The Role of Gallery Forests in the Zoogeography of the Cerrado's Non-volant Mammalian Fauna[1]

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ABSTRACT

The cerrado, one of the largest vegetation formations in Brazil, has been poorly studied. We present the first comprehensive list of the non-volant mammalian fauna and analyze its zoogeographic affinities. There are 11 endemic non-volant mammal species out of a total of 100 species. The cerrado flora is rich in endemics and shows pronounced adaptations to a xeric environment in contrast to the cerrado mammalian fauna. This is probably due to the fact that gallery forests have been present in the cerrado for a long time and have served as mesic enclaves, making xeric adaptations on the part of the mammalian species unnecessary. This contrast between cerrado flora and fauna is similar to the situation in the caatinga, although seemingly for different reasons.

ABSTRATO

O cerrado, apesar de ser a segunda maior formação vegetacional do Brasil, tem sido muito pouco estudado. Neste trabalho procura-se apresentar a primeira lista abrangente de mamíferos não-voadores da região, além de uma detalhada análise de suas afinidadas geográficas. Dentre os mamíferos não voadores encontrados no cerrado apenas onze em cada 100 espécies são endemicas. A flora do cerrado e rica em endemismos e contrastante com a fauna local de mamíferos apresenta acentuadas adaptações ao ambiente xérico. Este fato deve-se principalmente a que matas de galeria fazem parte do cerrado a milhares de anos e servem de enclaves úmidos, que dispensaram a mastofauna da região de produzirem adaptações ao ambiente xérico. O contraste encontrado entre a flora e fauna do cerrado e semelhante ao da caatinga, apesar das razões serem substancialmente diferentes.

THE CERRADO IS BRAZIL'S SECOND LARGEST vegetation formation, exceeding 1.4 million square kilometers in size (IBGE 1982) and occupying approximately 25 percent of the country (Joly 1970). The cerrado is a semideciduous, arboreal savanna composed of a mosaic of subunits grading from open grassland to dry forest. Threading through this mosaic, along water courses, are ribbons of mesophytic, evergreen, gallery forest.

The distribution of cerrado vegetation, in its broadest sense, is associated with the occurrence of a very predictable dry season, and the cerrado is usually defined as a xeromorphic vegetation type (Eiten 1972). The flora of the cerrado is highly adapted for dry conditions and contains many endemics (Eiten 1974).

The cerrado mammal fauna is one of the least studied of the South American vertebrate faunas. Earlier studies conflict in their conclusions regarding the nature of this fauna; some have described it as a depauperate fauna characteristic of open formations and lacking in endemics (Vanzolini 1963, Sick 1965, Avila-Pires 1966) while others have called it a savanna-adapted fauna rich in endemics (Muller 1973, 1979). Even though partial lists have been published (*e.g.*, Sick 1965, Muller 1979) no one has compiled a complete list of the species of mammals found in the cerrado and so resolution of these conflicting points of view has been impossible.

In this paper we present such a list based on the literature and examine the zoogeographic relationships between the non-volant mammalian fauna and the mammalian faunas of the surrounding biomes. From a previous paper analyzing the fauna of a small gallery forest in central Brazil (Fonseca & Redford 1985), we developed a hypothesis to be tested with the larger data set presented in this paper. This hypothesis is that the majority of the cerrado mammalian fauna is not characteristic of open vegetation formations *per se* but is composed of species which are found within the cerrado biome because of the presence of gallery forests. Subsequent to the development of this hypothesis an important paper by Mares

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et al. (1985) demonstrated that the mammalian fauna of the caatinga, a xeric biome adjacent to the cerrado, was extremely poor in endemics in sharp contrast to the flora. This conclusion and the explanations advanced by Mares *et al.* (1985) to explain the differences between faunal and floral patterns were compared with the results of our analysis.

