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DISTRIBUTION OF AMAZONIAN AND ATLANTIC BIRDS IN GALLERY FORESTS OF THE CERRADO REGION, SOUTH AMERICA

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Resumo. As distribuições de aves que tem os seus centros de distribuição na Amazônia (Elementos Amazônicos, 202 taxa) e no sul da Floresta Atlântica (Elementos Atlânticos, 79 taxa) nas florestas de galeria na região do Cerrado, a maior região de savanas da América do Sul, são analisadas. Em ambos os grupos, o número de espécies diminui com o aumento da distância em relação a seus centros de distribuição. Entretanto, elementos Atlânticos estendem suas distribuições muito mais no interior da região do Cerrado que os elementos Amazônicos. Há uma separação altitudinal entre elementos Amazônicos e Atlânticos, com os primeiros ocorrendo, em média, em altitudes mais baixas que os últimos. Elementos Amazônicos são restritos principalmente às depressões periféricas e planaltos baixos dentro da região do Cerrado, enquanto elementos Atlânticos são encontrados principalmente em planaltos altos. Fatores históricos (efeitos das mudanças climáticas durante o Quaternário sobre a estrutura e composição das florestas de galeria) e ecológicos (tolerância das espécies a trocas abruptas de temperatura durante o inverno) são sugeridos como possíveis explicações para as diferenças na distribuição dos elementos Amazônicos e Atlânticos dentro da região do Cerrado.

Abstract. Distributions of Amazonian (202 taxa) and Atlantic (79 taxa) bird elements in the system of the gallery forests of the Cerrado Region, the largest savanna region in South America, are analysed. In both categories, the number of species decreases with increasing distance from their source areas. However, more Atlantic elements extend their ranges considerably deeper into the Cerrado Region than do Amazonian elements. There is an altitudinal separation between Amazonian and Atlantic elements, with Amazonian taxa occurring, on average, at lower altitudes than Atlantic ones. Amazonian elements are mainly restricted to the peripheral depressions and low-altitude plateaus within the Cerrado Region, whereas Atlantic ones are found primarily at high plateaus. Both historical (effects of the cyclic climatic changes during the Quaternary on the structure and composition of gallery forests) and ecological (tolerance to abrupt changes in temperature during the winter) factors are suggested to have caused range differences between Amazonian and Atlantic elements within the Cerrado Region. *Accepted 2 October 1995.*

Key words: Biogeography, Central Brazil, Cerrado, gallery forests, paleoecology, dispersion, South America, avifauna.

INTRODUCTION

Biogeographic patterns within continental biotas are produced by successive cycles of vicariance (i.e., range fragmentation followed by differentiation) of widespread species, followed by cycles of population dispersion (i.e., progressive range expansion by occupying new areas that are suitable across a landscape) of descendant species that produce more widespread forms, followed by new cycles of vicariance (Cracraft 1988, Haffer 1993).

Modern historical biogeographers have focused their efforts on reconstructing the temporal sequence of fragmentation of the range of ancient widespread species during cycles of vicariance as well as searching for congruence between such sequences across different groups of organisms (Nelson & Platnick 1981, Humphries & Parenti 1986, Humphries 1992). Nonetheless, cycles of species dispersion are as important as are cycles of vicariance from an evolutionary viewpoint, as they promote biotal interchange

and ecological intermixing, phenomena that play important roles in augmenting the species richness at a regional scale as well as in the evolution of biological communities (Ricklefs & Schluter 1993).

A natural laboratory to study the historical and ecological factors involved in the promotion of biotal intermixing is the system of gallery forests within the Cerrado Region. The Cerrado Region is the second largest ecological region and the largest savanna region in South America, comprising between 1.5 and 1.8 million km² (Ab'Saber 1977a). Together with Chaco and Caatinga, two predominantly xeric regions, the Cerrado Region forms a broad open-vegetation corridor (Fig. 1) separating the large blocks of Amazonian and Atlantic forests (Vanzolini 1974, Ab'Saber 1977a). The development of this open-vegetation corridor during the Tertiary is generally acknowledged as an important paleoecological event which determined the disjunction and/or differentiation of several groups of forest-adapted species that currently have their centres of distribution in Amazonia or Atlantic Forest (Bigarella *et al.* 1975, Mori *et al.* 1981, Cracraft & Prum 1988).

The Cerrado Region is covered mainly by a savanna-like vegetation known as cerrado (Eiten 1972), but evergreen forests occur as narrow belts along rivers and streams. These forests are termed gallery forests (Eiten 1990). Gallery forests seem to be expanding in the Cerrado Region following the improvement of the ecological conditions (e.g., soil, microclimate) caused by the gradual dessication of ancient plateaus by fluvial erosion (Ab'Saber & Costa Júnior 1950, Cole 1986). Because of that, several researchers have suggested that gallery forests play an important role as mesic corridors, that open the way to the colonization of the Cerrado Region by forest-dependent organisms with ranges centered in the neighbouring Amazonian and Atlantic forests (Sick 1956, 1965, 1966; Rizzini 1979; Cerqueira 1990; Redford & Fonseca 1986; Willis 1992). Studies on the distribution patterns of plants (Smith 1962, Ratter *et al.* 1973, Rizzini 1979, Prance 1987, Mori *et al.* 1981, Ratter 1987), butterflies (Brown & Mielke 1967, Brown 1987), mammals (Bishop 1974, Cerqueira 1982, Redford & Fonseca 1986) and birds (Silva & Oniki 1988; Silva 1989; Willis & Oniki 1990, 1991; Willis

1992) have all provided numerous examples of Amazonian or Atlantic organisms whose range boundaries are located in the gallery forests within the Cerrado Region.

A point that still remains poorly investigated in all groups of organisms is how these forest-adapted species are distributed throughout the system of gallery forests of the Cerrado Region. Are they widely distributed throughout the gallery forest system of this region? Have they followed common pathways of colonization? What abiotic and biotic factors influence the ranges of these organisms within the Cerrado Region? Two hypotheses related to these questions have been proposed so far. The first suggests that Amazonian and Atlantic forest elements are not widely distributed within the Cerrado Region, but that their numbers decrease with increasing distance from the source areas (Cerqueira 1980, Silva & Oniki 1988). The second suggests that there is an altitudinal segregation between Amazonian and Atlantic species, with the former mainly occurring at low-altitude plateaus and peripheral depressions, and the latter mainly occurring at high plateaus (Silva 1989). Neither of these two hypotheses has been critically evaluated for any group of organisms.

In this paper, I present a list of forest-adapted birds that have their centres of distribution in Amazonia or southern Atlantic Forest, and range boundaries in the gallery forest system of the Cerrado Region. Thereafter, I shall evaluate how the distance from the source areas and altitude influence the distribution of these birds within the Cerrado Region.

