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Bamboo Specialization in Amazonian Birds.

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BAMBOO SPECIALIZATION IN AMAZONIAN BIRDS

A Dissertation

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

in

The Department of Zoology and Physiology

by

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DEDICATION

This dissertation is dedicated to the memory of
Theodore A. Parker, III
(1953-1993),
friend and colleague.

ACKNOWLEDGMENTS

This dissertation is dedicated to the memory of my friend and colleague Ted Parker. Not only did he set the stage for all studies of bamboo specialization by birds in the Neotropics, but he also helped me begin my research by inviting me on an expedition to the Ccollpa study site with Conservation International's Rapid Assessment Program, and taught me the "nuts and bolts" of specialization on bamboo by these fascinating birds. Learning my study subjects under the tutelage of perhaps the greatest field ornithologist ever will never be forgotten. Van Remsen, my Ph.D. advisor, has continually been helpful and inspiring during all phases of my research. He, along with the inspiration of the entire Section of Ornithology at the Museum of Natural Science at LSU, helped to transfer my energies from working on bamboo specialists in Asia to working on those in Amazonia. My graduate committee -Ken Brown, Bruce Williamson, Kam-biu Liu, Fred Sheldon, and Bob Zink - provided excellent assistance in formulating and carrying out this project. My field work in Peru in 1992 was made possible by Conservation International. Research in 1993 was funded by a Frank M. Chapman grant from the American Museum of Natural History, a Grants-in-Aid research award from Sigma Xi, Alexander Wetmore and AOU Council awards from the American Ornithologists' Union, and a Fugler Fellowship in Tropical Biology from the Museum of Natural Science, Louisiana State University. Walter Wust helped immeasurably with many administrative tasks in Lima. Fernando Cauper, Yoko Quintana, Ruperto "Chicuta" Fernandez, Pepe Moscoso, Julio Perez, Krista Lee, and Kathryn Deagon helped in the field. Amanda Stronza provided the copy of the INRENA report and gave me perspective on development in the Tambopata region. The staff of Rainforest Expeditions, especially Eduardo Nycander and Alvaro Del Campo, provided comfortable accommodations in the field, assistance in Lima, and valuable friendships. Finally, this dissertation is founded upon the inspiring atmosphere

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ABSTRACT

By spot-mapping territories of lowland forest birds in southeastern Peru, 19 “bamboo specialists” were documented to be restricted to thickets of bamboo (Guadua weberbaueri). Six specialists are restricted to thickets throughout their entire geographic range (obligate bamboo users); seven specialists may use other habitats sparingly away from southeastern Peru (near-obligate bamboo users); the remaining six species are frequent users of habitats lacking bamboo in area besides southeastern Peru (facultative bamboo users). The 19 specialists, all insectivorous, were classified into five guilds based on foraging maneuver and substrate preferences: four sallying tyrannid species; four arboreal antbirds; four stem-searching specialists; four dead-leaf-searching specialists; and three species that foraged low in bamboo thickets. I investigated niche-partitioning within the guilds along dimensions of habitat use and foraging behavior. Aside from pairs of specialists in the antbird and dead-leaf guilds, little niche-partitioning was found among the three structurally different types of bamboo thickets present in the study area (bluff-top, floodplain forest, and early successional bamboo). The specialists showed more partitioning in foraging behavior, particularly among the perch, attack and substrate variables. Except for the flycatcher guild, specialists showed high overlap among the continuous foraging variables (height, distance to canopy, perch size, perch foliage density), reflecting the small range of these variables in structurally uniform thickets. A distinction was made between species specializing only on the unique structure of bamboo thickets (habitat specialists) and those that showed signs of further specialization on unique bamboo substrates or prey bases available in bamboo. The probable habitat specialists included only one obligate specialist; all others were facultative or near-obligate specialists. Five of six obligate and two near-obligate specialists showed indications of substrate specialization. However, only one specialist, Simoxenops ucayalae, showed

morphological adaptations, which may be related to this species' unique foraging behavior. Using specialist densities from spot-mapping results and habitat areas from a satellite image of southeastern Peru and northern Bolivia, I made rough estimates of the regional population sizes of each specialist and discuss conservation implications of encroaching development in the area.

CHAPTER 1

INTRODUCTION

The great diversity of tropical ecosystems has long intrigued ecologists. Among many hypotheses explaining the high diversity, one is that the more benign and predictable conditions in the tropics allow increased specialization. This specialization can result in finer partitioning of a given resource among species, relative to more temperate latitudes, where unpredictable conditions promote generalized use of resources (Klopfer and MacArthur 1960, MacArthur et al 1966, Karr 1971). Thus more species can fit along a resource gradient in the tropics, all else being equal. An additional dimension of tropical specialization is the presence of resources unavailable to species in temperate latitudes (Orians 1969, Karr 1971, Terborgh 1980, Remsen 1985).

The recent discovery (Parker 1982) that many bird species in the Neotropics may be restricted to bamboo thickets provides another example of tropical specialization. Although bamboos are widespread in subtropical and tropical latitudes throughout the world, bamboo specialization by birds has received much more attention in the Neotropics than anywhere else. Outside the Neotropics, bamboo specialist bird species can be found in the Himalayan mountains of Asia (a number of parrotbill species - Paradoxornis sp. [Timaliidae]; Ali and Ripley 1971, Olson 1986). In subtropical North America , Bachman's Warbler (Vermivora bachmanii), which may be extinct, may have been restricted to bamboo (cane) thickets during the breeding season in southeastern North America (Remsen 1986). The most famous example of bamboo specialization is not a bird, however; the Giant Panda (Ailuropoda melanoleuca), restricted to vast bamboo thickets in montane central China (Schaller et al. 1985), may be the only bamboo specialist that forages only on bamboo leaves.

In the Neotropics, bamboo specialization may reach its greatest development in southwestern Amazonia. Here, a number of mostly unrelated insectivorous bird species are thought to be restricted to thickets of a single species of a large spiny bamboo (Guadua weberbaueri). Sites in southwestern Amazonia are also well-known for having the most diverse avifaunas in the world (e.g., over 550 species in <50 km² at Cocha Cashu Biological Station in Manu National Park [Robinson and Terborgh 1990] and at the Explorer's Inn Reserve Zone [Foster et al. 1994]). Additional Neotropical bamboo specialist communities can be found in southeastern Brazil and in the tropical Andes. These diverse communities of bamboo specialists offer a number of opportunities for study, but many questions ultimately reflect back to: What are the ecological and evolutionary factors driving bamboo specialization?

In this study I will look mainly at the ecological factors responsible for bamboo specialization. In two earlier papers, I discussed evolutionary pathways to bamboo specialization in a two taxa. The first was a cacique (Icteridae: Amblycercus holosericeus), with both bamboo specialist and non-specialist populations (Kratter 1993). The second was an assemblage of bamboo-specialized foliage-gleaners (Furnariidae: Anabazenops, Automolus, Simoxenops) (Kratter and Parker, in press). Bamboo specialization seems to be an evolutionary flexible strategy, having arisen a number of times in unrelated taxa. In some taxa, however, bamboo specialization is shared among sister taxa and thus probably represents an evolutionarily primitive character (e.g., in Claravis mondetoura/godefrida, Anabazenops, most Drymophila sp., Hemitriccus obsoletus/diops/flammulatus, Ramphotrigon megacephala/fuscicauda, Haplospiza: Parker 1982, Kratter and Parker in press). These taxa tend to show concurrent biogeographic patterns in the Andes, western Amazonia, and southeastern Peru (Parker 1982, Kratter and Parker in press).

Most bamboo specialists are poorly known. In fact, one species was only described recently (Cercomacra manu: Fitzpatrick and Willard 1990). Another

specialist (Cymbilaimus sanctaemariae) was until recently thought to be only a subspecies of its widespread congener (Cymbilaimus lineatus); however, they are sympatric throughout the distribution of C. sanctaemariae (Pierpont and Fitzpatrick 1983). Many other bamboo specialists are known only from a few sites, and fewer than 20 museum specimens exist (e.g., Celeus spectabilis, Simoxenops ucayalae, Poeciloriccus albifacies: Parker 1982). Although foraging behavior and habitat selection are probably instrumental in driving both the specialization and niche-partitioning of bamboo specialists, almost nothing has been published on the ecology of these species aside from qualitative descriptions of the behavior of a few individuals from a few sites (Parker 1982, Parker and Remsen 1987, Pierpont and Fitzpatrick 1983, Fitzpatrick and Willard 1990, Ridgely and Tudor 1994; however, see more detailed studies of Anabazenops fuscus [Rodrigues et al. 1994], Anabazenops dorsalis [Kratter and Parker in press], Automolus melanopezus and Myrmotherula ornata, [K. V. Rosenberg 1990a, 1990b, 1993] and Ramphotrigon fuscicauda [Fitzpatrick 1980]). Because elucidation of ecological principles and hypotheses ultimately stems from empirical observations of well-known systems (Wiens 1989), descriptive, quantitative analyses of the habitat selection, foraging behavior, and general ecology of the bamboo specialists are needed.

A primary question is determining the resource(s) upon which the bamboo specialists are specializing. Guadua bamboo in southwestern Amazonia affords two opportunities for birds to specialize: they can specialize on bamboo substrates (or, more precisely, their prey found on bamboo) or they can specialize on the structurally unique habitat that bamboo thickets offer. In the case of prey specialization, for example, the hollow Guadua bamboo stems, filled with water, harbor a diverse and specialized aquatic arthropod fauna, in addition to a few small vertebrates (Louton, et al. in press). Bird species may thus manipulate bamboo stems to prey on this hollow-stem fauna; these species would thus be specializing on bamboo stem substrates. In the case of

habitat specialization, bamboo grows in dense, often monotypic thickets, which can cover from < 1 ha (e.g., in treefall gaps in floodplain forest) to many square kilometers (on elevated sandy terraces). These thickets provide a structurally unique habitat, which is much less diverse than the nearby forest habitats that are renowned for their high plant diversities (e.g., Gentry 1988). In addition, the densely packed, small-diameter stems, and a very dense subcanopy of bamboo leaves differ as well.. A large part of the high diversity avifaunas in western Amazonia can be attributed to a high turnover of species among habitats (= β diversity, see Cody 1975) in this heterogeneous landscape (Terborgh 1985, Salo et al. 1986). Do bamboo specialists represent only another set of species restricted to a particular habitat or do they show further specialization on resources or substrates?

Another major question regarding tropical diversity and specialization is determining how similar species partition niche space. In bamboo, all specialists are sharing the same habitat (bamboo thickets) and taking relatively similar prey (arthropods) from the same substrates (bamboo). Even though bamboo appears to offer only a small range of opportunities for specialization, several closely related species' pairs appear to coexist. Further specialization on particular bamboo substrates or specialized and stereotyped foraging behavior may be expected.

Although niche-partitioning may not be important if the bird community is not at equilibrium, there is little reason to suspect non-equilibrium in the bamboo specialist avifauna. The specialists, as far as known, are all non-migratory and completely insectivorous. Their relatively stable prey base and year-round use of this resource should lead to equilibrium conditions unless predation pressures are severe. Bamboo specialists should be better at "tracking" their prey base than suspected non-equilibrium bird species like frugivores or nectarivores in the tropics or species in areas with more seasonal climates (e.g., Wiens 1989).

Lastly, these bamboo specialists are of special interest to conservationists. Many bamboo specialists have small geographic distributions relative to other tropical forest species. Within these small ranges, bamboo thickets, and thus the specialists, are patchily distributed across the landscape. It also should be noted that most bamboo thickets are probably ephemeral at any one spot because they represent temporary successional stages following disturbance. In addition, bamboo's unique phenology of mass-flowering and die-off (Janzen 1976) leads to disruptions in the occupancy of a site by bamboo specialists; such disruptions may lead to further endangerment of bamboo specialists with increasing isolation and fragmentation of this habitat caused by encroaching development. Finally, most Guadua bamboo thickets occur along rivers, the primary avenue for development in southwestern Amazonia (Foster et al. 1994). Guadua bamboo thickets also support populations of many specialist insects (Louton et al. in press), a species of poison-dart frog (Dendrobates biolat; L. Rodríguez pers. comm.), and a spiny rat (Dactylomys dactylinus; Emmons 1981). A ominous portent to the future threats that bamboo specialists in southwestern Amazonia may face can be found in southeastern Brazil, where a number of other bamboo specialists occur. In southeastern Brazil, less than 10 percent of native habitats are still extant (Oliver and Santos 1991) and four bamboo specialists are currently listed as threatened (Collar et al. 1991).

The primary questions I asked in this study were: 1) what species were restricted to bamboo thickets in southeastern Peru? 2) were these species bamboo specialists throughout their entire distributions? 3) what ecological and evolutionary factors were driving bamboo specialization? 4) how did bamboo specialists divide niche space? and 5) how large were the populations of bamboo specialists, and what were the threats to their long-term stability?

I present my analyses and findings in the following four main chapters. In Chapter 2, I begin by defining which bird species are bamboo specialists at a site in

southeastern Peru with a variety of tropical lowland habitats. I then used literature sources to evaluate evidence for bamboo specialization throughout each specialist's entire distribution, to determine which species are obligate users of bamboo. This chapter has been submitted to Biotropica. In Chapter 3, I investigate habitat selection and partitioning by bamboo specialists among three structurally different types of bamboo thickets. In Chapter 4, I describe the foraging behavior of the specialists and further investigate niche partitioning among potentially competing species. In Chapter 5, which will be submitted to Conservation Biology, I estimate regional population sizes of bamboo specialists, over approximately 35000 km² of lowland southeastern Peru and northern Bolivia, by using density estimates from spot-mapping and using habitat areas measured from a satellite image.

CHAPTER 2

BAMBOO SPECIALIZATION BY AMAZONIAN BIRDS

Lowland forest sites in western Amazonia are well-known for having the highest number of bird species in the world. For example, over 550 species have been recorded in the Explorer's Inn Reserve (Foster et al. 1994) and near the Cocha Cashu Biological Station in Manu National Park (Robinson and Terborgh 1990), both in southeastern Peru. One of the most often-cited reasons for this incredible diversity is the great habitat heterogeneity, resulting from various edaphic conditions and the successional processes associated with large rivers flowing out of the nearby Andes (Remsen and Parker 1983, Terborgh 1980, 1985, Salo, et al. 1986, G. H. Rosenberg 1990, Robinson and Terborgh 1990). In a small area (e.g., about 50 km² at Cocha Cashu), western Amazonian sites can have terra firme forests on upland soils, floodplain or transition forests in intermittently flooded areas, palm swamps in persistently flooded areas, distinctive vegetation around the margins of oxbow lakes, and the various early successional stages associated with primary succession along the margins of large rivers (Terborgh 1985, Salo et al. 1986, Robinson and Terborgh 1990). Although many studies have described use of habitats by birds in lowland forests in western Amazonia, only two (Terborgh and Weske 1969, Terborgh et al. 1990) quantified how tropical bird species respond to these landscapes of varying habitats. Determining habitat use of tropical forest bird species thus should be an important priority for understanding the processes responsible for these high diversity communities.

Bamboo thickets in western Amazonia provide an important habitat for several bird species, some of which may be restricted to such thickets (Parker 1982, Pierpont and Fitzpatrick 1983, Parker and Remsen 1987, Fitzpatrick and Willard 1990, Robinson and Terborgh 1990). In a number of ways, bamboo provides a distinct habitat for birds. Bamboo grows in dense, often monotypic stands, which is unusual in tropical plant

communities. The structure of bamboo stands is quite different from other habitats: bamboo thickets are densely packed with relatively thin-stemmed plants and have a thick subcanopy of similarly shaped leaves. Furthermore, most bamboos flower synchronously after many decades of vegetative growth, undergo mass seeding, and then die off over large areas (Janzen 1976). The use of bamboo habitats by these specialist bird species has yet to be quantified.

Specialization should lead to more efficient use of resources (Slobodkin and Sanders 1969, but see Fox and Morrow 1981), especially in bamboo thickets, where specialization on a single plant species that dominates the landscape is possible. One prediction that arises from specialization on this unique resource is: If the bamboo resource is abundant and extensive, then bamboo specialists should occur at higher densities in this habitat than species in "typical" tropical forests. These latter species are predicted to occur at lower densities because of the extreme diversity of plant species in tropical forests and the relative rarity of individual plant species. If forest species are specialized on particular plant species or substrates, they would need large home ranges because any one species would be rare; if they are generalized, then they should use foraging substrates less "efficiently" (Slobodkin and Sanders 1969).

In this study, I mapped territories of understory and subcanopy birds to determine which species were associated with bamboo thickets in southeastern Peru. I defined "bamboo specialists" by their frequency of occurrence in such thickets and their absence in all other habitats at the study sites. I then assessed the prevalence of the association between these bamboo specialists and bamboo thickets by comparing my results with published material regarding habitat use from other parts of the specialists' ranges.

STUDY AREA

My main study site was the Ccollpa de Guacamayos (hereafter, Ccollpa, the local Indian word for river banks where macaws and parrots gather to eat clay soil), on the west bank of the Río Tambopata, 75 km SSW of Puerto Maldonado, depto. Madre de Dios, Peru (Figure 2.1). The Ccollpa study site (13°08.5'S; 69°36.4'W), at approximately 350 m elevation, is dominated by an extensive stand of bamboo (Guadua weberbaueri) that stretches for 2.5 km along a 30-m tall bluff over the Río Tambopata and a smaller side channel of the river, and then for approximately 10 km inland along similar upland soils (= bluff-top bamboo; Figure 2.2). In the northern part of this study site, the ground is approximately 3 m above normal high-water level on the Tambopata, and tall floodplain or transition forest dominates. This forest probably floods every few years (E. Nycander V., pers. comm.). Bamboo stands (= floodplain forest bamboo) are common in this forest, primarily in tree-fall gaps and along slightly lower-elevation soils that probably flood more regularly. The vegetation at the Ccollpa study site is described in more detail in Foster et al. (1994).

Five other study sites with the same species of bamboo were also surveyed: four sites within 10 km of the Ccollpa, and a sixth site, the Explorer's Inn Reserve, at the mouth of the Río La Torre on the east bank of the lower Río Tambopata (Figure 2.1). Some habitats of limited extent at the Ccollpa study site (e.g., early primary successional vegetation) were more widespread at these additional sites (see Erwin 1984, Kratter in press). Cane (Gynerium sagittatum) thickets, a common component of river-edge habitats, have a somewhat similar physiognomic structure to bamboo thickets (see Discussion).

METHODS

DISTRIBUTION OF BAMBOO. - The distribution of bamboo at the Ccollpa study site was mapped along all 16.3 km of trail at the site. At 10 m intervals, the three closest stems (>3 cm DBH) to a point 2 m perpendicularly from the narrow footpaths

Figure 2.1. Map of Peru, showing study site locations and Cocha Cashu Biological Station. EIR is the Explorer's Inn Reserve (see text).

Figure 2.2. Habitat types at Ccollpa study site. Thin black lines show the trail system. Vegetation is mapped to 100 meters out along each trail.

were classified as either bamboo, palm, or non-bamboo. In addition, the height and class of vegetation intercepting a vertical line projected above the point were recorded. Disturbance associated with trail placement was minimal and no vegetation changes were noted.

To map the density of bamboo (Figure 2.2), the number of bamboo stems at a given point were summed with the two closest points on each side, thus summing over five points (15 total stems maximum) covering 40 m of trail. Similarly, the number of points with bamboo intercepting the vertical projection was totaled over the same 5 points. Bamboo density was then classified as either low density (0-4 bamboo stems and 0-2 points with bamboo intercepts) or high density (5-15 stems or 3+ points). In addition, the presence of bamboo away from the trail was visually inspected to a distance of 100 m and classified as either present or absent.

TERRITORY MAPPING. - At the Ccollpa study site, all trails were walked regularly during 178 days of field observation (22 May - 17 July, 1992 and 29 May - 18 September, 1993). The trails were marked with flagging at 50-m intervals. It is assumed that individual territories up to 75 m from the trail were detectable (see Terborgh et al. 1990). Individuals of all understory and subcanopy birds were encountered opportunistically as trails were walked, and followed for as long as possible; locations were registered on microcassette. To define territory boundaries, attention was focused on simultaneous registrations of the same species, almost always by hearing other individuals singing. Although females of many bamboo specialists sing (pers. obs.), their songs often differ from males. Furthermore, many species forage as pairs in mixed-species flocks (pers. obs., see also Munn and Terborgh 1979), and it was usually easy to tell if two individuals were traveling with the same flock. Species were considered not to be bamboo specialists and were dropped from intensive spot-mapping when a territory (i.e., an individual recorded regularly in the same general area) for that species was found away from bamboo. If a presumed bamboo specialist

was recorded away (but < 100 m) from the trail in habitat potentially without bamboo, the bird was located and the habitat recorded. This was important because although most species could be heard some distance from the trail, the presence of bamboo could not always be determined from the trail.

The location of each individual was then marked on a vegetation map of the site (Figure 2.2). Territories were defined by groups of registrations in near-vicinity (generally <100 m between points). Territory limits were defined by fitting polygons by sight to the outside points in groups of registrations. Simultaneous registrations (two singing individuals recorded at the same time) were used to define the borders of adjacent territories. If there was no adjoining neighbor, i.e. there was a large distance (>200 m) to the next group of registrations for a species and no simultaneous registrations, then each group of points was considered a separate territory. See Terborgh et al. (1990) and Thiollay (1994) for a review of using spot-mapping techniques for estimating habitat use and density of tropical forest birds.

A species was considered a "bamboo specialist" if all spot-mapped territories coincided with bamboo (as per Figure 2.2) and at least 95% of all registrations for that species were within bamboo habitats. Only species with more than three territories at the Ccollpa site were considered, because habitat selection in rarer species could not be assessed properly. Although the territories of specialists were only mapped at the Ccollpa study site, a species was not considered a specialist if regularly recorded away from bamboo at any of the other six study sites.

Population densities of bamboo specialists at the Ccollpa were compared with those of birds from the two other Amazonian sites where species have been spot-mapped. Terborgh et al. (1990) provided density estimates for 245 species on a 97 ha plot of floodplain forest at Cocha Cashu, about 350 km north of the Rio Tambopata. Thiollay (1994) gave density estimates for over 300 bird species spot-mapped in a mature terra firme forest in French Guiana.

RESULTS

Assuming that 75 m on either side of the trail was adequately surveyed, bamboo thickets covered approximately half (48.2%) of the 307 ha surveyed at the Ccollpa site (Figure 2.2). Most of the bamboo (108 ha) was continuous with the extensive bluff-top thicket. Within the 153 ha of floodplain forest surveyed were approximately 11 smaller bamboo patches, which totaled 40 ha. Small patches of terra firme forest (2.7% of area surveyed) and flooded palm swamp (1.2%) were found on the western edge of the study site. Although early successional habitats were sparse in the study area, this habitat was regularly visited at the peripheral sites (see above) and on the island in the Tambopata across from the Ccollpa.

Eighteen species (Table 2.1) met the criteria to be classified as bamboo specialists. A nineteenth species, Celeus spectabilis, was also included even though there were too few registrations to map territories. This quiet woodpecker, like many species in its genus, apparently had relatively large territories, making it difficult to record simultaneous registrations. All registrations were in bamboo at both the Ccollpa study site (Figure 2.3D) and three of the other study sites (n=22). All foraging observations (n=20) for this species were on bamboo stems (pers. obs.).

The 19 specialists can be broken down into five guilds based on foraging height and substrate preference (Figure 2.3, see Chapter 4). The first four guilds mainly occur 2- 12 m up, generally in the leafy portion of the bamboo thicket. Eight species regularly search live bamboo leaves; four of these are antbirds (Formicariidae) and four are flycatchers (Tyrannidae). Four species, two foliage-gleaners (Automolus and Anabazenops) and two antwrens (Myrmotherula), regularly search for insects hiding in dead leaves trapped in the bamboo foliage (see Remsen and Parker 1984, K. V. Rosenberg 1990a). Four species primarily search bamboo stems for insects and small vertebrates hiding in the hollow stems. The last guild, two antbirds and a furnariid, are mainly found within 1 m of the ground, where they search the leaf litter (antbirds) or

Table 2.1. Population size and density of bamboo specialists at Ccollpa study site.

species	# territories (# in bluff-top bamboo ¹)	density ² (territories /100 ha)	density ³ (territories / 100 ha)	total regi- strations
<i>Picumnus rufiventris</i>	7 (5)	2.3	4.7	41
<i>Celeus spectabilis</i>	2-3?	?	?	14
<i>Campylorhamphus trochilirostris</i>	26 (20)	8.5	17.6	262
<i>Synallaxis cabanisi</i>	4 (4)	1.3	2.7	28
<i>Simoxenops ucayalae</i>	8 (6)	2.6	5.4	71
<i>Anabazenops dorsalis</i>	23 (19)	7.5	15.5	265
<i>Automolus melanopezus</i>	11 (5**)	3.6	7.4	82
<i>Cymbilaimus sanctaemariae</i>	40 (30)	13.0	27.0	549
<i>Myrmotherula iheringi</i>	23 (15)	7.5	15.5	222
<i>Myrmotherula ornata</i>	23 (15)	7.5	15.5	176
<i>Microrhopias quixensis</i>	28 (15**)	9.1	18.9	271
<i>Drymophila devillei</i>	37 (22*)	12.1	25.0	651
<i>Percnostola lophotes</i>	52 (45**)	16.9	35.1	245
<i>Myrmeciza goeldii</i>	36 (26)	11.7	24.3	187
<i>Cercomacra manu</i>	37 (37***)	12.1	25.0	561
<i>Hemitriccus flammulatus</i>	22 (21**)	7.2	14.9	260
<i>Poecilatriccus albifacies</i>	21 (16)	6.8	14.2	272
<i>Ramphotrigon megacephala</i>	32 (23)	10.4	21.6	328
<i>Ramphotrigon fuscicauda</i>	9 (6)	2.9	6.1	62

¹ For χ^2 tests between number of territories in bluff-top bamboo and floodplain forest bamboo * = $0.05 < P < 0.10$, ** = $0.01 < P < 0.05$, *** = $P < 0.01$ (see Figure 2.2).

