# PATTERNS IN THREE FAMILIES OF NEOTROPICAL FORETS BIRDS: A TEST OF THE PLEISTOCENE REFUGIA MODEL*

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RESUMEN: Datos recientes sobre distribución de aves en manchas remanentes de selva en el Estado de São Paulo, Brasil (Willis, 1979), dan la oportunidad de extender a las mismas una prueba de la teoría que explica la diversificación de la biota neotropical por medio de refugios recientemente propuesta por Oren, 1981a, 1981b. El modelo predice que, a mayor superficie mínima de selva que requiere un taxón determinado, menor sería el número de refugios de selva donde el taxón podría haber sobrevivido durante el Pleistoceno. Estos deberían reflejarse hoy día en el número y distribución del taxón en cuestión. Este trabajo se refiere a las familias Dendrocolaptidae, Furnariidae y Formicariidae. En todos los casos el patrón actual resulta el predicho por el modelo. Esto refuerza el cúmulo de evidencias que indica que la selva neotropical estuvo fragmentada durante los picos glaciales del Pleistoceno.

The classic view of the tropical rain forest as a stable, unchanging environment over the eons was decisively challenged by Moreau, 1963, 1966, who used zoogeographic and geological evidence to show that the rain forests of Africa had undergone dramatic fluctuations in extent during the Pleistocene. Haffer, 1969, 1974, convincingly extended Moreau's hypothesis to South America, using the distributions of rain forest birds as his principal evidence. Corroborating data to support this theory have been presented for butterflies (Brown, 1977, 1979), arborescent plants (Prance, 1973,1981), and lizards (Vanzolini and Williams, 1970). According to the theory, which is known as the "Pleistocene refugia theory of Neotropical diversification," the geographical distributions of forest and nonforest taxa in South América were dramatically influenced by the retreat of the forest into "refugia" during dry periods of the Pleistocene, which correspond to glacial maxima in high latitudes. Dry adapted vegetations presumably expanded when the forest withdrew. There is a small but growing body of palynological evidence which appears to support the theory (Absy, 1981, Hammer, 1981). But at the same time there are strong critics of the theory (Benson, 1981, Endler, 1981). Several gobernments, particularly Brazil's, have used the theory to locate priority areas for conservation units (Wetterberg *et al.*, 1976), and it is critical to develop unbiased tests of the theory's validity.

Two data bases are used in the identification of putative refugia: 1) centers of endemism, and 2) centers of stable characters, with associated secondary contact zones between these centers. Both sets of data are used to demonstrate that there exist regions which have apparently been stable for long periods of time, in contrast to surrounding areas which show evidence of fluctuations.

Oren, 1981a, 1981b, formed a hypothesis regarding numbers and distributions of forest taxa using the notion of minimum area requirements to make a preliminary test of the refugia theory. The present work briefly reviews minimum area relations, outlines the

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hypothesis, and then extends the test to several genera of Dendrocolaptidae, Furnariidae, and Formicariidae based on data developed by Willis, 1979, in São Paulo State, Brazil.

## THE HYPOTHESIS

As pointed out by Haffer, 1981, and Williams, 1977, there are three possible outcomes for populations in refugia: 1) extinction; 2) isolation without differentiation; and 3) isolation with differentiation. If the forest enclaves existed in the Pleistocene, they would be expected to differ greatly in size, depending on local soil conditions, hydrology cycles, and water table relations. Some would be relatively mesic pockets of a few hectares in otherwise dry districts, others would be entire regions. One would expect different bird species to have been present in enclaves of different sizes depending on "minimun area requirements" of the taxa; that is, the area necessary for that taxon to survive through time (Diamond, 1978, Lovejoy and Oren, 1981). Based on work in Amazonian habitat patches (Oren, 1981b), the following patterns may be predicted for enclaves of different sizes. In small forest patches during the Pleistocene one would expect general extinction of forest specialist species, with the enclave inhabited exclusively by habitat generalists also found in the surrounding matrix of open vegetation. Such small forest patches could not have acted as refugia for forest birds. Medium-sized enclaves would be biased in favor of relatively dispersive species which move between forest patches. Given this gene flow, these species would not be expected to differentiate, except when the suitable forest patches were very widely separated geographically or by barriers such as rivers. In large forest enclaves many forest requiring habitat specialists would be maintained, including poor dispersers which do not cross light gaps. Such timidity toward light gaps is found in a large proportion of tropical forest bird species, especially those of the understory (Diamond, 1975, Sick 1967, Willis, 1974). This behavior reduces the chance of gene flow between patches, enhancing the probability of differentiation. Thus, only relatively large enclaves of forest could have served as effective centers of differentiation for birds, as the minimum critical area for the class of birds most likely to differentiate is relatively large. Given the technique used by Haffer, 1978, in locating putative refugia for birds, which is identifying centers of endemism and dispersal, only the largest of forest enclaves would be identified as effective avian refugia. This is not to say that small enclaves preserved no bird species, but simply that these enclaves, by virtue of being unlikely sites of differentiation, would not be identified as "refugia."