THE CERRADO REGION AND ITS GALLERY FORESTS

The Cerrado Region (see definition in Ab'Saber 1977a, 1986, and Vanzolini 1988) includes most of central Brazil and small extensions of north-east Paraguay and eastern Bolivia (Ab'Saber 1977a). It has borders with Amazonia, southern Atlantic Forest, Caatinga and Chaco (Fig. 1). The estimated length of the border between the Cerrado Region and Amazonia (7950 km) is more than three times as long as that between the Cerrado Region and southern Atlantic Forest (2630 km). The width of the transition zone separating the Cerrado Region from Amazonia



FIG. 1. Major South American morphoclimatic domains following Ab'Saber (1977a, 1986). Several small domains were combined in a single Andean Region. The domain of the plateaus with *Araucaria* has been merged with southern Atlantic Forest. The river dividing the Atlantic Forest in northern and southern regions is the São Francisco.

(Fig. 1) ranges from 20 to 430 km (mean = 150 km, s.d. = 30.5, $n = 14$ measuring points on a map with scale of 1: 1000000). The same measurement in the transition zone between the Cerrado Region from Atlantic Forest (Fig. 1) varies from 38.4 to 269.2 km (mean = 82.0, s.d. = 70.0, $n = 14$).

Most of the Cerrado Region consists of large blocks of crystalline or sedimentary plateaus,

whose continuity is broken by a network of peripheral or intermontane depressions (Ab'Saber 1983, Brasil & Alvarenga 1989). The altitude of these plateaus ranges from 500 to 1700 m. Most of the surface of the Cerrado Region plateaus was molded from the Upper Cretaceous to the Mid-Tertiary, during the Sul-Americano cycle of erosion (Braun 1971, Cole 1986). The resulting pedepain (Sul-Americana surface) was

then uplifted during the Plio-Pleistocene, with associated subsidence leading to the formation of the peripheral depressions, whose altitudes vary from 100 to 500 m (Braun 1971, Brasil & Alvarenga 1989, Del'Arco & Bezerra 1989). Peripheral depressions have been modified during the Quaternary by the recent cycles of erosion (Braun 1971). Geomorphological evidence suggest that during the cyclic global climatic fluctuations in the Pleistocene and Holocene, peripheral depressions were much more unstable and underwent more drastic ecological changes than the plateaus (Ab'Saber 1977b, 1983, 1988; Brasil & Alvarenga 1989).

On the plateaus, gallery forests occur as narrow and well-defined strips (no more than 100 m wide) along the rivers and streams (Fig. 2). On the peripheral depressions, gallery forests are generally wider than on the plateaus. In both plateaus and depressions, gallery forests grow on cambisols or hydromorphic soils rich in organic matter. Gallery forests are evergreen with trees on average 20–30 m tall, and a very humid un-

derstorey that harbors many ferns, epiphytes and palms (Ribeiro *et al.* 1983). The floristic composition of gallery forests is highly variable over the Cerrado Region (Eiten 1990).

Gallery forests form a dense network within the Cerrado Region. This is mainly because the headwaters of some of the major South American rivers (e.g., São Francisco, Tocantins, Araguaia, Paraguay) are located on the highest plateaus of the Cerrado Region (Innocencio 1989). From there, these rivers and their affluents flow in several directions (Fig. 3), making contact with hydrographic systems of almost all neighbouring ecological regions. Little is known about the evolution of the present-day drainage system of the Cerrado Region. It has certainly had a long and dynamic history associated with the geological changes in central Brazilian plateaus since the Paleozoic (Innocencio 1989). However, most of its modern features developed more recently, possibly in association with the Plio-Pleistocene uplift (Braun 1971, Petri & Fúlfaro 1983).

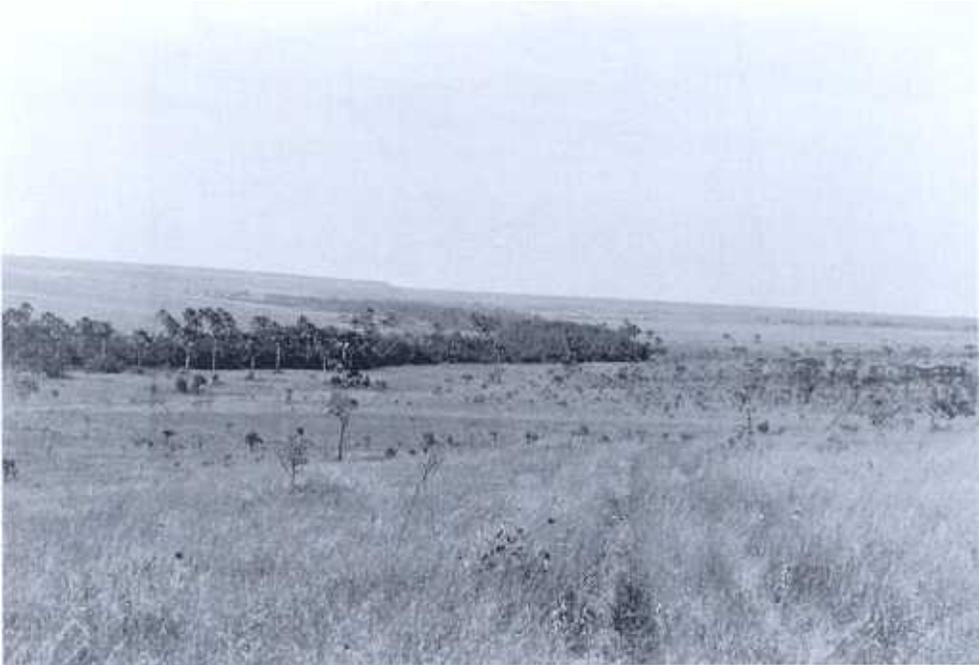


FIG. 2. Gallery forest on a high-plateau (ca. 1000 m) in the Cerrado Region. Notice the sharp separation between gallery forest and the adjacent cerrado. Photo by R. Constantino near Brasília, Distrito Federal, Brazil.

