

# ORNITOLOGIA NEOTROPICAL

Volume 3

1992

No. 1

ORNITOLOGIA NEOTROPICAL 3: 1–15, 1992  
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## ZOOGEOGRAPHICAL ORIGINS OF EASTERN BRAZILIAN BIRDS

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*Abstract.* Atlantic forests of eastern Brazil are separated from Amazonian and Andean ones by a semiopen region (the caatinga-cerrado-chaco zone). Fifty-seven water birds, 166 semiopen-zone birds, and 647 other nonmarine eastern breeding species are analyzed for zoogeographical patterns. Water birds rarely speciate or subspeciate, perhaps because few large areas of nesting habitat occur in eastern Brazil and because these birds wander widely. Semiopen-zone species center in the caatinga/cerrado zone and show links to Andean-Argentine species, to birds of depauperate small open patches in Amazonia, or to birds in the llanos of Colombia-Venezuela northward. Speciation in the open zone is often between caatinga and cerrado or this and chaco, subspeciation additionally across upland forests of western Goiás or across dry forests in northwestern Bahia. Forest-zone eastern birds sometimes have crossed from Amazonia via the north coast, more often "centrally" via the dry-forested Bahian zone or even further south, at times with double crossings forming a "ring". A "Madeiran" relationship, the eastern bird related to upper-Amazonian rather than lower-Amazonian forms, may result from such eastward movements well south of the Amazon. Absence of certain eastern birds north of Bahia may also result from south-central crossings. Subspeciation is frequent across dry zones in northeastern Bahia but also in southern Bahia. Various other eastern birds are related to Andean or Argentine groups, probably crossing through northern Argentina and central Paraguay rather than along forested edges of Bolivian-Brazilian cerrado plateaus. Andean birds tend to occur north along uplands in central Brazil, even to the central plateau or northeast Brazil. A few other forms seem closer to Guianan than to Andean ones. If not the result of central Andean rapid evolution ("leapfrog speciation"), crossing via former lower Amazonian dry forests is indicated. Amazonian and Andean forms may invade the "islands" of Central America and eastern Brazil, as if central species-rich zones "export" species in "taxon cycles". Invasion of the Andes from southeast Brazil may have occurred occasionally, just as northward spread of central Brazilian open-zone species has been proposed. *Accepted 10 November 1991*

*Key words:* Birds, Brazil, Atlantic forests, cerrado, caatinga, zoogeography, taxon cycles, leapfrog speciation, speciation, ring species, Andes, Amazonia.

### INTRODUCTION

Atlantic forests of Brazil are separated from Amazonian and Andean ones by a zone of semiopen savannas ("cerrado") and dry woodlands, the "chaco" southwestward and "caatinga" to the northeast. The avifauna of eastern Brazil is rich, while many genera, species and subspecies are endemic (Haffer 1974), as is the case for plants (Smith 1962), reptiles and amphibians (Müller 1968) and other fauna (Müller 1973). Birds of eastern Brazil are often related to Amazonian or (Miranda-Ribeiro 1906, Sick 1985a) Andean

ones. Here, I analyze in preliminary fashion the zoogeographic relationships of eastern Brazilian forms, especially the forest species.

### METHODS

Pinto (1944, 1978), Peters *et al.* (1934–1986), Belton (1984, 1985), Sick (1985b), Teixeira *et al.* (1987) and Silva (1989) were the main sources. Yoshika Oniki and I have concentrated our studies on São Paulo birds since 1975, but have done some work to Rio Grande do Sul, Paraíba, and Mato Grosso after earlier field studies in Maranhão.

hão, Ceará, Amazonia and the Andes. Here I exclude birds found only in the Uruguaiana region of Rio Grande do Sul, marine birds, and non-breeding species. Water and cerrado-caatinga (open-zone) birds are considered separately.

## RESULTS

### Water birds

Widespread herons, ducks, and other birds of large marshes and rivers are in Appendix 1. Although several show Andean and southern relationships ("S"), others cross central Brazil. Remarkably little speciation or subspeciation (except northern versus southern *Chloroceryle americana*) is involved in eastern Brazil, although Andean speciation has occurred (Fjeldsa 1985). *Mergus octosetaceus* might be included here, but I prefer to discuss it later as a "forest" bird.

### Open-zone birds

Birds of the semiopen formations of central Brazil, caatinga to the northeast and cerrado to the southwest, meeting on the west the swampy Bananal and Pantanal and grading into the Paraguayan and Argentine chaco, have been considered by several authors (Cracraft 1985, Haffer 1967, 1974, Short 1975). Included in the central-Brazilian part of this region are gallery woodlands, which become rather extensive woodlands of Atlantic type at high elevation in southwestern Goiás (the "Mato Grosso de Goiás"), plus dry woodlands along the northern edge of the Brasília plateau, to Maranhão and Bahia ("arboreal caatinga" of the "Mangabeiras bridge", noted below).

I have included 166 species (Appendix 2) as typical of the semiopen zones of central Brazil rather than of eastern Brazil, although many advance well into eastern Brazil in cerrado patches, in dry zones near Salvador, and wherever humans have cut forests. Since these or related birds often extend southwest into the open pampas of Argentina, thence northward along the Andes or along eastern Brazilian mountains at high elevations or in rain-shadow dry valleys, Andean/Argentinian relationships are common. In dry climatic cycles (Snethlage 1928, Haffer 1967, 1974), the open or semiopen formations connected, via Marajó Island and Santarém, to the savannas of Amapá, Surinam, and Venezuela-Colombia. Haffer and others have considered the

birds of northern savannas as recent derivatives of the Brazilian cerrado birds, with little endemism and several missing species (Cracraft 1985 does not list a center of endemism in the llanos.).

Some speciation has occurred within the Brazilian part of the semiopen zone, principally between deciduous caatinga and evergreen if patchy cerrado: *Bucco maculatus/chacuru*, *Penelope jacucaca/ochrogaster*, *Anodorhynchus leari/byacinthinus*, *Coryphospingus pileatus/cucullatus* (these occur northward, too), *Phaethornis gounelli/preteri*, *Furnarius figulus/leucopus*, *Phacellodomus rufifrons/ruber*, *Herpsilochmus pectoralis/longirostris*, *Euscarthmus meloryphus/rufomarginatus*, *Casiornis fusca/rufa*, *Empidonomus aurantioatrocristatus/variatus*. Certain of the preceding cases and *Phaethornis subochraceus/nattereri*, *Poospiza melanoleuca/cinerea*, *Melanopareia maximiliani/torquata*, and *Suiriri suiriri/affinis* are possible chaco/cerrado examples. *Emberizoides herbicola* of cerrado is related to *E. ypiranganus* in montane marshes southeastward, *Polystictus pectoralis* to *P. superciliaris* in high open zones, *Thamnophilus torquatus* to *ruficapilla*, *Knipolegus lophotes* to *nigerrimus*, *Neopelma pallescens* of woodlands to *aurifrons* of upland woods, *Pseudoleistes guirahuro* to *virescens* (both marshy grassland), *Cyanocorax cyanopogon* to *chrysops* (woodlands), *Helio-master furcifer* to *squamosus*, *Crax fasciolata* to *blumenbachii* (woodlands), *Schistochlamys melanopis* to *ruficapilla* (scrub), plus a swarm of perhaps polymorphic seedeaters on the marshy transition to pampas: *Sporophila bouvreuil* to *S. hypoxantha*, *S. ruficollis*, *S. palustris*, *S. melanogaster*, *S. cinnamomea* (and several Argentine or outside forms, *S. zelichi*, *S. hypochroma*, *S. nigrorufa*, *S. minuta*, *S. castaneiventris*). *Anodorhynchus leari/glaucus* are a similar example.

