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Can Avian Distribution Patterns in Northern Argentina be Related to Gallery-forest Expansion-Retraction Caused by Quaternary Climatic Changes?

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Nores (1992) presented an analysis of two bird distribution patterns in subtropical South America. The first is comprised of disjunct distribution of pairs of species and subspecies between the southern Yungas and the Paranaense forests, which are separated by 700 km of xerophytic Chaco vegetation. The second is a supposed zone of secondary contact located in the central Chaco, where some "nonforest" species and subspecies interact.

Nores proposed that both patterns were produced by vegetational changes in the central Chaco associated with the well-supported global climate changes during the Quaternary. He suggested that, when this region was more humid than today (possibly during interglacial periods), forests advanced from the Yungas and the Paranaense regions along the Pilcomayo and Bermejo rivers, forming a wide and continuous forest bridge. Forest birds from both regions presumably expanded their distributions during this epoch, whereas the ranges of nonforest birds were interrupted by this same ecological barrier. The opposite occurred when the forest bridge was fragmented during the following drier period. As the forest and nonforest species sharing the same distribution pattern show different "speciation" levels, Nores proposed that these vegetational shifts occurred several times in the recent past.

There are, however, several fundamental problems with the analysis of Nores that cause me to question the validity of his conclusions. These problems can be grouped in the following major topics: (a) problems with habitat classification; (b) the authenticity of a secondary contact zone in the central Chaco; (c) questionable assumptions; (d) lack of paleoecological support.

Habitat classification.—The first problem with Nores' analysis is the lack of a precise definition for forest and nonforest birds. This is an important point because his hypothesis can be considered as an appli-

cation of the refuge model (for review, see Lynch 1988) to a specific point in the subtropical region of South America. Therefore, it must require that the taxa involved present distributional concordance as well as rigid ecological fidelity (Vanzolini 1981, Lynch 1988). This problem is even bigger in Chaco, which comprises several different types of forests and woodlands (see Ramella and Spichiger 1989). Since Nores did not make a clear distinction between the different types of forests in the Chaco region, I assume that his "forest" within the Chaco region means only "tall humid gallery forest."

It is implicit in Nores' hypothesis that the present-day Chaco vegetation represents a major barrier to the dispersion of his forest birds. If this is correct, one would expect to find forest birds in this region only in gallery forests along the rivers. Nores convincingly showed that this is the case for many of his forest species (see Nores 1992:fig. 3).

However, he included in his list of forest birds some species that did not fit entirely this situation. *Nystalus chacuru* is a savanna species (Sick 1985, Silva 1992, Davis 1993). Some species are absent from the Argentine Chaco, but occur throughout Paraguayan and/or Bolivian Chaco and, thus, would not require belts of humid forests along the Pilcomayo and Bermejo rivers to reach the Yungas forests. This category of birds includes *Pionus maximiliani* (Smith 1960, Short 1975), *Piaya cayana* (Short 1975), *Veniliornis passerinus* (Short 1975, 1982), *Xenops rutilans* (Vaurie 1980), *Cyanocorax cyanomelas* (Short 1975), *Basileuterus culicivorus* (Short 1975, Ridgely and Tudor 1989, Davis 1993), and *Hemithraupis guira* (Short 1975, Isler and Isler 1987).

Other species (*Philydor rufus* and *Pipraeidea melano-nota*) avoid the Chaco region, but are distributed almost continuously from the Yungas forests to the Paranaense forests throughout central Brazil and southern Bolivia. In fact, this distribution pattern is shown so clearly in different groups of birds that

Remsen et al. (1991) recently named it as Circum-Amazonian.

Therefore, some disjunctions pointed out by Nores exist only in his rather limited study area in Argentina, but were not evident when the Chaco region and Yungas forests were studied as a whole. Besides, one of his disjunct species does not occur in the Paranaense region at all (*Dendrocolaptes picumnus*; see Short 1975, Pinto 1978). In another case (*Picumnus cirratus*), the two subspecies (*thamnophiloides* and *temmincki*), pointed out by Nores as disjunct, are separated by another subspecies inhabiting the Chaco region (*pilcomayensis*). Short (1982) has acknowledged that this latter species needs revision, but Nores did not present any evidence to modify this taxonomic arrangement. In fact, he included Short (1982) as one of his basic taxonomic references (Nores 1992:table 1). The remaining 30 species appear to represent genuine disjunctions between the Yungas and Paranaense regions.

