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APURIMAC VALLEY OF PERU WITH RESPECT TO  
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GRADUATE COLLEGE

THE DISTRIBUTION OF THE AVIFAUNA IN THE APURIMAC  
VALLEY OF PERU WITH RESPECT TO ENVIRONMENTAL  
GRADIENTS, HABITAT, AND RELATED SPECIES

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

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JOHN SEDDON WESKE

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1972

THE DISTRIBUTION OF THE AVIFAUNA IN THE APURIMAC  
VALLEY OF PERU WITH RESPECT TO ENVIRONMENTAL  
GRADIENTS, HABITAT, AND RELATED SPECIES

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## TABLE OF CONTENTS

	Page
ABSTRACT .....	iv
INTRODUCTION .....	1
DESCRIPTION OF THE AREA .....	3
Geography and Climate .....	3
Vegetation .....	7
HISTORY OF PREVIOUS RESEARCH IN THE AREA .....	13
METHODS .....	14
The Gradients .....	14
Field Data .....	15
Mist-netting .....	18
Weights .....	22
RESULTS AND DISCUSSION .....	23
Elevational Distribution Patterns .....	23
The Humidity Gradient .....	41
Ecological Sorting Mechanisms .....	47
Niche Relationships within Selected Genera .....	57
Ecological Specialists .....	84
ACKNOWLEDGEMENTS .....	88
LITERATURE CITED .....	90
FIGURES .....	93
TABLES .....	106
APPENDIX 1 .....	109
APPENDIX 2 .....	126

## ABSTRACT

Distribution patterns and ecological relationships of birds in a forested area of the eastern Andes were studied in order to shed light on problems of species diversity. Three gradients were selected: two elevational gradients in uniformly well-watered forest from 600 m to 3500 m and a moisture gradient at nearly constant elevation going from humid, evergreen forest to seasonally dry, deciduous forest. Data were gathered through mist-netting and field observation.

Along the elevational gradients, the number of species decreased with elevation. At 600 m, 162 species were present, compared to 53 at 3500 m. The percentage of suboscine species in the forest avifauna decreased with elevation, while the percentage of New World, nine-primaried oscine species increased. Lowland species appeared to have narrower vertical foraging ranges than highland ones.

Among congeneric species pairs with non-overlapping elevational ranges, the higher elevation member tended to be larger in size than its lowland congener. Statistical significance was not shown, however.

Along the moisture gradient, the number of forest species remained nearly constant. However, if species of both mature forest and riparian vegetation were considered, there was a decrease in species diversity correlated with increasing dryness. In genera where both a

riparian species and a forest species occurred in the humid area, the riparian species tended to be the sole representative in the dry forest. Frugivorous species were largely absent from the dry region, but species which feed on large insects were more numerous there than in the humid area.

Niche differences between closely related species were examined. The most prevalent means of ecological segregation between congeners was elevational replacement. Along the elevational gradients, there were numerous genera with two, three, or even four species whose elevational ranges were largely or entirely non-overlapping. In other cases, congeners were elevationally sympatric but differed in habitat preference, vertical stratification, feeding behavior, or size.

THE DISTRIBUTION OF THE AVIFAUNA IN THE APURIMAC  
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INTRODUCTION

In recent years, an increasing amount of attention has been devoted to ecological investigation of tropical avifaunas. At least two reasons for this interest can be cited. First, features of tropical biotas such as high species diversity offer worthwhile problems for study. Second, when compared to temperate regions, the stable, non-seasonal character and lack of human disturbance in certain tropical areas provide distinct advantages in reducing environmental variables.

Work to date has emphasized the ecological relationships of bird species at a single locality (Moreau, 1948; Slud, 1960; Miller, 1963), or the comparison of avifaunas at separate localities differing in such features as habitat area and isolation (Vuilleumier, 1970) or climate, elevation, and vegetation (Orians, 1969). Orians called attention to both the need for ecological study of South American avifaunas and the advantage in working along gradients, where certain potential variables can be measured and others can be considered as essentially constant. To date, the only analysis of avian distribution and ecology

along environmental gradients in the tropics is embodied in work published by Diamond (1972).

Therefore, in collaboration with J. W. Terborgh, I undertook a study of the birds along gradients in the Apurímac Valley of Peru, where the eastern slope of the Andes meets the Amazon Basin. In this area, a continuous sweep of climax humid forest on the valley's slopes affords an elevational gradient, and a more gradual gradient in humidity exists from south to north in lowland forest. The present paper seeks to: 1) describe and explain gradient-related patterns in species diversity, familial composition, and vertical stratification; and 2) analyze competitive relationships and niche differences among closely related species. Terborgh (1971) published a theoretical interpretation of distribution patterns along the elevational gradient, with particular emphasis on the alternative factors which limit elevational ranges of species.

Field work in the Apurímac Valley was carried out between June and September in 1965, 1966, 1967, 1968, and 1970. In the pages that follow, the pronouns "we," "us," and "our" refer collectively to members of the various field parties, all of whom contributed to the information reported here.

## DESCRIPTION OF THE AREA

### Geography and Climate

The Río Apurímac is a major tributary of the Amazon. Our base was Hacienda Luisiana (12°39' S, 73°44' W, elev 600 m) on the Apurímac's west bank in the Department of Ayacucho, Perú (Figure 1). Across from Luisiana, in the Department of Cuzco, rises the northern portion of the Cordillera Vilcabamba. This range, whose peaks are believed to be over 4000 m high, is one of the largest areas of undisturbed wilderness remaining in the tropics (Baekeland, 1964). It is bordered on the west by the Río Apurímac-Ene-Tambo river system and on the east by Río Urubamba. At the range's northern tip the Tambo and Urubamba join to form the Río Ucayali which in turn empties into the Amazon far to the north. To the south, the range is separated from the rest of the Cordillera Vilcabamba, a section of the Andes, by a pass between the Urubamba and Apurímac Valleys which is 2000 m in elevation. Thus, the northern Vilcabamba at elevations above 2000 m is effectively an island, isolated by lowlands from corresponding elevations in the Andean cordillera. Because of the lack of accurate topographic maps, one cannot determine the area of this insular portion. The entire northern Vilcabamba covers more than 20,000 sq km.

The west slope of the Apurímac Valley is the eastern face of an unnamed range which is part of the Cordillera Oriental of the Andes. The highest peaks in this range are about 5000 m and passes are about 4000 m.

The range is contiguous with the Peruvian "Sierra," the semi-arid highland area running the length of Peru which has been under extensive human use for centuries. The forest of the west slope has not been disturbed significantly by man above the 1150 m level. The straight-line distance across the valley in the Luisiana area from the crest of the western range to the crest of the northern Vilcabamba is about 50 km.

The topography of both sides of the valley is rugged. Fast-flowing tributaries of the Apurímac descend through canyons which are as much as 1000 m deep. Adjacent canyons are separated by steep-sided ridges. In some places mountain slopes rise directly from the Apurímac. In others, there is an area of flatland forming a valley floor between the river and two mountain slopes. The land comprising Luisiana is part of one of the largest such areas of flat or gently rising land, extending up to 10 km westward from the river.

Prior to the early 1960's, the Apurímac Valley was thinly settled, because of difficult access. A sparse, indigenous population of Campa Indians lived in the valley by hunting, fishing, and limited agriculture. A few pioneer farmers of mestizo or European descent have been present since the latter part of the 19th Century. A series of rapids on the Apurímac and the great distance to major settlements on the Amazon river system made contact between the valley and downstream points difficult. Contact with towns in the Sierra required an arduous three-day trip on foot or by mule over the west range. Coca and barbasco (the source of rotenone) were exported from the valley, but settlers lived mainly by subsistence agriculture. The disturbance of the natural vegetation by man was limited and localized. In 1962 a road was completed from the

Sierra to Puerto San Francisco on the river 18 km downstream from Luisiana. During the past decade there has been a great influx of settlers, mainly Quechua Indians from the adjacent Sierra, and the population of the valley, now estimated at 50,000, continues to grow rapidly.

Luisiana has a humid tropical climate. No official weather data are available, but our own observations indicate that the average daily maximum and minimum temperatures in July and August were approximately 31° and 19°C. There was little day-to-day variation. According to Sr. José Parodi, the owner of Hacienda Luisiana, annual rainfall averages 2900 mm. The driest months are June through September. Typically, dawn at Luisiana was damp and overcast, but by 08:00 or 09:00 the clouds dispersed, and bright sunshine and clear skies prevailed for the rest of the day. Occasionally, there was a cloudy day, and showers occurred at least once a week. We experienced a week in August 1965 with rain for part of each day. There is rarely any prolonged dry period.

On the valley slopes, of course, temperatures vary with elevation (Terborgh, 1971, figure 1). At 3000 m there are occasional frosts. At the higher elevations it is typically clear at dawn, and one looks down upon the valley filled with a sea of cloud. By 08:00 clouds begin to rise up the mountain slopes, and by mid-morning elevations above 1500-1800 m are normally "socked in" with clouds and fog. Rain is nearly a daily occurrence. At higher elevations we experienced afternoon thunderstorms, and the ground was covered once with sleet. At dusk the clouds dissipate rapidly, and the nights are almost always clear. No data on annual rainfall are available for the valley slopes, but they are well-watered.

at all seasons. It was our impression that in the "dry" season at least, rain was more frequent but not as heavy as at Luisiana.

Once or twice a year the valley experiences a storm, probably of temperate zone origin. These result in heavy precipitation, strong winds, and temperatures up to 6° C below normal. After one such storm the puna grassland above 3500 m on the west side of the valley was covered with snow. However, snow-cover does not normally persist in either range.

Winds at all elevations are usually very light or calm, even on exposed ridges. The only exception occurs on the valley floor after several rainless days, when convectional activity may cause moderately windy conditions even within the forest.

As one proceeds along the Apurímac downstream from Luisiana, the valley gradually broadens. At the mouth of the Río Mantaro, some 50 km north of Luisiana, the ranges to both east and west are distant and the valley is very wide. The Río Ene, formed by the waters of the Apurímac and the Mantaro, continues northward with no ranges close at hand. However, the terrain is often hilly and the river passes through a steep-sided water gap at one point. Tall, humid forest flanks the Apurímac and the upper Ene, but the lower Ene passes through a dry area perhaps 60 km in length and of unknown width where a lower, mostly deciduous forest occurs. Farther downstream, one reenters the zone of abundant rainfall. Below the confluence of the Ene and the Perene, forming the Tambo, evergreen humid forest again prevails. Settlements and farms occur along much of the lower Apurímac, but few colonists have reached the Ene. Population along this river is limited to a few Campa villages.

## Vegetation

Several naturally-occurring vegetational formations can be distinguished in the Apurímac-Ene valley:

Lowland humid forest.--The climax vegetation of the valley floor is tall, humid, evergreen forest. Like forests in areas of similar climate throughout the tropics (Richards, 1966), it is characterized by four distinct "layers": the understory, the subcanopy, the canopy, and huge emergent trees 50 m or more high whose crowns exceed the canopy. The understory, where ferns, arums, and cyclanths grow abundantly, is open enough to allow a person to walk with little or no cutting. Aside from leaf-litter there is no undecomposed organic matter atop the soil. In the canopy and sub-canopy lianas are common, but other epiphytes like bromeliads and mosses are not.

Matorral.--Along the river in areas affected by seasonal flooding or changes in the water table, one encounters a distinctive riparian formation. Immediately adjacent to the shore it consists of canebrakes and leguminous shrubs. On higher ground grows a woodland of balsa, Cecropia, and leguminous trees like Erythrina over-standing an often impenetrable undergrowth of vine tangles, bamboo, Heliconia sp, etc. This varied habitat contains an avifauna quite distinct from that of lowland forest (Terborgh and Weske, 1969).

Hill forest.--On the lower mountain slopes the forest resembles lowland humid forest but differs in several respects. The four-layered character is present, but in general the trees tend to be smaller. Fewer emergents are present, and the understory is somewhat thicker. A few tree ferns, absent in lowland forest, are found here. Hill forest occurs

on slopes right across the Apurímac from Luisiana. Its differences probably result from factors associated with sloping terrain like drainage and soil thickness, rather than from any elevational change. Hill forest extends upward to an elevation of about 1390 m on the Vilcabamba side and 1660 m on the west side.

Cloud forest.--Replacing the hill forest above these elevations is cloud forest. The transition is not abrupt, and one may consider an elevational belt of 50 m on either side of the elevations given above to be the hill forest/ cloud forest ecotone. However, in view of the apparent structural uniformity of hill forest over an elevational span of several hundred meters, the change occurs in a surprisingly short distance. Cloud forest is marked by the following features: 1) presence of moss jackets on limbs and trunks of trees; 2) abundance of other epiphytes like bromeliads, climbing ferns, and orchids festooning tree limbs; 3) an accumulation of undecomposed organic detritus on the ground; 4) increase in the number of palms and tree ferns; 5) denser understory with (on the Vilcabamba side) an abundance of climbing bamboo (Chusquea sp). The cloud forest, like forests at lower elevations, contains some very large trees reaching 40 m or more in height, but the layered character of the forest is not apparent and the canopy is often more open. Cloud forest extends upward to 2500 m in the Vilcabamba and to 3300 m on the west side. It is important to note that though the features listed above occur throughout the cloud forest zone, the forest at 2200 m does not look the same as that at 1600 m. The differences are of degree 2200 m in the Vilcabamba one finds the quintessence of cloud forest: luxuriant epiphytic growth, an abundance of tree ferns, moss

jackets on trunks which make saplings appear to have thrice their actual diameter, a deep and constantly wet mat of organic matter on the ground, and lush stands of Chusquea. At yet higher elevations the trees tend to be shorter and more contorted, with moss-covered, above-ground root systems.

The lower limit of cloud forest coincides roughly with the lower limit of the cloud layer which forms daily on the mountain slopes. It appears that this "ceiling" forms somewhat lower on the Vilcabamba side, on the average, than on the west side, a fact we cannot explain. This feature may account in part for the higher elevation of the hill forest/cloud forest boundary in the west side. Another explanation rests on the exposure to the drying effects of sunshine. Both slopes are normally free of cloud each day until perhaps 09:00. The west-facing Vilcabamba slope does not receive the sun's rays directly in the morning hours, but the west side does. In the afternoon, when the sun shines directly on the Vilcabamba slope of the valley, the vegetation above 1600 m is almost always shrouded by clouds. It was our impression that the cloud forests of the entire west slope are less wet and not as lush in epiphytic growth as on the Vilcabamba side. Average temperatures at the same elevations on the two slopes do not differ appreciably.

