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NULL MODELS AND RAPOPORT'S EFFECT IN NEOTROPICAL FALCONIFORMES

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Resumo. – Modelos nulos e efeito Rapoport em Falconiformes Neotropicais. – O efeito Rapoport prediz que a área de distribuição geográfica das espécies aumenta em direção às latitudes mais elevadas, refletindo provavelmente processos adaptativos a condições climáticas extremas, o que aumenta a sua tolerância ecológica e, consequentemente, permite a dispersão dessas espécies para áreas maiores. Entretanto, trabalhos recentes sobre padrões de riqueza de espécies e sua área de distribuição têm demonstrado que muitos deles podem estar associados à geometria do continente. Em função desses efeitos puramente geométricos, um efeito Rapoport simples dificilmente seria encontrado em algumas regiões do mundo, como a região Neotropical. Neste trabalho, nós aplicamos um modelo nulo a fim de avaliar o efeito Rapoport em Falconiformes neotropicais, simulando as extensões latitudinais das espécies dentro dos valores máximos permitidos pela posição do pontos médios latitudinais. Como o coeficiente angular observado para a relação entre extensão latitudinal e latitude foi significativamente menor do que a obtida em 5000 simulações, é possível concluir que o "espírito" do efeito Rapoport pode ser mantido. Assim, embora as distribuições geográficas das espécies temperadas sejam, em termos absolutos, menores do que o as das espécies tropicais, elas tendem a ocupar um proporção relativamente maior da área disponível para colonização. Embora seja difícil encontrar um explicação causal para esse efeito subjacente à restrição continental, processos adaptativos e ecológicos podem ser invocados para explicá-lo, uma vez que o modelo nulo baseado em um efeito puramente geométrico para o padrão espacial foi rejeitado.

Abstract. – The Rapoport effect predicts that species geographic range sizes will increase toward higher latitudes probably reflecting adaptations to extreme climatic conditions that increase species tolerance and, consequently, permit dispersion to larger areas. However, in recent years, studies about species richness and geographic range size suggested that spatial patterns may be associated with the geometry of species' ranges in relation to continental boundaries. This ensures that, for some regions of the world, as Neotropics, the Rapoport simple pattern could hardly be found. In this paper, we applied a null model to evaluate the Rapoport effect in Neotropical Falconiformes, simulating latitudinal extents constrained by position of latitudinal midpoints along South American domain. Since the slope observed for the relationship between latitudinal extent and latitude is significantly smaller than all 5000 simulated slopes, it is possible to conclude that species in the southern parts of the continent possess relatively large extents, as expected if the "spirit" of the Rapoport effect could be maintained. So, although the geographic ranges of temperate species are, in absolute terms, smaller than those of tropical species, they tend to occupy a greater proportion of the total space available to them than the latter ones. Although it is usually difficult to find a primary

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cause for large-scale patterns, rejection of null model indicate that adaptive ecological and evolutionary processes should be invoked to explain this pattern in Falconiformes. *Accepted 2 December 2001.*

Key words: Rapoport effect, Falconiformes, null models, geographic range size, latitudinal extent, Neotropics

INTRODUCTION

The Rapoport effect predicts that species geographic range sizes will increase toward higher latitudes probably reflecting adaptations to extreme climatic conditions that increase species tolerance and, consequently, permit dispersion to larger areas (Stevens 1989; see also Rapoport 1975). This controversial ecogeographical pattern has been widely discussed in the last few years, specially because of its possible link with latitudinal gradients in species richness (Stevens 1989). Despite many recent papers showing that no link seems to exist between the Rapoport effect and latitudinal gradient (Gaston 1999, Kerr 1999, Taylor & Gaines 1999), the increase of geographic ranges toward higher latitudes is still of interest and the associated ecological and evolutionary processes explaining it could be reconsidered. Gaston *et al.* (1998) showed that at least five processes could be involved with this pattern.