² Density for entire Ccollpa study site (307 ha).

³ Density only in bamboo at the Ccollpa study site (148 ha).

Figure 2.3A. Territory maps of antbird guild.

Hemitriccus flammulatus

Poecilotriccus albifacies

Ramphotrigon megacephala

Ramphotrigon fuscicauda

Figure 2.3B. Territory maps of flycatcher guild. See Figure 2.3A for legend.

Figure 2.3C. Territory maps of dead-leaf guild. See Figure 2.3A for legend.

Figure 2.3D. Territory maps of stem guild. See Figure 2.3A for legend

Figure 2.3E. Territory maps of undergrowth guild. Areas where more than one territory (terrs) could not be mapped accurately are indicated. See Figure 2.3A for legend

low tangles (furnariid). The foraging ecology of the nineteen specialists will be described in Chapter 4; dietary specialization will be described in a later paper.

Some territories (Figure 2.3) may have included portions without bamboo (e.g., the northernmost territory of Simoxenops ucayalae in Figure 2.3D): this almost always resulted when a few registrations were recorded from two nearby bamboo patches with non-bamboo habitat between them. If there was no reason to suspect two individual territories (i.e., no simultaneous registrations), then the resulting territory would include the portion without bamboo, even though the bird may have never been recorded in the non-bamboo portion of its territory.

Percnostola lophotes and Myrmeciza goeldii were difficult to spot-map precisely, because females sang identical songs to males in both of these common species. Although territories consisted of male-female pairs (pers. obs.), it was often possible to hear six or more singing individuals from one place. In some areas of high density, clumps of 2-4 territories were mapped without precise borders (Figure 2.3).

The most abundant bamboo specialist was Percnostola lophotes (Table 2.1), a rather large, undergrowth antbird. Celeus spectabilis, a woodpecker that specializes on ants found inside hollow bamboo stems (see Chapter 4), was probably the rarest, but I was unable to estimate density (see above). Densities for the 18 bamboo specialists with measurable densities at the Ccollpa (Table 2.1) were significantly different (Kruskal-Wallis $H' = 17.006$, $P = 0.0002$) from samples of Amazonian birds from floodplain forests at Cocha Cashu (Terborgh et al. 1990) and from terra firme forests in French Guiana (Thiollay 1994). Both the Cocha Cashu ($n=51$) and the French Guiana ($n=48$) samples included only those species with densities greater than 2.6 territories/100 ha, the density of the rarest bamboo specialist (Table 2.1). All samples included only species from the same families as the bamboo specialists (Picidae, Dendrocolaptidae, Furnariidae, Formicariidae, Tyrannidae). Six specialists at the Ccollpa had higher densities than the most common species at Cocha Cashu. These

differences in density were evident even though some of the most common species in bamboo at the Ccollpa site were not included because they also occurred in habitats lacking bamboo (e.g., *Thamnomanes schistogynus*, *Hypocnemis cantator*, and *Lathrotriccus euleri*; unpubl. data).

Even though bamboo specialists appear to be relatively abundant, the bamboo specialists were not evenly distributed across the bamboo habitat at the study site (Figure 2.3). For each species, a χ^2 test was used to determine if the number of territories in either floodplain forest or bluff-top bamboo differed from expected. The expected number of territories was based on relative areas of each bamboo habitat (Figure 2.2). Five species showed significantly different distributions than expected (Table 2.1). *Cercomacra manu*, *Pernostola lophotes*, and *Hemitriccus flammulatus* were more common in the bluff-top bamboo than expected ($P < 0.05$); in fact, all 36 territories of *Cercomacra manu* and all four of *Synallaxis cabanisi* were in bluff-top bamboo. Two species (*Automolus melanopezus* and *Microrhopias quixensis*) were more common in the floodplain forest bamboo ($P < 0.05$) than expected and the distribution of another species (*Drymophila devillei*) was nearly significantly more common ($P=0.07$) in the floodplain forest bamboo. The other 13 specialists were distributed as expected.

In addition to the 19 specialists, six other species (Table 2.2) were also found only in bamboo thickets, but were considered too rare to assess whether they were bamboo specialists or too few registrations were recorded to map territories adequately. Local populations of an additional seven species (Table 2.2) were closely associated with bamboo, but had a few territories (<10% of total) in areas away from bamboo.

The 19 species of bamboo specialists form an important part of the avifauna at the Ccollpa site, representing 4.3% of the 440 land-bird species recorded there (Foster et al. 1994; pers. obs.). The percentage rises above 7% when the 13 other species closely associated with bamboo (Table 2.2) are included.

Table 2.2. Additional species closely associated with bamboo

A. Common in bamboo, but also found in other habitats (RE = river edge <u>Gynerium/Cecropia</u> ; TG = tree-fall gaps in floodplain forest)	
<u>Crypterellus atrocapillus</u>	RE
<u>Automolus rufipileatus</u>	RE
<u>Cercomacra nigrescens</u>	RE
<u>Hypocnemis cantator</u>	TG
<u>Myiophobus fasciatus</u>	RE, TG
<u>Lathrotriccus eulerei</u>	TG
<u>Thryothorus genibarbis</u>	RE, TG
B. Apparent bamboo specialists, but too few registrations.	
<u>Dromococcyx pavoninus</u>	
<u>Bucco macrodactylus</u>	
<u>Monasa flavirostris</u>	
<u>Nonnula ruficapilla</u>	
<u>Automolus rubiginosus</u>	
<u>Sporophila schistacea</u>	

DISCUSSION

Bamboo specialization provokes interesting questions of the relative roles that vegetative structure (physiognomy) and plant species composition (floristics) play in determining habitat selection of birds (e.g., Rotenberry 1985). Obviously, bamboo specialists represent the extreme contribution of floristics: bamboo specialists are absent if a single species of plant -bamboo - is absent. This extreme is only pertinent, however, if floristics and structure represent opposite endpoints in a continuum. Bamboo thickets, however, are structurally different as well (see Chapter 3), and the specialists may be selecting these thickets not because bamboo (and prey bases associated with bamboo) is present, but only because the habitat structure differs from other habitats. In this case, a more appropriate distinction would be the relative contributions of habitat selection versus substrate specialization, instead of floristics versus structure. This topic will be discussed in greater detail in Chapter 4. Although this question is perhaps best asked on a species-by-species basis, community-wide patterns can reveal some insights.

Bamboo specialists appear to occur at higher densities relative to species in nearby forest habitats. Robinson and Terborgh (1990) also noted that territory sizes, as determined by song censuses, were larger for birds in mature forests than those in early successional habitats; thus, forest birds occurred at lower densities. Like bamboo, early successional stages in Amazonia have a number of specialist bird species (Remsen and Parker 1983, G. H. Rosenberg 1990). Bamboo and early successional habitats are structurally similar. Both are characterized by dense vegetation close to the ground, extremely reduced plant diversity, and low canopy cover. In southeastern Peru, some bird species are shared between these habitats (Table 2.2, see below) even though the dominant understory plant species are quite different (pers. obs.). These similarities

suggest that the structure of these habitats may be more important than floristics in determining their relatively high density of birds.

As is the case in this study, specialization is usually studied only locally, and few studies have looked at specialization throughout a species' distribution (but see Fox and Morrow 1981). The rich assemblage of bamboo specialists (19 species), the wide range in their areas of distribution (see below), and nearly two decades of increased ornithological work in Amazonia (e.g., Karr et al. 1990) have provided an opportunity to look at bamboo specialization across a broad geographical scale. In particular, do non-bamboo habitats support populations of these species outside the study area?

To determine the prevalence of specialization by these specialists on bamboo thickets, I reviewed habitat associations for these species in the literature (Table 2.3). In southeastern Peru, at least, 10 of the 19 specialists (Celeus spectabilis, Simoxenops ucayalae, Anabazenops dorsalis, Automolus melanopezus, Myrmotherula ornata, Cercomacra manu, Dryophila devillei, Hemitriccus flammulatus, Poecilatriccus albifacies, and Ramphotrigon megacephala) appear to be entirely restricted to bamboo thickets composed of Guadua sp. (Parker 1982, Pierpont and Fitzpatrick 1983, Fitzpatrick and Willard 1990, Karr et al. 1990, Ridgely and Tudor 1994). In Cocha Cashu, all 10 of these species were absent on the 97 ha plot (see above), which lacked significant stands of bamboo (T. A. Parker pers. comm., Terborgh et al. 1990). All 10 specialists, however, were found in nearby bamboo thickets outside their study plot (Karr et al. 1990); the only specialist not found in the Cocha Cashu area is Synallaxis cabanisi (Karr et al. 1990). Of the seven bamboo specialists that occur both on the 97-ha plot at Cocha Cashu and at the Ccollpa, only one (Picumnus rufiventris) was less dense at the Ccollpa site; the other six species had densities 3-32 times higher at the Ccollpa than at Cocha Cashu (Table 2.1).

Six bamboo specialists appear to be entirely restricted to bamboo thickets throughout their ranges: Celeus spectabilis, Cercomacra manu, Dryophila devillei,

Table 2.3. Previous references to habitats and micro-habitats used by bamboo specialists. Although habitats are not necessarily mutually exclusive, if bamboo was mentioned, e.g., "found in river-edge bamboo thickets," the habitat here is given as bamboo thickets, not river edge. * = definitively stated only occurs in areas with bamboo.

degree of bamboo specialization	habitat ^{1,2}
obligate	
<u>Celeus spectabilis</u>	BT (3,11*)
<u>Drymophila devillei</u>	BT (1*,3,4*,6*,7*,11*,12)
<u>Cercomacra manu</u>	BT (2,3*,4*,6*,7*,11*)
<u>Ramphotrigon megacephala</u>	BT (3*,4*,6*,7,8*,11*,12)
<u>Hemitriccus flammulatus</u>	BT (1,3*,4*,6,11*)
<u>Poecilatriccus albigularis</u>	BT (1*,3*,4*,6*,11*)
near-obligate	
<u>Simoxenops ucayalae</u>	BT (1,2,3*,4*,6,7*11*), FU (1,6)
<u>Anabazenops dorsalis</u>	BT (3,4*,6,7,11*), VT(7), RE (5,9), VA (9), FU (6,12), SG (6,9), ED (6)
<u>Automolus melanopezus</u>	BT (1*,2,3,4,6), FU (11)
<u>Cymbilaimus sanctaemariae</u>	BT (4*,6*,7,11*), VT (7,13), FU (13)
<u>Percnostola lophotes</u>	BT (1,2,4,6,11), RE (1,6,10,11), FU (11), ED (11)
<u>Myrmeciza goeldii</u>	BT (1,2,6), RE (6,10,11), FU (2,11), ED (11)
<u>Ramphotrigon fuscicauda</u>	BT (6,7,8,12), VT (6,7), FU (6,11), ED(10)
facultative	
<u>Picumnus rufiventris</u>	BT (11), ED (9), SG (9), RE (9,11), FU (10,11)
<u>Campylorhamphus trochilirostris</u>	BT (4,11), VA (4,6), ED (10), FU (11)
<u>Synallaxis cabanisi</u>	BT (7), RE (6,7,14), SG (6,7)
<u>Myrmotherula ornata</u>	BT (3,4*,6,11*), VT (6), ED (6)
<u>Myrmotherula iheringi</u>	BT (1,6,11), FU (2,6,10,11)
<u>Microrhopias quixensis</u>	BT (4,6,11), ED (6,9,10), FU (6,11), SG (6), VT (9)

¹ habitats given for Amazonian races only

² BT=bamboo thickets; VA=varzea, RE=river-edge (includes early successional vegetation with Gynerium, Cecropia, Heliconia), SG=secondary growth, VT=vine tangles, FU=forest undergrowth or subcanopy, ED=edge (includes tree fall gaps, borders)

³ citations: 1 = Parker 1982; 2 = Parker and Remsen 1987; 3 = Pierpont and Fitzpatrick 1983; 4 = Fitzpatrick and Willard 1990; 5 = Terborgh 1985; 6 = Ridgely and Tudor 1994; 7 = T. A. Parker, III, D. F. Stotz, and J. W. Fitzpatrick, unpubl. ms.; 8 = Parker 1984; 9 = Hilty and Brown 1986; 10 = Terborgh et al. 1990; 11 = Karr et al. 1990; 12 = Kratter et al. 1992; 13 = Davis et al. 1991; 14 = Terborgh and Weske 1969.

Hemitriccus flammulatus, Poecilotriccus albifacies, and Ramphotrigon megacephala (Table 2.3). I define these as "obligate bamboo users." Seven of the other 13 species (Table 2.3), defined as "near-obligate bamboo users," appear to occur almost wholly within or near bamboo thickets, but were occasionally recorded in habitats lacking bamboo. Most accounts stated that these species "prefer" bamboo. From published accounts, however, it was often impossible to determine if the records outside of bamboo thickets were of individuals from stable "non-bamboo" territories, wanderers from nearby "bamboo" territories, or non-territorial individuals dispersing between bamboo patches. These latter individuals are especially likely to be caught in mist nets (Remsen and Parker 1983), which are commonly used to assess habitat use in the Neotropics (e.g., Terborgh and Weske 1969, Karr 1990, Karr et al. 1990, Blake et al. 1990, Bierregaard 1990, Thiollay 1994). In addition, the presence of bamboo patches near the observation may have been missed. For example, Percnostola lophotes and Myrmeciza goeldii are often cited as preferring bamboo thickets, but also occurring in river-edge Gynerium thickets (references in Table 2.3). On the Tambopata, however, I found both species only in those Gynerium thickets that had some bamboo mixed in or had bamboo thickets nearby. In Gynerium thickets isolated from bamboo, e.g., on the island across from the lodge at the Ccollpa study site, neither species was found (pers. obs.).

The six remaining specialists ("facultative bamboo users", Table 2.3) definitely and regularly use non-bamboo habitats outside the study area. All six facultative bamboo users may be wholly or partially dependent on the presence of bamboo to support populations in southeastern Peru, and perhaps in other parts of their ranges as well.

The non-bamboo habitats used by the specialists can give some indication of the type of habitat use that may give rise, either evolutionarily or ecologically, to species that prefer bamboo. Of the 20 near-obligate and facultative bamboo specialists (Table

2.3) and species closely associated with bamboo at the Ccollpa (Table 2.2), 15 are also found in generally dense habitats with low canopy cover. Twelve species are also found in edge habitats, including tree-fall gaps (which could presumably include bamboo), and 10 are also found in early-successional river-edge habitats. The use of forested habitats is less striking: nine species are also found in forest undergrowth, and five are also found in vine tangles (Table 2.3).

It is not surprising that species are shared between river-edge habitats and bamboo thickets. Gynerium, or cane, forms thickets along rivers that have a somewhat similar physiognomic structure to bamboo thickets. Both habitats are composed of densely packed, hollow-stemmed, monotypic thickets with a dense low canopy of long linear leaves. Guadua bamboo thickets, however, tend to be taller, have greater canopy cover, and have more dead leaves trapped above the ground than Gynerium thickets (pers. obs.); in addition, Guadua stems have a greater variety of stem surfaces, including nodes, thorns, and clasping leaf-like sheaths. In addition to the 10 specialists that occasionally use river-edge habitats without bamboo, a congener (Automolus rufipileatus) of the specialist A. melanopezus, is also found in river-edge vegetation (Remsen and Parker 1983), including bamboo (see Table 2.2)

Within forested habitats, vine tangles probably offer the physiognomically most similar micro-habitat to bamboo thickets, with both providing very dense cover and interlocking networks of small branches. Aside from the five specialists that sometimes use this micro-habitat (Table 2.3), two sympatric species (Cymbilaimus lineatus and Cercomacra cinerascens) replace their two congeneric specialists in vine tangles within forests in southeastern Peru (pers. obs.).

A high percentage of the obligate and near-obligate bamboo users have small ranges relative to other species in Amazonia (Table 2.4; distributions from Sibley and Monroe [1990] and Ridgely and Tudor [1994]). Six of these are restricted to southwestern Amazonia, occurring no further north than central Peru and no further

Table 2.4. Biogeography of bamboo specialists

A. Restricted to southwestern Amazonia
<u>Cymbilaimus sanctaemariae</u>
<u>Cercomacra manu</u>
<u>Pernostola lophotes</u>
<u>Myrmeciza goeldii</u>
<u>Hemitriccus flammulatus</u>
<u>Poeciloriccus albifacies</u>
B. Southwestern Amazonia with populations further east in Brazil
<u>Celeus spectabilis</u> (distinct subspecies in Pará, Brazil)
<u>Simoxenops ucayalae</u>
C. Southwestern Amazonia with populations north to Amazonian Colombia
<u>Automolus melanopezus</u>
<u>Automolus dorsalis</u>
<u>Drymophila devillei</u>
<u>Ramphotrigon fuscicauda</u>
D. Western Amazonia with additional populations in southeastern Brazil
<u>Ramphotrigon megacephala</u>

east than northern Mato Grosso, Brazil. This area corresponds to Cracraft's (1985) South Amazon (Inambari) area of endemism. Six other species are somewhat more widespread, but these peripheral populations, outside of southwestern Amazonia, tend to be very local (references in Table 2.3). Two of these species occur somewhat further east, south of the Amazon River, and four occur north to southern Colombia along the base of the Andes. Only one of these 13 species (Ramphotrigon megacephala) has populations outside of Amazonia: the nominate subspecies occurs in southeastern Brazil.

In contrast, the six facultative specialists are more widespread. Only one (Synallaxis cabanisi) is restricted to southwestern Amazonia. One species (Picumnus rufiventris) occurs along the eastern base of the Andes north to Colombia; Myrmotherula iheringi and M. ornata are widely distributed south of the Amazon, with ornata also having a separate population found from northern Peru to southern Colombia. The last two species, Campylorhamphus trochilirostris and Microrhophias quixensis, are widespread in Amazonia. Other subspecies of these two species are distributed from Mexico south through most of tropical, and for Campylorhamphus trochilirostris, subtropical South America.

Bamboo specialization in Amazonia appears to be rare outside southwestern Amazonia. The only other Amazonian species considered to be a bamboo specialist is Lophotriccus eulophotes (Pierpont and Fitzpatrick 1983, Parker and Remsen 1987, Robinson and Terborgh 1990, Ridgely and Tudor 1994), another southwestern Amazonian endemic. It apparently does not occur south of the Río Madre de Dios (T. A. Parker, pers. comm.), hence its absence at my study sites. Therefore, almost all bamboo specialists in Amazonia, especially the obligate and near-obligate specialists, are either restricted to southwestern Amazonia, or, if they occur outside this area, they apparently use non-bamboo habitats.

Some Amazonian bamboo specialists (Anabazenops dorsalis, Drymophila devillei along with the Andean D. caudacuta, Hemitriccus flammulatus, Ramphotrigon megacephala bolivianus) have sister taxa that are also bamboo specialists in southeastern Brazil (Parker 1982, unpubl. data). This is the only prevalent biogeographic pattern among the clades that include bamboo specialists in southwestern Amazonia. Sister taxon relationships of the other specialists are either unclear, or, if a presumed sister taxon has been suggested, it is not a bamboo specialist (i.e., Simoxenops ucayalae/S. striatus, Parker et al. 1992; Cymbilaimus sanctaemariae/C. lineatus, Pierpont and Fitzpatrick 1983; Myrmotherula iheringi/M. sunensis, Whitney 1994; “gray backed” Myrmotherula ornata / “red -backed” M. ornata, Ridgely and Tudor 1994; Cercomacra manu/C. melanaria, Fitzpatrick and Willard 1990; Myrmeciza goeldii/M. melanocephala, Parker 1982; Poecilotriccus albifacies/P. capitale, Ridgely and Tudor 1994). Thus, if the sister taxon to the southwestern Amazonian specialist is also a bamboo specialist, then it occurs in southeastern Brazil.

The sharing of bamboo specialists between southwestern Amazonia and southeastern Brazil suggests that, for some taxa, bamboo specialization arose when these two avifaunas were connected. Although Kratter (1993) showed that bamboo specialization can arise convergently in two populations of a species (highland Amblycercus holosericeus), the common pattern across four species suggests that bamboo specialists in southeastern Brazil and southwestern Amazonia shared their specialization as a plesiomorphic condition. Subsequent to the faunal bridge between these areas, the regions became isolated and specialized populations differentiated in each area. Other specialists, those without sister taxa in southeastern Brazil, may have evolved in southwestern Amazonia following isolation of bamboo with southeastern Brazil. Other species with similar habitat requirements (e.g., species in river-edge Gynerium thickets or in vine tangles in forests; see above) may locally “invade” bamboo thickets. The present isolation of many bamboo specialists in southwestern

Amazonia and southeastern Brazil, both distinct avifaunal areas (Cracraft 1985), may only reflect the biogeographic history of the species, although appropriate habitat (extensive thickets of Guadua bamboo) may be lacking away from these areas. The genus Guadua, however, is widespread in the Americas from Mexico to Argentina (Soderstrom et al. 1988) and can form extensive thickets outside of southwestern Amazonia and southeastern Brazil (e.g., “guaduales” of Guadua angustifolia in inter-Andean valleys of central Colombia; Londoño 1990). Apart from Guadua, the Amazon basin is relatively poor in woody bamboos (Soderstrom et al. 1988). Unless specialization is a recently derived character in these taxa, and the sister taxa relationships mentioned above suggest that it is not, the diversity of bamboo specialists and the degree of their specialization indicate that bamboo thickets have been a evolutionarily persistent feature in southwestern Amazonia. The scarcity of bamboo specialists in other parts of Amazonia suggests that either appropriate habitat is currently missing or, if bamboo thickets are present, such as in Colombia, they have may not have had a continuous history in the area.

The conservation of birds hinges on our ability to identify and protect appropriate habitats. Although most bamboo specialists have previously been considered to be rare or uncommon (e.g., Parker 1982, Ridgely and Tudor 1994), populations sizes found in this study indicate that these species can be relatively abundant where their preferred habitat is extensive. Such areas should receive priority in conservation strategies. The Ccollpa area, currently part of the Tambopata-Candamo Reserved Zone in which some development is allowed, is under consideration by the Peruvian government to be included as a national park, which would give much greater protection (Foster et al. 1994; see Chapter 5).

CHAPTER 3

HABITAT SELECTION AND SEGREGATION

IN BAMBOO SPECIALIST BIRDS

High diversity communities offer great potential for investigating ecological principles; among the most important may be how sympatric species partition resources. Habitat segregation is one means by which potentially competing species may be able to occur sympatrically. Birds have dominated studies of habitat selection (e.g., Cody 1985). However, our knowledge of habitat selection (even at a macro-scale) in the most diverse ecosystems, lowland tropical forests, is primitive, as witnessed by the recent discovery of the importance of bamboo thickets for many tropical bird species (Parker 1982, Pierpont and Fitzpatrick 1983, Parker and Remsen 1987, Fitzpatrick and Willard 1990, Rodrigues et al. 1994, Chapter 2). Few studies have quantified habitat selection in tropical birds. In a recent volume on habitat selection (Cody 1985), only one (Terborgh 1985) of 16 chapters considered tropical species. Even fewer studies have attempted to quantify habitat partitioning among potentially competing species in the tropics, although this has been a frequent descriptive explanation for the high diversity of some tropical forests (e.g., Karr 1971, Terborgh 1980, 1985, Remsen and Parker 1983). Although the greater diversity of tropical forests could increase competition (Diamond 1978) and in turn increase habitat segregation, most studies of habitat selection and partitioning have taken place in relatively low-diversity temperate habitats, where competition may be less important.

