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Effects of Riverine Barriers on Genetic Differentiation of Amazonian Forest Undergrowth Birds (Peru).

Angelo Paul Capparella
Louisiana State University and Agricultural & Mechanical College

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Effects of riverine barriers on genetic differentiation of Amazonian forest undergrowth birds

Capparella, Angelo Paul, Ph.D.

The Louisiana State University and Agricultural and Mechanical Col., 1987

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EFFECTS OF RIVERINE BARRIERS ON GENETIC DIFFERENTIATION OF AMAZONIAN FOREST UNDERGROWTH BIRDS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Zoology and Physiology

by
Angelo Paul Capparella
B.A., The University of North Carolina at Chapel Hill, 1974
M.A., Texas Tech University, 1977
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ABSTRACT

The high frequency with which rivers delimit phenotypically differentiated bird taxa is unique to Amazonia, where major rivers often form the boundaries between allospecies and subspecies pairs of understory terra firme forest birds. In contrast, many such forest species with life history traits similar to these differentiated forms show no variation in plumage across even the largest rivers. To determine whether such species are nonetheless genetically differentiated, I obtained tissue samples from populations of forest understory birds from opposite banks of the Napo and Amazon rivers of northeastern Peru. These included three species that are not phenotypically differentiated across the Amazon and three species that are not phenotypically differentiated across the Napo, as well as two species that are phenotypically differentiated across the Amazon. Protein electrophoretic analysis of allozymes revealed substantial genetic differences among river-separated birds that do and do not show plumage differences.

The prevailing historical hypothesis to explain the high number of species of Amazonian birds states that isolation in Pleistocene forest fragments was the important vicariant event that permitted speciation. An alternative is that isolation on opposite banks of rivers after the formation of the Amazonian

river system was the important vicariant event. The pattern of genetic variation reported in this study supports the latter hypothesis.

Wright's coefficient F_{ST} was used as an indirect index of the extent of gene flow among populations in contiguous forest. For some Amazonian species, F_{ST} values are high compared to most temperate zone birds, especially considering the geographic proximity (<90 km) among the compared Amazonian populations. Increased population subdivision due to reduced effective population size or reduced effective dispersal distance, coupled with an aversion to crossing habitat discontinuities exposed to full sunlight, could explain the effect of riverine barriers on genetic differentiation within such species. The increased population subdivision and response to riverine barriers in understory terra firme forest birds suggests that the genetic continuity of these birds will be disrupted severely by the fragmentation of formerly contiguous forest through the building of roads and associated agricultural clearing currently underway in the Amazon basin.

INTRODUCTION

The genetic population structure of birds is an area of increasing research interest. Measures of genetic differences among conspecific populations and between species provide critical baseline information for understanding population dynamics, modes of speciation, and the significance of phenotypic diversity (Templeton 1980; Barrowclough 1983). Before the 1970s, ornithologists estimated genetic diversity indirectly by examining phenotypic diversity within species. With the application of protein electrophoresis, it became possible to survey genetic diversity more directly (Lewontin and Hubby 1966). In the last ten years, electrophoretic surveys of birds have become more frequent, although there are still relatively few empirical surveys of avian population genetic structure or interspecific patterns of genetic variation (Nevo et al. 1984; Zink 1986; Zink and Remsen 1987; Barrowclough and Baker in press). In addition, most studies have examined temperate zone oscine birds (Barrowclough et al. 1985; Capparella in press), and only three (Braun and Parker 1985; Capparella and Lanyon 1985) have examined birds of the Amazon basin. Therefore, because of geographic and taxonomic biases and the absence of an extensive data base, the generality of conclusions about the genetic population structure of birds is unknown.

An important determinant of genetic population structure is gene flow, the dispersal and subsequent incorporation of immigrants' genes into a conspecific population's gene pool. The cessation of gene flow between previously interbreeding populations is a necessary first step leading to the development of genetic and phenotypic divergence. Under the geographic or allopatric model of speciation, it is the physical separation of such populations through the interposition of a barrier to dispersal that causes this disruption of gene flow (Mayr 1963). For this reason, the role of gene flow and barriers to dispersal are critical aspects for understanding how new species originate. Most studies of gene flow have examined organisms in the temperate zone (Ehrlich and Raven 1969), and therefore studies of gene flow in the tropical rain forest, which has the highest number of species, and where bird species are, on the average, more sedentary, are critical.

For birds, the Amazon basin of South America is the center of highest alpha (single-point) and gamma (regional) species diversity (Amadon 1973; Pearson 1977; Remsen and Parker 1983). Hypotheses to explain this high level of diversity are ecological and historical. Ecological hypotheses have included increased number of resources ("more niches available"), greater degree of specialization ("narrower niches"), and greater species-packing ("more broadly overlapping niches") (for summaries, see Orians 1969; Karr 1975; Terborgh 1980; Remsen 1985). These explanations address the causes of high single-point diversity, but they do not

address adequately the high regional diversity. To explain the latter, historical hypotheses have been offered.

Of the historical hypotheses advanced, the Pleistocene refugia hypothesis is favored by most workers (Prance 1982). This explanation proposes that the high regional diversity of species in Amazonia is attributable to the periodic fragmentation and coalescence of the forest during Pleistocene climatic fluctuations. The isolation of forest fragments (refugia) is proposed as the major promoter of speciation, and rivers constitute, at times, a partial barrier to species' reexpansion following climatic amelioration.

An alternative historical hypothesis, suggested by the congruence of many bird ranges and rivers, is that the formation of the extensive Amazonian river system after the uplift of the Andes induced speciation in forest-dwelling birds by fragmenting their ranges and prohibiting gene flow. Under this hypothesis, the high regional species diversity in Amazonia would derive from riverine barriers interrupting gene flow (Sick 1967).

The early naturalists and taxonomists who studied Amazonian forest birds recognized that rivers are often coincident with the geographic limits of subspecies and allospecies (Sclater and Salvin 1867; Wallace 1889; Snethlage 1913; Hellmayr 1910), and this observation has been made by recent workers as well (e.g., Willis 1969). The delimitation of ranges by rivers occurs in spite of the observation that the habitats on each side of most Amazonian rivers appear to be identical (Willis 1969; pers. obs.).

Congruence between distribution limits and rivers is especially evident in many species of common, widespread birds confined to the understory of terra firme (nonflooded) forest, particularly passerine birds of the families Pipridae (the manakins), Dendrocolaptidae (the woodcreepers), and Formicariidae (the antbirds) (Haffer 1974). In the dendrocolaptids, for example, among the approximately 82 taxa (species and subspecies) that occur in Amazonia, about 50 (62%) have at least one border of their range demarcated by a river (Table 1). Of these 50, about 32 (64%) are members of opposite bank replacement taxa in which sister subspecies and species are found on opposite banks of a river.

The taxa of Dendrocolaptidae and other families that show this phenomenon are largely confined to the understory of the nonflooded terra firme forest. Because the riverine habitats that flank the rivers of Amazonia are unsuitable habitats for these terra firme species (Remsen and Parker 1983), the extensive bands of riverine habitats can provide an additional barrier. Opposite bank replacement taxa are found rarely in non-terra firme forest birds (e.g., the parrots Pionites melanocephala and P. leucogaster occurr in the canopy of tall riverine forest and replace one another across the Amazon) and in canopy terra firme forest species (e.g., the tanagers Tachyphonus surinamus brevipes and T. s. napensis replace one another across the Amazon). In addition, circumstantial evidence suggests that interior forest species are less likely to cross open or alien environments

(Willis 1974; Terborgh 1975), and hence the Amazon and its major tributaries could provide a substantial barrier to gene flow in understory terra firme forest birds.

Rivers may (riverine hypothesis) or may not (refugia hypothesis) be the principal cause of genetic differentation and speciation in understory terra firme forest Amazonian birds. The first process—a vicariant event—gives a primary role to rivers as a barrier to gene flow. The second process—limiting reexpansion—treats rivers as places at which secondary contact zones stabilize, and therefore rivers play a secondary role.

Complicating the interpretation of the role of riverine barriers in speciation is the observation that not all taxon boundaries are coincident with rivers. Some birds that exhibit phenotypic differentiation across a river (primarily in plumage) have congeners that do not, and some birds that show phenotypic differentiation across one river do not show it across other rivers of similar size. Also, some birds show differentiation that is not congruent with rivers (e.g., the boundary between Pipra c. coronata and P. c. exquisita is not coincident with any known geographic barrier; Haffer 1970). The lack of a consistent pattern of phenotypic differentiation congruent with rivers, coupled with the current popularity of the Pleistocene refugia hypothesis (Prance 1982), have led to the de-emphasis of the role of rivers in promoting differentiation of birds in Amazonia. A critical question is: to what extent do rivers induce genetic differentiation, a necessary (but not sufficient) stage in the

speciation process?

The contrast between related taxa with similar life history traits, some of which do and do not exhibit phenotypic differentiation across the same rivers, provides a useful context in which to study the role of rivers as barriers to gene flow. It seems that phenotypic and allozymic evolution are not always concordant (Zink 1982; Capparella and Lanyon 1985). For genetic differences in proteins as assessed by electrophoresis, empirical evidence suggests that differences accrue in a selectively neutral and time-dependent manner (Barrowclough et al. 1985). The evolution of phenotypic differences after cessation of gene flow is influenced not only by the time since divergence but probably also by selection (Lande 1985). Therefore, an examination of genetic differentiation will be an important "yardstick" with which to measure the effects of rivers, especially for species with and without congruence in phenotypic patterns of variation and riverine barriers.

The primary purpose of this study is to measure the degree of avian genetic differentiation associated with Amazonian rivers using protein electrophoresis. The specific objectives of this study are threefold: (1) documentation of phenotypic differentiation in birds that is associated with the lower Napo and adjacent Amazon rivers; (2) electrophoretic analysis of the genetic differentiation among phenotypically differentiated birds; and (3) determination of the extent (if any) of genetic differentiation among phenotypically undifferentiated birds. This

data base will be used to examine evidence for rivers as barriers to gene flow, and to consider the importance of riverine barriers in speciation of Amazonian forest birds. Additionally, it will provide information on the genetic population structure of Neotropical terra firme forest birds.

This study is the first to search systematically for taxa delimited by rivers using specimens accompanied by precise locality information. Many older specimens collected from Amazonia have imprecise or inaccurate locality data that make difficult the determination of congruence between rivers and range. In addition, this is the first study to measure genetic differentiation associated with Amazonian rivers and to characterize genetic population structure among Amazonian birds. The data base generated in this study is expected to provide a perspective on avian genetic population structure, on the role of gene flow in Neotropical birds, and on the historical effects of evolutionary processes in these birds.

METHODS AND MATERIALS

Background Information

The study area in northeastern Peru, Department of Loreto, encompasses the upper Amazon River and the lower Napo River near their confluence 70 km northeast of Iquitos (Fig. 1). In this region the Amazon is 3200 km from its mouth, yet it measures approximately 3 km in water width (up to 10 km in water + riverine habitat). The Napo flows into the Amazon from the northwest and is typical in size of upper Amazonian tributaries, approximately 1.5 km in water width (up to 3 km in water + riverine habitat).

The primary study objective was to compare the extent of genetic differentiation within species of understory terra firme forest bird populations separated by contiguous forest and two different-sized rivers, the Napo and Amazon. A secondary study objective was to determine the identity of phenotypically-differentiated birds separated by the Napo and Amazon rivers. To accomplish the primary objective, the sites sampled in contiguous forest needed to be separated by a distance at least equivalent to the river-separated populations to control for effects of geographic distance alone. Therefore, sampling localities had to be in largely undisturbed terra firme forest that was contiguous with other such forest (i.e., not isolated or on a peninsula), and there had to be no intervening barriers or

habitat discontinuities among the control sites. Implementation of this sampling design was complicated by several factors: (1) terra firme forest undisturbed by man rarely abuts the major rivers, and therefore travel up small tributaries is required to reach intact forest; (2) the average width of the rivers and accompanying riverine habitat was impossible to assess accurately from the ground; (3) the presence of uninterrupted terra firme forest between control sites could not be determined from the ground; and (4) reliable, detailed maps of this area do not exist.

To circumvent these problems, Landsat images were used. These satellite images can be obtained in several wavelengths (bands), of which band 7 is the best for highlighting the difference between water and land, as well as differentiating between riverine habitat and terra firme forest (Instituto de Pesquisas Espaciais 1981). Landsat images facilitated: (1) determination of the location of all tributaries that did not have closed canopy forest; (2) measurement of the average river and riverine habitat width, and distance between sample sites; (3) location of disturbed and intact terra firme forest; and (4) conditions between the control sites. The two Landsat images used in this study (Fig. 2) were taken on 7 December 1973 (scene identification #8150214314500) and 24 September 1975 (#8224514160500), and are available from the U.S. Geological Survey, EROS Data Center, Sioux Falls, South Dakota.

Study Sites

Five study sites were selected: three along the north bank of

the Napo and Amazon rivers in contiguous forest, one on the south bank of the Napo, and one on the south bank of the Amazon (Figs. 1, 2). The sites were designated on specimen labels as follows (Río = river, Quebrada = stream):

North bank sites. Site 1: lower Río Napo region, east bank of the Río Yanayacu, ca 90 km north of Iquitos, 120 m elevation. Site 2: 1 km N of the Río Napo, 157 km by river NNE of Iquitos, 110 m. Site 3: south of the Río Amazonas, ca 10 km SSW of the Río Napo mouth, on the east bank of the Quebrada Vainilla, 100 m.

South bank Napo. Site 4: 1.5 km south of Libertad, south bank of the Río Napo, ca 50 km north of Iquitos, 120 m.

South bank Amazon. Site 5: south of the Río Amazonas, ca 10 km SSW of the Río Napo mouth on the east bank of the Quebrada Vainilla, 100 m.

Site 1 (3° 55′S, 73° 05′W; Instituto Geografico Militar del Perú 1967)--This is east of the eastern tributary of the small Yanayacu River (= Yana-yacu River; Stephens and Traylor 1983) River, approximately 15 km from its mouth on the Napo. The terrain is gently undulating and has undisturbed terra firme forest that is occasionally used for hunting. Collecting occurred from 6 June 1983 to 1 July 1983.

Site 2 (3° 16′S, 72° 54′W; Stephens and Traylor 1983)--This is west of the small Sucusari River and about 1 km north of the Napo. Nearby are a tourist lodge and small farm plots. An unused logging road passes near the site. The terra firme forest was largely intact, although crisscrossed by hunting trails, and the

terrain is gently undulating. Collecting occurred from 28 May 1982 to 26 June 1982.

Site 3 (3° 25′S, 72° 35′W; Instituto Geografico Militar del Perú 1967)--This is to the west of the small Quebrada Orán (= Quebrada Yanayacu de Orán; Instituto Geografico Militar del Perú 1967), approximately 5 km north of the Amazon. The terrain is gently undulating and has relatively undisturbed terra firme forest. Hunting trails crisscross the forest, and logging to support the sawmill at the mouth of the Orán is encroaching gradually on the site. Collecting occurred from 6 June 1984 to 3 July 1984.

Site 4 (3° 02′S, 73° 20′W; Stephens and Traylor 1983)--This is to the east of the Quebrada Navarro, about 1.5 km south of the Napo. Although disturbance and clearings extend along the stream for about 1 km, this site is in largely undisturbed terra firme forest, with some hunting trails, on gently undulating terrain. Collecting occurred from 10 July 1982 to 9 August 1982.