Speciation between caatinga/cerrado and Argentina or the Andes occurred in 21 cases: *Nothura minor/darwinii* or *maculatus/darwinii*, *Theristicus caudatus/melanopis*, *Buteo albicaudatus/poecilochrous*, *Harpophalietus coronatus/solitarius*, *Milvago chimachima/chimango*, *Vanellus chilensis/resplendens*, *Gallinago undulata/stricklandii*, *Columba picazuro/maculosa*, *Colibri serrivostris/coruscans*, *Colaptes campestris/rupicola*, *Picoides mixtus/lignarius*, *Geobates poeciloptera/cunicularia*, *Pseudoseisura cristata/lophotes*, *Automolus rectirostris/erythrocephalus*, *Phyllomyias reiseri/*

virescens, *Phylloscartes roquettei/flaviventris*, *Xolmis cinerea/coronata*, *Knipolegus franciscanus/aterrimus*, *Alectrurus tricolor/risoria*, *Anthus nattereri/bellmayri*, and *Basileuterus leucophrys/leucoblepharus*. These examples suggest an earlier corridor of wet forest separating the open belt in northern Argentina or nearby (see below).

Direction of relationship is uncertain in *Penelope* (*jacucaca* and *ochrogaster* via Andean *obscura* or Amazonian *jacquacu*?) and *Xiphocolaptes falcirostris* via southern *albicollis* or central-northern *promeropirhynchus*?).

Speciation between caatinga-cerrado and Amazonian semiopen zones, forest edges or the llanos occurred in 20 cases: *Cathartes burrovianus/melambrotus*, *Crax fasciolata/globulosa*, *Laterallus xenopterus/melanophaius*, *Aratinga cactorum/pertinax*, *Caprimulgus candicans/cayennensis*, *Hydropsalis brasiliensis/climacocerca*, *Polytmus guainumbi/theresia*, *Lophornis magnifica/stictolopha*, *Hyllocharis chrysuras/sapphirina*, *Picumnus pygmaeus/varzeae*, *Synallaxis scutata/kollari*, *Formicivora melanogaster/grisea*, *Sublegatus modestus/obscurior*, *Stigmatura budytoides/napensis*, *Neopelma pallescens/sulphureiventer*, *Tyrannus albogularis/melancholicus*, *Polioptila dumicola/plumbea*, *Paroaria dominicana/gularis*, *Saltator coerulescens/maximus*, and *Ammodramus humeralis/aurifrons*.

In genera, about as many are Amazonian (54) as Andean/Argentine (52) ("F" and "G" in Appendix 2). Of species without obvious relatives, 32 seem closest to Andean/Argentine and 24 to Amazonian forms ("S" and "N" in Appendix 2).

Subspeciation (asterisks in Appendix 2) is frequent in the chaco and Argentina (16 cases, plus 3 just northward in Mato Grosso do Sul), the Andes or Peru (16 cases), and in the open zones of Amazonia or the llanos (31 cases, plus one on the Serra do Cachimbo). Internal subspeciation ("I" in Appendix 2) occurs in 39 species, in four of them twice and in *Sporophila bouvreuil* three times. The major patterns are of subspeciation across the "Mato Grosso de Goiás", or region, some 19 cases, or across the dry woodlands of the Tocantins-Bahia region ("Mangabeiras bridge"), 13 cases. These cases suggest the former existence of major forest barriers in these regions (see below). Nine cases occur near western São Paulo, where the Atlantic forest dips into Paraguay as far as Asunción. The marshy-prairie *S. bouvreuil*

cases fit no pattern, one isolate in Rio de Janeiro and one in eastern São Paulo as well as a main division across the "Mato Grosso". *Laterallus* rails and *Phacellodomus* in marshes have also been hard to place in preceding sections.

Strong subspecies occur in differing places northward (*Crax fasciolata*, *Picumnus limae*, *Gnorimopsar chopi*), southward (*Colaptes campestris*), and near western São Paulo (*Picoides mixtus*, *Philydor dimidiatus*) as well as in *S. bouvreuil*. *Arremon flavirostris*, almost an open-zone bird, has strong subspecies near western São Paulo, and *Cyanocorax chrysops/cyanopogon* meet there.

#### Forest species

*Northern-crossing widespread species.* Of the 870 species of east-Brazilian birds under consideration (647 when the 57 water and 166 open-zone species are excluded), 8 scrub, mangrove and coastal birds probably came along the coast, via existing habitat: *Nycticorax violaceus*, *Eudocimus ruber*, *Buteogallus aequinoctialis*, *Rallus longirostris*, *Aramides mangle*, *Columbina passerina*,



FIG. 1. Distribution of *Pteroglossus incriptus*, an aracari likely to have reached eastern Brazil by a northern route (after Haffer 1974).

*Mimus gilvus*, and *Conirostrum bicolor*. None have subspeciated. *Noctilio* fishing-bats have a similar coastal distribution (Emmons 1990), as do marine birds not considered here.

Thirteen other widespread birds range in eastern Brazil only to the Pernambucan region, north of the São Francisco River: *Crypturellus strigulosus*, *Mitu m. mitu*, *Glaucidium hardyi*, *Chaetura spinicauda*, *Pteroglossus inscriptus* (Fig. 1), *Dendrocincla fuliginosa taunayi*, *Dendrocolaptes certhia*, *Thamnophilus aethiops*, *Pyriglena leuconota pernambucensis*, *Cercomacra laeta sabinoi* (by R. Bierregaard, pers. comm.), *Zimmerius gra-*

*cilipes*, *Hemitriccus zosterops naumburgae*, and *Procnias averano*. In the five indicated cases, local subspecies are different from Amazonian ones. Unless these 13 came from the southwest, perhaps with later extinction in Bahia, a northern crossing seems possible. H. Sneath (1928: 539) suggested that earlier dry-forest links allowed *P. averano* to cross to or from Venezuela. Some mammals (Emmons 1990) show a similar pattern: a pygmy anteater, a howler monkey, *Pteronotus* bats.

Teixeira *et al.* (1987) show that *Cissopis l. leve-riana* of northern Amazonia occurs in Alagoas,



FIG. 2. Distribution of *Pteroglossus aracari* and *P. castanotis*. Related toucanets that probably reached eastern Brazil by different routes (after Haffer 1974).

not *C. l. major* of the south. *Veniliornis affinis ruficeps* occurs from Amazonia to Alagoas, then *V. a. affinis* south to Rio de Janeiro. *Dysithamnus mentalis emiliae* occurs from Pará to Alagoas, *D. m. mentalis* southward.

Some species that now range coastally south of Alagoas, such as *V. affinis*, may also have entered from the north. Several mammals, notably bats and two opossums, have this completely coastal pattern (Emmons 1990). *Pteroglossus aracari* (Fig. 2) shows one such pattern, where *P. castanotis* seems to block more southern entry. This "ring" pattern, discussed later, brings us to the next category.

*Central crossing.* As Haffer (1974) suggested, most east-Brazilian species of wide distribution probably crossed the central Brazilian semiopen zones. *P. castanotis* (Fig. 2), though a forest-edge bird, wanders in groups across wide clearings and open cerrados between gallery woodlands, easily reaching eastern Brazil today. Other species rarely leave forest, and must have needed forest to cross in wet epochs.

