Biogeographic Patterns and Conservation in the South American Cerrado: A Tropical Savanna Hotspot

JOSÉ MARIA CARDOSO DA SILVA AND JOHN M. BATES

Tropical savannas cover between 15 and 24.6 x 10^6 square kilometers (km^2) of the land surface in South America, Africa, and Asia. Most people know these savannas because of their unique assemblages of abundant and exquisite wildlife; however, they have only recently begun to receive the kind of attention from a conservation viewpoint that has been given to tropical rain forests (Myers et al. 2000). The largest, richest, and possibly most threatened tropical savanna in the world is the Cerrado, a large region that occupies the center of South America. In an effort to identify the world's most important biodiversity hotspots, Myers and colleagues (2000) ranked the Cerrado among the 25 most important terrestrial hotspots. It is the only region on their list dominated by tropical savannas. The biodiversity of the Cerrado is impressive; in an area of 1.86 million km^2, 10,000 plant species, 161 mammal species, 837 bird species, 120 reptile species, and 150 amphibian species have been recorded (Myers et al. 2000). However, the present-day situation of the Cerrado's biodiversity is tragic, because by some estimates, only 20% of the region remains undisturbed and only 1.2% is preserved in protected areas (Mittermeier et al. 2000).

Although the Cerrado has been recognized as an important South American area of endemism for several groups of organisms (Müller 1973, Rizzini 1979, Cracraft 1985, Haffer 1985), its biogeography remains poorly known. Here we present an overview of the main biogeographic patterns found for birds in the Cerrado, comparing these patterns with those found in other groups of organisms, and we examine how this information can be brought to bear on efforts to conserve the region's biotic diversity.

> THE CERRADO, WHICH INCLUDES BOTH FOREST AND SAVANNA HABITATS, IS THE SECOND LARGEST SOUTH AMERICAN BIOME, AND AMONG THE MOST THREATENED ON THE CONTINENT

The Cerrado: Geographic setting

Tropical savannas are an important component of the terrestrial vegetation in South America. In some regions, such as the Llanos of northern South America and Cerrado, savannas dominate the landscape, whereas forests are found only along the rivers or in small isolated patches. In contrast, in large forested regions such as Amazonia and Atlantic Forest, savannas occur as more or less isolated patches amidst a continuous cover of forests. Cerrado, Llanos, Roraima (or Grã-Sabana), Llanos de Mojos, and Pantanal are the largest continuous blocks of savanna in South America (Figure 1).

The Cerrado is by far the largest savanna region in South America. It is also the second largest South American biome, exceeded only by Amazonia. It includes much of central Brazil and parts of northeastern Paraguay and eastern Bolivia (Ab'Saber 1977). As a result, the Cerrado occupies a central position in relation to other large South American biomes

José Maria Cardoso da Silva (e-mail: j.silva@conservation.org.br) is director for Amazonia, Conservation International do Brasil, Av. Nazaré 541/310, 66035-170, Belém, Pará, Brazil. His research is focused on biogeography, systematics, ecology, and conservation of Neotropical birds. John M. Bates is an associate curator of birds at the Field Museum of Natural History, Department of Zoology, 1400 S. Lake Shore Drive, Chicago, Illinois, 60605-2496. His research interests are in genetic diversity of tropical birds and the implications of this diversity for evolution and conservation.

Figure 1. Distribution of major lowland tropical biomes in South America. The Cerrado occupies a central position in relation to other lowland tropical biomes on the continent. Other major savanna regions are the Llanos, Roraima, the Llanos de Mojos, and the Pantanal. Note the presence of several savanna patches within Amazonia and Atlantic Forest.

(Figure 1), with extensive borders with the two largest forest biomes (Amazonia and Atlantic Forest) as well as with the two largest dry regions (Caatinga and Chaco).

The Cerrado region has a tropical wet and dry climate with intermediate rainfall between the wetter regions to the northwest and southeast and the drier areas to the northeast. Average annual rainfall varies between 125 and 200 cm and average annual temperature between 20° and 26° C (Nimer 1979, Ab'Saber 1983). The dry period lasts from 3 to 5 consecutive months (generally between May and September or October), during the winter of the Southern Hemisphere (Nimer 1979, Sarmiento 1983).

Most of the Cerrado is on plateaus of crystalline or sedimentary blocks, whose continuity is broken by an extensive network of peripheral or interplateau depressions (Brasil and Alvarenga 1989). This geomorphological variation explains much of the distribution of plants in the Cerrado (Cole 1986). Savannas are by far the dominant vegetation, covering around 72% of the region, but patches of dry forests and complex belts composed of both dry forests and savannas give the region a mosaic-like aspect (Figure 2). We estimate that 24% of the region represents this mosaic that we call savanna–forest transition, with a remaining 4% being dry forest.

The tops of the plateaus are flat, gently rolling surfaces at elevations ranging from 500 to 1700 meters (m). They are covered primarily by cerrado, a semideciduous to evergreen savanna-like vegetation growing on the deep, well-drained, and nutrient-poor soils (Eiten 1972, 1990, Furley and Ratter 1988). Throughout, cerrado vegetation varies in physiognomy and composition (Furley and Ratter 1988, Ribeiro and Walter 1998). Five main structural types of cerrado are recognized by botanists (Eiten 1972):

1. *cerradão,* a dense forest type (8–15 m tall) that often has a completely closed canopy

2. *cerrado sensu stricto,* a woodland (5–8 m tall) with closed scrub and more scattered trees than in cerradão (Figure 3c)

3. *campo cerrado,* an open scrubland (3–6 m tall) with few trees (Figure 3a)