At a lowland forest site in southeastern Peru, 19 insectivorous bird species are restricted to bamboo thickets (Chapter 2). These "bamboo specialists" are part of the richest assemblage of bird species in the world; over 550 species have been recorded at nearby lowland forest sites (Robinson and Terborgh 1990, Foster et al. 1994). Bamboo specialists provide an excellent opportunity to explore habitat selection and resource

partitioning. The required bamboo habitat is easily determined: bamboo thickets occur as discrete patches in a mosaic of habitats lacking bamboo. Many of these bird species are completely restricted to bamboo thickets throughout their geographical ranges (Chapter 2), and many use bamboo substrates in nearly all (> 95% for many species) of their foraging maneuvers (see Chapter 4). Therefore, common guild members (see below) use the same resource (arthropods in bamboo) at the same sites in more or less similar manners throughout their ranges. How do these species segregate ecologically?

The 19 specialists, all insectivorous, can be classified into five guilds, based on substrate preferences and foraging maneuvers (Table 3.1; see Chapter 4). The first four guilds forage in the leafy portion of bamboo thickets, generally from 2- 12 m up. Eight species regularly search live bamboo leaves; four of these are antbirds (Formicariidae; = antbird guild) that generally glean prey from leaves and four are flycatchers (Tyrannidae; = flycatcher guild) that sally-strike to leaves for prey (see Remsen and Robinson [1990] for foraging behavior terminology). Four species, two foliage-gleaners (*Automolus melanopezus* and *Anabazenops dorsalis*) and two antwrens (*Myrmotherula* sp.), regularly search for insects hiding in dead leaves trapped in the bamboo foliage (= dead-leaf guild; see Remsen and Parker 1984, K. V. Rosenberg 1990a, 1990b, 1993). Four species primarily search and manipulate bamboo stems (stem guild) for insects and small vertebrates hiding in the hollow stems. The last guild, two antbirds and a furnariid (= undergrowth guild), are mainly found within 2 m of the ground, searching the low vegetation (all three) or the leaf litter (antbirds).

During initial studies of habitat selection of these specialists, I noted that the bamboo specialists were not evenly distributed within the available bamboo habitat (see territory maps in Chapter 2); a major distinction was discovered between species found in "bluff-top bamboo" that occurred on raised terraces, and those in "floodplain forest bamboo" that occurred as smaller patches in low-lying floodplain forest. In this paper, I expand my investigation of habitat selection in these bamboo specialists to include

Table 3.1. Guild membership of bamboo specialists and closely related and potentially competing species replacements in other habitats. Four-letter species codes follow species name. Habitat associations from Terborgh et al. (1984), Karr et al. (1990), Ridgely and Tudor (1994), Foster et al. (1994), and pers. obs.

guild bamboo specialist	floodplain forest replacement	early successional replacement
antbird guild		
<u>Cymbilaimus sanctaemariae</u> (CYSA)	<u>C. lineatus</u>	
<u>Microrhopias quixensis</u> (MIQU)		
<u>Cercomacra manu</u> (CEMA)	<u>C. cinerascens</u>	
<u>Drymophila devillei</u> (DRDE)		
flycatcher guild		
<u>Hemitriccus flammulatus</u> (HEFL)	<u>H. zosterops</u>	<u>H. iohannis</u>
<u>Poecilotriccus albifacies</u> (POAL)		
<u>Ramphotrigon megacephala</u> (RAME)	<u>R. ruficauda</u>	
<u>Ramphotrigon fuscicauda</u> (RAFU)	<u>R. ruficauda</u>	
dead-leaf guild		
<u>Automolus melanopezus</u> (AUME)	<u>A. infuscatus</u>	<u>A. rufipileatus</u>
<u>Anabazenops dorsalis</u> (ANDO)		
<u>Myrmotherula iheringi</u> (MYIH)	<u>M. longipennis</u>	
<u>Myrmotherula ornata</u> (MYOR)	<u>M. leucophthalma</u>	
stem guild		
<u>Picumnus rufiventris</u> (PIRU)	<u>P. aurifrons</u>	
<u>Celeus spectabilis</u> (CESP)	<u>C. elegans/torquatus</u>	
<u>Campylorhamphus trochilirostris</u> (CATR)		
<u>Simoxenops ucayalae</u> (SIUC)		
undergrowth guild		
<u>Synallaxis cabanisi</u> (SYCA)	<u>S. rutilans</u>	<u>S. gujanensis/albigularis</u>
<u>Pernostola lophotes</u> (PELO)		
<u>Myrmeciza goeldii</u> (MYGO)	<u>M. fortis/ hyperythra</u>	

several sites, covering a greater portion of the range of bamboo thicket types available for the specialists in lowland southeastern Peru. I will look for structural differences in the vegetation among thicket types and see how bamboo specialists are distributed across sites. In particular, I test whether habitat segregation is occurring among common guild members (see Table 3.1).

I assume here that the bird community in bamboo at equilibrium. As has been pointed out for some temperate bird communities (see Wiens 1989), potentially competing species can occur together without segregating if the prey base is not limiting. I argue that such a non-equilibrium condition is unlikely for bamboo specialists. The relatively stable climate of tropical forests guarantees a relatively stable prey base (the arthropod fauna) in comparison to the "boom and bust" seasonality of temperate communities. Non-migratory insectivorous bird populations in the tropics should be better able to "track" an arthropod resource base than either frugivorous or nectarivorous species in the tropics or species in areas with more seasonal climates. None of the bamboo specialists are known to be migratory, and, as far as known, all occupy territories year-round (T. A. Parker, pers. comm.). Most specialists occupy nearly all the available habitat given their habitat preferences (see above: territory maps in Chapter 2); furthermore, many of the specialists occur at relatively high densities for tropical forest birds (Chapter 2). This spatial saturation of habitat suggests that populations are near carrying capacity, although this should be further tested. Some sort of ecological segregation is thus expected among the specialists that share similar foraging substrates and behavior.

STUDY SITES

Habitat selection and partitioning were studied at six sites along the Río Tambopata in southeastern Peru. The lowland portion of the river has two physiographically distinct sections. Between the mouth of the Tambopata at Puerto Maldonado and the mouth of the Río Malinowski, the river channel is narrow (ca. 200

m wide) and deep; vegetated river islands are absent and tall floodplain forest generally extends to the edges of the river channel. Upstream from the Río Malinowski the river changes to a 1.7 - 15-km wide river channel, with a 200 - 900-m-wide main channel, numerous smaller channels, and many vegetated river islands. The river is bordered in many sections by early, primary-successional vegetation, which includes bamboo (= early successional bamboo) at older sites. A few sections along the upper part of the river have extensive stands of bamboo on 30 - 50-m bluffs (= bluff-top bamboo), but most river-edge is only a few meters above normal high water. The floodplain forests on these low-lying soils regularly flood from river overflow or accumulation of waters during the wet season. Bamboo thickets in this forest (= floodplain forest bamboo) are common in both the upper and lower sections of the river.

Five study sites were on the upper portion of the Río Tambopata, including the major study site at Ccollpa de Guacamayos (= "Ccollpa", Site 1). At this site, described in Foster et al., (1994), both bluff-top and floodplain forest bamboo are present. Site 2 (2 km northeast of the Ccollpa), a small, early successional bamboo stand with dense Heliconia, stretches for approximately 600m along the east bank of the Río Tambopata. Site 3 (3 km south of the Ccollpa) is a 800-m long floodplain forest bamboo stand along the west bank of the Río Tambopata. Site 4 (8 km south of the Ccollpa), an extensive stand of bluff-top bamboo, is on the west bank of the Río Tambopata. Site 5 (2.5 km south-southeast of the Ccollpa) is a 600-m-long, early-successional bamboo stand with some Heliconia and wild bananas along the east bank of the Tambopata.

The Explorer's Inn Reserve (= EIR, Site 6), on the lower part of the river, has three distinct bamboo thickets: a floodplain forest thicket spans the Tapir and Main trails, extending east to the Bamboo trail; a second floodplain forest thicket spans the Katicocha and Swamp trails; and a more early successional thicket is above the Río La Torre along the Heliconia Trail. Nearly all bamboo at Explorer's Inn flowered, seeded,

and died recently, from 1989 - 1992 (K. V. Rosenberg, pers. comm.). Only a few old stems with seeds remained in 1992, at the north end of the bamboo thicket on the Tapir Trail. New bamboo stems, however, had regenerated in the same sites as the old thickets, although the stems had yet to reach the same girth and stature of stems before flowering (T. A. Parker, pers. comm.). The vegetation of the EIR is described in Erwin (1984) and Foster et al. (1994).

The extensive bluff-top bamboo thickets at sites 1 and 4 are identifiable in a satellite image of extreme southeastern Peru (Earth Observation Satellite Company 1991). These thickets probably share similar edaphic conditions. Both sites occur on approximately 30 - 50-m-tall terraces above the river; in addition, both sites also occur on what appear to be alluvial deposits from the last (northernmost) topographically dissected terrain from the Andes identifiable on the satellite image. The floodplain forest bamboo thickets at the other sites, which occur in different edaphic conditions (see above), are too small to be seen in this image. Early successional vegetation is visibly distinct in the image, but stands with bamboo cannot be differentiated.

METHODS

First, I quantified structural differences between bamboo thickets and forests without bamboo. I compared the vertical distribution of vegetation in a bluff-top bamboo thicket with that in mature floodplain forest without bamboo. A general area that represented each habitat type was chosen (see Figure 2.1 in Chapter 2) along a 300-m section of trail at the Ccollpa site, and 15 50-foot line transects were randomly placed in each habitat type. The start of each transect was randomly placed along the section of trail, as was the direction, as long as the transect did not re-intersect the trail. The vertical distribution of vegetation was broken down into 12 height strata (Table 3.2), and the percent cover of green vegetation over the transect line in each stratum was estimated for each 10-foot horizontal interval. Likewise, the number of stems (> 4 cm diameter) intersecting the transect line was also recorded in eight height strata

Table 3.2. Average percent cover of green vegetation (A) and average number of stems (B) at different height strata in mature floodplain forest and bluff-top bamboo thickets. *post-hoc t -test significant at $P < 0.01$.

A. green vegetation												
FOREST TYPE	average % cover vegetation											
	HEIGHT (m)											
	0-0.5	0.5-1	1-2*	2-3	3-4	4-5*	5-7*	7-9*	9-11	11-15	15-20*	20+
bamboo	54.4	38.0	33.2	25.3	34.8	44.8	80.7	68.0	36.7	13.3	3.3	38.3
floodplain forest	64.4	15.1	37.0	27.6	24.4	24.4	40.0	37.7	30.1	22.9	31.2	67.6

B. stems							
FOREST TYPE	average number of stems > 4 cm diameter						
	HEIGHT (m)						
	0-1*	1-2*	2-3*	3-4*	4-5	5-7*	7+
bamboo	3.2	3.9	2.5	1.8	1.0	3.0	1.9
floodplain forest	0.5	0.4	0.1	0.3	0.3	0.5	0.2

below 15 m above the ground (Table 3.2). The percent cover and number of stems at each stratum for bamboo thickets and floodplain forest were compared using a split-plot ANOVA (treatment = bamboo and floodplain forest; dependent variable = percent cover or number of stems, at 12 and 8 strata for vegetation and stems, respectively, over 15 replications for each treatment).

Second, I quantified habitat structure among the different types of bamboo thickets; this necessitated a somewhat different transect methodology. At least 1 km of trail was cut at sites 2 - 5; the main Ccollpa site already had over 15 km of cut trails and the EIR had over 25 km of trails. The vegetation at sites 2 - 5 was quantified along transects (800 -1300 m long). A 30x1-m vegetation sub-transect, horizontal to, but two meters away from the cut trail, was randomly placed within each 100-m section of trail at each site. For example, the 1300-m of trail at site 3 had 13 such sub-transects. At site 1, two vegetation transects (1-A and 1-B) were placed in the same manner along two 1000-m stretches of trail in bluff-top bamboo thickets. Similarly three 1000 m transects (6-M, 6-S, 6-H, letter refers to trail name, see above) were placed in the three distinct thickets at site 6. The following variables were measured on each sub-transect: the number of (1) bamboo stems, (2) Heliconia stems, and (3) non-bamboo stems > 3 cm DBH; the diameter of each (4) bamboo and (5) non-bamboo stem (all Heliconia stems were 3 - 4 cm diameter); (6) the percent cover bamboo; (7) the average height of bamboo; and (8) the average canopy height. The correlation matrix of standardized variables was used to reduce variation in the matrix to a few axes using Principal Component Analysis (PCA).

Sites 2-5 were visited for at least four days in May-June 1993 with weather conducive for bird-finding (i.e., calm and no rain); site 1 was visited from May - July 1992 and May- September 1993; site 6 was visited for 18 days in July- August 1992 and August 1993. The trails at each site were walked repeatedly over the course of the day to search for the 19 specialist species. In addition, mist-nets were used to capture

birds at sites 1-5. At least six 6 x 2m or 12 x 2 m nets were set in bamboo thickets. Sampling with mist nets varied among sites, from 200 net hours at site 5 to over 800 net hours at site 1. Although mist nets were not used at site 6, this area is among the most intensively worked areas in Amazonia (see Foster et al. 1994); the presence and abundance of specialists in my observations generally matched those recorded previously (Foster et al. 1994, T. A. Parker, pers comm., K. V. Rosenberg pers. comm., although see discussion). Although sampling intensity varied among sites, there was ample time to record which specialists were present at each site. All bamboo specialists were vocal throughout the study period (per. obs.), although two woodpeckers, Celeus spectabilis and Picumnus rufiventris, were relatively quiet. Celeus spectabilis, however, makes distinctive and easily found holes in bamboo stems while foraging (used to confirm this species' presence at sites), and Picumnus rufiventris is frequently caught in mist nets.

In addition to the survey of specialists among sites, the territories of 18 of the bamboo specialists were spot-mapped over 180 days in 1992-93 at site 1; Celeus spectabilis was excluded because I lacked a sufficient number of registrations to spot-map effectively (see Chapter 2 for spot-map methodology and maps of all 19 specialists). These maps were used to measure territory overlap among the specialists (see below). For these analyses, an additional species, Lathrotriccus euleri, was included in the flycatcher guild. This tyrannid, one of the most common species in bamboo at the Ccollpa site, had similar foraging behavior to the two flatbill (Ramphotrigon sp.) species in this guild (see Chapter 4) and is a potential competitor of the flycatchers. It is not considered a specialist because it occurred sparingly in habitats other than bamboo (see Chapter 2).

Analysis of habitat segregation focused on two sets of potentially competing bamboo specialists. The first set consists of the six pairs of specialists: two flatbill flycatchers (Ramphotrigon megacephala and R. fuscicauda), two tody-tyrants

(*Poecilotriccus albiglacies* and *Hemitriccus flammulatus*), two arboreal antbirds (*Cercomacra manu* and *Drymophila devillei*), two antwrens (*Myrmotherula ornata* and *M. iheringi*), two foliage-gleaners (*Anabazenops dorsalis* and *Automolus melanopezus*), and two undergrowth antbirds (*Percnostola lophotes* and *Myrmeciza goeldii*). These pairs have the highest potential for interspecific competition, because of similar use of foraging substrates, similar foraging behavior, and relatively similar size (pers. obs.; see Parker and Remsen 1987 for reasons to consider the arboreal antbird pair). The members of each pair are generally closely related as well: the members of two pairs are congeneric (see Kratter and Parker [in press] for why *Anabazenops dorsalis* is probably not an *Automolus*); the members of other pairs are all in the same subfamily. The second set consists of the five guilds (Table 3.1).

Habitat segregation was analyzed by comparing overlap among sites (see below) or territories (see Figure 2.3 in Chapter 2) in the two sets of putatively competing species. Percent overlap for two species (x, y) was calculated as:

$$\text{percent overlap} = 2 (\# \text{ overlapping territories}) / t_x + t_y$$

where t_x and t_y are the number of territories of species x and y, respectively. If two territories of x overlapped one territory of y, the overlap was considered two. For the species pairs, paired t-tests were used to test if overlap within the set of potentially competing species was less than overlap with species outside the sets. For the guild set of species, the average overlap within the guild was compared (using unpaired t-tests) with the average overlap among non-guild members of bamboo specialists

RESULTS

The vertical distribution of vegetation differed significantly between the bluff-top bamboo thickets and mature floodplain forests without bamboo in both the percent cover of vegetation ($F_{15,209} = 12.21$, $P < 0.0001$) and the number of stems intersecting the transects ($F_{15,359} = 6.74$, $P < 0.0001$). Below 4 m the two habitats were similar (Table 3.2). A relatively dense layer (> 50% cover) of vegetation was found near the

ground (< 1 m in forest and < 0.5 m in bamboo thickets); sparser vegetation was found up to 4 m. In bamboo thickets, a very dense layer of bamboo leaves occurred from 4 - 9 m; floodplain forests were much less dense in these strata (Table 3.2). The situation was reversed in the subcanopy and canopy: floodplain forests were denser than bamboo thickets above 11 m, significantly so from 15-20 m (Table 3.2). At all heights, more stems intersected the transects in bamboo thickets (Table 3.2), significantly so below 4 m and at 5-7 m, where the differences were significantly different.

Among the seven bamboo sites, all vegetation variables varied significantly (ANOVA, $P < 0.05$), except the size of non-bamboo stems (Table 3.3). Of the seven significant variables, five grouped the bluff-top bamboo transects together in Student-Newman-Kuel's post-ANOVA tests (number, size and density of bamboo stems, and number of *Heliconia* and non-bamboo stems). Five variables grouped the floodplain forest bamboo transects together (number bamboo, *Heliconia* and non-bamboo stems, percent cover bamboo, canopy height). Four variables grouped the early successional sites together (number bamboo and non-bamboo stems, and percent cover and height bamboo).

In the PCA of the vegetation structure of the sites (Figure 3.1, Table 3.4), the first axis, accounting for 34.8 percent of the variation in the model, reflected the degree to which bamboo dominated the transect. The number of bamboo stems and percent bamboo had high positive loadings on this axis; the number of non-bamboo stems and average canopy height had high negative loadings. PCA2, accounting for 21.9 % of the total variation in the model, reflected the stature or age of the bamboo thicket. Thickets with large stems and tall bamboo loaded positively on this axis; the number of *Heliconia* stems, which were associated with early successional sites, loaded negatively. Although the eigenvalue for PCA3 (1.08) was marginally large enough to include in the analyses, this factor largely reflected the one variable

Table 3.3. Vegetation of transects and Principal Component Analysis scores. Means over n sub-transects are given for each transect. * $P < 0.01$ for ANOVA of given variable.

tran- sect	n	variable										PCA1	PCA2	PCA3
		bamboo number *	bamboo diameter *	non- bamboo number *	non- bamboo diameter	Heliconia number *	percent bamboo stems *	bamboo height (m) *	canopy height (m) *					
1-A	10	11.7	4.2	6.5	9.8	10.1	60.3	5.1	15.7	1.918	0.312	0.036		
1-B	13	3.7	5.4	11.2	10.0	0	46.5	8.5	20.7	0.623	1.329	0.622		
2	10	9.9	6.3	7.0	9.2	1.5	94.0	7.5	17.7	0.386	-0.978	-0.612		
3	8	12.8	3.5	5.4	9.6	10.9	75.6	3.6	11.2	-1.052	1.266	-0.278		
4	10	14.4	6.1	4.7	11.7	0	100.0	4.8	12.0	0.851	1.237	-0.232		
5	10	10.5	6.8	9.4	16.6	0	96.0	6.9	21.5	1.157	-1.867	-0.690		
6-M	10	5.3	3.2	12.8	12.6	0	58.0	5.1	23.7	-1.295	-0.484	0.124		
6-S	10	5.8	3.6	13.4	11.3	0	40.5	4.2	21.2	-1.331	-0.698	0.018		
6-H	10	6.0	3.2	7.3	16.5	0	62.5	4.7	25.8	-0.710	-0.871	0.956

Figure 3.1. Principal Component Analysis plot of vegetation variables. Variables with greatest loadings are shown where at a maximum.

Table 3.4. Variable loadings and percent of variation explained for Principle Component Analysis.

eigen-vectors	bamboo number	bamboo diameter	non-bamboo number	non-bamboo diameter	Heliconia number	percent bamboo stems	bamboo height	canopy height	percent total	culm-lative %
PCA1	0.53	0.23	-0.45	0.07	0.04	0.48	-0.09	-0.47	0.348	0.348
PCA2	-0.06	0.58	0.14	-0.18	-0.44	0.15	0.63	0.05	0.219	0.567
PCA3	-0.04	0.00	-0.12	0.84	-0.42	0.10	-0.08	0.28	0.134	0.702

(diameter non-bamboo stems) that did not show significant variation among sites and therefore is not considered further.

The plot of the mean scores for each transect on PCA1 and PCA2 (Figure 3.1) showed that the three bamboo types, as previously assigned, grouped together. The three transects with bluff-top bamboo were in the most extreme bamboo-dominated/mature bamboo region of the figure. The floodplain forest bamboo transects were grouped on the least bamboo dominant side of the plot; these transects had high canopy cover and middle-aged to mature bamboo. The early successional sites were somewhat more dominated by bamboo than floodplain forest transects, but had the least mature bamboo. The transect through the "early successional" thicket at EIR (6-H) was intermediate between the early successional sites upriver and the floodplain forest transects at EIR. The occurrences of each of the 19 specialists among transects on this plot of PCA1 and PCA2 are given in Figure 3.2.

The transects with the greatest number of bamboo specialists were in bluff-top bamboo thickets: transects 1-A and 4 had 18 of the 19 specialists (Figure 3.3), with only Synallaxis cabanisi absent in both; the other transect in bluff-top bamboo (1-B) had 15 specialists. Two specialists (Poecilotriccus albifacies and Cercomacra manu) were found only on these three bluff-top bamboo transects. In general, the other types of bamboo were less diverse in terms of bamboo specialists (Figure 3.3), although one transect in floodplain forest bamboo (transect 3) had as many species as least diverse bluff-top transect (1-B). The least diverse transects were the three in early successional bamboo (10, 11, and 12 specialists). These latter two bamboo types lacked exclusive species.

Seven bamboo specialists were present at all nine sites (Figure 3.2). The other 12 specialists were generally widely distributed, but still indicated selection of particular bamboo habitats (Figure 3.2). Two species (Myrmotherula ornata, Ramphotrigon fuscicauda) were on all transects except the most early successional

Figure 3.3. Diversity of bamboo specialists at each site. The sites are plotted on a Principal Component Analysis of vegetation variables (see Figure 3.2).

(site 5); Hemitriccus flammulatus was distributed likewise, but was absent from all three early successional sites (2, 5, and 6-H). Three species (Myrmotherula iheringi, Automolus melanopezus, Drymophila devillei) generally avoided early successional (negative PCA2) and bamboo-dominated sites (positive PCA1). Synallaxis cabanisi had the opposite pattern: this specialist was restricted to the two early successional sites with the strongest bamboo component. Another three species (Microrhopias quixensis, Anabazenops dorsalis, Picumnus rufiventris) were only absent from the three transects at site 6.

Generally, a high degree of overlap was shown by the set of six pairs of potentially competing species for both territories and sites (Table 3.5). Overlap was not significantly less than expected for either the sites ($P = 0.588$) or territories ($P = 0.576$). Among the nine sites, none of the six pairs showed mutually exclusive distributions among pair members; in fact, in four cases the overlap between pair members was higher than the average with other specialists, opposite the expected trend. The only pairs indicating preferences for different types of thickets were Cercomacra manu / Drymophila devillei and Anabazenops dorsalis / Automolus melanopezus (Figure 3.2, Table 3.5). Both pairs sorted somewhat similarly: one member of the pair (Drymophila devillei or Automolus melanopezus) was found in older bamboo with high canopy cover (mainly floodplain bamboo thickets); the second member was restricted to bluff-top bamboo thickets (Cercomacra manu) or widely distributed among bamboo-dominated sites (Anabazenops dorsalis). These distinctions separating members of both pairs were evident in their spot-mapped territories as well (Chapter 2).