A composite satellite photograph of world vegetation (Van Sant & Warren 1991) clearly shows a dark green dry-forest zone up the Grande and Preto rivers just south of the Chapada das Mangabeiras in northwestern Bahia, almost reaching Amazonian forests just northwest. On flights to and from the I Congress of Brazilian Ornithology in Belém in July, 1991, via Brasília, I noted forests on north escarpments at the border of Goiás and Tocantins states as a possible link westward (the "Paraná depression", studied by Silva 1989 and authors cited therein; in 1989 I saw forests below the nearby Parque Nacional Chapada dos Veadeiros, on a visit courtesy of R. B. Cavalcanti), but then a very long stretch of dry cerrados along the unforested Tocantins, and finally gallery forests on side rivers south of Araguaiana. I propose that the link northwestern Bahia/Amazonia may have been forested in wet climatic cycles, and that this formed a "Mangabeiras bridge" for forest bird movement from the Araguaiana and/or Paraná regions.

The Mangabeiras bridge (Fig. 3) is not the only possible crossing between east and west. The "Mato Grosso de Goiás", now deforested, does not show up on satellite photographs. While it now seems an area of highland birds, un-

likely to have been a bridge for Amazonian birds unless climates were much warmer, there were once large forest areas in northern Minas Gerais as far south as Januária, forests which could have formed a bridge (the "Januária bridge") from the Paraná basin to the headwaters of the rios Jequitinhonha and Doce. Before deforestation, these woodlands would have showed up on satellite photos. We know this zone from 1977–78 (Willis & Y. Oniki, in press) and found the habitat east of Brasília rather scruffy cerrado, the arboreal caatinga near Januária rather patchy, and the mountain ridge to the east (Serra do Cipó) rather open and full of southern birds nowadays. However, with wetter forests in warm and humid epochs, Amazonian birds could have crossed the Januária bridge directly to Espírito Santo and spread north to Bahia, rather than south from Bahia as suggested by the Mangabeiras hypothesis.

Some 318 east-Brazilian birds fall in the "central" group: of these, 92 probably entered northward, on the Mangabeiras bridge (whether via the southern escarpments or Araguaiana region), 21 southward like *P. castanotis*, and the rest cross widely or cannot yet be assigned. Mammals suggesting the Mangabeiras pattern are a sloth, an agouti, a marmoset (?), and several bats, while the southwestern "Mato Grosso de Goiás" or Januária pattern includes another agouti, a howler monkey, and other bats (Emmons 1990). One lower-Amazonian opossum (*Caluromys philander*) today even traverses southward over the cerrado, east of the Araguaia, to Rio de Janeiro/Bahia.

In some bird cases, the pattern is of a "Madeiran" type, first noted in *Heliothryx aurita*: the Purus-Araguaia *H. a. auriculata* reappears in Bahia to São Paulo, while another subspecies (*H. a. phainolaema*) seems closer geographically on the lower Amazon. Hinkelmann (1989) registered *Phaethornis malaris* (?) *margarettae* of coastal Brazil as more like *P. m.* (?) *bolivianus* of the upper Madeira-Tapajoz than like *P. superciliosus muelleri* of the lower Amazon. We should watch for other possible examples, which seem to indicate entry into eastern Brazil via the escarpments north of Brasília.

I should note that little is known about species or subspecies distributions in northern Mato Grosso, and that certain Madeiran birds go

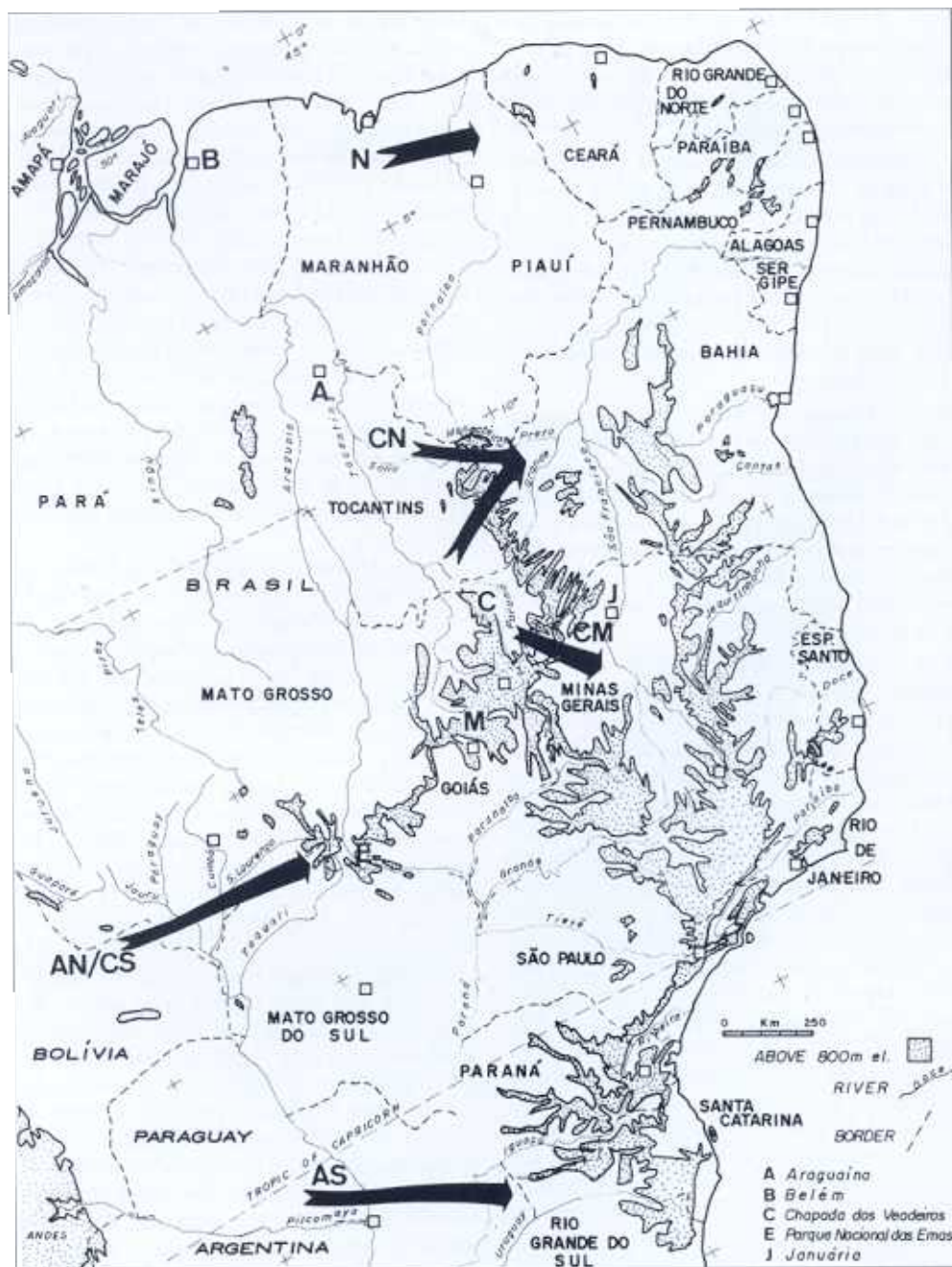


FIG. 3: Eastern Brazil, showing some routes by which birds could have reached coastal forests in former wet or more forested periods. N-North coastal route. CN-Central (northern) route via "Mangabeiras bridge" of north-western Bahia. CM-Central (middle) route via "Januária bridge". AN/CS - Andean-north or center-south route, AS - Andean-south route. M - "Mato Grosso de Goiás".

further east in the headwaters than they do along the Amazon. In *Hylophylax poicilinota*, the Madeira subspecies swings eastward south of Amazon subspecies. Haffer & Fitzpatrick (1985) show a tongue of higher rainfall from Peru across the southern Amazonian headwaters, separated from the Amazon-mouth Guianan tongue of high rainfall. However, the wide cerrado zone of the central Tocantins today suggests that connection with the Mangabeiras bridge was southward, at the Brasília escarpments.