Recently, studies about spatial variation in species richness and geographic range sizes suggested that peaks in species richness might be associated with the geometry of species' ranges in relation to continental boundaries, the so-called "mid-domain effect" (Colwell & Lees 2000). These ideas have been particularly stimulated by the application of analytical methods and computer-intensive simulation strategies to generate null models for variation in species richness and range overlap at large geographical scales (Colwell & Hurt 1994, Willig & Lyons 1998, Lees *et al.* 1999, Colwell & Lees 2000, Veech 2000, Jetz & Rahbek 2001). Beyond predicting expected species richness, the knowledge of these constraints ensures that, for some regions of the world, the Rapoport simple pattern could hardly be found (Lyons & Willig 1997).

The Neotropics provides an unique opportunity to study the effect of geometric constraints on range sizes and shapes and how ecological processes may be counteracted and obscured by them. The South American continent decreases in area toward southern higher latitudes in such a way that, under a simple geometric null model of geographic range sizes, an inverted Rapoport effect is expected. The opposite pattern is expected in North America, where the increase in available area for colonization implies that a clear Rapoport-like pattern would be expected by chance only, without ecological and evolutionary mechanisms affecting geographic range sizes. In this context, Lyons & Willig (1997) proposed that the "spirit" of the Rapoport effect would be maintained if the geographic range sizes of species living in the southern regions of South America are larger than expected by a null model that takes into account the geometric constraint caused by continent shape (see Fig. 8 of Lyons & Willig 1997).

In this paper, we applied a null model to evaluate the latitudinal extent of Neotropical Falconiformes, showing that despite their ranges tends to decrease toward southern latitudes (against the expected pattern under Rapoport effect) they decrease slower than expected by continent boundaries. Thus, in relative terms, temperate species can be considered to have larger ranges than their tropical counterparts, maintaining the so-called "spirit" of Rapoport effect.

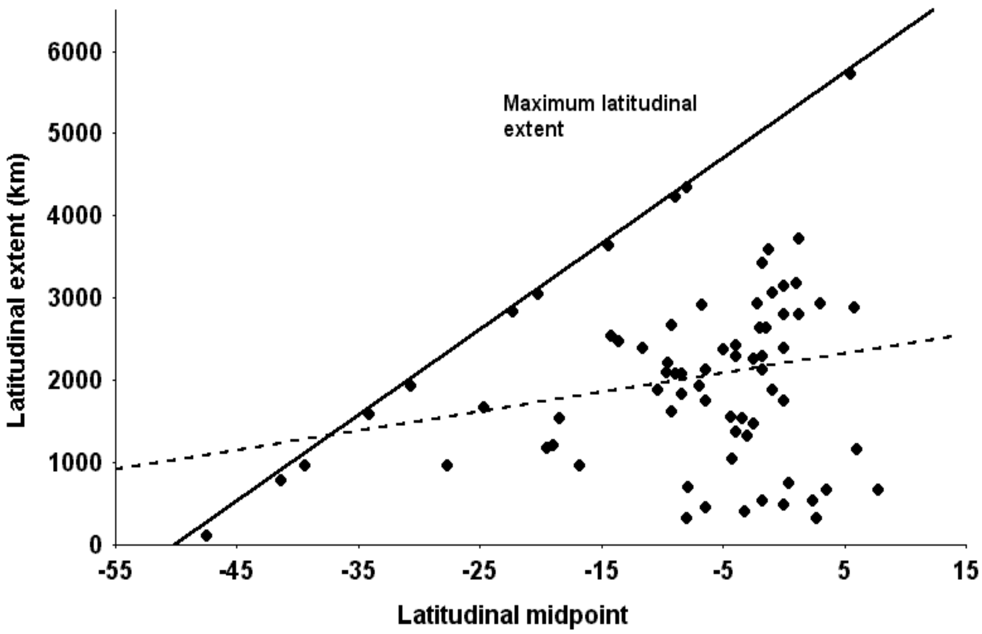

FIG. 1. Relationship between latitudinal extent and latitudinal midpoint for 78 species of Neotropical Falconiformes. The solid line shows the maximum possible extent in the South American domain (caused by the geometry of the estimate), while the dashed line indicates the regression line of the real data. Negative latitudinal midpoints indicate southern latitudes.