Given the overlap mentioned above for the potentially competing pairs, it is not surprising that overlap was also high within the guilds (Table 3.6): none of the guilds showed significantly less overlap than expected. Overlap in the spot-mapped territories of guild members was actually higher within four guilds than with non-guild members

Table 3.5. Percent territory and site overlap within pairs of bamboo specialists compared with average over all other specialists.

pair	TERRITORIES		SITES	
	within pair	with other spp.	within pair	with other spp.
<u>Poecilotriccus albifacies/</u> <u>Hemitriccus flammulatus</u>	0.698	0.694	0.667	0.661
<u>Ramphotrigon megacephala/</u> <u>R. fuscicauda</u>	0.927	0.783	0.941	0.772
<u>Drymophila devillei/</u> <u>Cercomacra manu</u>	0.432	0.697	0.500	0.623
<u>Automolus melanopezus/</u> <u>Anabazenops dorsalis</u>	0.471	0.648	0.400	0.665
<u>Myrmotherula iheringi/</u> <u>M. ornata</u>	0.862	0.685	0.857	0.707
<u>Myrmeciza goeldii/</u> <u>Percnostola lophotes</u>	1.000	0.765	1.000	0.794
t-test	t = 0.237, P = 0.589		t = 0.312, P = 0.616	

Table 3.6. Percent territory and site overlap ($\bar{x} \pm \text{SD}$) within guilds of bamboo specialists compared with non-guild specialists. Percentages are average overlap of between species pairs within each group. *P*-values give results of one-tailed paired *t*-tests between guilds and non-guild species.

guild	TERRITORIES			SITES		
	guild	non-guild	<i>P</i>	guild	non-guild	<i>P</i>
flycatcher	0.76 $\pm$ 0.17	0.73 $\pm$ 0.22	0.676	0.72 $\pm$ 0.18	0.73 $\pm$ 0.20	0.454
antbird	0.70 $\pm$ 0.18	0.70 $\pm$ 0.25	0.511	0.62 $\pm$ 0.12	0.70 $\pm$ 0.20	0.173
dead-leaf	0.71 $\pm$ 0.16	0.66 $\pm$ 0.24	0.693	0.66 $\pm$ 0.18	0.69 $\pm$ 0.22	0.364
stem	0.50 $\pm$ 0.03	0.68 $\pm$ 0.23	0.090	0.89 $\pm$ 0.13	0.76 $\pm$ 0.20	0.925
undergrowth	0.53 $\pm$ 0.41	0.61 $\pm$ 0.32	0.344	0.58 $\pm$ 0.37	0.66 $\pm$ 0.30	0.330

(Table 3.6). The only guilds showing lower overlap of territories within the guild were the two guilds with only three species (stem, understory); one of these (stem) showed higher overlap within the guild than with non-guild members in the analysis of sites.

DISCUSSION

Bamboo specialization exemplifies the sort of narrow resource use often associated with tropical forest birds. The results here indicate that bamboo specialization is even narrower than previously thought: in lowland forests in western Amazonia, different types of bamboo thickets harbored different assemblages of bamboo specialists. These results indicate that bamboo specialists are not just selecting habitats based on the presence of Guadua bamboo, but also appear to be selecting certain structural components of bamboo thickets. Thickets appropriate for some specialists (e.g., Synallaxis cabanisi in early successional bamboo) may be entirely inappropriate for other specialists (e.g., Automolus melanopezus or Drymophila devillei).

Certain types of bamboo thickets, however, namely those on bluff-top sites with some tall canopy cover, may contain almost all 19 bamboo specialists. The diversity of specialists drops off in either less dense thickets in floodplain forest or denser thickets in bluff-top or earlier successional sites. The high diversity of the bluff-top transects, however, probably results from intermediate or mixed conditions; both transects were centrally located on the gradient represented by the first PCA factor and diversity decreased toward either extreme along this axis (see Figure 3.3). The transects did not represent a particular "type" of thicket to which certain specialists were restricted. In fact, none of the 19 specialists was restricted to transects which had intermediate scores on either PCA axis (Figure 3.2); the specialists appeared to prefer thickets toward the extremes, which more or less coincided with the a priori designations of bluff-top, floodplain forest, and early successional bamboo thickets. Identifying appropriate

habitat for these species, many of which have geographically restricted ranges, has important conservation applications, which will be discussed in Chapter 5.

Another factor that may be very important in determining which bamboo specialists will be present is the phenology of the bamboo thicket. When bamboo thickets flower, seed, and die (see Janzen 1976), the habitat for specialists locally disappears. To survive, specialists would presumably have to disperse to other non-flowering thickets. If bamboo regenerates at the same site following flowering (e.g., at EIR, see below), specialists would not only have to recolonize from other thickets, but they would also have to wait until the structure of the thicket met their habitat requirements. Unfortunately, the periodicity and geographical extent of cohorts of Guadua bamboo in the area are unknown.

Bamboo specialists may have been missing from the three transects at EIR because of the recent flowering, seeding, and dying of almost all bamboo in the area from 1989-1992 (K. V. Rosenberg pers. comm., pers. obs.). Small populations of Anabazenops dorsalis, Cercomacra manu, Microrhopias quixensis, and Poecilatriccus albifacies were present in the EIR area before 1992 (T. A. Parker pers. comm., K. V. Rosenberg pers. comm.). In 1992, only one Poecilatriccus albifacies and one Cercomacra manu were present along transects 6-S and 6-H, respectively. None of these four species, however, was present in 1993, when the transect data were collected. Although much of the bamboo had regenerated at EIR, the stems were smaller and the canopy of bamboo leaves was lower than before the flowering event (T. A. Parker pers. comm.). In 1993, these specialists may have been absent from EIR either because the thickets had yet to attain appropriate stature or because the specialists had not yet recolonized the area from other populations where the bamboo did not flower (e.g., along the upper Río Tambopata). Although the only other transect with floodplain forest bamboo (at site 3) did have larger stems and taller bamboo canopy than at EIR (Table 3.3), only two of these four specialists missing at EIR were present

(*Microhospas quixensis* and *Anabazenops dorsalis*). Nonetheless, small numbers of all four specialists may use floodplain forest bamboo thickets on occasion (e.g., 250 km northwest in Manu National Park [Fitzpatrick and Willard 1990] or at the Ccollpa study site - excepting *Cercomacra manu* [Chapter 2]).

Although differences in habitat selection may be pronounced in bamboo specialists, very few of these differences appear to be related to broad-scale habitat segregation among potentially competing bamboo specialists. The only cases where segregation appeared to be important were between the *Cercomacra manu* / *Drymophila devillei* pair, and, to a lesser extent, the *Anabazenops dorsalis* / *Automolus melanopezus* pair. Similar habitat differences between *Cercomacra manu* and *Drymophila devillei* were noted by Parker and Remsen (1987) in northern Bolivia. However, many territories of both species pairs overlapped at site 1 (Chapter 2) and it was not unusual to see either pair foraging side-by-side, often in mixed-species flocks (see Munn and Terborgh 1979). Three of these species were almost always associated with such flocks; the fourth (*Cercomacra manu*) was not a habitual member of such flocks, although pairs often attended them when they were passing through territories (pers. obs.). For the four other pairs of specialists and within guilds as whole, the specialists appear to be able to occur sympatrically without segregating by habitat.

As mentioned above, bamboo specialization provides a context for competition among specialists belonging to the same guilds: they are using the same insect prey base in roughly similar manners. If competition affects these species and if they are not segregating by partitioning their habitat, they should either be segregating by differences in foraging behavior, at a finer scale than the guild designation followed herein, or in diet. The former is investigated in Chapter 4; I will investigate dietary overlap in a future paper.

The high overlap within guilds of bamboo specialists combined with the rather narrow habitat preferences of some of these species (excluding the widespread

specialists) indicates that factors other than competition, such as shelter from predators or abundance of potential prey, are driving habitat selection of these species, at least within habitats with bamboo. The initial selection of bamboo habitats by the specialists may be driven by competition with sympatric non-specialist species. This may be the case for the 12 specialists that have closely related, sympatric species in adjacent forest or early successional habitats (Table 3.6). The competitive influence of these sympatric species is impossible to gauge without more in-depth studies (e.g., Robinson and Terborgh 1995). However, Terborgh (1985) noted that one bamboo specialist species, Anabazenops dorsalis, apparently experienced niche expansion in the absence of the potentially competing Automolus rufipileatus, thus providing indirect evidence that competition may drive selection of bamboo thickets by one bamboo specialist species. Bamboo specialization in the seven specialists that lack sympatric, closely-related or ecologically similar species probably results from factors other than competition.

CHAPTER 4

FORAGING ECOLOGY OF BAMBOO SPECIALIST BIRDS

The great diversity of tropical ecosystems, as compared to those at more temperate latitudes, results in part from greater partitioning of niche space along resource gradients (Klopfer and MacArthur 1960). Species can divide a given resource gradient in three separate ways: 1) The gradient could be longer; for example there is a stable prey base of large insects for birds at tropical, but not temperate, latitudes (Schoener 1971). The resource gradient (insect prey) is thus larger in the tropics, and more bird species can fit into this niche space, all else being equal. 2) Species could occupy a smaller portion of the resource gradient (narrower niches) either along habitat gradients (MacArthur et al. 1966, Karr 1971) or along behavioral (e.g., foraging) gradients (Klopfer and MacArthur 1960); this is commonly thought of as greater specialization. 3) Lastly, species could have greater overlap along the resource gradient. However, ecological pressures (e.g., competition) to segregate in tropical communities should be as high, if not higher, than temperate communities, because resource bases in the tropics are relatively stable and predictable. This may be especially true for insectivorous tropical forest birds; in comparison to the unpredictable resource base and migratory habits of many temperate bird species, most tropical forest bird species are non-migratory and they tend to have year-round, relatively stable resources.

The means by which ecologically similar tropical birds divide niche space, however, remain largely unexplored. Detailed quantified descriptions of foraging patterns in tropical communities are rare; few have been of entire avian communities (except Remsen 1985, G. H. Rosenberg 1990). Most have been of some subset of an avifaunal community, including piscivores (Remsen 1990), dead-leaf specialists (K. V.

Rosenberg 1990, 1993), tropical raptors (Robinson 1994), or epiphyte specialists (Sillett 1994).

The pressures that lead to niche-partitioning, and thus ecological specialization, should be at a maximum where species diversity is the highest. The world's richest bird communities are found in lowland forests in southwestern Amazonia: over 550 species have been recorded in small areas of southeastern Peru (e.g., <50 km² at Cocha Cashu Biological Station in Mantu National Park: Robinson and Terborgh 1990). Two of the studies mentioned above (Rosenberg, Robinson) explored niche partitioning in these rich avian communities.

Part of this rich avifauna is restricted to locally distributed thickets of spiny bamboo (Guadua weberbaueri); these species are known as "bamboo specialists." (Parker 1982, Parker and Remsen 1987, Pierpont and Fitzpatrick 1983, Fitzpatrick and Willard 1990, Chapter 2). A distinct avifaunal community of 19 species of bamboo specialists co-occur in bamboo thickets at a lowland site in southeastern Peru (Chapter 2); all are insectivorous as far as known. Bamboo thickets are characterized by expansive areas of near-monotypic stands of this single species of bamboo. Thus the 19 specialists are sharing, and most are completely limited to, the same habitat; they are also eating similar prey (arthropods), and they are largely foraging from a single plant species with a limited number of potential substrates (mostly leaves, nodes, internodes). Bamboo specialists thus provide a unique opportunity to study niche partitioning in ecologically similar species. Nevertheless, except for four specialists (Anabazenops dorsalis; Kratter and Parker, in press; Automolus melanopezus and Myrmotherula ornata, K. V. Rosenberg 1990a, 1990b, 1993; and Ramphotrigon fuscicauda: Fitzpatrick 1980), the foraging ecology of bamboo specialists has received little attention, aside from qualitative descriptions at scattered sites (Parker 1982, Pierpont and Fitzpatrick 1983, Parker and Remsen 1987, Fitzpatrick and Willard 1990, Ridgely and Tudor 1994).

Bamboo thickets are a unique habitat, on which birds may specialize, and bamboo provides unique, locally abundant, substrates. In Chapter 3, I investigated habitat selection and partitioning by bamboo specialists among three structurally different types of bamboo thickets (all composed of the same bamboo species). In general, I found a great deal of overlap among potentially competing specialists. In this chapter, I have three goals: first, I will describe the foraging patterns in this bird assemblage and compare them with other tropical communities. Second, I will attempt to differentiate between habitat and foraging specialization. Finally, I will investigate how bamboo specialists partition niche space, especially among potentially competing species.

METHODS

STUDY SITES - All foraging observations were collected in lowland bamboo thickets along the Río Tambopata in depto. Madre de Dios in southeastern Peru (ca. 13°S; 69°W). The seven study sites, which include three structurally different types of bamboo thickets, but all were comprised of the same species of bamboo, have been described in chapters 2 and 3 and in Kratter (in press).

FIELD OBSERVATIONS - Foraging observations were taken over 178 days (22 May - 17 July, 1992 and 29 May - 18 September, 1993) during trail surveys at the six sites. Observations were recorded on a microcassette recorder. In general, many individuals of each specialist (see territory maps in Chapter 2) were sampled, thereby reducing problems associated with pseudo-replication. Nevertheless, at each encounter with an individual, no more than three consecutive observations were taken to limit biases resulting from pseudo-replication. For the three specialists with less than 25 total observations, only the first observation was used in consecutive series. In general, terms and variables used in classifying foraging behavior followed Remsen and Robinson (1989). In addition to the 19 specialists, a twentieth species (Lathrotriccus euleri) was also included; this flycatcher (Tyrannidae) was one of the most common

birds in bamboo thickets, although it did not meet the criteria to be a bamboo specialist because some (ca. 5%) of its territories were not in bamboo at my study sites (Chapter 2). Except where noted, *L. euleri* is considered a "specialist."

The following variables were estimated and recorded for each foraging observation: 1) height above ground. 2) distance below canopy. Height and distance below canopy were then added to create canopy height, which was used only in univariate analyses. 3) perch size. 4) perch angle, relative to horizontal. 5) substrate size (length and width for leaves, diameter for stems). 6) perch foliage density (in 6 classes 0-5, 5 being densest; see Remsen and Robinson 1990). Three categorical variables were also recorded: 7) perch (generally bamboo or non-bamboo, live or dead; if bamboo stem, on node or internode). 8) attack maneuver; and 9) substrate (leaf, stem, leaf litter, or air; bamboo or non-bamboo; node or internode; live or dead). The following variables were added when active attack maneuvers were used, such as jumps, lunges, or sallies: 10) sally (or jump or lunge) distance; 11) sally (or jump or lunge) angle, relative to horizontal; and substrate foliage density (if different than perch foliage density). In general, the variables recorded, the terminology, and the strategy for recording foraging observations followed Remsen and Robinson (1990).

ANALYSES - To define guilds, I began by analyzing all specialists together. Terborgh and Robinson (1986) presented a five-level hierarchy for classifying species into guilds. I was able to skip the first three levels because: for level 1 (taxon), the bamboo specialists represent a rather homogeneous group morphologically (Table 4.1) and taxonomically (two woodpeckers and 17 suboscine passerines); for level 2 (trophic level/diet) all specialists are insectivorous; and for level 3 (microhabitat), all species forage in bamboo thickets. I therefore was able to classify species into guilds using only the final two levels: substrate and foraging behavior. I used multiple correspondence analysis (MCA) of the substrate and attack variables to plot species in multi-dimensional space. Clusters of species, determined by sight, were considered

Table 4.1. Bamboo specialist codes, mass, bill measurements, and species loadings on multiple correspondence analysis axes (CA1, CA2, CA3). Morphological measurements were taken for at least five specimens of each species, except where noted. *samples not large enough for MCA.

SPECIES	4 letter code	mass (g)	bill length (mm)	bill width (mm)	CA1	CA2	CA3
<u>Anabazenops dorsalis</u>	ANDO	34.4	23.2	5.1	1.11	-0.23	-0.13
<u>Automolus melanopezus</u>	AUME	30.2	22.4	4.8	1.06	-0.66	0.02
<u>Campylorhamphus trochilirostris</u>	CATR	41.3	61.4	3.6	1.16	1.50	-0.63
* <u>Celeus spectabilis</u>	CESP	112.8	31.6	9.5			
<u>Cercomacra manu</u>	CEMA (n=3)	18.2	20.0	5.2	-0.59	0.12	0.51
<u>Cymbilaimus sanctaemariae</u>	CYSA (n=1)	30.9	21.3	7.2	-0.68	0.21	0.59
<u>Drymophila devillei</u>	DRDE	10.4	15.1	4.1	-0.67	0.01	0.26
<u>Hemitriccus flammulatus</u>	HEFL	11.4	13.6	4.5	-1.09	-0.11	-0.69
<u>Lathrotriccus euleri</u>	LAEU	10.2	14.1	5.2	-1.20	-0.07	-0.80
<u>Microrhopias quixensis</u>	MIQU	9.4	16.1	4.1	-0.61	-0.04	0.03
<u>Myrmeciza goeldii</u>	MYGO	43.4	24.8	5.4	-0.26	1.06	3.97
<u>Myrmotherula iheringi</u>	MYIH (n=3)	8.1	13.8	3.4	1.00	-0.50	-0.04
<u>Myrmotherula ornata</u>	MYOR	9.7	15.3	4.0	1.08	-1.08	0.00
<u>Percnostola lophotes</u>	PELO	30.0	21.2	5.3	0.11	1.07	2.58
<u>Picumnus rufiventris</u>	PIRU	22.7	7.6	4.8	1.26	4.25	-1.35
<u>Poecilatriccus albifacies</u>	POAL (n=1)	5.5	11.9	5.5	-1.21	-0.07	-0.75
<u>Ramphotrigon megacephala</u>	RAME	14.0	15.2	5.7	-1.19	-0.08	-0.76
* <u>Ramphotrigon fuscicauda</u>	RAFU	18.0	17.4	6.8			
<u>Simoxenops ucayalae</u>	SIUC	52.7	25.5	5.0	1.34	3.50	-1.26
* <u>Synallaxis cabanisi</u>	SYCA	18.8	16.1	3.6			

guilds. Species in these clusters thus had similar foraging behavior and substrate preferences. Differences among guilds were then investigated with univariate statistics (see below). I then analyzed each guild separately, using appropriate continuous and categorical variables.

Univariate statistical analyses consisted of analyses of variance (ANOVAs) for continuous variables and X^2 tests for categorical data. Scheffe's post-hoc tests were used to investigate differences between pairs of either guilds or species in ANOVAs. Residuals (observed minus expected values) in contingency tables were analyzed to see which cells contributed to significant X^2 tests (Siegel and Castellan 1988). Critical P values of 0.01 were used because the number of cells in most tables exceeded 20. When possible, I lumped similar categories if an expected value was less than one for any cell or if 20% of expected values were below five for any contingency table (see Cochran 1954). Lumping strategies depended on what appeared important for the species or guild in question. For example, species in both the dead-leaf and antbird guilds used many different types of hang maneuvers (for attack variable), but hangs were relatively rare in the antbird guild. Therefore, for the dead-leaf guild I was able to include all four types of hang maneuver, but all hang maneuvers had to be lumped into one category for the antbird guild (see below) to meet the criteria for contingency table analyses. Lumping was not always possible; for example, there was no ecologically similar substrate with which to lump the substrate "air," so this category was retained when recorded, even though expected values may have dropped below one for species with low samples sizes. For univariate investigation of continuous variables among guilds, frequencies of behaviors were averaged over each species in the guild, and ANOVAs were used to test for differences among guilds.

Multiple correspondence analysis (SAS Institute 1992) was used to see how the three categorical variables covaried in multivariate-space within each guild. For example, if non-bamboo perches were used, then it may be expected that non-bamboo

substrates would be used. This multivariate investigative technique, which is especially appropriate for foraging data (Moser et al. 1990), gives "biplots" in which the "dependent" variables (species) and "independent" variables (perch, attack, and substrate) are plotted simultaneously. Continuous variables were investigated in multivariate space using discriminant function analyses (DFA) (SYSTAT 1992). The three specialist species with small samples sizes ($n < 25$: Celeus spectabilis, Ramphotrigon fuscicauda, Synallaxis cabanisi) were excluded from multivariate and contingency table analyses.

RESULTS

ALL SPECIALISTS - The MCA of attack and substrate variables for the 17 specialists with large enough samples clustered the species into five distinct groups (Figure 4.1, tables 4.1-4.2). The first axis (CA1) separated those species foraging from live leaves (strongly negative) from those foraging from stems and dead leaves (positive). The eight species using live leaves clustered into two guilds based on attack. The first group contained four sallying species (Figure 4.1, tables 4.3-4.5), all flycatchers (Tyrannidae: Hemitriccus flammulatus, Poecilatriccus albifacies, Ramphotrigon megacephala, Lathrotriccus euleri). These species also were associated with the air substrate. The first two species are morphologically similar members of a group of related flycatchers known as tody-tyrants (Lanyon 1988). The latter two species are unrelated, but share similar size and morphology (Table 4.1). Another bamboo specialist, also in the genus Ramphotrigon, R. fuscicauda (Chapter 2), undoubtedly belongs with this guild. Although there were too few foraging observations to include R. fuscicauda in this analysis, all foraging observations of this somewhat rare tyrannid (Parker 1982, Ridgely and Tudor 1994, pers. obs.) were sallies, 89% of which were to live bamboo leaves (Table 4.5). These five species form the "flycatcher guild."

Figure 4.1. Multiple Correspondence Analysis for substrate and attack variables. Clusters of species define guilds and are numbered. The associated attack maneuvers and substrates are circled with the guild. Overlap between circles indicates shared behaviors. Large solid dot is the origin. Percent variation accounted for by each axis follows axis label. See Tables 4.1-4.2 for species codes, attack and substrate categories, and individual loadings on axes.

Table 4.2. Attack and substrate categories and loadings on multiple correspondence analysis axes (CA1, CA2, CA3). See text and Remsen and Robinson (1990) for descriptions of attack and substrate categories.

ATTACK		CA1	CA2	CA3
G	glean	0.20	0.27	0.53
HD	hang-down, includes hang-upside-down	1.05	-0.75	-0.14
HSW	hang-sideways	1.07	-0.62	-0.09
HU	hang-up	1.06	0.47	-0.46
J	jump, includes hop,	-0.75	0.11	0.63
JH	jump-hang	-0.85	-0.00	0.17
L	lunge	-0.70	0.60	2.37
PECK	peck, includes pry, rummage, plow	1.41	4.05	-1.47
R	reach	0.27	-0.45	0.30
SS	sally-strike, includes all wing-powered maneuvers	-1.09	-0.08	-0.63
SUBSTRATE				
A	air	-1.06	-0.05	-0.38
B	live bamboo stem	0.69	1.82	0.23
BD	dead bamboo stem	1.16	2.25	-0.78
BDL	dead bamboo leaf	1.03	-0.91	-0.05
BH	hole in bamboo stem internode	1.23	1.82	-0.82
BL	live bamboo leaf	-0.88	-0.02	-0.15
BSP	bamboo spine, includes clasping sheaths and nodes	1.03	0.24	-0.18
DL	non-bamboo dead leaf	1.04	-0.67	0.04
L	non-bamboo leaf	-0.59	-0.02	0.19
LL	leaf litter	-0.23	1.26	4.84
N	non-bamboo stem	0.90	1.28	-0.24

Table 4.3. Means, standard deviations, and sample sizes for continuous variables in the flycatcher guild. Canonical loadings of variables on first two axes of discriminant function analysis (Figure 4.6) are given for each species. *variable or species not included in discriminant function analyses.

SPECIES	height (m)	distance to canopy (m)	canopy (m)*	perch size (cm)	perch angle
<i>Hemitriccus flammulatus</i>	3.5±1.6 (99)	11.9±9.8 (95)	15.3±9.7 (95)	1.0±0.9 (89)	7.6±15.7 (85)
<i>Poecilotriccus albifacies</i>	4.9±2.0 (178)	12.5±9.7 (172)	18.4±9.9 (172)	0.7±0.4 (161)	6.8±16.3 (153)
<i>Ramphotrigon megacephala</i>	5.7±1.8 (111)	13.4±9.9 (108)	19.1±10.4 (108)	0.9±0.64 (99)	8.1±17.3 (91)
* <i>Ramphotrigon fuscicauda</i>	5.4±1.9 (9)	12.0±13.3 (7)	17.9±14.8 (7)	0.6±0.2 (6)	12.9±22.0 (7)
<i>Lathrotriccus euleri</i>	4.0±1.9 (83)	13.0±9.8 (83)	17.0±10.0 (83)	1.4±1.5 (77)	6.7±15.0 (76)
DFA1	-0.118	-0.034		-0.217	-0.046
DFA2	0.655	0.015		-0.359	0.005

SPECIES	perch foliage density	substrate foliage density	sally distance (m)	sally angle
<i>Hemitriccus flammulatus</i>	2.4±0.8 (80)	2.9±0.7 (95)	0.35±0.23 (97)	38.5±39.5 (97)
<i>Poecilotriccus albifacies</i>	3.0±0.7 (150)	3.4±0.7 (163)	0.32±0.21 (177)	46.8±38.9 (171)
<i>Ramphotrigon megacephala</i>	2.3±0.7 (92)	2.8±0.7 (109)	0.77±0.42 (109)	29.0±33.3 (105)
* <i>Ramphotrigon fuscicauda</i>	2.6±0.9 (9)	2.4±0.5 (8)	1.06±0.53 (9)	18.8±26.3 (8)
<i>Lathrotriccus euleri</i>	1.9±0.7 (66)	2.5±0.9 (73)	0.78±0.70 (80)	34.1±34.7 (76)
DFA1	0.543	0.401	-0.791	0.277
DFA2	0.426	0.320	0.277	-0.011

Table 4.4. Significant differences in continuous variables of the flycatcher guild. Given variables have $P < 0.05$ in Scheffe's post-hoc tests in single factor ANOVAs.