Cloud forest begins at varying elevations in other parts of the Neotropics. For example, in the Sira Range in central Perú's Department of Huánuco, where we did field work in 1969, the highest peak rises to only 2200 m and the lower boundary of cloud forest was at 1300 m. On low peaks in Panamá, Myers (1969) found cloud forest below 1000 m, an elevation where hill forest is found on taller peaks. It seems to be a general rule that the lower the range, the lower the cloud forest extends.

Elfin forest.--At higher elevations in the Vilcabamba, the vegetational formation is elfin forest. Along our access trail to the summit, the cloud forest/ elfin forest ecotone was narrow. The trail led up a wide, steep mountain slope through cloud forest to a small peak which formed the lower terminus of a ridge leading ultimately to the crest of the range. As one attained this first 2500 m summit, one experienced a pronounced change in the vegetation within 50 meters of trail. The trees decreased in height from 20 m to little more than head-high, they had a distinct shrubby character with many branches, the leaves of most were tiny and densely grouped, and the ground was covered with a deep, springy mat of sphagnum and other plants. Many of the plants were of the Ericaceae. Small trees of the genus Clusia with rather large, thick, elliptical leaves were also present. These features distinguish the elfin forest in its most extreme form, as found on exposed ridges and peaks and at timberline. On broader portions of a ridge, trees 5 to 15 m tall with crooked trunks and limbs and thick epiphyte jackets occur along with the shrubby vegetation. Walking is often treacherous because one treads on elevated root systems, not the earth, and easily puts one's leg up to the thigh through a gap in the roots.

Actually, elfin forest is a rather varied formation, and it is hard to select one elevation as the elfin forest/ cloud forest boundary. Even at 3000 m, in ravines, sheltered dips along ridges, or on steep slopes continually in contact with rising clouds, one encounters forest which closely resembles cloud forest except that the trees are somewhat shorter than at lower elevations. In general, however, the vegetation assumes a more uniformly elfin forest character with increasing elevation. Because our trail, camps, and netlines were necessarily placed on ridges,

we found it expedient to consider the area over 2500 m as the elfin forest zone. From 3280 m to the crest of the range at 3530 m, a mixture of elfin forest and grassland occurs. The grass is extremely dense and over head-high in places. Trees grow even along the crest, and there is no well-defined treeline.

On the west side the cloud forest extends to much higher elevations. It changes somewhat in character with elevation, as the average height of trees decreases and some microphyllous trees appear, but a forest of 20 m high trees forming a fairly closed canopy can be found over 3000 m. An apt term for these upper cloud forests is "moss forest." The shrubby microphyllous elfin forest occurs only at treeline proper, often as border between cloud forest and puna grassland, or as tongues of woody vegetation extending out into the puna. On this side tree-line is well-defined, and the grass is waist-high or less.

Dry, deciduous forest.--The xeric zone along the lower Río Ene, centered at about 11°20' S, 74°15' W, supports a dry forest in which more than 80 percent of the trees are without leaves during the dry season. The tallest trees do not exceed 30 m and most are considerably lower. The canopy is broken, much light reaches the ground, and the layered character of humid forest (Richards, 1966) is not apparent. Among the more conspicuous plants are arborescent cacti attaining a height of 10 m and a deciduous tree of the family Bombacaceae with smooth, reddish bark, a bulbous trunk, and very soft wood. Ferns and arums are scarce or absent, but vine tangles and terrestrial bromeliad are abundant.

Around the edges of the dry zone is a transitional type of forest which retains the layered structure of humid forest and contains

numerous trees over 30 m in height, but which clearly shows the influence of the drier climate. The understory is more open than in humid forest, and more light reaches the forest floor because of occasional deciduous trees and appreciable leaf loss among the remainder. One of the commoner small trees is a spiny palm. Terrain has a strong influence on the height and character of vegetation in this area. On flat ground close to the river grows the tall and largely evergreen forest, but slopes immediately adjacent have a lower forest that was close to 50 percent deciduous.

## HISTORY OF PREVIOUS RESEARCH IN THE AREA

Prior to our expeditions, little ornithological work had been done in the Apurímac Valley, and none to our knowledge along the Ene. In the 19th Century, Jelski collected at Monterico, about 30 km northwest of Luisiana. His work led to the discovery and description of a number of new forms (Cabanis, 1873). In 1963 H.-W. Koepcke and C. Koford were attached to a National Geographic Society Expedition which sought to establish an airstrip and explore the heights of the northern Vilcabamba (Baekeland, 1964). This goal was not achieved, but the two zoologists collected at Luisiana, and Koepcke reached 1500 m elevation in the Vilcabamba by entering the range on foot along the Río Pichari. The 1963 collections were available to me.

Chapman (1921) reported on his expedition to the Urubamba Valley. In this report he applied to the birds of the Peruvian Andean slope the concepts of life zones which he had developed in the northern Andes. The area he worked lies only about 130 km southeast of Luisiana but is located in the southern portion of the Vilcabamba and appears to be a somewhat drier region than that we studied, although humid habitats like cloud forest occur. Thus, the avifauna he investigated differs in numerous respects from ours. It has nevertheless been useful to compare our results with his and test his ideas of zonation on our elevational gradients.

## METHODS

### The Gradients

To study avian distribution along an elevational gradient in humid forest we made transects of the Apurímac Valley's east and west slopes at the level of Luisiana. The east slope, formed by the northern Wilcabamba range, was especially advantageous for this purpose and provides an example of our tactics and methods.

A continuous sweep of well-watered, undisturbed climax forest occurs from the river to the top of the range, all within a straightline distance of 20 to 25 km. We established a series of nine wilderness camps along the transect (Figure 2). Placement depended upon the availability of water and suitable tent sites, but we attempted to locate camps at elevations roughly an equal distance apart. Entry to the range was made initially along a mountain stream, the Río Mapitunari, but it became necessary to leave the chasm of the stream and cut a trail up the mountain slopes and along the ridges from 850 m to the summit. Travel was on foot, and all food and equipment were transported in backpacks.

The transect of the west side was made in similar fashion except for an existing trail linking the settlements of the valley with those in the Sierra. Because cargo can now be transported by road, only an occasional caravan still used the trail. It provided us with easy access to the west slope and permitted the use of mules to carry our baggage.

The forest from 1150 m to treeline is uninhabited and undisturbed by man except for one abandoned farm along the trail at 1660 m.

The lowland transect of a humidity gradient was accomplished by traveling downriver on two balsa rafts and establishing camps in forest back from the river at several convenient localities.

#### Field Data

Along each transect we sought to obtain the following: 1) a complete list of the species of birds present; 2) the elevational range of each species; 3) an index of the abundance of each species at points within its range; 4) information on habitat selection of each species and the stratum of the forest it uses--its foraging height; 5) data on foraging behavior; and 6) measurements of weight and wing-length of all species. Principal methods of gathering data were mist-netting and observation. In order to avoid misidentifications, we tried to secure at least one specimen of all species encountered during the study. Terborgh and I shared equally the work of netting and processing live birds, surveying the avifauna, and determining elevational ranges. He carried out most of the observational work on foraging heights and behavior, a report of which he will publish separately (although certain information is included below). I collected and prepared most of the specimens. About 1300 study skins, along with several hundred formalin specimens, were obtained. The skins are located in the American Museum of Natural History and will be the subject of a separate taxonomic report.

Virtually no avifaunal survey of a Neotropical continental area is complete, and ours is no exception. Although 598 species have been

recorded in the valley, we have a few unidentified descriptions of birds which could not be collected or which were not seen adequately. Other species elude notice entirely. In particular, because the canopy often prevents one from seeing what is flying overhead, we were unable to gain a complete familiarity with the hawks and parrots at lowland and cloud forest camps. Again, because of the poor visibility we also have a less complete knowledge of birds of the cloud forest canopy above 2000 m than of canopy birds at lower elevations.

To determine elevations we used a Thommen altimeter which was set for standard barometric pressure of 760 mm. The elevation of each camp was determined by averaging the readings obtained over a number of days under different weather conditions, and a correction was made for temperature due to differences between observed temperatures and those for the Standard Atmosphere (Byers, 1959). With camps as reference points, elevations of intermediate locations were calculated by adding or subtracting the incremental elevation from the nearest camp.

If a bird was noted at elevation A and elevation B, its range was generally considered to span the region in between. There are several qualifications to this rule. Juvenal or immature birds occasionally wander outside of the normal elevational range of the species, a fact particularly evident for the Pipridae. In this family one can determine the presumed elevational breeding range by the presence of adult males, which have distinctive plumages. An immature male Pipra chloromeros, for example was netted at 2120 m, although upper limit of the species' regular range is 1360 m. The phenomenon is not limited to manakins. We

encountered a juvenal solitaire, Myadestes ralloides, at Luisiana, more than 1000 m below the cloud forests which are its normal habitat.

Allowance must also be made for the occasional record of a lone individual considerably outside its species' otherwise well-defined range, even if juvenal wandering cannot be proved. An example is provided by the honeycreeper Diglossa glauca, which is a common and conspicuous inhabitant of cloud forest between 1520 m and 2200 m, but which turned up once at 2830 m. In rugged country an anomaly like this may easily happen if a bird temporarily leaves its usual range to cross a higher ridge to get to similar habitat on the other side. Our banding has shown that individual birds do make local movements of up to 5 km. A third consideration is the change in ranges that can result from destruction by man of the natural forest (Mayr and Gilliard, 1954). For example, we found that two warblers, Myioborus miniatus and M. melanocephalus, occupy mutually exclusive elevational ranges in undisturbed forest, but Eugene Eisenmann (pers. comm.) informs me that they occur together in second-growth near the rail depot below Machu Picchu in the Urubamba Valley. Fortunately, it was possible to do nearly all our work along the gradients in habitat unaffected by man's activities, where competitive relationships are often simpler and more easily understood. Habitat disturbance alters niches in various ways. Forest canopy birds, for instance, frequently forage much closer to the ground in second-growth, as Pearson (1971) and Orians (1969) also noted.

It may be argued that since our data on ranges were obtained in only four months of the year, when rather few birds were breeding, they

may not provide a reliable pattern of elevational distribution. However, the lack of a sharply defined breeding time for the avifauna as a whole and of any marked seasonality in the availability of resources would suggest a fairly stable situation. Although competitive pressures might be more intense during the breeding season, competition is a year-round phenomenon, and spatial relationships would always be expected to reflect its effects.

### Mist-netting

The use of Japanese mist-nets to capture birds is essential to a study of avian distribution in the humid Neotropics. Otherwise, many common understory species of birds with elusive habits would be thought rare or would be overlooked altogether. On the other hand, the catch in nets is strongly biased toward understory birds. Observation is equally important in making a thorough species inventory, and since canopy birds are relatively more easily seen, the two techniques of netting and observation complement each other nicely. Most likely to escape detection by either method are shy species of the forest floor which seldom fly, such as tinamous, quail, and ant-pittas.

At each study site 14 to 52 nets, each 12 m long, were strung along lanes approximately  $1\frac{1}{2}$  m wide cut through the forest understory. Northeastern Bird-Banding Association Type A nets, with four shelves and a stretched mesh size of 36 mm, were used throughout. A net is normally set so that it covers the air space between 30 cm and 2 m above the ground. Because of irregular terrain the top of a net might sometimes

be as much as 3 m above the ground, but no attempt was made to net in the canopy. Most frequently nets were placed in a simple, long line along the main access trail so that an elevational extent of up to 100 m or more might be sampled. Occasionally, nets were set along the contours in two or three parallel lines 30 to 60 m apart.

The catch in nets is greatest for the initial day or two but then decreases as birds with net-experience apparently learn to recognize and avoid nets. We returned to some camps in subsequent years in order to capture more birds and increase the size of our sample. While in operation, nets were checked several times each day. Most of the catch was banded and released, while a minority was collected. The principal reason for banding was to recognize birds which had previously been caught and counted. Banding also provided information on survivorship from year to year and, in a few cases, of movements by birds from one camp to another.

By calculating the percentage of the total catch comprised by the catch of individuals of a given species, one obtains a measure of relative abundance of the species. Particularly when comparing different species and sometimes when comparing the status of the same species at different stations, relative abundance figures are biased by a number of factors. These include the foraging height of the bird, its size, the height of the vegetation, the topography of the net-line area, and the birds' competitive relationships. As noted above, species which inhabit the understory are efficiently sampled and form a disproportionately large part of the net sample with respect to the whole avifauna.

Subcanopy and canopy species which occasionally enter the understory are inefficiently sampled, and some canopy species are not sampled at all. The mesh-size we used is perhaps the best for non-selectivity, but no mesh is equally effective for all sizes of birds (Heimerdinger and Leberman, 1966); 36 mm nets probably catch birds weighing from 15 to 40 grams most efficiently. Smaller species sometimes slip through, and larger ones, especially columbids, entangle themselves less readily and may escape. Birds of any size will occasionally bounce off the net and not get caught.

When comparing status at two different stations, the height of the vegetation must be taken into consideration. Certain tanagers which inhabit both elfin forest and cloud forest are readily netted in the former habitat but only sparingly in the latter, because they remain in the upper part of the vegetational column. Also, in areas of tall forest, a net-line situated on a ridgetop occasionally will capture canopy birds that momentarily fly close to the ground while moving from one slope to another, while a net-line at the foot of a slope almost never would.

The change in foraging height resulting from the change with elevation in a bird's competitive relationships is sometimes reflected in its net-sample abundance. Two flycatchers of the genus Leptopogon provide an example, which Terborgh called to my attention. L. amaurocephalus ranges from 340 m to 930 m and L. superciliaris from 685 m to 1620 m. The former species inhabits mainly the understory and is readily netted. In the elevational zone it shares with L. amaurocephalus, L. superciliaris is netted infrequently since it forages mainly in the subcanopy, above

net-level and above the stratum occupied by its congener. Over 930 m elevation, however, superciliaris occurs alone and inhabits both subcanopy and understory, and at these elevations its presence in the understory is reflected in greater relative abundance in the net-sample.

With the above-noted qualifications in mind, one can use net-catch data to measure relative abundance of the more readily netted species. The abundance figures, which can be plotted graphically, are especially useful in comparing the status of the same species or of related species at different stations on a gradient.

