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Characteristic avifauna of white-sand forests in Northern Peruvian Amazonia

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**CHARACTERISTIC AVIFAUNA
OF WHITE-SAND FORESTS
IN NORTHERN PERUVIAN AMAZONIA**

A Thesis

**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
Master of Science**

in

The School of Renewable Natural Resources

by

**José Alvarez Alonso
B.S., Universidad Nacional de la Amazonía Peruana, 1995
August, 2002**

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Abstract

Recently, it has been shown that the high species richness in western Amazonia is related to habitat heterogeneity. Some habitats are rapidly disappearing or deteriorating as a result of anthropogenic activities, resulting in loss of species. One such unique habitat is white-sand forest (hereafter WSF), which is patchily distributed and restricted to a few areas in the northern Peruvian Amazonia. Although it is known that these unique forests are rich in endemic plants, very few studies of the fauna or ecology of these habitats have been conducted. I evaluated and determined the species composition of the avifauna of the white-sand forests at five localities in the region. I sampled the surrounding habitats and determined that a group of birds is restricted to white-sand habitats. Thirty-two bird species, belonging to thirteen families, were found to have some degree of specialization on white-sand forests: nine were classified as “obligate” white-sand forest specialists, thirteen as “near-obligate” white-sand forest specialists, and ten as “facultative” white-sand forest users. I also documented patterns of local distribution of *Zimmerius villarejoi* and *Percnostola arenarum* within distinguishable types of WSF and demonstrated that both species are restricted to certain types of white-sand forests in which two species of plants, a palm and a leguminous tree, are dominant. The assessment of the uniqueness and restricted distribution of the WSF avifauna will facilitate the determination of the biological importance of this habitat and will help to promote conservation and management measures.

Introduction

Western Amazonia is known for its exceptional biodiversity of many taxa. Recently it has been shown that high heterogeneity of habitats that have been derived from different edaphic and ecological conditions is a factor that contributes to this superb species richness (Terborgh 1985; Salo et al. 1985; Gentry 1986, Ruokolainen and Tuomisto 1993, 1998; Tuomisto et al. 1995). Ecological heterogeneity has been shown to be much higher in western Amazonia than previously reported (Tuomisto et al. 1995). In this area, several vegetation types occur within small areas and grow over a mosaic of soils derived from sediments of different origin, age, nutrient content, texture and state of leaching. This soil heterogeneity has been caused by an array of historical, geographical, and ecological factors. They include the changing channels of rivers and fluvial site-turnover processes, marine intrusions from the Caribbean Sea, avulsions, and other geological phenomena related to the impact of Andean foreland dynamics (Liu and Colinvaux 1985; Linna 1993; Räsänen 1993, Räsänen et al. 1987, 1993, 1998).

Western Amazonia is one of the richest areas in species in the world due to this unique heterogeneity. The Iquitos region is famous because of its world records of biodiversity in terms of tree species per unit area, as well as for amphibians and reptiles (Dixon and Soini 1986; Gentry 1988a; Rodríguez and Duellman 1994). South of the Amazon, in the area between the Ucayali and Yavarí rivers, the highest species richness in the world has been reported for palms (Henderson et al. 1995), primates (Puertas and Bodmer 1993), and perhaps mammals in general (Puertas and Bodmer 1993; Valqui 1995).

Unfortunately, some of these habitats are rapidly being lost or are deteriorating as a result of anthropogenic activities. Such activities sometimes cause loss of species, some of which are endemic to the region. Little is known about many habitats, and some could vanish before there is enough information to develop a management plan to effectively conserve or manage them. One unique habitat vulnerable to anthropogenic activities is the white-sand forest (WSF), also known as "heath forest" or "Amazon caatinga". It is locally known in the Iquitos area as "varillal".

Several types of varillal in northeastern Peruvian Amazonia are distinguishable by sight. They have different vegetation structure and floristic composition, as well as different soil conditions. All are distributed in small patches throughout the upland rainforests in the northern Peruvian Amazon. These habitats have several distinguishing characteristics that usually include white-sand soil, small or stunted trees and an open understory. More importantly, the varillales of Iquitos harbor several dozen endemic plant species, and about 100 or more species restricted to WSF within South America.

Unfortunately, few studies of the fauna or ecology of these habitats have been conducted in Peru or elsewhere. From preliminary surveys carried out in the area in 1998 and 1999 by researchers of the Peruvian Amazon Research Institute (IIAP), was found that WSF also harbors a unique community of frogs and birds. Several species new to science and to Peru have so far been discovered in the WSF (Rivera 1999; Whitney and Alvarez 1998; Alvarez et al. 1999; Alvarez and Whitney 2001; Isler et al. 2001; Alvarez and Whitney, in pre.).

The greatest known concentration of WSF in Peruvian Amazonia, easily distinguishable in satellite images, occurs near the city of Iquitos, in the lower Nanay River basin. A new road, which passes through these WSF, is being built between Iquitos and the city of Nauta, and the Peruvian Government has made cheap loans available to clear the forests for agriculture. This government program unfortunately did not consider the quality of the soils, which are not suitable for agriculture. The loan program has resulted in clearing or logging of thousands of hectares of this varillales near the city and along the road. A reserve was created in 1999 to protect the relicts of these forests. Despite the legal status of the area as a reserve, there are no economic alternatives to clearing, and the local people continue with their traditional activities of shifting agriculture and extraction of resources from the forest for their living. The impact of these activities on the unique fauna and flora is not known. It is necessary to determine if the survival of some of the unique species is at risk, or if the unique habitat persists after this kind of pressure.

South of the Amazon, and related to the same geological feature (the “Iquitos Arch”; see Räsänen 1993), there are small, scattered pockets of WSF surrounded by other types of terra firme forest. Some of them have already been destroyed and converted to pastures. A road to connect the Ucayali and Yavarí rivers was been partially completed in this area in the 1980s. Along with this road, a joint project by the Peruvian Government and the Swiss Technical Cooperation Agency has been carried out to “develop” the area, and thousands of hectares of forest have been cleared to promote cattle ranching. Fortunately, this effort is not continuing.

Two other areas are known to have pockets of WSF: 1) the terra firme region between the Huallaga and the Marañón rivers, where hundreds of hectares have been cleared for agriculture near the town of Jeberos over the past century; and 2) the terra firme region between the Mayuriaga and lower Morona rivers. The last area is included in the boundaries of the newly created Santiago-Comaina Reserved Zone, but opposition to this reserve by local indigenous communities makes its future uncertain.

A biological assessment of these white-sand habitats in northern Peruvian Amazonia is urgently needed to determine their uniqueness and to propose management and conservation measures if necessary before more decisions are made about agricultural projects, logging and oil drilling concessions, and other kinds of development. Recently the Peruvian Congress issued a new Forest and Wildlife Law that may result in granting logging concessions of up to 40,000 hectares in the Amazonia (Ley Forestal y de Fauna # 27308, 07.05.2000).

In this study, I use birds as indicator species to assess the biological uniqueness and state of conservation of WSF in the Peruvian Amazonia. It is the first comprehensive assessment of the avifauna of the WSF in the Peruvian Amazonia.

Previous Work and Present Outlook

White-sand forests have been described from several tropical areas in the world; they are widespread but patchily distributed in Amazonia (Pires 1974, Pires and Prance 1985, Richards 1996). In western Amazonia, white-sand patches occur in various types at different locations, usually above the level of the floodplains. Although from the ecological viewpoint

they appear very similar, each has a separate and unique origin (Ab'Sáber 1982). In Amazonian Peru, they are even scarcer and more patchy, and they are restricted to a few areas in the northeast, as explained above (Gentry 1977; Ruokolainen and Tuomisto 1993). In northern Amazonia they are known from Venezuela, Surinam, Guyana, and Amazonian Brazil (Sampaio 1945; Richards 1996; Ducke and Black 1953; Heyligers 1963; Herrera 1977; Klinge et al. 1978, all cited by Anderson 1981 and Anderson et al. 1975), and Colombia (Duivenvoorden 1996; K. Ruokolainen, pers. com). Researchers in Brazil have described various types of vegetation associated with white-sand soils. They have different local names, as “caatinga baixa” and “caatinga alta”, “campina”, “campinarana” (Brazil), “wallaba forest” and “muri bush” (Guyana), “bana”, “cunuri”, and “yaguacanan” (Venezuela) (Jordan 1985).

Relatively small in extent, these ecosystems are fragile and ecologically unique, and should have a high priority for conservation. They have highly distinctive vegetation, characterized by pronounced sclerophylly, distinctive physiognomy, low diversity, and high endemism, among other features (Janzen 1974; Anderson 1981; Medina et al. 1990). Other common characteristics among the different types of WSF are the high density of trees, the scarcity of large emergent trees, large lianas, and herbs, and the absence of a marked buttressing of the trunks (Anderson 1981; Richards 1996). Probably because of nutrient and water constraints, the vegetation growing on white-sand is very specialized. Many of the trees and shrubs have small sclerophyllous foliage with xeromorphic appearance, and have evolved such anti-herbivore defenses, as coriaceous leaves and secondary compounds, especially phenolics and tannins (Janzen 1974, Anderson 1981).

Another distinctive feature is the thick humus layer, due to the extremely low decomposition rates. Some WSF can have nearly a meter of litter over the almost pure sand (Stark 1970, and pers. obs.) There are several potential reasons for such an unusual accumulation of organic matter in a humid tropical soil: high acidity of the soil, high content of toxic compounds in the litter, low nutrient quality of the litter, and removal of proteinaceous nutrients by complexing with phenols (Janzen 1974).

The absence of such layers in some types of WSF could be explained by the “changes in water levels, that are flushing out secondary compounds and oxygenating the substrate, so that fungi and bacteria can decompose the phenolics and other toxic chemicals” (Janzen 1974: 94). The nutrient content of plants growing on white-sand soils is much poorer than those of plants growing on lateritic or clayey soils (Stark 1970; Hardon, 1936, cited by Janzen 1974).

Roots are abundant in the litter layer of this type of forest, but they do not penetrate into the sand. The percentage of roots in the plant biomass is much higher in white-sand plants than in that growing in other types of soils (Klinge and Herrera 1978).

Trees tend to have long-lived leaves that are well protected against attacks by herbivores through physical (toughness) and chemical (secondary compounds) defenses. Leaves tend to have a heavy waxy cuticle that is probably an adaptation to minimize leaching of nutrients by rain. All these characteristics are probably adaptations to the scarcity of nutrients in the soil, as has been shown in other poor soils in the world.

Another unusual feature of these forests is that in contrast to most Amazonian (and tropical) forests, including those surrounding the WSF patches, they have comparatively low species richness, especially in plants, and a pronounced tendency toward dominance by one or a few species (called by some “tendency to gregariousness” (Jordan 1985; Richards 1996).

Knowledge of the existence of areas of endemism of birds (and other animals) in lowland Amazonia is not new (see Haffer 1974, Cracraft 1985), but interest in the white-sand habitats has occurred only recently. For example, Fjeldså and Rahbek (1997) stated that there are no or few bird endemics to the lowland central Amazon basin, when in fact WSF has many such endemics. Although WSF have been much less studied by zoologists than by botanists, the occurrence of some species of birds, mammals, and butterflies, restricted to these habitats in central and northern Amazonia has been reported (Anderson 1981; Oren 1982).

Emmons (1984), in a comprehensive study of Amazonian non-flying mammals, reported that large differences exist between the abundance (numbers of individuals) and richness (numbers of species) of certain kinds of animals encountered at different localities. She found that mammalian densities were highest in white-water and mixed-water alluvial soils and volcanic

soils, lowest on sandy, weathered Tertiary sediments of the Guianan Shield , and intermediate on upland latosols. Eisenberg (1979), as cited by Emmons (1984), also showed that primate diversity is lower in black-water areas of the Guianan Shield in Venezuela and Guyana compared to white-water areas.

It has been known for many years that the WSF have drastically depauperate animal communities. Not only do they have reduced density or abundance of individuals, but also reduced species richness. For example, it is known that the Brazilian WSF have few species of ants and termites, and no earthworms (Stark 1970). The scarcity of birds and other vertebrates in WSF had been noted by several (Heyligers 1963; Harrison 1965; Rothschild 1971, all as cited by Janzen 1974). As the last author stated, referring to the scarcity of birds, the WSF “can be defined by its silence” (op. cit. p. 79). Although the causes have not been well documented, presumably something related to the low productivity and high content in toxins of the vegetation reduces the biomass available to animals (Janzen 1974).

Oren (1981), using mostly published data of others, made a comprehensive analysis of the zoogeography of the white-sand avifauna from Amazonia. There were no data available to him from western Amazonia. Stotz et al. (1996), in their comprehensive analysis of Neotropical birds, listed 20 species of birds as ‘indicators’ (i.e, more or less specialized on this habitat) of WSF in northern Amazonia.

Hilty and Brown (1986) described the distribution of several dozen species of birds from the Colombian Amazonia in terms like: 1) "known only from white-sandy soil forests of upper Rio Negro" (*Myrmotherula ambigua*); 2) "found mainly in white-sandy soil forests" (*Percnostola rufifrons*); 3) "scrubby sandy-belt forest undergrowth" (*Myrmeciza disjuncta*); 4) "not well known. Sandy-belt and gallery forests" (*Heterocercus flavivertex*); 5) "not well known. Eastward found primarily in sandy savanna woodland" (*Neopelma chrysocephalum*); 6) "humid sandy-belt forest and second growth in blackwater regions" (*Cotinga cotinga*); 7) "fairly common in sandy-belt forest, and savanna and gallery woodland in NE Guianania" (*Xipholena punicea*); 8) "humid sandy-belt forest" (*Selenidera nattereri*); 9) "open lower levels of humid sandy-belt forest near Mitu. Few recs. in Colombia" (*Platyrrinchus*

platyrhynchos); 10) "humid forest. Colombian recs. are from sandy-belt forest" (*Platyrinchus saturatus*); 11) "common inside sandy-belt forest and tall savanna woodland of the extreme east; less often forest edges or swampy woodland" (*Lophotriccus galeatus*); 12) "apparently confined to sandy-belt forest and blackwater regions of the extreme east" (*Hylophilus brunneiceps*); 13) "apparently confined to sandy-belt scrub and adjacent savanna woodland" (*Rhytipterna immunda*); 14) "sandy savanna woodland edges, and open savanna with scattered high bushes, thickets, and patches of woodland" (*Tachyphonus phoenicius*).

Ridgely and Tudor (1989, 1994) also mentioned some birds of WSF but often in vague terms, for example: 1) "occurs mostly in vegetation growing on sandy soils" (*Myrmotherula cherriei*); 2) "favors areas with sandy soils, though by no means confined to them" (*Lophotriccus galeatus*); 3) "in west Amazonia perhaps mostly found in forest growing on sandy soil (*Platyrinchus saturatus*); 4) "often occurs in areas with sandy soil" (*Xenopipo atronitens*); 5) "...including (primarily?) forest and woodland in areas with sandy soil ('sandy-belt forest' or 'savanna forest') (*Cotinga cotinga*)".

Zimmer and Hilty (1997), in their description of the avifauna of a locality in the upper Orinoco River in Venezuela, where WSF is widespread, remarked that local bird distributions were often sharply delineated between the WSF and clay-soil or flooded forests. They reported some species restricted to white-sand habitats. Whitney and Alvarez (1998) reported that the distribution of the new species *Herpsilochmus gentryi* (Ancient Antwren) described for northwestern Amazonia (Peru and adjacent Ecuador) is clearly related to edaphic properties of the soil. This species is found only in terra firme forest with poor, leached soil, and especially in WSF. Alvarez and Whitney (2001) and Isler et al. (2001) also reported another two new species of birds, *Zimmerius villarejoi* (Mishana Tyrannulet) and *Pernostola arenarum* (Allpahuayo Antbird) as restricted to certain types of WSF in western Peruvian Amazonia.

The specialization of some birds to particular habitats or microhabitats has been shown to be one factor that contributes strongly to the high species richness in the Neotropics (Terborgh 1980, 1985; Parker and Parker 1982; Remsen 1985; Robinson and Terborgh 1990; Marra and Remsen 1997; Rosenberg 1990; Cohn-Haft et al. 1997). Despite this, specific

studies relating the birds to different types of forests or habitats in the Amazonia are scarce, although references about preferences of some species to a particular type of habitat are common, as was discussed above. Remsen and Parker (1983) remarked that 15%, or 64 species, of the non-aquatic avifauna of the Amazon basin is restricted to river-created habitats. These, in turn, were subdivided into six categories or microhabitats, and the birds restricted to them can be considered to be "habitat specialists".

Rosenberg (1990), in a study of habitat specialization on the islands of the lower Napo River near Iquitos, found that 19 bird species appeared to be restricted to habitats found exclusively on islands; obligate island species had a higher degree of microhabitat specialization than did non-obligate island species. Kratter (1997) in the lowland forests of southeastern Peru found that 19 bird species are restricted to bamboo thickets (*Guadua weberbaueri*) and defined them as "bamboo specialists". Of these species, four are "obligate bamboo specialists", nine are specialists that may use other habitats sparingly (away from southeastern Peru), or "near-obligate bamboo specialists", and six are frequent users of other habitats away from this region, or "facultative bamboo specialists". Stotz et al. (1996) not only described 41 habitat categories in the Neotropics and listed preferences of each species, but presented a list of indicator species of birds for each habitat. They presented a list of 20 species of "indicator" birds for WSF of northern Amazonia.

In the Peruvian Amazonia, perhaps because the WSF are much scarcer and less known than in the western Amazonia, zoologists have not emphasized them. The WSF of the Iquitos area were until recently the only known examples in the Peruvian lowland Amazonia (Gentry 1977). In spite of their biological importance, ecological uniqueness and accessibility, the WSF in the Iquitos area are little known biologically. Thus far, only the vegetation has been thoroughly studied, and only in some places (see below). Some preliminary classifications of the forest types in the white-sand ecosystems have been published (Revilla 1978; Ruokolainen and Tuomisto 1998; Alvarez et al. 1999; García et al. 2002), but these take into account only the floristic composition and the forest structure as ecological criteria.

Through preliminary inventories of the floristic composition (Gentry 1988a; Gentry and Ortiz 1993; Vásquez Martínez 1997; Ruokolainen and Tuomisto 1998), researchers found a unique plant community, with dozens of endemic and restricted plant species. In fact, almost 90% of the plant species in the Iquitos varillales are WSF specialists, many of them endemic (Gentry 1986; Vásquez 1997). New species for science, as well as many found for the first time in Peru, are found almost every year in Peruvian WSF (IIAP 1997; R. Vásquez, A. Tuomisto and K. Ruokolainen, com. pers.)

Studies on fauna of the varillales in Peruvian Amazonia are even scarcer. Dixon and Soini (1986) inventoried the herpetofauna of the Iquitos region in the 1970s, and published the longest list of reptiles for any locality in the world: 142 spp. of lizards and snakes. Although they sampled some of the WSF in the lower Nanay River, they did not record the type of habitat where each species was collected. Kinzey and his students (1974, 1977a, b, 1978, 1981) studied the yellow-handed titi monkey (*Callicebus torquatus*) for several years in the WSF of the lower Nanay. This species is apparently restricted to this habitat (Kinzey and Gentry 1979).