	HEFL	LAEU	POAL	RAFU	RAME
<i>Hemitriccus flammulatus</i>	-	SFD PFD SF	HT PFD SD	SFD	HT SFD
<i>Poecilotriccus albifacies</i>		-	HT PS SFD PFD SD		HT PS PFD
<i>Ramphotrigon megacephala</i>			-	SFD SD	HT SFD SA PFD SD
<i>Ramphotrigon fuscicauda</i>				-	
<i>Lathrotriccus euleri</i>					-

variable codes: HT=height, PS=perch size, PFD=perch foliage density, SD=sally distance, SA=sally angle, SFD=substrate foliage density

Table 4.5 Percentages of categorical variables (with n observations) in the flycatcher guild. In contingency table analyses categories with $P < 0.01$ (see text) are given a "+" if residual was significant and positive (the species used that behavior significantly more often than expected) and a "-" if residual was negative (significantly less use than expected). Contingency table design, Chi-squared statistic, and P -value are given for each variable at bottom. * removed from contingency table and correspondence analyses.

SPECIES	PERCH	ATTACK	SUBSTRATE
<u>Hemitriccus</u> <u>flammulatus</u>	-B: 80.4 (74) +N: 19.6 (18)	SS: 95.0 (94) SH: 3.0 (3) *G: 2.0 (2)	-BL: 78.35 (76) A: 0 +NL: 21.6 (21)
<u>Poecilatriccus</u> <u>albifacies</u>	+B: 95.2 (160) -N: 4.8 (8)	+SS: 97.8 (175) -SH: 1.1 (2) *G: 1.1 (2)	+BL: 98.9 (174) -A: 0 -NL: 1.1 (2)
<u>Ramphotrigon</u> <u>megacephala</u>	B: 86.7 (85) N: 13.3 (13)	-SS: 85.0 (96) +SH: 15.0 (17)	BL: 89.4 (101) A: 0.9 (1) NL: 9.7 (11)
<u>Ramphotrigon</u> <u>fuscicauda</u> *	B: 88.9 (8) N: 11.1 (1)	SS: 88.9 (8) SH: 11.1 (1)	BL: 88.9 (8) A: 0 NL: 11.1 (1)
<u>Lathrotriccus</u> <u>euleri</u>	B: 84.7 (61) N 15.3 (11)	SS: 92.8 (77) SH: 7.3 (6)	BL: 84.2 (69) +A: 11.0 (9) NL: 4.8 (4)
PERCH	$X^2_{(4 \times 2)} = 15.0$, $P = 0.0018$ B=all bamboo perches N=all non-bamboo perches		
ATTACK:	$X^2_{(4 \times 2)} = 25.7$, $P < 0.0001$ G=all stationary maneuvers, including glean, lunge, reach, hop SS=sally-strike SH=sally-hover		
SUBSTRATE	$X^2_{(4 \times 3)} = 90.9$, $P = 0.0001$ A=air NL=all non-bamboo substrates except A		
	BL=all bamboo substrates		

The other four specialists preferring live bamboo leaf substrates were all antbirds (Formicariidae: Cercomacra manu, Cymbilaimus sanctaemariae, Drymophila devillei, Microrhopias quixensis). In the MCA (Figure 4.1), these four species, the "antbird guild" (tables 4.6-4.8), were associated with active, near-perch attack maneuvers (jump, jump-hang, lunge) and live non-bamboo leaf substrates, although this substrate was rarely used (maximum 11%, Table 4.8). They had similar scores on CA2 to the flycatcher guild, but scored somewhat higher on CA3 (Figure 4.1)

Two other antbird species (Pernostola lophotes and Myrmeciza goeldii) were isolated from other specialists on CA1 and CA2, but scored near zero on both, indicating more generalized attack and substrate use relative to other species on these axes (Figure 4.1). These two antbirds did separate from other specialists on CA3, however, associated strongly with the leaf litter substrate. Neither species associated with any particular attack maneuver; they were closest to reach and glean, the most generalized attack maneuvers among all specialists (scores near zero on all three axes; Table 4.2). Both of these antbirds foraged lower than other species (see below), often dropping to the leaf litter to glean arthropods. These two antbirds were placed in the "undergrowth guild," along with the specialist Synallaxis cabanisi, the only other species that averaged below 1m in foraging height (tables 4.9-4.11); this species had too few observations to include in multivariate analyses.

The other seven specialists (with positive scores on the CA1) separated into two groups on CA2 (Figure 4.1). Two foliage-gleaners - Anabazenops dorsalis (see Kratter and Parker, in press, for reasons why this species is not an Automolus) and Automolus melanopezus - and two antwrens (Myrmotherula ornata and M. iheringi) formed a tight cluster associated with two of three hang attack maneuvers and the two dead leaf substrates (Figure 4.1). These four species form the "dead-leaf guild"

Table 4.6. Means, standard deviations, and sample sizes for continuous variables in antbird guild. Canonical loadings of variables on first two axes of discriminant function analysis (Figure 4.4) are given for each species. *=subset including only active maneuvers (see text). **variable not included in discriminant function analyses.

SPECIES	height(m)	distance to canopy (m)	canopy (m)**	perch size (cm)	perch angle
<i>Cercomacra manu</i>	5.9±2.3 (97)	13.7±9.9 (94)	19.7±11.0 (94)	0.6±0.3 (88)	16.8±28.4 (86)
<i>Cymbilaimus sanctaemariae</i>	5.8±2.1 (101)	14.1±8.8 (100)	19.9±9.1 (100)	1.0±0.6 (86)	10.1±21.5 (91)
<i>Drymophila devillei</i>	6.5±2.0 (219)	15.8±9.2 (211)	22.3±9.2 (211)	0.5±0.2 (202)	10.6±22.6 (189)
<i>Microrhophias quixensis</i>	5.7±2.2 (236)	15.2±10.1 (229)	20.9±10.5 (229)	0.5±0.4 (223)	17.7±27.6 (192)
DFA1	-0.037	-0.172		0.781	-0.066
DFA2	0.176	0.016		-0.564	0.147
*DFA1	0.052	0.001		0.648	-0.449
*DFA2	-0.509	-0.074		0.583	0.255

SPECIES	perch foliage density	sally distance (m)	sally angle (°)
<i>Cercomacra manu</i>	4.3±0.7 (98)	0.20±0.11 (34)	7.9±33.9 (17)
<i>Cymbilaimus sanctaemariae</i>	3.8±0.8 (97)	0.29±0.23 (52)	32.5±49.3 (34)
<i>Drymophila devillei</i>	3.7±0.8 (219)	0.19±0.20 (106)	20.1±45.5 (68)
<i>Microrhophias quixensis</i>	3.5±0.8 (232)	0.27±0.34 (106)	20.1±48.3 (78)
DFA1	0.516		
DFA2	0.802		
*DFA1	0.496	-0.090	-0.260
*DFA2	-0.416	0.418	0.202

Table 4.7. Significant differences in continuous variables of the antbird guild. Given variables have $P < 0.05$ in Scheffe's post-hoc tests in single factor ANOVAs.

	CEMA	CYSA	DRDE	MIQU
<i>Cercomacra manu</i>	-	PS PFD	PFD	PFD
<i>Cymbilaimus sanctaemariae</i>		-	PS	PS PFD
<i>Drymophila devillei</i>			-	HT PFD
<i>Microrhophias quixensis</i>				-

variable codes: HT=height, PS=perch size, PFD=perch foliage density

Table 4.8. Percentages of categorical variables (with n observations) in the antbird guild. In contingency table analyses, categories with $P < 0.01$ (see text) are given a "+" if residual was significant and positive (the species used that behavior significantly more often than expected) and a "-" if residual was negative (significantly less use than expected). Contingency table design, Chi-squared statistic, and P -value are given for each variable at bottom.

SPECIES	PERCH	ATTACK			SUBSTRATE
CEMA	+B: 100 (96) -N: 0	+G: 40.8 (40) R: 9.2 (9) -SS: 5.1 (5)	JH: 6.1 (6) J: 7.1 (7) H: 9.2 (9)	SH: 1.1 (1) +L: 17.3 (17) FC: 4.7 (4)	BL: 95.9 (93) NL: 3.1 (3) A: 1.0 (1)
CYSA	B: 87.6 (85) N: 12.4 (12)	G: 31.4 (32) R: 11.8 (12) SS: 12.7 (13)	JH: 4.9 (5) J: 15.7 (16) -H: 1.0 (1)	SH: 1.0 (1) +L: 20.6 (21) FC: 1.0 (1)	BL: 87.2 (89) NL: 11.8 (12) A: 1.0 (1)
DRDE	+B: 97.7 (212) -N: 2.3 (5)	G: 25.3 (56) R: 14.5 (32) SS: 8.6 (19)	+JH: 19.0 (42) J: 14.0 (31) H: 7.7 (17)	-SH: 1.8 (4) L: 8.1 (18) FC: 0.9 (2)	BL: 96.8 (214) NL: 2.3 (5) A: 0.9 (2)
MIQU	-B: 87.8 (202) +N: 12.2 (28)	G: 28.9 (69) R: 8.8 (21) +SS: 12.6 (30)	JH: 3.8 (9) J: 10.5 (25) +H: 13.4 (32)	SH: 12.1 (29) L: 4.6 (11) +FC: 5.4 (13)	-BL: 86.6 (206) +NL: 10.5 (25) A: 2.9 (7)
PERCH	$X^2_{(4 \times 2)} = 15.0$, $P = 0.0018$ B=all bamboo perches N=all non-bamboo perches				
ATTACK:	$X^2_{(4 \times 9)} = 25.7$, $P < 0.0001$ G=glean J=foot-powered jump away from perch SH=sally hover R=all reaches H=all hangs FC=flutter chase SS=sally strike JH=jump and hang on substrate L=lunge, includes hop and lunge along perch				
SUBSTRATE	$X^2_{(4 \times 4)} = 90.9$, $P = 0.003$ A=air BL=bamboo leaf, includes all bamboo substrates NL=non-bamboo leaf, includes all non-bamboo substrates except A				

Table 4.9. Means, standard deviations, and sample sizes for continuous variables in undergrowth guild. Discriminant Function Analyses was not significant for this guild

SPECIES	height (m)	distance to canopy (m)	canopy (m)**
<u>Synallaxis cabanisi</u>	0.7±0.5 (13)	6.4±1.6 (13)	7.2±1.8 (13)
<u>Myrmeciza goeldii</u>	0.4±0.6 (57)	16.1±7.4 (57)	16.4±7.4 (57)
<u>Pernostola lophotes</u>	0.5±0.7 (47)	14.2±9.9 (45)	15.2±10.0 (43)
SPECIES	perch size (cm)	perch angle	perch foliage density
<u>Synallaxis cabanisi</u>	3.1±2.4 (12)	4.2±10.0 (12)	3.5±0.8 (13)
<u>Myrmeciza goeldii</u>	3.7±2.5 (32)	14.4±27.8 (35)	2.3±0.9 (51)
<u>Pernostola lophotes</u>	3.4±3.9 (29)	10.7±22.8 (27)	2.7±1.5 (47)

Table 4.10. Differences in continuous variables of the undergrowth guild. Given variables have $P < 0.05$ in Scheffe's post-hoc tests in single factor ANOVAs.

	MYGO	PELO	SYCA
<u>Myrmeciza goeldii</u>	-		DC PFD CN
<u>Pernostola lophotes</u>		-	DC PFD CN
<u>Synallaxis cabanisi</u>			-

variable codes: DC= distance to canopy, CN = canopy, PFD = perch foliage density

Table 4.11. Percentages of categorical variables (with n observations) in the undergrowth guild. In contingency table analyses categories with $P < 0.01$ (see text) are given a "+" if residual was significant and positive (the species used that behavior significantly more often than expected) and a "-" if residual was negative (significantly less use than expected). Contingency table design, Chi-squared statistic, and P-value are given for each variable at bottom. *species not included in contingency table analyses.

SPECIES	PERCH	ATTACK	SUBSTRATE
MYGO	B: 45.6 (26) N: 15.8 (9) G: 38.6 (22)	-G: 42.1 (24) J: 19.3 (11) +HOP: 38.6 (22)	LL: 59.6 (34) L: 21.0 (12) A: 3.5 (2) S: 15.8 (9)
PELO	B: 44.9 (22) N: 16.3 (8) G: 38.8 (19)	+G: 77.6 (38) J: 14.3 (7) -HOP: 8.2 (4)	LL: 40.8 (20) L: 20.4 (10) A: 20.0 (1) S: 36.7 (18)
SYCA*	B: 71.4 (10) N: 28.6 (4) G: 0	G: 100 (14)	L: 78.6 (11) S: 21.4 (3)

PERCH $X^2_{(2 \times 3)} = 0.01, P = 0.99$

B=all bamboo perches

G=ground

N=all non-bamboo perches, except G

ATTACK: $X^2_{(2 \times 3)} = 16.0, P = 0.003$

G=glean, includes all stationary maneuvers

J=jump, includes jump (see above), sally-strike, jump-hang,

HOP=hop, foot-powered movements along substrate, includes lunge

SUBSTRATE $X^2_{(2 \times 4)} = 6.6, P = 0.087$

LL=leaf litter

A=air

L=leaf

(tables 4.12-4.14), a common foraging mode in these three Amazonia genera (Remsen and Parker 1984, K. V. Rosenberg 1990a, 1990b, 1993, Kratter and Parker in press).

The other three specialists were less tightly clustered, but all foraged from stem substrates (Figure 4.1). They shared the hang-up maneuver with the dead-leaf guild, along with live bamboo stems and non-bamboo stem substrates. A furnariid, Simoxenops ucayalae, and a woodpecker, Picumnus rufiventris (Picidae), were associated with the peck attack; a woodcreeper, Campylorhamphus trochilirostris (Dendrocolaptidae), was associated with the bamboo hole substrate and shared hang attacks with species in the dead-leaf guild (Figure 4.1). Celeus spectabilis, another woodpecker, clearly belongs here, although the small number of foraging observations prevented its inclusion in the multivariate analyses. All substrates in foraging observations of this species were bamboo stems, and 75% of the attack maneuvers were pecks. These four form the "stem guild" (tables 4.15-4.17). The loose clustering of this guild is reflected in its taxonomic and morphologic diversity: the two woodpeckers are differ dramatically in size (Table 4.1); the woodcreeper has an unusual long decurved bill, and the furnariid has a strange heavy bill, with a radically upturned mandible.

ANTBIRD GUILD - The four species in this guild were rather stereotyped behaviorally: they used diverse attacks (Table 4.8), used a high percentage of live bamboo leaf substrates (average 87.6%; Table 4.8), and foraged on small and high perches in dense vegetation (Table 4.6). Although on average they used a diversity of attack maneuvers, they differed significantly from all other guilds in only one maneuver - the jump-hang (Table 4.18). They also had significantly shorter sally distances than the flycatcher guild (Table 4.19).

Within the guild, D. devillei and Cercomacra manu used bamboo perches significantly more than expected; M. quixensis used them significantly less (Table 4.8). Drymophila devillei also used bamboo substrates more than expected and M. quixensis used non-bamboo substrates more often than expected. In attack,

Table 4.12. Means, standard deviations, and sample sizes for continuous variables in dead-leaf guild. Canonical loadings of variables on first two axes of discriminant function analysis (Figure 4.8) are given for each species. *variable not included in discriminant function analyses.

SPECIES	height (m)	distance to canopy (m)	canopy (m)*
<u>Anabazenops dorsalis</u>	5.5±2.3 (157)	18.9±8.7 (149)	24.5±9.1 (149)
<u>Automolus melanopezus</u>	5.6±2.2 (112)	18.6±7.2 (109)	24.2±7.3 (109)
<u>Myrmotherula iheringi</u>	5.2±1.9 (258)	18.4±9.7 (249)	23.6±8.5 (249)
<u>Myrmotherula ornata</u>	4.6±2.4 (216)	16.1±9.9 (215)	20.7±10.5 (211)
DFA1	0.233	0.027	
DFA2	-0.133	-0.131	

SPECIES	perch size (cm)	perch angle	perch foliage density
<u>Anabazenops dorsalis</u>	2.1±1.9 (124)	45.8±40.9 (107)	3.0±0.8 (154)
<u>Automolus melanopezus</u>	1.8±1.2 (82)	43.5±41.0 (71)	3.5±0.8 (112)
<u>Myrmotherula iheringi</u>	0.9±1.1 (228)	42.6±39.2 (199)	2.7±0.7 (256)
<u>Myrmotherula ornata</u>	0.8±2.8 (203)	37.6±38.4 (155)	3.1±0.8 (222)
DFA1	0.957	0.069	-0.194
DFA2	0.115	-0.044	0.940

Table 4.13. Differences in continuous variables of the dead-leaf guild. Given variables have $P < 0.05$ in Scheffe's post-hoc tests in single factor ANOVAs.

	ANDO	AUME	MYIH	MYOR
<u>Anabazenops dorsalis</u>	-	PS PFD	PS PFD	HT DC PS CN
<u>Automolus melanopezus</u>		-	PFD	HT PFD CN
<u>Myrmotherula iheringi</u>			-	HT PFD CN
<u>Myrmotherula ornata</u>				-

variable codes: HT=height, DC=distance to canopy, CN=Canopy, PS=perch size, PFD=perch foliage density

Table 4.14. Percentages of categorical variables (with n observations) in the dead-leaf guild. In contingency table analyses categories with $P < 0.01$ (see text) are given a "+" if residual was significant and positive (the species used that behavior significantly more often than expected) and a "-" if residual was negative (significantly less use than expected). Contingency table design, Chi-squared statistic, and P -value are given for each variable at bottom.

SPECIES	PERCH	ATTACK		SUBSTRATE
<u>Anabazenops dorsalis</u>	B: 63.4 (97) N: 20.3 (31) DL: 8.5 (13) +BNO: 7.8 (12)	HSW: 32.7 (51) -HD: 14.1 (22) +G: 27.6 (43) +HUD: 7.0 (11)	+HU: 12.2 (19) -R: 3.8 (6) PRY: 1.9 (3) FC: 0.6 (1)	-BDL: 26.0 (41) +BSP: 22.2 (35) +B: 12.7 (20) NDL: 34.2 (54) N: 3.8 (6) BL: 1.3 (2)
<u>Automolus melanopeus</u>	-B: 59.3 (67) N: 27.4 (31) DL: 9.7 (11) BNO: 3.5 (4)	HSW: 29.3 (34) -HD: 7.8 (9) G: 25.9 (30) HUD: 5.2 (6)	+HU: 17.2 (20) R: 11.2 (13) PRY: 1.7 (2) FC: 1.7 (2)	-BDL: 35.6 (41) BSP: 6.1 (7) -B: 0.9 (1) +NDL: 53.9 (62) N: 0 BL: 3.5 (4)
<u>Myrmotherula iheringi</u>	+B: 75.2 (179) N: 18.5 (44) -DL: 3.4 (8) BNO: 2.9 (7)	HSW: 24.3 (64) +HD: 36.1 (95) G: 18.2 (48) -HUD: 0.8 (2)	-HU: 1.9 (5) R: 14.1 (37) PRY: 0 FC: 4.6 (12)	BDL: 47.5 (124) BSP: 4.6 (12) -B: 16.1 (42) -NDL: 21.1 (55) +N: 4.6 (12) +BL: 6.1 (16)
<u>Myrmotherula ornata</u>	B: 73.2 (150) N: 19.5 (40) DL: 6.8 (14) -BNO: 0.5 (1)	HSW: 27.0 (62) +HD: 32.2 (74) -G: 14.4 (33) HUD: 0.9 (2)	-HU: 3.5 (8) +R: 17.8 (41) PRY: 0.4 (1) FC: 3.9 (9)	+BDL: 69.0 (158) -BSP: 1.3 (3) -B: 0 NDL: 28.0 (64) -N: 0 BL: 1.8 (4)

PERCH $X^2_{(4 \times 2)} = 27.9, P = 0.001$

B = bamboo stem

N = non-bamboo stem (live or dead)

DL = dead leaf
sheaths

BNO = bamboo node, including spines and

ATTACK: $X^2_{(4 \times 8)} = 134.1, P < 0.0001$

G = glean, includes all stationary maneuvers except reaches and hangs

SS = sally-strike, includes all sallies, flutter-chases, jumps, and lunges

R = all reaches

HUD = hang-upside-down

HU = hang-up

HD = hang-down

PRY = pry, includes rummage, flake, tear

SUBSTRATE $X^2_{(4 \times 6)} = 204.8, P < 0.0001$

BL = live bamboo leaf

BDL = dead bamboo leaf

NDL = dead non-bamboo leaf

BSP = bamboo spine, includes spines, sheaths

B = bamboo stem, includes all bamboo stem substrates except BSP

N = non-bamboo stem

Table 4.15. Means, standard deviations , and sample sizes for continuous variables in stem guild. Canonical loadings of variables on first two axes of discriminant function analysis (Figure 4.10) are given for each species. *variable or species not included in discriminant function analyses.

SPECIES	height (m)	distance to canopy (m)	canopy (m)**	perch size (cm)
<u>Campylorhamphus trochilirostris</u>	5.3±2.8 (64)	15.2±9.0 (61)	20.4±10.1 (61)	8.3±8.2 (61)
* <u>Celeus spectabilis</u>	2.9±1.7 (12)	16.1±10.0 (12)	19.0±9.6 (12)	4.8±1.3 (12)
<u>Picumnus rufiventris</u>	1.2±0.6 (23)	14.0±10.7 (22)	15.2±10.7 (22)	3.6±2.6 (23)
<u>Simoxenops ucayalae</u>	2.8±2.2 (59)	17.6±9.3 (59)	20.4±10.1 (59)	3.2±1.8 (56)
	DFA1	0.735	-0.169	0.564
	DFA2	-0.603	-0.311	0.181

SPECIES	substrate size (cm)	perch angle	perch foliage density
<u>Campylorhamphus trochilirostris</u>	6.34±4.23 (35)	63.6±36.2 (56)	2.5±0.8 (62)
* <u>Celeus spectabilis</u>	5±1.18 (11)	53.3±34.6 (12)	2.7±0.5 (12)
<u>Picumnus rufiventris</u>	3.43±2.70 (21)	61.7±35.4 (21)	3.0±0.6 (22)
<u>Simoxenops ucayalae</u>	4.36±7.84 (46)	37.6±33.8 (53)	2.8±0.9 (58)
	DFA1	0.354	-0.340
	DFA2	0.783	0.220

Table 4.16. Differences in continuous variables of the stem guild. Given variables have $P < 0.05$ in Scheffe's post-hoc tests in single factor ANOVAs.

	CATR	CESP	PIRU	SIUC
<u>Campylorhamphus trochilirostris</u>	-	HT	HT PS	HT PS PA
<u>Celeus spectabilis</u>		-		
<u>Picumnus rufiventris</u>			-	
<u>Simoxenops ucayalae</u>				-

variable codes: HT=height, PS=perch size, PA=perch angle

Table 4.17. Percentages of categorical variables (with n observations) in the stem guild. In contingency table analyses categories with $P < 0.01$ (see text) are given a "+" if residual was significant and positive (the species used that behavior significantly more often than expected) and a "-" if residual was negative (significantly less use than expected). Contingency table design, Chi-squared statistic, and P-value are given for each variable at bottom. *species not included in contingency table analyses.