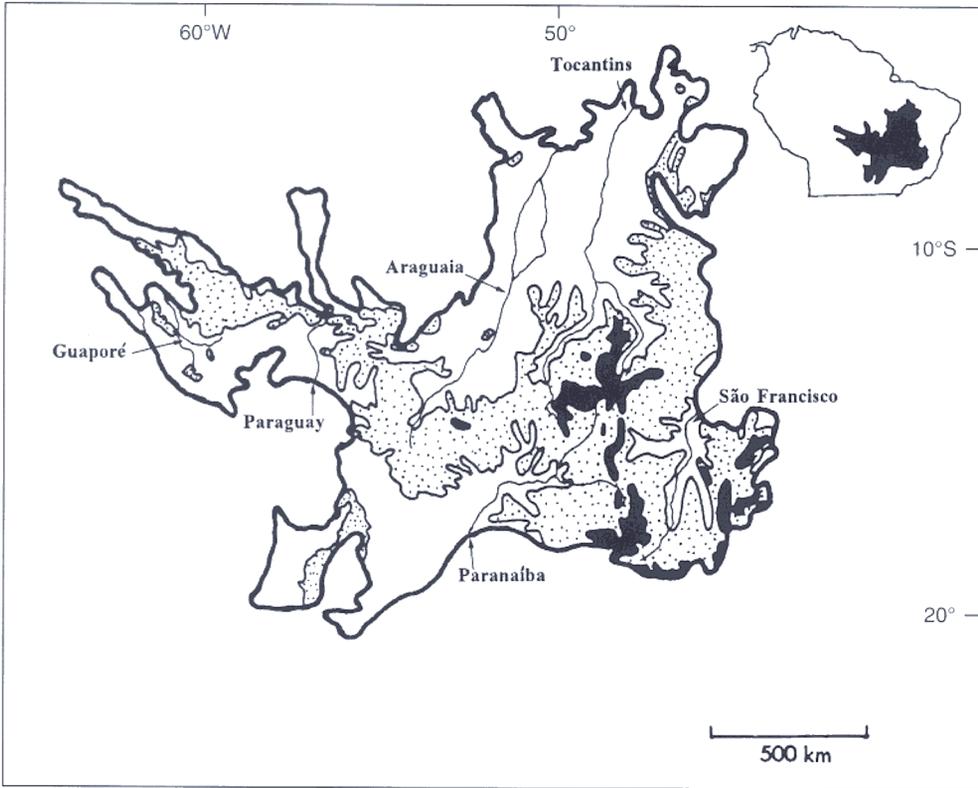


FIG. 3. Altitude and major rivers within the Cerrado Region. Black, areas with altitude equal or more than 1000 m. Stippled, areas with altitude ranging from 500 to 1000 m. Blank, areas with altitude below 500 m.

The Cerrado Region has a tropical seasonal climate with a dry period (May to August–September) coincident with the coldest months of the year (Nimer 1979). The average annual rainfall in this region varies between 1250 and 2000 mm, and the average annual temperature between 20° and 26°C (Nimer 1979, Ab'Saber 1983).

METHODS

From a list of bird species that are known or assumed to breed in the Cerrado Region (Silva 1995), I selected all those species or well-marked subspecies that: (a) were recorded mainly in gallery forests, (b) have their centres of distribution in Amazonia (Amazonian elements, see Fig. 4) or southern Atlantic Forest (Atlantic elements, see Fig. 5), and, finally, (c) have their range

boundaries within the Cerrado Region. I assume that these species have expanded and/or are expanding their ranges into the Cerrado Region from their centres of distribution after a phase of isolation caused by the fragmentation of an ancient humid forest biota.

Among the selected species, 11 species or well-marked subspecies (see Appendix) have disjunct populations in Amazonia and southern Atlantic Forest and no differentiation at all in external morphology. For each of these latter taxa, I measured the distance from its innermost record in the Cerrado Region to the nearest record in both Amazonia and southern Atlantic Forest. Then, I used the criterion of minimum distance between these points for determining whether populations in the Cerrado Region are more parsimoniously (from a geographical pers-

pective) interpreted as expansions from Amazonian or Atlantic populations (see Fig. 4a for an example).

Some Atlantic taxa that occur in the Cerrado Region and have closest relatives in the Andean Region (e.g., *Tigrisoma fasciatum*, *Otus atricapillus*, *Lochmias nematura*, *Philydor rufosuperciliatus*, *Philydor rufus*, *Elaenia obscura*, *Todirostrum plumbeiceps*, *Pyroderus scutatus*, *Oxyruncus cristatus*, *Pipraeida melanota*, *Euphonia musica*) were excluded from this analysis, because their presence in the gallery forests of the Cerrado Region might be as relicts of a pattern of distribution involving southern Atlantic Forest, part of the Cerrado Region and the Andes (Remsen *et al.* 1991) rather than due to comparatively recent range expansion from southern Atlantic Forest (Silva, unpubl.).

I evaluated the maximum distance that Amazonian and Atlantic elements extend into the Cerrado Region by estimating for each taxon the distance from its innermost record in the Cerrado Region to the nearest point at the border between the Cerrado Region and its centre of distribution. I classified each taxon in one of the following distance categories: (a) 0–250 km, (b)

251–500 km, (c) 501–750 km, (d) 751–1000 km, and (e) more than 1000 km. I tested the null hypothesis that Amazonian and Atlantic elements are similarly distributed across these five distance categories by using G-test.

To test the null hypothesis that Amazonian and Atlantic elements have similar altitudinal ranges within the Cerrado Region, I listed all localities within this region where one or more taxa of each of these two biogeographic categories had been recorded. After that, I checked the altitude for each of these localities in Paynter & Traylor (1991). Finally, I compared the altitude of these two sets of localities by using the non-parametric Mann-Whitney U-test.

To examine if the maximum distance reached by Amazonian and Cerrado elements into the Cerrado Region is associated with some of their ecological characteristics, I classified each taxon in broad categories of diet and habitat use. Diet categories are as follows: (a) nectarivores, species that feed mainly on nectar, perhaps including some arthropods in their diet; (b) frugivores, species whose diet is primarily based on fruits, with insects being included only rarely; (c) frugivores-insectivores, species whose diet may

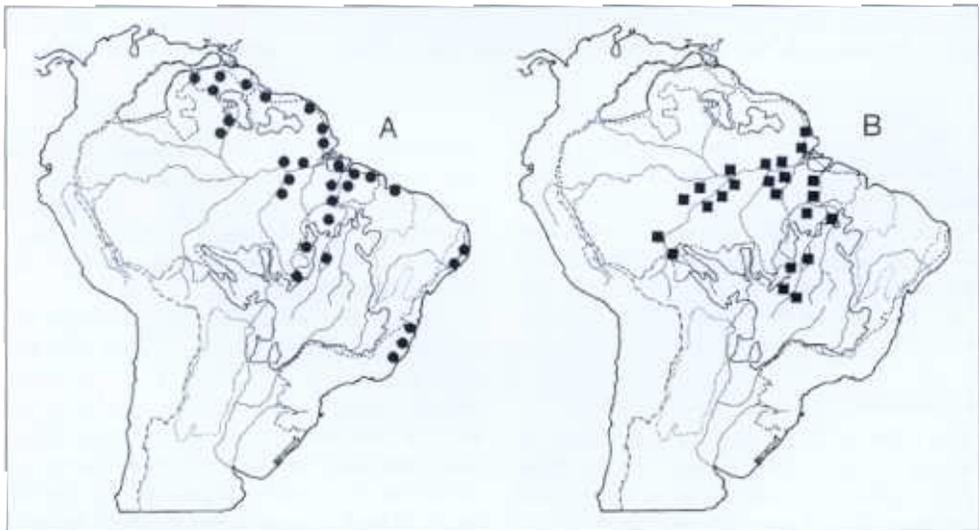


FIG. 4. Two examples of distribution of Amazonian elements recorded in the Cerrado Region: (A) *Chiroxiphia p. pareola*, (B) *Sakesphorus luctuosus*. Note that *C. p. pareola* has disjunct populations in Amazonia and the Atlantic Forest. Records within the Cerrado Region were assigned to Amazonian populations by using the criterion of minimum distance.