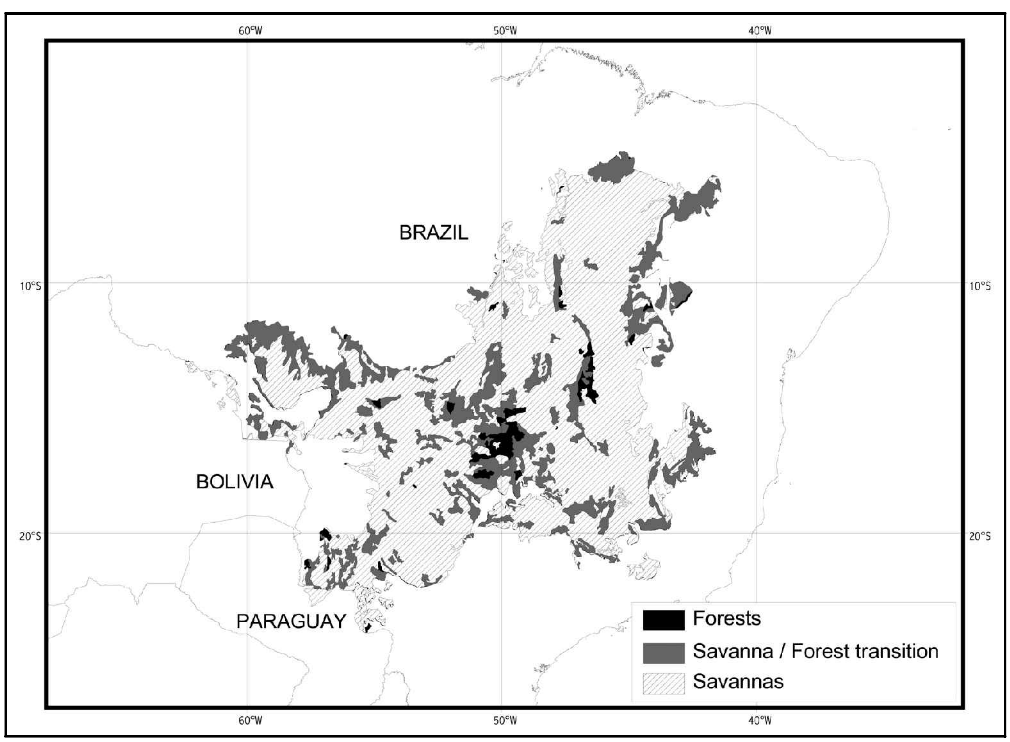

Figure 2. Major vegetation types in the Cerrado. The savanna–forest transition is a mosaic composed of patches of forest and savannas.

Figure 3. Examples of several of the structural habitat types that grade into one another across the Cerrado. Bird species endemic to the cerrado region and typical of these habitats are given in parentheses (Table 1). (a) Campo rupestre (blue finch, **Porphyrospiza caerulescens***), campo sujo (collared crescent-chest,* **Melanopareia torquata***), and campo cerrado (black-throated saltator,* **Saltator atricollis***, and curl-crested jay,* **Cyanocorax cristatellus***) atop the Serranía de Huanchaca. (b) Campo limpo (campo miner,* **Geobates poecilopterus***) with a small finger of gallery forest (helmeted manakin,* **Antilophia galeata***) in the distance. (c) Campo cerrado (chapada fly-catcher,* **Suiriri islerorum***). (d) Cerrado sensu stricto (coal-crested finch,* **Charitospiza eucosma***). All photographs taken at Noel Kempff Mercado National Park, Bolivia.*

4. *campo sujo*, grassland (2–3 m tall) with scattered shrubs
5. *campo limpo*, grassland with few or no shrubs or taller woody plants (Figure 3b)

Tree species common in the cerrado vegetation are *Annona crassiflora, Astronium fraxinifolium, Byrsonima coccolobifolia, B. verbascifolia, Hancornia speciosa, Kielmeyera coriacea, Qualea grandifolia,* and *Q. parviflora,* among others (Ratter and Dargie 1992). Besides cerrado, other types of distinct savanna vegetation, called campos rupestres (Figure 3a), and miscellaneous lithosolic campos occur on rocky outcrops. These habitats are limited to small patches on the plateaus and have a highly endemic flora (Giullietti and Pirani 1988, Eiten 1990). Narrow fringes of gallery forest often border small rivers and streams of the region. Gallery forests on the plateaus grow on narrow belts of soils rich in organic matter (Eiten 1990). They are evergreen, have trees that are on average 20–30 m tall, and possess a dense understory of low stature (Ribeiro and Walter 1998). Associated with gallery forests are stands of a species of palm, *Mauritia flexuosa,* locally known as *veredas.*

The peripheral depressions are generally flat surfaces of little relief (100–500 m in elevation) that are ocasionally interrupted by the presence of steep-sided hills. The landscape pattern on these depressions is much more heterogeneous than that of the plateaus in that it includes more habitats (riverine forests, tropical dry forests, all types of cerrado, and marshlands) distributed in a mosaic fashion. Riverine forests (called *matas ciliares*; Ribeiro and Walter 1998) differ from gallery forests because they are found only along the large rivers in the Cerrado. They are not wide (up to 100 m from each side of the river) and can be semideciduous to evergreen. Trees are 20–30 m tall. Common species are *Anadenanthera* spp., *Apeiba tibourbou, Aspidosperma* spp., *Tabebuia* spp., and *Trema micrantha,* among others (Ribeiro and Walter 1998). Tropical dry forests (*matas secas*) are particularly associated with peripheral depressions and, in some areas (e.g., in the Paranã River valley), are the dominant vegetation type. They are deciduous or semideciduous and grow on patches of moderately productive soils derived from basic rocks such as limestone (Ratter et al. 1978, Prado and Gibbs 1993). Canopy height averages 20–45 m (Ribeiro and Walter 1998). Tree species common in dry forests include *Astronium urundeuva, Piptadenia macrocarpa, Chorisia speciosa., Tabebuia* spp., *Cavanillesia arborea,* and *Cedrella fissilis* (Ratter et al. 1978).