While mist-netting provides a measure of the relative abundance of species which enter nets, attempts to determine relative abundance and population density of all species in an area were not successful and were abandoned. Spot-mapping techniques employed in the breeding season in temperate zone areas to count and map territories of singing males were unsuitable for several reasons: 1) Only a small percentage of birds in the area were singing. Even fewer showed territorial behavior. 2) What singing did occur was largely limited to the first half-hour of daylight, when visibility was very poor in the forest. We were in some cases unable ever to identify vocalizations which were heard morning after morning because we were unable to see and collect or identify the singer. 3) Individuals of many species customarily move about in roving, mixed-species flocks. The home ranges of members of such flocks, and thus the numbers of individuals per unit area, are exceedingly difficult to ascertain. It is possible to make a subjective estimate of whether a species is common or uncommon, based on the frequency with which it is

seen. Such estimates are biased toward species which have conspicuous habits, and this bias is shown by comparison of data obtained through observation with data obtained through net samples.

### Weights

Weights of live or freshly killed birds were taken with Pesola spring balances. Up to 100 grams the weight was read to the nearest 0.1 g and over 100 grams to the nearest 0.5 g. Unfortunately, weights were not obtained in the Apurímac Valley until the 1970 expedition, because we did not previously have available balances which were both accurate enough to be useful and, on the other hand, light, rugged, and compact enough to be carried along the netlines. Therefore, we lack weight data for some species and for others have very little. Ideally, interspecific weight comparisons should be made between sizeable samples of birds of known sex. In practice, it has been necessary in many cases to use average weights of small samples of unsexed birds. Such data may provide a poor estimate of the population's average weight. Weights of juvenal birds have been excluded from calculations. For a few species where no weights from the Apurímac Valley were available, data from the Sira Range has been used. Weight information is given in Appendix 1.

## RESULTS AND DISCUSSION

### Elevational Distribution Patterns

Species diversity.--The number of species of forest birds present along the elevational transect decreases with elevation (Figure 3). At 600 m, 162 species were detected, against 53 at 3500 m. These figures accord with ones for similar Costa Rican habitats, where Orians (1969) found about one-half as many species at 2000 m as at sea level. To account for this pattern, one may cite the reduced productivity of the environment at higher elevations. Connell and Orias (1964) associated species diversity with the level of productivity and considered humid lowland tropical forest to be the most productive environment. At upper elevations on the Apurímac Valley slopes, productivity would be lessened by the lower average temperature and the reduction in sunlight due to cloud cover. Probably related to reduced productivity is a lessened volume of habitat owing to the lower height of the forest. Both of these features result in a lower food supply. To sustain itself with the same amount of effort as a lowland bird, a highland bird would be expected to accept a broader variety of food items--i.e., to be less of a specialist than a lowland bird. Consequently, one could expect that niches at higher elevations would be broader and fewer and, therefore, that fewer species would be present. Furthermore, a lower food supply would be expected to

yield a low population density of birds in general. Although we have been unable to measure density, our impression based on daily observations at various elevations supports the idea of an inverse relationship between elevation and avian abundance. Under conditions of low density, a substantial number of different species cannot continue to exist because the number of individuals of each species is reduced to the point where extinction may result due to random fluctuations in population size or to poor reproductive success because of difficulty in finding mates. An avifauna of fewer species, with the population density of the average species approximating that of the average species in species-richer environments at lower elevations, would be expected to exist. The fact that species at the higher elevations have larger elevational ranges is probably also a consequence of the relationship between population size and extinction (Terborgh, 1971).

Replacement and Conation.---Accompanying a progressive reduction in species diversity with increasing elevation, there is a change in species composition of the avifauna between one elevational station and the next. Biologists have long been aware of elevational differences in avifaunas of montane areas of North America and have found that the limits of the elevational ranges of many species coincide with the boundaries of the vegetational associations in which they occur (Swarth, 1914). Thus, it has been convenient to classify birds ecologically according to the vegetational zone they inhabit. A certain group of bird species would characteristically be found throughout a particular plant community. Chapman (1921) applied a broad zonal concept to the Andean eastern slope in Perú,

identifying six zones and noting which bird species were characteristic of each. Terborgh (1971), however, found that the distributions of birds in the Apurímac Valley do not conform to zonal patterns. Less than 20 percent of elevational range limits coincided with boundaries of plant associations. The remaining range limits could be attributed to competitive exclusion interactions with related species or to intrinsic responses to physical conditions like temperature which change gradually along the gradient. He found that species replacement along the gradient occurred progressively at an approximate rate of 1 percent of the avifauna for every 10 m change in elevation. There was only a slight indication of an increase in replacement at vegetational boundaries.

One reason for the difference in bird distribution between temperate and tropical mountains lies in the nature of the zones themselves. In North America, a zone is characterized by a few common species of plants which tend to make it uniform vegetationally over its entire elevational extent. Within the Navahonian biotic province in the southern Rockies, the montane "life belt" is recognized by the presence of western yellow pine (Pinus ponderosa) and Douglas fir (Pseudotsuga menziesii), the sabinal belt by pinyon pine (Pinus edulis) and junipers (Juniperus sp), etc. (Dice, 1943). On tropical mountains many more species of plants are present, and zones are defined on the basis of vegetational characteristics and structure, not by indicator species. As I have noted above, continuing, progressive vegetational change with elevation occurs within zones, and zonal boundaries are marked by more extensive changes but not by abrupt discontinuities. With these facts in mind it is easier to understand a progressive elevational replacement in the avifauna.

At the hill forest/ cloud forest ecotone, canopy and understory species of birds react differently. Among the latter group, replacement occurs at about the same rate as within the respective vegetational zones. For canopy species, however, the ecotone is a boundary between two groups of species (Figure 4). Below the ecotone, over a broad elevational range in lowland humid forest and hill forest, occur an assemblage of tanagers and honeycreepers which often form mixed-species canopy flocks. Above the ecotone, this group is replaced by another of similar familial composition and canopy-flocking habits. Only three species (Cyanerpes caeruleus, Chlorophonia cyanea, and Tangara gyrola) are found both above and below the vegetational boundary. Remarkably, there is an elevational belt from about 1300 m to 1450 m where tanager-coerebid flocks of any sort are very scarce.

Familial composition.--There are also some sharp changes with elevation in the familial composition of the avifauna (Table 1). In particular, the percentage abundance of two groups of passerine families, the suboscines and the New World nine-primaried oscines, shifts along the gradient (Figure 5). From the valley floor to 1700 m about 40 percent of the species are suboscines, but above this elevation the percentage decreases until at the top of the range less than a quarter of the avifauna is comprised by this group. Parallel to this decrease with elevation is an increase in the percentage of nine-primaried oscines. The percentage of all other species holds fairly constant. In absolute terms, the number of nine-primaried oscines declines moderately along the gradient, increasing percentage-wise as the total number of species drops, while the

number of suboscines decreases from 60 at 600 m to 12 at the crest of the range. There are several possible reasons for the pattern described. One rests upon food supply. Most suboscine species are insectivorous, while the nine-primaried group includes insect, fruit, nectar, and seed-eaters. There is a marked decrease in the number and variety of insects encountered with increasing elevation in the Vilcabamba.

Perhaps the best indication of this trend was provided by night insects. These may not be entirely available to day-flying birds, but it seems reasonable that their number and diversity reflect the situation for all insects at a locality. During evenings in camp, the glow of the pressure lantern attracted insects to the windows of our tent. In the lowlands, large numbers of moths, cicadas, etc., representing many species, collected on the cloth screening. At higher elevations insects were much fewer in number and variety, and at the crest of the range one saw only an occasional moth. On the other hand, food in the form of fruits, seeds, and flowers was available in quantity at higher elevations. Indeed, the botanists of the expedition had their greatest success in collecting plant specimens with fruits and flowers in the elfin forest, but noted a relative scarcity of plants in fruit or flower at some stations lower down. One may argue that flowering is apt to be more seasonal at lower elevations and that the tall canopy in those areas makes finding fruits and flowers much more difficult. Nonetheless, the food supply available to birds seemed to shift to the disadvantage of insect feeders as we went higher along the gradient.

In familial composition, avifaunas of montane Neotropical forests resemble those of north temperate forests (MacArthur, 1971). The avifauna

at higher elevations in the Apurímac Valley is no exception. However, contrary to MacArthur's statement that tropical mountains have temperate-like forests, the montane forests of the valley are quite unlike any I have seen in North America. Orians (1969) contrasted the stability of tropical montane environments with the strong seasonality of temperate ones and noted that these dissimilar conditions nevertheless support similar avifaunas.

Increases in the abundance of certain families are due to vegetational features present along only part of the gradient. For example, several species of furnariids (including Syndactyla subalaris, S. rufosuperciliata, and Premnoplex brunnescens) feed on insects by searching and probing into the thick growth of bromeliads, orchids, and other epiphytes which cover tree limbs. Below the cloud forest there is rather little epiphytic growth. At the lowest cloud forest station, the number of furnariids increases to 12, compared to 6 at lower stations. As one goes higher, the number decreases again, not from the lack of epiphytes that provide feeding habitat but rather perhaps because of a decrease in the quantity of insects. Similarly, three species of woodcreepers and several species of antbirds gain most of their food by capturing insects flushed by army ant swarms (see p. 86). Army ants do not occur above about 1200 m in the Vilcabamba, and the loss of ant-following niches is reflected in the decrease in formicariids and dendrocolaptid species with elevation.

In the Cotingidae, a change in niches occupied by members of the family is not reflected by any marked change in the percentage abundance

of the family. At lower elevations, most of the cotingids which occur are insectivores, but at the three highest camps the family is represented only by the frugivorous genera Ampelion and Pipreola.

The families Thraupidae and Trochilidae form a substantial portion of the avifauna all along the gradient. The same is true of one of the two common suboscine families, the Tyrannidae. At higher elevations there still appear to be niches for birds which perch and sally after flying insects, niches which no oscine species seem to be able to occupy. Also, some tyrannids, notably Mionectes, eat fruits. Orians (1969) pointed out that the Tyrannidae is also the only Neotropical suboscine family to colonize north temperate environments successfully. The valley's other most common suboscine family, the Formicariidae, shows a striking drop in species along the gradient, due in part to the disappearance of ant-following niches. The inability of antbirds to colonize high-elevation environments may also be attributable to physiological limitations such as intolerance to low temperatures. Above 2200 m only members of the rather distinct Grallariine group occur. It is conceivable that with respect to certain niches they occupy in the lowlands, antbirds are replaced by species of other families higher up. The warblers are potentially a replacing group, since these small insectivores are represented by only one species, a stream-loving specialist, in lowland humid forest where the antbirds are most abundant, but by several species where antbirds are fewer. For example, the general niches of Myrmotherula and Herpsilochmus may be taken over to some degree by Myioborus and Basileuterus (even though some species of these genera overlap). The

factors which make one form competitively superior to another in a given habitat are often subtle. Among the ant-following birds he studied, Edwin Willis (pers. comm.) has suggested that species which perch easily on vertical perches are at an advantage because horizontal perches are scarce in the understory of lowland forest. Ant-following formicariids appear to perch readily on vertical perches. If we assume that this perching ability is a characteristic of understory formicariids in general (not just ant-followers), it might be one of the evolutionary factors responsible for the diversity and abundance of formicariids in the lowlands. In cloud forest, however, the understory is denser and more varied, with no lack of horizontal perches. In this habitat one might predict that understory species of other families would compete more effectively with antbirds. I have no direct evidence that the sort of perches available has in fact influenced the diversity of antbirds or other families at different elevations, but it is this sort of environmental feature which could be operating.

A less conjectural example of elevational niche replacement of certain species of one family by species of another is provided by the Dendrocolaptidae and Furnariidae. At lower elevations, six species of dendrocolaptids occur, of which two follow ant swarms and four are typical woodcreepers, searching the bark for insects as they climb tree trunks and limbs. In the higher part of the gradient, the number of dendrocolaptid species drops. Only one occurs above 2300 m, and none above 2900 m. Above 2000 m there also occur two furnariids which, besides searching epiphytes, glean food from the surface of bark--a large species

(Pseudocolaptes boissonneautii) and a small one (Margarornis squamiger). They are far more generalized in foraging behavior than woodcreepers, reminding the North American observer at times of nuthatches and at times of titmice. However, both species occasionally move and forage along trunks or limbs in characteristic dendrocolaptid fashion. There is a narrow elevational zone around 2100 m where these two furnariids and five dendrocolaptids coexist. The vegetation in that zone is a tall varied forest of large trees. Higher up, however, where trees are smaller and arboreal habitat is reduced, the foraging opportunities for a woodcreeper are greatly lessened. With one exception, the woodcreeper niches appear to be taken over by Pseudocolaptes and Margarornis. These two species have less rigid behavior and can be "part-time woodcreepers," while foraging in a tit-like or nuthatch-like fashion at other times. The exception is an uncommon dendrocolaptid (Campylorhamphus pucheranii) with a long sickle bill which is considerably larger than the two furnariids. One would infer from its unusual bill and large size that it exploits feeding opportunities not available to the two furnariids and that it is not in strong competition with them. The other four cloud forest dendrocolaptids are more similar in body size and bill shape to the two furnariids whose elevational ranges they overlap narrowly.

Vertical distribution.--Although the total number of species at a locality is greatest in lowland humid forest and decreases with increasing elevation, the number of species captured in nets reaches a maximum in cloud forest at about the 1500 m level. The percentage of species present which were netted increased with elevation, rising from 32 percent at

600 m and 46 percent at 685 m to 80 percent at 3475 m (Figure 6). Because less time was devoted to netting at 600 m and a smaller sample was captured there than at any other station but one, the 32 percent figure at this elevation cannot properly be compared with the other stations. At camps between 685 m and 3300 m, however, roughly similar samples (442 to 630 individuals) were made. Also, a larger netting sample usually means more time spent at a camp and more observational time, which is reflected in a higher count of total species present at the locality.