From preliminary surveys carried out in the area in 1998 and 1999 by researchers of the Peruvian Amazonia Research Institute (IIAP), the WSF of Iquitos area was found to harbor a unique community of frogs and birds. Several species new to science and to the country have been discovered to be restricted to the WSF (Rivera 1999, Whitney and Alvarez 1998; Alvarez et al. 1999; Alvarez and Whitney 2001; Alvarez and Whitney in prep.; Isler et al. 2001; Isler et al. 2002). From preliminary data we know that some of these species are restricted to some types of forests within the WSF pockets, and that their total population consists of only a few individuals. After these discoveries, the IIAP proposed to the Peruvian Government the creation of a new reserve in the lower Nanay River basin, close to the city of Iquitos. In March 1999, the decree was issued to create the 57,600 ha Allpahuayo-Mishana Reserve. This protects the largest concentration of WSF so far known in the Peruvian Amazonia (J. Salo, R. Kalliola, in litt.)

Scientists have visited other pockets of WSF in Peruvian Amazonia even less. In the 19th century, apparently by chance, the naturalist Bartlett collected birds in a WSF located on the highlands between the lower Huallaga and the Marañón rivers in the locality of Jeberos (Sclater and Salvin 1973). A few botanical inventories have been carried out in a small patch of WSF south of the Amazon River (Freitas Alvarado 1996), but no zoologist has studied this area until recently.

In this study, my main objectives are:

- 1) To document the avifauna and to assess the patterns of regional distribution of the community of birds inhabiting white-sand habitats in the northeastern Peruvian Amazonia.
- 2) To describe and compare the local distribution and habitat use of two of the white-sand specialists (*Zimmerius villarejoi* sp. nov. and *Percnostola arenarum* sp. nov.) within the WSFs.
- 3) To propose conservation measures.

Study Area

The department of Loreto is covered with humid rainforest with average canopy height of about 30 - 35 m, and elevation varying from 110 to 180 m above sea level. Most of the terrain is flat or gently undulating *terra firme*, with seasonally or permanently flooded habitats along rivers, lakes, and swamps. River levels generally are highest April to June (with another period of elevated levels October-November), and lowest July through September. Annual precipitation at Iquitos is at least 2500 mm (average 3087 mm), with a mean annual temperature of 24°C (maximum annual means between 28-30°C and minimum means of 17-20°C; Johnson 1976; Marengo 1998).

The study area is characterized by an exceptionally diverse mosaic of biotopes with contrasting site qualities caused by high spatial variation in soil properties (Salo 1993; Gentry and Ortiz 1993; Whitney and Alvarez 1998). In particular, *terra firme* soils vary considerably in their origin, age, texture, and geochemistry; this heterogeneity is the result of millions of years of Andean orogeny, weathering and fluvial perturbation in the northwestern Amazon basin (e.g., Räsänen et al. 1987; 1992; 1993; Puhakka et al. 1992). Phytogeographic patterns are closely correlated with edaphic properties (e.g., Gentry 1988a; Gentry and Ortiz 1993; Ruokolainen and Tuomisto 1993; 1998; Tuomisto and Ruokolainen 1994; Tuomisto et al. 1995; Poulsen and Tuomisto 1996; Tuomisto and Poulsen 1996).

To assess the patterns of regional distribution of the community of birds inhabiting white-sand habitats in the northeastern Peruvian Amazonia, I conducted systematic surveys of white-sand forests (WSF) and mixed forests (MF) on clay and loamy soils at five localities, and of flooded or varzea forests (VF) in two localities. The five localities are: **North of the Amazon and Marañón rivers**: Nanay River basin, especially in Allpahuayo-Misahana Reserve (hereafter AMR), located at 03° 57' S; 73° 24' W, but also upper Nanay River (aprox. at 03°06'S, 74°48'W); and Tierra Blanca site in the lower Morona River, close to the confluence with the Mayuriaga River (hereafter Morona), located at 04°16' S; 77°14' W (Fig. 1). **South of the Amazon and Marañón rivers**: Jeberos, in the Aypena - Huallaga rivers interfluvium, located at 05°18' S; 76° 16' W ; Jenaro Herrera, east of the Ucayali River,

located at 04° 51' S; 73° 36' W; and Tamshiyacu, south of the Amazon, located at 03° 59' 13" S; 73° 04' 47" W (both cited together, because their close proximity and lack of biogeographical barriers between them, as J. Herrera (Fig. 1 and Table 1).

As in most areas near the Equator in western Amazonia, there is no marked seasonal climatic pattern or a clearly defined “dry” and “wet” season in Depto. Loreto. Nevertheless the period from February to May with somewhat more rainfall is hereafter referred to as the “wet season” and the rest of the year as the “dry season”. Some bird species breed in Loreto at the beginning of the “wet season”, from November through March or April, such as some species in the Psittacidae and Cracidae (pers. obs.); but I have frequently found nests of many species, specially those of Thamnophilidae, Tyrannidae and Thraupidae, in other months of the year.

The first part of the study was conducted at the “Zona Reservada Allpahuayo-Mishana”, a 57,000 ha national reserve 25 km southwest of Iquitos in northeastern Peru. The reserve, the only one of the study sites studied ornithologically previously, comprises eight major habitats. The flora of Allpahuayo-Mishana has been described in detail (Vásquez Martínez 1997). The flora of the Reserve is diverse, with over 1,900 species. About 110 species have either highly restricted distributions in Peru (ca. 70 spp.) or are endemic to the WSF (ca. 40 spp.; Vásquez Martínez 1997; Alvarez et al. 1999). The WSF are unique to the reserve and a few other sites in Peruvian Amazonia. The upland of Allpahuayo-Mishana can be classified into two major types: those on sandy soils and those on clay soils (Vásquez Martínez 1997; Alvarez et al. 1999).

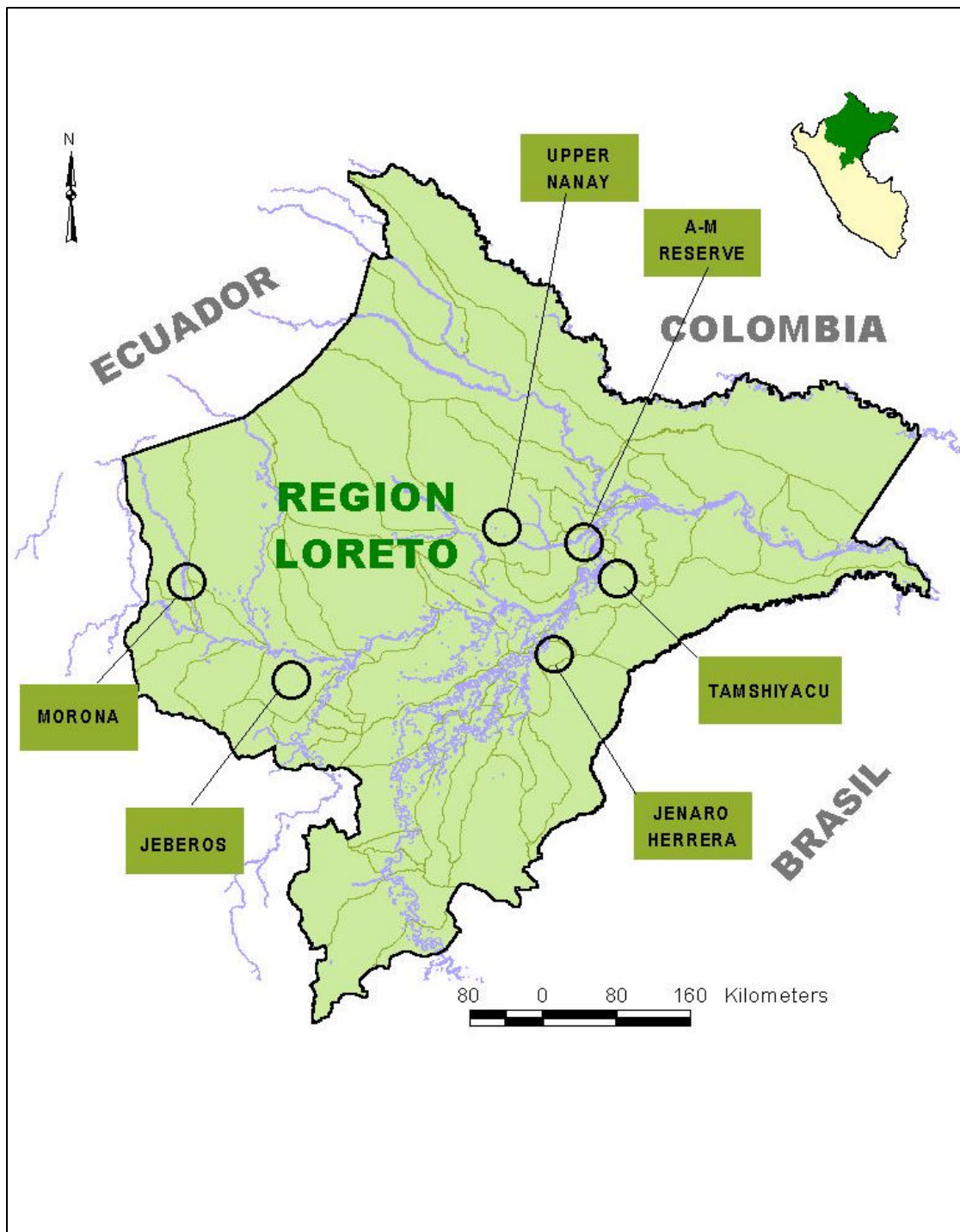


Fig.1. Study area, with location of study sites in northern Peruvian Amazonia.

Materials and Methods

Patterns of Distribution of Birds in White-Sand Forests on Northern Peruvian Amazonia

In addition to the systematic surveys of bird communities in WSF, MF and VF in the five localities cited above, I compared my results with those found in other well-studied sites from the northern Peruvian Amazonia. These studies, mostly unpublished, were made in the same geographical areas but were conducted in habitats different from WSF; they were in both terra firme and flooded forests in: 1) The lower Napo River around Sucusari River, north of the Amazon River (T. A. Parker, T. S. Schulenberg, B. M. Whitney, A. P. Capparella, S. W. Cardiff, R. H. Wiley, G. H. Rosenberg, A. Whittaker, S. L. Hilty, R. S. Ridgely, and others, in litt.) 2) six localities south of the Amazon: Santa Cecilia, Padre Isla, Manítí River, Orosa River, Tahuayo River, Tapiche River (Robbins et al. 1991; C. Siegel, C. Bouton, R. S. Ridgely, R. H. Wiley, in litt.) 3) the Pacaya Samiria Reserve (Begazo and Valqui 1998; P. Soini, R. S. Ridgely, in litt.; J. Alvarez, unpubl. data). 4) Tigre and Corrientes rivers (Alvarez 1994; Prum et al. 1993); Pastaza River (J. Alvarez, unpubl. data; Prum et al. 1993; E. O. Willis, in litt.) 5) the upper Putumayo River and tributaries (J. Alvarez, unpubl. data).

I used two techniques: “point counts” and “line transects”. Both have advantages. Point counts are better for sampling smaller patches of habitats that are diverse and that occur in small pockets, as is the case with WSF. Transects sample larger areas and thus record many more individuals and species. Consequently, I used transects when possible, but when patches were small, or when I could not place transects of sufficient length, I used point counts.

I surveyed the trails in the early morning, when the birds are more active (from 5:15 am to 11:00 am approximately). I used binoculars (8 x 40) for visual detections and a professional-grade tape-recorder (Sony TCD 5000) with directional microphone (Sennheiser, Mod. ME88) to lure in birds with unfamiliar voices. A GPS unit was used to locate the study sites and collecting localities on the map. I only collected specimens when necessary to identify species or as voucher specimens when a new taxon was found. For that purpose, I used a shotgun or mist nets.

- Point Counts: When using point counts (Ralph et al. 1981; Ralph et al. 1993), I stopped for fixed periods at sites selected at random or in a systematic array within the habitats of interest to record bird presence and abundance, usually within a certain distance of the point. At each point, I also recorded (see below) the type of habitat (i.e., type of forest, among several broad categories; see Encarnación 1985). Locations of the birds were scored with respect to distance from the observer in two categories: $d < 25$ m; and $25 < d < 50$. To ensure that the species recorded are actually in a specific habitat, i.e., white-sand forest vs. not white-sand forest, I recorded only the birds observed by sight or heard within 50 m of the point.

I counted for 10 minutes at each stop, which were separated from other stops by at least 250 m to reduce the possibility of counting the same individual twice, and to make point counts statistically independent. I discarded from the analysis potentially duplicated individuals, i.e., those moving in the direction of the next point count for species found at that next point. Particularly in WSF, which occur in small pockets of habitat where the changes in the soil are sharply defined, I determined in each case whether the habitat was homogeneous within 50 m of the point.

Because I have more than 15 years experience in Amazonian forests, I can distinguish among the different 'broad' categories of habitats, such as terra firme, varzea, swampy, palm, or transitional forest, etc. Within terra firme forest, I distinguished WSF from MF by sampling the soil itself for sand and by sampling the vegetation, which differs dramatically for WSF (only about 10% of the plant species of WSF is shared with non-white-sand ones; Vásquez Martínez 1997).

- Line Transects: This technique is widely used in faunal surveys. Lines transects were located randomly at the study sites. Transects were 1,200 m. long; this roughly corresponded to the length of the white-sand patches evaluated. When possible, transects were made along existing trails and were surveyed once a day. These transects took from 3.2 to 4.1 hrs to complete. The starting times of transects varied, but were interspersed among habitats, so that the results were not influenced by variation in starting time. One transect was surveyed each day. A transect survey consisted of walking the line at a slow pace (0.3 – 0.5 km/hour) as

silently as possible and identifying and recording the position of the all birds detected, by sight or sound, from both sides of the trail.

The assumptions that apply to the line transect and point count techniques are that: 1) each bird species has the same probability of being detected in the different habitats; 2) margin of error in calculating the distances of the birds to the observer is the same for each habitat and species; 3) temporal variation is the same among habitats; 4) errors from multiple counting are independent of habitat; and 5) no biases existed in weather-induced bird detectability among transects. These assumptions seemed to be met in my study. Because there may be temporal variation in detectability of the birds, I carefully controlled the timing of the sampling to ensure that sampling intensity of each habitat be the same by time. Because the weather is highly variable in Amazonia on an hourly and daily basis, but almost uniform along the year in northwestern Peruvian Amazonia, I assumed that it has no influence on the analysis. Transects were not conducted under weather conditions that adversely affected detectability. Because counts were carried out by me alone, biases related to individual variations in detecting birds (Cyr 1981; Bart and James 1984) were avoided.

The following information was collected for each bird encountered: species, perpendicular distance between the bird and transect or to the center of the point count, time of day, and height within the vertical strata of the forest. If a bird was heard only, I identified the species and obtain as much of the information mentioned above as possible.

To test the hypothesis that some bird species are specialized on WSF, I compared the data sets from WSF to those from MF and VF. To minimize the bias of the data set being weighted towards the AMR, where I worked throughout the year, I compared data sets for some of the analysis by blocks of time, those of the same season of the year in the same analysis. To do so, I divided the months of the year in three four-month blocks: from November through February, the peak of the breeding season; from March through July, the "rainy season", and from August through October, the "dry season".

I considered a species to be other than white-sand forest specialist if I record one or several individuals regularly in the same general area away from white-sand forest, or if this

species has been recorded repeatedly in other type of habitat different from white-sand forest by myself or by recognized ornithologists in the region in other studies, as those quoted above (see Kratter 1997; Rosenberg 1990, and data analysis below).

Over 400 species of birds were found during this study of white-sand forests (WSF) at five localities in the northeastern Peruvian Amazonia. More than 5,800 individual bird records, visual and auditory, were made on the 150 transects analyzed in this part of the study, and a similar number were recorded during the more than 700 point counts made in the same period (Table 1; the database of this study will be accessible at <http://www.siamazonia.org>). To determine if some of the presumed white-sand specialists are also absent in the seasonally flooded forest or varzea forest (VF), some sampling was done in this habitat in AMR - Nanay River basin and in Morona site. In Jeberos and J. Herrera sites, the VF was too far from WSF patches to sample it.

Table 1. Study sites, period of study, and number of transects and point counts at each site

LOCALITY	Coordinates (approximate)	Period of study	# of transects per habitat type			# point counts per habitat type		
			WSF	MF	VF	WSF	MF	VF
NAYAY- A- M RESERVE *	03° 57'5" S 73°24'31" W	1999- 2002*	49	20	13	272	128	53
MORONA	04° 16'51" S 77°14'17" W	May-June 2001	11	6	8	38	29	24
JEBEROS	05°18'46" S 76°16'26" W	July 2001	13	7	-	42	21	-
J. HERRERA- TAMSHIY.	04°51'55" S 73°36'29" W	Dec 2001 May 2002	13	10	-	93	34	-

* All trails, and most point-counts from the Nanay River basin varillales, are in the Allpahuayo-Mishana Reserve. Coordinates are from the varillal where most evaluation trails were located. However, some point counts were made during two trips to upper Nanay River in 2000 and 2001.

Patterns of Distribution of Two White-Sand Forest Specialists in Allpahuayo - Mishana Reserve

To determine if there is some pattern of distribution of the avifauna within the WSF patches in the AMR, I tested the hypothesis that two species of white-sand specialists are restricted to certain sub-habitats -or types of varillal- within WSF. In this reserve, preliminary botanical studies have identified several kinds of varillal distinguishable by the floristic composition, structure of the vegetation and soil moisture (Revilla 1978; Alvarez et al. 1999; Ruokolainen and Tuomisto 1999; García Villacorta et al. 2002). My preliminary studies indicated that most white-sand specialists are not evenly distributed within the white-sand patches, but occupy preferentially some distinguishable types of forest. For testing this hypothesis, I evaluated two bird species new to science recently discovered in the WSF of Nanay River basin: *Zimmerius villarejoi* sp. nov. (Tyrannidae), and *Percnostola arenarum* sp. nov. (Thamnophilidae). These species are apparently obligate white-sand specialists and as far as is known are restricted to particular types of WSF.

- ***Zimmerius villarejoi* sp. nov.** (Alvarez and Whitney 2001) seems to be restricted to the canopy of patches of white-sand forest that have a very well drained soil, and medium or low canopy height where a species of tree of the family Leguminosae, *Dicymbe uaiparuensis*, is abundant. This tree species does not seem to occur in wet varillales or in varillales with a mean canopy of more than 20-25 m. high (Revilla 1978; Alvarez et al. 1999). *Dicymbe* spp. is the only genus in the terra firme forest that has a multicaulous or multi-stemmed trunk in northern Amazonia, and its entire species are restricted to WSF: *D. altsoni*, *D. corymbosa* and other species in eastern and northeastern Amazonia, and *D. uaiparuensis* in Peruvian Amazonia (Richards 1996). Because of this feature, it is very easy to recognize, even at a distance.