SPECIES	PERCH	ATTACK	SUBSTRATE
CATR	-B: 55.4 (36) BD: 18.5 (12) +N: 26.2 (17)	-PECK: 0 -PRY: 1.5 (1) H: 7.7 (5) +P: 90.8 (59)	-B: 8.1 (5) N: 25.8 (16) BNO: 19.4 (12) +BHO: 46.8 (29)
CESP*	B: 75 (9) BD: 3 (25) N: 0	PECK: 75 (9) PRY: 0 H: 0 P: 25 (3)	B: 72.3 (8) N: 0 BNO: 0 BHO: 27.4 (3)
PIRU	B: 47.8 (11) BD: 30.4 (7) N: 17.4 (4)	+PECK: 78.3 (18) PRY: 0 H: 0 -P: 21.7 (5)	+B: 69.6 (16) N: 26.1 (6) BNO: 4.4 (1) -BHO: 0
SIUC	B: 47.5 (28) +BD: 45.8 (27) -N: 6.8 (1)	PECK: 32.2 (19) +PRY: 25.4 (15) H: 15.2 (9) -P: 27.1 (16)	+B: 62.1 (36) -N: 5.2 (3) BNO: 8.6 (5) BHO: 24.1 (14)

PERCH	$X^2_{(4 \times 3)} = 14.6$, $P = 0.005$ B=live bamboo perches D=dead bamboo perches N=all non-bamboo perches
ATTACK:	$X^2_{(4 \times 4)} = 95.3$, $P < 0.0001$ PECK=peck, PRY=pry, includes any maneuver that used bill to manipulate substrate except peck, e.g., pry, pull, plow, rummage H=all hangs except hang-up P=probe, includes all hang up maneuvers, except PRY or PECK, and glean and reach maneuvers
SUBSTRATE	$X^2_{(4 \times 4)} = 54.0$, $P < 0.0001$ N=all non-bamboo stems B=bamboo stem internodes, except BHO BHO=holes in bamboo stem internodes BNO=bamboo stem nodes, includes sheaths and spines

Table 4.18. Significant differences between guilds in attack and substrate. The frequencies (averaged over all species in the guild) for attack (above diagonal) and substrate (below diagonal) variables are compared using post-hoc Scheffe's tests in single factor ANOVAs. $P < 0.05$ for all categories listed.

GUILD	dead-leaf	flycatcher	antbird	stem	undergrowth
dead-leaf	-	R G HD HS SS	HD HS JH SS L J	R HD HS PRY	G HD HS L J
flycatcher	BL DL BDL	-	R G JH SS L J	G PRY SS L	R G SS L J
antbird	BL DL BDL		-	R J PRY JH SS	JH
stem	BD DL B N BDL BHO	BL BD B N BHO	BL BD B N BHO	-	R G PRY L J
undergrowth	DL B BDL LL	BL B LL	BL LL	BD N BHO LL	-
SUBSTRATES		ATTACKS			
BL=bamboo live-leaf		G=glean			
BDL=bamboo dead-leaf		HD=hang-down			
B=bamboo green-stem		HS=hang sideways			
BD=bamboo dead-stem		J=jump			
BHO=bamboo stem-hole		H=jump-hang			
DL=non-bamboo dead-leaf		L=lunge			
LL=leaf-litter		PRY=pry			
N=non-bamboo stem (live or dead)		R=reach			
		SS=sally-strike			

Table 4.19. Significant differences between guilds in continuous variables. Variable compared using Post-hoc Scheffe's tests in ANOVAs. Variables below the diagonal are greater for the row guild; those above the diagonal are greater for the column guild. $P < 0.05$ for all categories listed.

GUILD	dead-leaf			flycatcher			antbird		stem		undergrowth			
dead-leaf	-			PA	PD		PA		HT	CN	HT	DC	CN	PA
flycatcher	DC	CN	PD	-			SD		HT		HT	CN		
antbird	DC	PD		PD			-		HT	PD	HT	CN	PD	
stem	PS	PA		DC	PS	PA	PS	PA	-		HT	CN		
undergrowth	PS			PS			PS		PA		-			

variables: HT=Height; DC=Distance to Canopy; CN=Canopy Height; PS=Perch Size; PA=Perch Angle; SD=Sally Distance

Cymbilaimus sanctaemariae and Cercomacra manu lunged significantly more often than expected; Cercomacra manu gleaned significantly more often. Drymophila devillei used jump-hang more often than expected. Microrhopias quixensis used active flight maneuvers (flutter-chase and sally-hover) more often than expected and avoided the lunge and jump-hang maneuvers. All variation in the MCA (Figure 4.2) was confined to CA1 (see Greenacre [1984] for calculations of principal inertias). Two species pairs were isolated from one another (Figure 4.1): D. devillei and Cercomacra manu clustered with two active, foot-powered, attack maneuvers (lunge and jump-hang); Cymbilaimus sanctaemariae and M. quixensis clustered with non-bamboo perches and substrates (leaves and air) and two wing-powered attacks (sally-strike and flutter-chase). The sharing of attack maneuvers among species in this guild is reflected in the clumping of most attack categories between the specialists. Jump-hang was exceptional, associated mainly with D. devillei: (Figure 4.2). Likewise, the bamboo substrate and bamboo perch were used frequently by all four specialists, but non-bamboo substrates and perches were associated M. quixensis (Figure 4.2).

All continuous variables differed significantly among the four species. Because DFA cannot include observations with missing values, two separate DFAs were needed for antbirds: the first, by including sally distance and sally angle variables, was able to include only observations (total n=174) with the sally, flutter-chase, lunge, jump-hang, and jump attack maneuvers; the second analysis, excluding these variables, was able to include many more observations (total n=507). The more inclusive analysis (Figure 4.3) showed very high overlap among the four species and had the highest rate of misclassification of any guild (Table 4.20). Although Cercomacra manu showed the least dispersion on either of the first two axes (resulting from its small sample size?), it had the greatest percentage of correct classifications. Cymbilaimus sanctaemariae showed the most dispersion (Figure 4.3), especially positively on DFA1, which was associated with perch foliage density and perch size (Table 4.6). The analysis that

Figure 4.2. Multiple Correspondence Analysis of antbird guild. All variation was accounted for by the first axis (CA1).

Figure 4.3. Discriminant Function Analysis of antbird guild. Wilks' $\lambda = 0.731$; $P < 0.0001$. Points represent individual observations and all points for a species are enclosed in a polygon (except extreme outliers). Variables with the greatest loadings (positive or negative; see Table 4.6) are shown where at a maximum, e.g., an observation with a large perch size would tend to have a high positive score on DFA1 and a low negative score on DFA2, and would be in the bottom right corner.

Table 4.20. Tabulated classification results of Discriminant Function Analyses (by guild). Number of correct classifications is bold-faced. DFA for the undergrowth guild was not significant.

ANTBIRD GUILD					
observed species	predicted species				% correct
	CYSA	CEMA	DRDE	MIQU	
all attacks					
<u>Cymbilaimus sanctaemariae</u>	43	8	11	15	56
<u>Cercomacra manu</u>	17	33	12	12	45
<u>Drymophila devillei</u>	38	17	76	45	43
<u>Microrhopias quixensis</u>	22	14	62	81	45
total					233/507=46.0%
active attack maneuvers only					
observed species	predicted species				% correct
	CYSA	CEMA	DRDE	MIQU	
all attacks	13	3	3	1	65
<u>Cymbilaimus sanctaemariae</u>					
<u>Cercomacra manu</u>	4	15	8	6	46
<u>Drymophila devillei</u>	9	4	34	13	40
<u>Microrhopias quixensis</u>	10	5	17	29	48
total					93/174= 52.3%
FLYCATCHER GUILD					
observed species	predicted species				% correct
	HEFL	POAL	RAME	LAEU	
<u>Hemitriccus flammulatus</u>	37	16	3	5	61
<u>Poecilatriccus albifacies</u>	27	76	10	3	66
<u>Ramphotrigon megacephala</u>	8	4	27	12	59
<u>Lathrotriccus euleri</u>	7	12	12	42	53
total					182/300=60.7%
DEAD-LEAF GUILD					
observed species	predicted species				% correct
	ANDO	AUME	MYIH	MYO R	
<u>Anabazenops dorsalis</u>	38	23	17	12	42.2
<u>Automolus melanopezus</u>	6	28	11	10	50.9
<u>Myrmotherula iheringi</u>	11	30	83	47	48.5
<u>Myrmotherula ornata</u>	4	32	30	68	50.7
total					227/450=50.4%
STEM GUILD					
observed species	predicted species			% correct	
	CATR	PIRU	SIUC		
<u>Campylorhamphus trochilirostris</u>	31	10	5	66.0	
<u>Picumnus rufiventris</u>	0	11	17	57.9	
<u>Simoxenops ucayalae</u>	5	17	27	55.1	
total				69/115=60%	

included only active maneuvers (Figure 4.4) showed less overlap than the more inclusive analysis. *Microhoppia quixensis* and *Cymbilaimus sanctaemariae* in particular showed areas on both axes where distributed uniquely (Figure 4.4). *Cymbilaimus sanctaemariae* was associated with denser and larger perches, and *M. quixensis* was associated with larger perches and longer attack maneuvers (Figure 4.4, Table 4.6). *Cercomacra manu* again showed the greatest percentage of correct classifications (Table 4.20).

FLYCATCHER GUILD -The flycatcher guild was most similar to the antbird guild; these two guilds differed significantly only in perch density and sally distance (antbirds greater in former and less in latter) among continuous variables (Table 4.19) and showed no significant differences in their use of substrates (mainly bamboo leaves) (Table 4.18). However, the flycatchers were very stereotyped in attack: their use of the sallying attacks (sally-strike and sally-hover) exceeded 98% for all species (Table 4.5), which was the only variable (continuous or categorical) that differed significantly between the flycatcher guild and all others (tables 4.18-4.19).

Within the guild, the five species were very similar (tables 4.3-4.5): in addition to their use of sally-strike attack, they all used bamboo perches over 80% of the time and bamboo leaf substrates over 70% of the time. Differences among the four species included in the MCA analysis thus reflect only behaviors used rarely. Not surprisingly, all variation in the MCA was accounted for by CA1. More interestingly, the two todotyrrants differed the most (Figure 4.5). The relatively high score of *H. flammulatus* resulted mostly from its infrequent but relatively high use of non-bamboo perches (20%) and non-bamboo leaf substrates (22%), including dead leaves. *Lathrotriccus euleri* took insects from the air more often than expected, and *R. megacephala* sally-hovered more often than the others (Table 4.5).

In contrast to their similarity in the categorical variable analyses, species in the flycatcher guild showed a higher percentage of correctly classified observations (60.7)

Figure 4.4. Discriminant Function Analysis of antbird guild, including only active attack maneuvers (see text). Wilks' $\lambda=0.643$; $P<0.0001$. See Figure 4.3 for more complete explanation of figure.

Figure 4.5. Multiple Correspondence Analysis of flycatcher guild. All variation was accounted for by the first axis (CA1).

in DFAs than any other guild (Table 4.20), indicating that the five species had relatively distinct foraging behaviors in these variables. The two larger flycatchers (R. megacephala and L. euleri) shared a fairly large area on DFA1 (Figure 4.6), associated with longer sallies and larger perches (Table 4.3), where they did not overlap with the tody-tyrants. The tody-tyrants also shared a large area of unique distribution (Figure 4.6, positive on DFA1) associated with greater perch and substrate density. Both the tody-tyrant pair and the L. euleri/R. megacephala pair were somewhat separated along DFA2 (Figure 4.6). This axis was associated mainly with foraging height and perch size and density (R. megacephala and P. albifacies higher and on more dense and smaller perches than L. euleri and H. flammulatus, respectively; Table 4.3). Misclassifications were more common within both the pair of tody -tyrants and the L. euleri /R. megacephala pair than between species outside these pairs (Table 4.20).

DEAD-LEAF GUILD - Not surprisingly, the four species in this guild searched dead-leaf substrates (both bamboo and non-bamboo) significantly more than all other guilds. Dead-leaf substrates comprised at least 60% of foraging attempts of all four and made up over 95% of the substrates searched by Myrmotherula ornata and Automolus melanopezus (Table 4.14). The other two species, Myrmotherula iheringi and Anabazenops dorsalis, searched stem substrates, including spines and nodes, in the bulk of their other foraging attempts (Table 4.14). The guild used two hang attack maneuvers (hang-down and hang-sideways) significantly more than all other guilds (Table 4.18). This guild foraged the greatest distance below the canopy and at sites with the highest canopy (Table 4.19), reflecting their at least partial dependence on canopy trees above the bamboo from which dead leaves fall and get caught in the bamboo layer.

Within the guild, attack maneuvers separated the antwrens (Myrmotherula spp.) from the foliage gleaners (Anabazenops dorsalis and Automolus melanopezus) (Table 4.14). Both antwrens used significantly more hang-down attacks than expected and

Figure 4.6. Discriminant Function Analysis of flycatcher guild. Wilks' $\lambda=0.404$, $P<0.0001$. See Figure 4.3 for more complete explanation of figure.

foliage-gleaners used significantly more hang-up maneuvers (Table 4.14).

Anabazenops dorsalis also used hang-upside-down and glean maneuvers more than expected. Each of the four species showed a unique pattern of substrate use (Table 4.14). Anabazenops dorsalis and M. iheringi showed preferences for stem substrates. Anabazenops dorsalis used bamboo spines (and perched on them). M. iheringi used bamboo and non-bamboo stems (along with live leaves) significantly more often than expected. The other two species showed more typical dead-leaf specialization (see K. V. Rosenberg 1990a, 1990b, 1993): Automolus melanopezus used dead non-bamboo leaves and M. ornata used dead bamboo leaves significantly more than expected (Table 4.14).

Regardless of the differences in substrate use between the related pair members, the MCA still grouped the two foliage-gleaners and two antwrens with one another (Figure 4.7). The two antwrens grouped together tightly and were associated with the flutter-chase, reach, and hang-down attack maneuvers, dead and live (infrequent) bamboo leaf substrates, and bamboo perches. They were quite separate from the two foliage-gleaners, which did not group tightly. Hang-up, hang-upside-down, and glean attack maneuvers, and non-bamboo perches were associated with both foliage-gleaners. Use of the bamboo spine and bamboo node substrates was nearly restricted to A. dorsalis (Table 4.14).

The two foliage-gleaners had greater dispersion along DFA1 than the antwrens (Figure 4.8), associated mainly with the greater range in perch sizes in the former (Table 4.12). The foliage-gleaners also showed somewhat greater dispersion on DFA2, which was associated with foraging height and distance to the canopy. In general, overlap was high among all four species in the DFA (Figure 4.8), and all four species had relatively low rates (ca. 50%) of correct classifications (Table 4.20).

STEM GUILD - The four members of this guild foraged significantly lower than all but the undergrowth guild (Table 4.19). They also used more vertical perches

Figure 4.7. Multiple Correspondence Analysis of dead-leaf guild. All variation was accounted for by the first two axes (CA1 and CA2).

Figure 4.8. Discriminant Function Analysis of dead-leaf guild. Wilks' $\lambda = 0.655$, $P < 0.0001$. See Figure 4.3 for more complete explanation of figure.

than all guilds, and larger perches than all but the undergrowth guild (Table 4.19). Not surprisingly, they averaged significantly greater use of all stem substrates, except bamboo stems, which were shared with the undergrowth guild (Table 4.18).

This guild showed the most unusual foraging behaviors. Campylorhamphus trochilirostris often used its long curved bill to probe between the large clasping sheath and the stem of bamboo, and also used its bill to probe into holes within the internodes of bamboo stems. It differed significantly from the other guild members in its increased use of the probe attack and its use of bamboo hole substrates (Table 4.14). Unlike the other three stem searchers, it never used the peck attack. Picumnus rufiventris and Celeus spectabilis used typical woodpecker pecking attacks. Simoxenops ucayalae often used its upcurved bill to split open bamboo stems using a prying motion (see also Parker 1982); its use of bamboo stem substrates and the pry attack maneuver was significantly greater than all others in the guild. In the MCA, Campylorhamphus trochilirostris was distinct from the P. rufiventris and S. ucayalae (Figure 4.9). This woodcreeper was most closely associated with the probe attack and non-bamboo perches and substrates. Simoxenops ucayalae and P. rufiventris grouped together and were most closely associated with the peck and pry (S. ucayalae only) attack maneuvers, live and dead bamboo stem substrates, and dead bamboo perches (S. ucayalae only).

In the DFA (Figure 4.10), P. rufiventris and S. ucayalae showed high overlap on DFA1 but were quite distinct from Campylorhamphus trochilirostris. The latter species, which had the highest rate of correct classification among all specialists (66%: Table 4.20), used generally larger perches at greater heights than the other two species (Table 4.12). Simoxenops ucayalae showed much greater dispersion negatively along DFA2, foraging at greater heights on more horizontal stems than others in the guild (Figure 4.10).

Figure 4.10. Discriminant Function Analysis of stem guild. Wilks' $\lambda=0.651$; $P<0.0001$ See Figure 4.3 for more complete explanation of figure.

UNDERGROWTH GUILD - In addition to the lower foraging heights, the three species in the undergrowth guild used the leaf litter substrate significantly more than all other guilds (Table 4.18), even though one species (Synallaxis cabanisi) did not use this substrate at all (Table 4.11).

Within the guild, frequency of perch or substrate categories did not differ significantly between the two species included in the analysis (Myrmeciza goeldii and Pernostola lophotes). They differed somewhat in attack: P. lophotes used significantly more near-perch maneuvers (gleans), and M. goeldii used significantly more hop maneuvers (Table 4.11). The MCA (Figure 4.11) split the two antbirds, associating M. goeldii with the hop attack, leaf litter substrate, and non-bamboo stem perches, and P. lophotes with most other attacks, perches, and substrates. Although P. lophotes often foraged on the ground, it rarely used the leaf litter substrates and hop attacks preferred by M. goeldii; instead it used stationary gleans or sally-strikes to low stems or leaves (Table 4.11). The two species did not differ significantly in the DFA (Wilk's Lambda = 0.978; $P=0.75$).

DISCUSSION

COMPARISON OF BAMBOO WITH OTHER HABITATS - Although species in bamboo thickets are completely different from those in other habitats in southeastern Peru (Chapter 2), the 19 bamboo specialists (excluding the non-specialist Lathrotriccus euleri) are ecologically similar to the avifauna found in nearby floodplain forests. These forests, such as at Coca Cashu Biological Station in Manu National Park (Terborgh et al. 1990) or at the Explorer's Inn Reserve (Foster et al. 1994), have at least one behaviorally similar representative for 11 of the 17 genera of bamboo specialists (Table 4.21). Additionally, Nasica longirostris, another long-billed woodcreeper, has been suggested as an ecological (but not taxonomic) replacement in varzea forests for Campylorhamphus trochilirostris (J. V. Remsen in Hilty and Brown 1986). Nasica also occurs in floodplain forests along the Río Tambopata (Foster et al. 1994; pers. obs.).

Figure 4.11. Multiple Correspondence Analysis of the undergrowth guild. All variation was accounted for by the first two axes (CA1 and CA2).

Table 4.21. Ecological equivalents between bamboo thickets, floodplain forests, and early successional vegetation. Habitat associations from Terborgh et al. (1990), Foster et al. (1994), Ridgely and Tudor (1994), and pers. obs.

BAMBOO SPECIALIST	FLOODPLAIN FOREST	EARLY SUCCESSIONAL
<u>Anabazenops dorsalis</u>	-	-
<u>Automolus melanopezus</u>	<u>A. infuscatus</u> <u>A. ochrolaemus</u>	<u>A. rufipileatus</u>
<u>Campylorhamphus trochilirostris</u>	<u>Nasica longirostris?</u>	-
<u>Celeus spectabilis</u>	<u>C. torquatus</u> <u>C. elegans</u>	-
<u>Cercomacra manu</u>	<u>C. cinerascens</u>	-
<u>Cymbilaimus sanctaemariae</u>	<u>C. lineatus</u>	-
<u>Dryophila devillei</u>	-	-
<u>Hemitriccus flammulatus</u>	<u>H. zosterops</u>	<u>H. iohannis</u> <u>H. striaticollis</u>
<u>Microhoppas quixensis</u>	-	-
<u>Myrmeciza goeldii</u>	<u>M. fortis</u>	-
<u>Myrmotherula iheringi</u>	<u>M. longipennis</u>	-
<u>Myrmotherula ornata</u>	<u>M. leucophthalma</u>	-
<u>Percnostola lophotes</u>	-	-
<u>Picumnus rufiventris</u>	<u>P. borbae</u>	-
<u>Poecilatriccus albifacies</u>	-	<u>Todirostrum latirostre</u>
<u>Ramphotrigon megacephala</u>	<u>R. ruficauda</u>	-
<u>Ramphotrigon fuscicauda</u>	<u>R. ruficauda</u>	-
<u>Simoxenops ucayalae</u>	-	-
<u>Synallaxis cabanisi</u>	<u>S. rutilans</u>	<u>S. guianensis</u> <u>S. albigularis</u>

Interestingly, all twelve of these generic replacements are widespread Amazonian taxa (Meyer de Schauensee 1966; Ridgely and Tudor 1994). In contrast, five of the six species without ecological replacements (Table 4.21, except *Microrhopias quixensis*) represent genera of restricted distribution in Amazonia (*P. lophotes* is probably not closely related to other *Pernostola*; Parker 1982, Ridgely and Tudor 1994). These five species include at least one member from each of the five bamboo specialist guilds. Of these, *Anabazenops dorsalis* and *Simoxenops ucayalae* show distinct behavioral adaptations for foraging on bamboo (see above, Kratter and Parker, in press); *Drymophila devillei* and *Poecilotriccus albifacies* show strikingly high preferences (above 96% of total for each) for bamboo substrates; and *Pernostola lophotes* is a rather generalized forager without an obvious replacement in forest habitats.

No bamboo specialist guild appears to be more diverse than similar guilds in floodplain forests. A possible exception are the three long-tailed, arboreal antbirds (*D. devillei*, *Cercomacra manu*, and *Microrhopias quixensis*). In floodplain forests at Coca Cashu (Terborgh et al. 1990) and at the Explorer's Inn Reserve (Foster et al. 1994), only two other arboreal, long-tailed antbirds are found: *Cercomacra cinerascens* occurs in vine-tangles in the subcanopy, and *Terenura humeralis* is found with mixed-species canopy flocks, which are largely absent in bamboo habitats (pers. obs.). Karr (1980) stated that among insectivorous understory birds, gleaners usually outnumber salliers; in this study, salliers (the five species in the flycatcher guild) have slightly higher diversity than the gleaners (the four species in the antbird guild). Bamboo, however, does not represent true understory: it occupies a distinct stratum between the understory and the subcanopy (Chapter 3). In addition, salliers (mostly flycatchers) are usually relatively more diverse in early successional habitats than in mature forested habitats (Robinson and Terborgh 1990). Bamboo thickets are often considered an early successional habitat.

One guild is particularly noteworthy in its near-absence among bamboo specialists. The bark-searching woodcreeper guild (*Dendrocolaptidae*), which is very diverse in nearby floodplain forests (up to 12 species; Foster et al. 1994), is represented by a sole species in bamboo. In addition, this bamboo specialist, *Campylorhamphus trochilirostris*, is morphologically different from other woodcreepers in Amazonia; its long, curved bill is often used to probe deeply into holes in bamboo stems (pers. obs.), in which a rich and unique arthropod and vertebrate prey base can be found (Louton et al., in press). The lack of textured surfaces on the slick bamboo stems may inhibit the establishment of the typical arthropod prey base found on trunks and branches, which consists of arthropods that use cracks and crevices for refuge. More "normally" foraging woodcreepers, which tend to have similar diets (Chapman and Rosenberg 1991), probably rely heavily on this prey base.

The ecological similarity is much less evident between the avifauna of bamboo thickets and those in nearby early successional habitats, such as cane (*Gynerium sagittatum*) thickets. Only three specialists are replaced by ecologically similar congeners in this habitat (Table 4.21); additionally, the tody-tyrant *Todirostrum latirostre*, restricted to early successional habitats on the Tambopata (Foster et al. 1994; pers. obs.), may replace the bamboo specialist *Poecilotriccus albifacies*. The antbird, stem, and dead-leaf guilds appear to be much better represented in bamboo thickets than in early successional habitats.

HABITAT VS. SUBSTRATE SPECIALIZATION - Increased specialization is one means by which more species in a community can fit along a resource gradient, that is, more species can occur syntopically and diversity can increase. Bamboo offers two different, but not mutually exclusive, opportunities for species to specialize. First, bamboo thickets are a structurally unique habitat (Chapter 3). Second, individual *Guadua* bamboo plants offer substrates (long narrow leaves, smooth stems, spines, large clasping sheaths) on which a species may specialize. All bamboo specialists, by

definition, are habitat specialists. The main question is, therefore, whether further specialization, on substrates or prey bases unavailable in other habitats, is occurring.

Specialization along habitat gradients is a prevalent mode of increasing avifaunal diversity in western Amazonia (e.g., from terra firme to floodplain to early successional forest: see Terborgh 1985, Robinson and Terborgh 1995), where high species turnover among habitats is found (= beta diversity: see Cody 1975). Congeneric species replacements among these structurally different habitats are common in southwestern Amazonian forests (e.g., in Hemitriccus [Fitzpatrick 1976]; Thamnomanes [Schulenberg 1983]; Myrmotherula [K. V. Rosenberg 1990a]; Pipra: [pers. obs.]; see Robinson and Terborgh 1995). Robinson and Terborgh (1995) show that members are interspecifically territorial in many of these species pairs. They attribute this territoriality to interspecific competition for limiting resources.