There are several possible explanations for the trend shown in Figure 6. Trivial ones include the lower height of the vegetation at high camps and the placement of nets along ridges where birds might be captured while passing uncharacteristically close to the ground. However, the relationship holds even below 2400 m, where tall forest occurs and where nets were not placed along exposed ridge tops. It may be that in cloud forest, where the understory is denser and the canopy is somewhat more broken than in lowland and hill forest, a greater proportion of the species present actually live in the understory, and fewer in the canopy than at lower elevations. Alternatively, a higher percentage of species netted would also result from broader vertical foraging ranges in a given stand of forest. If all species present in a forest forage from the ground to the top of the canopy, all will eventually be captured in nets placed in the understory provided they are not too large or small in size to escape from the net.

This situation is closely approached in the temperate zone in eastern North America. Nets placed in the understory of tall, humid,

floodplain forest in Maryland captured 431 birds, representing 91 percent of the species known to be present (Stamm, Davis, and Robbins, 1960). Not all species are caught with equal efficiency, but it is important to note that even characteristic canopy species occasionally fly close enough to the ground to be netted. In the tropics, many more species of humid lowland forest birds have relatively narrow foraging ranges. The antbird genus Myrmotherula serves as an example (Terborgh and Weske, 1969). Species which confine their activities to the air space more than two meters above the ground will escape capture no matter how common they may be. My data for the slopes of the Apurímac Valley suggest that in tall forest, bird species at higher elevations tend to have broader foraging ranges than members of lower elevation avifaunas. At no point on the gradient do the data indicate that foraging zones are as broad as in the Maryland study, however.

Body size.--It has been shown that for a number of polytypic species, a subspecies occurring at higher elevations will average larger in size than a lower elevation subspecies (Rand, 1936; Traylor, 1950). Examples were taken from the avifauna of New Guinea and the Bolivian Andes. The results provide an illustration of Bergmann's ecogeographic rule (Mayr, 1963). One of the species which Traylor tested, the flycatcher Myiarchus tuberculifer, occurs in the Apurímac Valley. The race tuberculifer occurs in the lowlands and the race atriceps in cloud forest at middle elevations. This species was not recorded between 600 m and 1520 m. We do not have sufficient data to make a weight comparison, but individuals of the highland form appear larger, as one would expect

from Traylor's work. No other case of intraspecific variation in size correlated with elevation was noted. Indeed, M. tuberculifer is the only species we are aware of in the Apurímac Valley which is represented by elevational subspecies and the only species which has a discontinuous range between the valley floor and the crest, with two discrete populations present. Among other species with wide elevational ranges, populations are continuous, and gene flow appears sufficient to overcome any tendency that might exist for elevational variation.

However, there are numerous examples of genera with two or more species occupying different elevational ranges. Among these are 61 congeneric pairs which are wholly or almost wholly elevationally allopatric. In addition, the respective ranges of these pairs do not appreciably overlap that of any other congener. The size ratios of these pairs were computed in order to test for a pattern which was correlated with elevation. In the case of a series of three or four species (A-B-C, or A-B-C-D), the pairs selected comprised species with adjacent ranges (A-B, B-C, etc.). If appreciable range overlap existed between pair members or between another congener and a pair member, the pair was excluded from consideration. In such cases competitive interactions between coexisting congeners may influence their niches and possibly result in selection for size differences which have nothing to do with elevation. Unquestionably, competition can also occur between individuals which are not congeners and which may lack any close relationship. It is not possible to neutralize this factor completely.

Of the 61 pairs available, weights for one or both members were lacking in 32 cases, leaving 29 in which a comparison could be made

(Table 2). The ratio of average weights of each pair (the higher elevation member to the lower) was computed. Ratios ranged from 0.56 to 2.52. In a pair whose ratio exceeded 1.00 by any amount, the higher elevation member was considered heavier. This occurred in 19 cases. In the other 10, a ratio less than one indicated that the lower elevation species was larger. These results fall short of significance ( $0.05 < P < 0.10$ ), but they do suggest that higher elevation species tend to be larger than their lower elevation congeners. More examples need to be tested in order to confirm this indication, and additional weight data for all species would give more reliable ratios. The median ratio was 1.075; a higher elevation member averages 7.5 percent heavier than its counterpart.

A statistically significant demonstration that highland Andean species are larger than their lowland relatives would be one of the few examples to extend Bergmann's rule to the interspecific level. Other investigations of interspecific size variation have usually not shown a trend. Snow (1954), for instance, found no tendency for species of Parus in cold climates to be greater in size than those in warmer climates. However, Hesse, Allee, and Schmidt (1951) showed that species of penguins with more southern ranges are larger than those ranging nearer the Equator.

The West Side Gradient.---The study of bird distribution along an elevational gradient on the Apurímac Valley's west side was undertaken for two reasons. First, we wished to compare distribution patterns on opposing valley slopes. Second, we needed a knowledge of the species composition on the slope of the Andes proper to have a standard for

evaluating the insular nature of the northern Vilcabamba in terms of endemism and species diversity.

Several difficulties arose in gathering and evaluating data from the west side. Below about 1100 m the climax forest has been largely destroyed, except for an undisturbed area about Luisiana. We were not able, therefore, to secure data on forest birds at lower elevations. At 1660 m, we had a camp at Huanhuachayo, an abandoned, overgrown coffee plantation surrounded by forest. This proved to be an excellent site, rich in birds and conveniently located at the hill forest/ cloud forest boundary. Although most of our effort was concentrated in the primary forest, we netted and observed in secondary habitats as well. It became apparent that lowland species of birds often occur above their "normal" ranges in patches of secondary growth like the Cecropia woodland which had grown up on the plantation. While this fact is itself of interest, it provided records of lowland species at elevations higher than would be expected under undisturbed conditions and tended to give a distorted picture of elevational relationships between species. Therefore, I have in the discussion that follows attempted to use only data which were obtained in primary forest.

A second problem arose because our coverage of the west side was less complete than of the Vilcabamba. In particular, we had only one netline--at 2600 m--between 1900 m and treeline. Although we took observational data along the entire gradient, some portions of it were not thoroughly covered.

There are a number of species which we located in the Vilcabamba but not in the west side, or vice versa. In these situations it is

difficult to judge if a missing species was indeed absent or merely overlooked. One can sometimes judge by the habits of the species: a canopy tanager which is commonly and conspicuously present on one side but not seen on the other is probably really absent there, while little can be said for sure about elusive and rarely encountered forms like the Grallaria ant-pittas.

The trends in bird distribution occurring along the west side gradient were very similar to those present in the Vilcabamba. In particular, the elevational ranges of species relative to each other showed little difference. What changes did occur often involved species whose exact limits are difficult to determine because they are uncommon or hard to detect. However, there was a general upward shift in the ranges of most species with respect to elevation. The birds which are perhaps most conspicuous and whose ranges are thus most easily determined are the canopy tanagers and coerebids. The ranges of these species on the west side are shown in Figure 7, which can be compared with Figure 4 for the Vilcabamba. There is elevational replacement of one group by another, a hiatus where flocks of neither group appear to be present, and the bridging of the hiatus by several of the same species. The upward range shift of birds is explained by the upward shift of about 270 m in vegetational zones. However, the shift in bird ranges is less than that of the hill forest/ cloud forest boundary. This fact suggests that the birds are responding on the one hand to vegetational features and on the other to physical features--principally temperature--which are essentially the same at the same elevation on the two sides of the valley. In the absence

of interspecific competition, the range of a bird species would tend to be centered at the elevation which provided the best compromise between the birds' vegetational and physical optima. Superimposed upon this situation are effects from competitive interactions with other species which may result in a narrowing of the elevational range.

Not only canopy species show upward shifts. The ranges of a group of subcanopy or understory species whose ranges, I feel, are known with sufficient accuracy, are given in Figure 8. I emphasize the general area of the hill forest/ cloud forest boundary because our coverage and knowledge of this region is best.

Although for most species the populations of both sides of the valley are assigned to the same subspecies, there are a number of instances where the populations are considered racially distinct. Below 1700 m geographic isolation is apparently insufficient for differentiation of opposite slope populations to the degree usually required for subspecific designation. But two species which do have distinct forms on the east and west sides have their lower limits in the 1700-1800 m zone, the hummingbird Coeligena torquata and the wren Cinnycerthia peruana. The races of each are well-marked and separable at a glance. Isolation may even be sufficient for differentiation at the species level, since an Otus endemic to the northern Vilcabamba ranges down to 1730 m. However, we did not succeed in recording any Otus in corresponding area of the west side.

In montane areas of New Guinea, Diamond (1972) found that smaller, outlying mountain ranges have fewer bird species than the Central Range, which extends for about 1600 km. Likewise, for birds of northern Andean

páramos, species diversity is correlated with the area and degree of isolation of the páramo (Vuilleumier, 1970). The situation is similar to that for archipelagos, where the number of bird species varies positively with island size and inversely with its distance from the mainland (Hamilton, Barth, and Rubinoff, 1964; Diamond, 1969). Since the northern Vilcabamba can be seen as a large island in a sea of lowlands and the Andes proper as the "mainland," one would predict that the Vilcabamba would have fewer species than the west side. Without a truly complete survey it is difficult to make fine comparisons between localities on the two slopes, and one also is faced with compensating for the general shift in ranges mentioned in a previous paragraph. There are numerous instances of a species absent on one side and present on the other, but many involve species which were recorded only once or twice and whose true status, where they occur, is puzzling anyway. Among species common in the Vilcabamba but absent on the west side are the tanagers Creurgops dentata, Hemispingus superciliaris, and Dubusia taeniata, and the icterid Cacicus holosericeus. Missing from the Vilcabamba but present on the west side are the tanager Pipraeidea melanota and the coerebid Diglossa baritula (both conspicuous canopy flock members), the easily netted thrush Catharus dryas, and the motmot Momotus aequatorialis. The thrush Turdus nigriceps is common on the west slope but inexplicably scarce in the Vilcabamba where it may not have a resident breeding population.

An "island effect," reflected in an avifauna comprised of fewer species, would most likely be present at the uppermost elevations of the Vilcabamba, where the land area is most reduced and most isolated.

Between 3100 m and 3520 m in the Vilcabamba we noted 69 species during 31 days of work at two camps, with a netting sample of 708 birds. On the west side in similar habitat from 3370 to 3600 m we recorded 60 species while spending 10 days at two camps and netting about 320 birds. To allow a more valid comparison, the species total for the west side excludes several species of water, marsh, and puna birds, whose habitats do not exist in the portion of the Vilcabamba we studied. Clearly, the west side was surveyed less thoroughly than the Vilcabamba, and additional work would enlarge the species list for this area. It is not likely, however, that enough additions would be made to show that any substantial reduction in species diversity occurs at higher levels in the Vilcabamba. Similarly, on the basis of available data there seems to be no appreciable species deficit at middle elevations either. The prediction of lower species diversity in the Vilcabamba is not fulfilled.

There is a possibility, however, that the humid lowlands of the Apurímac Valley have a reduced avifauna compared to localities with similar habitats which are less peripherally situated in the Amazon basin. A long slender tongue of lowlands, bordered on each side by mountain ranges, connects Luisiana with the main Amazonian area. A portion of this strip has a dry climate and deciduous forest, which, as will be noted below, is unsuitable habitat for many bird species found at Luisiana. Bounded on three sides by highlands and on the fourth to at least a partial extent by drier vegetation, the humid lowlands of the upper Apurímac have an insular character. At typical Amazonian localities the lowland avifauna numbers about 400 species--for example, J. P. O'Neill (pers.

comm.) has encountered 409 during an extensive survey at 300 m elevation along the Río Curanja in Perú near the Brazilian border. At Luisiana we recorded 284 species in all habitats. Unquestionably, more field work would add to this number, since experience has shown that only a lengthy intensive study can approach completeness (Slud, 1960). And Luisiana would be expected to have a somewhat less diverse avifauna owing simply to its higher elevation. The question is how much of the substantial species deficit is attributable to coverage, how much to elevation, and how much to insularity.

#### The Humidity Gradient

In 1967 Terborgh made a brief raft trip down the Apurímac, Ene, and Tambo to the selva town of Atalaya. The trip was for pleasure, but it led to our awareness of the existence of the dry area along the Río Ene. For several reasons we determined to return to work on the birds of this area. First, it enabled us to work along a gradient where the principle variable and constant conditions of our elevational gradient were reversed: the avifauna could be studied at several stations with reasonably similar elevations but with markedly different annual precipitation. Second, the presence of a lowland area of strikingly different natural vegetation provided an opportunity for testing several predictions based on an earlier paper about colonization at Luisiana (Terborgh and Weske, 1969). Third, the Ene area offered the possibility of discovery of endemic forms, since the situation seemed to parallel that of the dry valley of the upper Río Marañon in northern Perú, which has a highly distinct avifauna.

Two qualifications concerning the results must be mentioned.

First, it was not possible to locate study areas at constant elevations because of the gradual decrease in elevation as the river descends. The highest camp (Boca Mantaro) was situated at 470 m and the lowest (Saoreni) lay 118 km to the north-northwest at 340 m elevation. Thus, some species replacement is expected because of elevation, not humidity. At a 1 percent per 10-meter change (the figure obtained on the elevational gradient by Terborgh, 1971), one would anticipate a 13 percent change from elevation alone. Second, time was not available for a thorough survey at each site, and the lists of species obtained are clearly incomplete. However, the amount of time spent (four or five days) and, consequently, the netting and observational coverage at each of the stations were roughly the same. It is therefore reasonable to make comparisons between the absolute figures obtained at each of the stations. Additionally, ratio figures obtained at stations along the gradient are compared with corresponding figures from Luisiana, since ratios are much less influenced by the thoroughness of coverage. In part of the following discussion Luisiana is considered the southernmost station on the humidity gradient just as it was the lowest on the elevational gradient.

The Boca Mantaro camp was located in humid lowland forest. The habitat was essentially identical to Luisiana, but the elevation was 130 m lower. The Quipachiari camp was situated in tall transitional forest at 360 m. Both Chiquireni (350 m) and Saoreni (340 m) were located near the center of the dry zone in deciduous forest. Because part of the Saoreni area consisted of an impoverished hillside, the height of the vegetation

was lower and the deciduous percentage greater than at Chiquireni. However, these two areas, which are about 22 km apart, have very similar ecological conditions and avifaunas.