I surveyed five plots of white-sand forest along a system of trails, and each time I recorded *Zimmerius villarejoi* by sight, by call, or by song, I localized and marked the spot at which the bird was first encountered, and measured the perpendicular distance to the trail and the distance to the nearest *Dicymbe* tree whose crown reaches the canopy.

Then, I chose at random a similar number of points in each plot and measured the distance to the nearest *Dicymbe* tree from each point. In both cases - 'bird points' and 'random points' - I measured only distances to the nearest *Dicymbe* tree as tall as 50 m, and considered the bigger ones as > 50 m. I compared both data sets to determine if there is a significant difference between the two sets of distances, and hence a preference of *Zimmerius villarejoi* for the habitat in which *D. uaiparuensis* is dominant.

- ***Percnostola arenarum* sp. nov.** (Isler et al. 2001) seems to be restricted to the understory of two clearly distinctive types of WSF: one whose understory is dominated by saplings of the white-sand specialist palm *Euterpe catinga* (Arecaceae), where the soil is very humid and has a very thick organic layer, and another whose understory is dominated by the small palm *Lepidocaryum tenue* (Arecaceae) that occurs over sandy soil or in very poor sandy-clayish soil, with a thick organic layer (Alvarez et al. 1999; Isler et al. 2001). Both palms are readily distinguishable by sight. The thick layer of organic matter is an indicator of very poor soils and high acidity, which reduces the abundance of soil fauna (Janzen 1974; Klinge and Herrera 1978; Anderson 1981). In AMR, *P. arenarum* apparently uses the first habitat type, whereas in the upper Nanay River basin and Tigre River basin, it uses preferentially the second one.

To test the hypothesis that this species is restricted in AMR to the varillal in which *E. catinga* is dominant, I surveyed four plots of white-sand through a system of trails. Each time I recorded *Percnostola arenarum*, by sight, by call or by song, I marked the spot where the bird was first recorded. In each spot, I counted the saplings (i.e. palms of < 3 m > 0.1 m height) of *Euterpe catinga* in a 5 x 5 m plot. In a similar way, as with the previous species, I chose at random a similar number of points in the same study area and measured the number of saplings of each palm species in a 5 x 5 m plot. I compared both data sets, i. e., fixed versus random distribution, to determine if there is a significant preference of *Percnostola arenarum* in AMR for the habitat in which either *E. catinga* is a dominant species.

Data Analysis

I determined which species are WSF specialists in the following way: I considered a species of bird as an “obligate white-sand specialist” when found only in WSF, and had at least five total observations. I considered a species of bird as “near-obligate white-sand specialist” when found only in WSF in the study area, but has been recorded outside this habitat in other regions. I considered a bird species as a “facultative white-sand user” when the species was found more commonly in WSF than in other forest types. To show that a species was more common in WSF, I used a chi square test to compare by species the number of observations in WSF and in not WSF. I used only species with more than five records to make the analyses.

To test the hypothesis that the mean distance of birds from the *Dicymbe* trees (in the case of *Zimmerius villarejoi*) was lower than that of the trees to random points, and that the mean palm density in the plots where *Percnostola arenarum* was observed was higher than that of the randomly selected points, a one tailed t-test was used. The hypothesis was supported if calculated p-values, in both cases, are below a probability level of 0.05.

Results

Patterns of Distribution of Birds in White-Sand Forests on Northern Peruvian Amazonia

Bird species and abundance differs strongly among the three main habitat types evaluated: white-sand forests, mixed terra firme forests, and varzea forests. Thirty-two bird species are virtually restricted to WSF (Tables 2 and 3). These 32 species are classified as having some degree of specialization or preference for WSF, according to the three categories used: **Obligate white-sand forest specialists**, **near-obligate white-sand forest specialists**, and **facultative white-sand forest users** (Table 4). All these white-sand specialists have been recorded more than five times in WSF, and never (the obligate ones) or very few times (the other two categories) in other habitat types.

The distribution of WSF specialists among 14 families is as follows: Tinamidae (2), Columbidae (1), Trochilidae (1), Trogonidae (1), Galbulidae (1), Bucconidae (1), Dendrocolaptidae (2), Furnariidae (1), Thamnophilidae (7), Tyrannidae (8), Pipridae (4), Cotingidae (1), Polioptilidae (1), and Thraupidae (1).

The number of records in WSF, combining point count and transect records, ranges from six of *Crypturellus strigilosus*, to 287 and 275 of *Herpsilochmus gentryi* and *Neopelma chrysocephalum*, respectively (Tables 2, 3). The number of records is not always a good indicator of relative abundance, because it is affected by major differences in detectability among the species.

Distribution of White-Sand Forest Specialists by Categories

• Obligate white-sand forest specialists

Nine species are classified as obligate WSF specialists, as they are entirely restricted to WSF throughout their ranges. Most species occur at multiple study sites: eight in Nanay basin and in AMR, of which three were not observed at the other sites, three at the J. Herrera and Tamshiyacu sites, two at the Morona site, and one at the Jeberos site (Table 4). *Pithys castanea* was the only species, among those found at J. Herrera, Morona and Jeberos sites, not found in Nanay basin (Tables 2 and 3; see Appendix for details of species' distributions).

Table 2. Number of records of white-sand forest specialists in transects in three habitat types

<i>Species</i>	WHITE SAND F (86)*					MIXED F (43)*				VARZEA (21)*		
	NA	MO	JE	JH	TOT	NA	MO	JE	JH	NA	MO	JE
<i>Crypturellus duidae</i>	5				5							
<i>Crypturellus strigilosus</i>				4	4							
<i>Polytmus theresiae</i>			17		17							
<i>Claravis pretiosa</i>	25				25							
<i>Trogon rufus</i>	6	2			8							
<i>Notharchus ordii</i>	16				16							
<i>Galbula dea</i>	15	4	2	2	23			1				
<i>Deconychura longicauda</i>	3	1		2	6							
<i>Lepidocolaptes albolineatus</i>	8				8							
<i>Sclerurus ruficularis</i>	23	4	1	4	32							
<i>Myrmotherula leucophthalma</i>		31			31							
<i>Pithys castanea</i>		4			4		1					
<i>Megastictus margaritatus</i>	29		8		37							
<i>Herpsilochmus gentryi</i>	105	16			121	15	9					
<i>Hypocnemis hypoxantha</i>	48	31		3	82		11					
<i>Pernostola arenarum</i>	28	49			77		3					
<i>Myrmeciza castanea</i>	82		4		86							
<i>Zimmerius villarejoi</i>	16				16							
<i>Hemitriccus minimus</i>	82			11	93							
<i>Ramphotrigon ruficauda</i>	12	14	7	17	50					1		
<i>Cnemotriccus (duidae).</i>	11		7	1	19							
<i>Platyrinchus saturatus</i>	8				8							
<i>Attila citriniventris</i>	21	6		12	39							
<i>Conopias parva</i>	15	5	6	6	32							
<i>Neopelma chrysocephalum</i>	120				120							
<i>Neopipo cinnamomea</i>	9	2		7	18							
<i>Heterocercus aurantiivertex</i>	13			6	19					1		
<i>Dixiphia pipra</i>	57	21	22	14	114							
<i>Xenopipo atronitens</i>			22		22							
<i>Xipholena punicea</i>	57	6			63							
<i>Polioptila sp. nov.</i>	21				21							
<i>Tachyphonus phoenicius</i>			22		22							

* Numbers of transects in each locality. NA: Nanay River (incl. AMR); MO: Morona River; JE: Jeberos; JH: Jenaro Herrera - Tamshiyacu

Table 3. Number of records of white-sand forest specialists in point counts in three habitat types

	WHITE SAND F (445)*					MIXED F (212)*				VARZEA (77)*		
<i>Species</i>	NA	MO	JE	JH	TOT	NA	MO	JE	JH	NA	MO	JE
<i>Crypturellus duidae</i>	15				15							
<i>Crypturellus strigilosus</i>				2	2							
<i>Polytmus theresiae</i>			6		6							
<i>Claravis pretiosa</i>	114				114							
<i>Trogon rufus</i>	6				6	1						
<i>Notharchus ordii</i>	25			3	28							
<i>Galbula dea</i>	18	1	1	5	25	1						
<i>Deconychura longicauda</i>	1				1		1					
<i>Lepidocolaptes albolineatus</i>	8				8							
<i>Sclerurus ruficularis</i>	7			2	9							
<i>Myrmotherula leucophthalma</i>		7			7							
<i>Megastictus margaritatus</i>	15				15							
<i>Herpsilochmus gentryi</i>	157	9			166	11	8					
<i>Hypocnemis hypoxantha</i>	33	8		1	42		4					
<i>Pernostola arenarum</i>	68	23			91		2					
<i>Myrmeciza castanea</i>	65				65							
<i>Zimmerius villarejoi</i>	25				25							
<i>Hemitriccus minimus</i>	77			19	96							
<i>Ramphotrigon ruficauda</i>	18	5	5	13	41					1		
<i>Cnemotriccus (duidae).</i>	9		12	4	25							
<i>Platyrinchus saturatus</i>	7				7							
<i>Attila citriniventris</i>	69	1		11	81							
<i>Conopias parva</i>	41	2	2	5	50							
<i>Neopelma chrysocephalum</i>	155				155							
<i>Neopipo cinnamomea</i>	9	1		10	21							
<i>Heterocercus aurantiivertex</i>	21			6	27					3		
<i>Dixiphia pipra</i>	38	11	9	8	66	2	8					
<i>Xenopipo atronitens</i>			14		14							
<i>Xipholena punicea</i>	44	4			48							
<i>Poliophtila sp. nov.</i>	7				7							
<i>Tachyphonus phoenicius</i>			5		5							

* Number of point counts in each locality. NA: Nanay River (incl. AMR); MO: Morona River; JE: Jeberos; JH: Jenaro Herrera - Tamshiyacu

Table 4. Distribution of white-sand forest specialists by categories

	OBLIGATE WSF SPECIALISTS	NEAR OBLIGATE WSF SPECIALISTS	FACULTATIVE WSF USERS
JEBEROS	<i>Cnemotriccus duidae</i>	<i>Conopias parva</i> <i>Tachyphonus phoenicius</i> <i>Xenopipo atronitens</i>	<i>Polytmus theresiae</i> <i>Sclerurus rufifigularis</i> <i>Megastictus margaritatus</i> <i>Ramphotrigon ruficauda</i>
MORONA	<i>Xipholena punicea</i> <i>Pithys castanea</i> †	<i>Lepidocolaptes albolineatus</i> <i>Pernostola arenarum</i> <i>Myrmotherula leucophthalma</i> <i>Neopipo cinnamomea</i> <i>Attila citriniventris</i> <i>Conopias parva</i>	<i>Trogon rufus</i> <i>Galbula dea</i> <i>Deconychura longicauda</i> <i>Sclerurus rufifigularis</i> <i>Herpsilochmus gentryi</i> <i>Hypocnemis hypoxantha</i> <i>Ramphotrigon ruficauda</i> <i>Dixiphia pipra</i>
NANAY - A-M RESERVE	<i>Crypturellus duidae</i> <i>Notharchus ordii</i> <i>Neopelma chryscephalum</i> <i>Xipholena punicea</i> <i>Zimmerius villarejoi</i> <i>Cnemotriccus duidae</i> <i>Hemitriccus minimus</i> <i>Polioptila sp. nov.</i>	<i>Lepidocolaptes albolineatus</i> <i>Pernostola arenarum</i> <i>Myrmeciza castanea</i> <i>Platyrhynchus saturatus</i> <i>Neopipo cinnamomea</i> <i>Attila citriniventris</i> <i>Conopias parva</i> <i>Heterocercus aurantiivertex</i>	<i>Claravis pretiosa</i> <i>Trogon rufus</i> <i>Galbula dea</i> <i>Deconychura longicauda.</i> <i>Sclerurus rufifigularis</i> <i>Megastictus margaritatus</i> <i>Herpsilochmus gentryi</i> <i>Hypocnemis hypoxantha</i> <i>Ramphotrigon ruficauda</i> <i>Dixiphia pipra</i>
JENARO HERRE RA	<i>Notharchus ordii</i> <i>Cnemotriccus duidae</i> <i>Hemitriccus minimus</i>	<i>Crypturellus strigilosus</i> <i>Neopipo cinnamomea</i> <i>Attila citriniventris</i> <i>Conopias parva</i> <i>Heterocercus aurantiivertex</i>	<i>Galbula dea</i> <i>Dechonychura longicauda</i> <i>Sclerurus rufifigularis</i> <i>Ramphotrigon ruficauda</i> <i>Dixiphia pipra</i>

† *P. castanea* has two records in clay-soil forest, but I provisionally consider it an obligate white-sand specialist (see Discussion and Appendix for details).

· **Near-obligate white-sand forest specialists**

Twelve species are classified as near-obligate WSF specialists, as they were found in the study sites only in WSF but have been recorded outside WSF in other regions: eight in the Nanay River basin and AMR, six at the Morona site, five at the J. Herrera site, and three at the Jeberos site (Table 4). *Platyrinchus saturatus* was found only at AMR, *Myrmotherula leucophthalma* was found only at Morona, and *Crypturellus strigilosus* was found only at the J. Herrera site. Two species were found only at Jeberos: *Xenopipo atronitens* and *Tachyphonus phoenicius*. The presence of these two species at Jeberos site is probably due to the existence there of a habitat missing from the other three localities: extensive grasslands and brushy forest growing on white-sand and other nutrient poor, sandy soils (Tables 2 and 3 and Appendix).

· **Facultative white-sand forest users**

Eleven species are classified as facultative white-sand users, because they are more common in WSF than in other habitats: ten at Nanay and AMR, eight at the Morona site, five at the J. Herrera site, and four at the Jeberos site. *Claravis pretiosa* was only found at AMR and *Polytmus theresiae* at Jeberos site (Tables 2 and 3 and Appendix).

AMR / Nanay River basin is the richest site in white-sand specialists in all categories in the study area, with 25 species, followed by Morona site, with 16 species, and finally by the Jenaro Herrera and Jeberos sites, with 13 and 8 species, respectively.

Another three species that I think are also white-sand specialists in the study area have not reached the five-record threshold to classify them as WSF specialists: *Crypturellus casiquiare*, *Myrmotherula cherriei*, and *Lophotriccus galeatus*. All have been found in Nanay River basin varillales and nearby right bank of the Tigre River. Another three species that may be specialists were not recorded during this study because they are nocturnal: *Nyctibius leucopterus*, whose only records in Peru are in WSF at the AMR, *Nyctibius bracteatus*, whose only two records I have for Loreto are in WSF, and *Nyctiprogne leucopyga latifacies*, a subspecies restricted in Peru to flooded black-water forest ('igapo') in

the Nanay River basin. Igapo forest occurs where a river drains white-sand or similar nutrient-poor soils, such the Rio Negro in Brazil (the only other area known for this subspecies).

Species of the second and third category, near obligate WSF specialists and facultative WSF users, although sometimes found in habitats different from WSF, usually are restricted to oligotrophic forest growing on similar nutrient-poor, deeply weathered soils. *Heterocercus aurantiivertex* and *Attila citriniventris* are found occasionally in oligotrophic, black-water swamps and igapo forests. I have also found *Myrmotherula cherriei* in similar habitats in Tigre River, and I recorded *Lophotriccus galeatus* in a *Mauritia* palm swamp on the Putumayo River in 1988.

There is a significant contribution of the WSF specialized avifauna to the regional biodiversity, because the community of WSF specialists constitute an important percentage of the avifauna of the study sites. For example, in AMR, where the avifauna has been thoroughly inventoried WSF specialists represent 5.2 percent of the 478 species so far recorded in the area (Alvarez et al. 1999).

Bird Species Rare or Absent From White-Sand Forest Patches

A number of bird species are fairly common in the terra firme mixed forests of the region and were scarce or absent inside the WSF at any of the five localities surveyed (Table 5). Other species are regularly found in WSF at some of the localities, but are clearly more abundant in the surrounding MF.

Patterns of Habitat Use by Two White-Sand Forest Specialists

Relationship of *Percnostola arenarum* to Abundance of *Euterpe* Palm Saplings

To determine whether the abundance of *Percnostola arenarum* was related to the abundance of *Euterpe* palm saplings, I only used data from three trails at AMR because only there the density of *P. arenarum* was large enough for statistical analysis. Despite this scarcity, *P. arenarum* is very vocal and I managed to record the species 12 times on one of the trails, 15 on the second one, and 5 in the third.

Table 5. Bird species rare or absent from white-sand forest patches

Species	Very rare in WSF	Absent from WSF
<i>Electron platyrhynchum</i>		x
<i>Galbula albirostris</i>		x
<i>Jacamerops aureus</i>		x
<i>Bucco tamatia</i>		x
<i>Monasa morphoeus</i>	x	
<i>Selenidera reinwardtii</i>	x	
<i>Melanerpes cruentatus</i>	x	
<i>Dryocopus lineatus</i>		x
<i>Campephilus melanoleucos</i>	x	
<i>Xiphorhynchus guttatus</i>	x ¹	
<i>Hylocistis subulatus</i>		x
<i>Automolus infuscatus</i>	x ¹	
<i>Cymbilaimus lineatus</i>		x
<i>Frederickena unduligera</i>		x
<i>Thamnophilus schistaceus</i>		x
<i>Pygiptila stellaris</i>	x	
<i>Thamnomanes ardesiacus</i>	x ²	
<i>Thamnomanes caesi</i>	x ²	
<i>Myrmotherula brachyura</i>		x
<i>Myrmotherula obscura</i>		x
<i>Cercomacra cinerascens</i>		x
<i>Pernostola leucostigma</i>	x ³	
<i>Myrmeciza fortis</i>		x
<i>Formicarius analis</i>		x
<i>Liosceles thoracicus</i>		x
<i>Myiopagis gaimardii</i>		x
<i>Todirostrum chrysocrotaphum</i>		x
<i>Platyrinchus coronatus</i>		x
<i>Myiobius barbatus</i>	x	
<i>Myiozetetes luteiventris</i>		x
<i>Tyrannetes stolzmanni</i>	x ²	
<i>Machaeropterus regulus</i>		x
<i>Manacus manacus</i>		x
<i>Pipra coronata</i>		x
<i>Campylorhynchus turdinus</i>		x
<i>Turdus lawrencii</i>		x
<i>Ramphocaenus melanurus</i>		x
<i>Saltator grossus</i>		x
<i>Cyanocopsa cyanoides</i>		x
<i>Habia rubica</i>		x
<i>Hylophilus ochraceiceps</i>	x	
<i>Psarocolius angustifrons</i>		x

x¹ : Only two and four records in Morona WSF, respectively

x² : Some records in Morona, Jeberos and J. Herrera WSF, but absent from AMR WSF

x³ : Only two records in AMR WSF

On all three trails, there was a highly significant statistical difference between the abundance of *Euterpe catinga* saplings on the plots selected at random and those plots where *P. arenarum* was recorded (t-test; $p < 0.01$). Variances applied in all cases were not significantly different (F-test; $p > 0.05$; see Table 6).