THE CERRADO.—Cerrado is a general name given to the major phytogeographic unit composed of xeromorphic arboreal vegetation, shrub communities, open savannas, and grasslands of central Brazil (Eiten 1972, 1974). The four major subunits of the cerrado are: 1) campos or open grasslands with a total absence of arboreal cover; 2) cerrados (*sensu strictu*), ot semi-arboreal scrubland; 3) cerradão or tall cerrado, characterized by a higher density of trees with a semi-open canopy; and 4) gallery forests, composed of evergreen trees usually with a sparse understory. The first three subunits account for approximately 80 percent of the cerrado area (Eiten 1978). The cerrado extends from approximately 7°30′S to 7°23′S (Fig. 1), although its precise boundaries are disputed.

When measuring total annual precipitation, the cerrado has a semi-humid, tropical climate, with an average of 1100–1600 mm per year (CODEPLAN 1976). During the long dry season which lasts from April–May to September the monthly mean rainfall is only 10–30 mm.

The cerrado is characterized by an ancient flora (Cole 1960) which is among the richest in the world in terms of number of vascular plant species per unit area (Eiten 1972, Sarmiento 1983). Rizzini (1963) lists 600 species of vascular plants and a total of 242 genera of plants for the cerrado, and undoubtedly many species remain to be described.

The trees and shrubs of the open canopy formations show adaptations for water stress (Joly 1970, Eiten 1972). These include hard, leathery leaves (Cole 1960) and a deep root system reaching 15 to 20 m down to the water table (Rizzini 1963). Cacti, found in the drier caatinga and chaco, are absent from most of the cerrado. Gallery forests are restricted to areas of year-round water availability: the borders of water courses or valleys where the water table is close to the surface. They are usually only a few hundred meters wide, and the vast majority of trees are evergreen. Although gallery forests comprise much less than 10 percent of the total area of the cerrado, they are found throughout the entire landscape.

The cerrado is bordered to the north by the Amazonian rainforest, to the east by the Atlantic coastal forest, to the northeast by the arid caatinga, and to the southwest by the dry chaco (Fig. 1). Like the cerrado, the caatinga and chaco are covered by xeromorphic vegetation, though in general these last two regions receive much less rain than does the cerrado (Hueck 1972). Both the Amazonian forest and the Atlantic coastal forest are mesophytic forests, a vegetation type represented within the cerrado zone by the gallery forests.

FIGURE 1. Distribution of the cerrado within Brazil with neighboring vegetation types.

THE CERRADO NON-VOLANT MAMMALIAN FAUNA.—The cerrado mammalian fauna is very poorly studied. New genera and species are still being described (Locke 1981, Borchert & Hansen 1983, Alho, in prep., Mares *et al.*, in prep.), and the majority of groups are in need of taxonomic revision. Because of this, the faunal list we compiled is a provisional one and will undoubtedly be revised as further collecting and analysis are done. In addition to a faunal list, we compiled data on the distribution of the different species. Each species was scored as present or absent in six biomes: the cerrado, the Amazonian forest, the caatinga, the chaco, the Atlantic forest, and "other" (all other areas, such as the pampas, the pantanal, and the Andes). We were concerned mainly with the first five areas.

The data base used for constructing the list of the cerrado non-volant mammalian fauna (Table 1) and for assessing the distribution of the species was compiled mainly from the works of Moojen (1952), Vieira (1955), and Cabrera (1958, 1961). Additional sources used were more recent taxonomic and zoogeographic reviews: Wetzel (1982) for edentates; Hershkovitz (1977) for primates; Streilein (1982) for marsupials; Mares *et al.* (1985) for mammals of the caatinga; Mares and Ojeda (1982) for hystricognath rodents; and Myers (1982, pers. comm.) for mammals of the chaco of Paraguay (see also sources for Table 1). The taxonomy, including synonymies, fol-

lows Honacki *et al.* (1982). Because the species list and distributional data are based on a literature review and because the taxonomy of many of the groups is unrevised, many of the specific data will undoubtedly be changed when additional work is done. However, this preliminary list can serve as a stimulus for further research. Previous lists were either not meant to be complete (Sick 1965) or else contain out-of-date interpretations of zoogeographic distributions (Avila-Pires 1966, Muller 1973).