I should stress that the enclave size classes are defined by a given taxon's response to patch size. A soil mite's "large" enclave is probably a birds's "small". Two factors determine the response: dispersability and minimum area requirements. These factors are not independent, as highly dispersive species are generally found in smaller habitat patches than relatively sedentary species (Diamond, 1975, Brown and Kodric-Brown, 1977), and therefore have correspondingly low minimum area requirements.

Within relatively sedentary forest birds there is expected to be a range of mimimum area requirements, depending on diverse factors such as territory size, social organization, fluctuations in food resources, and nest site availability. The analysis of which factors are most important in setting minimum area requirements is poorly developed, and should be a priority for field work.

## PREDICTION

The following prediction can be made for the relationship between the minimum area requirement of a relatively sedentary forest taxon and the numbers of Pleistocene refugia in which that taxon would be expected to have ocurred:

The smaller the minimum area requirement for a given taxon, the greater the number of refugia for that taxon; conversely, the greater the minimum area requirement for a taxon, the fewer the number of refugia.

This prediction provides a means of testing the Pleistocene refugia model, which assumes allopatric differentiation in isolated forest enclaves was of primary importance in producing current patterns in the Neotropical biota. If the model is true, the prediction should be borne out. It is impossible to measure directly the number of refugia a given taxon survived in. But since it is assumed that the refugia were sites of differentiation, the total number of subspecies within a given taxon should reflect the number of refugia where that taxon survived and differentiated.

## TESTING THE PREDICTION

A previous test of this hypothesis uses data from Willis, 1974, classic work on local extinctions of birds on Panamá's Barro Colorado Island, and Brown's, 1977, butterfly data (Oren, 1981a). Willis, 1979, has recently published excellent new data which provide an opportunity to extend the test. Willis worked in three areas of relict forest in Sao Paulo, Brazil, which varied from 21 to 1400 hectares. Table I summarizes data for three families of forest-requiring birds derived from the Willis study. Only taxa which showed clear patterns of minimum area requirements are used in the analysis.

Figure 1 plots the data for the fifteen genera in Willi's study, both lumped and for each family separately. In each regression, the number of subspecies is negatively correlated with minimum area requirements, and is highly significant ($p < .01$), for all except the furnariids. The sample size in the furnariids is so small, that even the correlation coefficient of $-.755$ is not significant.

## CONCLUSION

As predicted by the hypothesis, there is a negative correlation between minimum area requirement and total number of subspecies in the genus (although not statistically significantly for Furnariidae). For all three families tested the data are consistent with the notion that the Neotropical rain forest was fragmented into refugia during the Pleistocene

Although the data presented "pass" the test, this certainly does not constitute proof of the Pleistocene refugia theory. The most that can be confidently affirmed is that the data are consistent with the refugia model. The conclusions of the hypothesis applied here should be added to the rest of the body of work on biological differentiation in the Neotropics (see Prance, 1981). The combined research on the topic strongly suggests that Pleistocene forest fragmentations was indeed of key importance in producing contemporary biotic patterns in tropical America.