At least in these three areas, *P. arenarum* is associated with or restricted to the areas of the varillales where saplings of the palm *Euterpe catinga* are abundant (but see *Discussion* for patterns of distribution in other areas). These areas of the varillales are called locally as “low humid varillal” or “varillal bajo húmedo”, and they are one of the 8-10 types of varillal that are distinguished by local researchers (Revilla 1978; Alvarez et al. 1999, García Villacorta 2002).

Table 6. Mean number of *Euterpe catinga* palms in *Percnostola arenarum* plots and random plots

Trails	N° of points	<i>Percnostola</i> plots Mean \pm SD	Random plots Mean \pm SD	F-TEST	T-TEST
Nueva Esperanza Trail	12	14.8 \pm 7.1	5.9 \pm 5.4	p = 0.44	p = 0.001
El Dorado I-D Trail	15	19.7 \pm 7.7	9.6 \pm 7.7	p = 0.99	p = 0.0006
Fundo Piura Trail	6	12 \pm 3.7	2.8 \pm 4.9	p = 0.55	p = 0.0005

Relationship of *Zimmerius villarejoi* to *Dicymbe* Trees

Fifty-two records of *Zimmerius villarejoi* were made on six trails surveyed at AMR. At the Nueva Esperanza varillal, there was no significant difference between the distances from the bird detection points and from the random points to the nearest *Dicymbe* tree (t-test; $p > 0.05$; Table 7). I conclude that in this varillal there was no clear relationship between *Z. villarejoi* and *Dicymbe* trees, and consequently, *Z. villarejoi* is not associated with this tree species.

In contrast, on the other four trails (at the El Dorado and Fundo Piura varillales), the difference between the set of distances from the bird points to the respective nearest *Dicymbe* tree differed significantly from those from the set of random points (t-test; $p < 0.05$; Table 7). Thus, at these varillales, the distribution of *Z. villarejoi* seems clearly related to the type of white-sand forest in which the *Dicymbe* trees are dominant. The possible reasons for this contrasting pattern are analyzed in the Discussion chapter.

Table 7. Mean distances to *Dicymbe* trees in *Zimmerius villarejoi* points and random points

Trails	N° of points	<i>Z. villarejoi</i> points Mean \pm SD	Random points Mean \pm SD	F-TEST	T-TEST
Nueva Esperanza Trail	13	29.6 \pm 21.7	30.1 \pm 22.1	p = 0.96	p = 0.47
El Dorado I-A Trail	9	8.1 \pm 13.8	31.6 \pm 22.5	p = 0.19	p = 0.008
El Dorado I-C Trail	11	8.8 \pm 14.9	25.7 \pm 21.2	p = 0.28	p = 0.02
El dorado I-D Trail	19	7.7 \pm 14.8	23.3 \pm 21.1	p = 0.20	p = 0.004
Fundo Piura Trail	7	0.5 \pm 1.1	25.5 \pm 23.6	p = 0.002	p = 0.007

Discussion

The existence of community of birds specialized for WSF is evidence that habitat specialization is one of the factors contributing strongly to the high species richness in the Neotropics (Remsen 1985; Robinson and Terborgh 1990; Rosenberg 1990; Kratter 1997; Marra and Remsen 1997; Cohn-Haft et al. 1997). The Iquitos region is well known because of the high levels of both alpha and beta biodiversity, especially in plants and some vertebrate groups. With respect to the avifauna, within a radius of 100 km. at 100 m altitude around Iquitos, more than 650 bird species can be found (H. Wiley, in litt.; J. Alvarez, unpubl. data). At AMR, the only site thoroughly studied among the five study sites, the WSF specialized avifauna represents 4.5 % of the total avifauna. If we add to the 25 species reported in this study for AMR those not considered because they are nocturnal or I have insufficient records for the analysis, but which I consider “potential WSF specialists”, the percentage rises to 6.7 %. Similar patterns also occur in plants (R. Vásquez, com. pers.), and at least in some groups of insects (I. E. Saaksjarvi, com. pers.)

The contribution of floristics, both species composition and structure, to habitat selection and diversification in birds, already shown by Remsen and Parker (1983) with river created habitats, Rosenberg (1990) with river islands, Kratter (1997) with bamboo, Borges et al. (2000) with black water inundated forests, and others, is also very clear with the WSF. The absence of a single species such as bamboo (*Guadua weberbaueri*) in Southern Peruvian Amazonia, for example, can mean the absence of a group of 19 bamboo specialists (Kratter 1990). In a similar way, the absence of the community of WSF plant specialists means the absence of the 25 plus bird species in Northern Peruvian Amazonia.

Biogeography and Affinities of White-Sand Forests Specialists

Among the white-sand specialists of the first two categories (obligate and near obligate white-sand specialists) there are three clearly different groups or classes: The first one consists of those species shared with the Guianan Shield and nearby white-sand formations in northeastern Amazonia. It is supposed that these originated there, because the most extensive WSF in Amazonia are in northern Brazil, the Guianas, eastern Colombia and south Venezuela

and these areas harbor the majority of each of these bird species (see Appendix for more details). These species are the obligate white-sand specialists *Crypturellus duidae*, *Notharchus ordii*, *Neopelma chrysocephalum*, *Xipholena punicea*, *Cnemotriccus duidae* and *Hemitriccus minimus*, and the near obligate white-sand specialists *Xenopipo atronitens*, *Platyrinchus saturatus*, *Conopias parva*, *Attila citriniventris* and *Neopipo cinnamomea*.

The second group consists of bird species that do not occur in the Guianan Shield and are endemic to the white-sand forests and similar nutrient-poor forests of northwestern Amazonia, four of them were recently described as new for science. These species are restricted to the “Napo Ecoregion” (Dinerstein et al. 1995), an area characterized by high bird species richness and endemism. These species are: the obligate white-sand specialists *Zimmerius villarejoi*, *Polioptila* sp. nov., and *Pithys castanea*; the near obligate *Percnostola arenarum*, *Myrmeciza castanea*, and *Heterocercus aurantiivertex*; we can add to these also the facultative white-sand user *Herpsilochmus gentryi*.

The third group (*Crypturellus strigilosus*, *Lepidocolaptes albolineatus*, *Myrmotherula leucophthalma*, and *Tachyphonus phoenicius*) are widespread in Amazonia or have not a population in the Guianan Shield area. *Crypturellus strigilosus* was recorded during this study only in the varillales south of the Amazon, both at J. Herrera and Tamshiyacu, but farther south has been found in habitats other than white-sand forest. The other three species have also been recorded in habitats other than WSF in Amazonia.

Because of the restricted patterns of distribution these WSF specialists have today, we can identify two potential centers of bird speciation in WSF: The Nanay River basin and the Morona – Pastaza area.

The Nanay River basin has two species strictly endemic to the area, *Zimmerius villarejoi* and *Polioptila* sp. nov., plus three other species endemic to a slightly larger area, shared with Morona varillal and other nutrient-poor habitats of the region: *Percnostola arenarum*, *Myrmeciza castanea*, *Herpsilochmus gentryi*, and *Heterocercus aurantiivertex*.

The Morona – Pastaza area has *Pithys castanea*, of which only one old specimen is known from the middle-upper Pastaza River, relatively close to Morona varillal. Populations of

two other birds also occur in this region, that probably represent undescribed new subspecies (pending detailed studies): *Myrmotherula leucophthalma* and *Percnostola arenarum*.

At least two of the species in these groups, *Percnostola arenarum* and *Polioptila* sp. nov., have sister species in the Guianan Shield area, from which presumably both originated or differentiated: *Percnostola rufifrons* and *Polioptila guianensis* respectively (Whitney and Alvarez, in prep.; Isler et al. 2001).

The Nanay River basin harbors not only more endemics, but also almost every species of all the three groups. Only *Pithys castanea* and *Myrmotherula leucophthalma* subsp. nov. are absent from Iquitos and restricted to Morona varillal. The reasons for these patterns could be **historical** (age and origin of the white-sand formations), **ecological** (related to habitat heterogeneity, extension, and clumping of the white-sand patches), or **geographical** (distance and isolation from the presumed center of dispersal, the Guianan Shield).

Some species are classified in different categories of specialization at different sites; thus, the patterns of habitat preference may vary among sites. For example, *Myrmeciza castanea* is classified as a near-obligate white-sand forest specialist in the AMR, where recorded only in white-sand forest, whereas at the Jeberos site, it is more abundant in clay-soil forest than in white-sand forest (see Appendix for details).

White-Sand Forests as “Functional Islands”

Because patches of WSF, with their specialized flora and fauna, are surrounded by a matrix of other forest types, varillales function as “islands” in terms of their biogeography and isolation. Although the WSF islands in Amazonia occur at similar elevations as the surrounding habitats, they reflect depositional conditions different from the morphogenetic and hydrological systems prevailing in lowland Amazonia today (Ab’Sáber 1982). The WSF islands usually occur only in some areas of tectonic uplift, or ‘anticlinal emerging arches’, where very ancient lacustrine and fluvial sediments from the late Tertiary, originally covered by Quaternary fluvial deposits, appear in the surface because of intensive denudation. They are surrounded by younger, more extensive, and nutrient-rich Quaternary fluvial sediments (Räsänen et al. 1987; Räsänen 1993). Such cases of “high endemism may be promoted by the older age of the areas

and by possible isolation effects caused by gradational age differences on separating fluvial areas” (Räsänen et al. 1987)

Most of the specialized birds and plants present in the Peruvian WSF are shared with the Guianan Shield in Brazil and nearby Colombia and Venezuela (Brako and Zarucchi 1993; Stotz et al 1996; Alvarez and Whitney, in prep.). This ancient geological formation and related areas have been hypothesized as being not only the original source-pool of the white-sand specialized biota found in northwestern Amazonia (Herskovitz 1963; Alvarez and Whitney, in prep.; K. Ruokolainen, com. pers.; R. Vásquez, com. pers.; Whitney and Alvarez 1998), but also the source of the same white-sand sediments of Iquitos area (Linna 1993; Räsänen 1993).

Many species of plants and animals associated with WSF and related igapo forest currently show a distinctive pattern of disjunct distribution between the Guianan Shield - Rio Negro basin and Nanay river basin and the other WSF area in western Amazonia. I presume that the Nanay river basin, as a result of its older age, geographical localization and higher species richness in WSF specialists, was the first archipelago to be colonized, or the one with a longest history of persistence of WSF habitats (see below). In fact, some of the other forest patches, particularly the presumed younger WSF archipelagoes of Jeberos and Morona, may have acquired most or all of their WSF avifauna and flora from the Nanay basin rather than independently from Guianan Shield areas farther east.

The manner in which this dispersal originated is not obvious. We can hypothesize at least three alternative explanations for the presence of this specialized biota on the WSF islands in western Amazonia, so distant and isolated by great biogeographical barriers from the Guianan Shield.

- **Dispersal hypothesis.** Perhaps these species have colonized the Nanay basin, and subsequently the other WSF islands, by dispersing from the population source in Guianan Shield. These could be certainly the case of some mobile/vagile species, such as medium-size species of the canopy such as *Xipholena punicea* or primates such as *Callicebus torquatus*. But this possibility seems less likely for understory or terrestrial bird species, which rarely dare to cross ‘open areas’ a few dozens of meters wide and are known for having

different taxa at both sides of rivers such as Napo and Amazonas (Capparella 1988, 1991) or for some tree species, especially those that have heavy fruits that do not float (Gentry and Ortiz 1993; Prance 1982), or for some other small animals as spiders, reptiles, and subcanopy bats that also show the “disjunct” distribution pattern between WSF ‘islands’ in Loreto and Rio Negro-Guianan Shield (B. Lamar, pers. com.; C. Hice, pers. com.).

I think this could be the pattern of colonization for the Jeberos varillales, the impoverished WSF communities of which might reflect the ‘relaxation’ phenomenon related to ‘island effects’, that is, depauperate WSF avifauna and flora, or the increasing difficulties to colonization that dispersing species from Guianan Shield and Nanay basin sources face. According to this model, the Peruvian WSF would be considered a “neorefugia”, i.e., a habitat patch formed more recently than the matrix (Nekola 1999).

- **Relictual distribution hypothesis.** Perhaps the WSF patches are relicts of a formerly more widespread habitat, as proposed for WSF plants in northern Brazil by Prance (1982). The WSF were much more extensive in the past in Brazilian Amazonia at least during the Pleistocene (Oren 1982, Ab’Sáber 1982). However, the oldest WSF ‘islands’ in Perú (Nanay and J. Herrera ones) are at most eight million years old (Räsänen et al. 1998). This region was covered during late Miocene, 18 to 2 million years BP, by a huge lake called “Pebas Lake” that was eventually connected with the Caribbean, and whose bottom sediments, the “Pebas formation”, underlie the white-sand sediments in many places (Hoorn 1993; Räsänen 1993; Räsänen et al. 1998). So it is very unlikely that the WSF islands could harbor a “resilient” bird community in the same area previous to the occurrence of the marine intrusions and the formation of the “Pebas Lake” in western Amazonia.

According to Nekola’s model (1999), some characteristics of islands of the Nanay archipelago suggest that it is a “paleorefugium”, i.e., now fragmented relicts of a formerly widespread matrix, whereas Jeberos, and perhaps Morona, seem to be “neorefugia”, i.e., islands formed more recently than the matrix. Some features that seem to support this hypothesis are: a) the Morona, Jeberos, and J. Herrera areas are enriched with highly vagile species relative to the Nanay paleorefugium (such as *Cnemotriccus duidae*, *Hemitriccus*

minimus, *Conopias parva*, *Attila citriniventris* and *Xipholena punicea*, widespread in Amazonia), which is richer in less vagile species (such as *Crypturellus duidae*, *Neopelma chrysocephalum*, *Zimmerius villarejoi*, and *Polioptila plumbea*, with very restricted distributions); b) the Nanay archipelago seems to possess more and stronger correlations between community composition and environmental covariables, such as soil chemistry and habitat structure, as we will see later; c) The negative relationship between archipelago isolation and WSF species richness, in specialists at least, seems to be stronger in the hypothesized neorefugia than in Nanay archipelago (Table 4).

- **Metapopulation dynamics hypothesis.** Another possible scenario, that combines both previous ones, is as follows: perhaps WSF islands are ephemeral habitats in geological time, that is, thousands or millions of years, analogous to the contemporary and much shorter-lived Amazonian river islands. These islands, although highly ephemeral (fewer than 10 years for some) preserve a highly specialized community of birds that manage to migrate from one island to another and colonize even small young islands, although they can be distant and isolated by great stretches of open water.

Throughout Amazonia, the white-sand patches have developed at different times from diverse geological formations, from fossil beaches to in-situ weathering of quartzites (Ab'Sáber 1982). The WSF avifauna could have survived migrating from one WSF patch to another as they appeared and disappeared by erosion in interfluvial ridges through the millennia. This scenario could help to explain the presence in Nanay river basin WSF of bird species with low vagility and of plants with large seeds that seem unlikely to have colonized this 'island' by crossing huge biogeographical barriers as the Napo, Putumayo, Caquetá, and Rio Negro floodplains. This WSF biota is perhaps a relict of a more extensive Miocene white-sand forests growing on sediments derived from the Guianan Shield, and could have survived through this "stepping stone process", moving among island habitats (Brown 1971) through millions of years of geological and ecological changes.

It is difficult to evaluate which of the hypothesis is more likely to be true with the available data from the Peruvian Amazon, and with the low number of known WSF patches to

make any analysis. Nevertheless, as a working hypothesis, let us consider the Guianan Shield as the ‘mainland’, ‘continent’ or ‘source pool’ from which the white-sand bird species have originated. I will use with caution the “island metaphor” for mainland isolates (Haila 2002), given the challenges that island biogeography theory assumptions applied to mainland have suffered in the last decade. I heed the warnings of Terborgh (1974), Heaney (2000), Ricketts (2001), Haila (2002) and others in that both situations, real islands and patches of habitat, are analogous but not equivalent because the habitats surrounding the WSF archipelagoes are not as hostile to specialized birds as open water; in other words, the surrounding matrix quality can significantly influence the “effective isolation” of WSF patches. Also, the intrinsic instability due to their relative geological ephemeral existence and the natural pre-fragmentation conditions were probably not uniform.

Certainly, the bird community of a white-sand patch is not as isolated as an oceanic island, which receives comparatively few immigrants, and the mixed forest surrounding the white-sand patches theoretically allows the constant movement and immigration of individuals and species. Some of the species, especially those that I have classified as “near-obligate white-sand specialists” and “facultative white-sand users” can live, and perhaps even eventually breed, in ‘mixed’ or non white-sand forest, although in the study area they show a clear preference for this habitat. In fact, most of the species in these two categories use the mixed forest in a regular basis in other parts of Amazonia and South America. Every category, even the obligate WSF specialists, can probably use in a temporary basis the mixed forest while moving from one white-sand patch to another.

Various authors have tried to explain patterns of distribution of mainland species of restricted distribution in naturally occurring patchy habitats using the theoretical model of the island biogeography of MacArthur and Wilson (1967). For example, Culver (1970) and Vuilleumier (1970) have shown that aquatic arthropods in caves and Andean birds in isolated paramo habitats, respectively, are distributed as predicted by the equilibrium theory of MacArthur and Wilson. Sánchez and Parmenter (2002) showed that arthropod assemblages on ‘islands’ of creosotebush in the desert of New Mexico conformed fully to the species

richness-island area and species richness-island distance relationships of island biogeography theory.

In contrast, Brown (1971) showed that the diversity and distribution of small mammalian faunas of the montane “islands” of the Great Basin in western United States cannot be explained in terms of equilibrium between colonization and extinction, as island biogeography theory states. His hypothesis proposes a scenario analogous to that of WSF in western Amazonia: all islands were inhabited by a common pool of species at some time in the past, and subsequent extinctions have reduced the number of species on individual islands to their present level. The best predictor of the number of species of each island is their size (Brown 1971).

The comparison of Amazonian WSF patches with islands has already been made by at least two studies in Brazilian Amazon, in order to explain the patterns of distribution and dispersal of plants in white-sand “campinas” (the Brazilian equivalent of the Peruvian varillales: (Macedo and Prance 1978), as well as for specialized birds (Oren 1982). Macedo and Prance found that about 76% of the plant species in campinas have the potential for long-distance dispersal, of which about 60 % are bird-dispersed. This pattern differs clearly from the dispersal strategy prevailing in their surrounding matrix of forest, in which the “diaspores tend to be heavy, gravity-dispersed fruits with a short-range potential for distribution”. According to the authors, this tendency towards long-distance dispersal, and especially towards ornithochory, is characteristic of islands.