There are at least 67 genera and 100 species of mammals found in the cerrado region (Table 1). Most of these species are rodents (41) and carnivores (21). Of the 100 cerrado species, 55 are also found in the Amazon, 39 in the caatinga, 53 in the chaco, 64 in the Atlantic forest, and 78 in "other."

There is clearly a high degree of overlap between the fauna of the cerrado and those of neighboring biomes. The Atlantic forest biome (700,000 km^2: IBGE 1982) shares the most species with the cerrado region with 64, followed by the Amazon (6,000,000 km^2: Pires and Prance 1977) with 55. The chaco (1,000,000 km^2: Short 1975) has the third largest faunal overlap with 53. The arid caatinga (825,000 km^2: IBGE 1982) has the least number of shared species (39). The size of a neighboring biome is clearly not related to the degree of overlap.

Distributional patterns of cerrado species (Fig. 2) were analyzed a second way. Species were placed in categories based on their occurrence in biomes adjacent to the cerrado. Species classified as occurring in "forest" were found in the Amazon and/or the Atlantic forests, species classified as occurring in "savanna" were found in the caatinga and/or the chaco, "wide-ranging" species were found in one "forest" type plus one "savanna" type, "endemic" species were those found only in the cerrado, and "other" species were those found in one of the other areas (see above).

The analysis of the similarity between the faunas of the cerrado and the surrounding biomes shows that 50 percent of the cerrado species are characterized as wide-ranging (found in both forest and savanna biomes). This "wide-ranging" characteristic is found across all of the cerrado's mammalian orders: 31.2 percent of the rodents and lagomorphs; 81.8 percent of the edentates; 71.4 percent of the carnivores; 38.5 percent of the marsupials; 71.4 percent of the artiodactyls and perissodactyls; and 66.7 percent of the primates. Typical wide-ranging species include the collared peccary (*Tayassu tajacu*), the giant anteater (*Myrmecophaga tridactyla*), the capuchin monkey (*Cebus apella*), and the mouse (*Bolomys lasiurus*).

Of the remaining species (*i.e.*, those that are not wide-ranging) there are twenty "forest forms"; species like the woolly opossum *Caluromys philander*, the water rat *Nectomys squamipes*, and the kinkajou *Potos flavus*. Four cerrado species are also found only in other biomes: the rodents *Kunsia tomentosus*, *Ctenomys natterei*, *C. minutus*, and *Clyomys laticeps*.

Eleven percent of the non-volant cerrado mammals are endemic. This number is in agreement with most previous observations (Vanzolini 1963, Sick 1965) (Table 1) but contradicts Muller (1973) who said 23 percent of the species were endemic. Of these 11, there are one marsupial, one carnivore, and nine rodents. This number is even lower than previous estimates (see Avila-Pires 1966).

There are 13 species with a savanna distribution. These include the mouse *Calomys callosus* and the armadillo *Euphractus sexcinctus*. Adding the endemics to these 13 species gives only 24 species out of 100 distributed in open vegetation biomes. However, despite being classified as species occurring in such open, savanna-like biomes, most of the cerrado endemics do not actually live in local habitats of this description. Three of the endemic rodents, *Oryzomys lamia*, *Pseudoryzomys simplex*, and *Echimys braziliensis*, are probably obligate gallery forest dwellers (Mello & Moojen 1979; Alho 1981a, 1982; Fonseca & Redford 1985). A fourth species *Oryzomys utiariatensis* probably is also a gallery forest dweller based on its morphology (but see Myers & Carleton 1981 who suggest this species may be a composite). Another set of endemic species, *Ctenomys brasiliensis*, *Carterodon sulcidens*, and *Juscelinomys candango*, apparently spend the majority of their time underground (Moojen 1965), thus avoiding the environmental extremes faced by other savanna dwellers (see Hershkovitz 1969). Thus, there are only four endemic mammals, the mouse *Akodon reinhardti*, the cavy *Galea flavidens*, the fox *Dusicyon vetulus*, and the short-tailed opossum *Monodelphis umbistriata* that can be called characteristic of the above-ground savanna-like vegetation types of the cerrado region.

