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Semideciduous Atlantic Forest mammals and the role of the Paraná River as a riverine barrier

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Abstract

The role of the Paraná River as an effective barrier for mammalian dispersal was evaluated. Four species were analyzed based on their characteristics and distributions along river margins: *Caluromys lanatus* (Didelphimorphia), *Hylaeamys megacephalus*, *Oecomys bicolor* (Rodentia), and *Alouatta caraya* (Atelidae). Considering their characteristics of small body sizes, arboreal life styles (of most species), and distributions in both river margins, the Paraná River is suggested to be a weak geographic barrier for mammal dispersal.

Key words: *Alouatta caraya*, *Caluromys lanatus*, *Hylaeamys megacephalus*, riverine hypothesis, semideciduous Atlantic forest.

Introduction

In tropical South America, several studies have carried out to understand the diversification patterns of vertebrate species (Myers, 1982; Patton *et al*., 1994; Vivo, 1997; Silva and Patton, 1998; Lougheed *et al*., 1999; Moritz *et al*., 2000; Carmignotto, 2004; Cáceres *et al*., in press b). Currently, the main hypotheses to explain these diversification patterns in this region are: the riverine hypothesis and the Pleistocene refugia hypothesis (Patton *et al*., 1994; Moritz *et al*., 2000). This paper focuses only on the first hypothesis and its applicability to a large river of South America.

The riverine hypothesis postulates that large rivers reduce or impede gene flow between populations that occur in the opposite margins. In the long term, this process can lead to speciation. A second prediction postulates that, because headwaters are narrower than river mouths, the strength of a fluvial barrier will decrease from the river mouth to the headwaters. Consequently, higher probabilities to occur vicariant processes in the low parts of the river are expected (Lougheed *et al.*, 1999; Gascon *et al*., 2000).

Whether the large Paraná River, a major tributary of the La Plata River, can function as an effective barrier to dispersal of organisms, a variety of consequences in the species diversification would take place. The river would impede species dispersal or even gene flow due to the incapacity of species to cross the river, leading to speciation over the long term. The fact that the Paraná River crosses a transitional floristic zone between the Cerrado and the

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Atlantic Forest, but also serves as an obstacle between two large portions of the semideciduous Atlantic Forest, places it as an important geographic cue for the understanding of biogeographic faunal patterns that currently occur in central South America. For the Paraguay River, another large tributary of the La Plata River, Myers (1982) has concluded that the river is not a barrier for small mammal dispersal, based on the geographic distribution of species. This author hypothesized differences in soil and biomes as the main factors for the faunal divergence found in both margins of that river, a hypothesis supported by the bat fauna in the same region (Willig *et al*., 2000).

Small mammal species have a high degree of endemicity in the biomes of South America, but some species have wide distributions across them, occurring extensively in two or more biomes. This is true for the didelphid woolly opossum *Caluromys lanatus* (Olfers, 1818) and the cricetid rice rat *Hylaeamys megacephalus* (Fischer, 1814) that range from the Amazon basin south to the Cerrado of central Brazil and the seasonal semideciduous forests of eastern Brazil, northeastern Argentina, and eastern Paraguay. Other species analyzed is the cricetid arboreal rat *Oecomys bicolor* (Tomes, 1860), whose range is mainly the Cerrado and the Amazon forest. The last species analyzed is *Alouatta caraya* (Humboldt, 1812), a medium sized atelid primate, which ranges from central Bolivia to southern Brazil, crossing the Cerrado biome and reaching the seasonal forests of southern Brazil (Fonseca *et al*., 1996; Anderson, 1997; Emmons and Feer, 1997; Eisenberg and Redford, 1999; Carmignotto, 2004; Carleton and Musser, 2005).

This paper examines the distribution patterns of these four mammal species across the Paraná River: *C. lanatus*, *H. megacephalus*, *O. bicolor*, and *A. caraya*, which are typical of the semideciduous Atlantic Forest in their southern distribution. The main goal is to discuss the role of the Paraná River as a geographic barrier for dispersal of these arboreal or terrestrial mammals, since their range is interrupted by this river. These southern limits of distribution give conditions to analyze this large river as a plausible geographic barrier, since species would not have many alternative routes for dispersal. To date, nothing is known on the role of the Paraná River as a possible barrier for mammal dispersal.

Material and Methods

The study region is in central to southern Brazil, in the region drained by the Paraná River, comprising mainly the states of Mato Grosso do Sul, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, in Brazil. Records in eastern Paraguay and northeastern Argentina were also included, mainly based on data from Redford and Eisenberg (1992) and Chebez (1996) data.