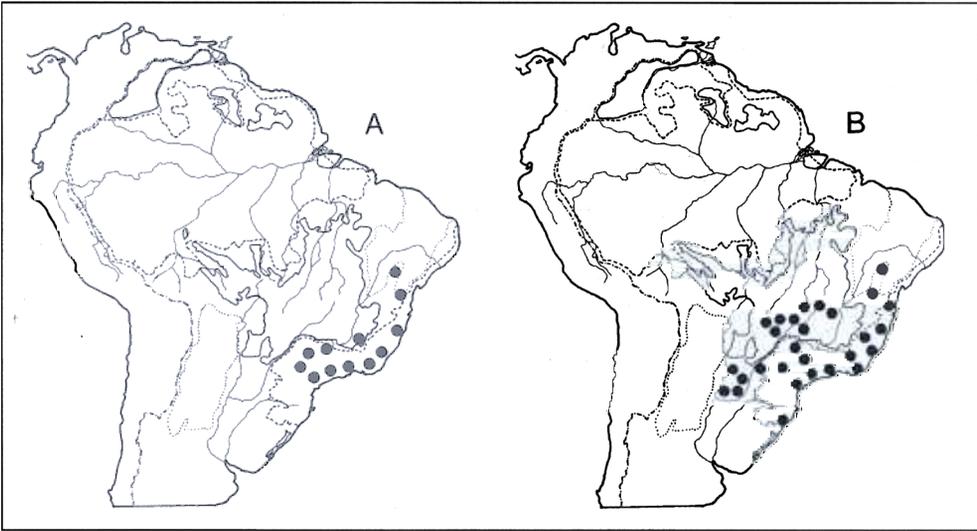


FIG. 5. Two examples of Atlantic Forest elements recorded in the Cerrado Region: (A) *Amazilia l. lactea*, (B) *Lepidocolaptes f. fuscus*.

include similar proportions of fruits and insects (and other arthropods); (d) insectivores, species which include only insects (and other arthropods) in their diets; (e) others, a mixed category composed of groups poorly represented in the set of species analysed, such as carnivores (raptors) and granivores (seedeaters). Habitat-use categories are the following: (a) species that concentrate their activities mainly on the interior of gallery forests (understorey and sub-canopy); (b) species that concentrate their activities on the external regions of the gallery forests (canopy and/or borders); (c) species that use both internal and external regions of the gallery forests.

Data about the natural history of species were collected during my field work in the Cerrado Region (several one-month expeditions from 1985 to 1994). Distribution and taxonomy of the gallery forests birds in the Cerrado Region were based on studies in museums (American Museum of Natural History, New York, United States; Museu Paraense Emílio Goeldi, Belém, Brazil; Museu Nacional, Rio de Janeiro, Brazil; Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; and Zoological Museum, University of Copenhagen, Copenhagen, Denmark) supplemented by a literature survey.

RESULTS

A total of 276 species (278 taxa, because two species, *Ciccaba hubbula* and *Cissopis leveriana*, are represented in the Cerrado Region by two subspecies) were included in this analysis (Appendix). Amazonian elements include 200 taxa whilst the Atlantic ones include 78 taxa (Table 1).

Eleven pairs of Amazonian and Atlantic sister taxa were recorded within the Cerrado Region (Table 2). None of them are known to have established a contact zone (e.g., a narrow zone of sympatry, hybridization or intergradation) within this region.

The distributions of Amazonian and Atlantic elements in the categories of maximum distance reached within the Cerrado Region differ significantly ($G = 61.2$, $df = 2$, $P < 0.001$; three categories with > 500 km were grouped to avoid the problem of categories with frequencies < 1). Most Amazonian elements (86%) do not extend more than 250 km into the Cerrado Region and no element extends more than 750 km (Table 1). In contrast, only 50% of the Atlantic elements are known to be restricted to the 1-250 km distance category, and 14% extend

TABLE 1. Distribution of Amazonian (AM) and Atlantic (AT) elements by categories of diet, habitat use, and distance reached into the Cerrado Region. Diet categories are nectarivores (NE), frugivores (FR), frugivore-insectivores (FI), insectivores (IN) and others (OT). Distance categories are (A) 1–250 km, (B) 251–500 km, (C) 501–750 km, (D) 751–1000 km, (E) > 1000 km.

Distance		Forest Interior					Forest Exterior					Both					Total
		NE	FR	FI	IN	OT	NE	FR	FI	IN	OT	NE	FR	FI	IN	OT	
A	AM	0	10	10	56	1	0	13	20	10	2	5	4	17	19	5	172
	AT	0	3	1	10	0	0	0	5	2	0	5	0	2	9	2	39
B	AM	0	0	1	6	1	0	0	1	1	1	1	0	7	4	0	23
	AT	0	0	1	3	0	0	0	4	0	0	0	0	1	0	0	9
C	AM	0	1	0	0	0	0	0	2	2	0	0	0	0	0	0	5
	AT	0	2	3	3	0	0	2	1	0	0	2	0	3	1	0	17
D	AM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AT	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2
E	AM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AT	0	1	0	5	0	0	0	0	1	0	0	0	2	2	0	11
Total	AM	0	11	11	62	2	0	13	23	13	6	4		23	5		
	AT	0	6	5	22	0	0	2	10	2	7	0		13	2		

more than 1000 km into the Cerrado Region (Table 1).

No clear pattern of association between diet, habitat use and distance reached into the Cerrado Region was found for Amazonian or Atlantic elements (Table 1). In general, most of the species assemblages formed by the combination of diet and habitat-use categories have increasingly fewer species within the Cerrado Region with increasing distance from their centres of distribution.

Localities where Amazonian elements have been recorded (n = 58) are mainly within the peripheral depressions or along the borders of

the main plateaus in the western part of the Cerrado Region (Fig. 6a). On the other hand, localities in which Atlantic elements have been recorded (n = 103) are mainly on the top of plateaus, in the eastern part of the Cerrado Region (Fig. 6b). Altitudes of Amazonian localities (mean = 396 m, s.d. = 213.4, n = 55) differ from those of the Atlantic ones (mean = 705 m, s.d. = 279.8 m, n = 96). This difference is statistically significant (Mann-Whitney U-test, U = 998.5, P < 0.001).

DISCUSSION

Both distance from their centres of distribution and altitude influence the distribution of Amazonian and Atlantic elements over the gallery forest system of the Cerrado Region. The hypothesis that the number of these elements within the Cerrado Region decreases with increasing distance from their centres of distribution (Cerqueira 1982, Silva & Oniki 1988) is supported. Nonetheless, Atlantic elements extend their ranges significantly deeper into the Cerrado Region than do Amazonian ones (Table 1). The hypothesis of differences in altitudinal distribution between Amazonian and Atlantic elements within the Cerrado Region (Silva 1989) is also supported, because Amazonian elements occur at significantly lower altitudes than Atlantic ones.

TABLE 2. Pairs of Amazonian and Atlantic allopatric sister taxa in the system of gallery forests of the Cerrado Region.