In order to further analyze the relationship between the cerrado fauna and the gallery forest, we classified each of the 65 cerrado mammalian genera into three categories by preference for local habitats: "never occurs in gallery forest," "occurs in but not dependent on gallery forest" and "relatively dependent on gallery forest" (Table 2). This classification was done using the sources listed for Table 1, data compiled from another study (Fonseca & Redford 1985), and our field experience. The aquatic carnivores *Pteronura* and *Lutra* were excluded as they are dependent on rivers and streams rather than the gallery forest, itself. The analysis was done only at the generic level because of lack of ecological data for all of the species. Even at the generic level there is probably geographic variation in habitat utilization so Table 2 should be interpreted as applying only to mammal populations dwelling in the cerrado. About 86 percent of the genera use the gallery forest obligately or opportunistically (Table 2). This contrasts sharply with the fact that only about

TABLE 1. *Distribution of cerrado non-volant mammal species.*

	Cerrado	Am. Forest	Caatinga	Chaco	At. Forest	Other
Marsupialia						
Didelphis albiventris	X		X	X		X
Marmosa cinerea	X	X	X	X	X	X
M. murina	X	X			X	X
M. agilis	X	X	X	X	X	X
M. incana	X				X	
M. velutina	X				X	X
Monodelphis domestica	X	X	X	X	X	X
Caluromys philander	X	X			X	X
Lutreolina crassicaudata	X	X		X	X	X
Philander opossum	X	X		X	X	X
Chironectes minimus	X	X				X
Metachirus nudicaudatus	X	X			X	X
Total	13	9	4	6	11	11
Rodentia						
Oryzomys nigripes (=*eliurus*)	X		X		X	X
O. ratticeps	X					X
O. subflavus	X		X		X	
O. capito (=oniscus)	X	X			X	X
O. lamia	X					
O. utiaritensis	X					
O. concolor (=*roberti*)	X	X		X		X
Pseudoryzomys simplex	X					
Wiedomys pyrrhorhinos	X		X		X	X
Nectomys squamipes	X	X			X	X
Rhipidomys mastacalis	X	X	X		X	X
Juscelinomys candango	X					
Akodon reinhardti (=*lasiotis*)	X					
Bolomys lasiurus	X	X	X	X	X	X
Oxymycterus roberti	X				X	
O. rutilans	X				X	X
Calomys callosus (=*expulsus*)	X		X	X		X
Holochilus brasiliensis	X	X	X	X		X
Neacomys spinosus	X	X			X	X
Blarinomys breviceps	X				X	
Kunsia fronto	X			X		
K. tomentosus	X					X
Coendou prehensilis	X	X				X
Sphiggurus (=*Coendou*) *villosus*	X				X	X
Proechimys longicaudatus	X	X		X		X
Clyomys laticeps	X					
Carterodon sulcidens	X					
Thrichomys apereoides	X		X	X		X
Echimys braziliensis	X					
Ctenomys brasiliensis	X					
C. minutus	X					X
C. natterei	X					X
Galea flavidens	X					
G. spixii	X	X	X			X
Cavia aperea	X				X	X
Kerodon rupestris	X		X			
Hydrochaeris hydrochaeris	X	X	X	X	X	X
Dasyprocta azarae	X			X	X	X
D. punctata	X	X				X
D. prymnolopha	X	X	X			
Agouti (=*Cuniculus*) *paca*	X	X		X	X	X
Total	41	14	12	10	17	26
Carnivora						
Chrysocyon brachyurus	X			X		X
Speothos venaticus	X	X			X	X