Site 5 (3° 35′S, 72° 45′W; Instituto Geografico Militar del Perú 1967)--This site is to the east of the small Quebrada Vainilla (= Río Vanilla, Stephens and Traylor 1983; probably = Río Marupa Cano, Instituto Geografico Militar del Perú). Most vegetation along the stream is highly disturbed, but about 0.5 km to the east is terra firme forest on relatively level terrain that is largely undisturbed except for some small, man-made clearings and hunting trails. Collecting occurred from 13 July 1983 to 9 August 1983.

Distances between the three north bank sites are slightly greater than distances between the across-river sites (accuracy within 5 km; Fig. 1). Therefore, the north bank site comparisons served as appropriate controls for assessing genetic differentiation due to geographic distance. Note that the distance between sites 2 and 3 is not straight-line but curves along the terra firme forest around the Sucusari River. As can be seen from the Landsat image (Fig. 2), no other intervening barrier is visible. The forest between the three north bank sites has a similar spectral signature, and therefore is assumed to be more-or-less equivalent and inhabited by all sampled species.

Target Species

The species targeted for the primary objective had to be: (1) confined (largely) to the understory of terra firme forest; (2) representative of several different life history strategies and familial assignments; (3) widespread; and (4) abundant. The first criterion was necessary to minimize habitat differences among the compared species. The second requirement ensured that the target species were representative of the diversity in social system, foraging method, and phylogenetic history found in understory terra firme forest birds. Widespread species were necessary to assure presence at all collection sites. Finally, without knowing a priori the degree (if any) of genetic differentiation to be found, it was necessary to collect many individuals. These considerations resulted in the selection of species in the Suborder Tyranni (tyrant flycatchers and allies), because these

are the most widespread and abundant birds of the terra firme understory.

The target species examined are of two basic types: (1) species phenotypically differentiated (by plumage) across the Amazon; and (2) species not phenotypically differentiated across the Amazon or Napo. Selection of taxa in the first group was done after the study, and therefore the sample sizes are smaller than those in the second group. Target species in the second group were selected from those captured most frequently in the field at the first collecting locality. A threshold of twenty individuals was used, but this was not met at all sites for some species. Fewer comparisons were possible across the Napo because the liquid nitrogen tank at site 4 failed towards the end of the camp, and the tissue of very few species could be saved. Those salvaged were not damaged.

Two members of the Family Pipridae (manakins), Pipra erythrocephala (Flame-headed Manakin) sensu lato and Chiroxiphia pareola (Blue-headed Manakin), represented the phenotypically differentiated taxa analyzed. Pipra erythrocephala sensu lato is currently divided into the allospecies P. erythrocephala (Golden-headed Manakin), found on the north bank of the Amazon and both banks of the Napo, and P. rubrocapilla (Red-headed Manakin), found on the south bank of the Amazon (Snow 1979; pers. obs.). The differences between P. erythrocephala and P. rubrocapilla are: (1) golden versus red top and sides of the head; (2) black versus white underwing coverts; (3) short versus long tail; and (4)

smaller bill in P. erythrocephala (Meyer de Schauensee 1966, 1970). Subsequent referral to P. erythrocephala will be sensu stricto. These manakins are all frugivorous, sexually dimorphic, and polygynous (Snow 1962; Sick 1985).

The non-phenotypically differentiated species analyzed are: Pipra coronata (Blue-crowned Manakin, Family Pipridae); Glyphorynchus spirurus (Wedge-billed Woodcreeper, Family Dendrocolaptidae); Pithys albifrons (White-plumed Antbird, Family Formicariidae); and Myrmoborus myotherinus (Black-faced Antbird, Family Formicariidae). Samples of the first two were collected at all five sites. Samples of Pithys albifrons were collected only at the north bank sites and on the south bank of the Napo; it is not found south of the Amazon in Peru. Samples of Myrmoborus myotherinus were collected only at the north bank sites and on the south bank of the Amazon; the south Napo samples were lost due to the liquid-nitrogen tank failure.

Like the other manakins, Pipra coronata is frugivorous, sexually dimorphic, and polygynous (Hilty and Brown 1986). Glyphorynchus spirurus is insectivorous, forages on bark substrates, regularly follows mixed-species flocks, and is sexually monomorphic and monogamous (Gradwohl and Greenberg 1980; Hilty and Brown 1986). Pithys albifrons is insectivorous, an obligate army ant follower, sexually monomorphic, and monogamous (Hilty and Brown 1986; Willis 1972). Myrmoborus myotherinus is insectivorous, forages on generalized substrates, does not follow mixed-species flocks, and is sexually dimorphic and monogamous

(Hilty and Brown 1986).

Sampling Protocol for General Collecting

Mist nets were placed in terra firme forest within a 1-2 sq km area. Nets were placed in multiple lines and were added at a rate of 5-10 per three days until about 60 were operating. In addition, shotguns were used to collect species considered unlikely to be caught in mist nets. Specimens were deposited at the Louisiana State University Museum of Zoology (LSUMZ), where identification to species and subspecies was accomplished by comparison to specimens and published descriptions.

Sampling Protocol for Electrophoresis

Birds for the electrophoretic analysis were removed from mist nets, returned to the preparation tent, and held alive in paper bags until humanely dispatched. Tissues were then extracted within 15 minutes after death and placed in liquid nitrogen, and the specimen was prepared as a study skin or skeleton. All tissue samples, skins, and skeletons are deposited at the LSUMZ.

Electrophoresis Protocol

Tissue samples were stored at -60^{o} C. Samples collected at site 5 were slightly stressed judging from the inactivity of GAPDH (see Table 2 for enzyme abbreviations). No other signs of unusual degradation (e.g., lack of clarity, extensive subbanding) were noted at other loci. Samples of breast muscle, heart, and liver were homogenized together in an equal volume of either deionized, distilled water or a 2 mM MgCl2, 0.2 mM dithiothreitol, 0.25 M sucrose solution and clarified by centrifugation. Horizontal

starch-gel electrophoresis was carried out on 11.5% or 12% gels. Most enzymes were examined on two or more buffer systems to determine which buffer system had the highest resolving power and to detect hidden alleles. Previous work on birds has shown that the detection of hidden alleles using multiple buffer systems is uncommon and does not affect overall genetic distance measures (Avise et al. 1980). This study found only one instance of hidden alleles--the GPD locus in Pithys albifrons.

When two or more loci were scored, they were numbered in sequence beginning with the most anodally locus. Similarly, multiple alleles at a locus were designated alphabetically, beginning with the most anodal allele. Staining procedures used to identify specific enzymes were modified from those given by Selander et al. (1979) and Harris and Hopkinson (1976).

The number of loci and number of individuals analyzed per species per population are given in Table 3. The same suite of loci was examined in all species, but the suite that could be reliably scored in each species varied slightly. Most individuals of every species could be scored for every locus. An average of 29 loci were scored per individual.

Data Analysis

Electrophoretic data were entered as individual genotypic scores into the BIOSYS-1 computer program of Swofford and Selander (1981) for each population of each species. A table of allele frequencies for each locus was compiled for each population of

each species. The following measures of within-population genetic variability were computed: (1) the percent of loci polymorphic; (2) the average number of alleles per polymorphic locus; and (3) the average individual heterozygosity.

The genetic distance measures of Nei (1978) and Rogers (1972) were calculated to estimate divergence among the populations of each species. Nei's 1978 measure is an improvement over his 1972 value because it corrects for small sample size. Also, Nei's 1978 measure permits comparison with Barrowclough's (1980) survey of genetic distance values among various avian taxa. Rogers' distance was calculated because it is a metric measure and therefore permits the construction of robust phenograms (Rogers 1972). The UPGMA algorithm (Sneath and Sokal 1973) was applied to the Rogers' distance values to construct phenograms.

Wright's (1978) F_{ST} statistic corrected for sample size was used to characterize the degree of genetic differentiation and population substructuring among populations separated by rivers and by contiguous forest. Values were compared to those recalculated by Barrowclough (1983) from studies of temperate birds and non-Amazonian Neotropical zone species. The F_{ST} value for Myrmoborus myotherinus was calculated without the sample from site 2 because it was too small (2 individuals) for meaningful comparison.

RESULTS AND DISCUSSION

Phenotypic Differentiation

The results of the general collecting documented that the number of understory terra firme forest taxa delimited by the lower Napo River (4 taxa) is less than those delimited by the wider Amazon River (24) (Table 4). For comparison, Hellmayr (1910) found that the Madeira River, which flows into the Amazon in eastern Brazil, delimits the range of 67 taxa. Snethlage (1913) reports that the lower Amazon River delimits the range of 80 taxa, and that the large tributaries of lower Amazonia, the Tocantins, Xingu, and Tapajoz, delimit 37, 22, and 12 taxa, respectively. Because the lower tributaries are wider than the Napo and upper Amazon, it is not surprising that they delimit (with one exception, the Tapajoz) more taxa. The relationship between the number of taxa delimited by specific rivers partially depends on the history of that river. Although it is suspected that some Amazonian tributaries have changed their course over time (Willis 1969), and that others were affected by sea incursions due to eustatic sea level changes (Haffer 1978), there is little direct geological evidence regarding the timing or extent of such events.

In addition to tabulations by river, authors have noted the congruence of rivers with the ranges of their study taxa (e.g.,

Myrmeciza, Todd 1927; Rhegmatorhina, Willis 1969). Despite tabulations based on specific rivers and birds, a complete accounting of the number of taxa delimited by rivers in Amazonia is lacking, and remains difficult to compile because of the uncertainty regarding the ranges of Amazonian birds. Additional collections, such as the one reported here, are needed to document fully this phenomenon.

An additional uncertainty in compiling such lists is illustrated by comparing the species collected at the three sites in contiguous forest along the north bank of the Napo and Amazon rivers (Appendix). Although there is considerable similarity in species composition and number, some species (e.g., Percnostola rufifrons) were collected at only one of the three camps. This may complicate the determination of rivers delimiting species ranges because a sample at a single trans-river site may not detect the species, even though it is present at other sites on the same bank.

Three factors, other than sampling error, may explain these between-site changes in understory avifauna: (1) differences in microhabitat availability; (2) differences in seasonal or mobile resources; and (3) differences in bird density. Salo et al. (1986) reported that riverine forest consists of a mosaic of habitat types. If terra firme forest is similarly heterogeneous, then the differences in species composition of netted birds may be due to differences in microhabitats sampled. Although every effort was made to deploy nets in all discernible microhabitats

for this study (e.g., streamside vegetation, treefall gaps, vine tangles), the structure perceived by birds probably encompasses a greater variety (and different scales) of microhabitats. Specialization on seasonal, patchy, or mobile resources can affect the distribution of birds within the forest. For example, obligate ant-following birds are dependent on moving army ant swarms. Therefore, the likelihood of capture of these birds depends on the proximity of an army ant swarm and the distance that these birds move when searching for swarms. Finally, differences in density between sites potentially can affect capture success. These factors must be evaluated when determining the likelihood that a species is truely absent from a particular region and interpreting such absence as indicative that its range is delimited by a river.

Within-population Genetic Variability

The percent of loci loci, average number of alleles per polymorphic locus, and average individual heterozygosity (Table 5) were calculated from the allelic frequencies for each locus for all species analyzed (Tables 6-11). These values are equivalent to those reported for three other species of Amazonian birds: Synallaxis rutilans, Mionectes oleagineus, and M. macconnelli (Braun and Parker 1985; Capparella and Lanyon 1985; Table 5). In addition, these Neotropical birds have heterozygosity levels (0.051 $\pm$ 0.017 s.d.) similar to those (0.051 $\pm$ 0.029 s.d.) compiled by Nevo et al. (1984) from 46 species of primarily temperate zone oscines and vertebrates in general (0.054 $\pm$ 0.059

s.d.). Similarly, the percent of polymorphic loci (19.2 ± 4.1 s.d.) resembles that compiled by Nevo et al. (1984) for other birds (30.2 ± 14.3 s.d.) and vertebrates in general (22.6 ± 14.6 s.d.). Therefore, the amount of genetic (allozymic) variability in Neotropical birds is equivalent to that found in other vertebrates.

Genotypic Differentiation

The genetic distance values between the subspecies of Chiroxiphia pareola (0.069) and the allospecies Pipra erythrocephala/P. rubrocapilla (0.101) (Table 13) exceed the mean value for temperate zone species (0.0440 ± 0.0221 s.d., Barrowclough 1980), but are less than the mean value for temperate zone genera (0.2136 ± 0.1659 s.d., Barrowclough 1980). Nevertheless, the genetic distance between the allospecies P. erythrocephala and P. rubrocapilla and between the subspecies of Chiroxiphia pareola is consistent with taxonomic ranking as determined from plumage. The presence of fixed allelic differences at two loci between P. erythrocephala and P. rubrocapilla, and the lack of any fixed differences between the two subspecies of Chiroxiphia pareola, is also consistent with the phenotypic differences. Determination that the pigments found in the crown feathers of P. erythrocephala and P. rubrocapilla are different further supports the genetic distinctiveness of these two allospecies (Brush and Capparella, ms). Thus, both phenotypic and genetic differentiation are congruent with each other and with the river.

Phenotypic differentiation (as measured by plumage and external morphology) and genotypic differentiation (as measured by protein electrophoresis) are not always congruent (Zink 1982; Capparella and Lanyon 1985). The taxonomic ranking of species for Pipra erythrocephala/P. rubrocapilla versus subspecies for Chiroxiphia pareola napensis/C. p. regina is interesting because they both differ in a similar manner in their crown color (red versus yellow on opposite banks of the Amazon). This reflects the finding that P. erythrocephala and P. rubrocapilla both occur in the lower Huallaga Valley of Peru where they do not intergrade (Meyer de Schauensee 1966). No area of sympatry between C. p. napensis and C. p. regina is known, and therefore it is difficult to assess the level of reproductive isolation between these two subspecies would interbreed if they overlapped.

The genetic distance values among the samples of phenotypically undifferentiated populations for each species showed genetic differentiation across the Amazon and (with one exception) the Napo. For the trans-Amazon comparisons, genetic differentiation is high in all three species compared: (1) Pipra coronata ($\bar{x}$ = 0.039 for Nei's D; Table 13, Fig. 3); (2) Glyphorynchus spirurus ($\bar{x}$ = 0.053; Table 14, Fig. 4); and (3) Myrmoborus myotherinus ($\bar{x}$ = 0.061; Table 15, Fig. 5). The trans-Amazon genetic distances are comparable to the mean value for avian species (0.0440 $\pm$ 0.0221, Barrowclough 1980). A correlation coefficient between geographic distance and Nei's genetic distance for Pipra coronata is -0.25. This indicates that

increased genetic differences are not due to geographic distance but apparently reflect the presence of the intervening Amazon.

For the trans-Napo comparisons, the genetic differentiation is lower. Pipra coronata (Table 13, Fig. 6) and Pithys albifrons (Table 16, Fig. 8) both show greater differentiation across the Napo ($\bar{x}$ = 0.013 and 0.004, respectively) than would be expected from geographic distance alone. However, Glyphorynchus spirurus (Table 14, Fig. 7) does not show greater differentiation across the Napo in comparison to the control sites.