Biogeographic patterns

Forest organisms in a tropical savanna region. The most basic question about the biota of a region is how it is distributed in major vegetation types. In the Cerrado, one might expect that most of the biota would inhabit the savannas that dominate the region. However, studies of mammals, birds, and plants do not support this hypothesis. Redford and Fonseca (1986) found that most (56.3%) of the nonvolant mammal species in the Cerrado inhabit forests. Similarly, Silva (1995b) classified the 759 birds species known or assumed to breed in the Cerrado as independent (occurring exclusively in forests), semidependent (occurring in both forests and open vegetation), or dependent (occurring exclusively in open vegetation). The majority of species (393, or 51.8%) are dependent on the various forest habitats, 20.8% (158) are semidependent, and 27.4% (208) are independent species. Thus, approximately 82.6% of Cerrado birds require forests to some degree. Mendonça and colleagues (1998) listed 6671 plant taxa (species and varieties) for the Cerrado; of these, 38% occur only in forests.

In general, these data support the hypothesis that gallery and dry forests, which occupy less than 20% of the Cerrado, are necessary for a large portion of regional biodiversity. How did this pattern evolve? Silva (1995b) suggested that biotic diversity of the Cerrado region increased through interchange with adjacent regions during the Quaternary climatic–vegetational fluctuations. Thus, Atlantic and Amazonian forest species expanded their ranges into the Cerrado during the wet periods following the expansion of the riverine–gallery forest network (Silva 1995b), whereas Caatinga and Chaco elements colonized the Cerrado during the Quaternary dry periods as part of the coalescence of dry forests in peripheral depressions (Ab'Saber 1983, Pennington et al. 2000). These species probably originated in adjacent regions and maintained viable populations within the Cerrado region because their forest habitats did not vanish entirely during the paleoclimatic period that followed their range expansion. In a fashion similar to what is seen today, large rivers and streams must have provided suitable environmental conditions to maintain wide gallery–riverine forests during the dry periods (Ab'Saber 1983), whereas large patches of soils derived from limestone were important for maintaining dry forests during the wet periods (Prado and Gibbs 1993, Pennington et al. 2000).

Endemic species: Origin and evolution. The percentage of species endemic to the Cerrado varies across different groups of organisms: vascular plants (44%), amphibians (30%), reptiles (20%), mammals (11.8%), and birds (1.4%) (Silva 1995a, Myers et al. 2000). However, because large areas of the Cerrado remain unexplored (Silva 1995c), these numbers will likely change when additional biological inventories are conducted. At present, we still know little about how these endemic species are distributed across the Cerrado or how they evolved. A key question for conservation purposes is whether one can identify subareas of endemism within the large Cerrado region.

To determine if there are subareas of endemism within the Cerrado, Silva (1997) mapped and created overlays of all endemic bird species' ranges smaller than 60,000 km^2. Only 10 of the 30 endemic species met this requirement (Table 1). The ranges of these species delimit three main areas:

- Espinhaço Plateau: Four species that inhabit campos rupestres are *Augastes scutatus* (Trochilidae), *Asthenes luizae* (Furnariidae), *Polystictus superciliaris* (Tyrannidae), and *Embernagra longicauda* (Emberizidae).
- Araguaia River Valley: Three species that inhabit gallery forests are *Synallaxis simoni* (Furnariidae), *Cercomacra ferdinandi* (Thamnophilidae), and *Paroaria baeri* (Emberizidae).
- Paranã River Valley: Two species found only in tropical dry forests are *Pyrrhura pfrimeri* (Psittacidae) and *Knipolegus franciscanus* (Tyrannidae) (Figure 4).

The subareas of endemism identified for birds are at least partially supported by studies of other groups of organisms. The Espinhaço Plateau is well known for its unique biota, composed of hundreds of endemic species of plants (Giullieti and Pirani 1988, Harley 1988) and some endemic species of other vertebrates, such as lizards and amphibians (Haddad et al. 1988, Rodrigues 1988). The Araguaia and Paranã river valleys are still poorly known for nonavian groups, but the riverine forests and dry forests likely harbor endemic species of other organisms also. For example, a very distinctive species of rodent of the genus *Kerodon* was described recently from Paranã dry forests (Moojen et al. 1997). Although not known to possess endemic birds, several other areas possess endemic taxa from other groups. For instance, Erwin and Pogue (1988)

Table 1. Endemic bird species of the Cerrado region.[a]

Species	Age[b]	Habitat[c]
Nothura minor	P	N
Taoniscus nanus[d]	P	N
Penelope ochrogaster	N	F
Columbina cyanopis	P	N
Pyrrhura pfrimeri	N	F
Amazona xanthops	P	N
Caprimulgus candicans	P	N
Augastes scutatus	N	N
Geobates poecilopterus[d]	P	N
Synallaxis simoni	N	F
Asthenes luizae	N	N
Philydor dimidiatus	N	F
Automolus rectirostris	N	F
Herpsilochmus longirostris	N	F
Cercomacra ferdinandi	N	F
Melanopareia torquata	N	N
Scytalopus novacapitalis	N	F
Phyllomyias reiseri	N	F
Suiriri islerorum	N	F
Polystictus superciliaris	P	N
Knipolegus fraciscanus	N	F
Antilophia galeata	N	F
Poospiza cinerea	N	N
Embernagra longicauda	N	N
Charitospiza eucosma[d]	P	N
Paroaria baeri	N	F
Saltator atricollis	P	N
Porphyrospiza caerulescens[d]	P	N
Basileuterus leucophrys	N	F
Cyanocorax cristatellus	P	N

a. This data set has been modified from Silva (1997), as *Geobates poecilopterus* (a monotypic genus) has been moved from neoendemic to paleoendemic, and *Antilophia galeata* has been changed to neoendemic because of the recent discovery of *Antilophia bokermanni* (Coelho and Silva 1998). *Suiriri islerorum* is a newly described endemic species (Zimmer et al. 2001).

b. P, paleoendemic; N, neoendemic.

c. N, nonforest; F, forest.

d. Monotypic genus.

indicated that the Mato Grosso Plateau is an important area of endemism for beetles of the genus *Agra*. Thus, bird distributions indicate three subareas of endemism; however, this number is almost certainly an underestimate for other groups such as some insects, vascular plants, and amphibians. From a taxonomic perspective, these groups are still too poorly known to be used for assessing patterns of endemism within the Cerrado.