Oren (1982) found in Brazilian campinas that the presence of habitat specialists in birds was related to the size of the WSF patches: campinas of less than three ha did not have any white-sand specialist, only generalists, whereas campinas of 5-100 ha had some relatively high vagility specialists, and those of more than 100 ha had the low vagility, habitat specialists, that tend to have the more restricted geographical ranges. However, Oren did not consider other factors that can influence the presence of bird species in a given white-sand patch, as it happens with island avifaunas, such as habitat quality and heterogeneity, individual history and origin of every patch, and distance from the “source pool” or “mainland”, in this case, the Guianan Shield. At least one study (Kadmon and Pulliam 1993) showed that distance from the mainland

has more influence on species composition of an island than the area or the habitat quality. They showed, for example, that islands isolated from each other but with a similar distance to the ‘continent’ are more likely to have species in common than are two islands relatively close to each other but differ in their distance to the ‘continent’.

In the Peruvian Amazon, the white-sand patches are arranged in a way somehow different than those in Brazil. Rather than single islands, they are more like ‘archipelagoes’, where the varillal patches are more or less clumped or connected according to geological formations. They are clustered in four areas. In two of them, Jeberos and Morona sites, the white-sand patches are relatively close to the foothills of the Andes, and their origin is probably related to the uplifting of these mountains in the late Miocene, and especially in the Quaternary (Díaz et al. 1998). The other two, the Nanay and Jenaro Herrera - Tamshiyacu sites, are both related to a geological formation, the ‘Iquitos Arch’, that is a Tertiary anticlinal emerging among more modern Quaternary sediments (Räsänen 1993).

I think that here the size of individual WSF patches is not so important for determining the composition of species as other factors, like size of the “archipelago”, age and history, isolation in relation with the ‘mainland’ -the Guianan Shield-, and habitat heterogeneity. I have observed that many of the smallest WSF patches, regardless the size and distance to other patches, are used by most of the WSF specialists found in a given locality.

Metapopulation Dynamics Model Applied to White-Sand Forest Islands

Small populations, such as those of the small islands and small forest patches, are relatively likely to become extinct due to stochastic factors (Lande 1988; Thomas 1990, 1994). On the other hand, many WSF patches, a few hectares in extent, are presumably too small to sustain a viable population of most of the white-sand specialists, some of which use only some types of varillal inside a given WSF patch, as was shown before. Because local extinctions of fragmented or isolated populations, such as those of islands or forest patches, are common, it follows that recolonization after local extinctions is critical for regional survival of these populations (Fahrig and Merriam 1994). If these populations are not self-sustaining, the populations of the white-sand specialists found in some of the smaller white-sand forest patches

are probably dependent on re-colonizations from the “mainland” as well from other nearby WSF patches. The maintenance of those fragmented and scattered sub populations could be explained by the metapopulation dynamics model (Gilpin and Hanski 1991; Thomas 1994).

I suspect that the most widespread white-sand specialists have evolved not only the capacity to exploit this unique habitat resource but some are also highly vagile, allowing them to maintain a genetically and demographically viable population in a highly fragmented complex of ‘archipelagos’ of white-sand forest patches in the Amazon. This probably is possible through the occurrence of a constant flux of individuals and genes among the different WSF patches, and possible recolonizations of patches where local populations became extinct due to stochastic events. This has allowed the WSF species to exploit a resource that is scarce but widespread, and under-exploited by other species. As has been remarked, this archipelago complex is unique in the sense that the islands are not isolated by an almost unsurpassable barrier such as a stretch of ocean, but a matrix of forest of different type. Two other communities of birds, those specialized on bamboo thickets and those on river islands, show a similar pattern of distribution and have probably similar strategies of dispersal and colonization (Rosenberg 1990, Kratter 1997).

Some of the WSF specialists with wider distributions are fairly small, but seem to be very good dispersers. For example, *H. minimus*, widespread in white-sand patches throughout the central Amazon, although apparently absent in Morona and Jeberos sites, is a small tyrant flycatcher barely 10 cm. long and barely 7 g in weight. The slightly bigger *Cnemotriccus duidae* sp. nov., which lives in the subcanopy of stunted WSF, is found in almost every small patch forest with this physiognomy, regardless of size or degree of isolation (B. Whitney, pers. com.; Alvarez, pers. obs.) I have recorded *C. duidae*, for example, in the highly isolated Jeberos WSF, and both flycatchers in a small shrubby WSF patch of no more than 500 m. in diameter in Jenaro Herrera, south of the Amazon and east of the Ucayali. The suitable habitat for *C. duidae* in this WSF patch (stunted varillal) was perhaps no more than two or three hectares, and I doubt that more than one to three pairs could live there. This small WSF patch was at least 10 km from the nearest WSF patch in the region.

Both species move slowly among the branches of the trees when foraging and never sally outside the tree canopies. I have never seen any of them flying more than five or eight meters in a flight. But given that they seem to be so successful in colonizing the smallest suitable white-sand patches, they probably have some adaptive behavior or dispersal trait that improves the probability of dispersers finding suitable habitat patches (Fahrig and Merriam 1994).

I have no data to test these hypotheses, and studies of population genetics of these isolated WSF populations and phenotypic indicators of genetic differences (or lack of them), as subtle differences in color, measurements, voice, etc., are required to determine if gene flow exists among the individual WSF patches, as well as among the five WSF “archipelagos” known so far in Northern Peruvian Amazonia. Also, concise analysis of the characteristics of the resource and habitat use by WSF specialists, i.e., canopy vs. undergrowth, frugivore/nectarivore vs. insectivore, and other indirect measures of potential dispersal ability or persistence would perhaps provide clues for understanding the origin and explain the patterns of distribution of this unique avifauna.

Presence of Some White-Sand Forest Specialists in Other Forest Types

Some of the WSF specialists, mainly in the near-obligate category, have been found occasionally in habitats other than WSF. This occurrence could have two explanations, which are not mutually exclusive: 1) dispersal of juveniles of white-sand specialists among the patches of varillal through the “matrix”; 2) the “mass effect” and “sink and source” models (Pulliam 1988; Shmida and Wilson 1985). When one species is abundant in its preferred habitat or “source”, it could occasionally persist or attempt to breed in less suitable nearby habitats or “sink”, although in these sink habitats the population may persist only maintained by continued immigration from nearby source area. Only careful studies of marked birds will resolve which of these explanations applies.

Patterns of Distribution of White-Sand Specialists among Four Localities

Not only the WSF bird assemblage, but also the WSF plant assemblage is reduced at the Jeberos site, and as well at Morona site (Tables 2 and 8; P. Fine, pers. com., and pers. obs.), as compared with the Nanay river basin WSF communities. The absence of some of the

white-sand specialists in Morona and Jeberos varillales could have several alternative explanations.

Table 8. Common bird species missing from two study sites

JEBEROS	MORONA
<i>Hyloctistes subulatus</i> <i>Cymbilaimus lineatus</i> <i>Thamnophilus schistaceus</i> <i>Thamnomanes ardesiacus</i> <i>Thamnomanes caesi</i> <i>Cercomacra cinerascens</i> <i>Hypocnemis hypoxantha</i> <i>Pithys albifrons</i> <i>Formicarius analis</i> <i>Corythopis torquata</i> <i>Todirostrum chrysocrotaphum</i> <i>Hemitriccus minimus</i> * <i>Tolmomyias flaviventris</i> <i>Cnipodectes subbrunneus</i> <i>Piprites chloris</i> <i>Pipra coronata</i> <i>Xipholena punicea</i> * <i>Campylorhynchus turdinus</i> <i>Liosceles thoracicus</i> <i>Hylophilus hypoxanthus</i> <i>Cyanocorax violaceus</i>	<i>Celeus grammicus</i> <i>Automolus ochrolaemus</i> <i>Megastictus margaritatus</i> * <i>Formicarius colma</i> <i>Hemitriccus minimus</i> * <i>Cnemotriccus duidae</i> * <i>Cnipodectes subbrunneus</i>

* WSF specialists

- **Isolation and age.** Geographic isolation has been shown to affect species composition on islands (Kadmon and Pulliam 1993), as well as species richness (MacArthur and Wilson 1967). Historical factors might also account for some of the patterns of distribution of species not explained by environmental conditions (Louks 1970; Pearson 1975; 1977; 1982). The ancient and huge Guianan Shield probably functions as the “source pool” for the biota that found in the scattered “white-sand” forest patches or “archipelagoes” throughout northwestern Amazon (Linna 1983; Räsänen 1983). That a great percentage of the WSF

specialized flora and fauna and the largest populations of WSF specialists, both plants and animals, are found there also supports the notion that the Guianan Shield is the source region.

I suspect that some of these species did not manage to colonize the Morona and Jeberos varillales for two reasons: a) both are farther from the Guianan Shield; and b) the Jeberos WSF, and perhaps the Morona ones, are probably of younger origin than Iquitos ones (F. Rodríguez pers. com.; Díaz et al. 1998; Räsänen et al. 1998). The presence of important biogeographical barriers to bird dispersal, like the Marañon, Tigre, Pastaza, and Morona rivers, and the flood plains with extensive transitional and swampy forests associated with them, could explain the absence of these species.

On the other hand, in situ speciation accounts for some of the differences among islands, which cannot be explained by island biogeography theory (Lomolino 2000): the occurrence of two species restricted to Nanay archipelago, *Zimmerius villarejoi* and *Polioptila* sp. nov., two others shared between Nanay and Morona archipelagos, *Percnostola arenarum* and *Herpsilochmus gentryi*, and at least one endemic at Morona site, *Pithys castanea*, suggest that these archipelagos have undergone the process of phylogenetic diversification, which is characteristic of a long history of isolation (Heaney 2000).

- **Size.** Island biogeography theory states that area alone accounts for most variation of species numbers in islands (MacArthur and Wilson 1967). As far as is known, the total area of the varillales is much smaller in the Jeberos than in the Nanay areas. The size of the Morona varillales is not known, but they could be smaller than the Nanay basin ones. A smaller habitat patch, with some degree of isolation, not only is less likely to be colonized by species (MacArthur and Wilson 1967), but also is prone to loss of species by phenomenon such as “relaxation” (Diamond 1972; Wilcox 1980) or population fluctuations (Karr 1982). Species dependent on resources likely to be variable or patchy in their distribution, particularly frugivores and nectarivores, are evidently more prone to extinction (Terborgh and Winter 1980). Coincidentally, some of the species missing in Morona and Jeberos are probably frugivores (*Neopelma* and *Xipholena* in Jeberos, *Neopelma* in Morona). However, the

presence in Jeberos of the presumably frugivore *Xenopipo atronitens*, whose closest population is more than 1000 km. away in southern Peru, seems to contradict this hypothesis.

- **Habitat heterogeneity.** Habitat heterogeneity or diversity has been proposed as a determinant of species diversity and distribution (Shmida and Wilson 1985; Tuomisto et al 1995, and others) It has been shown recently that habitat diversity, not considered initially by MacArthur and Wilson among the factors influencing island species richness, is one of the best predictors of species richness (Ricklefs and Lovette 1999; Fox and Fox 2000). The Nanay River varillales are by far the most heterogeneous among the study sites: more than eight types of varillal, different in vegetation stature, structure and composition, and organic layers in the soil have been classified and can be distinguished by sight in this area (Revilla 1978; Alvarez et al. 1999; García Villacorta et al. 2002). Only three types of varillal were recognized in Jeberos site, and only one in Morona site. As shown in the second part of this study, some of the WSF specialists are segregated by habitat and restricted to one or two types of varillal. This extreme habitat specialization probably allows the coexistence of so many species in the area.

I suggest that some of the most strange or unexplained patterns of distribution of some widespread Amazonian bird species, such as highly patchy distributions or extreme rarity, are related to some kind of habitat specialization, so far unknown to ornithologists, analogous to the patterns of distribution and specialization of WSF bird species (and bamboo bird species, as stated by Kratter 1997). This specialization, as happens with some WSF specialists, can change in different localities depending of the “species-packing” or species saturation and habitat quality (Pearson 1975). Some species, as has been described for insects (Fox and Morrow 1981) and some vertebrates (Watson 1970) can show a pattern of “local specialization”; that is, they have geographically variable diets or habitat use, being specialists with restricted diets or habitats at a local scale, and generalized diets or habitats over their geographical ranges. Coincidentally, the unexplained variance in field data of botanists when dealing with correlation of ecological distance with differences in environmental conditions has been labeled in the past as “noise”; more recently, it has been explained by other determinants (Shmida and Wilson 1985; Tuomisto et al. 1995). Recent studies have shown that spatial

variation in abundance in North American birds largely reflects the extent to which local sites satisfy the niche requirements of the species (Brown et al. 1995)

Jeberos Site: A Non-saturated Bird Community?

The striking pattern of habitat use by *M. castanea* in Jeberos could also be explained by the “ecological release”, “density compensation” and “habitat expansion” mechanisms typical of oceanic islands and continental isolates (MacArthur et al. 1972; Cox and Ricklefs 1977; Terborgh et al. 1997; Pearson 1975, and others). In contrast to AMT, where it is an obligate white-sand specialist, here the abundance of this species is much higher in clay-soil forest than in white-sand forest: 2.14 ind/km vs. 0.47 ind/km, respectively (t-test, $p < 0.001$). Because Jeberos has a depauperate avifauna, the absence of competitors as *Pernostola arenarum* and perhaps other bird species, and even other animals, could allow *M. castanea* to use unexploited resources, in this case habitats, including the clay-soil forest, which can sustain higher bird densities because of greater productivity.

Another possible example of ecological release was observed in *Cnemotriccus duidae* sp. nov., which had a similar pattern of wider habitat utilization in Jeberos than in AMR varillales, where is restricted to varillal with stunted vegetation, the so called “chamizal”, especially the “chamizal seco”. Although always restricted to white-sand, at Jeberos I found this species using tall varillal, secondary forest on white-sand, as well as a type of “chamizal húmedo” similar to those in AMR.

Bird Species Rare or Absent from White-Sand Forest Patches

There are at least three possible explanations of the conspicuous absence or extreme rarity of a number of species from the WSF patches that are fairly common in the surrounding MF (Table 4).

1) Habitat quality / productivity. Some of the characteristics of the WSF include a) nutrient deficiencies and hence low productivity, b) the abundance of toxic secondary compounds and physical defenses in the foliage, and c) as a consequence, reduced arthropod and other small animals' fauna (Stark 1970; Hardon 1937; Klinge and Herrera 1978; Anderson

1981). This scarcity could explain at least the absence of some of the more exigent the insectivorous/omnivorous species.

2) Lack or scarcity of microhabitats and substrata used by some species. This can be the case, I think, of some species that regularly use vine-tangles and structurally similar thickets, which are very scarce in the WSF. Examples are *Cymbilaimus lineatus*, *Cercomacra cinerascens*, or *Thamnophilus schistaceus* (Marra and Remsen 1997).

3) Competitive exclusion by other species (habitat segregation). This could be the case, for example, of some species that have potential ecological substitutes in some of the WSF specialists: for example, *Pernostola leucostigma*, whose substitute in WSF probably is *P. arenarum*; *Myrmotherula brachyura*, whose substitute in WSF could be *Herpsilochmus gentryi*; or *Xiphorhynchus guttatus*, whose substitute in WSF could be the abundant *X. ocellatus*.

Patterns of Habitat Use by *P. arenarum* and *Z. villarejoi*

The patchy pattern of distribution that both *P. arenarum* and *Z. villarejoi* have is not unusual in many tropical vertebrate species, including birds (Arita et al. 1990; Karr 1977; Terborgh and Winter 1980). Although some cases have been explained as related to patchy environments, often there is no obvious explanation (Wiens 1976). In the case of the white-sand forest bird species, given the scarcity and isolation of the varillales in a matrix of mixed forests, possible stochastic processes could determine the presence/absence patterns of some of the species in a given locality. These processes are related to colonization, extinction and survival, and determined by patch size, habitat quality and distance from the dispersion centers - according to the island biogeography model, as it was seen before (MacArthur and Wilson 1967; Terborgh et al. 1997).

Different Patterns of Habitat Use in Different Localities by *P. arenarum*

In 3 years of study in the AMR and Nanay river basin, I have very few records of *P. arenarum* in varillal types other than that waterlogged WSF in which the saplings of the palm *E. catanga* were abundant. This varillal is called locally “varillal bajo húmedo” (Alvarez et al. 1999; Isler et al. 2001). At least in some of these cases, these birds probably represent either

transient individuals, moving from one suitable patch of forest to another, or immature individuals that were looking for a territory.

I have never recorded a permanent territory of *P. arenarum* in AMR away from dense stands of *E. catinga*, except for one possible, exceptional case in a varillal 10 km west of the Iquitos-Nauta road, at approximately km. 38 in the so-called “Parcelación Ex-Petroleros”- There, during five days, I recorded a *Percnostola* pair occupying a patch of very dense, secondary white-sand forest. The area had been cleared for a road construction 15 years before, but the road had never been built. The regrowth vegetation structurally resembled the patches of *E. catinga* saplings commonly used by *P. arenarum* in the area. However, the palm was relatively uncommon there.

The hypothesis that the population of *P. arenarum* is limited in AMR by the availability of this type of white-sand forest in which *E. catinga* is dominant -“varillal bajo humedo”- is supported by one observation: When gathering data for the description of this species, I collected two males and one female from the same territory in a patch of “varillal bajo humedo” close to the village of Mishana, inside the AMR. Other types of varillal less waterlogged surrounded this varillal patch, where the *E. catinga* saplings were absent or not abundant. I did not record a permanent territory of *P. arenarum* in these drier habitats. But when I collected the first female in September 1998, another female occupied the same territory at the “varillal bajo humedo” the following day, singing and marking the territory along with the male. Similarly, when I collected the male a few days latter, another male occupied the territory and was singing the next day. I collected this male a few days later, and I found the territory occupied by yet other male when I returned to the site ten days afterwards.

Records of *Percnostola arenarum* Outside the *E. catinga*-dominated Stands and Outside Allpahuayo-Mishana Reserve

A different pattern of habitat use is shown by *P. arenarum* in the upper Nanay river basin, and in the nearby area on the right bank of the Tigre river, where this species was recorded for the first time. In this area I have not observed varillales of the kind that *P. arenarum* commonly uses in AMR, but I have sometimes recorded *P. arenarum* at both sites

in a completely different type of habitat, a closed-canopy and taller forest growing on lateritic soil that is called locally as “irapayal”, because the understory is dominated by the palm *Lepidocaryum tenue* (Isler et al. 2001).

These “irapayales”, although widespread, are locally distributed in certain types of terra firme forest in the Iquitos region, but *P. arenarum* is only present, in very low densities, in some of them. I have observed and recorded this species only at those irapayales presumably growing on the most deeply weathered lateritic soils, probably very poor in nutrients, as revealed by the somewhat stunted vegetation and the presence of a thick organic layer in the soil of decomposing leaves, twigs and roots, one of the features of very nutrient poor soils (Klinge and Herrera 1978; Richards 1996). These ‘irapayales’ are commonly related with late Tertiary sediments, both clayey and white-sand soils.