The detection of genetic differentiation between river-separated populations of species that do not differ in plumage suggests that the number of genetically differentiated forms delimited by rivers is greater than predicted from consideration of plumage alone. Altogether, river-associated differentiation is found in four monomorphic, forest understory birds representing three different families. Additionally, two different Amazonian rivers (Amazon and Napo) show this effect. Only Glyphorynchus spirurus did not show a pattern of genetic differentiation congruent with the Napo, although it did with the Amazon. If Glyphorynchus spirurus is more tolerant of riverine habitats than are the other taxa, then it would be more likely carried across when sections of the Napo River change channel, uniting riverine habitat from one bank to another. The extensive bends and oxbows evident in this river, as compared to the Amazon (Fig. 2), could account for the differences in the two trans-river analyses. Further information on this species is needed to

understand this difference in genetic differentiation across the Napo and Amazon rivers.

Population Substructuring

Although characterization of the amount of genetic variation within avian demes is informative, the amount of genetic variance partitioned among component populations of a species is important also for inferring modes of speciation (Barrowclough 1983). Among the three different F coefficients developed by Wright (1978) to describe the arrangement of genetic variation within a species, the coefficient F_{ST} is a measure of the genetic differentiation among populations. Values of F_{ST} can range from zero (no differences among populations) to one (fixation of alternate alleles apparent lack of gene exchange among populations).

F_{ST} values for the Amazonian species Pipra erythrocephala, Pipra coronata, Glyphorynchus spirurus, Pithys albifrons, and Myrmoborus myotherinus were calculated for north bank and trans-river populations, and for the north bank populations only (Tables 17, 18). These values are compared to those of temperate zone birds (Table 17) and those of non-Amazonian, tropical latitude birds (Table 18) using data from Barrowclough (1983). F_{ST} values for the Amazonian species average considerably higher (0.125 $\pm$ 0.065 s.d.) than the mean for birds (0.022 $\pm$ 0.011 s.d.) calculated principally from temperate zone species. Surprisingly, the F_{ST} values for the same-bank populations are also average higher (0.055 $\pm$ s.d.) for Amazonian species, although these populations are separated by less than 90 km of continuous forest.

Generally, greater geographic distance among compared samples increases F_{ST}, yet even distant samples of temperate zone birds, including trans-river populations, average lower than values for these Amazonian species, and thus indicates greater population subdivision and reduced gene flow. The only comparable values are those for Galapagos finches (Table 20). These birds are confined to the arid Galapagos Islands in the Pacific, which are separated by ocean barriers. Although their dispersal capability is high, as evidenced by their colonization of islands, they periodically go through population crashes which would lower their effective population size, and thus provide one mechanism for increasing F_{ST} values as discussed below.

Factors that can increase population subdivision as measured by F_{ST} include decreased effective population size and decreased effective dispersal distance. Effective population size refers to the actual number of individuals contributing to the gene pool of the subsequent generation. It is noteworthy that the two highest F_{ST} values belong to the manakins, which have an unusual polygynous social system (communal courtship in leks), and thus may have a low effective population size (Gilliard 1959, Snow 1971, Lill 1976). Effective dispersal distance refers to the distance moved between birth site and breeding site. The high F_{ST} values found for Glyphorynchus spirurus could be a consequence of decreased effective dispersal distance (i.e., increased sedentariness), although there are no data on dispersal distance with which to evaluate this explanation. In comparison, the

meaning of the low F_{ST} values for the antbirds, Pithys albifrons Myrmoborus myotherinus is unclear. Nevertheless, this analysis suggests that some understory terra firme forest birds are different in their demography or vagility from temperate zone birds.

Rivers versus Refugia

The riverine barrier and Pleistocene refugia hypotheses both state that rivers can serve as barriers, although they differ regarding the importance of the effect of rivers on Neotropical bird speciation. This makes it difficult to develop predictions to distinguish them. To explore this problem further, I will apply both theories to reconstruct the history of the three manakin taxa analyzed earlier, and will then develop predictions by which to test the competing historical hypotheses.

Under the Pleistocene refugia hypothesis, the progenitors of Pipra erythrocephala sensu lato and Chiroxiphia pareola were isolated in the Napo and Inambari refugia, respectively (Fig. 9), during the glacial periods of the Pleistocene. This geographic isolation permited differentiation. When the forest coalesced during the interglacial periods, either the Amazon was a sufficient barrier that neither species was able to cross or the Amazon was a partial barrier that limited crossing, and those that crossed possessed post-reproductive isolating mechanisms that prevented interbreeding. In contrast, under the riverine barrier hypothesis, the progenitors' ranges of these two manakins were fragmented by the formation of the Amazon. As the width of the

river and associated riverine habitat increased, these barriers prevented gene flow and thereby permitted differentiation.

The application of these two hypotheses to the Pipra coronata case requires further description of geographic variation within this species. Nominate coronata is the black-bodied subspecies found on both sides of the Amazon. As one proceeds further south of the Amazon, it is replaced by a green-bodied subspecies. The nature of the transition zone is unknown, but specimens taken in southern and northern Peru suggest that the zone is located in an area of central Peru where there is no known geographic barrier (Haffer 1970). Under the Pleistocene refugia hypothesis, the green subspecies originated in the Inambari refugium and the black subspecies in the Napo refugium. Because the latter is closer to the Amazon, when the forest re-expanded, the black-bodied subspecies could reach and cross the Amazon prior to the arrival of the northwardly expanding green-bodied subspecies. A contact zone presumably has formed in central Peru between these two subspecies.

The observation of phenotypic differentiation not congruent with a river conflicts with expectations under the riverine barrier hypothesis. The observation that two north bank manakins, Pipra erythrocephala and Chiroxiphia pareola napensis, did not cross the Amazon but that one north bank manakin, Pipra coronata, did cross conflicts with expectations under the refugia hypothesis. One can postulate differences in their dispersal capabilities, but there is no evidence with which to evaluate this

possibility. Instead, I shall present three predictions regarding the effect of refuges and rivers on allozymic variation that can be used to distinguish between the refugia and riverine hypotheses as applied to all three manakin taxa.

Prediction 1. Heterozygosity values will decrease outward from the core of the refugium. The expansion of the formerly restricted taxa into newly arising forest would involve a stepwise series of founder events. A transect through the refugium will find a central core of high heterozygosity with a decrease as one moves away from the core, assuming that the expanding peripheral populations have not reached equilibrium. This pattern is not expected under the riverine barrier hypothesis.

Prediction 2. The number of rare alleles will increase outward from the core of the refugium. If the founder populations are still increasing in number, then theoretical models predict that there will be an excess of rare alleles in those populations (Maruyama and Fuerst 1984). This prediction also assumes that the peripheral populations have not rebounded to reach an equilibrium. This pattern is not expected under the riverine barrier hypothesis.

Prediction 3. The calibrated genetic distance value between sister taxa separated by a river will be older under the riverine barrier hypothesis than the Pleistocene refugia hypothesis. This is because the development of the riverine system began in the Late Pliocene over 2 million years ago (m.y.a.), whereas the Pleistocene climatic fluctuations began 0.8 m.y.a. (Haffer 1974).

Of the three predictions, numbers 1 and 2 can only rule out the riverine hypothesis if a positive result is obtained. Negative results are consistent with both hypotheses if these populations have reached equilibrium. Prediction 3 can distinguish between these hypotheses regardless of the equilibrium complication. In addition, the data base presented in this study cannot be used to test the first two predictions because transects through putative refugia are lacking.

The neutral mutation model of the evolution of electrophoretic characters states that they evolve in a roughly time-dependent manner (Barrowclough 1983, Gûtierrez et al. 1983)). This has led to the utilization of genetic distances to date divergence events (Gûtierrez et al. 1983). Although this use is theoretically feasible, the choice of the proper calibration time remains controversial (Gûtierrez et al. 1983; Martin and Johnson 1986). I used a suggested value for birds of one unit of Nei's (1978) genetic distance equals 26.3 m.y.a. (Gûtierrez et al. 1983) to compute the divergence time between the three groups of Amazon-separated manakin taxa. The times calculated for Pipra erythrocephala/P. rubrocapilla, Chiroxiphia pareola napensis/C. p. regina, and Pipra coronata north bank/south bank sister taxa are 2.65, 1.73, and 0.92 m.y.a., respectively. These all predate the beginning of the Pleistocene climatic fluctuations, and thus the results based on this particular calibration value all support the riverine barrier hypothesis. Needed are additional comparisons and refined dating of the geological events in the Amazon, as well

as further calibration of the rate of change as measured by genetic distance.

There are other tests of refugia theory that do not rely on allozyme analysis. These involve examination of the geologic and biogeographic data used to infer the prior existence of refugia (Haffer 1969, 1974). It is clear from the geologic evidence that parts of South America outside of the basin were affected by the Pleistocene climatic fluctuations (Prance 1982). The only evidence from within the basin, however, is an undated core sample from Rondonia in southwestern Brazil (Colinvaux and Liu in press). Although this core does show forest alternating with savanna, it is not useful for inferring vegetational type in the basin as a whole, because Rondonia is on the periphery of the basin, near contemporary savanna, and a local alteration in vegetation cover could have occurred without affecting the basin as a whole. To date, no core samples from the Pleistocene have been taken from the interior of the basin, and therefore the evidence for the existence of extensive non-forest areas within Amazonia is weak (Colinvaux and Liu in press).

Liu and Colinvaux (1986) found that montane Andean forest covered most of the putative Napo refugium. Therefore, understory terra firme forest birds could not have inhabited that site. These authors argue that the decrease in precipitation was not sufficient to cause fragmentation of the forest and invasion by savanna. Instead, it was depression of average temperature that allowed life zones to decrease in altitude and thereby compress

the terra firme forest towards the center of its current distribution. Under this interpretation, forms that partially differentiated because of rivers, but were still crossing at the headwaters, would now be unable to cross the larger courses of the rivers downstream.

The utilization of current areas of high precipitation to map refugia (Haffer 1969) has been challenged by Colinvaux et al. (1985, in press). They reported fluctuations in precipitation in sedimentation patterns of local lakes that suggest variation in storm tracks over the basin. Areas of high precipitation within the basin have not been constant through time, and therefore past patterns cannot be inferred from present patterns. The impact of catastrophic Holocene flooding events because of Andean glacial lake release on putative refugia must be considered also (Campbell et al. 1985).

The evidence from biogeography does not strongly support refugia theory. Attempts to superimpose maps of endemism from different species show that there is no concordance (Beven et al. 1984). In addition, statistical analysis of the density of avian species' distributional boundaries show that they are distributed randomly and independently, contrary to the prediction of refugia theory (Beven et al. 1984). Other tests using biogeographic data cannot distinguish between the riverine and refugia hypothesis (e.g., Oren 1983, Mayr and O'Hara 1986) because equivalent distribution patterns are expected under both models.

The necessity for postulating the existence of forest refugia

in which Amazonian birds differentiated is due partially to the supposition that rivers are insufficient in themselves to induce speciation (Haffer 1974). The finding of congruence between genetic differentiation and rivers in Amazonian understory birds enhances the importance of rivers as barriers to gene flow. These data suggest that rivers serve a direct role in permitting speciation. Therefore, these results temper the postulation of Pleistocene refugia as causal factors for the high regional species diversity in Amazonia.

Conservation

The distinction between the riverine barrier hypothesis and the Pleistocene refugia hypothesis is important from the standpoint of conservation. Currently, the targeting of forest areas for reserves involves the determination of putative refugia because these are considered to be the source areas for the present-day biotic diversity (Wetterberg 1976; Gentry 1986). The documentation of the importance of rivers to genetic differentiation and the geologic evidence presented earlier casts doubt on the necessity for postulating refugia and the reality of such refugia. If refugia are not the centers of biotic diversity, then this method of identifying areas for preserves is ill-advised. If rivers are the chief agents enhancing regional species diversity, then only thorough inventory of many sites within the Amazon basin will permit the identification of regions of highest biotic diversity for preservation.

The increasing deforestation of the Neotropical terra firme

forest is leading to the fragmentation of formerly contiguous forest (see papers in Soulé 1986). This deforestation typically begins as road cuts and progresses to the clearing of forest flanking the roads for agriculture and settlements. These linear features resemble rivers in that they are open areas devoid of the appropriate vegetation and subject to high light levels. The finding that understory forest birds show substantial genetic differentiation across rivers, and that these same birds have substantial population subdivision, suggests that they are sensitive to discontinuities in the forest. There is evidence that Neotropical birds that inhabit the dark understory of terra firme forest will not cross light gaps associated with discontinuities in forest habitat (Terborgh 1975; Wilson and Willis 1975), including water gaps of as little as 500 meters (Willis 1974). This may be a consequence of negative phototaxis, negative reaction to microclimate changes in open areas, or increased vulnerability to predators. For these reasons, man-made fragmentation could be disrupting the genetic continuity of understory terra firme forest birds. Further studies of the genetic population structure and dynamics of this important component of the Neotropical avifauna must proceed to fully understand the management implications of the patterns documented in this study.

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TABLE 1. Dendrocolaptid (woodcreeper) taxa delimited by rivers (compiled from Peters 1951).

River	Number of taxa*
Amazon	41
Madeira	17
Tapajoz	11
Tocantins	8
Negro	7
Jamunda	5
Jari	3
Obidos	3
Xingu	1
Guama	1
Cataniapo	1
Juruá	1

*Many taxa have more than one river delimiting their range. Number of taxa incorporates a total of 50 independent taxa.

TABLE 2. Protein loci used in this study. Abbreviation, full name, Enzyme Commission number, and number of subunits are given (compiled from Harris and Hopkinson 1976).

ABBREV.	FULL NAME	E.C.#	#SUBUNITS
ACON-1,2	Aconitase	4.2.1.3	1
ADA	Adenosine Deaminase	3.5.4.4	1
AK	Adenylate Kinase	2.7.4.3	1
ALD	Aldolase	4.1.2.13	4
CK-1,2	Creatine Kinase	2.7.3.2	2
DIA-1,2,3	NADH Diaphorase	1.6.2.2	1
ESTN-1,2	Esterase, napthyl propionate substrate	3.1.1.1	1
EST-D	Esterase-D (uv stain)	3.1.1.1	2
FUM	Fumarase	4.2.1.2	4
GAPDH	Glyceraldehyde-phosphate Dehydrogenase	1.2.1.12	4
GLUD	Glutamate Dehydrogenase	1.4.1.3	?
GOT-1,2	Glutamate-oxaloacetate Transaminase	2.6.1.1	2
GPD	Glycerol-3-phosphate Dehydrogenase	1.1.1.8	2
GPT	Glutamate Pyruvate Transaminase	2.6.1.2	2
GSR	Glutathionine Reductase	1.6.4.2	2
HK	Hexokinase	2.7.1.1	1
ICD-1,2	Isocitrate Dehydrogenase	1.1.1.42	2
LA	Leucyl-alanine Dipeptidase	3.4.*.*	1
LAP	Leucine Aminopeptidase	3.4.*.*	1
LDH-1,2	Lactate Dehydrogenase	1.1.1.27	4
LGG	Leucyl-glycyine-glycine Tripeptidase	3.4.*.*	1

ABBREV.	FULL NAME	E.C.#	#SUBUNITS
MDH-1,2	Malate Dehydrogenase	1.1.1.37	2
ME	Malic Enzyme	1.1.1.40	4
MPI	Mannose Phosphate Isomerase	5.3.1.8	1
NP	Purine Nucleoside Phosphorylase	2.4.2.1	3
ODH	Octanol Dehydrogenase	1.1.1.1	2
PGD	Phosphogluconate Dehydrogenase	1.1.1.44	2
PGI	Phosphoglucose Isomerase	5.3.1.9	2
PGM-1,2	Phosphoglucomutase	2.7.5.1	1
PHEPRO	Phenylalanyl-proline Dipeptidase	3.4.*.*	2
PK	Pyruvate Kinase	2.7.1.40	4
SOD-1,2	Superoxide Dismutase	1.15.1.1	2
SDH	Sorbitol Dehydrogenase	1.1.1.14	4
VL	Valine-leucine Dipeptidase	3.4.*.*	2
XDH	Xanthine Dehydrogenase	?	?