In order to confirm and analyze species distribution, distributional records of the four mammal species were obtained from the literature, museums (FZB at Porto Alegre; LAMAQ at Florianópolis; MHNCP at Curitiba; MZUSP at São Paulo, and MNRJ at Rio de Janeiro), and unpublished data of the author.

Results and Discussion

Distributional data around the Paraná River have shown important differences in the distributional patterns among species, with *A. caraya* exhibiting a slightly different one. Nonetheless, the distributions of the four mammal species illustrate the failure of the Paraná River as an effective riverine barrier, since at least two species exhibit obligatory ranges across the river. Therefore, these two species (*O. bicolor* and *A. caraya*) were intended as having no alternative route for dispersal being the Paraná River as the unique route to maintain gene flow. However, the specific habits of the four species still need to be analyzed to better understand the phenomenon of a riverine barrier on each, including alternatives routes of dispersal rather than over the Paraná River (Figure 1).

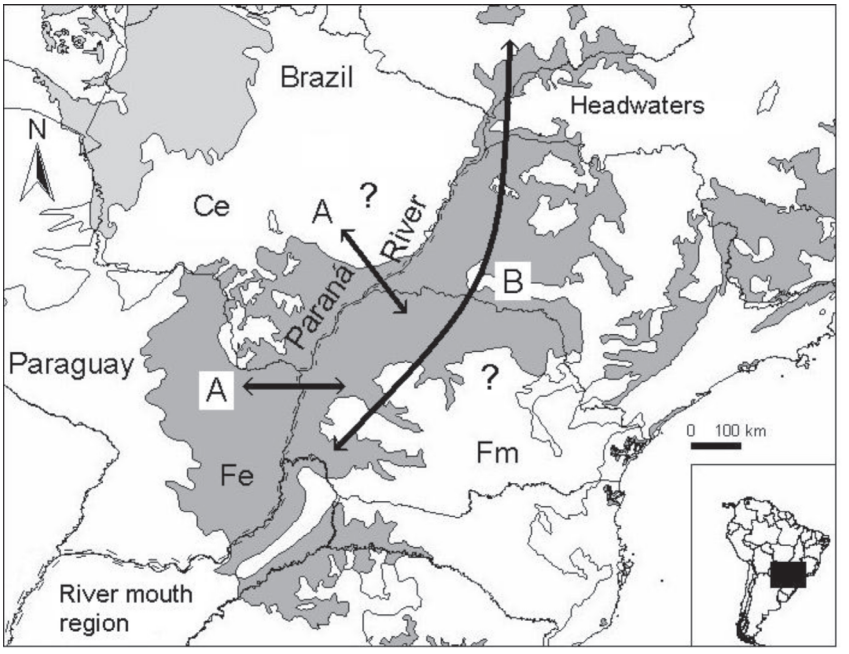

Figure 1. Hypotheses of dispersal or gene flow between populations of mammals east and west of the Paraná River in the La Plata basin, in eastern South America. A) free dispersal over the river; B) dispersal circumscribing the river via headwaters. Biomes: Ce – Cerrado; Fe – Semideciduous forest (in dark gray); Fm – Mixed ombrophyll forest; Pantanal is in light gray. Arrows indicate possible pathways of dispersal.

It is known that arboreal mammal species have more difficulty to cross open areas and, hence, to disperse or migrate (Fernandez and Pires, 2006). This difficulty would be greatly diminished if a given species was terrestrial and opportunistic.

All four species occur in the semideciduous Atlantic Forest of southern Brazil and in the adjacent Cerrado biome, in west and northward directions (regarding São Paulo and Paraná states). Nonetheless, *C. lanatus* (Figure 2) and *A. caraya* (Figure 3) also reach the deciduous forests of Santa Catarina and Rio Grande do Sul states at the southern latitudes. The ranges of neither *H. megacephalus* (Figure 4) nor *O. bicolor* extend that far south.

Caluromys lanatus and mainly *H. megacephalus* have wide distributions to the east, in the states of São Paulo and Paraná, and are clearly limited by the distribution of the seasonal, semideciduous Atlantic Forest (*census* IBGE, 1992) (Figure 2 and 4). However, *A. caraya* has its distribution restricted to the west (see Emmons and Feer, 1997), but just at the left margin of the Paraná River (thus, in western Paraná state) (Figure 3). *Oecomys bicolor* was recorded in western São Paulo state, east of the Paraná River, at a single locality (Aguapeí River; Cáceres *et al*., in press a). Hence, the range of *O. bicolor* in the semideciduous Atlantic forest is unknown.