If this competitive hypothesis is applied to habitat selection by bamboo specialists, one may expect to find patterns common to avifaunal turnover between other structurally different habitats in western Amazonia (e.g., terra firme and floodplain forests). The commonest pattern is for ecologically similar and taxonomically related species to be found in each habitat, with little or no morphological differences between the species; foraging behavior can be very similar (e.g., in Myrmotherula: K. V. Rosenberg 1990b). Therefore, if habitat selection by bamboo specialists is only mediated by competition, and substrate specialization is not important, then bamboo specialists would be expected to show neither an exaggerated preference for bamboo substrates within the thickets, nor morphological specialization, relative to related species. Species replacements between bamboo and non-bamboo habitats should be common.

If specialization on bamboo substrates is occurring, then more exclusive use of bamboo substrates would be expected among bamboo specialists; more morphological specialization may also be expected if this is the case. Foraging specialization is

hypothesized to have deeper evolutionary origins than habitat selection (Diamond 1986). In a phylogenetic analysis, Richman and Price (1992) showed that within a closely related group of species (all in the genus Phylloscopus, Sylviidae) the more closely related species tended to sort by habitat and the more distantly related species occurred syntopically, but sorted by foraging behavior. If this pattern can be applied generally, then in this case substrate specialists should show indications of a longer evolution of bamboo specialization, such as morphological adaptations and shared bamboo specialization among sister taxa, than strict habitat specialists. Substrate specialization may be most expected in the stem guild, where an apparently unique prey base of arthropods and a few vertebrates can be found in the hollow bamboo stems of Guadua (Louton et al., in press). I will look at the possibilities for each type of specialization across both guilds and species.

Substrate specialization shows pronounced development among few bamboo specialists. Only one specialist, Simoxenops ucayalae in the stem guild, shows morphological and behavioral adaptations that may be related to foraging on bamboo (see Results). However, the presumed sister taxon (S. striatus), which shares the unusual bill, does not appear to be a bamboo specialist (Parker et al. 1992). Three other specialists appear to have a phylogenetic history of bamboo specialization (Anabazenops dorsalis, Drymophila devillei, and Hemitriccus flammulatus: see Chapter 2). Drymophila devillei also shows very high preference for bamboo substrates (Table 4.22). Anabazenops dorsalis shares unusual foraging behavior and substrate choice with its sister species A. fuscus in southeastern Brazil (Kratte and Parker, in press). Although bamboo specialization is shared among H. flammulatus and its two presumed sister taxa (H. obsoletus and H. diops of southeastern Brazil: Ridgely and Tudor 1994), flammulatus does not show as high preference for bamboo substrates as other flycatchers (Table 4.22).

Table 4.22. Degree of specialization and percent bamboo substrate use by guild and species.

SPECIES	GUILD	DEGREE OF SPECIALIZATION	% BAMBOO SUBSTRATES
<u>Cercomacra manu</u>	antbird	obligate	0.959
<u>Drymophila devillei</u>	antbird	obligate	0.968
<u>Microrhopias quixensis</u>	antbird	facultative	0.874
<u>Cymbilaimus sanctaemariae</u>	antbird	near-obligate	0.863
<u>Hemitriccus flammulatus</u>	flycatcher	obligate	0.778
<u>Poecilatriccus albifacies</u>	flycatcher	obligate	0.983
<u>Ramphotrigon megacephala</u>	flycatcher	obligate	0.894
<u>*Ramphotrigon fuscicauda</u>	flycatcher	near-obligate	0.889
<u>Lathrotriccus eulerei</u>	flycatcher	facultative	0.817
<u>Campylorhamphus trochilirostris</u>	stem	facultative	0.742
<u>Celeus spectabilis</u>	stem	obligate	1.000
<u>Picumnus rufiventris</u>	stem	facultative	0.783
<u>Simoxenops ucayalae</u>	stem	near-obligate	0.948
<u>Anabazenops dorsalis</u>	dead-leaf	near-obligate	0.620
<u>Automolus melanopezus</u>	dead-leaf	near-obligate	0.452
<u>Myrmotherula ornata</u>	dead-leaf	facultative	0.707
<u>Myrmotherula iheringi</u>	dead-leaf	facultative	0.678
<u>Myrmeciza goeldii</u>	undergrowth	near-obligate	0.158
<u>Pernostola lophotes</u>	undergrowth	near-obligate	0.388
<u>Synallaxis cabanisi</u>	undergrowth	facultative	0.857

Seven specialists show high preferences for bamboo substrates, but do not appear to show phylogenetic, behavioral, or morphological characters associated with foraging from bamboo substrates. Three of these species show very high preferences (above 95% of total, Table 4.22) for bamboo substrates, indicating substrate specialization. Of these, Poecilotriccus albifacies lacks sympatric congeners in other habitats, Cercomacra manu is replaced in vine tangles in floodplain forests by a congener (C. cinerascens; Terborgh and Weske 1969), and Celeus spectabilis is replaced in floodplain and terra firme forest by two morphologically similar congeners (C. torquatus and C. elegans). The other four specialists in this group (Synallaxis cabanisi, Cymbilaimus sanctaemariae, Ramphotrigon megacephala, and R. fuscicauda) also have congeners in nearby non-bamboo habitats, but show somewhat less preferences for bamboo substrates (85-90%, Table 4.22).

Although Lathrotriccus euleri and Microhapias quixensis show high preferences for bamboo substrates (above 85% for each, Table 4.22) neither is restricted to bamboo thickets throughout its distribution (see Chapter 2, below). Although bamboo substrate specialization for these two species is not likely, different populations of some tropical insect species have shown localized substrate specialization (Fox and Morrow 1981).

The other seven bamboo specialists show relatively low preferences for bamboo substrates (less than 80% of total); these species may be selecting bamboo thickets only because of habitat structure, not because of their specialization on unique substrates or prey bases therein. Four of these species (Picumnus rufiventris, Automolus melanopezus, Myrmotherula ornata, Myrmeciza goeldii) have closely related and behaviorally similar congeners in nearby non-bamboo habitats (Table 4.21); Myrmotherula iheringi also has behaviorally similar (but not closely related? [see Whitney 1994]) congeners in nearby forests. The final two specialists

(*Campylorhamphus trochilirostris*, *Percnostola lophotes*) lack sympatric, closely related species, and do not seem to prefer bamboo substrates (both species < 75%, Table 4.22). Although *Campylorhamphus trochilirostris* uses its extraordinary bill to probe for arthropods within hollow bamboo stems, this may only be opportunistic behavior, as this species can be found in many habitats lacking bamboo (e.g., varzea forest, Chaco woodland: Ridgely and Tudor 1994). All seven of these species are probably solely specializing on the structural uniqueness of bamboo thickets, not on particular substrates.

Another way to look at this question is by analyzing these species' percent use of bamboo substrates, in respect to their degree of specialization on bamboo throughout their distributions. In Chapter 2, I classified six specialists as "obligate specialists," seven as "near-obligate," and six as "facultative" (Table 4.22). If specialization is based upon substrate rather than habitat preference, then the percentage use of bamboo substrates should be highest for obligate users and lowest for facultative specialists. Two of the five guilds (undergrowth and dead-leaf guild), however, are not represented among the obligate specialists. All seven species in these guilds used bamboo substrates in decreased quantity relative to other guilds. Aside from *Anabazenops dorsalis* (see Kratter and Parker, in press), the dead-leaf specialists are not dependent on bamboo substrates directly; they search curled dead leaves trapped in the intricate and dense network of branches found in bamboo thickets. Although a high proportion (45-71%) of the substrates used by all species in this guild are bamboo (Table 4.22), these specialists often searched non-bamboo dead leaves as well; they especially appeared to prefer the much larger *Cecropia* leaves (K. V. Rosenberg 1990; pers. obs.). *Cecropia* is a common overstory tree above more open bamboo thickets, and their dead leaves are a common component of the arboreal dead-leaf resource that becomes trapped in bamboo (pers. obs.)

Of the three undergrowth species, the two antbirds preferred leaf litter over arboreal substrates (Table 4.11); bamboo substrates were less than 40% of their totals (Table 4.22). Aside from bamboo stems, few bamboo substrates are close to the ground in a bamboo thicket (pers. obs.). However, the few foraging observations for the undergrowth guild member, *Synallaxis cabanisi*, a facultative specialist, showed a stronger preference for bamboo substrates than the other two species in this guild (86% of total, Table 4.22). These two guilds may be choosing bamboo habitats more on habitat structure than on the presence of bamboo substrates.

The specialists in the other guilds (the three with obligate specialists) showed the expected order (obligate > near-obligate > facultative) for percentage use of bamboo substrates; the test statistic was barely non-significant (ANOVA, $P = 0.08$). The high percentage use of bamboo substrates (average above 86% for all three guilds, Table 4.22) indicates that substrate specialization may be more important for obligate specialists.

In summary, most bamboo specialists appear to be specializing only on the unique habitat attributes that bamboo thickets offer. This is further evidence of how habitat heterogeneity in western Amazon and the resultant refined habitat selection and specialization by birds plays an important role in making these forests the most species-rich in the world. A small set of specialists, all unrelated, show some indications of further specialization on bamboo substrates.

NICHE PARTITIONING - In general, the tests and analyses looking for both within- and between-guild niche differences were more successful among the three categorical variables (perch and particularly attack and substrate) than in the six continuous variables (height, distance to canopy, canopy height, perch size, perch angle, perch foliage density, with two additional continuous variables - sally distance and sally angle - for the flycatcher and antbird guilds). This presumably reflects the structural uniformity of bamboo thickets, in which bamboo stems can make up from 40

to 100% of all stems > 3 cm diameter (Chapter 3). Therefore, only a limited range of these continuous variables is available in a bamboo thicket. Most leaves occurred from 5-10 m up, stem diameters did not exceed 8 cm, and most stems (of similar size) had similar orientation. This uniformity results in few opportunities for species to partition resources along these axes. However, the continuous variables were more useful in separating guild members in the antbird and flycatcher guilds, where perch, attack, and substrate were quite similar.

It will probably always be difficult, if not impossible, to determine exactly how much partitioning of resources is necessary for species to coexist. To unlock those behaviors by which species partition shared resources, we should thus turn to those situations in which many species use a limited resource and ecological pressures (e.g., competition) are expected to be high. Such a situation is most likely in tropical forests. For example, all species in MacArthur's (1958) classic documentation of niche-partitioning in wood-warblers (Parulidae) of northeastern North America were migratory, and each had different winter ranges; it thus could not be assumed that competition for resources on the breeding grounds was driving the differences in foraging behavior observed by MacArthur. In comparison, all bamboo specialists in this study are non-migratory, although breeding populations of the non-specialist *Lathrotriccus euleri* in the study area may be augmented by some populations that may only winter in the Peruvian Amazon (R. T. Chesser, pers. comm). The bamboo specialists have year-round territories, and, as far as known, do not switch to non-bamboo habitats or substrates at any time of the year (T. A. Parker, pers. comm.; pers. obs.). Bamboo specialization thus sets an excellent context for studying how similar species coexist.

Even though all bamboo specialists are largely foraging from a common substrate (bamboo), competitive pressure among guilds is probably relaxed. Different guilds either forage from different substrates within the bamboo thickets (flycatcher and

antbird guilds vs. dead-leaf vs. stem vs. undergrowth guilds,) or they use different attack behaviors (flycatcher vs. antbirds guilds). Within guilds, however, competitive pressures would be expected to be higher. Common guild members are using the same substrates with similar attack behavior.

The results indicate that resource overlap may be highest among the five species in the flycatcher guild. All five appear to use the same foraging mode, sally-strikes, and all preferentially foraged from live bamboo leaves (Table 4.5). In his subdivision of flycatcher foraging modes, Fitzpatrick (1980) put the tody-tyrant genera (including Hemitriccus and Poeciloriccus) and Ramphotrigon together as "upward strikers" (sally-strikes to leaves in the terminology used here), an observation consistent with this study. However, he classified Lathrotriccus (then in the genus Empidonax) as an "enclosed perch hawkler." He stated that species using this foraging mode (sally-strikes to air in my terminology) may also use other foraging modes, such as upward strikes, up to half the time. He did not present any quantitative data on L. euleri, however, and it is possible that Fitzpatrick had other Empidonax species in mind. Although I found that L. euleri used sally-strikes to air more than the other flycatchers (Table 4.5), it did so less than 10% of the time. It is possible that L. euleri has different foraging strategies depending on habitat. In bamboo thickets there may be structural constraints on the types of behavior possible for a sallying species, and L. euleri may converge in behavior towards the other flycatchers in the guild. Regardless of the similarities among the flycatchers, the results here indicate that the guild can be subdivided into two groups: the two tody-tyrants and the three larger species.

The two tody-tyrants, P. albifacies and H. flammulatus, used smaller perches and shorter and more vertical sallies than the other three species (tables 4.3-4.4). Determining nice-partitioning within the two tody-tyrants was more difficult. First, both are obligate bamboo specialists (Chapter 2), and both showed high overlap in territories (Chapter 2) and among different types of bamboo thickets (Chapter 3). The

behaviors observed at my study sites, therefore, were probably representative of these species throughout their area of sympatry (depto. Madre de Dios in southeastern Peru, the entire distribution of P. albifacies; Ridgely and Tudor 1994).

Lathrotriccus euleri differed from the two Ramphotrigon sp. in using larger diameter and less dense perches and made more sally-strikes to air. Differences between the two Ramphotrigon were less apparent. The quantitative results showed little partitioning by foraging behavior, perhaps due to the small sample of R. fuscicauda; the results for differences in habitat selection also showed little partitioning (Chapter 3). One qualitative difference was noted: R. fuscicauda tended to perch near the top of the dense layer of bamboo leaves (in part accounting for the few foraging observations) and then to make sally-strikes outwards to exposed bamboo leaves. Ramphotrigon megacephala, on the other hand, tended to perch below the leafy bamboo layer and made upward sally-strikes to the lower leaves of the bamboo canopy. Although the differences were not significant (Table 4.4), R. megacephala had shorter, more upward sallies. Unfortunately, I did not distinguish between the bamboo and non-bamboo canopy, so the relative positions of each species in the bamboo layer could not be determined. Lastly, the two species differ in size, especially in bill length (Table 4.1) and may take different size prey.

The antbird guild also showed high overlap in foraging behavior. The two mid-sized species (Drymophila devillei and Cercomacra manu; Table 4.1), which share a similar long-tailed body shape, clustered together in MCA space (Figure 4.2). These species, however, appear to prefer structurally different types of bamboo thickets (Chapter 3; Parker and Remsen 1987), although they showed some overlap in territories at one site (see maps in Chapter 2). Although habitat selection is the defining criterion for the bamboo specialists and the three types of bamboo thickets are structurally unique (Chapter 3), within this group of 19 species, only Cercomacra manu and D. devillei provide a strong example of habitat partitioning among the bamboo specialists.

As well as using more non-bamboo substrates, the small (Table 4.1) and relatively acrobatic Microhoppia quixensis was more active and agile in its attack maneuvers (sally-strikes, sally-hovers, flutter-chases, hangs) to forage from more exposed leaves (lower perch-substrate density) than others in the guild. At the other end of the size spectrum in this guild (Table 4.1), the antshrike, Cymbilaimus sanctaemariae, was widespread among bamboo thickets types (Chapter 3) and showed high overlap with all other species in the guild. The most noteworthy difference between Cymbilaimus sanctaemariae and the other three species was its use of larger perches (Table 4.6-4.7) and the lunge attack maneuver (Table 4.7).

Although the stem specialists showed high overlap in habitat (Chapter 3) and territories (Chapter 2), in general this guild had the lowest overlap in foraging behavior of any guild. Simoxenops ucayalae and Campylorhamphus trochilirostris showed unique foraging behaviors associated with their modified bills (see Results); these behaviors are probably critical for exploiting the prey base inside bamboo stems. The two most similar species ecologically are the two woodpeckers (Picumnus rufiventris and Celeus spectabilis); both species frequently use the peck attack maneuver on bamboo stems internodes (Table 4.17). However, P. rufiventris is less than 20% as large (in mass) as Celeus spectabilis and its bill is only 25% the length (Table 4.1). Not surprisingly, P. rufiventris forages on smaller stems than Celeus spectabilis (Table 4.15; almost significant: $t=1.823$; $df=20$; $P=0.078$). P. rufiventris may be absent from more mature bamboo stands because most bamboo stems in these thickets are too large (see Chapter 3).

The foraging behavior of Celeus spectabilis is most noteworthy. I observed three long bouts (>10 minutes) of foraging by this species, when the woodpecker repeatedly pecked holes in dead bamboo-stem internodes full of large red ants (including adults and eggs). After pecking the holes, the birds would sit there for minutes, using bursts of probe attack maneuvers interspersed with short waits (ca. 1

minute). The diet of this species consists largely of ants (Formicidae; pers. obs.), a frequent prey item for other Celeus species (Short 1982). The intervals between probes probably allowed the ants to move back into range of the bird's tongue. Foraging bouts at live stems (n=9) were much shorter in duration, and the species did not wait or probe after pecking the holes. It has been suggested by T. A. Parker (pers. comm.) that this species actually opens up holes in bamboo stems to allow ants and other arthropods to colonize (see Louton et al., in press) and returns later to "harvest" this resource. My foraging observations of this species support this fascinating hypothesis, but I lack enough data to draw strong conclusions. This behavior deserves further study.

In the undergrowth guild, Synallaxis cabanisi, a wholly arboreal forager, was quite separate from the two antbirds, which often dropped to the ground to forage in the leaf litter (Table 4.11). The two antbirds, however, shared many behaviors, had high overlap in territories (Chapter 2) and among bamboo habitats (Chapter 3), and differed only slightly in size (P. lophotes is 75% the mass of M. goeldii; Table 4.1). Both species were frequently observed at the periphery of army ant swarms, where M. goeldii often chased away the smaller P. lophotes (pers. obs.). The small differences between the species were mostly in the greater use of near-perch attack maneuvers by P. lophotes and the more frequent use of hops by M. goeldii (Table 4.11).

For some specialists, competition may actually be stronger with closely related, ecologically similar species in other habitats than with other species in the guild. This may be especially true for the dead-leaf guild. The two antwrens (Myrmotherula) foraged from different substrates (M. ornata almost entirely from dead leaves and M. iheringi at least in part from stems: Table 4.14) and had slightly different attack behavior (Table 4.14). Phylogenetically (Hackett and Rosenberg 1990), and most likely ecologically, the most similar sympatric species to M. ornata is M. leucophthalma, which sometimes occurs in bamboo thickets (as well as areas without bamboo) and also forages almost entirely from dead leaves (K. V. Rosenberg 1990a,

1990b). Remsen and Parker (1984) documented ecological release between these two species, which is indicative of a strong competitive interaction (Wiens 1989). A similar situation exists between the two bamboo specialist foliage-gleaners: Anabazenops dorsalis prefers stems and Automolus melanopezus prefers dead leaves. Automolus melanopezus is replaced by the ecologically similar and taxonomically related A. rufipileatus in younger bamboo stands and early successional vegetation (K. V. Rosenberg 1990b, pers. obs.). Anabazenops dorsalis, however, lacks an ecologically similar counterpart in non-bamboo habitats in the study area; it may be a substrate specialist (see above).

As mentioned above for the two Ramphotrigon species, another unexplored dimension may result in niche partitioning: species with common foraging behavior may be choosing different prey. The correlation of foraging behavior and diet, along with the influence of diet on niche partitioning within the bamboo specialist avifauna, remain to be studied.

CHAPTER 5

CONSERVATION OF HABITAT SPECIALIST BIRDS: USING SATELLITE IMAGERY TO ESTIMATE REGIONAL POPULATION SIZES

Conservation of most tropical birds is in its infancy. For many threatened species habitat requirements are unclear, nesting habits unknown, and exact distributions yet to be determined (e.g., Collar et al. 1990). Almost all tropical bird conservation measures therefore have been passive. Actions already taken in Amazonian lowland forests have largely relied on targeting and conserving large tracts of undisturbed areas (usually mature forests) in the hopes that these areas contain a major proportion of the important habitats and species in the area (e.g., in Manu National Park or the Tambopata-Candamo Reserve Zone in southeastern Peru, Foster et al. 1994). In contrast, bird conservation in the temperate zone has relied largely on single species approaches (e.g., the Endangered Species Act in the United States). Although the systematic approach in the tropics has many advantages over the species approach of the temperate zone, it may not insure the preservation of those species most at risk. Many threatened Neotropical species are habitat specialists with narrow distributions (see Collar et al. 1990); conservation of these species may best be approached by identifying and conserving key areas of importance (large tracts of critical habitat) in conjunction with the strategy of conserving large tracts of forest. In many cases, these restricted habitats (e.g., *Polylepis* woodlands in the Andes, Fjeldsø and Krabbe 1990) may contain a number of specialists with similar habitat preferences, so conservation measures aimed at one species often protect habitat for many other species.

Thickets of Guadua bamboo in southwestern Amazonia contain a number of "bamboo specialist" bird species. In Chapter 2, I documented that 13 species are

"obligate" or "near-obligate" bamboo specialists; these species appear to be restricted to bamboo throughout their distributions. Six "facultative" bamboo specialists are also restricted to bamboo in southeastern Peru, but may use other habitats away from this area.

Aside from ecological specialization, other factors make bamboo specialists of unique interest for conservation. First, many bamboo specialists, particularly the obligate and near-obligate users, have small geographic distributions relative to other tropical forest species (Chapter 2). Second, within these small ranges, bamboo thickets, and thus the specialists, are patchily distributed across the landscape. Third, bamboo thickets may be ephemeral at any one spot because of bamboo's unique phenology of mass-flowering, die-off, and regeneration (Janzen 1976), and because most thickets are a temporary successional stage following disturbance. Last, and perhaps most importantly, many Guadua bamboo thickets occur along rivers, which are usually the primary avenue along which development proceeds in southwestern Amazonia (Foster et al. 1994). Guadua bamboo thickets also support populations of specialist insects (Louton et al. in press), frogs (L. Rodríguez, pers. comm.), and mammals (Emmons 1984). An ominous portent to the future threats that bamboo specialists in southwestern Amazonia may face can be found in other regions with bamboo specialists. In southeastern Brazil, where several other bamboo specialists occur (Parker 1982), less than five percent of rainforest habitats still exist (Oliver and Santos 1991) and four bamboo specialists are currently listed as threatened and many more are listed as near-threatened (Collar et al. 1991). In the southeastern United States, the probably extinct Bachman's Warbler (Vermivora bachmanii) may have been restricted in the breeding season to expansive thickets of bamboo or cane (Arundinaria gigantea) (Remsen 1986). Bamboo is still common in the region, but there are no longer any expansive thickets (Remsen 1986).

Bamboo specialists provide an important opportunity to study the conservation implications of habitat specialization. In this paper, I approach conservation of these specialists by identifying key habitat and estimating densities of specialists. By using satellite imagery, I measure available habitat in southeastern Peru, and calculate regional population sizes of the specialists. Finally, I discuss the stability of these populations in light of development pressures and current conservation measures in the area.

METHODS

Field work took place at six study sites along the Río Tambopata in southeastern Peru, five near the Ccollpa de Guacamayos (sites 1-5) and a sixth (site 6) downriver at the Explorer's Inn Reserve (Foster et al. 1994, Kratter in press, Chapter 3). Three different types of bamboo thickets are found in this region, each with its own contingent of bamboo specialists (Chapter 3). Bluff-top bamboo occurs in vast thickets on uplifted terraces along the eastern flank of the Andes. Floodplain forest bamboo occurs in small patches within mature floodplain forest. River-edge bamboo occurs in a narrow band proximal to the disturbance-creating processes of large rivers flowing out of the Andes. Bluff-top bamboo was extensive at Site 1, the main "Ccollpa" study area, and Site 4. Floodplain forest bamboo was found at sites 1, 3, and 6. River-edge bamboo was found at sites 2, 5, and 6 (along the Río La Torre) (Chapter 3).

A Landsat satellite image (Earth Observation Satellite Company 1991; see color frontispiece in Foster et al. 1994), covering approximately 12°15' - 13°32' S and 68°10' - 69°40' W of lowland southeastern Peru (deptos. Madre de Dios and Puno) and northern depto. La Paz, Bolivia, was used to measure the extent of habitats (Figure 5.1). The image includes the entire lowland portion of the Río Tambopata, a stretch of the Río Madre de Dios in Peru and Bolivia, and numerous other smaller rivers (Figure 5.1). Different colors in the image were associated with particular broad habitat types (see below) based on ground and river surveys and habitats given in Parker and Bailey

Figure 5.1. Habitats visible in satellite image of southeastern Peru and northern Bolivia.

(1991), Foster et al. (1994), and Phillips et al. (1994). Seven major habitat types are identifiable in the image: the extensive bluff-top bamboo thickets (bright green or brownish-green in image) mentioned above, early successional vegetation along rivers (mottled light green), mature floodplain forest (dark green, no stream development), mature *terra firme* forest (green, slightly dissected terrain), agriculture areas (pink or light green patches), grasslands (pink), low Andean foothills (dissected terrain), and rivers and beaches.