TABLE 1. *Continued.*

	Cerrado	Am. Forest	Caatinga	Chaco	At. Forest	Other
Dusicyon (=Cerdocyon) thous	X	X	X	X	X	X
D. vetulus	X					
Procyon cancrivorus	X	X	X	X	X	X
Nasua nasua	X	X		X	X	X
Potos flavus	X	X			X	X
Eira barbara	X	X		X	X	X
Galictis vitatta	X	X	X	X	X	X
C. cuja	X			X	X	X
Conepatus chinga (=chilensis)	X	X		X	X	X
C. semistriatus	X	X	X			X
Pteronura brasiliensis	X	X			X	X
Lutra longicaudis (=platensis)	X	X		X	X	X
Panthera onca	X	X	X	X	X	X
Felis colocolo	X			X		X
F. concolor	X	X	X	X	X	X
F. pardalis	X	X		X	X	X
F. wiedii	X	X		X	X	X
F. yagouaroundi	X	X	X	X	X	X
F. tigrina	X	X		X	X	X
Total	21	17	7	16	17	20
Lagomorpha						
Sylvilagus brasiliensis	X	X	X	X	X	X
Total	1	1	1	1	1	1
Edentata						
Myrmecophaga tridactyla	X	X	X	X	X	X
Tamandua tetradactyla	X	X	X	X	X	X
Bradypus variegatus	X	X	X	X	X	X
Dasypus septemcinctus	X		X	X	X	
D. novemcinctus	X	X	X	X	X	X
Tolypeutes matacus	X			X		X
T. tricinctus	X		X		X	X
Priodontes maximus	X	X		X	X	X
Cabassous unicinctus	X	X	X	X	X	X
C. tatouay	X				X	X
Euphractus sexcinctus	X		X	X		X
Total	11	6	8	9	9	9
Perissodactyla						
Tapirus terrestris	X	X		X	X	X
Total	1	1		1	1	1
Artiodactyla						
Tayassu tajacu	X	X	X	X	X	X
T. pecari	X	X	X	X	X	X
Mazama americana	X	X	X	X	X	X
M. gouazoubira	X	X	X	X	X	X
Ozotoceros bezoarticus	X		X	X		X
Blastocerus dichotomus	X			X		X
Total	6	4	5	6	4	6
Primates						
Callithrix penicillata	X				X	
C. argentata	X	X		X		X
C. jacchus	X		X		X	
Aotus trivirgatus	X	X		X	X	X
Cebus apella	X	X	X	X	X	X
Alouatta caraya	X			X		X
Total	6	3	2	4	4	4
Total Cerrado species	100	55	39	53	64	78

14 percent of the genera have not been trapped or observed in gallery forest.

DISCUSSION

THE ROLE OF THE GALLERY FOREST.—The results presented in this paper confirm the hypothesis that the greatest proportion of the cerrado mammalian fauna is composed not of species characteristic of open biomes but of ones characteristic of more closed, mesic biomes. Their existence in the cerrado is due to the mesic gallery forest. Gallery forests probably function to increase the species diversity of the cerrado mammalian fauna in two ways. First, they serve as mesic corridors allowing vast range extensions of species which are basically forest dwellers. In this way mammals which are Atlantic forest or Amazonian species become elements of the cerrado fauna (for similar conclusions for caviomorph rodents, see Bishop 1974; and for lizards, Vanzolini 1963). The second way in which gallery forests increase diversity is by providing refuge, food, or water for species not confined to forests. Maned wolves sleep in the gallery forest, nine-banded armadillos dig burrows there, and opossums and brocket deer use gallery forests to forage. Not only the water, which is always available in a gallery forest, but the structure of the forest itself helps sustain such species within the cerrado (August 1983).