Amazonian	Atlantic
<i>Tinamus tao</i>	<i>T. solitarius</i>
<i>Ciccaba bubula bubula</i>	<i>C. h. albomarginatus</i>
<i>Baryphthengus martii</i>	<i>B. ruficapillus</i>
<i>Selenidera gouldii</i>	<i>S. maculirostris</i>
<i>Melanerpes cruentatus</i>	<i>M. flavifrons</i>
<i>Dendrocincla fuliginosa</i>	<i>D. turdina</i>
<i>Pyrgilena leuconota</i>	<i>P. leucoptera</i>
<i>Corythopsis torquata</i>	<i>C. delalandi</i>
<i>Myiornis ecaudatus</i>	<i>M. auricularis</i>
<i>Cissopis leveriana leveriana</i>	<i>C. l. major</i>
<i>Euphonia rufiventris</i>	<i>E. pectoralis</i>

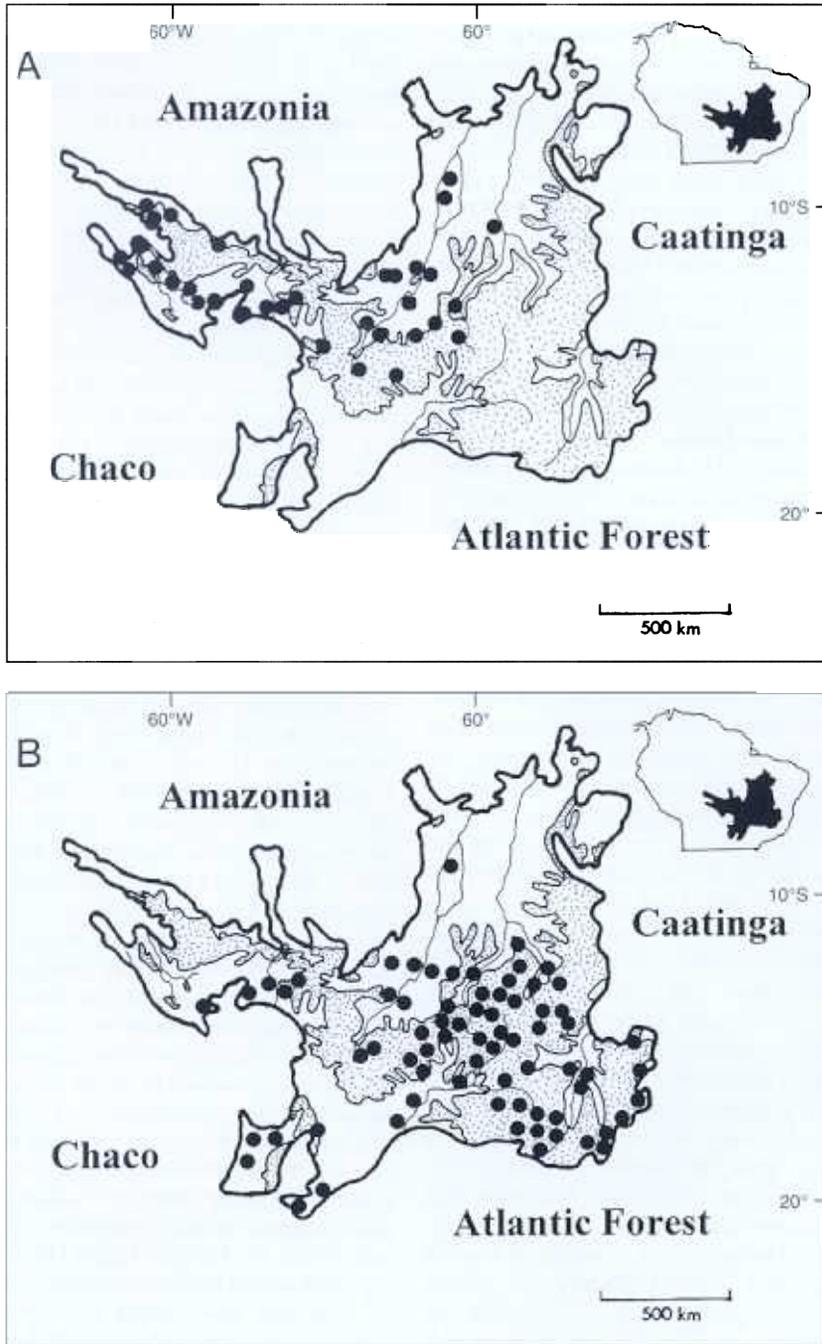


FIG. 6. Distribution of all localities where Amazonian (A) and Atlantic (B) elements have been recorded within the Cerrado Region. Some dots in both maps may represent more than one locality. Stippled, areas with altitude equal or more than 500 m.

The reduction of number of species from the main source area toward the centre of the region being colonized is the pattern expected if species are passively expanding their ranges in accordance with the improvement of the ecological conditions (Udvardy 1969). The number of Amazonian and Atlantic forest species expanding their ranges into the Cerrado Region is only a fraction of the pool of species living in the source regions. The limited area covered by forest habitats, differences in floristic composition and structure, and possibly the reduction of density of some key resources (e.g., army ants swarms and fruits) in the gallery forests of the Cerrado Region certainly constrain the range expansion of most of the Amazonian and Atlantic forest birds.

Amazonian and Atlantic elements follow different pathways to expand their ranges into the Cerrado Region. Connections with the Amazonian forests are made mainly through the gallery forests that follow the channels of the major rivers that flow toward the Amazon Basin (e.g., Araguaia, Tocantins, Guaporé). These rivers, in turn, flow mainly in the peripheral depressions. In contrast, links between the gallery forest system of the Cerrado Region and southern Atlantic Forest are made mainly by narrow gallery forests on the plateaus as well as by a broad corridor of tall evergreen and semi-deciduous forests growing on rich soils along the Paranaíba River and its tributaries (Brown & Ab'Saber 1979, Silva 1989).

Differences in the paleoecological history of these different pathways of colonization might explain the reason why more Atlantic elements expanded their ranges deeper into the Cerrado Region than Amazonian ones. Paleoecological information suggests that in the Cerrado Region, peripheral depressions were much more influenced by the drastic climatic fluctuations in the Quaternary than the plateaus (Ab'Saber 1977b, 1983, 1988). Consequently, one can expect that high frequency climatic shifts and their associated geomorphological and hydrological changes have disturbed more frequently the gallery forests on the peripheral depressions than the gallery forests on the plateaus or those on rich soils. I suggest that connections with Amazonian forests following peripheral depressions may have broken down several times during un-

favourable climatic periods. This could have had a negative effect on populations of Amazonian forest birds that were expanding their ranges into the Cerrado Region, promoting local extinctions or range retraction toward the borders of the source area. In contrast, gallery forests on the plateaus and those on rich soils were relatively more stable during the Quaternary climatic fluctuations (Ab'Saber & Brown 1979), providing Atlantic forest birds with more opportunities to expand and maintain their ranges into the Cerrado Region.

In addition to historical factors, present-day ecological factors also may help to explain the differences in ranges found between Amazonian and Atlantic elements within the Cerrado Region. Willis (1976) has documented that the drastic falls in temperature, which are so common during the winter of the Cerrado Region (Nimer 1979), affect negatively the behavior of Amazonian forest birds in areas close to their range boundaries in the Cerrado Region. In contrast, Atlantic elements seem to have developed different strategies (long or local migrations, wanderings, diet shifts) to avoid such short-term climatic changes (Willis 1990). If so, similarity between the climatic types of the Cerrado Region with parts of southern Atlantic Forest (Nimer 1979) may confer Atlantic elements more advantages for maintaining their ranges within the gallery forest system of the Cerrado Region than Amazonian ones.