The areas of major habitat types (see Figure 5.1), including bluff-top bamboo, were measured by cutting out continuous pieces of habitat from a photo-copied reproduction of the satellite image, and weighing each piece. The weights were converted to areas by a multiplying it by a scalar, which was determined by weighing square pieces of known area from the photo-copied image. Densities of bamboo specialists in bluff-top bamboo (Table 5.1) are available from the Ccollpa site (Chapter 2: Table 2.1, but using only bluff-top bamboo [108 ha]). Regional population sizes were then calculated by multiplying the area of bamboo and the species' densities.

Calculation of population sizes of specialists in river-edge bamboo and floodplain-forest bamboo is much more problematic. The distributions of specialists among patches of floodplain-forest bamboo and river-edge bamboo were not regular among sites. For example, some specialists present in floodplain forest bamboo thickets at sites 1 and 5 were rare or absent in seemingly similar thickets at site 6 (Chapter 3). Also, river-edge bamboo and floodplain-forest bamboo thickets are too small to be seen in the satellite image, so the extent of bamboo, and thus population sizes, had to be estimated in another way for these habitats (see below).

The proportional area of floodplain forest bamboo in floodplain forest was estimated at site 1 (Ccollpa) and site 6 (Explorer's Inn). A habitat map of the Ccollpa site, which shows floodplain forest bamboo thickets is given in Chapter 2 (Figure 2.2). At Explorer's Inn, the extent of all three main bamboo thickets (see Chapter 3) was m

Table 5.1. Density (pairs/km²) of bamboo specialists in various bamboo habitats. A zero denotes that the species was absent in that habitat. BTB=bluff-top bamboo; FFB=floodplain forest bamboo; REB=river-edge bamboo.

species	density BTB	density FFB	density REB
<u>Picumnus rufiventris</u> Rufous-breasted Piculet	4.63	5.0	5.0
<u>Celeus spectabilis</u> Rufous-headed Woodpecker	1.85	2.5	2.5
<u>Campylorhamphus trochilirostris</u> Red-billed Scythebill	18.52	15.0	15.0
<u>Synallaxis cabanisi</u> Cabanis's Spinetail	3.70	0	0
<u>Simoxenops ucayalae</u> Peruvian Recurvebill	5.56	5.0	5.0
<u>Anabazenops dorsalis</u> Dusky-cheeked Foliage-gleaner	17.59	10.0	10.0
<u>Automolus melanopezus</u> Brown-rumped Foliage-gleaner	4.60	15.0	0
<u>Cymbilaimus sanctaemariae</u> Bamboo Antshrike	27.78	25.0	25.0
<u>Myrmotherula lheringi</u> Lhering's Antwren	13.89	20.0	0
<u>Myrmotherula ornata</u> Ornate Antwren	13.89	20.0	20.0
<u>Microhoppia quixensis</u> Dot-winged Antwren	13.89	32.5	32.5
<u>Drymophila devillei</u> Striated Antbird	20.37	37.5	0
<u>Cercomacra manu</u> Manu Antbird	34.26	0	0
<u>Pernostola lophotes</u> White-lined Antbird	41.67	17.5	17.5
<u>Myrmeciza goeldii</u> Goeldi's Antbird	24.07	25.0	25.0
<u>Hemitriccus flammulatus</u> Flammulated Bamboo-tyrant	19.44	2.5	2.5
<u>Poecilotriccus albifacies</u> White-faced Tody-tyrant	14.82	12.5	0
<u>Ramphotrigon megacephala</u> Large-headed Flatbill	21.30	22.5	22.5
<u>Ramphotrigon fuscicauda</u> Dusky-tailed Flatbill	5.56	7.5	7.5

apped on a field map (unpublished) of the site. For both sites 1 and 6, I divided the area floodplain forest bamboo by the total area floodplain forest.

The extent of bamboo in floodplain forest varied by more than an order of magnitude between the two sites (1 and 6). Thus, I calculated a range of population values for bamboo specialists in floodplain-forest bamboo. As a maximum, I used the mean value of proportional bamboo in floodplain forest between the two sites; for the minimum value I used the proportional area of bamboo at site 6. The latter site is probably more representative of the extent of bamboo in most floodplain forests (T. A. Parker pers. comm.). The extent of bamboo in the floodplain forest at site 1 may be above average because of the proximity of the vast bluff-top bamboo thickets. Density values for the specialists in floodplain-forest bamboo from the Ccollpa site were used to calculate population sizes in this habitat (Chapter 2, Table 2.1, using 40 ha of floodplain-forest bamboo and number of territories in floodplain forest bamboo).

Riverside surveys of bamboo along the Río Tambopata, coupled with indications from the satellite image, showed that river-edge bamboo was largely restricted to a narrow band (50-100 m wide) where floodplain forest met the river (e.g., sites 2, 5, and 6). Using the satellite image, I measured the linear distance of the floodplain forest/river interface on all large rivers in the image (ríos Madre de Dios, Tambopata, Malinowski, La Torre, Piedras, Pariamanu, Heath, Asundra, Madidi; see Figure 5.1) and assumed a habitat width of 100 m for river-edge bamboo. Most of this habitat has been destroyed on the Río Tambopata between Puerto Maldonado and the mouth of the Río Malinowski (Foster et al. 1994; pers. obs.) and along the Río Madre de Dios (indicated by the satellite image). Densities of specialists in river-edge bamboo were similar to floodplain-forest bamboo for the 10 species that occur in both habitat types (Chapter 3). Bamboo thickets appear to be scarce in *terra firme* forests (aside from the bluff-top bamboo identified in the satellite image, T. A. Parker pers. comm.), agricultural habitats (A. Stronza pers. comm., pers. obs.), and most Andean foothills.

The large Guadua bamboo thickets on the lower portions of Andean foothill habitats in northern Bolivia mentioned in Parker and Bailey (1991) are probably part of the system of bluff-top bamboo thickets, and can be seen in the satellite image. These are greenish brown on the satellite image. Guadua bamboo is lacking in the riverine and pampa habitats.

RESULTS

The dominant habitat in the approximately 40,000 km² area represented in the satellite image is terra firme forests (39.7 %), followed by floodplain forests (22.3%) and Andean foothills (18.6%) (Table 5.2). Bluff-top bamboo occurred as nine easily identifiable bright patches in the satellite image (Figure 5.1); however, five similarly shaped and sized, light-brownish patches in similar situations (terraces at the periphery of dissected foothill terrain) further east were probably this habitat as well; these were included as bluff-top bamboo and made up 34.4 % of the total bluff-top bamboo habitat. The total extent of the 14 patches was 248 km², only 0.58 % of the image. Individual patches varied from 2.1 to 56.4 km² (average 17.8 ± 19.8 km²); the largest patch was continuous with the bluff-top bamboo at the Ccollpa site.

Estimated population sizes in bluff-top bamboo (Table 5.3) were above 1,000 pairs for all but two specialists: only 450 pairs of the large woodpecker Celeus spectabilis and 920 pairs of the spintail Synallaxis cabanisi were estimated in this habitat. The commonest specialists had fair-sized populations (e.g., 10,355 pairs of the undergrowth antbird Percnostola lophotes in bluff-top bamboo alone). Bamboo specialists may, on average, have higher densities within appropriate habitat than species in other lowland forest habitats (Chapter 2). All 19 specialists occurred in bluff-top bamboo thickets (Chapter 3).

Bamboo was estimated to account for between 1.2% (site 6) and 11.4 % (average of sites 11 and 6) of the floodplain forest. With the latter estimate, floodplain-forest bamboo was the most extensive type of bamboo (1076 km²); however, only

Table 5.2. Habitat areas and estimated extent of bamboo from satellite image. See text for differences between "green" and "brown" bluff-top bamboo.

habitat	area (km ²)	%bamboo	area bamboo (km ²)
bluff-top bamboo	249	100	249
green		163	163
brown		85	85
floodplain forest			
site 1	9,468	11.4	1,076
site 6	9,468	1.2	117
early-successional	348	0	0
river-edge bamboo	96	100	96
<u>terra firme</u> forest	16,867	0	0
pampas	2,655	0	0
agricultural	4,781	0	0
river	228	0	0
Andean foothill	7,904	0	0

Table 5.3. Estimated population sizes of bamboo specialists in southeastern Peru and northern Bolivia. See Figure 5.1 for area included. BTB=bluff-top bamboo; FFB=floodplain forest bamboo; REB=river-edge bamboo.

Species	POPULATION SIZE			
	BTB	FFB		REB
<u>Picumnus rufiventris</u>	1,151	587	- 5,380	479
<u>Celeus spectabilis</u>	460	294	- 2,690	239
<u>Campylorhamphus trochilirostris</u>	4,602	1,761	- 16,140	1,436
<u>Synallaxis cabanisi</u>	920	0		0
<u>Simoxenops ucayalae</u>	1,381	587	- 5,380	479
<u>Anabazenops dorsalis</u>	4,372	1,174	- 10,760	957
<u>Automolus melanopezus</u>	1,151	1,761	- 16,140	0
<u>Cymbilaimus sanctaemariae</u>	6,904	2,935	- 26,900	2,393
<u>Myrmotherula iheringi</u>	3,452	2,348	- 21,520	0
<u>Myrmotherula ornata</u>	3,452	2,348	- 21,520	1,914
<u>Microrhopias quixensis</u>	3,452	3,816	- 32,767	3,111
<u>Dryophila devillei</u>	5,063	4,402	- 32,767	0
<u>Cercomacra manu</u>	8,514	0		0
<u>Percnostola lophotes</u>	10,355	2,054	- 18,830	1,675
<u>Myrmeciza goeldii</u>	5,983	2,935	- 26,900	2,393
<u>Hemitriccus flammulatus</u>	4,833	294	- 2,690	239
<u>Poecilatriccus albifacies</u>	3,682	1,468	- 13,450	0
<u>Ramphotrigon megacephala</u>	5,293	2,642	- 24,210	2,154
<u>Ramphotrigon fuscicauda</u>	1,381	881	- 8,070	718

117.4 km² of floodplain-forest bamboo were estimated with the smaller figure. With the large difference in estimated areas, a large range of estimated population sizes was found for the 17 specialists that occur in floodplain-forest bamboo habitats (Table 5.1). If the larger area figure was used, than sixteen specialists had their greatest populations in floodplain-forest bamboo; the populations of 12 specialists were above 10,000 pairs. With the smaller estimate, only two species (*Automolus melanocephalus* and *Microtopias quixensis*) had their greatest populations in floodplain-forest bamboo, and no population was greater than 5000 pairs.

Only 10 specialists occur in river-edge bamboo thickets (Table 5.1). River-edge bamboo had the smallest extent of bamboo (95.7 km²) and the lowest population estimates of the three types of bamboo thickets for all specialists.

DISCUSSION

Much of the study area falls within the Tambopata-Candamo Reserve Zone (Foster et al. 1994) or the proposed Alto Madidi National Park in Bolivia (Parker and Bailey 1991). In Bolivia, the lowland area between the Río Asundra and the Peruvian border extending south to and including the foothills east of the Río Madidi (see Figure 5.2) is slated for protection, but the development activities that will be allowed therein have not been decided (E. Ortiz, pers. comm.). In Peru, the portion of the Tambopata upriver from the Malinowski extending east to the Bolivian border (Figure 5.2) will probably be given national park status (Bahuaia-Sonene National Park), in which the included therein should receive full protection (Foster et al. 1994). This proposal has yet to be approved by the Peruvian government. Fortunately, most bluff-top bamboo patches in the study area (11/15 or total 75% of total bluff-top bamboo area) occur within the area designated for Bahuaia-Sonene National Park (Figure 5.2). These thickets should not be at risk to habitat destruction. The types of development activities that will probably be permitted in the reserve area outside Bahuaia-Sonene National Park or in Alto Madidi National Park (timber harvest, colonization, ore extraction)

Figure. 5.2. Approximate limits of protected areas in study area, with locations of bluff-top bamboo thickets. See Figure 5.1 for complete habitats.

could have severe impacts on bamboo habitats, however (see below). Does protection of bluff-top bamboo thickets, as afforded by the Bahuaia-Sonene National Park protect adequate populations for the long-term persistence of specialists? To what extent can we rely on the stability of populations in floodplain-forest bamboo and river-edge bamboo?

The usefulness of the data presented here is dependent on the accuracy of measures of both habitat area and bird densities. For both reasons, the estimates of population sizes in bluff-top bamboo are the most accurate, although the floodplain-forest bamboo and river-edge bamboo habitats definitely add substantial populations of most specialists. Although not small enough to provoke immediate alarm, the population sizes of most specialists in bluff-top bamboo are not very large. In contrast, a rare bird in *terra firme* forest, for example a species with only 1 territory/km², would have a population of over 16,000 in the image area, larger than that of any bamboo specialist in bluff-top bamboo. In addition, these small regional populations of bamboo specialists are subdivided by the natural patchiness of the bamboo habitat. Bamboo thickets along rivers and in floodplain forests, however, may provide important “stepping stone” connections among the larger bluff-top thickets (see below).

In addition, the bluff-top bamboo populations of most specialists are augmented by sizable populations in floodplain-forest bamboo, and to a lesser extent river-edge bamboo, populations (Table 5.3). For the six facultative bamboo specialists (see Chapter 2), populations may be additionally augmented by populations in other habitats outside the study area. The species most at risk then are the six specialists (*Celeus spectabilis*, *Simoxenops ucayalae*, *Cercomacra manu*, *Hemitriccus flammulatus*, *Poecilotriccus albifacies*, *Ramphotrigon fuscicauda*) that are both obligate or near-obligate bamboo users (see Chapter 2) and are not common in floodplain-forest or river-edge bamboo. Of the two specialists with the smallest populations (*Celeus spectabilis* and *Synallaxis cabanisi*), the status of only the woodpecker should be of concern.

Whereas the spinetail can be common in habitats without bamboo (Chapter 2, Ridgely and Tudor 1994), the woodpecker is apparently restricted to bamboo throughout its range (Chapter 2).

Most of the satellite image falls within the Tambopata-Candamo Reserve Zone, although only a portion (ca. 25% or 1,000,000 ha) is to be designated within the Bahuaja-Sonene National Park (Foster et al. 1994). This national park includes approximately 30% of total floodplain forest in the satellite image. Approximately half the floodplain forest is included in the Alto Madidi National Park in Bolivia. Development pressures in and outside the national parks and reserve areas could threaten floodplain forest and river-edge bamboo thickets. For instance, along the lower Río Tambopata between Puerto Maldonado and the mouth of the Río Malinowski, colonization has led to the destruction of most river-edge habitats, including bamboo (pers. obs.), even though much of this area is in the Tambopata-Candamo Reserve Zone (Figure 5.2).

Because most development in the region occurs along rivers (Foster et al. 1994), the continuing expansion of the human population in the region undoubtedly endangers river-edge bamboo more than any other bamboo habitat. However, these pressures also threaten floodplain forests in the Tambopata region (Phillips et al. 1994) and, presumably, the bamboo thickets therein (but see Foster et al. [1994] and below). Both habitats may be important in providing corridors of habitat among bamboo patches. For bamboo specialists, habitat corridors are important for two reasons. First, bamboo specialists need to be able to move between thickets after the bamboo flowers, seeds, and dies en masse (see Janzen 1976 for the general phenology of bamboos). Presumably, all bamboo in a thicket would be of the same cohort, and would flower synchronously, although the phenology for any *Guadua* sp. has not been described. Following these episodes, it probably takes several years for bamboo to reach adequate stature to provide appropriate habitat. Specialists would then need to recolonize from

other bluff-top bamboo thickets (as long as they are not the same cohort) or from nearby floodplain-forest bamboo or river-edge bamboo thickets, where another species of bamboo (*Guadua angustifolia*) is often found (Foster et al. 1994). Second, bamboo is very patchily distributed across the landscape. Aside from the larger bluff-top bamboo thickets, populations in any one thicket are small. Often only one or two pairs of a specialist may be present in floodplain-forest bamboo patches (pers. obs.). Populations in these small thickets would therefore be very unstable unless specialists can move between thickets. In its natural state river-edge bamboo probably provides the most continuous bamboo habitat.

Foster et al. (1994) expressed concern that bamboo will dominate forest plots that are cleared, and later abandoned, in the region. This reasoning was based on the belief that the terraces held human communities before and during the rubber boom era (through approximately 1900) and that bamboo colonized the area and has persisted following abandonment of the communities (R. Foster pers. comm.). Although these terraces would be excellent sites for communities, the size, shape, and physiographic setting of bluff-top bamboo thickets indicated by the satellite image suggests that these thickets on the terraces are natural, not the result of secondary succession and persistence. The bluff-top thickets appear too large for village sites (many square kilometers), they have irregular perimeters that conform to the natural topography, and they occur repeatedly in similar physiographic situations, often far from rivers where villages would be expected. In addition, *Guadua* bamboo only invades cleared areas (or primary successional sites) where some canopy remains (e.g., edges) or does not become established until adequate canopy has developed (pers. obs.). The existence of a number of bamboo specialists endemic to the region indicates that bamboo thickets have been an extensive part of the natural landscape in Madre de Dios over evolutionary time, and are not a recent phenomenon.

The question remains, however, as to what extent bamboo thickets can secondarily become established in disturbed areas. Guadua bamboo does appear to colonize recently disturbed forest edges, such as riversides (naturally), along road cuts, and the forested edges of farms and other cleared areas, as long as some canopy trees remain (pers. obs.). These thickets can hold populations of some specialists (e.g., Cercomacra manu along roads in Pando, Bolivia, Parker and Remsen 1987), but bamboo probably cannot persist where development is intensive (e.g., along the lower Río Tambopata, pers. obs.). The rich floodplain soils in the region allow farms to be worked for many decades, first for crops and then for pasture, and the abandonment of farms or communities is currently rare in the region (A. Stronza, pers. comm.).

Estimation of population sizes can provide a strong foundation for conservation action, but aside from a similar earlier study in the study area (Kratter, in press), the approach taken here is unique for Amazonian birds. Although many studies have used remote sensing techniques to evaluate habitat suitability for birds (e.g., Breininger et al. 1991, Homer et al. 1993, Aspinall and Veitch 1993, Herr and Queen 1993), I could find only one previous study (Palmerim 1988) that used satellite imagery and bird densities from spot-mapping to estimate population sizes; this was for forest and grassland birds in central North America. Satellite imagery provides the best available means to estimate areas of habitat over large regions. Satellite imagery can also be used to monitor temporal changes of habitats, such as forest destruction. Similar approaches to the one used here may prove very useful to estimate population sizes and monitor changes in the avifaunas for a variety of habitats in southwestern Amazonia. Two habitats that deserve particular attention in southeastern Peru are floodplain forests and pampas (grasslands); both of these habitats are easily discerned on satellite images. Floodplain forests are also probably the most endangered forests of the region (Phillips et al. 1994).. As well as having an extremely diverse avifauna, many endemic birds species in southwestern Amazonia appear to be restricted to particular successional

stages found only in floodplain forests (Foster et al. 1994, Kratter, in press, S. K. Robinson and J. Terborgh, , manuscript). All other southeastern Peruvian endemics are bamboo specialists (Chapter 2). The small remnants of pampas in Peru along the Bolivian border (Figure 5.1) hold the only Peruvian populations of at least 16 bird species and four mammal species, including the endangered maned wolf (Chrysocyon brachyurus) and marsh deer (Blastocerus dichotomus); these grasslands appear to be in the process of being colonized by forest (Foster et al. 1994). The much more extensive grasslands in Bolivia (deptos. La Paz and Beni) are heavily used for cattle production (Foster et al. 1994).

The approach in this study, however, is also dependent on field methods for which absolute densities of birds can be estimated. Unfortunately, too many studies of Neotropical bird communities have relied on mist nets to estimate relative abundances, which give inaccurate estimates of density (Thiollay 1994, J. V. Remsen and D. A. Good ms). The coupling of appropriate field methods with satellite imagery has many promising applications.

This study provides an example of how basic natural history knowledge - avian bamboo specialization in this case - can provide a cornerstone for the conservation of an important ecosystem. Because habitat preferences of birds are, in general, much better known and more easily determined than other animal taxa, identifying habitat specialists should be a priority in devising conservation efforts. At least with bamboo thickets, preservation of the bird's habitat would allow a number of specialists of other taxa to "piggy-back" on conservation efforts to preserve bird habitats.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Here I briefly summarize the important results from each of the four main chapters and give a synopsis of the entire study.

Bamboo specialists are an important component of the lowland tropical forest avifauna in southwestern Amazonia. Of the 444 bird species recorded at the Ccollpa de Guacamayos on the Río Tambopata (Foster et al. 1994) approximately 150 are insectivorous (Rosenberg 1993). The 19 bamboo specialists thus comprise about 4.3% of the overall avifauna and over 12% of the insectivorous avifauna at this particular site. The southwestern Amazonian bamboo specialists may be the most diverse avifaunal community in the world that is completely dependent on a single plant species. Other keystone resources tend to be used seasonally (e.g., fruit, nectar), not year-round like bamboo thickets.

Of course, bamboo specialization is not an all-or-none phenomenon, especially when applied at a more regional scale. Six facultative specialists can be found in other habitats away from the Río Tambopata. Another seven, the near-obligate specialists, seem to prefer bamboo thickets throughout their distributions but may on occasion use other habitats, particularly dense habitats with little canopy cover, such as early successional vegetation along rivers and tree-fall gaps inside forest. The remaining six species, the obligate specialists, seem to be closely tied to bamboo thickets throughout their distributions. The obligate and near-obligate specialists tend to have small geographic ranges centered in southwestern Amazonia; three of these belong to clades with sister taxa in southeastern Brazil, suggesting a common biogeographic history of bamboo specialization between these areas. The facultative specialists are more widespread, perhaps reflecting their more generalized habitat preferences.

The high diversity of specialists tied to bamboo is unusual in that individual bamboo plants do not seem to provide many unique substrates or prey bases, except for the relatively inaccessible arthropod and small vertebrate fauna found inside the hollow bamboo stems. Most bamboo specialists may be more specialized on the unique structure that bamboo thickets provide, rather than particular substrates or prey bases; this may be particularly true for the facultative specialists. As is found among other southwestern Amazonian habitats (Terborgh 1980, 1985; Remsen and Parker 1983; Robinson and Terborgh 1995) many bamboo specialists are replaced in nearby habitats by ecologically similar, usually closely related, species. Among the six specialists that show substrate specialization, four are obligate and two are near-obligate specialists; only one, however, shows dramatic behavioral and morphological adaptations that are probably associated with foraging in bamboo. Substrate specialization in the other five species is indicated by either high preferences for bamboo substrates (above 95%) or a history of specialization within their clades.

The high diversity of specialists and the low diversity of substrates available in bamboo thickets also prompts questions concerning niche-partitioning. The 19 specialists were grouped into five distinct guilds based on foraging maneuver and substrate preferences. Apart from the guild that foraged on the hollow stem fauna, these guilds are representative of guilds found in more widespread forest habitats. Niche-partitioning in the guilds appeared to be mainly mediated by differences in foraging behavior. Within the guilds of arboreal antbirds and sallying flycatchers, the species mainly segregated by distance and angle of active foraging maneuvers (sallies, jumps, lunges, etc.), relative position in the strata of bamboo vegetation, perch size, and density of the foraging site. Members within the other guilds (dead-leaf searchers, stem searchers, and undergrowth inhabitants) mainly segregated by differences in substrate preference and foraging maneuver. Two species pairs also showed some niche-partitioning among the three different types of bamboo thickets found in the area, but

generally the specialists showed wide overlap in habitat selection. Productive areas for future research into niche-partitioning and habitat selection in bamboo specialists include studies of the dietary ecology of these species.

Even in southwestern Amazonia, bamboo is found very locally, and thickets occur as isolated clusters. The largest, most extensive thickets, which contained the highest diversity of bamboo specialists, are restricted to a narrow band of elevated terraces adjacent to the easternmost Andean foothills. Many bamboo specialists, particularly the obligate and near-obligate species, have small ranges relative to other Amazonian bird species. All of these factors, combined with bamboo's unique phenology and highly fragmented distribution, make bamboo specialists of special concern to conservationists. Using densities of specialists calculated from spot-mapping and the area of bamboo thickets measured from a satellite image of northern Bolivia and southeastern Peru, I estimated regional population sizes of the specialists. Estimated populations in this area, which represent most of the known populations of many species, were below 35,000 pairs for all specialists and may not exceed 10,000 for several species. Although the most extensive bamboo thickets in the region are slated for protection (they will be parts of a national parks in both Bolivia and Peru), several natural and anthropogenic factors may threaten the long-term stability of these populations.

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DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Andrew W. Kratter

Major Field: Zoology

Title of Dissertation: Bamboo Specialization in Amazonian Birds

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

April 7, 1995