Several Amazonian or widespread species, found in Bahia or southward, do not occur in the Pernambucan region. Mammals apparently present only north to Bahia include paca, *Oxymycterus* mice, tapir, jaguar, margay, puma, otter, coati, a bush dog, and a free-tailed bat (Emmons 1990). If not a result of undercollecting, recent human interference, or past extinctions northward, some birds may have been unable to spread north from Bahia or have not yet done so. It is not necessary to presume that these birds ever occurred in the Pernambucan region, for they could have crossed along the Mangabeiras bridge in northwestern Bahia or southward.

*Southern crossing.* Miranda-Ribeiro (1906) and Sick (1982a) emphasized that some eastern birds extend to the Andes or have close relatives there. The former, based on the connection, even argued that *Scytalopus speluncae* must be the same species as Andean *S. magellanicus*. Even excluding this case as unlikely, I count 79 widespread species that extend from eastern Brazil into Argentina or along the Andes (Appendix 3, including *Bubulcus ibis* as a species that came this way recently), 53 to or along the Andes. It is true that 8 of the 53 (19 of 79) barely enter eastern Brazil in the south (Rio Grande do Sul, "G"). Among mammals (Emmons 1990), only one agouti suggests this pattern or a very south-of-center one, but she probably excludes Andean and southern forms.

*Endemic species*

*With outside allopatric sister species.* In 49 cases, the outside sister species of an endemic (east Brazilian region) bird could be identified. In four cases, the crossing seems to have been northward, in twelve cases southward, and in 33 cases centrally. Among the 33, 8 seemed results of a

crossing rather southwestward and 18 via the Mangabeiras or Januária regions, northward.

The four possible northern cases are *Tinamus solitarius*, *Automolus leucophthalmus*, *Iodopleura pipra* (Pernambucan subspecies showing some intermediate features to *T. tao*, *A. infuscatus* and *I. isabellae*) and *Coccyzus euleri* (*C. americanus* is migrant from North America).

These could have come by the Mangabeiras bridge rather than coastally, of course. Since Ceará montane birds are often southeastern rather than Amazonian, one can even doubt any coastal movement of forest birds.

North-central cases are (eastern bird first, any geographically intermediate species being indicated) *Crypturellus noctivagus/erythropus*, *Leucopternis lacernulata/kuhli*, *Leucopternis polionota/albicollis*, *Odontophorus capueira/gujanensis*, *Crax blumenbachii/fasciolata/globulosus*, *Pyrrhura leucotis/pfimeri/picta* (species according to Silva 1989), *Chlorostilbon aureoventris/mellisuga*, *Malacoptila striata/rufa*, *Selenidera maculirostris/gouldii*, *Colaptes melanochloros/punctigula*, *Lepidocolaptes squamatus/albolineatus*, *Myrmotherula urosticta/longipennis*, *Myrmotherula fluminensis/iberingi*, *Cotinga maculata/cotinga*, *Xipholena atropurpurea/lamellipennis*, *Corythopsis delalandi/torquata*, *Mionectes rufiventris/macconnelli*, and *Pitylus fuliginosus/grossus*.

Examples of a possible Argentine crossing are *Amazona pretrei/tucumana*, *Pulsatrix koeniswaldiana/melanota*, *Otus atricapillus/hoyi*, *Cinclodes pabsti/fusca*, *Chamaea meruloides/turdina* (Willis, in press), *Elaenia parvirostris/albiceps*, *Elaenia mesoleuca/strepera*, *Cyanocorax caeruleus/cyanomelas*, *Haplospiza unicolor/rustica*, *Amaurospiza moesta/concolor*, and *Cacicus chrysopterus/leucoramphus*. The new *Asthenes luizae* from Minas Gerais has southern relatives (Vielliard 1990).

Central-southern sister species are *Pipile jacutinga/pipile*, *Ara maracana/auropilla*, *Pyrrhura frontalis/devillei*, *Pyrrhura cruentata/molinae*, *Sclerurus scansor/albigularis*, *Myiornis auricularis/albiventris*, *Turdus amaurochalinus/ignobilis* and *Sporophila falcirostris/schistacea*.

Difficult to assign, but central or central-northern are *Phaethornis pretrei/augusti*, *Celeus flavescens/lugubris*, *Dendrocolaptes platyrostris/picumnus*, *Xiphocolaptes albicollis/falcirostris/promeropirhynchus*, *Cercomacra brasiliiana/ferdinan-*

*di*, *Sporophila collaris/americana*, and *Euphonia pectoralis/rufiventris*.

#### "Reinvasion" of sibling

In 31 pairs, an endemic species represents a widespread bird that reaches eastern Brazil. In many of these pairs, the members are in contact or almost meet. In one case, the outside bird has been registered as a northern entrant, in three cases as a southern entrant, and in 27 cases centrally. Among the 27, six seem north-central, one south-central.

Amazon-mouth *Dendrocincla fuliginosa* meets or nearly meets its counterpart *D. turdina* across the lower São Francisco river. To the south *Philydor lichtensteini* meets *P. rufus*, *Saltator maxillosus* meets *aurantiostrius* and *Embernagra longicauda* meets *platensis* as "Andean" pairs.

North-centrally, *Harpagus diodon/bidentatus*, *Glaucis dohrri/hirsuta*, *Lipaugus lanioides/vociferans*, *Schiffornis virescens/turdinus*, *Chiroxiphia caudata/pareola*, and *Poliophtila lactea/plumbea* are pairs in which the second Amazonian bird reaches east Brazil. In *Brachygalba tridactyla/lugubris* the crossing was probably south-central. Central but unspecified are *Leptodon forbesi/cayanaensis*, *Aramides saracura/cajanea*, *Brotogeris tigris/versicolorus*, *Streptoprocne biscutata/zonaris*, *Ramphastos dicolorus/vitellinus*, *Campylorhamphus falcularius/trochilostrius*, *Synallaxis spixi/hypospodia*, *Dysithamnus stictothorax/mentalis*, *Formicivora serrana/grisea*, *Todirostrum poliocephalum/cinereum*, *Thryothorus longirostris/leucotis*, *Basileuterus hypoleucus/culicivorus*, *Hemithraupis ruficapilla/guira*, *Dacnis nigripes/cayana*, *Nemosia rourei/pileata*, *Thraupis cyanoptera/sayaca*, *Ramphocelus bresilius/carbo*, *Tachyphonus coronatus/rufus* and *Saltator similis/maximus*.

#### Multiple endemic species

In some 29 cases, there are two or more endemic species in eastern Brazil, which are either sympatric or allopatric. *Amazona brasiliensis/rhodocorytha* and extralimital *dufresniana* are coastal-woodland birds, following the northern route. *Tangara seledon/fastuosa* and Amazonian *chilensis* suggest a north-central route, as do *Touit melanonota/surda* to northern *purpurascens*, *Aratinga auricapillus/jandaya* to *solstitialis* and *Hyllopezus nattereri/ochroleucus* (Vielliard & H. Camargo, MS) to *berlepschi*.

Seven groups of Andean relationship are *Lepstasthenura setaria/striolata* as forms of *platensis*, *Synallaxis ruficapilla/infusca* as forms of *superciliosa*, *Cranioleuca semicincta/pallida/obsoleta* ending in *pyrrhophia* from Rio Grande do Sul west, *Scytalopus novacapitalis/speluncae* to Andean *magellanicus*, *Phylloscartes ceciliae*/sp. nov. (Willis & Oniki, MS) to Andean/southeastern *P. ventralis*, *Hemitriccus mirandae/kaempferi*/Andean *cinnamomeipectus*, and *Hemitriccus diops/obsoletus* to Andean *flammulatus*.