Investigation of the timing and mode of the evolution of the endemic species of the Cerrado is in its infancy, but nonetheless raises controversy. Some authors (e.g., Rizzini 1979) have suggested that the original vegetation in the Cerrado was forest rather than savanna. In this view, present-day savannas succeeded forests by natural processes such as fire and climatic changes. At the opposite extreme, Cole (1986) suggests that within the Cerrado, the savanna vegetation is older than the forests, based on geomorphological information. If one assumes that avian diversification within the Cerrado followed, at least roughly, the same trend as evolution of the landscape in this region, then one would predict, based on Rizzini's hypothesis, that older species are associated mainly with forest vegetation and younger species are associated mainly with savannas. Under Cole's hypothesis, the prediction would be inverted. To evaluate these two hypotheses, we classified each endemic species into one of two evolutionary age categories: *paleoendemics,* species that are either taxonomically distinct (i.e., well-differentiated, monotypic genera) or considered to be the sister taxon of a large radiation in which one or more members also occur in the Cerrado region; and *neoendemics,* species with sister taxa in adjacent South American regions. Based on recent molecular work on South American birds (Bates et al. 1999), we suggest that neoendemics are younger than the Pliocene–Pleistocene transition (about 1.8 million years ago), whereas paleoendemics originated before this period. This is only a tentative classification that must be evaluated in future molecular studies. In addition, we classified each avian endemic as either a forest or nonforest species. All 30 endemic species were analyzed (Table 1). We determined 12 species to be paleoendemics and 18 to be neoendemics. The majority (11 of 12) of the paleoendemic species are nonforest species, whereas most of the neoendemics (12 of 18) are forest birds. These results support Cole's rather than Rizzini's hypothesis.

An additional aspect of these data concerns recent suggestions that ecotones, or transition zones between two or more distinctive types of vegetation, provide important opportunities for speciation (Smith et al. 1997, Schlithuizen 2000). For the Cerrado avifauna, this does not appear to be well supported with respect to the ecotone between savanna and forest. Although 158 bird species inhabit both forest and

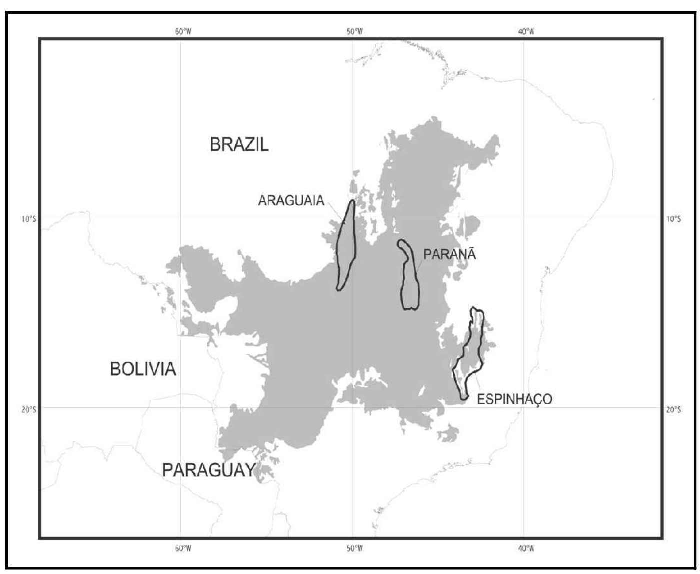

Figure 4. Three subareas of endemism are identified for birds within the Cerrado: Espinhaço Plateau (with four endemic species), Araguaia River Valley (with three endemic species), and Paranã River Valley (with two endemic species).

savanna, no single case of intraspecific differentiation across this transition has been reported so far. In addition, few genera have species in both forest and savanna. In cases in which avian genera do have species in both habitats, those species are generally considered distantly related.

Connections among Neotropical savannas. South American tropical savanna regions can be grouped into two major groups that are currently separated by the Amazon valley. The northern block is formed by Llanos, Roraima, Paru, Monte Alegre, Amapá, and Marajó, whereas the second block is formed by Cerrado, Pantanal, Llanos de Mojos, and patches of savannas located close to the transition between Amazonia and the Cerrado (Figure 5). Because South American savannas exhibit biotic similarity to one another (Sarmiento 1983), a consensus opinion is that these regions were connected in the recent past, and the biotic disjunctions observed today are the result of vicariance rather than long-distance dispersal across large expanses of Amazonian forest (Haffer 1967, Sarmiento 1983). Under this scenario, South American savannas are believed to have expanded and retracted their ranges during Quaternary climatic cycles. During the cold, dry periods, savannas expanded in Amazonia while humid forests retracted to peripheral ecological refuges. During moist and warm periods, humid forests spread again while savannas retracted to areas approximating their present-day ranges (Mayle et al. 2000). These Quaternary cyclic climatic–vegetational changes have been postulated by some biogeographers to be the most important factor driving the speciation process in both forest and savanna organisms in tropical South America (Whitmore and Prance 1987, Haffer 2001).