Similar critical remarks apply to Nores' nonforest birds. If the secondary contact zones between them are a result of expansion and retraction of the gallery forests along the Pilcomayo and Bermejo rivers, one could expect that this type of habitat would still be an important barrier to these nonforest species today.

Nores used 10 nonforest species to support his hypothesis. However, as he noted, some of these (e.g. *Thamnophilus caerulescens* and *Phacellodomus rufifrons*) also inhabit certain forest habitats. This information is supported by my personal experience with these species in the Cerrado and Caatinga. These morphoclimatic domains form, with the Chaco, the "open vegetation diagonal" instead of the "arid diagonal" as incorrectly quoted by Nores (1992; for exact definition, see Ab'Saber 1977). The Cerrado is not an "arid" region.

Thamnophilus caerulescens is mainly found in gallery or other types of evergreen and semideciduous forests (the same pattern was also found in southern Bolivia [J. Fjeldså pers. comm.] and in the Paranaense forests [F. C. Straube in litt.]), while *P. rufifrons* is found primarily in semideciduous and deciduous forests, but also in gallery forests. Two more of Nores' nonforest species should be able to live in forest habitats. For *Campylorhamphus trochilirostris*, one of the subspecies listed by Nores (1992) (*lafresnayanus*) inhabits gallery and dry forests in southeastern Mato Grosso (pers. obs.). Also, *Pseudoseisura cristata* inhabits both Caatinga woodland and high deciduous forest in northeastern Brazil. This latter species is able to cross wide tracts of gallery forests, through the canopy, without problems (pers. obs.). I think that these four species cannot be used as evidence for Nores' hypothesis, since their ranges would not necessarily be interrupted by a continuous gallery forest along the Pilcomayo and Bermejo rivers. The remaining six species can be regarded as nonforest (open vegetation) species.

In short, at least some species do not fit the habitat

classification employed by Nores, thus violating one important assumption of his hypothesis. However, I regard this as only a minor problem. If one excludes the problematic species from the analysis, both distribution patterns discussed by Nores appear to be supported by other taxa.

Secondary contact zones for birds in central Chaco.—Nores (1992) indicated that the region of the Pilcomayo river should be considered as a secondary contact zone for his nonforest birds. This proposal contrasts with that of Short (1975), who suggested that this region should be considered mainly as a zone of primary intergradation (Short 1975:fig. 82) rather than as a secondary contact zone (Short 1975:fig. 81). It has been suggested that without detailed knowledge of the evolutionary histories of populations involved it is difficult, if not impossible, to decide whether these zones are results of primary or secondary contact (Ender 1977, 1982, Barton and Hewitt 1985). However, some suggestions for explicit tests have been proposed (e.g. Thorpe 1984, 1987). Since Nores' hypothesis is more recent, he should have presented much more evidence to support it as well as falsify Short's hypothesis (e.g. by using more accurate maps to show the distribution of the different populations in the area [e.g. see Haffer 1974, Ford 1986] or by analyzing the geographical variation of some species [e.g. Haffer and Fitzpatrick 1985]). Instead, he used 10 rough maps, 8 of which were based on maps published by Short (1975), and did not present new detailed information. Consequently, we have two hypotheses, little detailed information available, and no critical tests.

When Nores (1992:354) proposed that "The distribution patterns of nonforest birds . . . also are consistent with the former existence of a forest belt along the Bermejo and Pilcomayo rivers," he implicitly assumed that the present-day location of this contact zone is in the same position as the barrier that separated the populations in the past. This likely is a false assumption because there is no evidence that the courses of the Bermejo and Pilcomayo rivers have always been the same as today (see below). Thus, I suggest that only with more detailed data and robust tests would it be possible to evaluate the Nores' hypothesis that there is a secondary contact zone for nonforest birds in the central Chaco.