MATERIAL AND METHODS

The geographic ranges of the 78 species of Falconiformes whose latitudinal midpoints can be found in the South American domain (below approximately 12° of northern latitude) were obtained from Sibley & Monroe (1990) and del Hoyo *et al.* (1994). The latitudinal extents of the geographic ranges (latitudinal ranges) (Gaston 1994) were recorded for each species as the difference between southern and northern extremes along latitude.

The Rapoport effect was measured simply by regressing latitudinal extent against latitudinal midpoint (Rohdes's *et al.* 1993 method; see also Gaston *et al.* 1998, Ruggiero 1999). This method was used because it reduces pseudo-replication of Stevens' method (caused by measuring successive averages of geographic ranges across latitudinal bands) and because of its higher statistical power (Lyons & Willig 1997). Since measures of geographic range size usually lack strong phylogenetic components (Brown 1995, Gaston & Blackburn 1997), we assume that problems associated to cross-species analyses cannot distort seriously the results in this case.

The maximum latitudinal extent in South American domain associated with each species latitudinal midpoint was obtained as in Lyons & Willig (1997). It was given by the geographic distance from each midpoint to southern extreme of the continent (because, in our analyses, all species are in the southern hemisphere domain). Also, since some species are found in the southern extreme of the continent, there is no need to distinguish

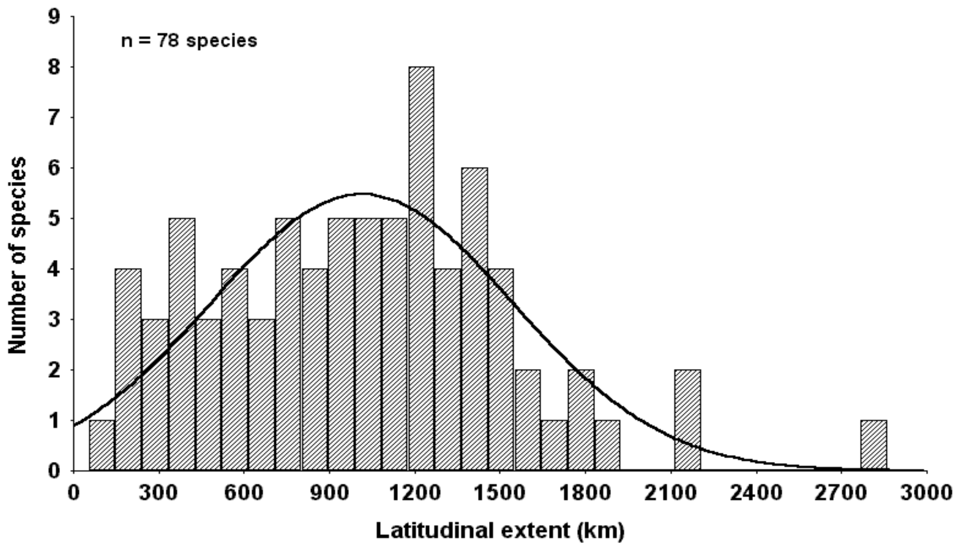

FIG. 2. Frequency distribution of latitudinal extents in the South American domain for 78 species of Neotropical Falconiformes, fitted by a normal curve.

between the different models used to define extreme limits (continental versus maximum distributional extent for the whole group, i.e., Falconiformes) (Lyons & Willig 1997, Koleff & Gaston 2001).

For each of the 78 species midpoint, random latitudinal extents were generated using a normal distribution of extents, limited to the maximum allowed by the associated midpoint. The average of the statistical distribution of the latitudinal extent for a given species was then given by half of the maximum extent allowed by the continent (that in turn is determined by its latitudinal midpoint). The standard deviation of this distribution was set in such a way that 99,9% of the randomly generated extents are within zero and maximum allowed extent. This procedure was then repeated 5000 times and, for each of these simulation, slopes were then estimated by regressing randomly generated latitudinal extents for the 78 species on their associated latitudinal midpoints. Under no continental boundaries, an average zero slope is expected for these regressions. However, since there are limits to the maximum latitudinal extents at a given latitudinal midpoint, a positively biased distribution is expected (since latitudes in the southern hemisphere are coded as negative values).