Altitudinal segregation between Amazonian and Atlantic elements may be viewed as a consequence of the topographic distribution of the connections between the gallery forest system of the Cerrado Region with the Amazonian and Atlantic forests as well as of the paleoecological histories of these connections. One could suggest that competition also might play an important role in the determination of this distribution pattern. However, potential competitors, i.e., pairs of closely related Amazonian and Atlantic taxa within the Cerrado Region (Table 2), only represent a small portion of the species identified as expanding their ranges into the Cerrado Region. In addition, the ranges of these closely related taxa are known to be separated by large distances, which makes any explanation based on competition unrealistic.

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APPENDIX. List of taxa included in this analysis (taxonomic sequence following Howard & Moore 1991). Pattern: (AM) Amazonian, (AT) Atlantic. Distance: (A) 1–250 km, (B) 251–500 km, (C) 501–750 km, (D) 751–1000 km, (E) > 1000 km. Habitat Use: (I) Interior (understorey and sub-canopy), (E) Exterior (canopy and borders), (B) Both. Diet: (NE) Nectarivores, (FR) Frugivores, (FI) Frugivore-Insectivores, (IN) Insectivores, (OT) others, including carnivores and granivores. Species preceded by # have disjunct and undifferentiated populations in Amazonia and southern Atlantic Forest.

Species	Pattern	Distance	Habitat	Diet
Tinamidae				
<i>Tinamus tao</i>	AM	B	I	FI
<i>Tinamus solitarius</i>	AT	B	I	FI
<i>Tinamus major</i>	AM	A	I	FI
<i>Tinamus guttatus</i>	AM	A	I	FI
<i>Crypturellus cinereus</i>	AM	A	I	FI
<i>Crypturellus obsoletus obsoletus</i>	AT	C	I	FI
<i>Crypturellus strigulosus</i>	AM	A	I	FI
<i>Crypturellus noctivagus noctivagus</i>	AT	A		FI
Ardeidae				
<i>Agamia agami</i>	AM	B	I	OT
<i>Zebrilus undulatus</i>	AM	A	B	IN
Anatidae				
<i>Mergus octosetaceus</i>	AT	E	E	OT
Accipitridae				
<i>Leucopternis kublí</i>	AM	A	E	OT
<i>Leucopternis albicollis</i>	AM	A	B	OT
<i>Spizaetus tyrannus serus</i>	AM	A	B	OT
Falconidae				
<i>Daptrius ater</i>	AM	A	B	FI
# <i>Micrastur gilvicollis gilvicollis</i>	AM	A	I	OT
Cracidae				
<i>Ortalis guttata guttata</i>	AM	A	B	FR
<i>Penelope jacquacu</i>	AM	A	B	FR
<i>Pipile pipile nattereri</i>	AM	A	B	FR
<i>Mitu tuberosa</i>	AM	A	B	FR
Phasianidae				
<i>Odontophorus gujanensis</i>	AM	A		FR
<i>Odontophorus capueira capueira</i>	AT	C		FR
<i>Odontophorus stellatus</i>	AM	A		FR
Rallidae				
<i>Eulabeornis saracura</i>	AT	A		IN
Euryptidae				
<i>Eurypyga helias</i>	AM	B		IN
Columbidae				
<i>Columba subvinacea</i>	AM	A	E	FR
<i>Claravis godefrida</i>	AT	A	I	FR
Psittacidae				
<i>Ara macao</i>	AM	A	E	FR
<i>Ara severa</i>	AM	A	E	FR
<i>Ara manilata</i>	AM	A	E	FR
<i>Aratinga auricapilla</i>	AT	C	E	FR
<i>Aratinga wedelli</i>	AM	A	E	FR
<i>Pyrrhura rhodogaster</i>	AM	A	E	FR
<i>Pyrrhura picta</i>	AM	A	E	FR
<i>Brotogeris tirica</i>	AT	C	E	FR
<i>Brotogeris cyanoptera</i>	AM	A	E	FR
<i>Pionus menstruus menstruus</i>	AM	A	E	FR
Opisthocomidae				
<i>Opisthocomus boazin</i>	AM	B	E	OT

Species	Pattern	Distance	Habitat	Diet
Cuculidae				
<i>Piaya melanogaster</i>	AM	A	E	IN
<i>Piaya minuta</i>	AM	C	E	IN
<i>Neomorphus geoffroyi geoffroyi</i>	AM	A	I	IN
Strigidae				
<i>Otus watsonii</i>	AM	A	B	OT
<i>Lophotrix cristata</i>	AM	A	B	OT
<i>Strix virgata borelliana</i>	AT	A	B	OT
<i>Ciccaba hubula hubula</i>	AM	A	B	OT
<i>Ciccaba hubula albomarginatus</i>	AT	A	B	OT
Nyctibiidae				
<i>Nyctibius aethereus aethereus</i>	AT	A	I	IN
<i>Nyctiprogne leucopyga</i>	AM	A	I	IN
Caprimulgidae				
≠ <i>Caprimulgus maculicaudus</i>	AM	A	B	IN
<i>Chaetura cinereiventris sclateri</i>	AM	A	E	IN
Trochilidae				
<i>Threnetes leucurus</i>	AM	A	B	NE
<i>Phaethornis hispidus</i>	AM	A	B	NE
<i>Florisuga mellivora</i>	AM	A	B	NE
<i>Melanotrochilus fuscus</i>	AT	A	B	NE
<i>Anthracoceros viridigula</i>	AM	B	B	NE
<i>Lophornis magnifica</i>	AT	C	B	NE
<i>Chlorostilbon mellisugus</i>	AM	A	B	NE
<i>Thalurania glaucopis</i>	AT	A	B	NE
<i>Leucochloris albicollis</i>	AT	A	B	NE
<i>Amazilia lactea lactea</i>	AT	A	B	NE
<i>Aphantochroa cirrochloris</i>	AT	C	B	NE
<i>Heliobryx aurita auriculata</i>	AT	A	B	NE
<i>Heliomaster longirostris</i>	AM	A	B	NE
Trogonidae				
<i>Trogon melanurus</i>	AM	B	B	FI
<i>Trogon viridis viridis</i>	AM	A	B	FI
<i>Trogon collaris collaris</i>	AM	A	B	FI
<i>Trogon rufus rufus</i>	AM	A	B	FI
<i>Trogon aurantius</i>	AT	A	B	FI
<i>Trogon violaceus</i>	AM	A	B	FI
<i>Electron platyrhynchum</i>	AM	B	B	FI
<i>Baryphthengus ruficapillus</i>	AT	E	B	FI
<i>Baryphthengus martii</i>	AM	A	B	FI
Galbulidae				
<i>Galbula cyanicollis</i>	AM	B	B	IN
<i>Galbula leucogastra</i>	AM	A	B	IN
<i>Jacamerops aurea</i>	AM	B	B	IN
Bucconidae				
<i>Notharchus macrorhynchus hyperrhynchus</i>	AM	A	B	IN
<i>Notharchus tectus</i>	AM	A	B	IN
<i>Bucco tamatia</i>	AM	A	B	IN
<i>Nystalus striolatus</i>	AM	A	B	IN
<i>Malacoptila striata striata</i>	AT	A	B	IN
<i>Malacoptila rufa</i>	AM	A	B	IN
<i>Nonnula ruficapilla</i>	AM	A	B	IN
<i>Monasa morphoeus</i>	AM	A	B	IN
Capitonidae				
<i>Capito dayi</i>	AM	A	B	FI

