophisticated methods that are available today for evaluating phylogenetic effects, such as phylogenetic autoregressive analysis (Cheverud et al. 1985, Gittleman and Kot 1990) and independent contrasts (Felsenstein 1985, Harvey and Pagel 1992), subtraction methods based on ANOVA are the most useful in this case, because they permit the establishment of distances in relation to the expected value at the minimum hierarchical level (family) analyzed. If Brown's model for optimal body size is correct, we expect that most of geographic range variation occurs at zero residuals, which are the expected level within families that balance the different ecological processes defining the

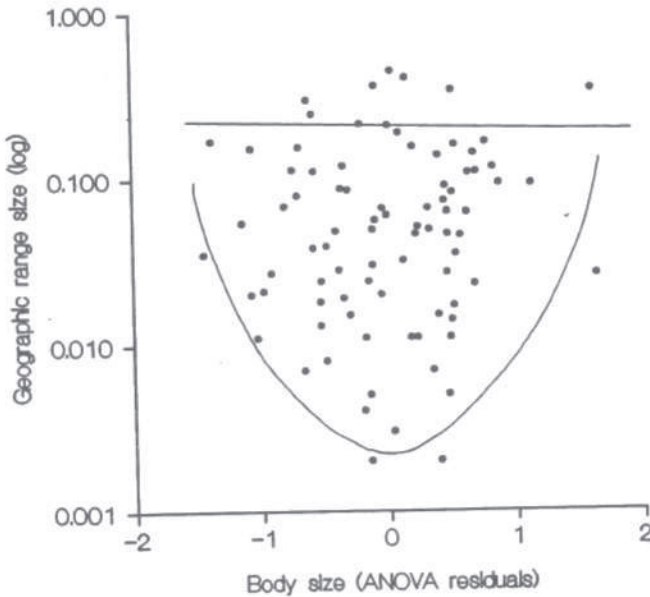


Figure 1. Relationship between geographic range size and body size, in logarithmic scale, for 87 Neotropical rainforest mammals. Linear and quadratic regressions were fitted to the borders of envelope constraint space using the method of Blackburn et al. (1992).

constraint space of GRS on BS.

All statistical analyses were performed with a PC/AT486 microcomputer, using SYSTAT/SYGRAPH (Wilkinson 1989).

Results

As expected, a plot of GRS against BS on logarithmic scale revealed a pattern similar to the one found by Brown and Maurer (1987, 1989) for North American birds and mammals, defined by constraint lines, as previously discussed (Figure 1). Using the method of Blackburn et al (1992), we fitted regressions to minimum and maximum GRS for 8 class intervals of body size. For maximum GRS against body size, a linear fit was obtained, with $r^2=0.54$, and the regression slope was only slightly different from zero ($P=0.04$). For minimum GRS, a good quadratic fit was obtained, with $r^2=0.93$ ($F=33.1$, $DF=2,5$; $P<0.001$). The advantage of a single quadratic fit in relation to two different linear regressions (below and above the optimum body size) is that it was not necessary to define *a priori* the value of optimum body size, and of course results would be sensitive to this choice.

The shape of the fitted curve indicates that the minimum GRS is found between 10^2 and 10^3 g of body size (Figure 1), and thus support the model of Brown and Maurer (1987, 1989), that proposes that there is a critical value of body size at which the largest variance in GRS is found. GRS increases for species with larger or smaller BS than this critical value. The minimum value of BS is also observed in our sample. Although maximum GRS is expected to be independent of body size, the very slight trend observed here must be a consequence of small number of lineages with small body size, in such a way that is less likely to sample species in all GRS values.