RESULTS

The latitudinal extents of South American Falconiformes tend to decrease toward southern latitudes, in the opposite direction expected under a simple Rapoport effect and according to expectations based on continent shape (Fig. 1). The slope for original data from the 78 species of Falconiformes was equal to 23.50 ± 10.83 (t = 2.17; $P = 0.033$), but the explanatory power was very small (5.8%), indicating anyway a very weak spatial pattern of latitudinal extents in South American domain. However, before rejecting any ecological or evolutionary process related to

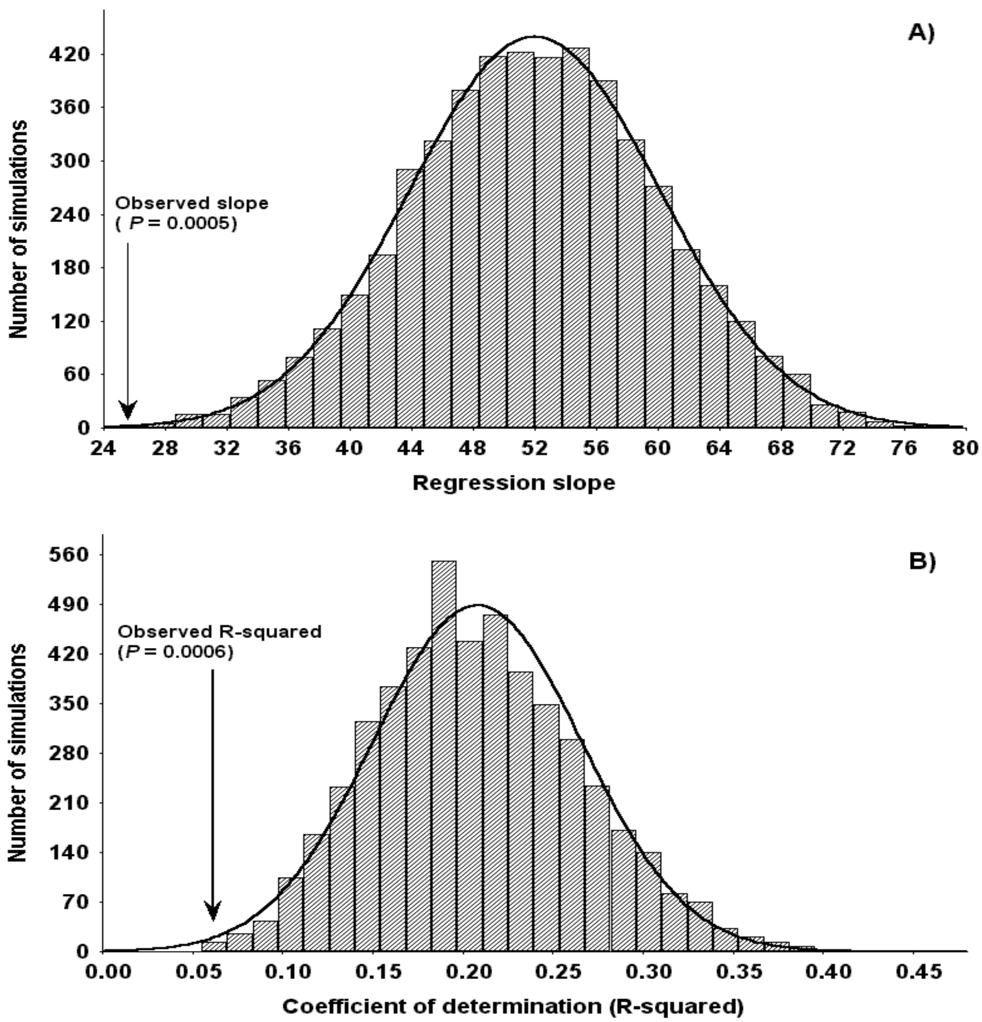

FIG. 3. (A) Frequency distribution of regression slopes and (B) of the coefficients of determination based on 5000 regressions of simulated extents against latitudinal midpoints. Arrows indicate the relative position of the statistics estimated using the real data from the 78 species of Falconiformes.

the Rapoport effect, it is necessary to control for the geometric constraints in the latitudinal extents by using a null model. The statistical distribution of latitudinal extents for the 78 species in South American domain (Fig. 2) does not significantly departs from normality (g1 = 0.508 and g2 = 0.786, for both $P > 0.05$), so using normally distributed random extents is adequate in this case.