TABLE 3. Number of loci and individuals analyzed per species.

SPECIES	INDIVIDUALS (Site #)	LOCI
Pipra coronata	30 (1)	32
	30 (2)	"
	30 (3)	"
	30 (4)	"
	30 (5)	"
Glyphorynchus spirurus	23 (1)	25
	22 (2)	"
	22 (3)	"
	24 (4)	"
	24 (5)	"
Myrmoborus myotherinus	11 (1)	27
	2 (2)	"
	11 (3)	"
	6 (5)	"
Pithys albifrons	13 (1)	31
	13 (2)	"
	13 (3)	"
	12 (4)	"

TABLE 4. Understory taxa delimited by the Napo and Amazon rivers, and number of specimens collected at each study site. Sites 1-3 are north bank sites. Site 4 is south bank Napo. Site 5 is south bank Amazon. Symbols: "-" = neither expected nor present; "?" = expected but not collected.

UNDERSTORY SPECIES	SITE 1	SITE 2	SITE 3	SITE 4	SITE 5
Phaethornis superciliosus moorei	2	24	19	-	-
Phaethornis superciliosus ucayali	-	-	-	-	13
Phaethornis bourcieri	11	12	9	7	-
Phaethornis philippi	-	-	-	-	25
Galbula albirostris chalcocephala	6	16	14	19	-
Galbula cyanicollis	-	-	-	-	25
Nonnula rubecula	4	2	2	-	5
Nonnula brunnea	-	-	-	-	4
Eubucco richardsoni nigriceps	1	4	-	-	-
Eubucco richardsoni richardsoni				1	
Eubucco richardsoni aurantiicollis	-	-	-	-	?
Dendrocolaptes certhia radiolatus	6	9	6	7	-
Dendrocolaptes certhia juruanus	-	-	-	-	7

UNDERSTORY SPECIES	SITE 1	SITE 2	SITE 3	SITE 4	SITE 5
Xiphorhynchus elegans ornatus	17	7	2	1	-
Xiphorhynchus spixii juruanus	-	-	-	-	41
Automolus ochrolaemus turdinus	8	0	0	2	-
Automolus ochrolaemus ochrolaemus	-	-	-	-	2
Thamnomanes ardesiacus ardesiacus	12	14	21	13	-
Thamnomanes saturninus	-	-	-	-	49
Thamnomanes caesius glaucus	22	17	24	10	-
Thamnomanes schistogynus	-	-	-	-	1
Myrmotherula menetriesii pallida	2	5	5	0	-
Myrmotherula menetriesii menetriesii	-	-	-	-	8
Cercomacra serva serva	4	7	0	0	-
Cercomacra serva hypomelaena	-	-	-	-	6
Hypocnemis cantator saturata	7	8	5	4	-
Hypocnemis cantator peruviana	-	-	-	-	8
Myrmeciza atrothorax tenebrosa	-	-	-	1	
Myrmeciza atrothorax obscurata	-	-	-	-	4
Gymnopithys leucaspis castanea	18	25	32	18	-
Gymnopithys salvini maculata	-	-	-	-	40

UNDERSTORY SPECIES	SITE 1	SITE 2	SITE 3	SITE 4	SITE 5
Rhegmatorhina melanosticta melanosticta		9	2	5	-
Rhegmatorhina melanosticta purusiana	-	-	-	-	4
Hylophylax poecilonota lepidonata	28	18	23	36	-
Hylophylax poecilonota gutturalis	-	-	-	-	16
Phlegopsis erythroptera erythroptera	0	3	6	11	-
Phlegopsis erythroptera ustulata	-	-	-	-	7
Myrmothera campanisona signata	4	3	-	-	-
Myrmothera campanisona minor	-	-	-	-	3
Conopophaga aurita occidentalis	5	12	18	-	
Conopophaga aurita australis	-	-	-	-	22
Conopophaga peruviana	-	-	-	9	-
Chiroxiphia pareola napensis	16	10	10	1	-
Chiroxiphia pareola regina	-	-	-	-	9
Pipra erythrocephala berlepschi	20	35	85	95	-
Pipra rubrocapilla	-	-	-	-	28
Lophotriccus vitiosus affinis	8	0	2	-	-
Lophotriccus vitiosus congener	-	-	-	-	7

UNDERSTORY SPECIES	SITE 1	SITE 2	SITE 3	SITE 4	SITE 5
Microbates collaris	-	7	12		
Microbates cinereiventris peruvianus	-	-	-	-	10
Lanio fulvus peruvianus	-	4	9	-	-
Lanio versicolor versicolor	-	-	-	-	7

TABLE 5. Heterozygosity values and per cent polymorphic loci (%P) in Amazon basin birds. N = number of individuals analyzed, S.E. = standard error.

Species	N	#loci	%P	Mean Heterozygosity ± S.E. Direct Count	Hardy-Weinberg Expected
FURNARIIDAE*@					
Synallaxis rutilans	5	30	23	0.08 ± 0.04	0.08 ± 0.03
TYRANNIDAE**$					
Mionectes macconnelli (Bolivia)	7	32	9	0.04 ± 0.03	0.04 ± 0.03
Mionectes oleaginea (Bolivia)	5	32	19	0.07 ± 0.03	0.07 ± 0.03
Mionectes oleaginea (Peru)	7	32	16	0.07 ± 0.03	0.08 ± 0.04
PIPRIDAE**					
Chiroxiphia pareola napensis	9	27	15	0.032 ± 0.028	0.050 ± 0.028
Pipra erythrocephala	10	27	22	0.052 ± 0.020	0.061 ± 0.027
Pipra rubrocapilla	3	27	15	0.056 ± 0.032	0.057 ± 0.027
Pipra coronata (1)***	30	31	26	0.028 ± 0.013	0.047 ± 0.021
" " (2)	30	31	19	0.036 ± 0.016	0.046 ± 0.021
" " (3)	30	31	19	0.030 ± 0.013	0.031 ± 0.013
" " (4)	30	31	23	0.068 ± 0.026	0.070 ± 0.026
" " (5)	30	31	19	0.046 ± 0.020	0.075 ± 0.029

Species	N	#loci	%P	Mean Heterozygosity + s.e. Direct Count	Hardy-Weinberg Expected
DENDROCOLAPTIDAE**					
Glyphorynchus spirurus (1)***	23	25	20	0.048 ± 0.038	0.048 ± 0.038
Glyphorynchus spirurus (2)	22	25	12	0.004 ± 0.004	0.032 ± 0.025
" " (3)	22	25	24	0.019 ± 0.009	0.055 ± 0.027
" " (4)	24	25	12	0.012 ± 0.009	0.022 ± 0.016
" " (5)	24	25	4	0.004 ± 0.004	0.022 ± 0.022
FORMICARIIDAE**					
Pithys albifrons (1)***	13	31	23	0.070 ± 0.030	0.061 ± 0.025
" " (2)	13	31	19	0.042 ± 0.020	0.053 ± 0.023
" " (3)	13	31	23	0.059 ± 0.022	0.068 ± 0.026
" " (4)	12	31	16	0.033 ± 0.022	0.041 ± 0.021
Myrmoborus myotherinus (1)***	11	27	33	0.085 ± 0.032	0.101 ± 0.035
" " (2)	2	27	19	0.074 ± 0.035	0.074 ± 0.031
" " (3)	11	27	30	0.085 ± 0.031	0.085 ± 0.032
" " (5)	6	27	26	0.073 ± 0.031	0.081 ± 0.031

*A locus was considered polymorphic if more than one allele was recorded.

**A locus was considered polymorphic if the frequency of the most common allele did not exceed 0.99.

***Numbers denote sites 1-5 as described previously.

@From Braun and Parker 1985.

$From Capparella and Lanyon 1985.

TABLE 6. Allele frequency data for 27 loci in Pipra erythrocephala (pooled samples from Sites 1-3) and in Pipra rubrocapilla (Site 5).

LOCUS	P. erythrocephala	P. rubrocapilla
ADA	a (0.889)	a (0.750)
	b (0.111)	b (0.250)
EST-D	a (0.150)	
	b (0.850)	b (1.000)
LGG	a (0.050)	
	b (0.950)	b (1.000)
ME		a (1.000)
	b (1.000)	
MPI	a (1.000)	a (0.833)
		b (0.167
NP		a (0.667)
	b (0.050)	
	c (0.900)	c (0.333)
	d (0.050)	
VL/LA	a (0.167)	
	a (0.833)	b (1.000)

LOCUS	P. erythrocephala	P. rubrocapilla
PGD		a (1.000)
	b (0.500)	
	c (0.250)	
	d (0.250)	
SOD-1		a (0.667)
	a (1.000)	
ACON-1	a (1.000)	a (1.000)
ACON-2	a (1.000)	a (1.000)
AK	a (1.000)	a (1.000)
ALD	a (1.000)	a (1.000)
CK-1	a (1.000)	a (1.000)
CK-2	a (1.000)	a (1.000)
GOT-1	a (1.000)	a (1.000)
GOT-2	a (1.000)	a (1.000)
LDH-1	a (1.000)	a (1.000)
LDH-2	a (1.000)	a (1.000)
MDH-1	a (1.000)	a (1.000)
MDH-2	a (1.000)	a (1.000)
ODH	a (1.000)	a (1.000)
PGI	a (1.000)	a (1.000)
PGM-1	a (1.000)	a (1.000)
PGM-2	a (1.000)	a (1.000)

TABLE 7. Allele frequency data for 27 loci in Chiroxiphia pareola napensis (pooled samples from Sites 1-3) and in Chiroxiphia pareola regina (Site 5).

LOCUS	C. p. napensis	C. p. regina
ADA	a (0.500)	
	b (0.125)	
	c (0.375)	c (1.000)
ME		a (0.333)
	b (1.000)	b (0.667)
NP	a (1.000)	a (0.500)
		b (0.500)
VL/LA	a (0.667)	a (1.000)
	b (0.333)	
PGD	a (0.111)	a (0.500)
	b (0.889)	b (0.500)
EST-D	a (1.000)	a (1.000)
LGG	a (1.000)	a (1.000)
SOD-1	a (1.000)	a (1.000)
ACON-1	a (1.000)	a (1.000)
AK	a (1.000)	a (1.000)
ALD	a (1.000)	a (1.000)
CK-1	a (1.000)	a (1.000)

LOCUS	C. p. napensis	C. p. regina
CK-2	a (1.000)	a (1.000)
GOT-1	a (1.000)	a (1.000)
GOT-2	a (1.000)	a (1.000)
ICD-1	a (1.000)	a (1.000)
ICD-2	a (1.000)	a (1.000)
LDH-1	a (1.000)	a (1.000)
LDH-2	a (1.000)	a (1.000)
MDH-1	a (1.000)	a (1.000)
MDH-2	a (1.000)	a (1.000)
ODH	a (1.000)	a (1.000)
PGI	a (1.000)	a (1.000)
PGM-1	a (1.000)	a (1.000)
VL	a (1.000)	a (1.000)

TABLE 8. Allele frequency data for 31 loci in 5 populations of Pipra coronata.

LOCUS	Site 1	Site 2	Site 3	Site 4	Site 5
ADA		a (0.019)	a (0.036)	a (0.050)	a (0.129)
	b (0.931)	b (0.907)	b (0.946)	b (0.767)	b (0.839)
	c (0.069)	c (0.074)	c (0.018)	c (0.183)	c (0.032)
EST-D	a (0.021)			a (0.019)	
	b (0.979)	b (1.000)	b (1.000)	b (0.926)	b (1.000)
				b (0.056)	
ICD-2	a (0.025)				
	b (0.975)	b (1.000)	b (1.000)	b (1.000)	b (1.000)
LGG	a (0.167)	a (0.159)	a (0.086)	a (0.173)	a (0.229)
	b (0.750)	b (0.795)	b (0.845)	b (0.827)	b (0.750)
	c (0.083)	c (0.045)	c (0.069)		c (0.021)
ME				a (0.125)	a (0.883)
				b (0.500)	b (0.100)
	c (0.966)	c (0.983)	c (0.931)	c (0.375)	c (0.017)
	d (0.034)	d (0.017)	d (0.069)		
NP	a (0.078)	a (0.050)	a (0.052)	a (0.150)	a (0.550)
	b (0.922)	b (0.950)	b (0.931)	b (0.800)	b (0.450)
			c (0.017)	c (0.050)	
PGM-1			a (0.038)		
	b (1.000)	b (1.000)	b (0.962)	b (1.000)	b (1.000)

LOCUS	Site 1	Site 2	Site 3	Site 4	Site 5
PHEPRO	a (0.500	a (0.500)		a (0.125)	a (0.375)
	b (0.500)	b (0.500)	b (1.000)	b (0.875)	b (0.625)
VL	a (0.038)	a (0.103)	a (0.097)	a (0.033)	a (0.315)
	b (0.942)	b (0.845)	b (0.855)	b (0.883)	b (0.630)
	c (0.019)	c (0.052)	c (0.048)	c (0.083)	c (0.056)
ACON-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ACON-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ACP	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
AK	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ALD	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
CK-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
DIA-3	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
FUM	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
GPD	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
GOT-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
GOT-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
HK	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
LAP	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
LDH	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
MDH-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
MDH-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
MPI	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ODH	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
PGD	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
PGM-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)

TABLE 9. Allele frequency data for 25 loci in 5 populations of *Glyphorynchus spirurus*.

LOCUS	Site 1	Site 2	Site 3	Site 4	Site 5
ICD-1				a (0.105)	a (0.579)
	b (0.595)	b (0.476)	b (0.533)	b (0.763)	b (0.316)
	c (0.357)	c (0.381)	c (0.333)	c (0.079)	c (0.053)
	d (0.048)	d (0.143)	d (0.133)	d (0.053)	d (0.053)
ICD-2	a (0.022)				
	b (0.978)	b (1.000)	b (1.000)	b (1.000)	b (1.000)
GOT-2			a (0.045)	a (0.042)	
	b (1.000)	b (1.000)	b (0.955)	b (0.958)	b (1.000)
MPI		a (0.045)	a (0.091)		
	b (0.522)	b (0.955)	b (0.909)	b (0.958)	b (1.000)
	c (0.478)			c (0.042)	
PGD	a (0.029)		a (0.194)		
	b (0.912)	b (0.938)	b (0.778)	b (1.000)	b (1.000)
	c (0.059)	c (0.063)	c (0.028)		
PGM-1	a (0.957)	a (1.000)	a (0.955)	a (1.000)	
	b (0.043)		b (0.045)		b (1.000)
LGG	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
FUM	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ME	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ESTN-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)

LOCUS	Site 1	Site 2	Site 3	Site 4	Site 5
SDH	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
MDH-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
GPD	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
LDH	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
SOD-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
PK	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
CK	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
LAP	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ALD	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
GLUD	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
PGI	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ODH	a (1.000)	a (1.000)	a (1.000)	a (1.000)	a (1.000)

TABLE 10. Allele frequency data for 27 loci in 4 populations of Myrmoborus myotherinus.