One might predict from the insular nature of the dry region and from the lower productivity of the environment that fewer species of forest birds would occur there than in humid forest. The data do not support this prediction, however. We recorded 66 species in the forest at Boca Mantaro, 65 at Quipachari, 67 at Chiquireni, and 50 at Saoreni. That the sharp drop in species number occurred between the two dry region camps is surprising but attributable to the impoverished nature of the habitat at Saoreni, where avian populations were low and the netting yielded a 30 percent smaller sample than at other camps. If one considers total species in all habitats at the camps, the figure for Boca Mantaro is 92, for Saoreni 52, and the others unchanged. The jump in species at Boca Mantaro results from extensive matorral habitat there, while little or no matorral occurred at the others. Therefore, more species would be expected at Boca Mantaro simply from its greater habitat diversity. However, as we shall discuss below, a portion of the dry forest avifauna consists of species limited to matorral in humid areas; so the presence of matorral habitats there would be expected to add relatively few additional species to the total avifauna of the area. More study is needed to determine unequivocally whether the dry region is species-poor compared to the nearest humid areas.

At Luisiana nearly all species which were found in secondary habitats were also found in at least one of two primary habitats, forest or matorral (Terborgh and Weske, 1969). Species could be therefore assigned

to three groups based on the primary habitats that they inhabited: forest species, matorral species, and "generalists" (species common to both). From the colonization work at Luisiana, one could venture two predictions about that portion of the dry region avifauna which was comprised by species found also at Luisiana: 1) Generalists, in view of their apparently greater latitude in habitat requirements, would be represented in greater proportion in the dry region than species found at Luisiana in just one of the primary habitats. 2) By a similar line of reasoning, species which colonize secondary habitats would be more likely to occur in the dry region than non-colonizers. Both these predictions are fulfilled, although the second must be qualified. Seventy-eight species were recorded in the study areas at Chiquireni or Saoreni, or at both. Of these, 14 species were not found at Luisiana and the source habitat of one other species found at Luisiana is unknown, leaving 63 species common to the dry region and Luisiana. We recorded 41.4 percent (18 species) of the Luisiana generalists, but only 28.3 percent (30 spp) of forest species and 24.0 percent (16 spp) of matorral species occurring at Luisiana. Of the generalists inhabiting the dry region, 94.4 percent were also known to be colonizers. A similar high proportion (86.7 percent) of matorral species were also colonizers, but only 53.3 percent of Luisiana forest species found in the dry region had colonizing habits at Luisiana. The second prediction, then, is confirmed for general and matorral species, but not for forest species. It appears that for humid forest species, the ability to colonize secondary habitats and the ability to inhabit deciduous forest are relatively independent. A substantial

portion of the humid forest species occur in dry forest not because of their ecological versatility but rather because the particular forest habitat features necessary to them still persist there despite increased seasonality and aridity.

Although matorral and the dry deciduous forest are structurally and floristically quite different, they share certain features. Compared to humid forest, both these habitats are drier and more sunlit, and have lower vegetation. It is therefore understandable that a number of matorral species which shun humid forest do inhabit the deciduous forest. In several genera a matorral species appears to be competitively superior in the dry region to a humid forest congener, which has been excluded: the dove Leptotila rufaxilla has been replaced in the dry forest by L. verreauxi, the puffbird Monasa morphoeus by M. nigrifrons, the spinetail Synallaxis cherriei by S. gujanensis, the antbird Myrmoborus myotherinus by M. leucophrys, the becard Pachyramphus marginatus by P. polychopterus, and all humid forest Euphonia species by E. lanirostris.

At Boca Mantaro 47.0 percent of all forest birds recorded were netted. For the other camps the figures are: Quipachiari, 49.2 percent; Chiquireni, 59.7 percent; Saoreni, 62.0 percent. The higher percentages at the dry camps are attributable to the lower height of the vegetational column there. At the same time, the figures reveal that fewer species in this area forage exclusively in the upper strata of the forest, suggesting that vertical distribution is less specialized than in humid forest.

The familial composition of the avifauna at the gradient's stations is shown in Table 3. The most conspicuous feature is the scarcity of frugivorous birds in the dry region. No toucans were present, only one

species each of trogon and pigeon, only two parrots and three tanagers. Conversely, certain insectivorous families form a greater portion of the dry region avifauna than in humid areas, notably the Tyrannidae. We were impressed in particular by the diversity and abundance of birds that feed on large insects. Two species each of caprimulgids, motmots, and cuckoos were present, along with the Boat-billed Flycatcher, Megarhynchus pitangua. While also occurring in humid areas, small owls of the genera Otus and Glaucidium were more numerous in the dry region, and the large puffbird Monasa nigrifrons was ubiquitous.

Of the bird species noted in the dry region, 17.9 percent (14 spp) were not found in humid forest at Luisiana or Boca Mantaro. Besides these 14, five more species were found only in the transitional forest at Quipachiari. Of the total of 19, we know from work in the Sira that four are humid forest birds. Of the remainder, three species--the gnatcatcher Polioptila plumbea, the cotinga Casiornis rufa, and the nightjar Caprimulgus rufus--are characteristically dry forest species. The latter two were not previously known from Perú. Their populations are endemic to the Río Ene dry region, and that of Casiornis is racially distinct. The preferred habitat of the remaining 12 species is unknown to me, but all occur elsewhere in Amazonian Perú, and most would therefore be expected to be either matorral or humid forest birds. What is clear is that the region of seasonally dry, deciduous forest shows little endemism in its avifauna, which is composed largely of species also occurring in adjacent humid areas. This result is in agreement with statements by MacArthur and Wilson (1967) on habitat islands in mainland situations.

Ecological Sorting Mechanisms

According to the competitive exclusion principle, two species which occupy the same niche cannot coexist (Mayr, 1963). One will prove to be competitively inferior to the other and will be eliminated. Niche similarities are normally greatest among closely related species because of their genetic similarities. It is therefore to be expected that competition would be most severe between sympatric congeneric species and that there would be strong selection for the evolution of differences which minimize competition (Lack, 1944). A glance at the list of species found in the Apurímac Valley (Appendix 1) shows that there are numerous genera represented by more than one species. In this section I shall examine these genera and the niche differences, called ecological sorting mechanisms by Diamond (1972), which have evolved to allow the coexistence of member species. Here and throughout this paper I follow Meyer de Schauensee (1966) on the taxonomic status of forms, except where noted otherwise. Elevational ranges and body weights of Apurímac Valley birds are found in Appendix 1, and data on relative abundance at various elevations are given in Appendix 2.

At the outset, it is important to note that the mere existence of niche differences does not prove that they arose in response to selective pressures for the reduction of competition. Selander (1971) and Mayr (1963) have emphasized this point. The ecological differences described in the pages that follow are facts, but it can only be inferred that they evolved in response to competition--other selective factors may be responsible. Some specific facets of this problem will be considered later.

Terborgh (1971) has shown that in many genera, the species occupy exclusive elevational ranges and do not, in fact, coexist with their congeners. This elevational separation occurs in more than 50 percent of the cases examined and is the most important and widespread ecological sorting mechanism in the Apurímac Valley. Others include habitat selection, vertical stratification, differences in feeding behavior and food habits, and differences in size and structure. The key features lessening niche overlap between close relatives are a high degree of spatial segregation or the exploitation of different food sources in the same habitat. For some species pairs, ecological differentiation involves one mechanism, while for others it is more complex, involving a combination of several. A discussion of the various sorting mechanisms follows.

Elevational segregation.—Two populations which were originally a single species may diverge genetically under conditions of geographic isolation until they are reproductively isolated. If secondary contact is established, they cannot successfully establish sympatry unless they have diverged ecologically (Lack, 1944). Otherwise, competitive exclusion will prevail. If two formerly conspecific, montane allospecies have diverged to the point where, while still similar in most ecological requirements, they have different elevational optima, it may be possible for each to invade that portion of the range of the other in which it is competitively superior. A situation very similar to the former geographic allopatry continues, for after the new ranges stabilize, the two forms are allopatric elevationally although sympatric in the geographic sense. They come into contact only on their common elevational boundary. Competitive interactions in the area of contact would be expected to

reinforce ecological divergence. It appears that this is the sort of segregation most readily evolved by geographic isolates, since it is the mechanism most frequently illustrated by congeners.

If speciation is recent, one would expect the forms to be similar in appearance, structure, behavior, and habitat preference, and to have elevational optima which were not widely separated. Under these conditions, one would expect the abundance of the lower elevational form to increase progressively at successively higher stations along an elevational gradient. Only slightly higher than the station of maximum abundance would come the upper boundary of its range, and it would be replaced by its congener, which would be at maximum abundance in the region just above its lower boundary. At still higher points along the gradient, the abundance of the higher elevation form would drop progressively. Because the region of the boundary is near-optimum habitat for each form in the absence of the other, one would expect no broad hiatus there which is unoccupied by either. Conversely, because their ecological similarity does not allow coexistence, one would expect the ranges not to overlap.

Among Apurímac Valley species, the situation described above is most nearly illustrated by the two Pseudotriccus flycatchers (Figure 9) and by the woodcreepers Xiphorhynchus ocellatus and X. triangularis (Figure 10). These and other genera are discussed in greater detail below. Sometimes there is a well-defined boundary with replacement in a short elevational distance, but the respective elevations with ecologically optimum conditions for each species are further apart, as in the flycatchers Ochthoeca pulchella and O. frontalis (Figure 11).

Other species pairs for which elevation is the sole apparent ecological sorting mechanism and for which the common boundary between elevational ranges is considered to be determined by competitive interaction are Tinamus major and T. tao, Geotrygon montana and G. frenata, Malacoptila fusca and M. fulvogularis, Eubucco richardsoni and E. versicolor, Picumnus aurifrons and P. cirrhatus, Xiphocolaptes orenocensis and X. promeropirhynchus, Philydor ruficaudatus and P. erythrocerus, Xenops minutus and X. rutilans, Chamaeza campanisona and C. mollissima, Grallaricula flavirostris and G. ferruginepectus, Scytalopus femoralis and S. unicolor, Chloropipo holochlora and G. unicolor, Myiodynastes maculatus and M. chrysocephalus, Rhynchocyclus olivaceus and R. fulvipectus, Pogonotriccus ophthalmicus and P. poecilotis, Vireo olivaceus and V. gilvus, Myioborus miniatus and M. melanocephalus, and Iridosornis analis and I. reinhardti. In each case the member of the pair with the lower elevational range is listed first. Elevational segregation appears to be present in the genera Pionus, Ciccaba, and Chalcostigma but in these genera one member of the species pair was so rare that we know little of its actual status and range.

Terborgh (1971) presented evidence that competitive interactions between congeners actually do determine elevational ranges. He showed that the larger the number of replacing species in a congeneric elevational series, the narrower the elevational range of each. The findings of Diamond (1972) in New Guinea are even more conclusive. In certain genera, two species form a replacing series on one mountain range, but on another range one of the species is absent. In such a case, the elevational range of the remaining congener is broader and includes most or all of

the gap where the missing member would have been expected to occur. Similar cases exist in the Andes (Terborgh and Weske, unpublished data).

On the other hand, one sometimes finds that the ranges of two congeners are separated by a broad elevational hiatus where neither occurs. There are several explanations for this situation. In some cases our survey may simply have failed to detect the presence of a member of the pair in the hiatus even though it occurred there. A second possibility is that the two species are prevented from expanding their ranges into the intervening area by the presence there of a competing form (or forms) which is closely related but not congeneric. The Cracidae and Momotidae seem to provide examples of such distributions. It is also possible, that the ranges are limited by competition with a less closely related species or with a group of species whose collective ecological requirements close the niche in the area of the hiatus. In such cases it is exceedingly difficult to identify which species are competitors, as relationship provides no clue. A possible example of woodcreeper niches occupied at higher elevations by furnariids was discussed earlier, although no hiatus was involved.

A final possibility for the existence of an elevational hiatus between two congeners is that their ranges are limited by factors other than competition. During geographic separation the ecological requirements of the incipient species may have diverged so markedly that they later, following the breakdown of geographic barriers, became macrogeographically sympatric without coming into actual contact. The congeners may differ greatly in their tolerance to temperature, cloudiness, or other physical features of the gradient. These differences did not arise

nor become reinforced as a response to mutual competition. Because of their differing elevational ranges, the congeners usually occur in dissimilar habitats, and it is impossible to judge whether they are responding directly to physical features of the gradient or indirectly, through preference for a particular type of vegetation. In some cases the intervening elevation may in other parts of the Andes be occupied by a third congener which because of local conditions is absent in the Apurímac Valley. Pairs of species with widely separated elevational ranges are Accipiter poliogaster and A. striatus, Buteo magnirostris and B. albigula, Claravis pretiosa and C. mondetoura, Caprimulgus rufus and C. longirostris, Dendrocincla fuliginosa and D. tyrannina, Cranioleuca curtata and C. albiceps, Lepidocolaptes albolineatus and L. affinis, Sclerurus caudacutus and S. mexicanus, Herpsilochmus rufimarginatus and H. pileatus, Drymophila devillei and D. caudata, Formicarius analis and F. rufipectus, Platypsaris minor and P. rufus, Miobius atricaudus and M. villosus, Cyanocorax violaceus and C. yncas, Thryothorus coraya and T. euophrys, and Troglodytes aedon and T. solstitialis.

In another group of genera, the species pairs are largely segregated elevationally but there is a limited overlap in ranges. The overlap zone may in some cases be attributable to the presence of wandering immature birds. In most cases of overlap, however, there is some other ecological sorting mechanism involved besides elevation.

Segregation by habitat.--I previously mentioned certain species which occur at different elevations and seem to have different habitat preferences as well. One example is the flycatcher genus Myiobius. M.

atricaudus occurs in matorral and second-growth on the valley floor. M. villosus inhabits hill forest. A third species, M. barbatus, which lives in lowland humid forest in other parts of Perú, was not found in the Apurímac Valley. There are a number of congeneric pairs which exist at the same elevation but are ecologically separate because of different habitat selection. In most cases one member inhabits matorral and the other the adjacent humid lowland forest on the valley floor. With the matorral species given first and the forest species second, some examples are: Leptotila verreauxi and L. rufaxilla, Monasa nigrifrons and M. morphoeus, Automolus dorsalis and A. ochrolaemus, Myrmoborus leucophrys and M. myotherinus, and Tityra inquisitor and T. semifasciata. Although occasionally seen together, the vulture Cathartes melambrotos forages mainly over undisturbed forest while C. aura soars over areas cleared for agriculture. The two Daptrius caracaras may separate ecologically in this manner also, with D. ater an open country bird and D. americanus more in the forest. The tanager Tachyphonus rufiventer is a common forest species while our lone observation of T. rufus was in sparse second-growth at the edge of a pasture. Myiornis ecaudatus is a tiny flycatcher inhabiting the subcanopy of humid lowland forest and hill forest. We also saw Myiornis albiventris once in humid forest, but it becomes abundant in the dry deciduous forest along the Río Ene where M. ecaudatus is absent. The Torrent Flycatcher, Serpophaga cinerea, is always found along rushing mountain streams, as its name suggests. Its congener, S. hypoleuca, was seen only at the edge of the Apurímac's broad sandy shore in a part of the matorral comprised of young, willow-like trees about three meters in height.