In addition, *Thalurania glaucopis/watertoni* are related to *furcata*, which reaches the region centrally; *Veniliornis spilogaster/maculifrons* may represent the widespread *affinis*, *Pyriglena leucoptera/atra* the Amazonian-Pernambucan *leucnota*, and *Tangara preciosa/peruviana* local forms of widespread *cayana*.

Thirteen other eastern groups are at the moment hard to relate to outside birds: *Augastes scutatus/lumacellus* may be related to Andean *Schistes*, *Phacellodomus erythrophthalmus/ferrugineigula* to cerrado *ruber*; but *Philydor novaesi/atricapillus*, *Mackenziaena severa/leachi*, *Terenura sicki/maculata*, *Drymophila ferruginea/rubricollis*, *Myrmeciza ruficauda/loricata/squamosa*, *Scytalopus psychopompus/indigoticus*, *Merulaxis stresemanni/ater*, *Tijuca condita/atra*, *Carpornis melanocephala/cucullata*, *Hyllophilus amaurocephalus/poicilotis*, and *Tangara cyanoventris/desmaresti* are of uncertain relationship, mostly rather Andean.

#### Endemic without obvious relatives

Eighty-eight of 229 east-Brazilian regional species have no obvious relative. Some 24 represent endemic genera (plus *Augastes*, *Mackenziaena*, *Merulaxis*, *Tijuca*, and *Carpornis* above): *Triclaria*, *Macropsalis*, *Eleothreptus*, *Ramphodon* (Amazonian *Glaucis*?), *Melanotrochilus* (Amazonian *Florisuga*), *Leucochloris* (Andean *Schistes*?), *Stephanoxis* (Andean?), *Aphantochroa* (Andean *Haplophaidia*?), *Clytolaema* (Andean *Heliodoxa*?), *Baillonius* (*Andigena*), *Oreophylax* (Andean *Schizoeca*), *Hypoedaleus*, *Biatas*, *Rhopornis* (Amazonian *Pyriglena*?), *Psiloramphus*, *Calyptura*, *Ilicura*, *Muscipipra*, *Satrapa*, *Stephanophorus* (Andean *Anisognathus*?), *Orchesticus*, *Orthogonys* (Andean *Chlorothraupis*?), *Pyrrhocoma* (Andean *Thlypopsis*), and *Donacospiza* (Andean *Poospiza*).



Since *Augastes* seems Andean, *Tijuca* seems related to Amazonian *Lipaugus* and *Carpornis* to Andean *Pipreola* (Snow 1982), *Eleothreptus* is southern, and the rhinocryptids (related to *Psiloramphus* and *Merulaxis*) generally Andean, more endemic genera have Andean relatives than Amazonian. This may indicate an old Andean forest connection.

Among 61 local endemic species, 30 with possible Andean links (*Mergus octosetaceus*, *Amazona vinacea*, *Cypseloides fumigatus*, *C. senex*, *Picumnus nebulosus*, *Thripophaga macroura*, *Philydor amaurotis*, *Xenops contaminatus*, *Drymophila squamata*, *D. malura*, *D. ochropyga*, *D. genei*, *Myrmotherula unicolor*, *Phyllomyias fasciatus*, *P. griseocapillus*, *Hemitriccus nidipendulus*, *H. orbitatus*, *H. furcatus*, *Phylloscartes sylviolus*, *P. difficilis*, *P. eximius*, *P. paulistus*, *P. oustaleti*, *Turdus rufiventris*, *Tangara cyanocephala*, *Euphonia chalybea*, *Thraupis ornata*, *Pospiza lateralis*, *P. thoracica*, *Carduelis yarrelli*) about equal 31 with seemingly Amazonian links (*Laterallus leucopyrrhus*, *Pionopsitta pileata*, *Chaetura andrei*, *Phaethornis eurynome*, *P. idaliae*, *P. squalidus*, *Heliomaster squamosus*, *Trogon surrucura*, *Piculus aurulentus*, *Melanerpes flavifrons*, *Dryocopus galeatus*, *Campephilus robustus*, *Lepidocolaptes fuscus*, *Synallaxis cinerascens* (via "*Poecilurus*" *scutatus*), *Phacellodomus dendrocolaptoides*, *Philydor leucophrys*, *P. fuscus*, *Myrmotherula gularis*, *Dysithamnus xanthopterus*, *Formicivora erythronota*, *F. iberingi*, *Conopophaga melanops*, *C. lineata*, *Procnias nudicollis*, *Piprites pileatus*, *Neopelma aurifrons*, *Platyrinchus leucocoryphus*, *Attila phoenicurus*, *A. rufus*, *Sporophila frontalis*, and *Schistochlamys ruficapillus*). Some Andean birds may have crossed Amazonia via the Guiana highlands, however (see below).

Endemic subspecies in eastern Brazil

Subspeciation is frequent between the Andes and eastern Brazil — of 53 Andean/eastern species, all but *Bubulcus ibis*, *Accipiter striatus*, *Buteo leucorhous*, *Rallus nigricans*, *R. sanguinolentus*, *Asio flammeus*, *Aegolius harristii*, *Notiochelidon cyano-leuca* (subspeciation southward), *Euphonia musica*, and *Trichothraupis melanops* have subspeciated, or 43 of 53. Strong subspecies occur in *Strix hylophila*, *Turdus nigricaps*, and *Pospiza nigrorufa*. Subspeciation is less common for centrally crossing species, 126 of 318, and for northern species, 5 of 22. Subspeciation in the two

groups is not significantly different, but the two differ from the Andean group ( $\chi^2$ ). Only 7 of the 23 other southern birds, extending only to Argentina, have subspeciated; *Serpophaga subcristata* has a strong subspecies (*S. s. munda*) westward. Of birds that cross northward, only *Mitu mitu* has strong subspecies; centrally, *Micrastur ruficollis*, *Brotogeris versicolurus*, *Ciccaba virgata*, *Nyctibius leucopterus*, *Lucoicalis semitorquata*, *Chlorestes notatus*, *Baryphthengus ruficapillus*, *Bucco macrorhynchus*, *Colaptes melanochloros*, *Formicarius colma*, *Myiodynastes maculatus*, *Tityra cayana*, *Arremon taciturnus*, *Arremon flavivestris*, *Habia rubica*, and *Icterus cayanensis* come to mind.

Internal subspeciation within eastern Brazil has occurred in 70 of the 340 northerly and centrally crossing species, only 6 of 78 southerly crossing birds, and in barely 37 of the 229 endemic east-Brazilian species (113 cases in 647).

Subspeciation within eastern Brazil is common (17 cases) across the dry region of the lower São Francisco River and in southern Bahia (47 cases). Strong subspecies northward are in *Tinamus*, *Iodopleura pipra*, *Turdus albicollis*, *Automolus leucophthalmus*, and *Cissopis*; *Sittasomus*, *Contopus* and *Crypturellus noctivagus* are rather distinct in the south-Bahian break. A dry zone almost reaches the coast at Salvador, along the lower Paraguaçu River, and separates *Pyriglena atra* from *P. leucoptera* of the southeast (Willis & Oniki 1984). However, some subspecies seem to cross this gap and change in southern Bahia; details need study.