Based on these facts, the arboreal *C. lanatus* and the terrestrial *H. megacephalus* could maintain dispersal between populations from the Cerrado and Semideciduous Forests at the left margin of the Paraná River (see Costa, 2003) through connecting populations northward around the headwaters of the Paraná River, where the river is narrower and the crossing is easier, rather by directly crossing it (Figure 1B). For *A. caraya* and *O. bicolor*, both being arboreal species, the mechanism is intended to be different because of its limitation of distribution (1) to the west regarding the two previous species distributions (*C. lanatus* and *H. megacephalus*), and (2) to the north along the left bank of the Paraná River.

The proximity of the Cerrado biome (in the Mato Grosso do Sul state) in relation to the left margin in the upper Paraná River is a possible explanation for

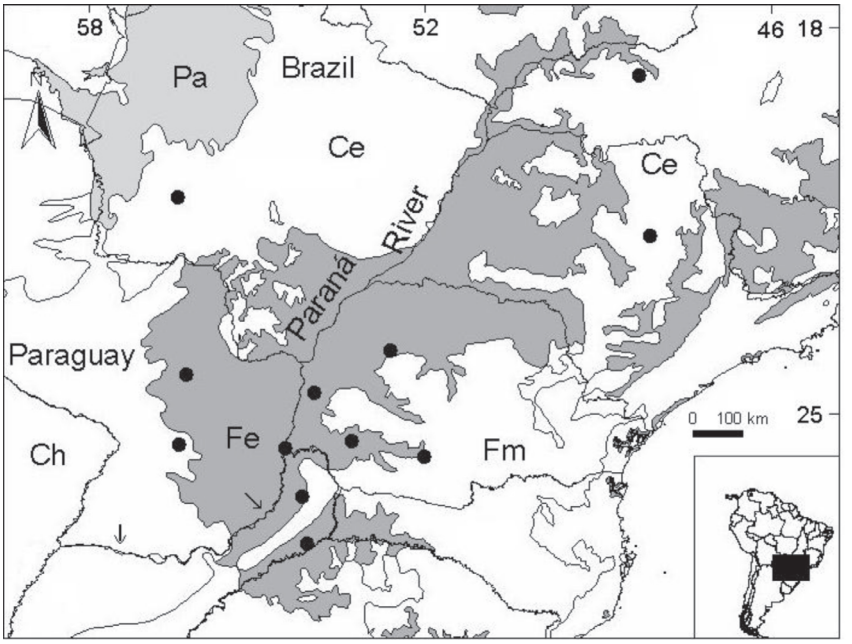

Figure 2. Localities of distribution of the wooly opossum *Caluromys lanatus* in its southern range. Records are based on Redford and Eisenberg (1992), Chebez (1996), Quadros *et al*. (2000), Costa (2003), Cáceres *et al*. (2007, in press b). Biomes: Ce – Cerrado; Ch – Humid chaco; Fe – Semideciduous forest (in dark gray); Fm – Mixed ombrophyll forest; Pa – Pantanal (in light gray). Arrows indicate the Paraná River.