Vertical stratification.--Closely related species can exist together in the same habitat if their foraging tends to be confined to mutually exclusive vegetational strata. The simplest and clearest example of this segregating mechanism is provided by the vireo genus Hylophilus (Terborgh and Weske, 1969). H. ochraceiceps inhabits the understory of humid lowland forest and hill forest, while H. hypoxanthus is a canopy dweller in this same habitat. The vertical foraging zones of the two species appear to be entirely separate.

It is possible that vertical foraging preferences like those of Hylophilus greenlets evolved during allopatry and not as a result of selection for mechanisms that avoid mutual competition. However, Willis (1966) has demonstrated that competitive interactions do affect the vertical dimensions of the foraging domain of the woodcreeper Dendrocincla fuliginosa.

As stated in a previous section, available evidence suggests that vertical stratification is a more important factor in restricting niches and reducing competition in tropical forests than in temperate zone forests. Additional examples are cited below.

Feeding behavior and food preference.--A significant cause of competition is eliminated if two species exploit different food resources. Either the food itself may be different or else the same food items may be obtained in separate ways. I have few examples from the Apurímac Valley of congeners which employ this mechanism to avoid competition because I analyzed stomach contents of very few specimens. Also, an

analysis of comparative feeding behavior requires an intensive study of a few forms, rather than a study which encompasses an entire avifauna.

Observation has provided some clues to niche differences in the tanager genus Tangara, where there are many species and ecological relationships are complex. Most of the species seem to feed on insects and fruit by foraging in canopy foliage in what can best be described as conventional tanager fashion. T. ruficervix and T. chrysotis, two cloud forest species, often feed in this manner, but each also obtains food in a way which, in my experience, is unique for the genus. T. ruficervix makes sallies and appears to hawk flying insects, a tyrannid-like behavior seen also in Lanio versicolor, a lowland tanager. T. chrysotis creeps along moss-covered branches, foraging in the manner of a nuthatch (Sitta). Certain similar-sized dendrocolaptids avoid niche overlap through differences in feeding behavior: Xiphorhynchus guttatus searches the surface of bark for food, whereas Dendrocolaptes woodcreepers feed primarily on insects flushed by army ants.

Structure and size.--Congeneric species which are dissimilar in size or in bill shape may be able to exploit different food sources and coexist, even if their behavior seems similar. A larger bird has greater strength, but a smaller one is more agile. Differences in bill shape facilitate securing food from different situations. The speciation process can be considered to be completed when morphological differentiation is sufficient to allow sympatry in the very closest sense (Lack, 1944).

Size appears to be the sorting mechanism permitting coexistence of the following pairs of species. In each case the larger is listed

first, and the ratio of average weights is given if data is available: the parakeets Aratinga leucophthalmus and A. weddellii, the hummingbirds Colibri coruscans and C. thalassinus (1.76), the woodcreepers Dendrocolaptes picumnus and D. certhia (1.19), the antbirds Hylophylax poecilonota and H. naevia (1.39), the flycatchers Mecocerculus leucophrys and M. stictopterus, and the tanagers Dubusia taeniata and D. castaneoventris (1.44). Although similar in size, the finches Catamenia homochroa and C. inornata have differently shaped bills and are able to coexist. Habitat as well as size differences reduce niche overlap in the finch genus Saltator. S. coerulescens exceeds S. maximus in weight by a factor of 1.37, and both inhabit matorral and second-growth, but S. maximus is found also in forest, where S. coerulescens is absent. A similar situation concerns the cuckoo genus Piaya, whose two species segregate by size, vertical stratification, and, partly, habitat. We lack weight data, but P. cayana is about double the size of P. minuta, with which it coexists in matorral and some second-growth formations. P. minuta lives close to the ground and is occasionally netted, but the commoner P. cayana stays high and does not enter nets. P. minuta is absent from mature forest and is strictly a lowland bird, while P. cayana inhabits various types of primary forest and ranges from the valley floor to the lower boundary of the elfin forest. A series of species which sort out ecologically by size need not be restricted to one genus. Along the lower Apurímac three kingfishers, representing two genera, occur together: the small-sized Chloroceryle americana, the medium-sized C. amazona, and the large Ceryle torquata. In Amazonia as a whole there are five species (including these

three) which form a size series (MacArthur, 1971). Certain differences in habitat preference exist, as well.

Nearly all the genera discussed so far are represented in the Apurímac Valley by two species. In the next section I discuss other genera in which niche relationships are often more complicated because three, four, or more species are present in the valley. Meanwhile, it is convenient to mention here several genera with two species for which the sorting mechanisms are not clear at present. These include the parakeets Bolborhynchus andecola and B. lineola, the quetzals Pharomachrus antisianus and P. pavoninus, the furnariids Syndactyla subalaris and S. rufosuperciliata, the flycatchers Myiozetetes similis and M. granadensis, the tanagers Ramphocelus carbo and R. nigrogularis, and the grosbeaks Pheucticus aureoventris and P. chrysopheplus. Some of the species listed above are rare in the valley and therefore poorly known to us. The hummingbirds Amazilia chionogaster and A. lactea segregate to some extent elevationally, but there is a broad zone of overlap where the niche differences are not apparent. The same situation applies to the flycatchers Mionectes striaticollis and M. olivaceus. Two honeycreepers of the lowland forest canopy, Dacnis cayana and D. lineata, may segregate on a size basis, but we lack weights for either species.

#### Niche Relationships Within Selected Genera

The accounts which follow illustrate the manner in which ecological sorting mechanisms lessen niche overlap in various genera represented by three or more species in the Apurímac Valley. Occasionally,

a discussion includes members of several related genera which appear to appear to interact ecologically.

Crypturellus.--Four species are present. In the humid lowlands, there are two small species in the forest, C. soui and C. tataupa, and one larger species, C. atrocapillus, which is in matorral and second-growth. All are replaced elevationally by C. obsoletus, a bird of hill forest and the lower cloud forest. How C. tataupa and C. soui segregate in lowland humid forest is not clear. In the dry forest C. tataupa and C. atrocapillus occur together and segregate by size, while C. soui is absent.

Broad elevational and habitat overlap occurs between Crypturellus and Tinamus. Sympatric forms seem to sort out by size: the larger T. tao and smaller C. obsoletus in hill forest, and the larger T. major and smaller C. soui and C. tataupa in lowland humid forest.

Falco (Falconidae).--F. deiroleucus and F. rufigularis coexist in humid forest and sort out by size, deiroleucus being the larger. F. sparverius, which was seen once, is probably a vagrant from the Sierra, where it is common.

Penelope and Aburria (Cracidae).--Three species of guans form an elevationally replacing series, the middle member of which belongs to a different genus from the end members. P. jacquacu inhabits the lowlands and hill forest. It is replaced in lower cloud forest by A. aburri, which in turn is replaced in upper cloud forest by P. montagnii.

Odontophorus (Phasianidae).--Four species form an elevationally replacing series. From lowest to highest they are O. stellatus, O.

gujanensis, O. speciosus, and O. balliviani. Members of this genus are shy and rarely encountered. We do not have a thorough knowledge of their ranges.

Columba (Columbidae).--The pigeons separate by habitat and elevation but there is some overlap. C. fasciata is limited to higher elevations, and C. plumbea is most common at middle elevations although it occurs also in lowland humid forest. C. speciosa is strictly a matorral species. C. cayennensis is present in both matorral and lowland forest. It is usually found in sizeable flocks, whereas plumbea and speciosa are seen singly or in groups of two or three.

Ara (Psittacidae).--We lack knowledge of the macaws, which occur only in the lowlands. All but A. severa are uncommon. There are two large species, A. macao and A. militaris, and two smaller ones, A. severa and A. couloni. The two larger species may segregate by nest-site preference, since A. militaris is regularly seen only in the vicinity of cliffs. How A. severa and A. couloni sort out is unknown.

Amazona (Psittacidae).--Two lowland species segregate by size, with A. farinosa larger and A. ochrocephala smaller. These are replaced at higher elevations by A. mercenaria.

The lowland parrot genera as a group form a size series comprised, from largest to smallest, of Ara, Amazona, Pionus, Aratinga, Pyrrhura, and Forpus. At higher elevations the series shortens to Amazona and Bolborhynchus.

Otus (Strigidae).--These small owls form an elevationally replacing series of four species with no apparent overlap. From lowest to highest

they are O. watsonii, O. ingens, Otus sp, and Otus albogularis. In hill forest there is a hiatus where we failed to locate an Otus. At this elevation in the Sira, O. guatemalae was present. We also did not find an Otus in matorral, a habitat occupied by O. choliba in other parts of Perú.

Glaucidium (Strigidae).--The pigmy-owls form a three-fold elevational series including G. brasilianum in the lowlands (principally matorral and dry forest), G. minutissimum (once in lower cloud forest), and G. jardiini (upper cloud forest and elfin forest). The situation may prove to be less neat than portrayed here since Paul Schwartz (pers. comm.) has tentatively identified a vocalization taped at night in transitional forest at 370 m as belonging to G. minutissimum. If verified, the broad overlap between brasilianum and minutissimum would need to be explained.

Phaethornis (Trochilidae).--Two larger species, P. superciliosus and P. guy, form an elevational series, meeting and overlapping slightly at the lowland humid forest-hill forest boundary. P. guy occurs in hill forest and lower cloud forest. Coexisting with superciliosus on the valley floor is P. hispidus. The two seem to segregate by a combination of size and habitat preference. P. hispidus is shorter-billed and somewhat lighter. Its preferred habitat is tall matorral, especially where Helioconia forms a part in the understory, although it is also found in forest. On the other hand, P. superciliosus is primarily a forest species which occasionally turns up in matorral. Both species also inhabit the dry forest. The weight and bill length ratios (superciliosus to hispidus)

are 1.17 and 1.16, respectively. The fourth member of this genus of understory hummingbirds in the Apurímac Valley is P. stuarti. The range of this tiny forest species overlaps those of its congeners, from which it sorts out by size. The weight ratios are 1.73 (guy to stuarti), 1.98 (superciliosus to stuarti), and 1.69 (hispidus to stuarti).

Heliodoxa (Trochilidae).--H. rubinoides and H. leadbeateri replace each other elevationally, with rubinoides having the higher range. In hill forest H. leadbeateri shares its range with H. branickii. Segregation is by size, for leadbeateri averages 1.59 times heavier than its smaller congener.

Coeligena (Trochilidae).--Three species of similar-sized hummingbirds in this genus form an elevational series, but there is substantial overlap in ranges (Figure 12). The broader overlap is between C. torquata and C. violifer, which seem to sort out by habitat preference. C. torquata is most common in upper cloud forest and C. violifer in elfin forest. Netting data indicates that their respective elevational optima are about 600 m apart. In the area where both exist, each can find its preferred habitat, for both elfin forest and cloud forest occur according to local conditions of topography and exposure. The overlap between C. torquata and the lowest member of the series, C. coeligena, is narrow, but each species is at near-maximum abundance in the presence of the other. Their elevational optima are only about 100 m apart. The sharp drop-off in the abundance of each species not far above or below its optimum elevation suggests that competitive exclusion determines elevational range limits. However, I am unaware of any differences in other aspects of the niches of

the two species which account for the fact that both coexist and are numerous from 2100 m to 2250 m.

Metallura.--In this genus of elfin forest hummingbirds, the same niche on opposite sides of the valley is occupied by different species. M. eupogon is abundant on the west side, while M. aeneocauda, a form similar in size and structure, occurs in the Vilcabamba and is uncommon. Coexisting with each of these allopatric species is the smaller form M. tyrianthina, which sorts out by size. Its weight ratio with M. eupogon is 1.27. We lack weights of M. aeneocauda.

Trogon (Trogonidae).--The trogons are puzzling ecologically since there is wide sympatry without conspicuous sorting mechanisms. The two species which resemble each other most, T. collaris and T. personatus, do however replace each other elevationally. We lack weights for the lowland species, but T. melanurus appears in skins to be larger than T. curucui and T. viridis and may segregate by size.

Momotidae.--The motmots form a three-fold elevationally replacing series in which the middle member, Baryphthengus ruficapillus, is generically different from the upper member (Momotus aequatorialis) and the lower (M. momotus). In the dry forest, M. momotus coexists with a smaller motmot, Electron platyrhynchum, from which it may sort out by size (weight ratio 1.71).

Eubucco and Capito (Capitonidae).--E. richardsoni and E. versicolor replace each other elevationally, as I have mentioned earlier. In the lowlands however, E. richardsoni coexists with C. niger. Both have similar feeding behavior--searching for insects in curled up, dead leaves

which have become caught in the canopy vegetation. Ecological segregation is by size, as C. niger probably weighs twice as much as E. richardsoni.

Aulacorhynchus (Ramphastidae).--Three toucanets of this genus comprise an elevationally replacing series, with a limited amount of overlap where ranges meet.

Picidae.--In the woodpeckers there is a pattern of elevational replacement within genera and ecological segregation by size between genera. Three-fold replacing series are comprised by Veniliornis affinis, V. dignus, and V. nigriceps, by Piculus leucolaemus, P. rubiginosus, and P. rivolii, and by Phloeocastes melanoleucos, P. rubricollis, and P. haematogaster. There is, in addition, a fourth species of Veniliornis which sorts out by habitat preference: V. passerinus and V. affinis both occur in the lowlands, but passerinus inhabits matorral and second-growth while affinis is strictly a forest bird.

In cloud forest and hill forest, there is customarily a large woodpecker (Phloeocastes), a medium-sized one (Piculus), and a small one (Veniliornis), with the particular species depending on the elevation. The weight ratio is approximately 5.0: 1.7: 1.0. Inclusion of the piculets (Picumnus), which weigh less than half as much as a Veniliornis, expands the size series to four. Correlated with the reduction in arboreal habitat, there is a reduction in number of woodpecker species at higher elevations. As one goes higher along the gradient, Phloeocastes reaches its upper limit at 2150 m and Piculus drops out at 2830 m. Only Veniliornis reaches tree-line.