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**TABLE I:** **Area requirements and total number of lowland tropical subspecies in genus. (Data from Willis, 1979, and Peters, 1951 ).**

| Species | Minimum Area | Total Lowland Tropical Subspecies in Genus |
|---|---|---|
| Dendrocolaptidae: | | |
| *Dendrocolaptes platyrostris* | 250 h | 12 |
| *Dendrocincla turdina* | 250 h | 16 |
| *Sittasomus griseicapillus* | 250 h | 12 |
| *Lepidocolaptes fuscus* | 250 h | 13 |
| *Campylorhamphus falcularius* | 250 h | 14 |
| *Xiphocolaptes albicollis* | 1400 h | 7 |
| Furnariidae: | | |
| *Synallaxis ruficapillus* | 21 h | 34 |
| *Automolus leucophthalmus* | 21 h | 17 |
| *Sclerurus scansor* | 1400 h | 15 |
| *Philydor atricapillus* | 1400 h | 11 |
| Formicariidae: | | |
| *Dysithamnus mentalis* | 21 h | 15 |
| *Herpsilochmus rufimarginatus* | 250 h | 11 |
| *Terenura maculata* | 1400 h | 7 |
| *Chamaeza campanisoma* | 1400 h | 6 |
| *Pyriglena leucoptera* | 1400 h | 8 |

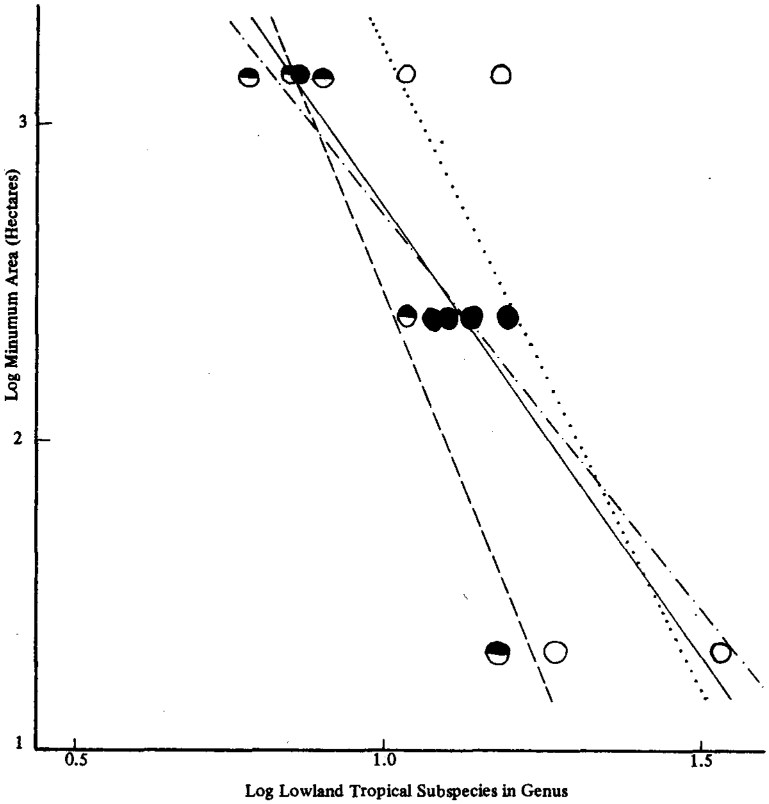

FIGURE 1: Relationship between log minimum area requirement and log lowland tropical subspecies in genus for selected birds from Willis (1979). Solid circles = Dendrocolaptidae; hollow circles = Furnariidae; half-shaded circles = Formicariidae. Regression lines: Dashes = Formicariidae; dots = Furnariidae; dashes and dots = Dendrocolaptidae; solid = lumped data for all three families.

## LITERATURE CITED

ABSY, M.L., 1981. Quaternary palynological studies in the Amazon basin. *In:* G.T. Prance (ed.), Biological diversification in the tropics. Columbia University Press, New York.

BENSON, W.W., 1981. Alternative models for infrageneric diversification in the humid tropics. *In:* G. T. Prance (ed.), Biological diversification in the tropics. Columbia University Press, New York.

BROWN, J.H. and A. KODRIC-BROWN, 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology,* 58:445-449.