LOCUS	Site 1	Site 2	Site 3	Site 4
ADA	a (0.045)			
	b (0.864)	b (1.000)	b (1.000)	
	c (0.091)			c (1.000)
ICD-1				a (0.083)
	b (1.000)	b (1.000)	b (1.000)	b (0.917)
GOT-1	a (0.045)		a (0.045)	
	b (0.955)	b (1.000)	b (0.955)	b (1.000)
MDH-2	a (0.091)			
	b (0.909)	b (1.000)	b (1.000)	b (1.000)
SOD-1				a (0.417)
	b (1.000)	b (1.000)	b (1.000)	b (0.583)
GPD			a (0.045)	
	b (1.000)	b (1.000)	b (0.955)	b (1.000)
ESTN-1	a (0.091)		a (0.045)	
	b (0.455)	b (0.250)	b (0.318)	
	c (0.455)	b (0.750)	b (1.000)	
PGI	a (0.045)			
	b (0.636)	b (0.750)	b (0.545)	b (0.917)
	c (0.318)	c (0.250)	c (0.455)	c (0.083)

LOCUS	Site 1	Site 2	Site 3	Site 4
GPD	a (1.000)	a (1.000)	a (1.000)	a (0.500)
				b (0.500)
VL	a (1.000)	a (1.000)	a (0.955)	a (1.000)
			b (0.045)	
PGM				a (0.083)
	b (0.955)	b (0.750)	b (1.000)	b (0.917)
	c (0.045)	c (0.250)		
PGD	a (0.944)	a (1.000)	a (0.850)	a (1.000)
	b (0.056)		b (0.150)	
NP			a (0.091)	a (0.083)
	b (0.409)	b (0.500)	b (0.182)	b (0.083)
	c (0.591)	c (0.500)	c (0.727)	c (0.833)
LGG			a (0.045)	
	b (0.409)	b (0.250)	b (0.182)	b (0.333)
	c (0.591)	b (0.750)	c (0.773)	c (0.667)
ICD-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)
GOT-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)
MDH-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)
SOD-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)
MPI	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ODH	a (1.000)	a (1.000)	a (1.000)	a (1.000)
HK	a (1.000)	a (1.000)	a (1.000)	a (1.000)
FUM	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ESTN-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)

LOCUS	Site 1	Site 2	Site 3	Site 4
LDH	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ACP	a (1.000)	a (1.000)	a (1.000)	a (1.000)
CK	a (1.000)	a (1.000)	a (1.000)	a (1.000)
AK	a (1.000)	a (1.000)	a (1.000)	a (1.000)

TABLE 11. Allele frequency data for 31 loci in 4 populations of *Pithys albifrons*.

LOCUS	Site 1	Site 2	Site 3	Site 4
ADA	a (1.000)	a (1.000)	a (1.000)	a (0.958)
				b (0.042)
ESTN	a (0.654)	a (0.654)	a (0.885)	a (1.000)
	b (0.346)	b (0.346)	b (0.115)	
GPD	a (1.000)	a (1.000)	a (1.000)	a (0.900)
				b (0.100)
ICD-1	a (0.308)	a (0.154)	a (0.333)	a (0.050)
	b (0.692)	b (0.846)	b (0.667)	b (0.950)
MDH-1	a (0.045)			
	b (0.955)	b (1.000)	b (1.000)	b (1.000)
ME	a (0.462)	a (0.462)	a (0.429)	0.417)
	b (0.538)	b (0.538)	b (0.571)	b (0.583)
NP		a (0.125)	a (0.154)	a (0.182)
	b (0.917)	b (0.875)	b (0.803)	b (0.727)
	c (0.083)		c (0.038)	c (0.091)
PGM-1	a (0.038)	a (0.038)		
	b (0.962)	b (0.962)	b (1.000)	b (1.000)
PGM-2	a (0.115)	a (0.077)	a (0.192)	
	b (0.885)	b (0.923)	b (0.808)	b (1.000)

LOCUS	Site 1	Site 2	Site 3	Site 4
VL	a (1.000)	a (1.000)	a (0.962)	a (1.000)
			b (0.038)	
SOD-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)
SOD-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ESTD	a (1.000)	a (1.000)	a (1.000)	a (1.000)
MPI	a (1.000)	a (1.000)	a (1.000)	a (1.000)
LAP	a (1.000)	a (1.000)	a (1.000)	a (1.000)
GOT-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)
LDH-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)
LDH-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)
LGG	a (1.000)	a (1.000)	a (1.000)	a (1.000)
PP	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ESTN-1	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ODH	a (1.000)	a (1.000)	a (1.000)	a (1.000)
GPD	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ALD	a (1.000)	a (1.000)	a (1.000)	a (1.000)
MDH-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)
PK	a (1.000)	a (1.000)	a (1.000)	a (1.000)
SDH	a (1.000)	a (1.000)	a (1.000)	a (1.000)
ICD-2	a (1.000)	a (1.000)	a (1.000)	a (1.000)
GPT	a (1.000)	a (1.000)	a (1.000)	a (1.000)

TABLE 12. Matrix of genetic distance (Rogers' D above diagonal, Nei's D below diagonal) for Pipra erythrocephala/rubrocapilla and Chiroxiphia pareola napensis/regina. North bank samples were pooled.

TAXON	P. erythro	P. rubro
P. erythrocephala	-----	0.140
P. rubrocapilla	0.101	-----

TAXON	C. p. napensis	C. p. regina
C. p. napensis	-----	0.075
C. p. regina	0.066	-----

TABLE 13. Matrix of genetic distance (Rogers' D above diagonal, Nei's D below diagonal) for Pipra coronata.

	GENETIC DISTANCE				
SAMPLE (Site #)	1	2	3	4	5
North Amazon (1)	-----	0.008	0.028	0.045	0.066
North Amazon (2)	0.000	-----	0.024	0.044	0.062
North Amazon (3)	0.007	0.006	-----	0.026	0.073
South Napo (4)	0.014	0.014	0.011	-----	0.062
South Amazon (5)	0.038	0.038	0.042	0.023	-----

TABLE 14. Matrix of genetic distance (Rogers' D above diagonal, Nei's D below diagonal) for Glyphorynchus spirurus.

	GENETIC DISTANCE				
SAMPLE (Site #)	1	2	3	4	5
North Amazon (1)	-----	0.026	0.031	0.035	0.081
North Amazon (2)	0.008	-----	0.017	0.018	0.064
North Amazon (3)	0.008	0.000	-----	0.026	0.073
South Napo (4)	0.010	0.004	0.004	-----	0.062
South Amazon (5)	0.059	0.052	0.050	0.050	-----

TABLE 15. Matrix of genetic distance (Rogers' D above diagonal, Nei's D below diagonal) for Myrmoborus myotherinus.

	GENETIC DISTANCE			
SAMPLE (Site #)	1	2	3	5
North Amazon (1)	-----	0.042	0.042	0.122
North Amazon (2)	0.000	-----	0.044	0.115
North Amazon (3)	0.002	0.000	-----	0.123
South Amazon (5)	0.063	0.054	0.067	-----

TABLE 16. Matrix of genetic distance (Rogers' D above diagonal, Nei's D below diagonal) for Pithys albifrons.

SAMPLE (Site #)	1	2	3	4
North Amazon (1)	-----	0.011	0.025	0.038
North Amazon (2)	0.000	-----	0.027	0.028
North Amazon (3)	0.001	0.002	-----	0.033
South Napo (4)	0.006	0.004	0.003	-----

TABLE 17. F_{ST} comparison between Amazonian and temperate (Barrowclough 1983) species. Value in parentheses for Amazonian species is F_{ST} when across-river populations are included.

AMAZONIAN SPECIES	F_{ST}	MAXIMUM DISTANCE (km) BETWEEN SAMPLES
Pipra erythrocephala	0.098 (0.166)	80
Pipra coronata	0.090	80
Glyphorynchus spirurus	0.073	80
Pithys albifrons	0.010 (0.033)	80
Myrmoborus myotherinus	0.002 (0.177)	80

TEMPERATE SPECIES	F_{ST}	MAXIMUM DISTANCE (km) BETWEEN SAMPLES
Zonotrichia leucophrys	0.032	1200
Picoides borealis	0.024	150
Melospiza georgiana	0.024	2300
Sphyrapicus nuchalis	0.019	1400
Passerella iliaca	0.016	1300

TABLE 18. F_{ST} comparison between Amazonian and non-Amazonian (Barrowclough 1983) species. Value in parentheses for Amazonian species is F_{ST} when across-river populations are included.

AMAZONIAN SPECIES	F_{ST}	MAXIMUM DISTANCE (km) BETWEEN SAMPLES
Pipra erythrocephala	0.098 (0.166)	80
Pipra coronata	0.090	80
Glyphorynchus spirurus	0.073	80
Pithys albifrons	0.010 (0.033)	80
Myrmoborus myotherinus	0.002 (0.177)	80

NON-AMAZONIAN SPECIES	F_{ST}	MAXIMUM DISTANCE (km) BETWEEN SAMPLES
Certhidea olivacea	0.125	300
Geospiza fortis	0.065	300
Camarhynchus parvulus	0.057	300
Geospiza fuliginosa	0.054	300
Geospiza magnirostris	0.046	300
Geospiza scandens	0.020	300
Zonotrichia capensis	0.015	20

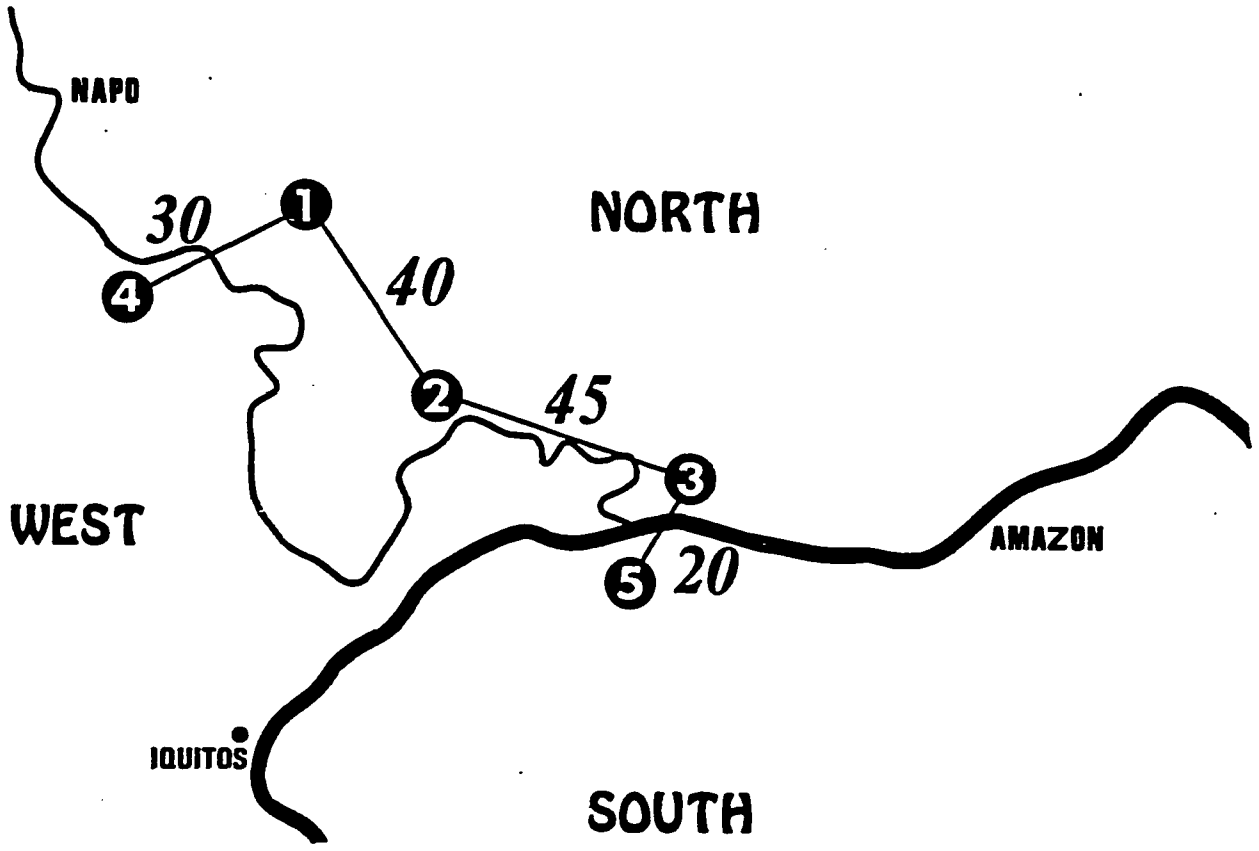

Figure 1. Location of study sites. The study area is in northeastern Peru in the region of the confluence of the Napo and Amazon rivers. Sample localities are 1 through 5. Distances (within 5 km) are straight-line except for that between sites 2 and 3, which was measured around a small stream.

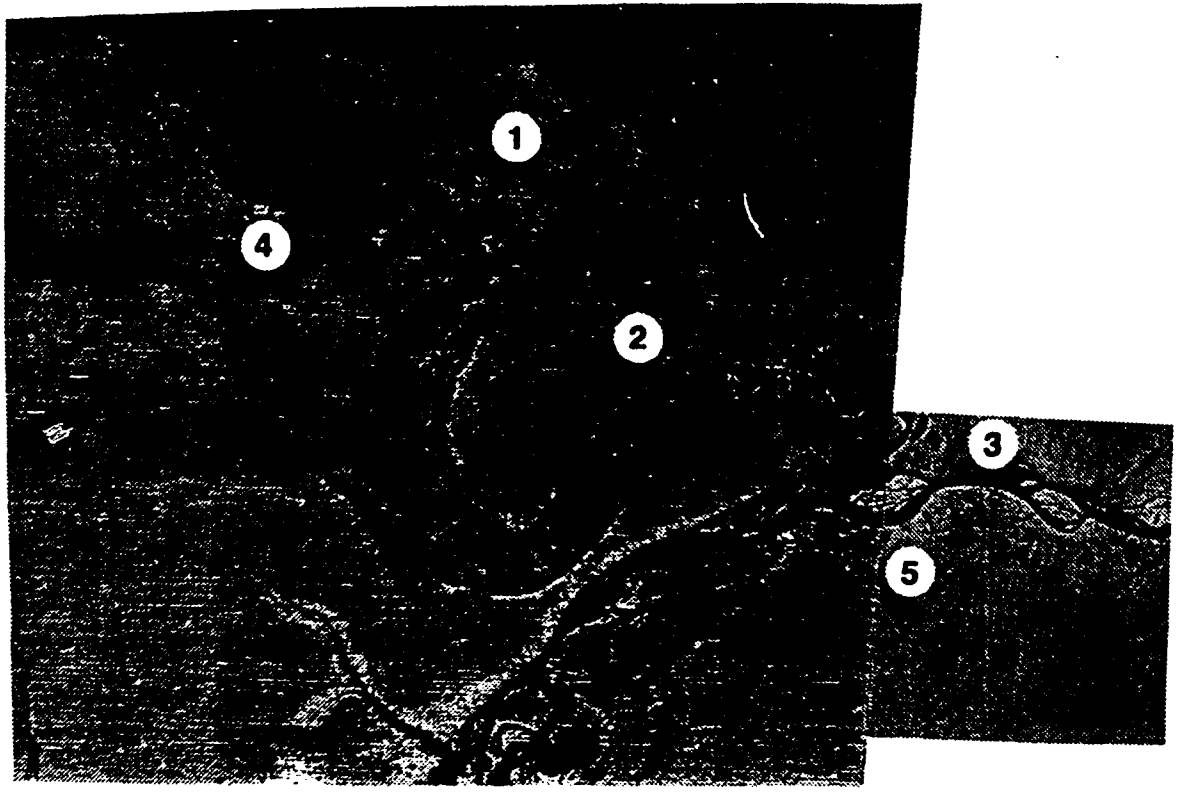

Figure 2. Landsat images of study area. This composite of two Landsat images shows the location of the five sampling localities, the width of the rivers, and the presence of riverine habitats and terra firme forest. Scale is 1 mm : 80 km.