In the lowlands, ecological relationships are more complex, since species of Centurus, Celeus, and Dryocopus are present in addition to members of genera given above. Segregation is accomplished by differences in feeding behavior (Short, 1970) as well as in size and habitat selection.

Xiphorhynchus (Dendrocolaptidae).--Three members of this genus of medium-sized woodcreepers are found in the valley and form an elevationally replacing series. The abundance curves for X. ocellatus and X. triangularis are truncated at the elevation where the two species meet, indicating that the common boundary to their ranges is determined by competitive exclusion (Figure 10).

Synallaxis and Schizoaeca (Furnariidae).--All members forage close to the ground. Four species of Synallaxis occur in the lowlands. These appear to segregate on the basis of habitat and size. S. cherriei is found in the understory of undisturbed humid forest. S. cabanisi, S. gujanensis and S. albigularis are all matorral birds. Their weight ratios are 1.37: 1.12: 1.00. Although all three are found together, albigularis is not common in the denser matorral areas, as its infrequency in our netting records reveals. It prefers edge habitats and sparser vegetation and is encountered most commonly in second-growth like hedgerows and brushy pastures. S. cabanisi, in contrast, is common in the dense matorral vine tangles and thickets. It colonizes second-growth that is sufficiently dense. S. gujanensis has the widest habitat preference, being found in dense and sparse matorral, the deciduous forest down-river, and various sorts of second-growth and cultivated areas. It also appears to be the most aggressive colonizer, since we found it once

on the west slope at Huanhuachayo in the abandoned plantation, which it could reach only by passing through over a mile of unsuitable forest habitat. We netted it once in forest at 600 m about one-fourth mile from proper habitat. A pair of S. cabanisi netted in "forest" at 685 m were in reality caught next to a stream flowing through a "bright" in the forest, created by a large gap in the canopy. The thick viny growth present closely resembled the typical habitat of the species.

Above the valley floor, there is a replacing series of species. S. azarae occurs at cloud forest elevations but not in undisturbed forest. We found it common at 1560 m in a large open area of unknown origin which was densely grown with Chusquea, at 1660 m in the Huanhauchayo plantation, and in several naturally occurring areas of second-growth. One may predict that when the cloud forests of the Apurímac Valley are cut, this species will be very common in the resulting disturbed habitats. In nature its preferred habitats probably occur most commonly on steep slopes when the vegetation grows back after landslides.

S. unirufa replaces azarae at somewhat higher elevations and is a bird of upper montane elfin and cloud forests. Elfin forest may be its preferred habitat, for on the West slope, where elfin forest is absent at "proper" elevations for this species, we failed to find it.

At still higher elevations, Schizoaecca fuliginosa overlaps unirufa elevationally and ultimately appears to replace it, ranging upward to the very limit of woody vegetation. This genus is closely related to Synallaxis, and fuliginosa resembles unirufa in size, structure, and foraging habits. How it and unirufa minimize competition in the zone of overlap is not apparent.

Thripadectes (Furnariidae).--The three members of this genus replace each other elevationally. Their ranges do not overlap at all.

Thamnophilus (Formicariidae).--This genus of antshrikes is large, with members which are diverse in plumage pattern and bill structure. Five species are present in the valley. The sole representative above the valley floor is T. caerulescens, which occurs in the lower portions of cloud forest. In the humid lowlands, T. doliatus occupies matorral and second-growth, while T. schistaceus and T. murinus inhabit the forest. The latter two are very similar in appearance and vocalizations, but segregate by structure and size. T. schistaceus has a decidedly heavier bill than murinus and outweighs it by a factor of 1.22. Niche separation is less clear-cut in the dry lowlands, where T. aethiops appears and where doliatus enters the forest. T. murinus continues to be present. T. aethiops, a rather large, heavy-billed species, may replace schistaceus in the dry region, although they coexist in the transitional forest.

Thamnomanes and Dysithamnus (Formicariidae).--On the basis of behavioral evidence communicated to him by E. Willis, Meyer de Schauensee (1966) transferred T. ardesiacus from the genus Dysithamnus to Thamnomanes. It therefore comes as a surprise--but may be only coincidental--that T. ardesiacus and Dysithamnus mentalis have mutually exclusive elevational ranges, suggesting replacement, while Thamnomanes schistogynus and T. ardesiacus occurred together in the humid lowland forest at 470 m. Willis (pers. comm.) informs me that schistogynus and ardesiacus have flycatching foraging habits and that the latter tends to feed nearer to the ground than the former. T. schistogynus has a tyrannid-like bill,

quite unlike that of ardesiacus, whose bill is remarkably similar to that of Thamnophilus murinus.

Myrmotherula (Formicariidae).--The lowland members of the genus Myrmotherula provide an excellent example of ecological segregation by vertical stratification (Terborgh and Weske, 1969). Five species coexist in lowland humid forest. M. brachyura forages in the lower canopy and upper subcanopy, M. menetriesii and M. ornata in the lower subcanopy, and M. axillaris and M. haematonota in the understory. M. brachyura and M. menetriesii were never taken in our forest nets, and M. ornata was caught only rarely. M. ornata, which possesses the stoutest bill of the group, probably sorts out by virtue of this structure and of larger body size from M. menetriesii. M. axillaris forages somewhat higher in the understory than M. haematonota although their vertical distributions overlap. M. haematonota is primarily a hill forest species and M. axillaris a bird of the flat lowlands. Where one is common, the other is scarce. A comparative behavioral study of these Myrmotherulas species might reveal additional mechanisms for segregation. Wiley (1971) has recently shown that in Panamá, M. axillaris and M. fulviventris sort out by foraging behavior. M. fulviventris, a species not present in Perú, probes curled dead leaves for food, whereas axillaris gleans from live foliage or makes sallies.

In the dry forest and the transitional forest, only two species were present: M. axillaris in the understory and M. brachyura in the higher strata. The valley's sixth species, M. schisticolor, is a cloud forest bird whose range lies entirely at elevations above those of the other five.

Grallaria and Myrmothera (Formicariidae).--Our information on elevational ranges indicates a replacing series of six species of ant-pittas, the largest series in the valley. There is no Grallaria in lowland humid forest, but an ant-pitta of the closely related genus Myrmothera (M. campanisona) is present there. Then, in order with increasing elevation, come Grallaria guatemalensis (in hill forest), G. squamigera (lower cloud forest), G. erythroleuca (upper cloud forest), G. rufula (elfin forest), and G. andecola (on west side only in isolated copses in the puna). Because ant-pittas are shy and because they are so terrestrial that they seldom enter nets, they are infrequently noted. A more thorough knowledge of their ranges might indicate some overlap, particularly between G. squamigera and G. erythroleuca, which were recorded at elevations not far apart. If they coexist, these two species could sort out on a size basis, since G. squamigera is the largest Grallaria in the valley.

At middle elevations, species of Grallaria coexist with Grallaricula ant-pittas. Besides being much smaller, members of Grallaricula (at least G. flavirostris) seem to be much less terrestrial, judging from the higher frequency of capture in nets.

Pipreola (Cotingidae).--Four species of these heavy-bodied, fruit-eating cotingas inhabit the valley's middle and upper elevations. They appear to form two elevational series of two replacing members each. P. frontalis and P. intermedia comprise one series, and P. pulchra and P. arcuata the other. There is no overlap in ranges between members of each species pair. However, pulchra and frontalis occur together at

middle elevations, as do arcuata and intermedia higher up. The coexisting congeners sort out by size. The weight ratio for pulchra/frontalis is 1.30 and for arcuata/intermedia it is 1.99. Pipreolas are much commoner on the west slope than in the Vilcabamba, except for P. arcuata, which is fairly numerous in both areas.

Pachyramphus (Cotingidae).--In this genus there is a three-fold elevational series of forest species whose ranges are exclusive and have rather wide hiatuses between. A fourth species, P. polychopterus, inhabits matorral and second-growth on the valley floor, remaining spacially separate by habitat preference from P. marginatus, the humid lowland forest species. In the dry forest, marginatus drops out and is replaced by polychopterus.

Coexisting at some stations with a Pachyramphus is a larger becard of the genus Platypsaris. The two genera are structurally similar, but size differences allow ecological segregation. Platypsaris rufus and Pachyramphus albogriseus occur together in cloud forest, and Platypsaris minor and Pachyramphus marginatus probably do in the lowlands. I lack weights for some of these species, but a ratio of about 2:1 is indicated in each case.

Pipra and Machaeropteryx (Pipridae).--The manakins also segregate by size and elevational distribution. The larger members of the genus Pipra form a three-fold replacing series. Distributional limits coincide fairly closely with the boundaries of habitat zones. P. pipra is found in cloud forest, P. chloromeros in hill forest, and P. fasciicauda in lowland forest, where it is exceedingly abundant. As remarked previously, young manakins wander widely. Because of these wanderings, the ranges of

the species appear to overlap broadly. There is, however, almost no overlap in the elevational ranges of the adult males, a fact which suggests mutually exclusive breeding ranges.

Over its entire range, P. pipra coexists with the much smaller P. caeruleicapilla. The ratio of their weights is 1.54. In other parts of Peruvian Amazonia, such as the Sira range, P. caeruleicapilla is replaced at lower elevations by a very similar congener, P. coronata, which is found with fasciicauda and chloromeros. P. coronata is inexplicably absent from the Apurímac Valley. On the valley floor, however, another small manakin, Machaeropteryx pyrocephalus, shares the forest understory with P. fasciicauda. The latter is 1.61 times heavier.

Myiotheretes (Tyrannidae).--The members of this genus of large, highland flycatchers are uncommon, and our knowledge of their distribution may be incomplete. The sole species found in the Vilcabamba, M. fumigatus, was not found on the west slope. Three species do occur on that side of the valley, however--M. fuscorufus in cloud forest and, at the elfin forest/puna border, M. erythropygius and M. striaticollis. How the latter two segregate is not evident. M. erythropygius perches on exposed branches of shrubs or trees at the very fringe of forest and makes long flights or sallies over the puna.

Ochthoeca (Tyrannidae).--The niches of the Ochthoeca flycatchers show nearly all of the available sorting mechanisms. The two most closely related species, probably comprising a superspecies, are O. pulchella and O. frontalis. In appearance they differ only in the details of head and wing markings. Both are rarely seen inhabitants of the dimly-lit interior of dense vegetation. They form a two-fold elevational series, without

overlap and with replacement occurring over a short distance (Figure 11). O. pulchella is the lower elevation member, present in cloud forest understory and in elfin forest, while O. frontalis is in elfin forest at higher elevations. O. rufipectoralis shares the ranges of these two species down to the lower limit of elfin forest. It is of similar size, but unlike the other two it forages in the well-lit outer portions of the vegetation where it is readily seen. Coexisting in low abundance with rufipectoralis and pulchella is O. cinnamomeiventris, a species whose niche differences are unknown but which may also involve aspects of habitat selection. The one time I saw O. cinnamomeiventris other than in a mist-net was in a rather dry area at 2100 m along the access road to the valley, where the habitat was less humid and lush than any encountered at similar elevations along our transects.

The fifth member of the genus in the valley is O. fumicolor, which occurs where elfin forest mixes with or meets grassland above 3200 m on both slopes. Like O. rufipectoralis, which resides in this same area, it perches and forages on the outer branches of trees and shrubs. However, it also feeds on the ground, dropping from a perch in a manner remarkably like bluebirds of the genus Sialia. In size it is the largest of the valley's Ochthoecas, with a weight ratio to O. rufipectoralis of 1.47.

Myiarchus (Tyrannidae).--M. ferox and the lowland race of M. tuberculifer (nominate tuberculifer) are found together in matorral and sort out by size. (The ferox/tuberculifer weight ratio is 1.32.) The larger highland race of tuberculifer (M. t. atriceps) and the species M. cephalotes occupy the cloud forest. Although the former has a broader range and

occurs at higher elevations in the absence of M. cephalotes, the two species have considerable elevational overlap. How their niches differ is not evident.

Myiophobus (Tyrannidae).--The flycatchers of this genus form a five-fold elevational series in the Vilcabamba consisting from lowest to highest of M. fasciatus, M. roraimae, M. inornatus, M. flavicans, and M. ochraceiventris. However, since M. fasciatus is not a forest bird and may be present only as a migrant or winterer, it is perhaps best to exclude it from the series. The range of M. inornatus is very narrow, with its population seemingly squeezed between those of roraimae and flavicans. On the west side, we failed to find inornatus, and the ranges of roraimae and flavicans apparently meet and overlap in this area.

Platyrinchus (Tyrannidae).--The two commoner flat-bills, P. platyrhynchus and P. mystaceus, replace each other elevationally with the former a lowland bird and the latter a hill forest and cloud forest form. The third species, P. flavigularis, is puzzling with respect to its general status and its ecological relationship to P. mystaceus. It occurred just once, in a net, at a locality within the range of mystaceus.

Tolmomyias (Tyrannidae).--These three lowland flycatchers form a size series consisting, from largest to smallest, of T. assimilis, T. flaviventris, and T. poliocephalus. The weight ratio of the trio is 1.61: 1.24: 1.00. They differ in habitat preference as well as size. T. assimilis is a canopy species in heavy, humid forest and is the only member not colonizing secondary habitats and not present in the dry forest along the Río Ene. T. flaviventris occurs in forest but is most abundant

along the forest edge, in tall second-growth woodland, and in the crowns of coffee plantation shade trees. The primary habitat of T. poliocephalus in the humid lowlands is unknown, but it is found in the same secondary habitats as T. flaviventris, which seems to forage somewhat higher above the ground than poliocephalus.

Todirostrum (Tyrannidae).--The tody-flycatchers avoid contact through differences in vertical stratification and habitat selection (Terborgh and Weske, 1969). T. chrysocrotaphum lives in the forest canopy and sub-canopy. Both T. latirostre and T. cinereum occupy the lower strata of matorral, but the former is a thicket bird, found in dense, dimly-lit vegetation. T. cinereum, on the other hand, inhabits the edges and sparser portions of matorral. It is particularly common in secondary habitats like citrus groves and fallow pastures where woody composites have invaded.