Species	Pattern	Distance	Habitat	Diet
Ramphastidae				
<i>Pteroglossus inscriptus</i>	AM	A	E	FI
<i>Pteroglossus bitorquatus</i>	AM	A	E	FI
<i>Selenidera gouldii</i>	AM	A	E	FI
<i>Selenidera maculirostris</i>	AT	A	E	FI
<i>Ramphastos dicolorus</i>	AT	B	E	FI
<i>Ramphastos tucanus</i>	AM	A	E	FI
Picidae				
<i>Picumnus aurifrons</i>	AM	A	B	IN
<i>Picumnus cirratus</i>	AT	A	B	IN
<i>Picumnus albosquamatus guttifer</i>	AT	E	B	IN
<i>Melanerpes cruentatus</i>	AM	B	B	FI
<i>Melanerpes flavifrons</i>	AT	E	B	FI
<i>Veniliornis maculifrons</i>	AT	A	B	FI
<i>Veniliornis affinis ruficeps</i>	AM	A	B	FI
<i>Piculus leucolaemus</i>	AM	A	B	FI
<i>Piculus flavigula erythropis</i>	AT	C	B	FI
<i>Celeus grammicus</i>	AM	A	B	FI
<i>Celeus flavus inornatus</i>	AM	A	B	FI
<i>Celeus torquatus occidentalis</i>	AM	B	B	FI
<i>Campephilus rubricollis</i>	AM	B	B	FI
<i>Campephilus robustus</i>	AT	C	B	FI
Dendrocolaptidae				
<i>Dendrocincla fuliginosa</i>	AM	A	I	IN
<i>Dendrocincla turdina</i>	AT	E	I	IN
<i>Dendrocincla merula</i>	AM	A	I	IN
<i>Glyphorhynchus spirurus inornatus</i>	AM	A	B	IN
<i>Nasica longirostris</i>	AM	A	I	IN
<i>Hylexetastes perrotii</i>	AM	B	I	IN
<i>Xiphocolaptes promeropirhynchus</i>	AM	A		IN
<i>Xiphocolaptes albicollis</i>	AT	E		IN
<i>Dendrocolaptes certhia</i>	AM	A	I	IN
<i>Xiphorhynchus obsoletus</i>	AM	A	I	IN
<i>Xiphorhynchus elegans</i>	AM	A	I	IN
<i>Lepidocolaptes squamatus squamatus</i>	AT	A	I	IN
<i>Lepidocolaptes fuscus fuscus</i>	AT	C	I	IN
<i>Lepidocolaptes albolineatus</i>	AM	A	I	IN
<i>Campylorhamphus falcularius</i>	AT	A	B	IN
Furnariidae				
<i>Synallaxis ruficapilla</i>	AT	A	B	IN
<i>Synallaxis spixi</i>	AT	C	B	IN
<i>Synallaxis cinerascens</i>	AT	A	B	IN
<i>Synallaxis rutilans</i>	AM	A	I	IN
<i>Cranioleuca pallida</i>	AT	A	B	IN
<i>Philydor erythrocerus</i>	AM	A	I	IN
<i>Philydor erythropterus</i>	AM	A	I	IN
<i>Philydor lichtensteini</i>	AT	E	I	IN
<i>Automolus ochrolaemus</i>	AM	A	I	IN
<i>Automolus leucophthalmus</i>	AT	D	B	IN
<i>Sclerurus rufigularis</i>	AM	A	I	IN
<i>Sclerurus scansor scansor</i>	AT	D	I	IN
<i>Xenops tenuirostris</i>	AM	A	B	IN
<i>Xenops minutus genibarbis</i>	AM	A	B	IN
Formicariidae				
<i>Cymbilaimus lineatus</i>	AM	A		IN
<i>Hypoedaleus guttatus</i>	AT	B		IN
<i>Mackenziaena severa</i>	AT	A		IN
<i>Sakesphorus luctuosus</i>	AM	B	B	IN

Species	Pattern	Distance	Habitat	Diet
# <i>Thamnophilus palliatus palliatus</i>	AM	A	E	IN
<i>Thamnophilus aethiops punctuliger</i>	AM	A	I	IN
<i>Thamnophilus schistaceus</i>	AM	A	I	IN
<i>Thamnophilus amazonicus</i>	AM	A	I	IN
<i>Dysithamnus mentalis mentalis</i>	AT	B		IN
<i>Thamnomanes saturninus</i>	AM	A		IN
<i>Thamnomanes caesius persimilis</i>	AM	A		IN
<i>Myrmotherula brachyura</i>	AM	A		IN
<i>Myrmotherula sclateri</i>	AM	A		IN
<i>Myrmotherula surinamensis</i>	AM	A	I	IN
<i>Myrmotherula hauxwelli</i>	AM	A	I	IN
<i>Myrmotherula leucophthalma</i>	AM	A	I	IN
<i>Myrmotherula ornata</i>	AM	A	I	IN
<i>Myrmotherula axillaris axillaris</i>	AM	A	I	IN
<i>Myrmotherula menetriesii</i>	AM	A	I	IN
<i>Herpsilochmus longirostris</i>	AT	E	B	IN
<i>Herpsilochmus rufimarginatus frater</i>	AM	A	I	IN
<i>Microrhopias quixensis</i>	AM	A	I	IN
<i>Formicivora serrana</i>	AT	A	B	IN
<i>Drymophila ferruginea</i>	AT	A	I	IN
<i>Drymophila ochropyga</i>	AT	A	I	IN
<i>Drymophila devillei</i>	AM	A	I	IN
<i>Cercomacra cinerascens</i>	AM	A		IN
<i>Cercomacra nigrescens</i>	AM	A		IN
<i>Pyriglena leuconota</i>	AM	B		IN
<i>Pyriglena leucoptera</i>	AT	A		IN
<i>Myrmoborus leucophrys</i>	AM	A		IN
<i>Myrmoborus myotherinus</i>	AM	A		IN
<i>Hypocnemis cantator</i>	AM	A		IN
<i>Hypocnemoides maculicauda</i>	AM	A		IN
<i>Sclateria naevia</i>	AM	A		IN
<i>Myrmeciza loricata</i>	AT	A	I	IN
<i>Myrmeciza hemimelaena</i>	AM	A	I	IN
<i>Myrmeciza atrothorax</i>	AM	B	B	IN
<i>Rhegmatorhina hoffmannsi</i>	AM	B	I	IN
<i>Hylophilax punctulata</i>	AM	A	I	IN
<i>Hylophilax poecilinota</i>	AM	B	I	IN
<i>Phlegopsis nigromaculata</i>	AM	A		IN
<i>Formicarius colma amazonicus</i>	AM	A		IN
<i>Formicarius analis</i>	AM	A		IN
<i>Hyllopezus berlepschi</i>	AM	A		IN
Conopophagidae				
<i>Conopophaga lineata</i>	AT	E		IN
Tyrannidae				
<i>Phyllomyias virescens</i>	AT	B	E	FI
# <i>Ornithion inermis</i>	AM	A	I	IN
<i>Mionectes oleagineus chloronotus</i>	AM	A	I	FR
<i>Mionectes rufiventris</i>	AT	C	I	FR
<i>Phylloscartes ventralis</i>	AT	A	E	IN
<i>Corythopsis delalandi</i>	AT	E	I	IN
<i>Corythopsis torquata</i>	AM	A		IN
<i>Myiornis auricularis</i>	AT	B	I	IN
<i>Myiornis ecaudatus</i>	AM	A	I	IN
<i>Hemitriccus minor</i>	AM	A	I	IN
<i>Hemitriccus diops</i>	AT	A	I	IN
<i>Hemitriccus flammulatus</i>	AM	A	B	IN
<i>Hemitriccus zosterops</i>	AM	A	B	IN
<i>Hemitriccus minimus</i>	AM	A	I	IN
# <i>Hemitriccus striaticollis</i>	AM	A	B	IN
<i>Hemitriccus nidipendulum</i>	AT	A	B	IN