Three main corridors connecting northern and southern savanna regions have been proposed (Haffer 1967, 1974; Webb 1991): (a) Andean, connecting the southern block of savannas directly with Llanos and Roraima through the Andean slopes; (b) central Amazonian, connecting the southern block of savannas directly with some patches of savannas located north of the Amazon, such as Monte Alegre and Paru, roughly following a belt of low precipitation across central Amazonia; and (c) coastal, connecting the southern and northern blocks through savanna patches located close to the Atlantic coast, such as Marajó and Amapá (Figure 5). Silva (1995a) examined the general distribution patterns of savanna-associated birds in the Cerrado region to determine how well these patterns fit with these three proposed corridors. It was assumed that if these corridors did exist, current patterns of distribution of savanna-adapted birds might show evidence of their legacy. Thus, we predicted spatial congruence should exist between species' ranges and the position of these past biotic corridors as mapped by their proponents (Figure 5).

Present-day ranges of savanna birds support two of the three hypothesized biogeographic corridors (Figure 6). The Andean connection is supported by the distribution of five species and links the Cerrado region with the Llanos and Grã-Sabana. The Atlantic coast savanna corridor is consistent with the distributions of 33 species. All these species occur in Amapá or Marajó with some of them extending their ranges in other savannas of the northern block (Pinto Henriques and Oren 1997, Silva et al. 1997). No single species was recorded only in the savannas that follow the central Amazonian savanna corridor (Silva 1995a). These two pieces of information suggest that a savanna corridor following a belt of low precipitation across the Amazon basin may not have existed, and the most recent biotic connections between Amazonian savannas and the Cerrado region were mostly through the savannas located along the Atlantic coast (Silva 1995a, Silva et al. 1997). Ávila-Pires (1995) analyzed the distribution patterns of all lizard species within Amazonia and also found little support for a central Amazonian savanna corridor. Thus, even though savanna biotas have expanded and contracted their ranges during the Quaternary climatic cycles (Mayle et al. 2000), there is little evidence to suggest that these changes resulted in a broad savanna corridor across central Amazonia. Pennington and colleagues (2000) suggested that several lines of evidence point to tropical dry forests rather than savannas as replacing rain forests in Amazonia during the coolest periods of the Quaternary.

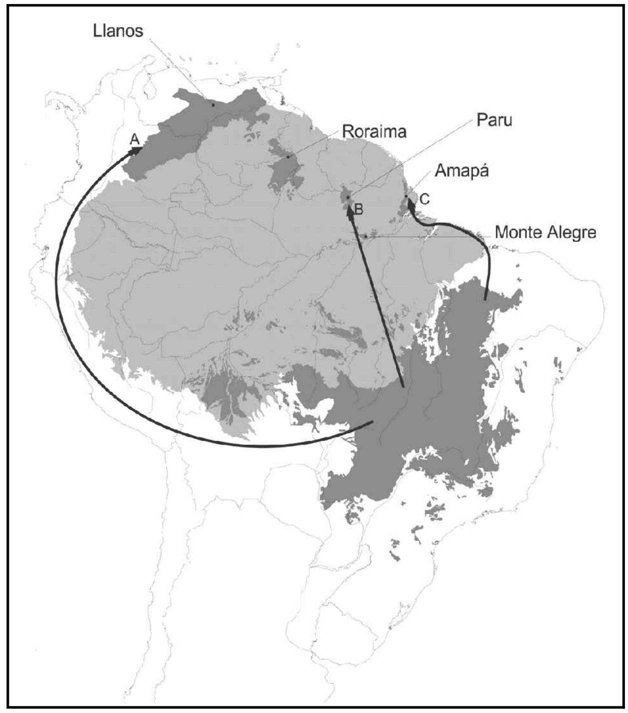

Figure 5. Major savanna corridors that have been hypothesized to historically connect northern and southern blocks of South American tropical savannas: (a) Andean corridor, (b) central Amazonian corridor, and (c) coastal corridor.

Biogeography and conservation

Until very recently, conservation of biological resources in the Cerrado had received little international attention. To date, less than 2% of the total area of the Cerrado is protected in reserves (Mittermeier et al. 2000), but there are important differences in how countries are approaching Cerrado conservation. The Bolivian government created Noel Kempff National Park in 1988, thereby protecting the country's largest cerrado (Killeen and Schulenberg 1998). These roughly 42,000 ha of unaltered cerrado near the western edge of the biome is one of the world's largest continuous protected parcels of this habitat (Figure 7). Because of the park's remoteness and Bolivia's comparatively low human population density (especially in the country's eastern lowlands), the most substantial human threats to this area come from burning associated with ranching operations in neighboring Brazil. Bolivia also possesses several smaller and more isolated plateaus with cerrado habitat; these remain unprotected and largely unexplored (Parker and Rocha 1991).

In Paraguay, at the southern limit of the biome, Cerrado is protected by two national parks: Serranías de San Luís and Cerro Corá (Clay et al. 1998, Robbins et al. 1999). Avian survey work has been conducted at both sites; however, the regions are still not considered to be thoroughly surveyed, and both Clay (1998) and Robbins and their colleagues (1999) emphasize that the rapid expansion of agricultural operations threaten all unprotected savanna regions in the country.

In Brazil, which possesses the vast majority of Cerrado, the situation is drastically worse. There are few large reserves (more than 25,000 hectares [ha]), and they are not distributed evenly across the biome (Figure 7). Consequently, an important part of the Cerrado's environmental diversity has not been incorporated in a network of protected areas. Large areas of Brazilian Cerrado and dry forests have been converted to soybean and rice plantations. Most of this large-scale habitat modification has not followed the most basic principles of environmental conservation, and problems of erosion and deterioration of important streams and rivers are increasing. International support for this alteration has come from major development agencies and some senior scientists who have encouraged increased land use in the Cerrado to reduce human pressure on Amazonian forests.