Questionable assumptions.—Since the reality of secondary contact zones still needs better support than that offered by Nores, only one genuine pattern of bird distribution is suitable for biogeographical interpretation in Nores' study area: the disjunct distribution of the 30 taxa of humid forest birds between the Yungas and Paranaense forest regions. Nores proposed that the Yungas and Paranaense forests were connected many times in the past due to expansion of gallery forests, thus allowing the dispersion of the forest bird species.

To interpret the different speciation levels shown by these taxa, Nores (1992:353–354) argued: "species

that crossed during the last connection would not yet have had time to differentiate. Another group of species that show differences at subspecies level presumably crossed during an earlier connection. . . . A third group could have crossed even earlier and differentiated to megasubspecies level. Finally, pairs of allopatric species probably represent differentiation that began very early. . . ."

In this quite simple hypothesis, there are three basic assumptions. The first is that the time between two cycles of humid-gallery-forest expansion was sufficient to permit the development of reproductive isolation and competitive superiority so that upon a new meeting, the different populations would serve as self barriers to the expansion of the other. This assumption is necessary to ensure that the two other possible results of the contraction-expansion of populations (i.e. fusion or sympatry) would not take place. The second assumption is that the amount of differentiation is proportional to the duration of the disjunction and, consequently, that the rate of change is equal for all characters and taxa (see discussion about this subject in Cracraft 1985). The third assumption is that different taxa showing this distribution pattern have different propensities for dispersal, since once the connection existed some species allegedly dispersed while others waited for another opportunity.

While it is possible to find some evidence for the first assumption, the second and third have no empirical or theoretical justification. Thus, Nores' argumentation can be regarded as insufficient. Besides these logical flaws, Nores' hypothesis is also a two-taxon statement and, as such, it is not particularly informative either from the standpoint of systematics or biogeography (Cracraft 1985).

Paleoecological background.—Nores' hypothesis rests on two main paleoecological assumptions: (a) that the courses of the Bermejo and Pilcomayo were constant during all of the Quaternary; (b) that the gallery forests along these rivers were stable (at least during the interglacial periods) and, thus, could function as faunistic corridors between the Yungas and Paranaense forests.

There is good evidence that the river drainage in the Chaco region was completely different from the present one (see review in Ramella and Spichiger 1989). In the case of the Pilcomayo River, it only reached its present-day course after the deposition of sediments from the Andes in the western Chaco region. This event has to be recent, but as Sennhauser (1991) commented: "These rivers (including the Pilcomayo and Bermejo rivers) have not yet reached their equilibrium profile, and consequently the fluvio-dynamic processes are still at work."

If one assumes that all events proposed by Nores took place after these rivers have reached their present-day courses, there still are difficulties. Sennhauser (1991) has pointed out that, currently, the persistence of humid gallery forests along the Pilcomayo and

Bermejo rivers is closely connected with the stability of the river course. However, the current drainages of these rivers are so unstable that according to Adamoli et al. (1990): "a river may abandon its present course and start to flow an ancient bed, all within a period measured in days."

Because of these remarkable dynamics, there are intense changes in composition and structure of gallery forests that can go forwards and backwards, in terms of centuries, from the xerophytic forests with Chaco elements to humid forests with the composition dominated by foreign elements (Sennhauser 1991). It follows that the humid gallery forests in the Chaco region can be considered as too unstable, at least in the time scale required by Nores' hypothesis, to function as biogeographical corridors such as those currently found in the Cerrado region (Redford and Fonseca 1986).

In fact, this conjecture is well supported by the comparison between gallery forests of these two regions made by Adamoli et al. (1990): "Gallery forests in the Chaco region grow mainly on river levee-banks, that is, on top of a positive relief structure with respect to the surrounding flat land. . . . In the Cerrados region, in contrast, gallery forests grow at bottom-of-the valley position, benefiting from the additional water supplied by the higher water table. . . . Consequently, Cerrados and all gallery forests growing at the bottom of valleys are more stable in time than those growing on elevated river levee-banks."