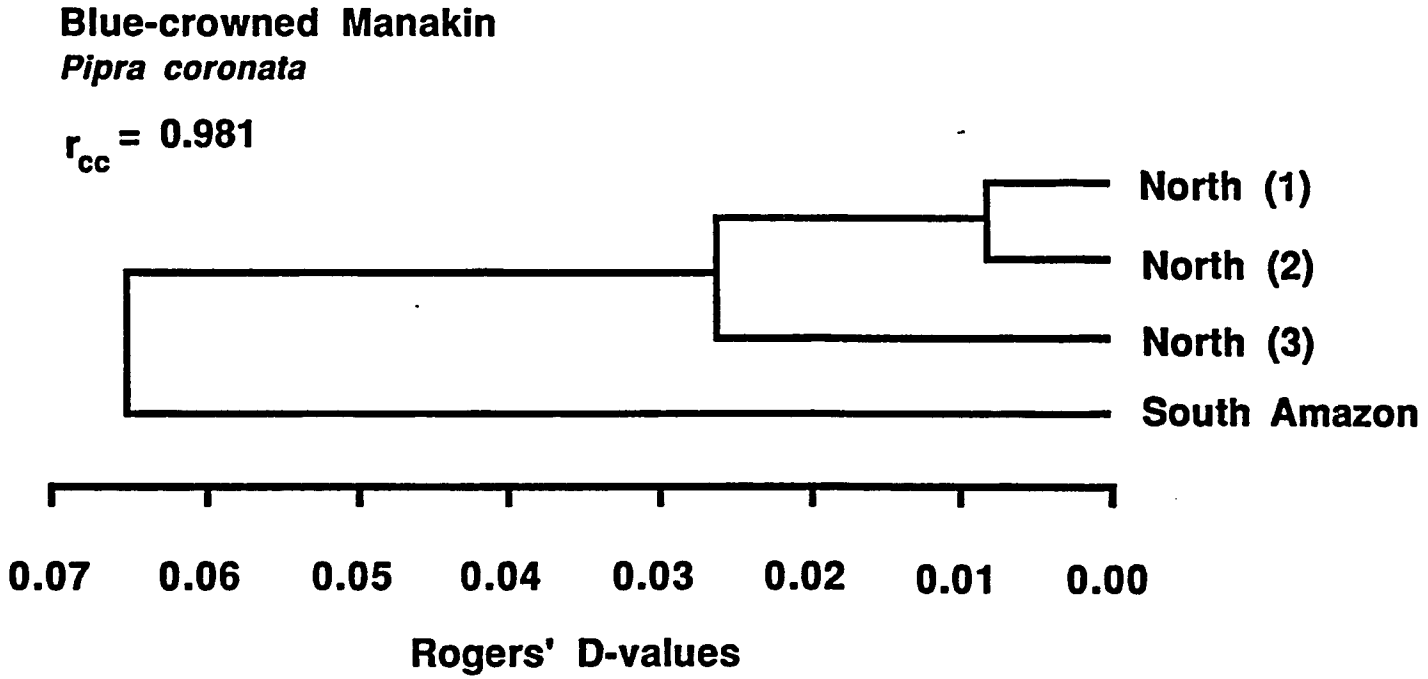

Figure 3. UPGMA phenogram for Pipra coronata samples compared across the Amazon River.

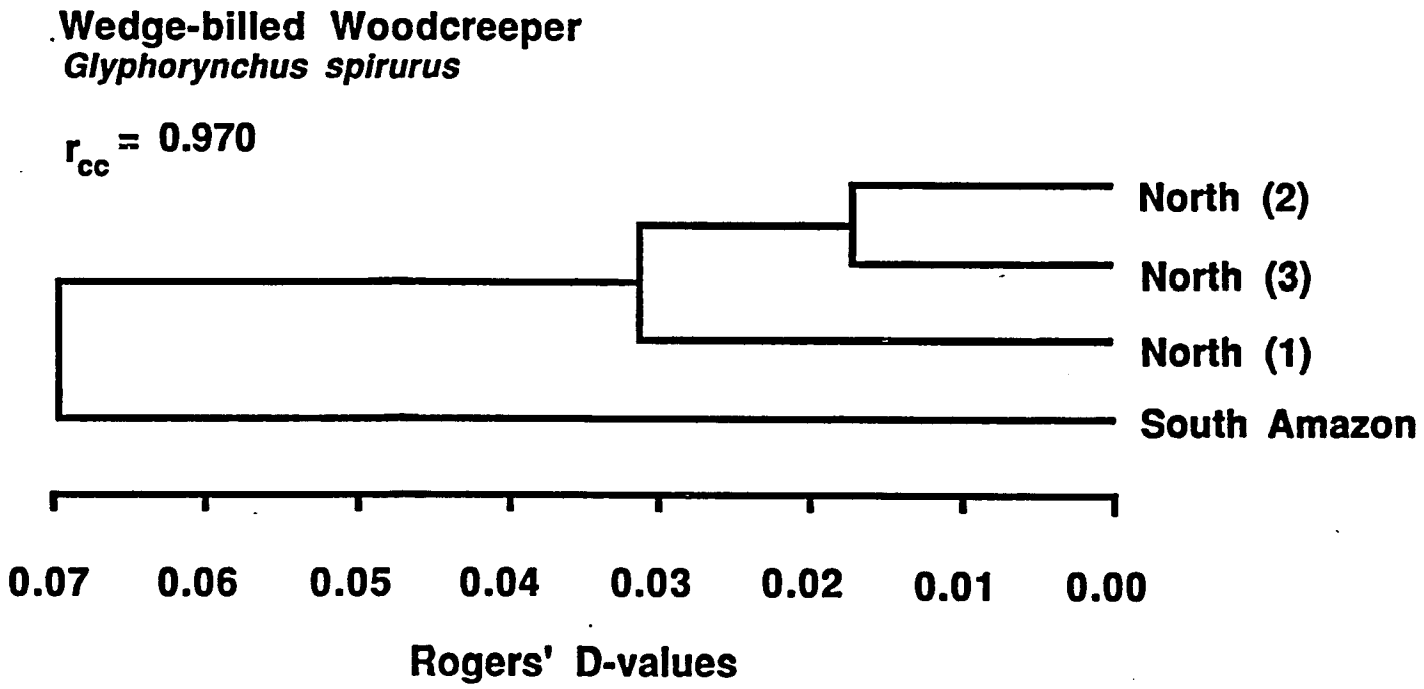

Figure 4. UPGMA phenogram for Glyphorynchus spirurus samples compared across the Amazon River.

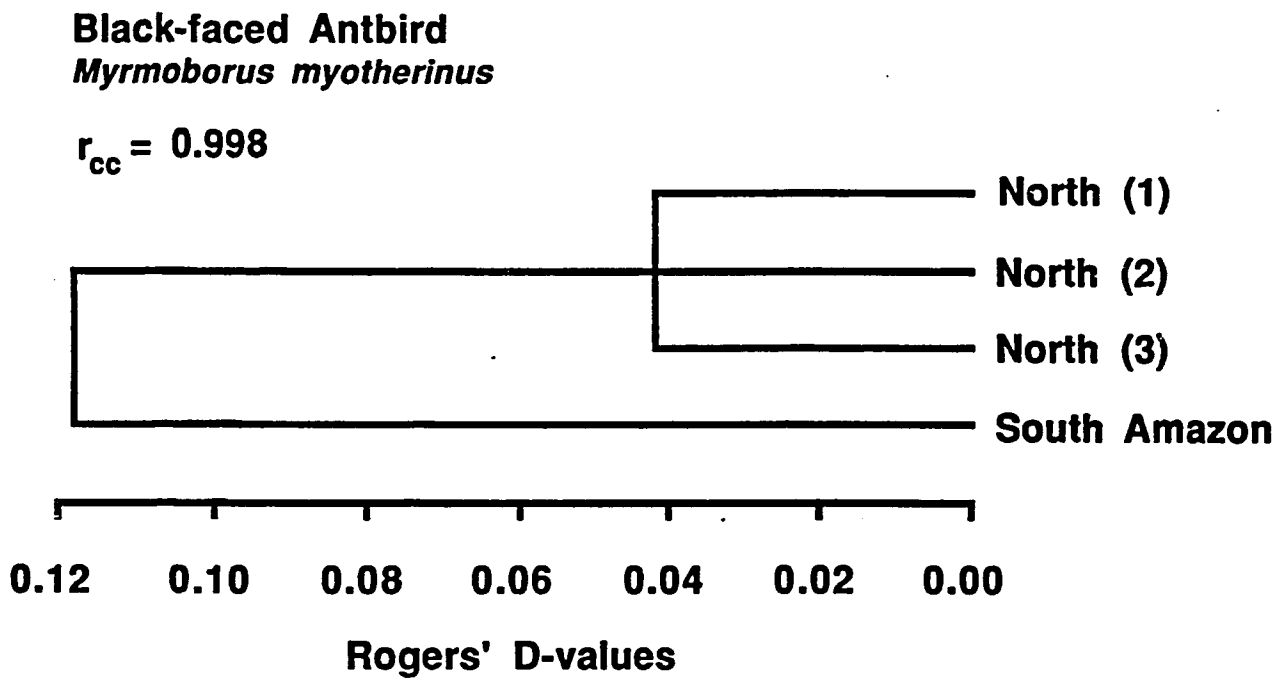

Figure 5. UPGMA phenogram for Myrmoborus myotherinus samples compared across the Amazon River.

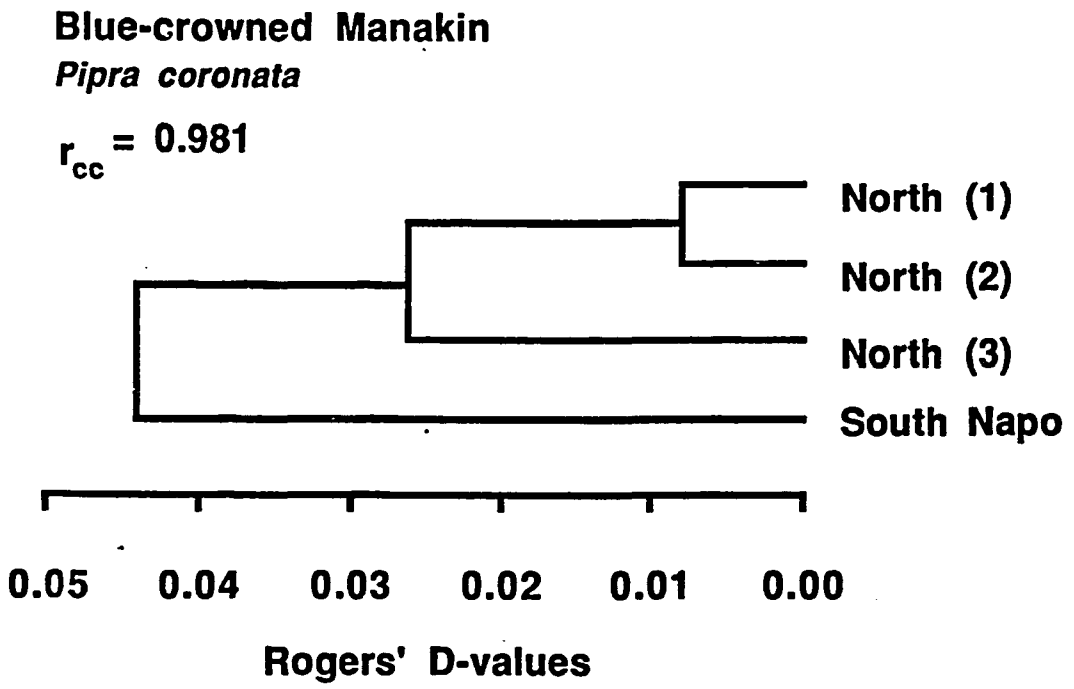

Figure 6. UPGMA phenogram for Pipra coronata samples compared across the Napo River.

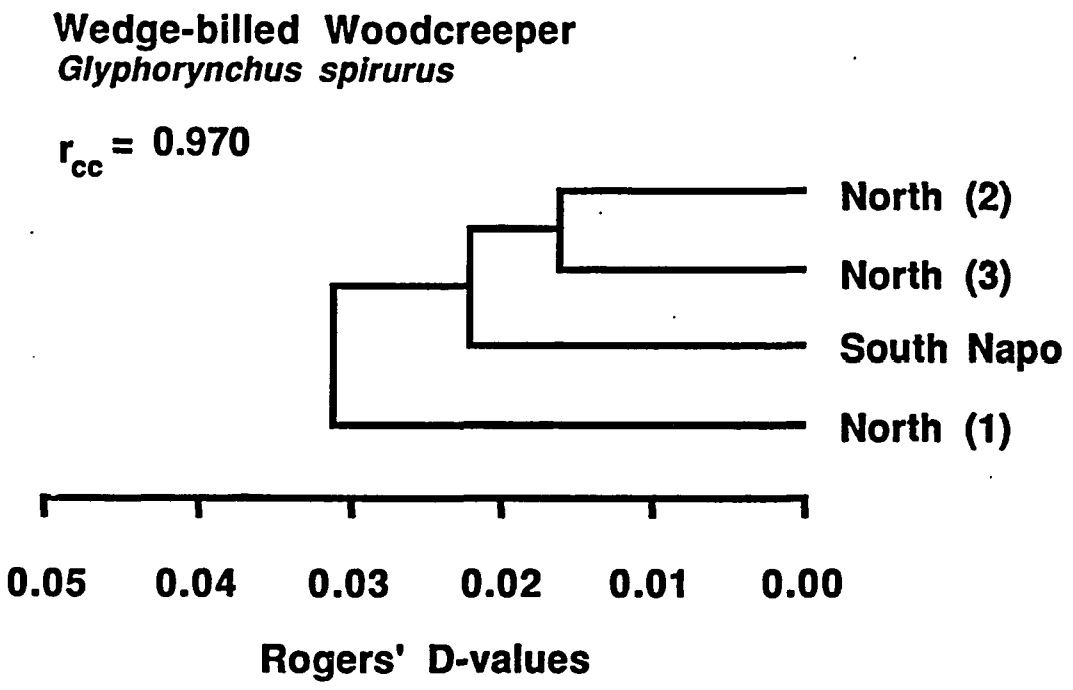

Figure 7. UPGMA phenogram for Glyphorynchus spirurus compared across the Napo River.