The Brazilian government's appreciation of the uniqueness of the Cerrado's biodiversity has developed slowly. The first major initiative occurred in 1997, when the Brazilian Ministry of Environment promoted a workshop, which included over 200 scientific experts on the region. This group met to define priority areas for conservation in the Brazilian Cerrado. It followed the same methodology applied earlier for the Atlantic Forest and Amazonia (Cavalcanti 1999). Several criteria for assessing biodiversity value were used, such as number of endemic species, species richness, presence of rare or endangered species or both, and sites of unique communities or key areas for migratory species. The group identified a total of 87 priority areas. The urgency for conservation action in a priority area was determined by cross-referencing biodiversity data with the human-pressure and land cover-change data (Cavalcanti 1999). As of August 1999, the Brazilian government has indicated that it will follow most of the recommendations of this workshop and that new protected areas and ecological corridors will be established. In fact, some important actions were taken during 2001, but two deserve special comments. The first was the expansion of the National Park of Chapada dos Veadeiros, an important reserve that includes pristine cerrados and patches of campos rupestres with several endemic plant species, from 60,000 to 235,000 ha. The second was the creation of the Ecological Station of Serra Geral do Tocantins with 716,306 ha close to the State Park of Jalapão with 158,885 ha. Together, these two areas form the world's largest continuous area of protected Cerrado (Figure 7).

How can the biogeographic information discussed here be used to help protect and preserve the Cerrado's biodiversity? First, we know now that the Cerrado's biota is not homogeneous, so additional distribution data for different groups of organisms must be collected and organized in a retrievable way to help conservationists determine whether there are additional unidentified subareas of endemism. Second, even though the three subareas of endemism identified here as harboring restricted-range endemic species of birds are partially covered by one or more reserves (for comparison, refer to Figures 4 and 7; Silva 1997), most reserves need to be more formally implemented and connected through biodiversity corridors to insure their preservation over the long term. Analyses of other, nonavian taxa are certain to uncover additional areas that are not currently protected by reserves. Third, despite occupying a relatively small part of the total landscape,

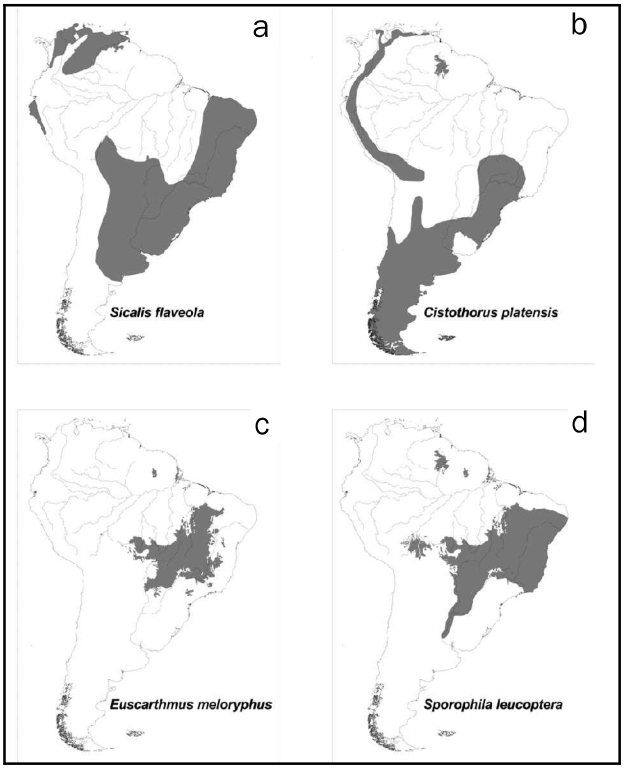

Figure 6. Examples of ranges of bird species supporting the hypothesis (a, b) of the Andean savanna corridor and (c, d) of the coastal savanna corridor.

gallery–riverine forest, cerradão, and dry forest have been shown to be key habitats for a substantial portion of the Cerrado's biodiversity. Thus, their conversion into pastures and agricultural fields should be halted and their connectivity maintained. Fourth, new projects in areas currently covered by cerrado or other types of open vegetation should be temporarily banned until their impact on the flora and fauna can be rigorously assessed and conservation strategies for those areas designed. Fifth, it is critical that agricultural technology be developed and implemented to help landowners increase productivity of lands already under cultivation (Macedo 1994, Silva 1998). This would reduce pressure on lands still covered by natural vegetation. Finally, a special conservation action plan must be developed to guarantee the conservation of at least part of the largest savannas in Amazonia and Atlantic Forest as they are important laboratories for ecological and evolutionary studies in tropical South America. It is urgent now because efforts are underway to establish soybean plantations in these enclaves.