Under these conditions, it is expected that a system of wide and continuous gallery forests such as that proposed by Nores would be almost inconceivable, even in more humid conditions. In fact, if during an interglacial period (such as the one we are now in) the Chaco region was more humid than it is today (because of its poor-drainage system and flat topography), there would be a trend to great and perhaps disastrous floods of rivers. These floods would be even more severe if we also consider the melting of the Andean glaciers and raising of sea level. Thus, the region could be somewhat like a hyperseasonal savanna, dominated by grasses, palms and perhaps with mosaics of unstable patches of humid and dry gallery forests in some points of rivers. Ramella and Spichiger (1989) suggested that such an environment, found currently only in the wet Chaco region, is a relict of a more widespread situation.

Nores also suggested that the presence of relict forest patches in dry riverbeds and the upper parts of the channels of the Bermejo and Pilcomayo rivers could support his hypothesis, since such forest patches would suggest the ancient extension of the humid gallery forests. I examined the list of plant species presented by him and found that many species listed occur also in different types of dry forests (for lists, see Ratter et al. 1978, 1989, Ramella and Spichiger 1989). These still poorly known forests are currently distributed as islands of variable size in northeastern

and central Brazil (Ratter et al. 1978), Bolivia (Davis 1993) and Paraguay (Ramella and Spichiger 1989). There is good evidence that they were more widely distributed in the past, but only during the dry periods of the Quaternary (Ab'Saber 1988) or Late Tertiary (Rizzini 1979, Ratter et al. 1989). Besides, for the dry river beds sampled by Nores to be interpreted as evidence of once-continuous gallery forest, it also would be necessary to suppose that they have approximately the same age. Considering the extraordinary dynamics of these rivers, I think this would be improbable.

In conclusion, I suggest that Nores' article exemplifies how a biogeographical analysis can be biased when researchers attempt to fit limited data into a crude refuge model. In order to fit the model, one must accept or create many unnecessary and sometimes questionable assumptions. Such an approach has been strongly criticized even by proponents of the refuge model (e.g. Vanzolini 1981, Whitmore and Prance 1987). In the specific example of Nores' analysis, the author ignored the dynamic geological history of his study area (Baez and Yané 1979, Ramella and Spichiger 1989, Ojeda and Mares 1989, Shapiro 1991, Taylor 1991). Thus, he did not consider the importance of other events (e.g. Plio-Pleistocene tectonism, flooding associated with changes in sea level) that might explain the observed pattern as (or more) parsimoniously than interpretations based on the refuge paradigm.

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Quaternary Vegetational Changes and Bird Differentiation in Subtropical South America

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In a recent paper (Nores 1992), I have concluded that the distribution of forest and nonforest birds in subtropical South America was the result of forest expansion along the Bermejo and Pilcomayo rivers that connected the southern Yungas to the Paranense region and interrupted the arid vegetation in the center of the Chaco. Silva (1994) questions practically all the points that I have discussed in that paper.

His first statement with which I do not agree is that my hypothesis can be considered as an application of the refuge model. The refuge model is related to forest retraction during arid periods and their expansion while humid conditions (like the present) prevailed. Arid periods have reduced forests to isolated blocks of various sizes that served as refugia for the fauna and flora (Haffer 1969, 1974, Vanzolini and Williams 1970, Prance 1974, Simpson and Haffer 1978, Mayr and O'Hara 1986).

My hypothesis is related to forest expansion during periods of higher than contemporary humidity and their subsequent shrinkage during periods when the climate was similar to the present. During the moister periods currently disjunct forests such as the Amazon/Atlantic regions, and the southern Yungas/Paranense regions, may have been connected. Many forest animals presumably expanded their ranges to form a continuous distribution and were separated into two populations during periods like the present. Concurrently, continuous nonforest habitats such as the Chaco-Cerrado-Caatinga diagonal would have been interrupted by forest belts of different size. Many nonforest animal ranges were presumably interrupted and the resulting differentiated populations came in contact when the forest belt disappeared (Nores 1989, 1992; see also Vanzolini 1968, 1974, 1981, Fitzpatrick 1980, Haffer 1985, Nores and Cerana 1990).