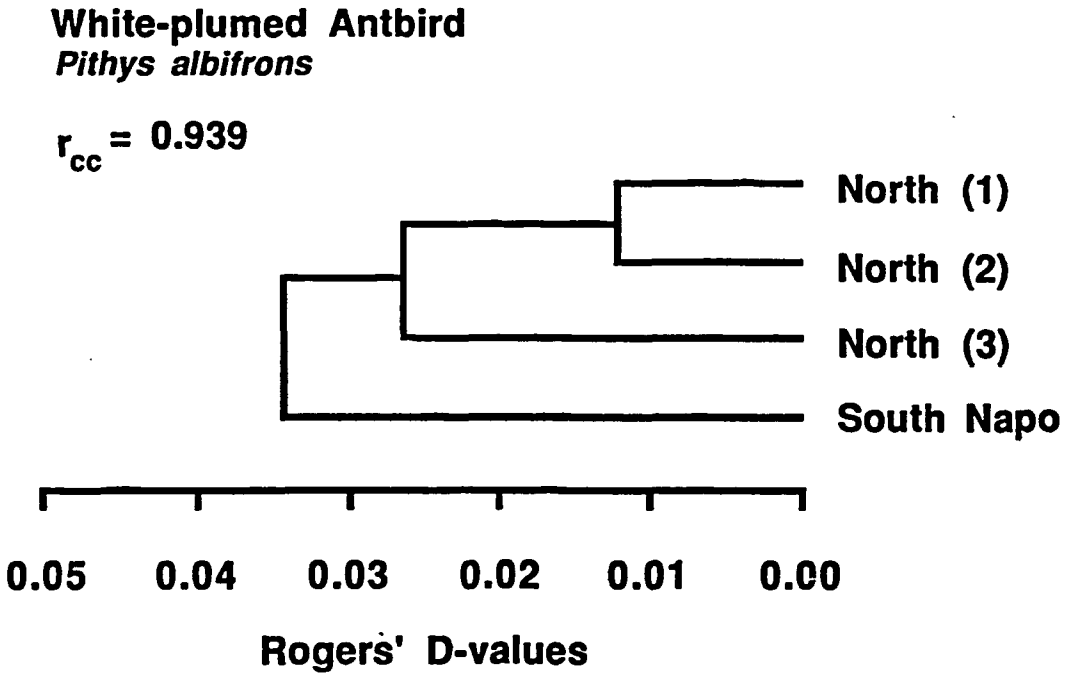

Figure 8. UPGMA phenogram for Pithys albifrons compared across the Napo River.

Figure 9. Map of proposed western Amazonian refugia (Napo and Inambari; from Haffer 1974).

Appendix. List of all species collected at sites 1 through 5.

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Tinamus major peruvianus	2	—	—	1	—
Tinamus guttatus	1	—	1	1	1
Crypturellus soui nigriceps	—	—	—	1	1
Crypturellus bartletti	2	—	—	2	1
Crypturellus variegatus	—	—	—	—	1
Agamia agami	—	—	—	1	—
Cathartes melambrotus	—	1	1	1	—
Leptodon cayanensis	—	—	1	1	—
Harpagus bidentatus bidentatus	2	—	1	2	3
Accipiter bicolor	—	—	—	1	—
Buteo magnirostris	—	1	—	—	1
Leucopternis albicollis albicollis	—	1	—	—	—
Leucopternis melanops	1	—	1	—	—
Leucopternis kuhli	—	—	—	—	2
Leucopternis schistacea	—	—	—	—	1
Morphnus guianensis	—	—	—	—	1
Harpia harpyja	—	—	—	1	—
Geranospiza caerulescens	1	—	—	—	—
Herpetotheres cachinnans	—	—	—	—	1
Micrastur mirandollei	—	—	—	—	12
Micrastur ruficollis	—	—	—	1	—
Micrastur gilvicollis	—	—	—	1	2

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Daptrius ater	1	—	—	1	—
Daptrius americanus	—	—	—	1	1
Milvago chimachima	—	1	—	—	—
Penelope jacquacu jacquacu	1	—	—	2	—
Nothocrax urumutum	—	—	—	1	—
Aramides cajanea cajanea	2	—	—	1	—
Anurolimnas castaneiceps castaneiceps	—	1	—	1	—
Heliornis fulica	—	—	—	1	—
Columba plumbea bogotensis	—	2	—	1	—
Columba plumbea delicata	—	—	—	—	1
Leptotila rufaxilla	1	—	—	—	1
Geotrygon montana	10	4	4	13	9
Ara macao	2	—	—	—	—
Aratinga weddellii	—	—	—	—	1
Pyrrhura picta	—	—	—	—	3
Pyrrhura melanura	1	—	6	2	—
Brotogeris cyanoptera cyanoptera	2	2	—	—	—
Touit huetii	2	—	—	—	—
Pionites melanocephala pallida	1	3	2	—	—
Pionites leucogaster xanthomeria	—	—	—	—	7
Amazona farinosa	—	—	—	—	1
Piaya cayana	1	2	1	2	1
Piaya melanogaster	—	1	2	1	—
Crotophaga major	1	—	—	—	—
Crotophaga ani	—	—	—	—	1

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Neomorphus pucheranii	1	—	—	—	1
Otus watsonii	2	2	1	1	2
Lophostrix cristata	1	—	—	—	—
Pulsatrix perspicillata	—	1	—	—	—
Ciccaba virgata	1	—	—	—	1
Nyctibius bracteatus	1	—	—	—	—
Lurocalis semitorquatus	—	—	—	1	—
Nyctidromus albicollis albicollis	1	1	—	—	2
Chaetura brachyura	—	—	—	—	1
Tachornis squamata	—	1	—	—	1
Glaucis hirsuta	—	1	4	—	1
Threnetes leucurus cervinicauda	5	4	5	7	9
Phaethornis superciliosus moorei	2	24	17	—	—
Phaethornis superciliosus ucayali	—	—	—	—	10
Phaethornis hispidus	—	2	—	6	4
Phaethornis bourcieri	9	12	8	7	—
Phaethornis philippi	—	—	—	—	23
Phaethornis ruber nigricinctus	—	1	1	1	—
Phaethornis longuemareus atrimentalis	—	—	—	5	—
Campylopterus largipennis aequatorialis	1	4	—	1	—
Florisuga mellivora	—	1	—	2	2
Anthracothorax nigricollis nigricollis	—	—	—	—	2
Popelairia langsdorffi melansternon	—	—	—	1	—
Chlorostilbon mellisugus	—	—	—	—	1
Thaluranis furcata viridipectus	3	4	2	2	12

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Amazilia fimbriata	—	—	—	1	2
Polyplancta aurescens	2	—	—	2	9
Heliodoxa schreibersii schreibersii	3	—	—	1	—
Heliothryx aurita	—	—	1-	—	—
Pharomachrus pavoninus	1	—	—	—	6
Trogon melanurus melanurus	—	1	1	1	2
Trogon viridis	4	—	1	3	2
Trogon collaris castaneus	2	—	—	1	—
Trogon rufus sulphurens	6	—	1	3	1
Trogon curucui peruvianus	1	1	—	—	—
Trogon violaceus crissalis	—	1	—	—	—
Ceryle torquata	—	—	1	—	—
Chloroceryle americana	—	—	—	1	—
Chloroceryle inda inda	3	1	3	2	—
Chloroceryle aenea aenea	5	3	1	5	7
Electron platyrhynchum pyrrholaemum	—	—	—	2	—
Baryphthengus martii	—	5	6	4	1
Momotus momota	5	—	—	3	—
Galbula albirostris chalcocephala	5	13	11	19	—
Galbula cyanicollis	—	—	—	—	23
Galbula chalcothorax	—	3	—	2	—
Galbula dea	—	—	—	—	5
Jacamerops aurea isidori	2	—	—	3	2
Notharchus macrorhynchus hyperrynchus	—	—	—	—	2
Bucco macrodactylus	1	3	1	—	1

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Bucco tamatia	—	—	—	—	1
Bucco capensis	6	4	4	5	5
Malacoptila fusca fusca	1	8	11	12	—
Malacoptila rufa rufa	1	—	—	—	—
Micromonacha lanceolata	3	1	—	—	—
Nonnula rubecula cineracea	4	2	2	—	5
Nonnula brunnea	—	—	—	4	—
Monasa nigrifrons nigrifrons	2	—	—	2	2
Monasa morphoeus peruana	—	1	2	4	1
Monasa flavirostris	—	—	4	6	—
Capito aurovirens	—	—	—	1	3
Capito niger	6	3	8	1	5
Eubucco richardsoni nigriceps	1	3	—	—	—
Eubucco richardsoni richardsoni	—	—	—	1	—
Pteroglossus pluricinctus	—	1	3	1	—
Pteroglossus flavirostris flavirostris	1	—	2	8	2
Pteroglossus beauharnaesii	—	—	—	—	4
Selenidera reinwardtii	1	3	—	3	—
Ramphastos vitellinus culminatus	2	2	2	—	—
Ramphastos tucanus cuvieri	1	1	—	—	—
Picumnus borbae juruanus	—	—	—	—	1
Picumnus aurifrons lafresnayi	—	—	—	1	—
Colaptes punctigula	—	—	—	1	—
Piculus flavigula flavigula	2	—	1	2	1
Piculus chrysochloros capistratus	3	1	1	8	—

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Celeus elegans	3	1	1	2	—
Celeus grammicus grammicus	3	2	10	2	1
Celeus flavus peruvianus	3	—	—	—	—
Dryocopus lineatus	—	—	—	1	—
Melanerpes cruentatus extensus	—	1	1	2	—
Veniliornis affinis hilaris	—	1	2	2	1
Phloeoceastes melanoleucos melanoleucos	—	1	—	—	—
Phloeoceastes rubricollis trachelopyrus	1	1	—	1	2
Dendrocincla fuliginosa phaeochroa	8	5	6	13	9
Dendrocincla merula bartletti	10	5	4	1	12
Deconychura longicauda connectens	—	—	—	2	5
Deconychura stictolaema secunda	3	4	6	4	10
Sittasomus griseicapillus amazonus	—	1	—	1	—
Glyphorynchus spirurus catelnaudii	76	79	122	34	54
Nasica longirostris	1	—	—	4	1
Dendrexetastes rufigula devillei	1	—	—	—	—
Xiphocolaptes promeropirhynchus berlepschi	1	—	—	—	—
Dendrocolaptes certhia radiolatus	3	7	5	7	—
Dendrocolaptes certhia juruanus	—	—	—	—	4
Dendrocolaptes picumnus validus	—	—	1	—	—
Xiphorhynchus picus peruvianus	—	—	—	—	3
Xiphorhynchus obsoletus palliatus	7	—	—	2	1
Xiphorhynchus ocellatus	3	6	10	10	4
Xiphorhynchus spixii juruanus	—	—	—	—	35
Xiphorhynchus elegans ornatus	13	6	1	1	—

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Xiphorhynchus guttatus guttatoides	5	9	6	10	6
Lepidocolaptes albolineatus fuscicapillus	—	—	—	3	—
Campylorhamphus trochilirostris napensis	—	—	—	2	—
Campylorhamphus procurvoides	—	—	3	—	—
Synallaxis rutilans caquetensis	—	4	—	4	—
Cranioleuca gutturata	1	—	1	—	2
Hyloctistes subulatus subulatus	1	—	5	1	6
Ancistrops strigilatus strigilatus	—	—	2	7	—
Philydor erythrocercus subfulvus	2	—	5	—	1
Philydor pyrrhodes	7	3	4	5	3
Philydor erythropterus erythropterus	—	—	1	—	—
Philydor ruficaudatus	—	—	1	—	—
Automolus infuscatus infuscatus	9	11	10	15	8
Automolus rubiginosus	—	3	—	—	—
Automolus ochrolaemus turdinus	7	—	—	2	—
Automolus ochrolaemus ochrolaemus	—	—	—	—	1
Xenops milleri	1	—	—	—	5
Xenops tenuirostris	—	—	—	—	1
Xenops minutus obsoletus	8	9	7	5	9
Sclerurus rufigularis	1	1	2	4	8
Sclerurus caudacutus brunneus	1	1	2	—	3
Cymbilaimus lineatus intermedius	3	1	1	2	5
Frederikena unduligera	3	2	—	6	3
Taraba major melanurus	1	1	—	1	—
Thamnophilus aethiops kapouni	—	—	—	—	4

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Thamnophilus schistaceus capitalis	8	5	2	3	—
Thamnophilus murinus canipennis	2	7	6	4	8
Pygiptila stellaris maculipennis	4	6	—	1	4
Megastictus margaritatus	7	—	9	5	—
Neoctantes niger	2	1	—	3	2
Thamnomanes ardesiacus ardesiacus	9	11	18	13	—
Thamnomanes saturninus	—	—	—	—	44
Thamnomanes caesius glaucus	22	17	24	10	—
Thamnomanes schistogynus	—	—	—	—	1
Myrmotherula brachyura brachyura	—	1	—	5	2
Myrmotherula obscura	2	—	—	7	1
Myrmotherula surinamensis multostriata	2	—	—	—	—
Myrmotherula hauxwelli suffusa	15	5	10	10	—
Myrmotherula haematonota haematonota	2	4	4	6	21
Myrmotherula axillaris melaena	13	28	15	17	13
Myrmotherula longipennis	—	—	2	7	—
Myrmotherula menetriesii pallida	2	5	4	—	—
Myrmotherula menetriesii menetriesii	—	—	—	—	5
Dichrozona cincta	3	2	2	2	7
Cercomacra cinerascens	1	2	2	2	—
Cercomacra serva serva	3	5	—	—	—
Cercomacra serva hypomelaena	—	—	—	—	4
Myrmoborus myotherinus napensis	17	12	16	24	7
Hypocnemis cantator saturata	5	6	4	4	—
Hypocnemis cantator peruviana	—	—	—	—	5

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Hypocnemis hypoxantha hypoxantha	17	7	9	—	8
Hypocnemoides melanopogon	6	—	—	6	—
Percnostola rufifrons	—	—	8	—	—
Percnostola schistacea	—	1	5	—	9
Percnostola leucostigma subplumbea	3	7	4	11	1
Sclateria naevia argentata	3	2	2	5	1
Myrmeciza hemimelaena hemimelaena	—	—	—	—	11
Myrmeciza hyperythra	—	—	—	6	—
Myrmeciza melanoceps	—	—	—	6	1
Myrmeciza fortis fortis	6	2	8	8	12
Myrmeciza atrothorax tenebrosa	—	—	—	1	—
Myrmeciza atrothorax obscurata	—	—	—	—	3
Pithys albifrons brevibarba	29	20	29	13	—
Gymnopithys salvini maculata	—	—	—	—	37
Gymnopithys lunulata	—	—	—	3	—
Gymnopithys leucaspis castanea	14	18	30	18	—
Rhegmatorhina melanosticta melanosticta	6	1	3	—	—
Rhegmatorhina melanosticta purusiana	—	—	—	—	2
Hylophylax naevia theresae	6	3	6	5	12
Hylophylax punctulata punctulata	8	—	—	3	—
Hylophylax poecilonota lepidonata	23	15	21	36	—
Hylophylax poecilonota gutturalis	—	—	—	—	13
Phlegopsis nigromaculata nigromaculata	—	3	1	7	—
Phlegopsis erythroptera erythroptera	—	2	5	11	—
Phlegopsis erythroptera ustulata	—	—	—	—	4