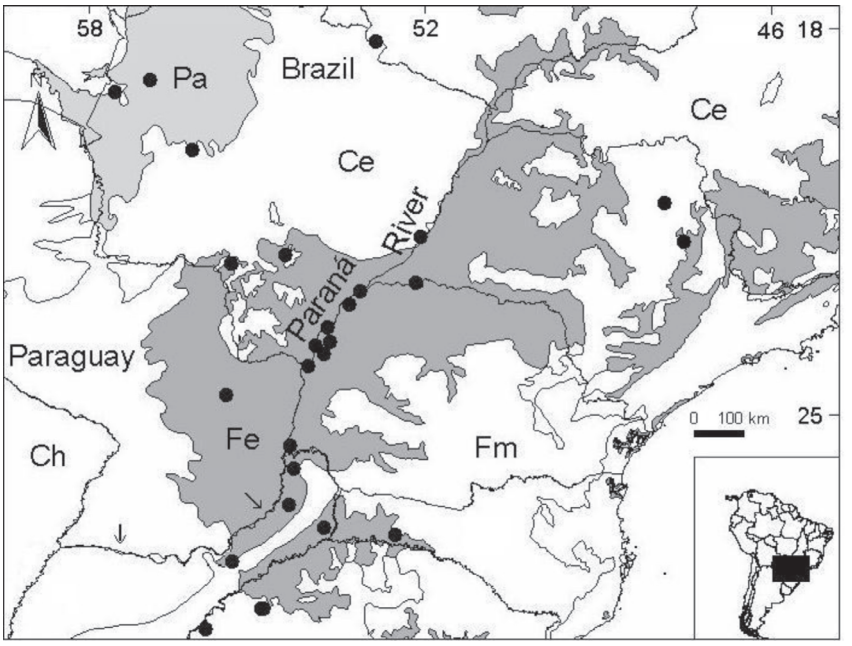

Figure 3. Localities of distribution of the black howler monkey *Alouatta caraya* in its central range. Records are from field data of the author, personal communications, museums, and literature based on Redford and Eisenberg (1992), Chebez (1996), Rodrigues *et al*. (2002), Cáceres *et al*. (in press b). Biomes: Ce – Cerrado; Ch – Humid chaco; Fe – Semideciduous forest; Fm – Mixed ombrophyll forest; Pa – Pantanal. Arrows indicate the Paraná River.

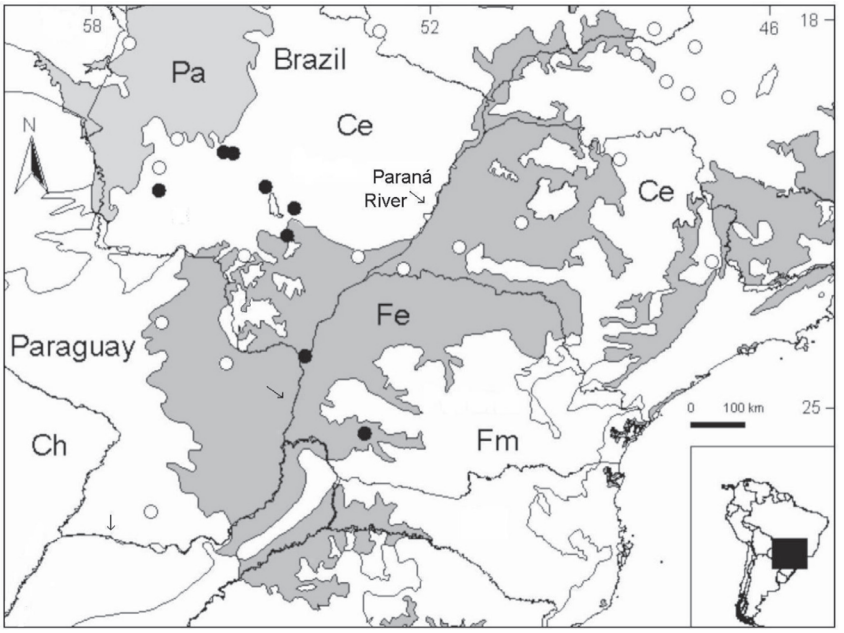

Figure 4. New (in black) and previous (in white) localities of *Hylaeamys megacephalus* southern distribution in South America. New records are base mainly on field collections of the author. Previous records are based on Musser *et al*. (1998), Percequillo (1998), Costa (2003), Carmignotto (2004), Emmons and Patton (2005). Biomes: Ce – Cerrado; Ch – Humid chaco; Fe – Semideciduous forest; Fm – Mixed ombrophyll forest; Pa – Pantanal.

the occurrence of *O. bicolor* in the semideciduous Atlantic forest of western São Paulo. This is based on the free dispersal of this species of arboreal rat over the Paraná River, as occurred for another arboreal rodent in the Amazon forest (Patton *et al*., 1994).

Clearly, *A. caraya* has its distribution limited to the Paraná River (in its left margin) at semideciduous forests of the Paraná state, but it reaches the deciduous forests and more distant areas from the river only at the southern latitudes, along the Uruguay River, in the deciduous forests (Figure 3). The main cause of this limitation in the semideciduous Atlantic forest is probably the tension/competition with the congeneric species, *A. guariba* (Humboldt, 1812), which has its occidental limit of distribution exactly in the oriental limit of distribution of *A. caraya* (Emmons and Feer, 1997; Cáceres *et al*., in press b; Passos *et al*., in press). Why *A. guariba* extends its distribution so far to the west in semideciduous and deciduous forests, but does not cross the Paraná River, is not known. It could be inferred that the simple presence of *A. caraya* along both margins of the Paraná River is an important reason for that, since these congeneric species are similar in habits. Competition is an important factor in determining spatial distribution, mainly between congeneric species (Ricklefs, 2003).