I suspect that the species with which *P. arenarum* faces competition in the terra firme forests is the closely related *Percnostola leucostigma*, although this could also be a case of “diffuse competition” with several species (MacArthur et al. 1972). Although these irapayales are occasionally used by *P. leucostigma*, and I have recorded both species in sympatry several times at the same locality, I have never observed them using the same habitat type in syntopy. I do not know with certainty how they can manage to share the habitat, but I suspect that they segregate among the different gradients determined by soil quality: *P. arenarum* being restricted to white-sand and very nutrient-poor irapayales, and *P. leucostigma* occupying a variety of richer and more extensive habitats. If this hypothesis is true, *P. leucostigma* would be the dominant species, and *P. arenarum* the subordinate one, sensu McNaughton and Wolf (1970). According to these authors, dominant species tend to have broader niches than less dominant species or subordinate species, and dominance is a characteristic of the most abundant species.

On the other hand, I have never recorded *P. leucostigma* in the patches of humid varillal dominated by *Euterpe* saplings used by *P. arenarum* at AMR. I have recorded *P. leucostigma* in other types of varillal only twice, both were of a single pair, along the 56.4 km of transects made on the white-sands, but perhaps these were vagrant or dispersing individuals, or a case of “mass effect” (Shmida and Wilson 1985). The fact that *P. leucostigma*, while

being fairly common in the nutrient richer clayey forests, never uses the contiguous varillales on a regular basis, reveals that both species seem to be segregated by the habitat type. Their pattern of distribution probably is related to the structure and composition of the vegetation, which in turn is related with the edaphic properties of the soil (Ruokolainen and Tuomisto 1998).

The few records of *P. arenarum* I have in the Morona site in the mixed forest could be also explained by the phenomena known as “mass effect” and “sink and source” (Pulliam 1988; Shmida and Wilson 1985). Because *P. arenarum* is so abundant in the nearby WSF or “source”, it could occasionally wander through less suitable nearby habitats or “sinks”, although in these sink habitats the population may persist only maintained by continued immigration from nearby WSF or source area.

***P. arenarum* in Morona River Varillales**

A new population of *Percnostola* was found in the Morona river varillales. Although this population apparently belongs to the same species, differences in the colors of the collected individuals, especially among the females, with the Nanay river population, suggest that they could represent a new taxon, perhaps a different subspecies.

The relative abundance of *P. arenarum* in this varillal, in which the understory was fairly open and the saplings of *E. catanga* somewhat scarce, was surprising (see relative abundances in previous chapter; also, Valqui et al., in prep.). Both the use of this type of varillal, and the high densities of *P. arenarum* in this varillal could have at least three possible explanations:

The first one, as was suggested in the previous chapter, could reside in the occurrence of some of the processes taking place on islands, such as ‘ecological release’, and its related ‘niche shift’ and ‘density compensation’ mechanisms. If I take the AMR as the “mainland” or “pool source”, in other areas as Morona varillal in the absence of the main competitor or competitors, the species may benefit from unexploited resources and niches and expand its habitat (MarArthur et al. 1972) and increase its abundance (MarArthur et al. 1972; Cox and Ricklefs 1977; Terborgh et al. 1997).

Although I do not know which species may compete with *P. arenarum* in the varillales, the absence of *Myrmeciza castanea* in the Morona varillal undergrowth, which perhaps is one

of the potential competitors of *P. arenarum*, offers some circumstantial evidence for this hypothesis. I have observed in AMR that *P. arenarum* was apparently substituted by *M. castanea* in the types of varillal in which the saplings of *E. catanga* palms were not present or were scarce -those with less humid soils and higher and closer canopy. The latter species has a slightly smaller size, overall similar behavior, and occupies thoroughly the same niche in the forest understory as *P. arenarum*, not only in varillales but also in irapayales of different quality. *M. castanea* has a more extensive distribution and uses a wider range of habitats (Isler et al. 2001; Isler et al. 2002, Alvarez, pers. obs.).

A second possible explanation for the different pattern of distribution of *P. arenarum* between AMR and Morona varillales could be related with the edaphic properties of the soil and the vegetation structure and composition. This species, being bigger and probably dominant over *M. castanea*, probably occupies the more suitable parts of the varillales in AMR, and excludes the latter species from them. The dense understory of the *E. catanga* clumps that it uses in AMR varillales could be advantageous compared with other more open habitats, in order to avoid predators. The thicker and more humid litter layer that characterizes the soil of this varillal type could have comparatively more arthropods than the lighter, drier parts of the varillal. In fact, it has been demonstrated that higher litter moisture content in forest floor is associated with increased arthropod populations (Levins and Windsor 1984).

In San Carlos, Venezuela, Klinge and Herrera (1978) studied the biomass and composite root mass in several types of white-sand forests or caatinga forest, that resemble in some way those of the Peruvian Amazon. They showed that the thickness of the litter and raw humus layer in the soil is related to the topography of the terrain, and hence the watertable level and the flux of nutrients. These features determine the litter decomposition and humus accumulation rates. The AMR varillales differ from those of San Carlos in the last ones being at different topographic levels. In AMR, the shape and disposition of the hardpan or spodic horizon under the surface is what determines the water table level and water fluxes, and could explain the different vegetation types at AMR sites (Ruokolainen, pers. com.)

In San Carlos, the ‘drier’ parts of the caatingas -called low caatinga or ‘bana’- are soaked with water during heavy rains, but because the drainage is good, due to the topography and the sandy texture of the soil, the water is rapidly drained and the banas may even experience drought during times of rain scarcity. Due to the rapid drainage, leaching is severe and the nutrients are exported to nearby lower areas, where the watertable remains constantly near the surface. The nutrients accumulate in those lower areas and allow the formation of higher vegetation, called tall caatinga or “yevaro” (Klinge and Herrera 1978). I think that an analogous phenomenon is occurring in the different types of varillal at AMR.

Although Klinge and Herrera (1978) did not describe the soil fauna in the different white-sand forest types, they mention the ‘poor soil life observed’ in these habitats. This is concomitant with the pattern of ‘reduced animal communities’ that has been observed in other tropical white-sand forests (Stark 1970; Janzen 1974). In any case, it seems very probable that those areas with greater litter accumulation and hence more nutrient-rich -tall caatinga or yevaro, equivalent to the “varillal bajo humedo” of AMR and the varillal at Morona site- should sustain a relatively richer arthropod fauna than the almost barren and drier ‘bana’. I suspect that this could be one of the reasons that *P. arenarum* uses the varillal bajo húmedo in AMR and Morona sites, while avoiding the drier types of varillal.

This hypothesis is supported by the abundance of predatory army-ants swarms that were observed at Morona varillal, where the soil litter was very thick and humid in all its extension, in contrast with AMR varillales, where the patches of varillal with a thick litter layer - the varillal bajo húmedo- are very scarce, and where I have never seen any army ants. Certainly, the Morona varillal had not only a very thick and permanently waterlogged layer of soil litter, but also a great abundance of palms -not less than eight species- and several herbaceous species. Both are very scarce in AMR varillales, and especially in the drier types of varillal, apparently from nutrient and water stress (K. Mejía, pers. com.; Alvarez, pers. obs.) The presumably more recent history and Andean origin of these white-sands soils (F. Rodríguez, pers. com.) could explain the edaphic differences between both sites.

Assuming that they belong to the same species as the AMR population, if the relatively dense population of the *P. arenarum* in the Morona varillal uses extensively a type of varillal with very open understory, I can not find any reason, other than subtle differences in habitat quality or possible competition with *M. castanea* and perhaps other species, why it cannot use structurally similar habitats in AMR.

Finally, a third possible explanation for the different pattern of distribution of *P. arenarum* and *M. castanea* in Nanay, Morona and Jeberos localities could be a phenomenon called “checkerboard distribution pattern”, initially described for islands, in which two or more closely related species occupy ecologically similar patches of insular habitats to the exclusion of each other in a geographically irregular array (MacArthur et al. 1972). In some cases, as these authors explain, “similar species are able to coexist on an island by dividing up the available habitats in mutually exclusive fashion, such that a species which would occupy all habitats in the absence of competitors becomes restricted to fewer habitats on species rich islands” (MacArthur et al. 1972: 339).

Some authors (i.e. Van Horne 1983) have warned about inferences of habitat quality from indices of animal abundance. Some habitats could be actual population “sinks” having nevertheless higher densities than better quality habitats. I think it is very unlikely that this is the case of *P. arenarum* in Morona varillal, because being a white-sand specialist, there is no other habitat that can function as a “source” of the population. The same observation can be made for the AMR, where the lack of records of *P. arenarum* outside the “varillal bajo húmedo” excludes the possibility of it functioning as a “source”.

I think this could be the situation at AMR, where the exceptional richness of varillal types and other habitats allow the coexistence of the similar *P. leucostigma*, *P. schistacea*, and perhaps *Myrmoborus myotherinus* in mixed forests, and *P. arenarum* and *M. castanea* in the nearby white-sand forests. The overall higher species richness of AMR terra firme forests, compared with Morona and Jeberos sites, could be explained by both ecological and evolutionary or historical processes (Pearson 1975; Srivastava 1999): The higher number of habitats in AMR permits the coexistence of species with effectively identical or near identical

niche and habitat requirements, being closer to species saturation than the other sites (Cohn-Haft et al. 1997; Thiollay 1990; Shmida and Wilson 1985) The longer history of the white-sand sediments have permitted a higher species accumulation (McArthur et al. 1972, and others). I hypothesize that, at least in some specialized insectivorous birds, it can be predicted that the richer the number of habitats in one given locality, the narrower the niche occupied by the species.

I do not have enough data to test this hypothesis, and further studies are needed in order to determine the real causes of bird distribution patterns in the Peruvian Amazon white-sand forests, as to determine in detail the interactions among these species, resource partition and niche utilization.

Some Potential Causes of the High *Pernostola* Specialization

It has been shown that the most abundant species have specialized on a wider range of habitats or resources, which forces other species into “peripheral specializations” (McNaughton and Wolf 1970). I think this could be the case of *P. arenarum*.

P. arenarum appears to have the narrowest niche in the white-sand forests of the lower Nanay river basin, where the habitat heterogeneity and the consequent “packing of species” seem to be highest. This pattern of or increased species richness and species-niche specialization in areas with high habitat heterogeneity, as determined by underlying soil mosaic, has been described for Amazonian plants (Duivenvoorden 1996; Ruokolainen and Tuomisto 1998; Tuomisto et al 1995); for birds (Pearson 1975; Cohn-Haft et al. 1997; Marra and Remsem 1997; Zimmer and Hilty 1997; Thiollay, 1990) and other organisms (i.e., Lim and Engstrom 2001).

On the other hand, the forest types in which I have observed *P. arenarum* are characterized not only by a dense understory of saplings of two species of palms, but by a thick layer of litter on the forest floor. This layer, as has been pointed out before, is characteristic of some extremely poor soils, especially white-sand (Janzen 1974; Richards 1996). As has been pointed out before, understory and floor invertebrates are very scarce in this kind of habitat. It has been suggested that extreme specialization is one adaptative response of some terrestrial

vertebrates in the rain forests of humid tropical lowlands, because the resources are scattered and uncommon (Kikkawa and Dwyer 1992).

I presume that *P. arenarum*, in response to these “scattered and uncommon resources”, combines extreme habitat specialization in lower Nanay varillales, in which the species richness and competition are probably higher, with some kind of flexibility in other more ornithologically depauperate areas, which allows it to use at least two other kind of habitats. Habitat and diet flexibility, along with idiosyncratic specialization, has been suggested as an adaptation to a challenging environment with scattered and scarce resources (Kikkawa and Dwyer 1992). However, as these authors suggest (1992: 305), both attributes “render each species taken separately and the system as a whole vulnerable to catastrophic disturbances”. The extensive destruction and extractive pressures put on the habitat of *P. arenarum* in Nanay river basin could be seen as a real threat to its survival, given its specialized habitat requirements and restricted distribution.

Patterns of Habitat Use by *Z. villarejoi*

Z. villarejoi seems to be restricted to one type of varillal where *Dicymbe uaiparuensis* is dominant, “varillal intermedio seco”, except in one locality, Nueva Esperanza varillal; there it was found in the “chamizal húmedo” where *D. uaiparuensis* is very scarce. At least three explanations could be considered to explain this apparent discordance.

The simplest explanation is that *Z. villarejoi* can also use occasionally this second type of varillal. In fact, I have recorded it occasionally in “chamizal húmedo” in other places in Nanay river basin, not only in Nueva Esperanza.

One question that comes to mind immediately is whether *Z. villarejoi* uses this “chamizal húmedo” on a permanent basis, or only as a “corridor” between patches of its preferred habitat. The stands of *Dicymbe* are not evenly distributed in many varillales, but occur in clumps of different sizes. They frequently occupy the higher and drier spots of the area, scattered throughout a matrix of more humid or taller varillal, in which *Dicymbe* is scarce or absent. Many of these clumps of *Dicymbe* are probably too small to sustain a territory for *Z. villarejoi*, but perhaps moving among several patches close enough it could manage to

supplement its resource intake. This phenomenon, observed in other organisms, has been called “landscape supplementation” (Dunning et al. 1992), and I think it is quite possible for a high mobile bird like *Z. villarejoi* to behave in this way. The quick movement of *Z. villarejoi* through the forest I have observed many times could then be explained by the bird moving from patch to patch of *D. uaiparuensis* through a matrix of less suitable habitat.

The second possible explanation of this pattern of habitat occupancy, as was suggested for *P. arenarum*, could be related with the “mass effect” and “sink and source” models (Shmida and Wilson 1985; Pulliam 1988). If *Z. villarejoi* is abundant in its preferred habitat or “sources”, it could occasionally wander through less suitable nearby habitats or “sinks”, although in these sink habitats the population may persist only by continued immigration from nearby source areas. Perhaps, by chance, the Nueva Esperanza census trail missed a preferred habitat patch of *Z. villarejoi* and passed through a nearby “marginal habitat”, where nevertheless several records of the species were made.

Finally, another possible explanation could be related to the local history. The case of Nueva Esperanza Varillal is unique among the study sites because it was being exploited heavily for timber at the time of this research. Only the sections of the forest with more stunted trees, that is, the “chamizal húmedo”, were untouched by the timber workers. Extensive areas of drier forest in the surrounding areas, in which *Dicymbe* was abundant, had been cleared in previous months, judging by the stumps left by the lumbermen. It is plausible that some *Z. villarejoi* were forced by the forest clearing to occupy unsuitable areas such as the “chamizal húmedo” in which I recorded it several times. It would be interesting to evaluate this trail again two or three years later, to find out if there is a self-sustainable population of *Z. villarejoi* in this “chamizal húmedo”.

Conclusions

Patterns of Distribution of Birds in White-sand Forests on Northern Peruvian Amazonia

This research is the first comprehensive study of the white-sand forest avifauna in the Peruvian Amazon. I used birds as an indicator group of the patterns of distribution and endemism of the fauna in the unique white-sand forest of northwestern Peruvian Amazon. Assessing the uniqueness of the avifauna will facilitate the determination of the biological importance of this habitat and will result in information useful to promote conservation and management measures.

At the time of this study, only a preliminary survey had been carried out by the author in the white-sand forests close to the city of Iquitos, and about a dozen species of birds new to Peru, some of them new to science, have been found. After these findings were reported, a new Reserve was proposed and created in the area in 1999 for the protection of these birds and the entire community of unique plant and animal species that are restricted to white-sand forests. After establishment of the Reserve, the local people continued with their traditional activities of extracting timber and hunting wild animals within the now protected forest of the reserve. Local government officials were reluctant to enforce the law, because of strong social and political pressures. There were not enough field data to show that there were species at risk if the harvesting activities continued. One of the purposes of this research was to show that at least some of the white-sand specialists have very limited distribution and are also restricted to certain types of white-sand forests. Continued logging activities in these kinds of forests could put at risk these species long term survival of those species.

The other three localities in which WSF pockets have been found in the Peruvian Amazon have not been surveyed ornithologically prior to this study. Many of these forests are also threatened by shifting agriculture, logging, and other human activities, because they don't have any protection status. It is important to study and, if necessary, protect these forests not only because they are biologically unique and home to a rich community of rare and range-restricted species, but also because they are so fragile that once disturbed, they may require hundreds or thousands of years to recover (Uhl et al. 1982). Many WSF specialists may never

recolonize regenerated white-sand forest patches, especially if they are separated from intact forest by open areas. Some animals, specially the obligate white-sand specialists, may be affected by minor disturbances of the forest, disturbances such as that caused by the selective timber extraction. More studies are required to precisely define habitat requirements of WSF species and to assess threats that various habitat changes would have on them. The patterns of distribution of some of the WSF specialists found in this study can help to understand the biogeography of the Amazon basin birds. The “patchy” distribution -or leap-frog pattern- of some of them is not yet explained.

Habitat Use by *P. arenarum* and *Z. villarejoi*

Although it is clear that these results are very preliminary, it can be safely concluded that both species have very specialized habitat requirements. If we use niche breadth as an inverse measure of ecological specialization (Colwell and Futuyma 1971), *P. arenarum* and *Z. villarejoi* are among the most specialized of the Amazonian birds (Alvarez and Whitney 2001; Isler et al. 2001). It is known that narrow-niched species are ill-adapted to uncertain environments (Smith 1981). This circumstance, together with the restricted and patchy distribution of both species, and the growing threats to their habitat, puts them among the most threatened bird species in Peruvian Amazonia.

Much more ecological and biogeographical studies need to be done before detailed patterns of distribution and causes of the high degree of specialization of these and other WSF specialists can be more fully understood. Moreover, more work is required before the scenario of the evolutionary origin of western Amazonian megadiverse biota can be reconstructed.

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Appendix: Notes on the Distribution of White-Sand Forest Birds in Northern Peruvian Amazonia

Obligate white-sand forest specialists

1. *Crypturellus duidae* (Gray-legged Tinamou)

The number of records of this tinamou during this study is very low, no doubt due to its secretive habits and low densities, as is usual in most members of the family. Actually, all 5 records of this species made during sampling periods in the transects, or 0.09 ind./km, and 15 records in the point counts, or 0.06 ind/pc, were made by voice because it is very difficult to see this drab-colored bird in the dense understory of the varillales. I have made many dozens of additional records outside the 50 m. limit of the evaluation areas, because the voice of *C. duidae* can be heard from 300 or 400 m. apart. It has never been recorded, however, outside the WSF patches, either during the study sampling periods, nor in the years I have worked in other places where this species has previously been recorded in Peru: upper Nanay River and a varillal in the right bank of the Tigre River. Because its strong and characteristic voice, it is very unlikely that it could be overlooked in other habitats. (For details about the transect and point count records for these and the following species, see Tables 2 and 3)

In two other areas of its known distribution, in Venezuela and Colombia, the literature is very vague about its habitat preferences: it says “forest” (i.e. de Schauensee 1982), “little known”; “apparently humid forest and scrubby open woodland (Hilty and Brown 1986); “dense tropical rain forest and open woodland and bushes”; “little known” (del Hoyo et al. 1992). Consequently, I will consider *C. duidae* tentatively as an obligate white-sand specialist.