Species	Pattern	Distance	Habitat	Diet
<i>Todirostrum poliocephalum</i>	AT	A	B	IN
<i>Ramphotrigon megacephala megacephala</i>	AM	A	I	IN
<i>Ramphotrigon ruficauda</i>	AM	B	I	IN
<i>Ramphotrigon fuscicauda</i>	AM	A	I	IN
<i>Tolmomyias assimilis</i>	AM	A	E	IN
<i>Platyrrhynchus platyrhynchus</i>	AM	A	I	IN
<i>Onychorhynchus coronatus swainsoni</i>	AT	C	I	IN
<i>Terenotriccus erythrurus</i>	AM	A	I	IN
<i>Myiobius barbatus mastacalis</i>	AT	C	I	IN
<i>Contopus cinereus cinereus</i>	AT	A	E	IN
<i>Knipolegus orenocensis</i>	AM	A	E	IN
<i>Attila bolivianus</i>	AM	B	E	FI
<i>Attila spadiceus</i>	AM	A	E	FI
<i>Rhytipterna simplex frederici</i>	AM	A	I	FI
# <i>Laniocera hypopyrra</i>	AM	A	I	FI
# <i>Myiarchus tuberculifer</i>	AM	B	E	IN
<i>Tyrannopsis sulphurea</i>	AM	B	B	FI
<i>Pachyrhamphus castaneus castaneus</i>	AT	B	B	FI
<i>Pachyrhamphus minor</i>	AM	A	B	FI
<i>Tityra semifasciata</i>	AM	A	B	FI
Pipridae				
<i>Schiffornis virescens</i>	AT	E		FR
<i>Schiffornis turdinus amazonus > wallacii</i>	AM	A		FR
<i>Piprites chloris bolivianus</i>	AM	A		FI
<i>Tyrannetes stolzmanni</i>	AM	A		FR
<i>Neopelma sulphureiventer</i>	AM	A		FI
<i>Heterocercus linteatus</i>	AM	A		FR
<i>Machaeropterus pyrocephalus</i>	AM	C		FR
<i>Manacus manacus subpurus</i>	AM	A		FR
<i>Illicura militaris</i>	AT	A		FR
# <i>Chiroxiphia pareola pareola</i>	AM	A		FR
<i>Chiroxiphia caudata</i>	AT	A		FR
<i>Pipra nattereri</i>	AM	A		FR
# <i>Pipra rubrocapilla</i>	AM	A		FR
Cotingidae				
# <i>Lipaugus vociferans</i>	AM	A	B	FI
<i>Xipholena punicea</i>	AM	A	E	FR
<i>Gymnoderus foetidus</i>	AM	A	E	FR
<i>Querula purpurata</i>	AM	A	E	FR
<i>Cephalopterus ornatus</i>	AM	A	E	FR
Troglodytidae				
<i>Odontorchilus cinereus</i>	AM	A	E	IN
<i>Microcerculus marginatus</i>	AM	A	I	IN
Turdidae				
# <i>Turdus fumigatus</i>	AM	A	B	FI
<i>Turdus hauxwelli</i>	AM	A	B	FI
Poliopitidae				
<i>Ramphocaenus melanurus sticturus</i>	AM	A	B	IN
Emberizidae				
<i>Sporophila schistacea</i>	AM	A	E	OT
<i>Arremon flavivrostris flavivrostris</i>	AT	C		FI
<i>Pitylus grossus</i>	AM	A		FI
<i>Cyanocopsa cyanoides</i>	AM	A	B	FI
<i>Cissopis leveriana leveriana</i>	AM	B	B	FI
<i>Cissopis leveriana major</i>	AT	C	B	FI
<i>Pyrrhocomma ruficeps</i>	AT	C	E	FI
<i>Hemithraupis ruficapilla</i>	AT	A	E	FI
<i>Hemithraupis flavicollis centralis</i>	AM	A	E	FI

Species	Pattern	Distance	Habitat	Diet
<i>Lanio versicolor</i>	AM	A	E	IN
<i>Tachyphonus luctuosus</i>	AM	A	E	FI
<i>Tachyphonus coronatus</i>	AT	B	E	FI
<i>Trichothraupis melanops</i>	AT	C	I	FI
<i>Habia rubica hesterna</i>	AM	A	I	FI
<i>Euphonia laniirostris</i>	AM	C	E	FI
<i>Euphonia chalybea</i>	AT	A	E	FI
<i>Euphonia chrysopasta</i>	AM	A	E	FI
<i>Euphonia minuta</i>	AM	A	E	FI
<i>Euphonia rufiventris</i>	AM	A	E	FI
<i>Euphonia pectoralis</i>	AT	B	E	FI
<i>Tangara mexicana boliviana</i>	AM	A	E	FI
<i>Tangara chilensis</i>	AM	A	E	FI
<i>Tangara seledon</i>	AT	A	E	FI
<i>Tangara cyanoventris</i>	AT	A	E	FI
<i>Tangara gyrola</i>	AM	A	E	FI
<i>Tangara cyanicollis melanogaster</i>	AM	A	E	FI
<i>Tangara nigrocincta</i>	AM	A	E	FI
<i>Dacnis lineata</i>	AM	A	E	FI
<i>Chlorophanes spiza caeruleus</i>	AM	A	E	FI
<i>Cyanerpes caeruleus</i>	AM	A	E	FI
<i>Cyanerpes cyaneus violaceus</i>	AM	A	E	FI
Parulidae				
<i>Basileuterus leucoblepharus</i>	AT	A	I	IN
<i>Basileuterus fulvicauda</i>	AM	A	I	IN
<i>Granatellus pelzelni</i>	AM	A	B	IN
Vireonidae				
<i>Hylophilus thonicus griseiventris</i>	AM	A	E	IN
<i>Hylophilus pectoralis</i>	AM	C	E	IN
<i>Hylophilus muscicapinus</i>	AM	A	E	IN
<i>Hylophilus hypoxanthus</i>	AM	A	E	IN
Icteridae				
<i>Psarocolius bifasciatus</i>	AM	A	E	FI
<i>Cacicus cela</i>	AM	C	E	FI