Therefore, the arboreal habit of *A. caraya* and its effective crossing over the Paraná River, without an actual possibility of circumscribing the river via the headwaters (Figure 3), leads to the inference that the Paraná River is not a barrier to mammal dispersal, even to the arboreal species, which is intended to be more difficult to disperse in open areas. The São Paulo state territory is highly dominated by the congeneric species, *A. guaryba*, with *A. caraya* occurring only in the extreme southwest (in semideciduous forest) and in the north-east (where the Cerrado biome has an important distribution; Figure 3).

For *Caluromys*, the limits of *C. lanatus* and *C. philander* distributions in the south of Brazil are apparently given by the limits of forest formations. *C. lanatus* is limited by the distribution of seasonal deciduous Atlantic forests and *C. philander* by the dense and probably the mixed forests (Cáceres and Carmignotto, 2006; Cáceres *et al*., in press b). For the "*Oryzomys*" group, three species occur in southern Brazil and northeastern Argentina, east of the Paraná River: *Sooretamys angouya*, *Euryoryzomys russatus*, and *Hylaeamys megacephalus* (Lange and Jablonski, 1981; Chebez, 1996; Musser *et al*., 1998; Quadros *et al*., 2000; Cherem *et al*., 2003; Pereira *et al*., 2005; U. Pardiñas, pers. comun.; and this study). The eastern limit of *H. megacephalus*, however, corresponds to the distribution of semideciduous forest in São Paulo and Paraná states (Figure 4). The coexistence of the three species at the same locality is apparently not supported (Musser *et al*., 1998), which results probably in spatial segregation between them (see Moritz *et al*., 2000). The Paraná River thus is not a barrier for the "*Oryzomys*" species group since all three species of the group cited here also occur in its right margin, in eastern Paraguay (Musser *et al*., 1998; Percequillo, 1998), in a portion where the river is larger, which presumably would difficult the crossing.

Corroborating the hypothesis of free dispersal over the Paraná River, there is a species group of small mammals strongly Atlantic in characteristics (except for one that occurs also in the Amazon forest), which never or not fully occurres in the Cerrado biome, but occurres in both margins of the Paraná River. These species are the marsupials *Didelphis aurita* (Wied-Neuwied, 1826), *Metachirus nudicaudatus* (Desmarest, 1817), and *Micoureus paraguayanus* (Tate, 1931), and the rodents *Akodon montensis* (Thomas, 1913), *Thaptomys nigrita* (Lichtenstein, 1821), and *Kannabateomys amblyonyx* (Wagner, 1845) (see Redford and Eisenberg, 1992; Emmons and Feer, 1997; Eisenberg and Redford, 1999; Cerqueira and Lemos, 2001; Costa, 2003; Cáceres *et al*., in press b). Since

the Paraná River headwater is mainly inserted in a biome different from the Atlantic Forest, the Cerrado (IBGE, 1992), this indicates that these six Atlantic forest species have to cross the river for their respective populations in order to maintain their genetic contact. However, despite the apparent weak riverine barrier performed by the Paraná River, to date there is at least an endemic rodent species of the semideciduous forest of the right margin of the Paraná River, which occurs in southern and eastern Mato Grosso do Sul state and northeastern Paraguay (Percequillo, 1998; Carmignotto, 2004). The species is *Cerradomys maracajuensis* (Langguth and Bonvicino, 2002), whose eastern limits of distribution is apparently given by the Paraná River.

The Paraná River has not a dynamic floodplain like many western Amazonian rivers or the Paraguay River (Myers, 1982; Patton *et al*., 2000). Then species populations can not become transferred from one bank to the other by the passive means of a dynamic channel shift over time (Myers, 1982). As the upper Paraná River is channeled (in uplands rather than in floodplains) then passive movement is unlikely. Then active movements over water must take place, mainly by natural rafts.

Large rivers such as the Paraná River seem to be weak barriers to mammal dispersal based on the present analysis. Even without passive movements of populations or gene flow over the river, because its channeled characteristic, dispersal over water takes place. Furthermore, other studies in South America have shown that small species could cross major rivers in South America (Myers, 1982; Gascon *et al*., 2000) being one of them with an arboreal mammal species (Patton *et al*., 1994). An important factor influencing mammal patterns of distribution in the La Plata River basin might be the biome distribution (i.e. habitat; Myers, 1982) rather than riverine barrier (see Patton *et al*., 2000). For *A. caraya*, the Paraná River is not properly a barrier but acts as a mechanism that promotes forest heterogeneity (see Moritz *et al*., 2000) along both margins (which are characteristically open, with a rather shrubland-like physiognomy, namely as pioneer formation, *census* IBGE, 1992). This characteristic has created a habitat suitable for this mostly open forest species of primate.

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