2. *Notharchus ordii* (Brown-banded Puffbird)

Although there is only a single sight record of this species in southeastern Peru (Zimmer et al. 1997), where apparently there is no WSF, this species has been recorded in Loreto so far only in this habitat. All the records made in AMR during this study (16 records in the transects, 0.28 ind/km, and 25 records in the point counts, 0.09 ind/pc), plus many others made either during this study outside of the transects, or in previous work at AMR and at the varillales of upper Nanay and Tigre Rivers; and those in J. Herrera varillales (1 record in the transects, 0.06

ind/km, and 3 in the point counts, 0.03 ind/pc), all occurred in WSF. I have never recorded this species, which is fairly vocal and can be heard from more than 150 away, in other habitat than WSF (Alvarez and Whitney, in prep). I think that it is a strong evidence that *N. ordii* is actually a white-sand specialist, at least in Loreto. Elsewhere in Amazonia, this species has been recorded in a few localities in Brazil and Venezuela, mostly in WSF of the upper Rio Negro basin (Zimmer et al. 1997) although the literature, again, is very vague in regard to its habitat preferences.

3. *Pithys castanea* (White-masked Antbird)

The only previous record of this rare species was a specimen collected in the upper Pastaza River in Peru in 1937 (Berlioz 1938, 1948). It was rediscovered in the Morona site by our team in July 2001 (Valqui et al., in prep.) *P. castanea* was actually fairly common in this varillal, as revealed by the high number of individuals captured in mist-nets. Because of its behavior as a professional ant-follower, it does not appear in the transects frequently: there are only four records in the 13.2 km. of transects made in WSF (0.3 ind/km), and one in the 7.2 km. of trails made on MF (0.1 ind/km). There were actually two records of *P. castanea* in the same MF and on the same day, they were separated by about 200 meters (one of them was outside the transect). I suspect that could be the same individual, that was vocalizing loudly as it was moving through the forest and looking, apparently, for some ant swarm, as the professional ant-follower birds usually do. In this area, the trail was actually no more than 300 or 400 hundred meters away from the WSF, so it could be one vagrant individual, or a case of “mass effect” (Shmida and Wilson 1985). Another individual was mist netted close to the varillal in a seasonally flooded forest, where an ant swarm it was following was marauding in this moment.

P. castanea was recorded many times more outside the sampling periods and trails, by myself and by other members of the team, always in WSF, and about 15 individuals were mist netted also in the WSF during our work there. I tentatively consider this species as a white-sand specialist, waiting for more studies describing in detail its distribution and habitat preferences.

4. *Zimmerius villarejoi* (Mishana Tyrannulet)

This is a recently described species (Alvarez and Whitney 2001), so far only found in WSF in the Nanay River basin, especially in AMR. The Moyobamba specimen deposited at the Field Museum of Natural History (No 49405), cited in the description paper, was collected in 1912 and, although it resembles in size and color this species, the label has no record of the habitat where it was collected, nor anything related to its voice or behavior. We know that there are some WSF patches in certain hilltops of the area, and this specimen could have been collected there.

Z. villarejoi is not an abundant bird (only 16 records in this study transects, 0.28 ind/km, and 25 records in the point counts, 0.09 ind/pc), but as is shown in the second part of this study, in its preferred habitat it is not rare at all. If the transects would cover only this type of varillal (specially that one dominated by *Dicymbe uauiparuensis* trees), the density of this species would without doubt be much higher. Although it is a fairly inconspicuous bird, its well known voice make it very unlikely that it could be overlooked in other habitats.

5. *Hemitriccus minimus* (Zimmer's Tody-Tyrant)

This little-known flycatcher has been only recorded in WSF in Loreto. It is especially common on those inside the AMR, where the first individual recorded in Peru was found in September 1996. After then, I have found *H. minimus* to be a fairly common species in various types of WSF in this reserve, as in some WSF in the upper Nanay River, outside the Reserve, and in J. Herrera site, south of the Amazon.

All *H. minimus* records made so far in Peru, as well as all records made in the last years by ornithologists as Bret Whitney and Mario Conh-Haft from diverse points in the Brazilian Amazon, are from forest on sandy-soil or similarly nutrient-poor soil on weathered ridge crests. This species has a highly patchy distribution in Brazil, and has been found in the drainage of the Rio Tapajós/Teles Pires; nw Acre; and in southern Amazonas In the Caxiuanã National Forest region of Pará, *H. minimus* inhabits mostly, perhaps exclusively, flooded blackwater forest (B. Withney, pers. comm.; Alvarez and Whitney, in prep.) In Bolivia, the only other country where it has been recorded, it seems to have the same habitat preference.

Ridgely and Tudor (1994) say about this species: “very local; birds in ne Bolivia were found in canopy of stunted forest on sandy soil”.

The density of this species in WSF is fairly high: 93 records in the transects (1.2 ind/km), and 96 in the point counts (0.3 ind/pc). It is very unlikely that this highly vocal species could be overlooked in other habitats. There are no other records of this species in other parts of Peru, except the recent one from J. Herrera cited above.

6. *Cnemotriccus (duidae) sp. nov.*

This form, considered until now as a subspecies of *Cnemotriccus fuscatus (duidae)*, is found only in WSF in terra firme all along the Amazon basin. This contrasts with the use of river island habitats by its closest relative *C. fuscatus*. Both forms are sympatric, but of course not syntopic. In addition to the differences in habitat use and some color patterns their voices differ strikingly. From this and other evidence, it seems that it is a new taxon (B. Whitney et al., in prep.)

C. duidae has been recorded only in some types of low stature, dense varillal (stunted WSF), in three of the four localities studied: 1) in Allpahuayo- Misahana and upper Nanay River basin, plus in the only varillal studied in the right bank of the Tigre River (Alvarez 1994), that is geologically related to the Nanay River basin; 2) in Jeberos, south of the Aypena River; and, 3) recently, in Jenaro Herrera, south of the Amazon, where one specimen was collected, and some others recorded. Although it is not an abundant bird, is very unlikely that its very distinctive voice had been overlooked in other types of habitats. B. Whitney (pers. comm.) has recorded this species in several places in Brazil; these were always WSF or similar deeply-weathered ridges with stunted vegetation.

C. duidae has been recorded 11 times in AMR transects (0.2 ind/km); 1 in J. Herrera transects and 7 in Jeberos (0.45 ind/km), where it seems to use a wider range of WSF types (perhaps other case of “ecological release”). Twenty-five additional records were made during the point counts in the three localities (0.06 ind/pc). As has been suggested for *Z. villarejoi*, the density of this species would be much higher if we could census transects cut only in its

habitat of preference (stunted WSF). Because this kind of habitat is very scarce in all localities, the density of this species appears low.

7. *Neopelma chrysocephalum* (Saffron-crested Tyrant-Manakin)

First recorded in Peru in the varillal in right bank of Tigre River and latter in numerous varillales in the contiguous Nanay basin, this species has been found, so far, only in WSF. Because of the abundance of records in the transects made during this study (120, or 2.1 ind/km), during the point counts (155, or 0.57 ind/pc), plus many more observations made outside the sampling transects and during other studies, there is little doubt that this species is a WSF specialist. In fact, it is one of the most conspicuous birds in the area. It is very unlikely that it could be overlooked in other habitats, because its very loud and distinctive vocalizations can be heard throughout the day year round.

In other areas of Amazonia, the literature says that this species, although “not well known”, is “found primarily in sandy savanna woodland” (Hilty and Brown, 1986: 437). Interestingly, in some areas in Brazil it seems also to be restricted to WSF, but not in extreme eastern Amazonia. Regarding this, Rigely and Tudor (1994: 697) say: “Uncommon to locally fairly common in lower growth of woodland and forest in savanna regions, and in areas with sandy soil; in some regions, i.e. north of Manaus, Brazil, seems confined to the rather scrubby vegetation (campinas) growing on such soil, and is absent from the surrounding, much more extensive areas of humid forest”.

8. *Xipholena punicea* (Pompadour Cotinga)

Although this cotinga is not very conspicuous in the upper canopy of the high varillales where it forages, it is easily detected because of its frequently given calls. *X. punicea* was recorded in Peru for the first time in Allpahuayo - Mishana Reserve in 1997 (Alvarez and Whitney, in prep). Since then, hundreds of records have been made during and outside the sampling periods of this study. It was always found in WSF inside this reserve and in the varillales of upper Nanay River. During the fieldwork in July 2001, a new population was recorded in the Morona River varillal. The number of records made during the transect samplings (57, or 1.0 ind/km. in Allpahuayo-Mishana Reserve, and 6, or 0.5 ind/km. in Morona

varillal), plus 48 records in total during the point counts (0.16 ind/pc, and 0.11 ind/pc respectively), leaves little doubt that this species is a obligate WSF specialist, because it is very unlikely that could be overlooked in the surrounding habitats.

In other localities *X. punicea* seems to be most abundant in WSF and restricted in general to similar nutrient-poor habitats. For example, in Colombia, Hilty and Brown (1986: 452) say that it is “fairly common in sandy-belt forest, and savanna and gallery woodland”. In Brazil, Ridgely and Tudor (1994: 756) say about this species: “Uncommon to locally fairly common in canopy and borders of humid forest and woodland (the latter especially in areas with sandy soils). Pompadour Cotingas are most numerous north of the Amazon; records either represent localized populations (in areas with sandy soil?) or merely wandering birds”. Other authors only describe its habitats as “humid forest” or “forest” (i.e., see de Schauensee and Phelps, 1978, Birds of Venezuela). Amazon from Guianas to e. Colombia; they are much less common in w. Amazonia, where the scatter of records either represent localized populations (in areas with sandy soil?) or merely wandering birds”. Other authors only describe its habitats as “humid forest” or “forest” (i.e., see de Schauensee and Phelps, 1978, Birds of Venezuela).

9. *Polioptila* sp. nov. (Allpahuayo Gnatcatcher)

This undescribed taxon has been recorded so far only in high canopy of WSF inside the Allpahuayo-Mishana Reserve. Although this small and drab colored bird is difficult to locate by sight in the upper strata of the forests where it usually forages, it is very unlikely that it could be overlooked in other habitats. Its frequently given voice, both call and song, is very different from other bird vocalizations of the area, and makes it fairly conspicuous once the vocalizations are learned. This is revealed in the relative abundance of records in the transects. Despite the fact that this bird is probably one of the scarcest on earth, 21 records, or 0.38 ind/km. of transect were taken; we must add to these the 7 records made during the point counts, or 0.026 ind/pc.

Polioptila usually follows mixed-species flocks in the canopy. It is seen in family groups of two to four individuals; they interact frequently among them, vocalizing almost constantly. It is very unlikely that it could be overlooked in other habitats, because of the time

and interest devoted by the researcher to the mixed-species flocks encountered on a given trail of MF or VF.

Near obligate white-sand forest specialists

1. *Crypturellus strigilosus* (Brazilian Tinamou)

As with the previous species, the secretive habits and low densities have rendered very few records of this tinamou: 4 and 2 in transects and point counts, respectively. All these records, plus several dozen more that were made outside the 50 m. limit of the transect/point count evaluation area, occurred in WSF. It is very unlikely that this species, whose characteristic voice can be heard from 300 or 400 m apart, were using regularly the mixed forest surrounding the WSF patches and were overlooked during the censuses.

C. strigilosus is known farther south in Peru, in a few localities, and farther east in Brazil, in habitats different of WSF, although it is certainly fairly scarce in Peru and poorly known throughout its range (del Hoyo et al. 1992). For this reason, I will consider tentatively as near-obligate WSF specialist.

2. *Lepidocolaptes albolineatus* (Lineated Woodcreeper)

This very inconspicuous woodcreeper uses the canopy and subcanopy of primary forest. It is probably overlooked frequently, because of its habits, the difficulty in differentiate it from other woodcreepers, and the fact that it sings very infrequently. There are only eight records in transects (0.13 ind/km) and eight in point counts (0.03 ind/pc), all in the WSF of AMR. It has been recorded in 5 of the 13 study sites in the Iquitos region - presumably only in terra firme, in weathered Tertiary ridges. The same pattern probably occurs elsewhere in Amazonia (B. Whitney, pers. comm.; also see Ridgely and Greenfield 2001; Hilty and Brown 1986)

3. *Myrmotherula leucophthalma* (White-eyed Antwren)

This antbird has been recorded for the first time north of the Amazon-Marañón Rivers in the Morona site. Although in southwestern Amazonia it is found in MF (B. Whitney, pers. comm.), in Morona was found only in WSF, where was fairly abundant: 31 records in WSF transects () and 7 in point counts (). Interestingly, in the MF immediate to the Morona varillal

was found *Myrmotherula haematonota*, so apparently both species displace each other in both habitats. Although the voice and physical characteristics of the Morona population of *M. leucophthalma* resembles closely those of the farther south form, it could represent a different taxon, given the existence of the big Amazon-Marañón biogeographical barrier.

4. *Pernostola arenarum* (Allpahuayo Antbird)

This recently described species (Isler et al. 2002) has been recorded so far in AMR only in WSF. It is very vocal and can hardly be overlooked. The abundance of 0.48 ind/km of transect (28 records), and 0.25 ind/pc, or 68 records in the point counts seems to be accurate. In fact, as shown in the first part of this research, this species only uses some types of varillal. At the Morona site, a new population of *Pernostola arenarum* was found that differs in color: this is probably a new subspecies. There was only one type of varillal at the Morona site. It had fairly open understory, and *Pernostola* was certainly abundant: 49 records, or 3.7 ind/km, and 23 records in the point counts, or 0.6 ind/pc. Three individuals were recorded in one of the trails on clayey soil (0.4 ind/km). In upper Nanay River and in the contiguous and geologically related terra firme of the right bank of the Tigre River -the only two other places in which this species has been so far recorded- *P. arenarum* uses also certain types of forest growing on very poor terra firme clayish soil, where the understory is dominated by the palm *Lepidocarym tenue* (Isler et al. 2002). However, although there are extensive stands of this understory palm growing on nutrient poor clayish soils in AMR, *P. arenarum* has never been recorded there.

The presence of the three specimens in MF growing on clayish soil at the Morona site could be explained by the phenomenon known as “mass effect” (Shmida and Wilson 1985) or “source” and “sink” (Pulliam 1988). In fact, this trail was very close to the WSF, and in the extreme point of the trail there was a small and somewhat isolated hill of WSF; some individuals could eventually use habitat close to their preferred habitat (see Discussion for details). Nevertheless, the difference in abundance in the WSF and in the MF in both localities was highly significant (t-test: $p < 0.001$). Therefore, I consider this species to be a facultative white-sand specialist.

5. *Myrmeciza castanea centuculorum* (Northern Chestnut-tailed Antbird)

This recently described subspecies is fairly common in the WSF of AMR – 82 records in transects, or 1.5 ind/km, and 65 in point counts, or 0.24 ind/pc- but is absent from all the trails in the MF and VF. In Morona and J. Herrera sites it is absent, while in Jeberos it is fairly common. In contrast with the Iquitos area, it is more abundant in MF forests than in WSF: 2.14 ind/km vs. 0.47 ind/km, respectively (t-test, $p < 0.001$). The possible causes of this striking pattern are analyzed in the Discussion.

M. castanea been recorded sometimes in terra firme forests other than WSF in the Colombia and Ecuador Amazonian lowlands and foothills, although it is apparently rare and local (Ridgely & Greenfield 2001; Hilty and Brown 1985). In Tigre and Corrientes Rivers Alvarez (1994) recorded this species in some forest growing on nutrient poor, lateritic soils - probably deeply weathered sediments from the Tertiary-, dominated by the understory palm *Lepidocaryum tenue*, Arecaceae.

6. *Platyrhinchus saturatus* (Cinnamon-crested Spadebill)

This species has been recorded in A-M Resreve only in WSF. The other two records for Peru are an old record in Indiana, at the left bank of the Amazon down river from Iquitos (Zimmer 1939; Hilty and Brown 1986), and two records in the terra firme of the middle Tigre River (Alvarez 1994, Alvarez and Whitney, in prep.). The Indiana specimen has no reference to the habitat where it was collected, although the terra firme in the area is dominated by nutrient-poor clayey hills (pers. obs.). One of the Tigre specimens was collected in WSF and the other in a MF growing on very poor clayey soil, with the understory dominated by the palm *Lepidocarym tenue*. *P. saturatus* is actually very scarce in Loreto: in AMR, where hundreds of hours has been spent in many different places surveying birds, only five individuals in total have been detected in five territories at different sites. The eight records from the transects (0.1 ind/km.) and the seven records from the point counts (0.03 ind/pc) are actually from two individuals with well-defined separated territories.

There is only one record in Ecuador of one mist-netted individual “in terra firme forest” in extreme northeast (Ridgely and Greenfield 2001). The few records from Colombia are “from

sandy-belt forest” (Hilty and Brown, 1986: 488). Ridgely and Tudor (1994: 544) say about this species that “in west Amazonia perhaps [is] mostly found in forest growing on sandy soil”. Actually, the records of Colombia are restricted to the Vaupes, a black-water river that drains an area dominated by sandy soil towards the Rio Negro.

This species is very inconspicuous because of its behavior, drab color, habitat preferences -usually dense understory-, and lack of frequent loud vocalizations. I recorded for the first time in AMR the ‘loud song’ of *P. saturatus*, whose only vocalization known prior to this time was a simple, sharp “kwip” call that was sometimes doubled or lengthened (Ridgely and Greenfield 2001: 493) or “a distinctive 2-noted “chip-it” (Ridgely and Tudor 1994). In fact, I managed to record this cryptic species several times during this study because of this dawn song, that is given only for a few minutes immediately after dawn, and for a few months - presumably during the breeding season-.

Consequently, it is possible that *P. saturatus* had been overlooked in other habitats in the localities surveyed in Loreto, although at the Allpahuayo-Mishana Reserve, where I have spent more than one thousand hours surveying different habitat types, it certainly seems restricted to WSF.

7. *Attila citriniventris* (Citron-bellied Attila)

This is another species only recorded in WSF in the sites surveyed during this study. *A. citriniventris* is a very vocal bird, and its distinctive voice can be heard from 100 or 150 m. apart. It is very unlikely that it had been overlooked in other habitats during this study, or by other researchers in some well studied localities in the Iquitos region. It is not certainly a common bird: 21 records, or 0.37 ind/km in AMR transects, 6 records or 0.76 ind/km in J. Herrera, and 12 records or 0.45 ind/km in Morona, plus 69 records in AMR point counts, or 0.25 ind/pc, 1 in Morona, or 0.03 ind/pc, and 11 in J. Herrera, or 0.1 ind/pc. I have also recorded it many times in dozens of varillales in the Nanay, Tigre, and Ucayali basins during this study, outside the 50 m. radius, and prior to this study. Therefore, the preference of this species for the WSF appears to be a well established behavior in the region. In two or three

opportunities, outside the censuses, I have recorded single individuals away from white-sand, in *Mauritia flexuosa* palm swamps: twice in middle Tigre River, and once in lower Morona River.