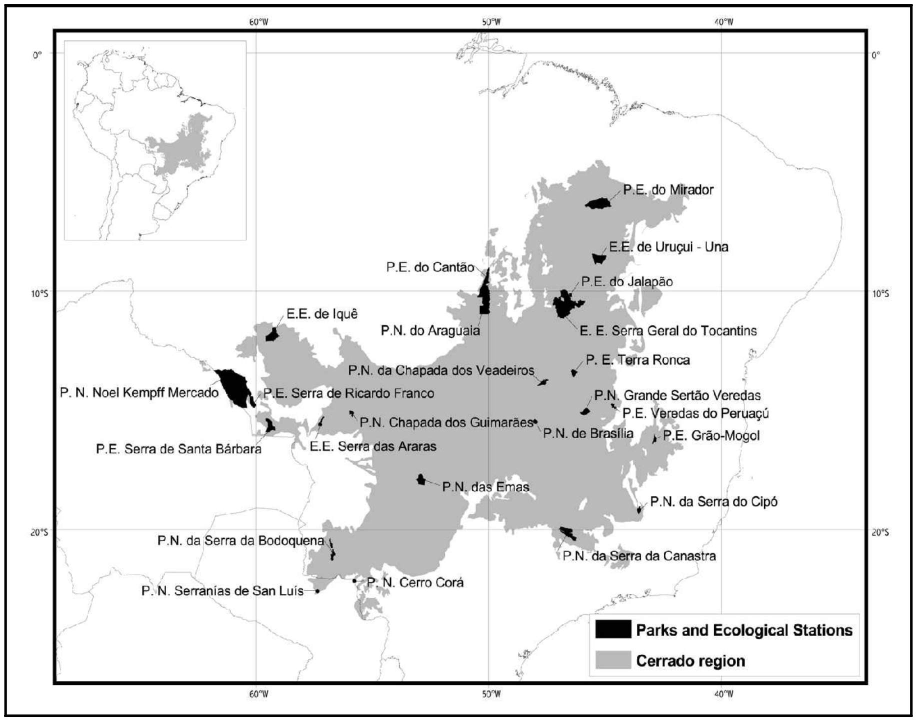

Figure 7. Parks and ecological stations in the Cerrado region. Only those reserves larger than 25,000 ha are shown in Brazil. P.E., state park; P.N., national park; E.E., ecological station.

The Cerrado's conservation is a challenge from both scientific and political viewpoints. Because important financial and political interests are involved in the destruction of the Cerrado, scientists and conservationists must be creative in gathering and synthesizing the best and most complete information possible to generate a viable strategy to insure conservation of the world's richest tropical savanna.

Acknowledgments

We thank Jon Fjeldså, David C. Oren, Roberto B. Cavalcanti, Fernando C. Novaes, Bent O. Poulsen, Mary E. Petersen, Townsend Peterson, Carsten Rahbek, James A. Ratter, Neiva Guedes, and Shannon J. Hackett for discussions about Cerrado biogeography and comments on the manuscript. Luis Barbosa produced the figures. Research support came from Conselho Nacional de Desenvolvimento Científico e Tecnológico (grant no. 302464/88-3), National Geographic Society (grant no. 4964-93), Danish Natural Science Research Council (grant J. no. 11-0390), Museu Paraense Emílio Goeldi, and Universidade de Brasília.

References cited

Ab'Saber AN. 1977. Os Domínios morfoclimáticos da América do Sul. Primeira Aproximação. Geomorfologia 52: 1–21.

———. 1983. O domínio dos cerrados: Introdução ao conhecimento. Revista do Servidor Público 111: 41–55.

Ávila-Pires TC. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). Zoologische Verhandelingen Leiden 299: 1–706.

Bates JM, Hackett SJ, Goerck J. 1999. High levels of mitochondrial DNA differentiation in two lineages of antbirds (*Drymophila* and *Hypocnemis*). The Auk 116:1093–1106.

Brasil AE, Alvarenga SM. 1989. Relevo. Pages 53–72 in Duarte AC, ed. Geografia do Brasil: Região Centro-Oeste. Rio de Janeiro: IBGE.

Cavalcanti RB, ed. 1999. Ações Prioritárias para a conservação da biodiversidade do Cerrado e Pantanal. Belo Horizonte: Conservation International do Brasil

Clay RP, Cooper DR, Mazar Barnett J, Burfiled IZ, Esquivel EZ, Fariña R, Kennedy CP, Perrens M, Pople RG. 1998. White-winged Nightjars *Caprimulgus candicans* and cerrado conservation: The key findings of project Aguará Nu 1997. Cotinga 9: 52–55.

Coelho G, Silva W. 1998. A new species of *Antilophia* (Paseriformes: Pipridae) from Chapada do Araripe, Ceará, Brazil. Ararajuba 6: 81–86.

Cole MM. 1986. The Savannas: Biogeography and Geobotany. London: Academic Press.

Cracraft J. 1985. Historical biogeography and patterns of differentiation within the South America avifauna. Areas of endemism. Ornithological Monographs 36: 49–84.

Eiten G. 1972. The Cerrado vegetation of Brazil. Botanical Review 38: 201–341.

———. 1990. Vegetação. Pages 9–65 in Pinto MN, ed. Cerrado: Caracterização, Ocupação e Perspectiva. Brasília: Universidade de Brasília and SEMATEC.

Erwin TL, Pogue MG. 1988. *Agra,* arboreal beetles of Neotropical forests: Biogeography and the forest refugium hypothesis (Carabidae). Pages 161–188 in Vanzolini PE, Heyer WR, eds. Proceedings of a Workshop on Neotropical Distribution Patterns. Rio de Janeiro: Academia Brasileira de Ciências.

Furley PA, Ratter JA. 1988. Soil resources and plant communities of the central Brazilian cerrado and their development. Journal of Biogeography 15: 97–108.

Giullietti AM, Pirani JR. 1988. Patterns of geographic distribution of some plant species from the Espinhaço Range, Minas Gerais and Bahia, Brazil.

Pages 39–69 in Vanzolini PE, Heyer WR, eds. Proceedings of a Workshop on Neotropical Distribution Patterns. Rio de Janeiro: Academia Brasileira de Ciências.

Haddad CFB, Andrade GV, Cardoso AJ. 1988. Anfíbios anuros do Parque Nacional da Serra da Canastra, estado de Minas Gerais. Brasil Florestal 64: 9–20.

Haffer J. 1967. Zoogeographical notes on the "nonforest" lowland bird faunas of northwestern South America. Hornero 10: 315–333.

———. 1974. Avian Speciation in South America. Publications of the Nuttall Ornithological Club 14: 1–390.

———. 1985. Avian zoogeography of the Neotropical lowlands. Ornithological Monographs 36: 113–146.

———. 2001. Hypotheses to explain the origin of species in Amazonia. Pages 45–118 in Vieira ICG, Silva JMC, Oren DC, D'Incao MA, eds. Biological and Cultural Diversity in Amazonia. Belém: Museu Paraense Emílio Goeldi.