Even though covering a small total area, gallery forests are responsible for both the presence in cerrado of forest-adapted mammals and the persistence of other species that make use of more open areas but nevertheless, rely on gallery forest. For the latter species, gallery forests may be particularly important during the dry season, as well as in years of decreased rainfall. In a previous study of cerrado mammals we found that of the 22 marsupial and rodent species trapped in different cerrado habitats, 21 could be found in gallery forests while 12 species were restricted to gallery forest (Fonseca & Redford 1985).

Several other authors have commented on the importance of gallery forests in maintaining faunal diversity. Alho (1981a) found diversity increased from cerradão and cerrado to gallery forest. August (1983) documented the increased diversity of mammals in gallery forests in the Venezuelan llanos and suggested that this was due to the increased diversity of food types available in the forest.

THE ROLE OF MESIC ENCLAVES IN XERIC ENVIRONMENTS.—

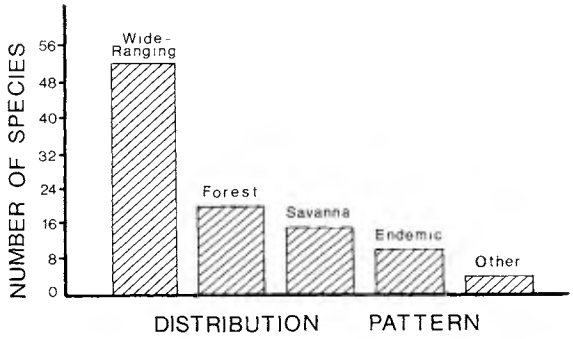

FIGURE 2. Classification of cerrado mammal species according to type of distribution (see text for definitions).

The results of the present analysis agree with previous studies in indicating that the non-volant mammalian fauna of the cerrado has a low number of endemic forms (Vanzolini 1963, Sick 1965). Instead, it is largely composed of either species primarily tied to forest habitats as discussed above or those which occur in both open and forested biomes.

Mello-Leitão (1946) was the first to indicate that most mammalian groups of the cerrado (which he defined as the "Guarani" faunal province) were represented by forms with large geographical ranges. This same trend has also been noted for vertebrate faunas in several other open vegetation formations: birds and bats of the Paraguayan Chaco (Short 1975, Myers & Wetzel 1983); non-volant mammals of the Venezuelan llanos (Eisenberg & Redford 1979); and bats, birds, lizards and non-volant mammals of the Brazilian caatinga (Sick 1965, Vanzolini 1976, Willig 1983, see Mares *et al.* [1985] for review).

In a recent analysis Mares *et al.* (1985) documented this lack of endemism in the caatinga mammalian fauna, showing that only one of the 32 non-volant mammalian species is endemic (but see Moojen 1952 who states that even this one endemic *Kerodon rupestris* may be distributed outside of the caatinga). Mares *et al.* (1985) concluded that the mammalian fauna of the caatinga is a depauperate subset of that of the cerrado, while Vanzolini (1976) expressed the same conclusion regarding lizards. However, as we have shown, there is no unique cerrado fauna; rather, it too is composed of a mix of open and forest biomes faunas.

References: Alho (1981a, 1982), Avila-Pires (1960, 1968, 1972), Avila-Pires and Gouvea (1977), Bishop (1974), Borchert and Hansen (1983), Brasil (1978), Cabrera (1958, 1961), Cabrera and Willink (1973), Carvalho (1962), Carvalho and Toccheton (1969), Cerqueira (1980), Costa *et al.* (1979), Davis (1947), Dietz (1983), Fonseca and Redford (1985), Handley (1976), Hershkovitz (1969, 1977), Mares *et al.* (1981), Mares and Ojeda (1982), Mello and Moojen (1979), Moojen (1952, 1965), Myers (1982, unpubl.), Nowak and Paradiso (1983), Peterson (in press), Peterson *et al.* (1981), Pine (1973), Redford (1983), Streilein (1982), Valle and Varejao (1981), Vieira (1955), Wetzel (1982), Wetzel and Lovett (1974), Wetzel and Mondolfi (1979).