A. citriniventris has been recorded in habitats other than WSF in 4 of the 13 localities surveyed by other researchers in the Iquitos region, all of them terra firme sites south of the Amazon River where I suspect that some of the Nanay River basin white-sand facultative specialists are not restricted to this habitat (see discussion). In Ecuador and Brazil it is considered to be “rare and seemingly local in subcanopy of terra firme forest” (Ridgely and Greenfield 2001: 518) and “not a well known bird” (Ridgely and Tudor 1994: 638). Interestingly, like *P. saturatus*, this species is restricted in Colombia to the Vaupes and Guiana regions, regions that are dominated by sandy soils (Hilty and Brown 1986)

8. *Conopias parva* (Yellow-throated Flycatcher)

This species has also been recorded so far in WSF in the study area. Although it dwells in the canopy of tall primary forest, it is a very vocal bird with a very distinctive voice difficult to overlook. It has been recorded in all four study sites. The densities are strikingly similar among sites: 0.27 ind/km in AMR, 0.38/ind/km in Jeberos, 0.35 in J. Herrera, and 0.38 in Morona. The pattern in point counts, where I have 50 records in all sites (0.11 ind/pc), is very similar.

C. parva has been recorded only in 2 of the 13 study sites of the Iquitos region. Both sites are in terra firme south of the Amazon River. In Ecuador it is considered to have a “status uncertain” and has only a few records in terra firme in Amazonia (Ridgely and Greenfield 2001).

Elsewhere in Amazonia (the pacific race is considered today as a distinct species, *Conopias albobittata* see Ridgely and Greenfield 2001) it is reported as being rare, local, or uncommon (see Hilty and Brown 1986, Ridgely and Tudor 1994). Perhaps this is due to, at least in west Amazonia, it being restricted to sandy or similar nutrient-poor soils. The few records that exist in Colombia occur again -as happens with the two previous species- in the extreme east, in Vaupes and Guiana, a region dominated by sandy soils, and where most of the white-sand related bird species occur in Colombia.

9. *Neopipo cinnamomea* (Cinnamon Neopipo)

This species seems to be rare everywhere in Amazonia, although it is more frequently observed in WSF. Because of its size and color, foraging position in the subcanopy, and somewhat secretive habits, *Neopipo* probably is commonly overlooked. During this study it has been recorded only in WSF, although very few times: nine at AMR, seven at J. Herrera, and two at Morona site. Seven of the records in AMR, and the seven records of J. Herrera were made during the more humid months from February to May, when it appears to be more vocal. The density calculated for the transects made in these more humid months at AMR (0.41 ind/km) seems to be more realistic (and to reflect more accurately the actual density of this species in WSF) than the density calculated by pooling together all transects of the year (0.16 ind/km). In the same way in J. Herrera: 0.64 ind/km for the humid months, vs. 0.41 ind/km pooling the records of all months.

There are only two other records of *N. cinnamomea* in other localities of the Iquitos area. Both are in terra firme forest (probably other than white-sand, although is not specified in the studies) and south of the Amazon. In the Tigre River basin, it has also been recorded only in white-sand or somewhat sandy soils in the right bank of the river where nutrient-poor Miocene deposits related with the Nanay basin predominate (Alvarez 1994).

Elsewhere in Amazonia, *Neopipo* has been recorded in terra firme forest other than white-sand, although it seems to be rare and local everywhere (perhaps because it is restricted to the more leached ridges with poor soil?) (Ridgely and Greenfield 2002; Ridgely and Tudor 1994; Hilty and Brown 1986).

10. *Xenopipo atronitens* (Black Manakin)

This manakin was only recorded in the shrubby, low stature varillal (called “chamizal” in Loreto) in Jeberos, where it actually was fairly abundant: 22 records in the transects (3.0 ind/km), and 14 in the point counts. There is no other record of *X. atronitens* in the study area, nor in other localities in Peru, except in the shrubby savannas of Pampas del Heath, in southern Peruvian Amazon.

It has been recorded in Colombia in “scrubby woodland”, mostly in sandy-belt regions of the extreme east, as well as in the heavily weathered cuatzitic table mountains region of Vaupes (Hilty and Brown 1986). Ridgely and Tudor (1994: 705) say about this species: “Fairly common in often dense lower growth of scrubby forest and woodland, and in gallery forest; often occurs in areas with sandy soil”.

Although *X. atronitens* sometimes occurs in other areas of Amazonia in habitats other than white-sand scrubby forest, in Loreto it has only been recorded in the “chamizal” of Jeberos, so I will consider it tentatively as a near obligate WSF specialist in the study area.

11. *Heterocercus aurantiivertex* (Orange-crested Manakin)

This species has been only recorded in WSF in the Allpahuayo-Mishana Reserve, but in upper Nanay River it occurs also in black water, seasonally flooded forest. In upper Tigre River it is fairly common in certain types of black water swamps and flooded forests, especially around old oxbow lakes (Alvarez 1999). It is not abundant in the AMR (0.23 ind/km), while in some upper Nanay varillales, where I did not make transects but only point counts, it seems to be one of the most common bird species (see Table 3). This species has not been recorded in other localities in Iquitos area with the exception of six records I made recently in the WSF at J. Herrera, south of the Amazon River. In eastern Ecuador, where is rare and local, it has been observed mainly in seasonally flooded forest (Ridgely and Greenfield 2001).

12. *Tachyphonus phoenicius* (Red-shouldered Tanager)

This species has only been recorded in the shrubby forest and savanna growing on white-sand or sandy soils in Jeberos, where actually it is fairly numerous: 22 records in the transects, or 3 ind/km, and 5 records in point counts. This species has not been recorded in any other place in Loreto. Actually, this Jeberos record is the only one that exists so far in Peru.

In Colombia, this species has been recorded especially in “sandy savanna woodland edges and open savanna with scattered high bushes...”, mostly in Vaupes and Guiana (Hilty and Brown 1986: 631).

Facultative white-sand forest users

1. *Claravis pretiosa* (Blue Ground-dove)

This small dove has 25 records in WSF transects, none in clayish forest, and only one in Nanay flooded forest: there were 0.44 individuals/km. of transect in white sand vs. 0.02/km in flooded forest (t-test, $p < 0.005$); in the point counts it has 114 records, or 0.42 ind/pc. This species has several records in secondary forest in other areas: the Tamshiyacu-Tahuayo Reserve, Orosa River, Sucusari Reserve, and Yanamono Island. Actually, this is a species associated with forest borders and secondary forest (Ridgely and Greenfield 2001, Hilty and Brown 1986), habitats not sampled in this study except in some river margins. Nevertheless, the abundance of this species in some types of WSF is surprising; and it is actually one of the most commonly heard birds in some months of the year. These WSF types, called locally as “varillal bajo” or low varillal (Alvarez et al. 1999), are of low stature and resemble, in some ways, the structure of the preferred habitat of this species in other areas.

2. *Polytmus theresiae* (Green-tailed Goldenthrout)

This hummingbird has been recorded during this study only in the grassy savanna and scrubby forest growing on very poor soils (mostly white sand, but also in secondary forest on nutrient poor loamy soils) at the Jeberos site. However, in other parts of Amazonia, especially in the Guianas, it is known to inhabit “shrubby intermixed with tall grass along rivers” (Ridgely and Greenfield 2001: 261). Jeberos is the only locality in Peru where this species is known so far, where Bartlett recorded it around 1860. In Ecuador it is known from only one old specimen in Amazonian lowlands, and in Colombia from “sandy-belt forest edge and savanna with scattered low to high bushes” (Hilty and Brown 1986).

3. *Trogon rufus* (Black-throated Trogon)

This trogon occurred in low numbers in WSF -six records in the transects of AMR, and two records at Morona, plus six records in AMR point counts-. However, it has never been recorded during the study outside the WSF. It has been observed, however, in non WSF habitats in 5 of the 13 localities studied in the region, as elsewhere in Amazonia (Ridgely and Greenfield 2001, Hilty and Brown 1986).

4. *Galbula dea* (Paradise Jacamar)

This species has been recorded so far in the AMR, J. Herrera, and Morona sites only in WSF (15 records, 2 and 4 respectively). In Jeberos, however, I have two records from WSF transects and one from WSF point counts, as well as one record from MF, a pattern that occurs here also with other species and has been addressed in Discussion. This species has been recorded in 2 of the 13 sites of the Iquitos region, all in terra firme forests. In River Tigre basin and elsewhere in Amazonia, it can be found sometimes in habitats other than WSF, but always in deeply weathered, nutrient poor terra firme clay or sandy soils (and once in a *Mauritia flexuosa* swamp in River Tigre). *G. dea* seems to be scarce everywhere in Amazonia, except in the sandy-belt forests of the East, where it “is more numerous” (Hilty and Brown 1986). This apparent scarcity could be an artifact of sub sampling and -as happens with many other habitat specialists- due to the lack of knowledge about its preferred habitat (B. Whitney, pers. comm.)

5. *Deconychura longicauda* (Long-tailed Woodcreeper)

I have only two records of this inconspicuous species in the WSF of AMR, two in WSF of J. Herrera, and none in MF or VF. I have made several records outside this study, and they were always in WSF. There is also one record in white-sand and one in clayish forest in the Morona site. This species is rare everywhere and vocalizes infrequently, so it is probably overlooked. It has been recorded in 4 of the 13 sites of the Iquitos region, as well as in Rio Tigre basin and elsewhere in Amazonia. It probably occurs only in terra firme forests growing on deeply weathered, nutrient poor soils, especially on white-sand (B. Whitney, pers. comm.; see also Alvarez 1994; Ridgely and Greenfield 2001; Hilty and Brown 1986).

6. *Sclerurus rufigularis* (Spot-throated Woodcreeper)

I found this species 23 times in the WSF of AMR, and none in the MF or VF. There are also one record at the Jeberos WSF, and four records both at J. Herrera and Morona WSF, and again none in the other forest types. In the study sites other than the AMR, this pattern is probably a sub sampling artifact, but the 23 records in WSF -0.4 ind/km of transect- plus 7 records in the point counts probably reflects a clear preference for this habitat in this

Reserve. In fact, this species has been recorded in terra firme forest other than white-sand in three of the Iquitos region study sites, and elsewhere in northern Amazonia (Ridgely and Greenfield 2001). Hilty and Brown (1986: 377) state that it can be found in Colombia and other parts of Amazonia “in humid forest, including sandy-belt and swampy forests”. In the River Tigre basin, for example, I have recorded this species both in terra firme clayey and swampy soils (Alvarez 1994).

7. *Megastictus margaritatus* (Pearly Antshrike)

The 29 records of this species -0.57ind /km- in the WSF transects of AMR contrast strikingly with the 3 records -0.12/km- of the MF of the same area (t-test, $p < 0.01$). This contrast is even bigger in the point counts: 15 records in WSF, and none in MF. *Megastictus margaritatus* was apparently absent from the two study trails open in the more fertile clayey soils of the hills close to the varillales, that belong to the so called “Pebas Formation”, whose soils have their origin in the bottom sediments of the late Miocene “Pebas” lake, rich in minerals and salts (Räsänen et al. 1998). This forest has a dense and tangled understory, rich in palms, epiphytes and lianas. The only trail outside WSF in which this species was present crossed a hilly area dominated by more weathered, nutrient-poorer clayish soils -upland latosols- that have their origin in the sediments deposited by a paleo Amazon River during the late Miocene, the so called “Canalización Canalizada de Nauta” (Räsänen et al. 1998). Not surprisingly, the understory of this forest was very open, and palms, lianas and herbaceous plants were very scarce. This understory resembles in some way that of some varillal types. On the contrary, in the ornithologically depauperate Jeberos site, *M. margaritatus* seems to use indistinctly both varillal and clayish forests: eight records in varillal -0.51/km- vs. three records in clayey-soil forest -0.35/km- (t-test, $p > 0.05$).

This species has also been recorded in 3 of the 13 Iquitos region study sites, but always in terra firme forest. Although it is scarce everywhere in Amazonia, it seems to be “fairly common” in other WSF, as happens in the “sandy-belt” forest of Vaupes area (Hilty and Brown 1986: 385). It has also been recorded elsewhere in Amazonia in places other than WSF; records usually are from forests growing on deeply weathered clay soils (B. Whitney, pers.

comm.; Alvarez 1994. Van ?Tienes la referencia del artículo de Bret sobre esta especie? No la he encontrado...). Ridgely and Tudor (1994: 702), for example, say about this species: “Rare to locally uncommon (perhaps most numerous in few places) in lower and middle growth of terra firme forest and secondary woodland, in some areas primarily where there is sandy soil”.

8. *Herpsilochmus gentryi* (Ancient Antwren)

This recently described species has been found only in primary forests growing on terra firme nutrient-poor soils. All occurrences were north of the Amazon and west of the Nanay River, at the upper Pastaza, close to the Ecuador-Peru border, and at the lower Morona River. Although it has been recorded regularly in forests growing on clayey weathered latosols in several places of the study area, the preference of this species for WSF is very clear in AMR: the 1.87 ind./km. of transect in WSF contrast clearly with the 0.62 ind./km in MF (t-test, $p < 0.001$), and 0.58 ind/pc in WSF point counts, vs. 0.09 ind/pc in MF. Like the pattern of the previous species in AMR, *H. gentryi* is very rare or absent in the trails that cross the “Pebas Formation” forest patches, where it is apparently substituted by two species of antwrens: *Myrmotherula brachyura* and *M. obscura*. This is not surprising for this canopy-dwelling species, because the canopy is very irregular in this type of forest, where tree falls and openings occur frequently.

H. gentryi seems to be more evenly distributed between the WSF/MF at the Morona site than at the AMR. At Morona it shows no significant difference in the abundance between both habitats: 1.2 ind./km vs. 1.25 ind./km (t-test, $p > 0.05$). In the other three places where this species has been recorded: the upper Tigre and Corrientes Rivers, upper Nanay River, and upper Pastaza River in Ecuador, *H. gentryi* is found only in nutrient-poor terra firme soils, both podzolic and quartzitic (Whitney & Alvarez 1998, Ridgely & Greenfield 2001)

9. *Hypocnemis hypoxantha* (Yellow-browed Antbird)

This species has been recorded only in WSF in the AMR, where it is fairly common – 48 records in transects, or 0.85 ind./km, and 90 in point counts, or 0.33 ind/pc-. It was absent at the Jeberos site, very scarce at J. Herrera, while at Morona, where the species was abundant -2.3 ind/km in white-sand, and 1.5 ind/km in clay soil forest- no statistical difference was found

between both habitats (t-test, $p > 0.05$). It has been recorded in 4 of the 23 localities in the Iquitos region. Elsewhere in Amazonia, the species has been found at numerous places, primarily -or exclusively?- in terra firme forest. Ridgely and Greenfield (2001: 419) state that it “favors areas with a fairly open understory, often on ridges”. According to B. Whitney (pers. comm.) *H. hypoxantha* is always more common in WSF, and is restricted to forests growing on weathered terra firme soils: latosols, podsoles and spodosols - sediments mostly originated in the Tertiary-.

10. *Ranphotrigon ruficauda* (Rufous-tailed Flatbill)

This species is not restricted to WSF in Nanay River basin, and has been occasionally recorded in some MF: Itaya site clayish hills trail, and in Morona site clayish hills trail, as well as in seasonally flooded forest -upper Nanay River. There is not a significant difference in the abundance between both forest types, WSF and MF in AMR (t-test, $p > 0.05$). Perhaps the reason for that is the fact that the trails cover different types of varillal: this species usually favors forest with open understory (Ridgely and Greenfield 2001, and pers. obs.), and *R. ruficauda* is fairly common in certain types of varillal that have this characteristic. In Jeberos site it was only recorded in white-sand. If we only consider the trails cut on tall varillal with open understory, the abundance is fairly high: 0.83 ind/km of transect. In Morona site it was clearly more abundant in WSF than on MF, perhaps because here all the varillal was of the same type, with fairly open understory: 1.06 ind/km in varillal vs. 0.28 ind./km in clay forest (t-test, $p < 0.05$). Similar pattern was found in J. Herrera WS, where the dominant varillal has also an open understory: 1.01 ind/km -it was apparently absent from MF-. We cannot separate the varillales with more open understory in AMR, in order to replicate this comparison more accurately, because` every trail passes through several types of varillal.

This species has been recorded only in two other localities around Iquitos, both in terra firme south of the Amazon River. In other areas, *R. ruficauda* is actually scarce and very local -perhaps restricted to forest growing on deeply weathered Tertiary sediments?- as everywhere in Amazonia, but again, it seems to be more abundant in WSF: for example, Hilty and Brown (1986: 484) state that *R. ruficauda* is “more common in sandy woodlands as at Mitú”.

11. *Dixiphia pipra* (White-crowned Manakin)

This manakin is significantly more abundant in WSF than in MF in AMR: here it reaches 1.32 ind/km in varillal, while in two of the three trails in MF it is absent, and in the third, located at the Itaya hills, in forest growing on nutrient-poor lateritic soils, has a density of 1.59 ind/km. There is a significantly higher density in white-sand when all the trails are grouped together (t-test, $p < 0.01$).

At Jeberos site, following the pattern of other species, *D. pipra* is more or less evenly distributed in both habitat types (2.6 vs. 2.4 ind/km, t-test, $p > 0.05$).

At Morona site it is also more or less evenly distributed in both habitats: 1.6 ind/km vs. 1.1 ind/km (t-test, $p > 0.05$), while at J. Herrera- Tamshiyacu has 0.71 ind/km in WSF and is absent in MF (see Discussion for possible explanations of this patterns).

This species has been recorded in eight localities in the Iquitos area, in habitats other than WSF, although always in terra firme forests and presumably, as previous species, in deeply weathered lateritic soils. It shows the same pattern elsewhere in Amazonia: for example, Hilty and Brown (1986: 431) describe this species as “common in sandy-belt forest of Orinoco and Negro drainage, much less numerous into Amazonia”.

Vita

José Álvarez Alonso was born on 17 February 1958 in León, Spain. He graduated from San Agustín High School in Zaragoza in 1975, and studied philosophy and theology at Estudio Teológico Agustiniiano of Valladolid, both in Spain, where he graduated in 1981. In January 1983 he moved to the Peruvian Amazon, where he worked as a missionary and studied biology. He received his bachelor degree in biology in 1990 and his title of Biologist in 1994 at Universidad Nacional de la Amazonía Peruana. Since 1996, when he married Elena Burga at Iquitos, Perú, he works for the Instituto de Investigaciones de la Amazonía Peruana in Iquitos. He entered Louisiana State University in August 2001, and is currently a candidate for the Master of Science degree in the School of Renewable Resources, thanks to a Fulbright scholarship.