Harley RM. 1988. Evolution and distribution of *Eriope* (Labiatae), and its relatives, in Brazil. Pages 71–120 in Vanzolini PE, Heyer WR, eds. Proceedings of a Workshop on Neotropical Distribution Patterns. Rio de Janeiro: Academia Brasileira de Ciências.

Killeen TJ, Schulenberg TS, eds. 1998. A biological assessment of Parque Nacional Noel Kempff Mercado, Bolivia. RAP working papers 10. Washington (DC): Conservation International.

Macedo J. 1994. Prospectives for the rational use of the Brazilian cerrados for food production. Anais da Academia Brasileira de Ciências 66 (supp. 1): 159–166.

Mayle FE, Burbridge B, Killeen TJ. 2000. Millennial-scale dynamics of southern Amazonian rain forests. Science 290: 2291–2294.

Mendonça RC, Felfili JM, Walter BMT, Júnior MCS, Rezende AV, Filgueiras TS, Nogueira PE. 1998. Flora vascular do Cerrado. Pages 289–556 in Sano SM, Almeida SP, eds. Cerrado: Ambiente e Flora. Brasília: EMBRAPA.

Mittermeier RA, Myers N, Mittermeier CG. 2000. Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. Mexico City: CEMEX.

Moojen J, Locks M, Langguth A. 1997. A new species of *Kerodon* Cuvier, 1825 from the state of Goiás, Brazil (Mammalia, Rodentia, Caviidae). Boletim do Museu Nacional, Zoologia, nova série 377: 1–10.

Müller P. 1973. The Dispersal Centers of Terrestrial Vertebrates in the Neotropical Realm. A Study in the Evolution of the Neotropical Biota and Its Native Landscapes. The Hague: Dr. W. Junk.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nimer E. 1979. Climatologia do Brasil. Rio de Janeiro: IBGE.

Parker TA III, Rocha O O. 1991. The avifauna of Cerro San Simon, an isolated campo rupestre locality in the Department of Beni, northern Bolivia. Ecologia en Bolivia 17: 15–29.

Pennington RT, Prado DE, Pendry CA. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography 27: 261–273.

Pinto Henriques M, Oren DC. 1997. The avifauna of Marajó, Caviana, and Mexiana islands, Amazon river estuary, Brazil. Revista Brasileira de Biologia 57: 357–382

Prado DE, Gibbs PE. 1993. Patterns of species distributions in the dry seasonal forests of South America. Annals of the Missouri Botanical Garden 80: 902–927.

Ratter JA, Dargie TCD. 1992. An analysis of the floristic composition of 26 cerrado areas in Brazil. Edinburgh Journal of Botany 49: 235–250.

Ratter JA, Askew GP, Montgomery RF, Gifford DR. 1978. Observations on forests of some mesotrophic soils in central Brazil. Revista Brasileira de Botânica 1: 47–58.

Redford KH, Fonseca GAB. 1986. The role of gallery forests in the zoogeography of the cerrado's non-volant mammalian fauna. Biotropica 18: 126–135.

Ribeiro JF, Walter BMT. 1998. Fitofisionomias do bioma Cerrado. Pages 91–166 in Sano SM, Almeida SP, eds. Cerrado: Ambiente e Flora. Brasília: EMBRAPA.

Rizzini CT. 1979. Tratado de Fitogeografia do Brasil. São Paulo: HUCITEC and EDUSP.

Robbins MB, Faucett RC, Rice NH. 1999. Avifauna of a Paraguayan cerrado locality: Parque Nacional Serrania San Luis, depto. Concepcion. Wilson Bulletin 111: 157–302.

Rodrigues MT. 1988. Distribution of lizards of the genus *Tropidurus* in Brazil (Sauria, Iguanidae). Pages 305–315 in Vanzolini PE, Heyer WR, eds. Proceedings of a Workshop on Neotropical Distribution Patterns. Rio de Janeiro: Academia Brasileira de Ciências.

Sarmiento G. 1983. The savannas of tropical America. Pages 245–288 in Bourliére F, ed. Ecosystems of the World, Vol. 13. Amsterdam: Elsevier.

Silva JMC. 1995a. Biogeographic analysis of the South American avifauna. Steenstrupia 21: 49–67.

———. 1995b. Birds of the Cerrado Region, South America. Steenstrupia 21: 69–92.

———. 1995c. Avian inventory of the Cerrado Region, South America: Implications for biological conservation. Bird Conservation International 5: 291–304.

———. 1997. Endemic bird species and conservation in the Cerrado Region, South America. Biodiversity and Conservation 6: 435–450.

———. 1998. Integrating Biogeography and Conservation: An example with birds and plants of the cerrado region. Anais da Academia Brasileira de Ciências 70: 881–888.

Silva JMC, Oren DC, Roma JC, Henriques LMP. 1997. Composition and distribution patterns of the avifauna of an Amazonian upland savanna, Amapá, Brazil. Ornithological Monographs 48: 743–762.

Schilthuize n M. 2000. Ecotone: Speciation-prone. Trends in Ecology and Evolution 15: 130–131.

Smith TB, Wayne RK, Girman DJ, Bruford MW. 1997. A role for ecotones in generating rainforest biodiversity. Science 276: 1855–1857.

Webb SD. 1991. Ecogeography and the Great American Interchange. Paleobiology 17: 266–280.

Whitmore TC, Prance GT. 1987. Biogeography and Quaternary History in Tropical America. Oxford (UK): Clarendon Press.

Zimmer KJ, Whittaker A, Oren DC. 2001. A cryptic new species of flycatcher (Tyrannidae: *Suiriri*) from the Cerrado region of central South America. Auk 118: 56–78.