In some cases, the wet Serra do Mar of southeastern Brazil longitudinally separates coastal and interior subspecies or species of less wet forests: *Amazilia fimbriata nigricauda* inland and *A. f. tephrocephala* coastally in dune ("restinga") vegetation, *Thryothorus leucotis* inland and *T. longirostris* coastally, *Phylloscartes ventralis* and *P. sp. nov.* (Willis & Oniki, MS), etc. *Formicivora* antbirds have speciated (*F. erythronota*) and subspeciated (Gonzaga & Pacheco 1990) coastally in dry patches, Reptile, frog, and insect papers suggest many local barriers, dry zones in dunes or across to the coast for dry-woodland groups, wet zones coastwise for humid-zone groups.

In birds, subspeciation parallel to the coast is rather common, somewhat in the dry woodlands of the interior versus the wetter coastal

ones: 23 cases. An additional 9 cases separate subspecies of northwestern Bahia from coastal ones, but these might also be grouped with birds two paragraphs back. All resemble subspeciation across the open center of Brazil, but are displaced eastward. Strong forms occur in *Crypturellus noctivagus*, *Amazilia fimbriata* and *versicolor*, *Colaptes melanochloros*, *Dysithamnus mentalis*, *Tolmomyias sulphurescens*, *Contopus cinereus*, *Cnemotriccus fuscatus*, *Myiarchus swainsoni*, *Piranga flava*, and *Cyclarhis gujanensis*.

Minor subspeciation breaks occur in São Paulo (14 cases, including rather different forms in *Aramides cajanea* [D. Stotz, pers. comm.], *Otus atricapillus*, *Stephanoxis*, *Picummus cirratus*, *Xenops contaminatus* [J.M.C. Silva, pers. comm.], and *Lepidocolaptes squamatus*) in Espírito Santo (8 cases) and Rio de Janeiro (11; jointly, 19; different forms in *Myiozetetes cayanensis* but others weak). Only 3 cases are from Paraná and 3 from Santa Catarina.

## DISCUSSION

### Water and open-zone birds

Water birds are remarkably nonspeciose in southeastern Brazil, either because they fly everywhere or never developed large local populations due to relative lack of major freshwater habitats. Marsh birds have speciated somewhat more noticeably, at least some rails and icterines.

Open-area birds have speciated rather strongly in central to eastern Brazil. Although their zoogeography is somewhat outside the range of this report, some cases of speciation and subspeciation could have been caused by former forest links which are here suggested to transversely connect Amazonia or the Andes with eastern Brazil.

The north-central "Mangabeiras" link proposed here would have separated caatinga from cerrado birds, for instance. The possible "Mato Grosso de Goiás" link, Januária to south-central Andean link, and the northern Argentine link could have separated others. A rather similar situation is suggested for subspecies and species of coastal birds, where dry links perpendicular to the coast would separate wet-forest birds at the time of dry climatic cycles, while longitudinal montane wet forests would cut coastal dry-woodland birds off at the time of wet epochs. The

number of possible patterns, especially as suggested by plant and reptile or amphibian workers, is great.

Otherwise, open-zone species of birds show links with open areas in Argentina and the Andes, as well as to the Amazon open zones and llanos, more or less as proposed by various authors.

## Forest birds

### Amazonian links

The analysis of east-Brazilian forest birds suggests that a few species entered along the north coast, but that most Amazonian species crossed to or from the region off to the south, across what are called "central" links.

One likely place for the north-central link with Amazonia is via the northern and eastern edges of the central Brazilian uplands, notably via the dry-forested upper Tocantins and its branch, the Paranã River of eastern Goiás (Silva 1989). These dry forests almost meet northwestern Bahian ones (the "Mangabeiras bridge") across the north-south Serra Geral between Bahia and Tocantins. Connection across the north end of the Serra Geral, from the Chapada das Mangabeiras northwest in dry forests of southern Maranhão and northern Tocantins, is also possible. Contacts in slightly wetter climatic cycles, use of evergreen "grottoes" like ones we have seen near Brejo de Amparo ("Brejo Januária") in northern Minas Gerais, or even entry in the green summer followed by desperate wandering in the dry winter, could provide a link for such species as *Neomorphus geoffroyi* and others to reach Bahia but not Pernambuco. Birds could also have used the Januária bridge, across central Minas Gerais, from the Paranã River.

Southwestward, the former semievergreen forest on the uplands of western Goiás ("Mato Grosso de Goiás") could be another link. However, birds and plants of this region are often Atlantic forms, more of an extension of Andean forms northward than a pathway for Amazonian birds (Silva 1989). Still, some Amazonian birds like *Saltator maximus* do reach Brasília, along with Andean birds like *Euphonia musica* (J.C. Motta Jr., pers. comm.). Several Amazonian mammals seem to occur across the Mato Grosso, but no Amazonian bird species seem to have

crossed. The mammal distribution may be along the Januária/Paraná connection, of course.

The entry of Amazonian birds north-centrally, rather than on the coast, is further suggested by a few confirmed "Madeiran" subspecies. The possibility that eastern birds are more closely related to Madeiran or upper Amazonian subspecies or species than to birds from the lower Amazon should be kept in mind in future analyses.

#### Andean/Argentine links

There are many species and genera related to Andean forms, an idea emphasized by Miranda-Ribeiro (1906) and briefly reviewed by Sick (1985a). In most cases these birds occupy montane forests and limited alpine grasslands of eastern Brazil, even to the uplands of 1000–1600 meters in the Brasília region and others east of the São Francisco River in Minas Gerais and Bahia. A few reach the interior uplands of Alagoas and Pernambuco, where Teixeira *et al.* (1987 and elsewhere) have detected species of southern Brazilian birds only a few hundred meters above Amazonian lowland species.

Some Andean birds may have moved along a south-central route, along the evergreen forests of bases of the central Brazilian "chapadas" or tablelands. Migratory and nocturnal species could pass along this route even today, as there are large chapadas even west of the Guaporé River, on the Brazilian-Bolivian border, close to the serra dos Parecís and other western fingers of the Brazilian tablelands. However, there is little evidence of passage. A more likely route is via gallery forests of Paraguay and northern Argentina, direct from eastern forests near Asunción, in wetter climatic periods than today. M. Nores (1991 Ornithological Congress in Cidade del Este, Paraguay) noted that gallery forests west along the Pilcomayo and Bermejo rivers, to within 400 km of Andean woodlands, have forest birds even today. Other species may have crossed further south, through central Argentina.

Failure to realize the importance of Andean links southeastward may have led to some incorrect taxonomic decisions, as pointed out by Sick (1985a). For instance, southeastern *Pyrrhocoma ruficeps* is probably just another peri-Andean *Thlypopsis*, while *Carpornis* sp. of the southeast seem like Andean *Pipreola*.

#### Double links

In some cases, there may have been "ring" formation or double entry into (or exit from) eastern Brazil. The *Pteroglossus* of Fig. 2 are one likely case of central + north crossings, as are the two subspecies of *Cissopis leveriana* and of *Ramphastos vitellinus*. *Glaucidium hardyi* seems Amazonian, *G. minutissimum* Andean, *Dendrocincla turdina* calls more like Madeiran *D. fuliginosa atrirostris* than like other forms of *D. fuliginosa*, including *taunayi* of Alagoas. *Pyriglena leucopetra* females look rather like those of Madeiran *P. leuconota maura*, while *P. leuconota pernambucensis* is definitely northern. On the other hand, *Sporophila nigricollis/caerulescens* show the uncertainties of this type of analysis, for the latter is more likely an invader of Bolivia than the reverse; the center of the ring seems in eastern Brazil, with hybrid "*S. ardeola*" as the link. Ring forms can be species generators, since any break in the ring center causes separation of populations.