TABLE 2. *Dependency of Cerrado mammals on gallery forests within Cerrado.*

Family/dependence	No. of genera	Genera
Marsupialia		
1. Never occurs	0	
2. Occurs, but not dependent	4	*Didelphis, Marmosa, Monodelphis, Lutreolina*
3. Relatively dependent	4	*Caluromys, Philander, Chironectes, Metachirus*
Rodentia		
1. Never occurs	5	*Juscelinomys, Clyomys, Carterodon, Ctenomys, Kerodon*
2. Occurs, but not dependent	15	*Oryzomys, Pseudoryzomys, Weidomys, Akodon, Bolomys, Oxymycterus, Calomys, Holochilus, Neacomys, Kunsia, Thrichomys, Galea, Cavia, Hydrochaeris, Dasyprocta*
3. Relatively dependent	8	*Nectomys, Rhipidomys, Blarinomys, Proechimys, Echimys, Agouti, Coendou, Sphiggurus*
Carnivora		
1. Never occurs	0	
2. Occurs, but not dependent	8	*Procyon, Nasua, Galictis, Conepatus, Chrysocyon, Dusicyon, Panthera, Felis*
3. Relatively dependent	3	*Potos, Eira, Speothos*
Lagomorpha		
1. Never occurs	0	
2. Occurs, but not dependent	0	
3. Relatively dependent	1	*Sylvilagus*
Edentata		
1. Never occurs	2	*Tolypeutes, Cabassous*
2. Occurs, but not dependent	5	*Myrmecophaga, Tamandua, Dasypus, Priodontes, Euphractus*
3. Relatively dependent	1	*Bradypus*
Perissodactyla		
1. Never occurs	0	
2. Occurs, but not dependent	1	*Tapirus*
3. Relatively dependent	0	
Artiodactyla		
1. Never occurs	2	*Ozotoceros, Blastocerus*
2. Occurs, but not dependent	2	*Tayassu, Mazama*
3. Relatively dependent	0	
Primates		
1. Never occurs	0	
2. Occurs, but not dependent	1	*Callithrix*
3. Relatively dependent	3	*Aotus, Cebus, Alouatta*
Cerrado total		
1. Never occurs	9	13.8%
2. Occurs, but not dependent	36	55.4%
3. Relatively dependent	20	30.8%

Mares *et al.* (1985) also demonstrated that none of the caatinga mammals show adaptations to xeric conditions, a conclusion substantiated for caatinga lizards by Vanzolini (1976). The explanation offered for the persistence of non-xeric-adapted vertebrates within the caatinga is the presence of mesic enclaves within the caatinga which serve as refuges. In this way the fauna in one of the driest parts of South America is in fact composed of species characteristic of mesic environments. The continued existence of such species is due entirely to the presence of these mesic enclaves.

The cerrado is not nearly as xeric an environment as the caatinga, and there are mammalian species which exist there independent of mesic environments. However, as we have shown, more than three-quarters of the mammalian species in the cerrado rely on the gallery forests, the mesic enclaves within the cerrado biome. The findings of Mares *et al.* (1985) for the caatinga are directly applicable to the cerrado. The presence of many of the species found in the caatinga, the cerrado, and probably the chaco as well is due to the ability of these species to colonize and persist in mesic enclaves within these otherwise xeric biomes.

THE EVOLUTION OF THE CERRADO FAUNA.—Recent evidence has suggested that the neotropical region has undergone

several cycles of climatic fluctuation which were accompanied by correspondent modification of the relative position and absolute size of different vegetation types (Haffer 1969, Vuilleumier 1971, Prance 1978, Brown & Ab'-Saber 1979). During the mesic phases it seems clear that savanna and other open vegetation formations contracted into isolated pockets surrounded by more mesic forest formations (Bigarella & Andrade 1965, Tricart 1974). Within these more xeric islands what are now the floras of the caatinga and cerrado developed high levels of endemism and a preponderance of xeric-adapted species (Sarmiento 1983, references in Mares *et al.* 1985).