Regression slope distribution (Fig. 3A) obtained in the simulations, as expected, is positively biased, with average slope equal to 52.01 ± 8.15, varying between 25.05 and 78.03, reflecting then the geometric constraints in the latitudinal extents. The probability of obtaining the slope estimated for the

78 species from this null distribution was then equal to 0.0005 (1/5000). So, the observed slope is significantly smaller (less inclined) than expected by chance alone. Also, the distribution of coefficients of determination (R^2) indicates that, under simple continent constraints, spatial patterns in latitudinal extents would be much stronger than the observed ($P = 0.0006$) (Fig. 3B).

DISCUSSION

The spatial patterns of latitudinal extents in South American Falconiformes does not follow a simple Rapoport effect, in which the geographic ranges decrease toward higher latitudes. Instead, latitudinal extents of Falconiformes decrease toward the southern part of the continent, as expected if hard boundaries of continent borders constraint the geographic ranges.

The original interpretations of the Rapoport effect, however, does not take into account other factors than adaptations and evolutionary processes changing geographic ranges, such as continent geometry. Specially in Neotropics, this geometric effect may impose strong forces limiting ranges in the southern part of the continent that can obscure interpretations of ecological and evolutionary processes invoked in Rapoport effect (Gaston *et al.* 1998). So, as for other areas of recent ecological research (Gotelli & Graves 1996), null models must be used to overcome this problem and establish the expected distribution of the statistics under these constraints.

Confidence intervals of the null distribution obtained from the simulated data exclude zero ($P < 0.05$) in such a way that, under simple geometric constraints, the relationship between latitudinal extents and latitudinal midpoints are usually strongly positive for Neotropics, as predicted by the Lyons & Willig (1997) null model. Since the slope observed for the 78 species of Falconiformes is significantly smaller than all simulated slopes (see Figs 1 and 3), it is possible to conclude that species in the southern parts of the continent possess relatively large extents, as expected if the "spirit" of the Rapoport effect could be maintained (Lyons & Willig 1997). In other words, although the geographic ranges of temperate species (i.e., whose range centered south from 25°S) are, in absolute terms, smaller than those of tropical species, they tend to occupy a greater proportion of the total space available to them than the latter ones. Thus, in relative terms, they can be considered to have larger ranges than their northern conterparts.

Although it is usually difficult to find a primary cause for large-scale patterns, adaptive ecological and evolutionary processes should now be invoked to explain this pattern in Falconiformes. Although there is a clear gradient is species diversity in Neotropical birds, they cannot be used to explain the Rapoport effect based on low competition caused by low richness (Blackburn & Gaston 1996a, 1996b, Taylor & Gaines 1999). On the other hand, it is interesting to point out that the composition of raptor assemblages is different across altitudinal gradients (Thiollay 1996), reflecting adaptations to climatic and overall conditions for the different species. This variation in environmental tolerance is, in fact, the base of many mechanisms proposed to explain the Rapoport effect, causing range expansion, differential extinction or creating different biogeographic boundaries (structuring species assemblages) (see mechanisms 2, 3 and 5 in Gaston *et al.* 1998; see also Ruggiero & Lawton 1998, Kerr 1998).

A test of these different, but not mutually exclusive, mechanisms would require much more information about phylogeny, life-history variation, ecological tolerance and community structure variation for the studied species at continental scales. This study shows that spatial patterns in latitudinal extents of South American Falconiformes depart from null expectation caused by the geometry of the continent. This departure occurs in the direction expected if an underlying Rapoport effect explains at least part of the variation in these extents. Evaluation of how these departures occur is indeed a crucial step toward understanding the ecological and evolutionary factors explaining spatial variation in geographic range sizes.

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