#### Guianan links

In a few cases, eastern Brazil and the northern Andes have similar birds; a more different bird may live between, on the central Andes: *Platycichla flavipes* (*leucops* centrally), *Cichlopsis leucogenys* (Andean subspecies different), *Basileuterus flaveolus* (*signatus* in the Andes). These may be cases of "leapfrog speciation", but could be cases where the species crossed directly from the Guianas to southeastern Brazil, perhaps via mountains like the serra dos Carajás in southern Pará or via dry forests at the Amazon mouth (Snethlage 1928). The latter author suggested crossing for *Procnias averano* and *Basileuterus culicivorus*, this last being another form with very different subspecies along the Andes.

Taxon cycles and Andean-Amazonian dominance  
It seems possible that eastern Brazilian forests are like an island, being repeatedly invaded by species that enter from Amazonia or from the Andes in what could be considered "taxon cycles". Haffer (1967a,b) has suggested that Amazonian forms are constantly moving into northwestern Colombia and Central America, taking the place of birds already present, in more or less the sort of taxon cycle proposed here. If so, the Amazon and Andes could be constantly "exporting species",

which would either have some competitive advantage over peripheral species or would take over at climatically unfavorable periods.

It may be that Haffer and I have overlooked possible reverse cases, due to our "extra-Amazonian" points of view. One could argue that *Pteroglossus aracari* (Fig. 2) started in the east and invaded the Amazon, for instance. I found few other likely cases northward, but there seem several possible cases southward: *Sporophila caerulea*, *Trichothraupis melanops*, *Phibalura flavirostris*, and *Batara cinerea* may have invaded the Andes rather than the reverse.

In any such hypothesis, of course, high-altitude and open-country forms would invade from their own centers of distribution. Fjeldsá (1985) suggests that Patagonian forms invaded the Andes during cool periods after warm epochs eliminated local forms. Haffer (1974) and others have suggested that central Brazil furnishes species for the llanos northward, where areas of habitat are smaller and extinctions more likely. Old-World families invading South America when the Panama isthmus arose in the late Pliocene were moving from their own rich faunas, which collectively overshadow the Amazonian and Andean centers.

An alternative would be that central regions receive a few successful new forms from each of several side regions (such as eastern Brazil), plus locally evolved forms, and that each side region then receives more than it gives.

## ACKNOWLEDGEMENTS

I appreciate a fellowship from the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) and Deutsche Akademische Austauschdienst (DAAD) for preparation of the manuscript at the Museum Alexander Koenig at Bonn, Germany in 1990. I especially thank Karl-L. Schuchmann for help at the Museum, J. Haffer for suggestions on the manuscript and letting me use his range maps, and J.M. C. Silva for unpublished material based on his studies in central Brazil. Aerial study of the Brasília-Araguaiana axis was incidentally provided by the Museu Paraense "Emílio Goeldi" to attend the I Congresso Brasileiro de Ornitologia in Belém.

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APPENDIX 1. Widespread vernal and marsh birds in E Brazil. Explanation of letters and asterisk see text.

<i>Tachybaptus dominicus</i>	<i>Jabiru mycteria</i>	<i>Oxyura dominica</i>
<i>Podilymbus podiceps</i>	<i>Plegadis chihi</i> S	<i>Neochen jubata</i>
<i>Podiceps rolland</i> S	<i>Platalea ajaja</i>	<i>Chauna torquata</i> S
<i>Phalacrocorax brasilianus</i>	<i>Rostrhamus sociabilis</i>	<i>Gallinula chloropus</i> S
<i>Anhinga anhinga</i>	<i>Buteogallus urubitinga</i>	<i>Fulica rufifrons</i> S
<i>Pilberodius pileatus</i>	<i>Busarellus nigricollis</i>	<i>Fulica armillata</i> S
<i>Ardea cocoi</i>	<i>Dendrocygna bicolor</i> S	<i>Fulica leucoptera</i> S
<i>Florida caerulea</i>	<i>Dendrocygna viduata</i>	<i>Vanellus cayanus</i>
<i>Egretta alba</i>	<i>Dendrocygna autumnalis</i>	<i>Charadrius collaris</i>
<i>Egretta thula</i>	<i>Coscoroba coscoroba</i> S	<i>Himantopus himantopus</i> *
<i>Butorides striatus</i>	<i>Cygnus melancoryphus</i> S	<i>Sterna simplex</i>
<i>Nycticorax nycticorax</i>	<i>Cairina moschata</i>	<i>Sterna supercilii</i>
<i>Cochlearius cochlearius</i>	<i>Sarkidiornis melanotos</i>	<i>Rynchops niger</i> *
<i>Tigrisoma lineatum</i>	<i>Amazonetta brasiliensis</i>	<i>Ceryle torquata</i>
<i>Ixobrychus involucris</i>	<i>Anas bahamensis</i>	<i>Chloroceryle amazona</i>
<i>Ixobrychus exilis</i>	<i>Anas versicolor</i> S	<i>Chloroceryle americana</i> I
<i>Botaurus pinnatus</i>	<i>Anas georgica</i> S	<i>Chloroceryle inda</i>
<i>Mycteria americana</i>	<i>Netta erythrophthalma</i>	<i>Chloroceryle aenea</i>
<i>Ciconia maguari</i>	<i>Netta peposaca</i> S	<i>Atticora melanoleuca</i>

APPENDIX 2. Open-zone birds of eastern Brazil. Explanation of letters and asterisk see text.

<i>Rhea americana</i> *GIS	<i>Caracara plancus</i> GS	<i>Columbina minuta</i> N
<i>Nothura bonaquira</i> GS	<i>Milvago chimachima</i> G	<i>Uropelia campestris</i>
<i>Nothura minor</i>	<i>Falco sparverius</i> GIS	<i>Anodorhynchus hyacinthinus</i> F
<i>Nothura maculosa</i> *I	<i>Falco femoralis</i> S	<i>Anodorhynchus leari</i>
<i>Taoniscus nanus</i> GS	<i>Penelope ochrogaster</i> F	<i>Anodorhynchus glaucus</i>
<i>Rhynchotus rufescens</i> *GIS	<i>Penelope jacucaca</i>	<i>Cyanopsitta spixi</i> F
<i>Syrigma sibilatrix</i> GS	<i>Crax fasciolata</i> FI	<i>Ara nobilis</i> FIN
<i>Phimosus infuscatus</i> *GS	<i>Aramides ypecaba</i> FN	<i>Phacellodomus ruber</i> F
<i>Theristicus caudatus</i> G	<i>Laterallus xenopterus</i> FN	<i>Phacellodomus rufifrons</i> *F
<i>Cathartes burrovianus</i> F	<i>Micropterygia schomburgkii</i> F	<i>Aratinga cactorum</i> F
<i>Gampsonyx swainsoni</i> G	<i>Cariama cristata</i> GS	<i>Aratinga aurea</i> N
<i>Elanus caeruleus</i>	<i>Vanellus chilensis</i> F	<i>Aratinga acuticaudata</i> IN
<i>Circus buffoni</i> S	<i>Gallinago undulata</i>	<i>Pyrrhura pfrimeri</i> FN
<i>Buteogallus meridionalis</i> FN	<i>Columba picazuro</i> FI	<i>Amazona xanthops</i> FN
<i>Parabuteo unicinctus</i> GS	<i>Zenaida auriculata</i> I	<i>Guira guira</i> GS
<i>Buteo albicaudatus</i> F	<i>Columbina cyanopsis</i>	<i>Bubo virginianus</i> GIS
<i>Harpyhaliaetus coronatus</i> G	<i>Columbina picui</i> IS	<i>Athene cunicularia</i> GS