This contrasts sharply with the low level of endemism and the absence of xeric-adapted species which typifies both the caatinga and the cerrado mammal faunas. Mares *et al.* (1985) suggested two explanations for this: 1) the xeric refugia within the caatinga were apparently not large enough to support viable populations of arid-adapted mammals; and 2) the irregular and lengthy droughts precluded adaptation to xeric conditions.

For the cerrado, the first of these explanations probably applies as well though a more important explanation may involve the presence of mesic vegetation enclaves (gallery forests). Gallery forests have a long history of coexistence with the cerrado vegetation (Laboriau 1963). Their association with geomorphologic and topographic characteristics rather than climatic ones may have allowed their persistence in the cerrado region even during the peaks of arid cycles. The long coexistence of cerrado and gallery forest may explain the fact that the cerrado mammalian fauna is characterized by a large number of mesic-adapted species which are distributed in both savanna and forest but rely on the existence of gallery forests. The persistence of gallery forests would have also served as a continuous source of new colonists coming from the adjacent Amazon and Atlantic forests, preventing local differentiation (Cerqueira 1982).

Another factor that could have influenced the present composition of the cerrado non-volant mammalian fauna is the high frequency of savanna fires in the cerrado region. Most vascular plant species of the cerrado are fire resistant and flush rapidly after burning. Ferri (1955) has suggested that the savanna vegetation of central Brazil represents a fire climax. Whether fires are responsible for the occurrence of savannas or are only an additional characteristic, one would expect that the terrestrial fauna should be affected by them.

Both terrestrial and arboreal mammal species inhabiting open areas should be adversely affected by fire. Gallery forests can serve as temporary refugia during a fire and may also serve as sources of colonization following a fire. After a cerrado fire, sudden increases in population densities of rodent species that range both in the cerrado and the gallery forest have been observed within the gallery forest (Alho 1981b). If such fires are indeed frequent and extensive in magnitude, they could severely affect savanna species which are not protected by fossorial habits or gallery forests.

The frequency and intensity of burning in the cerrado has increased with increased cattle ranching. Fires occurring at frequent intervals are capable of destroying otherwise resistant gallery forest (Redford 1985). Evidence of this is common throughout central Brazil. The gallery forests are keystone habitats within the cerrado and are responsible for maintaining both floral and faunal diversity. More attention needs to be paid to their preservation if the rich and varied life they contain is to be conserved.

CONCLUSIONS

As we have shown, the cerrado has only 11 endemic species of non-volant mammals, many less than the 26 reported by Muller (1973). The majority of the mammalian species found in the cerrado are tied to the mesic gallery forests. The lack of species clearly adapted to arid conditions and the relatively low level of endemism found in the cerrado mammal fauna stand in sharp contrast to the cerrado flora which is strongly xeromorphic and has many endemic species. In this contrast the cerrado is very much like the caatinga (Mares *et al.* 1985). For the cerrado, the lack of a fauna well suited to living in a relatively xeric environment is probably due to the long history of association between the cerrado vegetation and the mesic gallery forests. As Sick (1965) has pointed out, the lack of a fauna characteristic of just the cerrado is due to the fact that the cerrado is defined phytosociologically not faunistically.

An equivalent study has not been done for the chaco, but we would predict that based on the work of Myers (1982) a sharp contrast between the chaco flora and fauna will not be found due to the proximity of the Andes. This area could have been a source of arid-adapted plant and animal forms that invaded the chaco. The cerrado and caatinga are shielded as a source of colonists by the highly mesic Pantanal from the Andes.

There remains much taxonomic and ecological work to be done on the mammals of the cerrado. As this work is done there undoubtedly will prove to be more species of non-volant mammals endemic to the cerrado. However, we predict they will be primarily restricted to the gallery forests or, less likely, confined to the open cerrado.

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