The two variables analyzed revealed some hierarchical structure across the two taxonomic levels, but with very different magnitudes. The r^2 values derived from the two-level nested ANOVA for BS and GRS were 0.88 and 0.35, respectively. These two values indicate the part of variation in the traits that can be explained by hierarchical trends, although they are clearly different. This difference is also

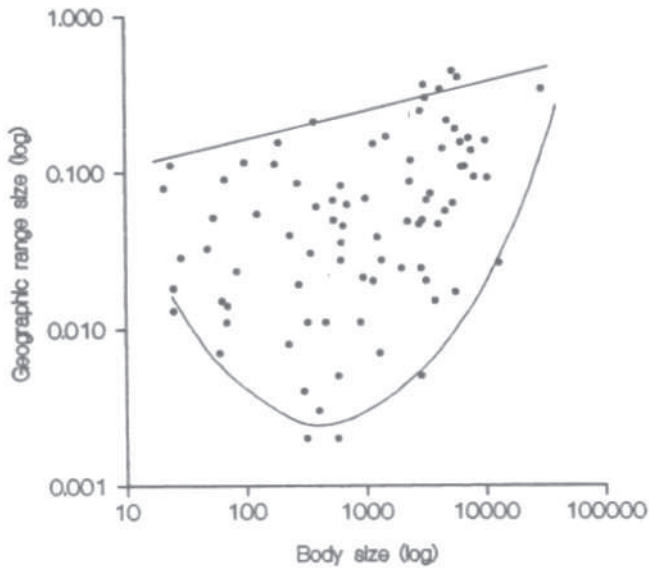


Figure 2. Relationship between geographic range size and body size of 87 Neotropical rainforest mammals, after removing large-scale hierarchical trends (orders and families) by nested ANOVA. Linear and quadratic regressions were fitted to the borders of envelope constraint space using the method of Blackburn et al. (1992).

confirmed by the F-values of the two ANOVA models, at the two levels (orders and families). For GRS, only the family level showed significant F-value, only at 5% level ($F=3.0$; $P=0.03$), but the order effect was not significant ($F=2.0$; $P=0.10$). For BS, however, the two F-values were highly significant ($F=4.11$ and 25.1 for order and family effects, respectively, with $P < 0.01$).

Since a strong hierarchical trend was detected for BS, we plotted the residuals of the ANOVA model, expressing the within-family variation for BS, against the original GRS values. In the new plot of GRS against the residuals of BS (Figure 2), the constraint space is still present, and there is a negative correlation, at both sides of predicted values for BS (residual equal to zero), between GRS and residuals of BS derived from nested ANOVA. A quadratic regression was also fitted to minimum GRS against residuals of BS, using the method of Blackburn et al. (1992), and r^2 was 0.91 ($P=0.002$). The minimum value for GRS trend was very close to the zero residual in BS. Also, and more interesting, maximum GRS was independent of body size according to a linear regression ($r^2=0.01$; $P=0.87$), which is indeed expected if significant inclination detected before removing phylogenetic trends was a consequence of sampling a few species in lineages with small body size. So, both minimum geographic range size and the maximum amplitude of variation in geographic range size was found when species were close to the expected value for their respective family. When plotting residuals of the two variables derived from nested ANOVA models, results were also very similar in the terms discussed above, which is expected by considering the low hierarchical trends in GRS.

Discussion

The analysis of macroecological variables in South American rainforest mammals supports the model proposed by Brown and Maurer (1987, 1989), in which species fall within a limited envelope space, limited by constraints. In our analyses, the minimum GRS is found approximately when $BS = 10^{2.5}$ g, which is within the limits established by Brown's et al. (1993) model for optimal body size in mammals (especially considering that number of small mammals, such as rodents, are clearly underestimated in our sample). So, although our sample is relatively small, it preserves the main macroecological patterns

of the group. However, since body size possesses phylogenetic trends, it is important to remove them before inferring that macroecological patterns can be explained by ecological constraints of life-history leading to optimal body size.