BROWN, K.S., 1977. Centros de evoluçâo, refugios quaternários e conservaçâo de patrimônios genéticos na regiâo neotropical: padrôes de diferenciaçâo em Ithomiinae (Lepidoptera: Nymphalidae). *Acta Amazonica,* 7:75-137.

———,1979. Evoluçâo e diferenciaçao em Ithominae neotropicais (Lepidoptera: Nymphalidae). Unpublished Ph. D. thesis, Universidade Estadual de Campinas, Campinas, Sâo Paulo, Brazil.
zil.

DIAMOND, J.M., 1975, Assembly of species communities. *In:* M.L. Cody and J.M. Diamond (eds.), Ecology and evolution of communities, pp. 342-444. Belknap Press, Cambridge, Massachusetts.

———,1978. Critical areas for maintaining viable populations of species. *In:* M.W. Holdgate and M.J. Woodman (eds.), The breakdown and restoration of ecosystems, pp. 27-39. Plenum Press, New York.

ENDLER, J.A., 1981. Biological diversification in the tropics: clines or refugia? *In:* G.T. Prance (ed.) Biological diversification in the tropics. Columbia University Press, New York.

HAFFER, J., 1969. Speciation in Amazonian forest birds. *Science,* 165:131-137.

——— ,1974. Avian speciation in tropical South America. *Publ. Nuttall Ornith. Club,* 14:1-390.

——— ,1978. Distribution of Amazon forest birds. *Bonn. zool. Beitr.,* 29:38-78.

——— ,1981. General aspects of refuge theory. *In:* G.T. Prance (ed.), Biological diversification in the tropics. Columbia University Press, New York.

HAMMEN, T. VAN DER, 1981. Paleoecology of tropical South America. *In:* G.T. Prance (ed.), Biological diversification in the tropics. Columbia University Press, New York.

LOVEJOY, T.E. and D.C. OREN, 1981. Minimum critical size of ecosystems. *In:* L.M. Graves (ed.), Forest islands in man-dominated landscapes. Springer Verlag, New York.

MOREAU, R.E., 1963. The distribution of tropical African birds as an indicator of past climatic changes. *In:* F.C.Howell and F. Bourliere (eds.), African ecology and human evolution, pp. 28-42. Aldine Publ., Chicago.

———, 1966. The bird faunas of Africa and its islands Academic Press, New York.

OREN, D.C., 1981a. Testing the refugia model for South America: a hypothesis to evaluate discrepancies in refugia number across taxa. *In:* G.T. Prance (ed.), Biological diversification in the tropics. Columbia University Press, New York.

———, 1981 b. Zoogeographical analysis of the white sand campina avifauna of Amazonia. Unpublished Ph. D. thesis, Harvard University, Cambridge, Massachusetts.

PETERS, J.L., 1951. Check-list of birds of the world, vol. VII. Museum of Comparative Zoology, Cambridge, Mass.

PRANCE, G.T., 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae, and Lecythidaceae. *Acta Amazonica,* 3:5-28.

——— 1981.Biologicaldiversification in the tropics. Columbia University Press, New York.

SICK, H., 1967. Rios e enchentes na Amazônia como obstáculo para a avifauna. *Atas Simp. Biota Amazonica,* Vol. 5 *(Zool.)* :495-520.

VANZOLINI, P.E. and E.E.WILLIAMS, 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepi* species group (Sauria, Iguanidae). *Arq. Zool. S. Paulo,* 19: 1-298.

WILLIAMS, E.E., 1977. The Belém park effect and vanishing refugia. *Anolis Newsletter,* 3.

WILLIS, E.O., 1974. Populations and local extinctions of birds on Barro Colorado Island, Panamá. *Ecol. Monog.,* 44:153-169.

———, 1979. The composition of avian communities in remanescent woodlots in southern Brazil. *Pap. Avul. Zool. S. Paulo,* 33 (1): 1-25.

WETTERBERG, G.B., M.T. JORGE PADUA, C.S. DE CASTRO, and J.M.C. DE VASCONCELLOS, 1976. Um análise de prioridades em conservação de natureza na Amazônia. Ministério da Agricultura, PNUD/FAO/IBDF, Brasília.