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Chamaeza nobilis rubida	—	—	1	1	—
Chamaeza nobilis nobilis	—	—	—	—	1
Formicarius colma nigrifrons	10	—	1	11	4
Formicarius analis zamorae	1	—	—	5	—
Myrmornis torquata torquata	—	—	—	1	—
Grallaria varia	—	1	—	—	—
Myrmothera campanisona signata	2	2	—	—	—
Myrmothera campanisona minor	—	—	—	—	2
Conopophaga peruviana	—	—	—	9	—
Conopophaga aurita occidentalis	4	9	14	—	—
Conopophaga aurita australis	—	—	—	—	19
Liosceles thoracicus erithacus	—	4	3	4	1
Phoenicircus nigricollis	1	1	—	7	—
Iodopleura isabellae isabellae	2	—	—	1	—
Lipaugus vociferans	1	4	5	4	—
Porphyrolaema porphyrolaema	—	—	1	—	—
Cotinga maynana	—	—	—	—	1
Cotinga cayana cayana	—	2	1	—	2
Gymnoderus foetidus	—	1	—	—	—
Querula purpurata	1	4	—	2	—
Schiffornis major major	1	—	—	1	6
Schiffornis turdinus amazonus	13	1	3	1	15
Piprites chloris tschudi	—	1	—	—	2
Tyranneutes stolzmanni	3	—	—	3	—
Machaeropterus regulus striolatus	6	15	5	39	8

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Manacus manacus interior	1	16	—	26	17
Chiroxiphia pareola napensis	12	9	5	1	5
Chiroxiphia pareola regina	—	—	—	—	5
Pipra pipra discolor	4	26	21	47	27
Pipra coronata coronata	71	129	106	60	49
Pipra filicauda filicauda	9	—	—	5	19
Pipra erythrocephala berlepschi	16	37	70	95	—
Pipra rubrocapilla	—	—	—	—	24
Zimmerius gracilipes gracilipes	2	—	2	—	2
Ornithion inerme	—	—	—	—	1
Tyrannulus elatus	—	—	—	—	1
Myiopagis gaimardii guianensis	—	3	—	2	1
Myiopagis caniceps cinerea	—	—	—	1	1
Mionectes oleagineus hauxwelli	30	21	10	33	41
Leptopogon amaurocephalus peruvianus	—	—	—	—	3
Corythopis torquata sarayacuensis	13	9	5	9	10
Myiornis ecaudatus ecaudatus	—	—	—	—	2
Lophotriccus vitiosus affinis	5	—	1	—	—
Lophotriccus vitiosus congener	—	—	—	—	4
Todirostrum capitale	—	2	1	—	—
Todirostrum latirostre caniceps	—	1	—	—	1
Todirostrum chrysocrotaphum	—	—	—	—	1
Todirostrum calopterum calopterum	—	—	—	2	—
Cnipodectes subbrunneus minor	8	10	1	3	9
Ramphotrigon ruficauda	3	—	—	1	4

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Rhynchocyclus olivaceus aequinoctialis	1	2	—	—	7
Tolmomyias assimilis obscuriceps	—	1	1	4	—
Tolmomyias assimilis clarus	1	—	—	—	2
Tolmomyias poliocephalus	—	—	—	—	5
Tolmomyias flaviventris viridiceps	1	1	—	2	3
Platyrinchus coronatus coronatus	2	—	2	—	9
Onychorhynchus coronatus castelnaui	6	2	2	5	2
Terenotriccus erythrurus signatus	—	14	19	18	—
Terenotriccus erythrurus brunneifrons	—	—	—	—	10
Myiobius barbatus barbatus	12	8	—	6	—
Myiobius barbatus amazonicus	—	—	6	—	6
Myiobius atricaudus adjacens	—	—	—	—	1
Attila cinnamomeus	—	—	—	—	2
Attila citriniventris	1	—	—	—	3
Attila spadiceus spadiceus	—	—	2	—	1
Rhytipterna simplex	—	—	1	6	1
Laniocera hypopyrrha	2	—	—	6	3
Myiarchus tuberculifer tuberculifer	—	—	—	1	1
Myiarchus swainsoni	—	—	—	—	1
Myiarchus ferox ferox	—	—	1	—	2
Pitangus sulphuratus sulphuratus	—	—	—	—	1
Megarhynchus pitangua pitangua	—	—	—	—	2
Myiozetetes similis similis	—	1	—	—	—
Myiozetetes granadensis obscurior	—	1	—	—	—
Myiozetetes luteiventris luteiventris	—	—	1	—	4

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Myiodynastes maculatus solitarius	—	1	—	—	1
Myiodynastes maculatus maculatus	—	—	—	1	—
Empidonomus aurantioatricristatus	—	1	—	1	2
Tyrannus melancholicus melancholicus	—	1	—	—	2
Pachyrhamphus polychopterus tenebrosus	—	—	—	—	2
Pachyrhamphus marginatus marginatus	1	—	1	—	—
Pachyrhamphus marginatus nanus	—	—	—	3	—
Pachyrhamphus minor	—	—	1	4	—
Stelgidopteryx ruficollis ruficollis	—	—	—	—	7
Thryothorus coraya griseipectus	5	11	1	6	—
Troglodytes aedon	—	1	—	—	—
Microcerculus marginatus marginatus	1	9	2	6	9
Cyphorhinus aradus salvini	9	3	9	3	2
Turdus lawrencii	—	1	—	—	—
Turdus hauxwelli	—	—	—	—	1
Turdus albicollis spodiolaemus	6	10	3	11	4
Microbates collaris	—	6	9	—	—
Microbates cinereiventris peruvianus	—	—	—	9	—
Ramphocaenus melanurus amazonus	—	—	—	—	3
Vireolanius leucotis simplex	—	—	—	—	2
Vireo olivaceus solimoensis	—	1	—	—	1
Hylophilus hypoxanthus fuscicapillus	3	—	—	1	1
Hylophilus thoracicus semulus	—	—	—	—	2
Hylophilus ochraceiceps ferrugineifrons	—	2	4	2	4
Molothrus bonariensis	—	—	—	—	1

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Psarocolius oseryi	—	—	1	5	—
Psarocolius decumanus decumanus	—	—	—	1	—
Psarocolius angustifrons angustifrons	—	—	—	—	2
Cacicus cela cela	—	1	—	2	2
Cacicus haemorrhous haemorrhous	—	—	—	11	—
Icterus cayanensis chrysocephalus	1	—	—	4	—
Phaeothlypis fulvicauda fulvicauda	—	—	2	—	—
Cyanerpes nitidus	—	1	—	6	—
Cyanerpes caeruleus microrhynchus	1	1	—	1	1
Chlorophanes spiza caerulescens	—	8	4	7	1
Dacnis cayana glaucogularis	—	—	—	2	1
Dacnis lineata lineata	—	2	—	2	1
Dacnis flaviventer	1	—	—	1	3
Tersina viridis	—	2	—	—	—
Euphonia xanthogaster dilutior	3	8	2	4	2
Euphonia minuta minuta	—	—	—	—	3
Euphonia laniirostris melanura	—	—	—	—	1
Euphonia rufiventris	1	1	—	1	—
Euphonia chrysopasta	1	—	—	—	—
Tangara velia iridina	—	1	—	2	1
Tangara callophrys	—	1	—	2	1
Tangara chilensis chilensis	—	3	1	2	1
Tangara schrankii schrankii	4	6	—	—	6
Tangara xanthogastra xanthogastra	—	3	—	—	2
Tangara mexicana boliviana	—	1	—	1	1

Species	Site 1	Site 2	Site 3	Site 4	Site 5
Tangara gyrola parva	1	—	1	—	—
Thraupis palmarum melanoptera	—	2	—	1	2
Ramphocelus carbo carbo	2	8	—	—	14
Ramphocelus nigrogularis	1	3	—	—	—
Habia rubica rhodinolaema	4	4	11	—	—
Lanio fulvus peruvianus	—	4	9	—	—
Lanio versicolor versicolor	—	—	—	—	7
Tachyphonus cristatus cristatellus	1	3	—	6	—
Tachyphonus surinamus brevipes	—	7	11	6	—
Tachyphonus surinamus napensis	—	—	—	—	18
Tachyphonus rufiventer	—	—	—	—	1
Eucometis penicillata penicillata	—	—	—	2	—
Hemithraupis flavicollis peruana	2	—	—	—	1
Cissopis leveriana leveriana	—	—	—	1	1
Saltator maximus maximus	2	1	—	3	5
Caryothraustes humeralis	1	—	—	1	—
Pitylus grossus grossus	2	2	—	1	—
Passerina cyanoides rothschildii	5	7	5	6	6
Oryzoborus angolensis torridus	—	10	—	1	9

CURRICULUM VITAE: ANGELO P. CAPPARELLA

May 1987

PERSONAL DATA:

Born: 25 September 1952
Birthplace: Raleigh, North Carolina

ADDRESS:

Museum of Zoology
Louisiana State University
Baton Rouge, Louisiana 70803-3216
Phone: 504/388-2855

EDUCATION:

B.A.: Zoology and Geology double major, University of North Carolina at Chapel Hill, August 1974.

M.A.: Museum Science, Texas Tech University, Lubbock, December 1978.

Ph.D.: Zoology major, Biochemistry minor, Louisiana State University, Baton Rouge, expected May 1987. Dissertation: "Rivers as barriers to gene flow in Amazonian forest understory birds." (Research advisors: Dr. J. V. Remsen, Jr. and Dr. Robert M. Zink).

MUSEUM PROFESSIONAL POSITIONS:

1983 - present: Curatorial Assistant, Museum of Zoology, Lousinna State University; all aspects of the collection, curation, and maintenance of bird frozen tissues, skins, skeletons, and alcoholics.

1978 - 1979: Field Technician, North Carolina State Museum of Natural History, Raleigh; to study biology of Necturus lewisi (Neuse river waterdog).

1979 (summer): Instructor, North Carolina State Museum of Natural History, Raleigh; Ornithology and Mammalogy summer classes for preteens.

1978 (6 months): Museum Intern, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; research collections of Birds, Mammals, and Amphibians and Reptiles.

1977 - 1978: Research Assistant, The Museum, Texas Tech University; mammal research collection.

OTHER PROFESSIONAL POSITIONS:

1981 - 1986	Teaching Assistant, Department of Zoology and Physiology, Louisiana State University; laboratory sections of Comparative Anatomy, Introductory Biology, Introductory Zoology, and Ornithology.
1979 - 1980	Biologist/Environmental Protection Specialist, Environmental Criteria and Assessment Office, U.S. Environmental Protection Agency, North Carolina; assisted with the preparation of air quality criteria assessment documents.

FIELD EXPERIENCE:

1973 - 1980	Active in amateur ornithological and herpetological fieldwork in North Carolina.
1977 (2 months)	Participated in expedition from Mexico to Costa Rica to collect bats for Texas Tech University.
1977 (1 month)	Personal trip to Ecuador to study the avifauna of the tropical rain forest.
September 1978	Assisted in processing birds at the Carnegie Museum of Natural History's bird banding station at Powdermill Nature Reserve in western Pennsylvania.
Summer 1981	Member of Louisiana State University Museum of Zoology research expedition to Bolivia to study birds along an altitudinal transect.
1982 - 1984	Leader of Louisiana State University Museum of Zoology summer research expeditions to the Amazon/Napo River area of northeastern Peru to gather dissertation material and bird specimens.

PUBLICATIONS:

Capparella, A. P. and S. M. Lanyon. 1985. Biochemical and morphometric analysis of the sympatric, neotropical, sibling species, Mionectes macconnelli and M. oleagineus. Pp. 347-355. In: P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley (eds.). Neotropical Ornithology. Ornithol. Monogr. No. 36.

Capparella, A. P. 1986. First record of Yellow-collared Chlorophonia for Middle America. American Birds 40:194-195.

Capparella, A. P. In press. Genetic variation in neotropical birds: Implications for the speciation process. In: Proc. XIX Internat. Ornithol. Congr., Ottawa, Canada.

ACTIVE MANUSCRIPTS:

Brush, A. C. and A. P. Capparella. Pigment differences in crown color among between Pipra erythrocephala and Pipra rubrocapilla, with comments on their nomenclature.

Capparella, A. P. Mechanisms of speciation in Amazonian birds: the significance of rivers.

Capparella, A. P. Genetic population structure of some neotropical suboscine birds: inferences from Wright's F statistics.

Capparella, A. P. and G. H. Rosenberg. Two new bird species for Peru, with other distributional records from northern Departamento de Loreto.

Rosenberg, G. H. and A. P. Capparella. A new subspecies of Percnostola rufifrons.

INVITED PRESENTATIONS:

Capparella, A. P. 1986. Genetic variation in neotropical birds: Implications for the speciation process. Presented at the Symposium on the Genetic Structure of Avian Populations, International Ornithological Congress, Ottawa, Canada.

OTHER PAPERS PRESENTED AT MEETINGS:

Capparella, A. P. and S. M. Lanyon. 1983. Biochemical and morphometric analysis of a sibling species pair, Mionectes macconnelli and M. oleagineus (Tyrannidae). American Ornithologists' Union meeting, American Museum of Natural History. Abstract #146.

Capparella, A. P. 1985. Gene flow in a tropical forest bird: Effects of riverine barriers on the Blue-crowned Manakin (Pipra coronata). American Ornithologists' Union meeting, Arizona State University. Abstract #165.

Capparella, A. P. 1986. Population structure of neotropical forest birds: Inferences from electrophoretic data. American Ornithologists' Union meeting, Mississippi State University. Abstract #94.

RESEARCH INTERESTS:

Genetic population structure, speciation processes, and zoogeography of neotropical and temperate birds.

Phylogenetic relationships of neotropical and temperate birds using molecular and morphological analyses.

Theory and application of biochemical techniques (DNA analysis, protein electrophoresis) in evolutionary biology.

SOCIETY MEMBERSHIPS:

American Association for the Advancement of Science
American Ornithologists' Union
Cooper Ornithological Society
Society of Sigma Xi
Society for the Study of Evolution

GRANTS/FELLOWSHIPS

1. Grant from Frank M. Chapman Memorial Fund of the American Museum of Natural History for purchase of Landsat images, 1982.

2. Grant from L.S.U. Museum of Zoology Expedition Fund for fieldwork in Peru, 1982.

3. Travel funds from the L.S.U. Organizational Relief Fund to attend American Ornithologists' Union meeting, 1983.

4. Grant from L.S.U. Museum of Zoology Expedition Fund for fieldwork in Peru, 1983.

5. Grant from L.S.U. Museum of Zoology Expedition Fund for fieldwork in Peru, 1984.

6. Grant from L.S.U. Chapter of the Society of Sigma Xi for chemicals, 1985.

7. Grant from Alexander Wetmore Fund of the American Ornithologists' Union for chemicals, 1985.

8. Grant from Frank M. Chapman Memorial Fund of the American Museum of Natural History for chemicals, 1985.

9. Charles Fugler Fellowship in Tropical Vertebrate Biology, Museum of Zoology, Louisiana State University, 1985.

10. Travel funds from the L.S.U. Organizational Relief Fund to attend International Ornithological Congress, 1986.

GRADUATE COURSES:

Biochemistry Laboratory, Biochemistry of Nucleic Acids, Biochemistry Seminar, Ethology, Experimental Statistics, Herpetology, Mammalogy, Molecular Evolution (course and seminars), Neotropical Ornithology Seminars, Ornithology, Parasitology, Population Genetics, Principles of Biochemistry (two semester course), Survey of Birds of the World, Systematic Zoology, Taxonomy of Vascular Plants, Vertebrate Paleontology, Zoogeography.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Angelo Paul Capparella

Major Field: Zoology

Title of Dissertation: Effects of Riverine Barriers on Genetic Differentiation of Amazonian Forest Undergrowth Birds

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

April 28, 1987