The elevated magnitude of hierarchical effects in body size detected in our study has been found for many distinct taxonomic groups, and usually explained by phylogenetic inertia (closely related species are more similar) (Cheverud et al. 1985, Gittleman and Kot 1990, Geffen et al. 1996) or by trends in body size evolution, as a consequence of the empirical Cope's "rule", well-known among paleontologists (Grantham 1995). These trends in body size evolution have been explained recently by local adaptations at the organismic level (driven trends) or by processes at species level, such as the "passive diffusion", in which variance in body size increases along evolutionary time even in the absence of direction selection within-species (Grantham 1995). On the other hand, our analyses confirms that geographic range size has low phylogenetic inertia, confirming previous work (Taylor and Gotelli 1994, Brown 1995). This is expected because geographic range is a very "plastic" trait, usually being subjected to strong shifts and fluctuations, tracking macroclimatic variations. Brown (1995) showed similar hierarchical effects on these two variables, for North American mammals, but analyzing variation at generic level.

The constraint space is still present when hierarchical (phylogenetic) effects are statistically removed from the data. So, models based on life-history evolution and species dynamics can be used to explain it, since species are affected independently by the combined effects of geographic range size and body size, determining the final shape of constraint space.

In this new constraint space, the maximum amplitude of geographic range size variation among species appears when residuals of body size are close to zero, giving support to a relationship between the shape of the envelope constraint space and Brown's et al. (1993) model for optimal body size. This pattern in the residuals of BS may be understood by assuming that the expected value of body size derived from ANOVA (residual equal to zero) is close to theoretical optimal body size, within a given taxonomic level (in this case, family). This assumption may be justified because, at low taxonomic levels, distributions of body size are usually log-normal (Blackburn and Gaston 1994) and because ecological and life-history characteristics at family level do not necessarily affect body size gradients within families, which may be better explained by inertial evolution (Cheverud et al. 1985, Geffen et al. 1996). Ecological mechanisms explaining this constraint space after removing hierarchical trends may be as follows.

At the optimal size in a given evolutionary lineage, equilibrium between different body size-related ecological processes maximizes probabilities of survival of species, by increasing or decreasing speciation or extinction rates, respectively. The value of optimal body size and the magnitude of these two rates, however, must take into account the different ecological and life-history traits within groups (Blackburn and Gaston 1996), producing then a large number of species close to optimal body size and with a large variation in geographic range size, depending both on modes of speciation and colonization capacity of each species. Shifts in the ecological conditions that constrain body size should then produce a new optimal body size, and the process goes on again. At each optimal body size, maximum variation in geographic range size is determined by absolute probability of extinction at minimum size, as proposed by Brown and Maurer (1987). The consequence of this model is that the overall macroecological constraint space observed should be viewed as a fractal structure, composed of successive triangles containing phylogenetically related species in which the same ecological and life-history traits constrain body size evolution, and in each of them the maximum variation in geographic range size occurs at optimal body size.

Taylor and Gotelli (1994) recently evaluated the influence of autocorrelation effects, at spatial and phylogenetic dimensions, on the macroecology of North American fishes of the genus *Cyprinella*. However, they considered mainly the signal of the relationship between geographic range and body size to give support to macroecological models derived by Brown and Maurer (1987, 1989) or Gaston and Lawton (1988a,6). Also, since they did not consider analytically the overall shape of the constraint space, they used multiple Mantel tests (Sokal and Rohlf 1995) to remove spatial and phylogenetic trends, and only discussed that pairwise matrices of differences in geographic range and body size are

not significantly associated after removing these trends. In fact, they tested only for a linear (or monotonic) relationship between geographic range size and body size. However, since the relationship between these two variables is much more complex (forming the constraint space), the absence of a significant correlation by Mantel tests does not imply that constraint spaces will not be present after removing the phylogenetic trends, as we found in this paper.

Our reanalysis of macroecological variables of South American rainforest mammals supports both the constraint space previously observed in North American species and the ecological and evolutionary processes developed to explain it, by considering patterns of relationship between body size and geographic range size before and after removing large-scale phylogenetic effects. The most important aspect of this analysis is that the optimal body size model proposed by Brown et al. (1993) can explain the shape of constraint space after removing these large-scale phylogenetic trends, providing a useful theoretical framework to understand how ecological and life-history body size-related processes can lead to the observed macroecological patterns.

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