*Chordeiles pusillus* FIN  
*Caprimulgus candicans* F  
*Caprimulgus maculicaudus* N  
*Caprimulgus hirundinaceus* N  
*Podager nacunda* GS  
*Hydropsalis brasiliiana* FI  
*Tachyornis squamata* FN  
*Phaethornis gounellei* F  
*Polytmus guainumbi* F  
*Colibri serrirostris* G  
*Eupetomena macroura* FIN  
*Lophornis magnifica* F  
*Heliactin cornuta* F  
*Heliomaster furcifer* F  
*Hylocharis chrysura* F  
*Bucco maculatus* \*FI  
*Bucco chacuru*  
*Ramphastos toco* FN  
*Picumnus limae* FIN  
*Picumnus pygmaeus*  
*Colaptes campestris* \*GI  
*Picooides mixtus* \*GI  
*Melanerpes candidus* G  
*Xiphocolaptes falcirostris* F  
*Lepidocolaptes angustirostris* \*FIN  
*Geositta poeciloptera* G  
*Furnarius leucopus* G  
*Furnarius figulus*  
*Synallaxis phryganophila* GIS  
*Synallaxis scutata* \*  
*Synallaxis hellmayri*  
*Synallaxis frontalis* \*  
*Xenopsaris albinucha* F  
*Phaeoprogne tapera* F  
*Alopecelidon fucata* FN  
*Pseudoseisura cristata* GI  
*Philydor dimidiatus* FIN  
*Automolus rectirostris* G  
*Megaxenops parnaguae*

*Thamnophilus torquatus* G  
*Sakesphorus cristatus* FN  
*Formicivora rufa* FI  
*Formicivora melanogaster* I  
*Herpilochmus pileatus*  
*Herpilochmus longirostris*  
*Herpilochmus pectoralis*  
*Myrmorchilus strigilatus* FIN  
*Melanopareia torquata* GI  
*Antilophia galeata* FN  
*Polystictus pectoralis* G  
*Culicivora caudacuta* GS  
*Phyllomyias reiseri* F  
*Phylloscartes roquettei* G  
*Elaenia cristata* FN  
*Elaenia chiriquensis* N  
*Sublegatus modestus* \*F  
*Stigmatura budytoides* \*F  
*Stigmatura napensis*  
*Suiriri affinis* GI  
*Fluvicola nengeta* F  
*Euscarthmus rufomarginatus*  
*Euscarthmus meloryphus* G  
*Xolmis velata* GS  
*Xolmis cinerea* I  
*Xolmis irupero* IS  
*Knipolegus lophotes* GS  
*Knipolegus franciscanus* S  
*Alectrurus tricolor* G  
*Gubernetes yetapa* GS  
*Casiornis fusca* F  
*Casiornis rufa*  
*Machetornis rixosus* G  
*Neopelma pallescens* F  
*Empidonomus varius* FI  
*E. aurantioatrocristatus* I  
*Tyrannus albogularis* F  
*Tyrannus savana* N

*Cyanocorax cristatellus*  
*Cyanocorax cyanopogon*  
*Mimus saturninus* \*GIS  
*Anthus nattereri* G  
*Poliophtila dumicola* G  
*Basileuterus leucophris* G  
*Neothraupis fasciata*  
*Cypsnagra hirundinacea* I  
*Compsothraupis loricata* GS  
*Schistochlamys melanopsis* \*  
*Paroaria dominicana* F  
*Charitospiza eucosma*  
*Coryphospingus cucullatus* \*  
*Coryphospingus pileatus*  
*Saltator atricollis*  
*Saltator caerulescens* FI  
*Sicalis citrina* GS  
*Sicalis columbiana* N  
*Sicalis luteola* S  
*Sporophila bouvreuil* FI  
*Sporophila hypoxantha*  
*Sporophila ruficollis*  
*Sporophila palustris*  
*Sporophila melanogaster*  
*Sporophila cinnamomea*  
*Sporophila plumbea*  
*Sporophila albogularis* S  
*Poopyrispiza caerulescens* S  
*Poospiza cinerea* G  
*Coryphaspiza melanotis*  
*Ammodramus humeralis* GI  
*Emberizoides herbicola* G  
*Curaeus forbesi*  
*Gnorimopsar chopi* I  
*Molothrus badius* GIS  
*Molothrus rufoaxillaris* S  
*Pseudoleistes guirahuro* G  
*Pseudoleistes virescens*

### APPENDIX 3. Andean-Argentine birds in east Brazil. Explanation of letters and asterisk see text.

*Bubulcus ibis* A  
*Tigrisoma fasciatum* \*A  
*Accipiter striatus* A  
*Geranoaetus melanoleucus* \*  
*Buteo leucorhous* A  
*Milvago chimango* G  
*Penelope obscura* \*AI  
*Rallus nigricans* A  
*Rallus sanguinolentus* A  
*Porphyriops melanops* \*A  
*Nycticyphes semicollaris*  
*Myiopsitta monachus* \*G  
*Pionus maximiliani* \*  
*Strix hylophila* \*A  
*Asio flammeus* AG

*Aegolius harristii* A  
*Glaucidium minutissimum* \*A  
*Nyctibius aethereus* \*A  
*Caprimulgus longirostris* \*A  
*Amazilia lactea* \*A  
*Picumnus cirratus* \*AI  
*Geositta cunicularia* \*AG  
*Phleocryptes melanops* \*A  
*Phacelodomus striaticollis* \*AG  
*Furnarius rufus* \*I  
*Anumbius anumbi*  
*Certhiaxis sulphurifera* G  
*Spartanoica maluroides* G  
*Limnornis rectirostris* G  
*Limnornis curvirostris* G

*Lochmias nematura* \*A  
*Philydor rufosuperciliatus* \*AI  
*Dysithamnus plumbeus* \*A  
*Thamnophilus ruficapillus* \*A  
*Batara cinerea* \*A  
*Chamaeza campanisona* \*A  
*Chamaeza* sp. \*A  
*Laniusoma elegans* \*A  
*Phibalura flavirostris* \*A  
*Pyroderus scutatus* \*A  
*Xolmis dominicana* \*  
*Knipolegus cyanirostris* \*  
*Serpophaga subcristata* \*  
*Serpophaga nigricans*  
*Phylloscartes ventralis* \*

*Phyllomyias burmeisteri* \*A  
*Elaenia obscura* \*A  
*Tachuris rubrogastra* \*A  
*Pseudocolopteryx sclateri*  
*Todirostrum plumbeiceps* \*AI  
*Pyrocephalus rubinus* \*AG  
*Ramphotrigon megacephala* \*A  
*Tachycineta leucorrhoa*  
*Notiochelidon cyanoleuca* A  
*Cistothorus platensis* \*A  
*Cichlopsis leucogenys* \*A  
*Platycichla flavipes* \*A

*Turdus nigriceps* \*A  
*Anthus bellmayri* \*A  
*Anthus furcatus* \*AG  
*Anthus correndera* \*G  
*Basileuterus leucoblepharus*  
*Euphonia musica* A  
*Chlorophonia cyanea* \*A  
*Pipraeidea melanonota* \*A  
*Thraupis bonariensis* \*A  
*Trichothraupis melanops* A  
*Saltator aurantiirostris* \*AG

*Paroaria coronata* G  
*Passerina glaucocerulea*  
*Embernagra platensis*  
*Poospiza nigrorufa* \*AG  
*Poospiza melanoleuca* G  
*Sporophila caerulea* \*A  
*Zonotrichia capensis* \*AI  
*Xanthopsar flavus* G  
*Agelaius thilius* \*AG  
*Amblycercus holosericeus* G  
*Carduelis magellanica* \*A