Lophotriccus and Idioptilon (Tyrannidae).--L. pileatus and I. granadense provide an example of a two-fold elevational series whose members are of different genera. Both are tiny, short-winged flycatchers which forage at lower levels in the forest. Along the gradient, Idioptilon replaces Lophotriccus above 2000 m.

Elaenia (Tyrannidae).--Of five species of Elaenia in the valley, only three have resident breeding populations. The other two (E. albiceps and E. spectabilis) nest in the South Temperate Zone and winter in the tropics (Zimmer, 1941). E. spectabilis was found only once, well above ground in matorral. E. albiceps is common at lower and middle elevations, particularly in second-growth, where it often feeds on small fruits. The resident species are E. pallatangae, a small forest Elaenia of middle and

higher elevations, and two lowland birds, E. flavogaster and E. gigas. The latter two occur together in sparse matorral, young second-growth, and cultivated habitats. I have insufficient weight data, but they seem to sort out by size, with gigas the larger as its name would suggest.

Tyranniscus (Tyrannidae).--Two species, T. nigrocapillus and T. uropygialis, are very similar in appearance and habits. They form an elevational series--the former in cloud forest and the latter in elfin forest. The third member of the genus, T. bolivianus, has a wide range which bridges that of its two congeners. Differences in feeding behavior provide a means for segregation. T. bolivianus perches motionless on exposed branches and sallies after insects, while T. nigrocapillus seemed to me to feed like a kinglet (Regulus), with active hops or flights from branch to branch. I have no observations of T. uropygialis.

Leptopogon (Tyrannidae).--There is a three-fold elevational series in this genus, with broad overlap in ranges of the lower member, L. amaurocephalus, and the middle one, L. superciliaris. At higher elevations, L. taczanowskii replaces L. superciliaris. Their ranges are mutually exclusive.

In a previous section I described vertical partitioning of the habitat by L. amaurocephalus and L. superciliaris in the area of range overlap. Where its congener is absent, the vertical foraging range of L. superciliaris is broader.

Notiochelidon (Hirundinidae).--The valley's three species of Notiochelidon swallows do not come in contact. N. cyanoleuca is found on the valley floor in cleared areas. At higher elevations in the

Vilcabamba N. flavipes is present, but at treeline on the west side N. murina occurs--a case of allopatric replacement similar to that in the hummingbird genus Metallura.

Troglodytidae.--The niches of the wrens seem fairly well differentiated. Ten species are present in the valley. In the lowlands there are three: a mainly terrestrial forest species (Microcerculus marginatus), a large matorral species (Thryothorus coraya), and a small matorral species (Troglodytes aedon). In the cloud forest, one encounters a medium-sized understory wren (Henicorhina leucophrys), two large understory wrens which do not overlap elevationally (Cyphorhinus thoracicus and Cinnycerthia peruana), a small arboreal wren which forages among hanging vines and other epiphytes (Troglodytes solstitialis), and a small arboreal species (Odontorchilus branickii) which forages along limbs in the manner of the nuthatch Sitta pusilla. Thryothorus coraya ranges upward to the lower cloud forest but is strictly limited to second-growth vegetation in clearings. At higher elevations there is a grassland species (Cistothorus platensis) and a large Thryothorus (T. euophrys) about which we know little since it was recorded just once. Troglodytes solstitialis inhabits elfin forest, but Cinnycerthia peruana and Henicorhina leucophrys are present at higher elevations only where cloud forest vegetation persists.

Turdus (Turdidae).--Four members occur in the valley. T. ignobilis occupies matorral in the lowlands. To our surprise, there appears to be no robin in the lowland forest. T. nigriceps is a bird of hill forest and lower cloud forest, replaced at higher elevations by T. fuscater and T. serranus, which overlap broadly. These two species sort out by size,

for fuscater is very large and outweighs serranus by a factor of 1.78. There is one other robin present, Platycichla leucops, which is occasionally placed in the genus Turdus and which coexists with T. nigriceps on the west side. Other than rather modest differences in body size and bill structure, I am not aware of niche differences between leucops and nigriceps.

Psarocolius (Icteridae).--The oropendolas segregate by elevational range and habitat preference, although occasionally two or even all three species are found together. P. decumanus and P. angustifrons share the lowlands, but the former is more a forest species and the latter more a bird of matorral and second-growth. It is the nests of angustifrons that one sees hanging from solitary large trees that are left standing after land is cleared for cultivation, and it is angustifrons which causes occasional depredations on bananas and papayas. The third species, P. atrovirens, is the elevational replacement in cloud forest.

Cacicus (Icteridae).--Three canopy-dwelling caciques which form an elevational series are C. cela, C. uropygialis, and C. leucoramphus. In the lowlands, C. cela comes in contact with C. solitarius, a species of the matorral understory, but the two avoid niche overlap by their differing vertical distribution. A somewhat similar relationship prevails at higher elevations where the ranges of C. leucoramphus and C. holosericeus overlap. The latter forages in dense vegetation near the ground and, in addition, is smaller than leucoramphus, with a differently shaped bill. Their ranges suggest elevational replacement (Terborgh, 1971), but that situation is probably coincidental, since their niches appear to be quite distinct otherwise.

Basileuterus (Parulidae).--Of five species of the genus in the valley, one stands ecologically apart. This is the stream-side specialist B. rivularis, which in actions, appearance, call notes, and habitat closely resembles the North American waterthrushes of the genus Seiurus. The other four Basileuterus warblers occupy more similar niches in forest vegetation and form an elevational series. Occurring successively higher along the gradient are B. chrysogaster, B. tristriatus, B. coronatus, and B. luteoviridis (Figure 13). There is considerable range overlap between adjacent pairs of the latter three--only the lowest member, B. chrysogaster, has an exclusive range. Coexistence between tristriatus and coronatus is accounted for by differences in size and vertical distribution. Although both occur in the understory, tristriatus commonly forages in the sub-canopy as well. B. coronatus outweighs it by a factor of 1.26. Both B. coronatus and B. luteoviridis are large warblers of the dense cloud forest understory, with the latter also inhabiting the elfin forest. Their netting abundance curves are skewed toward the elevations where their ranges come together, indicating that competitive interactions compress these ranges (Terborgh, 1971). It is perplexing that from 2100 m to 2200 m, each species is quite common in the presence of the other. If, or how, they segregate ecologically in this zone is unknown. The situation for this species pair is comparable to that for the hummingbirds Coeligena coeligena and C. torquata, whose ranges meet at the same elevations.

Conirostrum (Coerebidae).--The species of this genus reduce niche overlap by elevational replacement and differential habitat selection.

C. speciosum, in the lowlands, and C. albifrons, a cloud forest bird, have exclusive ranges. C. sitticolor, C. ferrugineiventre, and C. cinereum are found in elfin forest and are sometimes seen together. C. sitticolor inhabits solid stands of elfin forest and ranges to a lower elevation than the other two, while C. ferrugineiventre is an edge species found only at treeline where elfin forest and grassland meet. C. cinereum also occurs at treeline and is common in patches of sparse, low shrubbery surrounded by puna. However, cinereum is really a characteristic species of the Sierra (the "Arid Temperate Zone" of Chapman, 1921), and its population at the crest of the valley's west slope can be considered a spill-over from the adjacent Sierra. C. cinereum was not found in the Vilcabamba, where no dry highland habitat is nearby.

Diglossa (Coerebidae).--Like Conirostrum, Diglossa is a mainly highland genus which is well-represented in the valley. As many as four species may coexist, sorting out by size and habitat preference. At the risk of oversimplification, I offer a capsule description of the niche of each: 1) D. glauca is a small species of cloud forest canopy and subcanopy. 2) D. albilatera is a small species of upper cloud forest and elfin forest--the elevational replacement for glauca. 3) D. carbonaria, another small species, replaces albilatera and inhabits the elfin forest/puna ecotone. 4) D. caerulescens, a medium-sized cloud forest species overlaps glauca and is uncommon in the valley. From the Sira Range we know that this is an abundant species in the elfin forest that occurs around 2000 m. The elfin forest does not come that low in the Apurímac Valley, but caerulescens probably finds sufficient elements of that type

of vegetation to maintain a population and sort out from glauca by habitat preference. 5) D. baritula is a very small species found only on the west side in cloud forest at middle elevations. No weight data are available, but one may conjecture that baritula segregates ecologically by size from the somewhat larger species glauca and caerulescens, with which it coexists. 6) D. lafresnayii is a larger species whose range is strictly determined by the presence of shrubby, microphyllous elfin forest vegetation. It ranges down to 2500 m in the Vilcabamba but is found only near treeline on the west slope, where low elfin forest is limited to high elevations. 7) D. cyanea, the largest and most wide-ranging member, is common in upper cloud forest and elfin forest. This species and lafresnayii coexist commonly over a broad span, are fairly close in size, and are occasionally seen together. D. lafresnayii seems usually to be solitary, but cyanea is normally a member of mixed-species tanager-honeycreeper flocks. D. cyanea occurs in shrubby elfin forest but is even more a species of taller trees and the unbroken forest. It is not found in the scattered low copses of the puna edge where D. lafresnayii, D. carbonaria, and Conirostrum cinereum are abundant.

Segregation by size occurs between these combinations of coexisting species: cyanea/albilatera (weight ratio = 1.46), cyanea/caerulescens (1.22), cyanea/glauca (1.40), lafresnayii/albilatera (1.31), and lafresnayii/carbonaria (1.27).

Our records of D. carbonaria in the Vilcabamba are of only two individuals, both immatures, suggesting that there may be no breeding population there. Like Conirostrum cinereum, D. carbonaria is a species

of the Sierra whose range barely extends into the upper fringe of the humid Apurímac Valley.

Euphonia (Thraupidae).--Seven species of euphonias occur in the valley. E. chlorotica and E. lanirostris are matorral birds which sort out by size and structure, for the latter is larger and has a stouter bill. E. chlorotica is especially numerous in rather open cultivated habitats--citrus plantations, Hibiscus hedgerows, and scattered trees in pastureland. There are four lowland forest species whose niche differences are unknown, although there are some size differences: E. chrysopasta, E. xanthogaster, E. rufiventris, and E. minuta. E. minuta is exceedingly similar to E. chlorotica in appearance and small size but remains separate by habitat selection. E. xanthogaster has a broad range which extends from the valley floor well into the cloud forest. In the latter habitat it bridges the range of E. mesochrysa, a smaller species from which it sorts out by size.

Tangara (Thraupidae).--A full explanation of the ecological relationships of the members of this genus of canopy tanagers must await an intensive analysis as done by MacArthur (1958) on the Dendroica warblers of eastern North America. Seventeen Tangaras are found in the valley; frequently, four of five species will be seen in the same flock feeding in the same tree. I call attention to niche differences which so far have become evident. The elevational replacement between a lowland group and a middle elevation group was mentioned earlier (See Figure 4.), as was specialized feeding behavior in T. chrysotis and T. ruficervix. There can also be segregation by size and structure: T. pardzudakii is probably the largest of the cloud forest group and outweighs T. nigroviridis,

a species with which it often associates, by a factor of 1.7; T. callophrys has a longer, more slender bill than its congeners. T. schrankii was the only lowland Tangara to be netted, and it was occasionally seen in the C-story (subcanopy) of lowland forest. Others of the genus seem to remain in the canopy. T. punctata and T. xanthogastra may form a superspecies; they are very similar in plumage pattern and in their small size, and they seem to replace each other elevationally.

Anisognathus (Thraupidae).---Three members of this genus of mountain tanagers are present in the valley. A. flavinucha is a common species of the forest canopy and subcanopy at middle elevations. Its elevational range does not overlap those of A. lacrymosus and A. igniventris, which coexist broadly at higher elevations and often join the same mixed-species feeding flocks. Segregation between the latter two is partly by size: igniventris outweighs lacrymosus by a factor of 1.12. There are, in addition, differences in habitat preference and elevational range. A. lacrymosus has a somewhat lower range and was found in the upper cloud forest but not in the elfin forest at treeline on the west side. Conversely, A. igniventris was never seen below the elfin forest zone, but it ranged to the upper limit of woody vegetation in the elfin forest / puna ecotone.

The Anisognathus tanagers coexist throughout the cloud and elfin forest with tanagers of the genus Iridosornis--A. flavinucha with I. analis, and A. lacrymosus and A. igniventris with I. reinhardti. These five colorful species are among the most abundant tanagers in the valley. Respective members of the two genera sort out by size, for the two

Iridosornis are about 25 percent smaller. Also, A. flavinucha and I. analis differ in vertical stratification. The former forages higher and usually stays above net level, but the latter feeds in both subcanopy and understory, and is regularly netted.

Chlorospingus (Thraupidae).--In this genus of tanagers there appear to be two pairs of species whose members are ecologically similar and replace each other elevationally. C. ophthalmicus replaces C. canigularis, and C. parvirostris replaces C. flavigularis. Segregation between the two pairs is by habitat selection. C. parvirostris and C. flavigularis seem to prefer vegetation bordering or near mountain streams, while C. ophthalmicus and C. canigularis are found in cloud forest not necessarily near water. C. ophthalmicus was abundant in elfin forest around 2000 m in the Sira Range, where this forest type is found lower than in the Apurímac Valley. Its status parallels that of the coerebid Diglossa caerulescens.

Hemispingus (Thraupidae).--Another genus of tanagers which is well-represented in the valley is Hemispingus. Terborgh pointed out to me that one member, H. xanthophthalmus, has a distinctive behavior which sets it off from the rest. In search of food, it walks about on the tops of leaf clusters of small elfin forest trees.

The species with the lowest elevational range is H. frontalis, which occupies the subcanopy in lower cloud forest. It shares this range with H. melanotis, an uncommon species which I have never seen aside from four occasions when it was netted. How frontalis and melanotis sort out is unknown. At somewhat higher elevations, frontalis is replaced by two coexisting species, H. superciliaris and H. atropileus, which in turn are

replaced above 3300 m in the Vilcabamba by Hemispingus sp. Segregation between atropileus and superciliaris is by size: the weight ratio of the former to the latter is 1.62. On the west side, the distributional picture at higher elevations is altered. Hemispingus superciliaris and Hemispingus sp are absent from that side of the valley. A species not found in the Vilcabamba, H. trifasciatus, is the allopatric replacement for H. superciliaris, which closely resembles it in plumage details and size. H. trifasciatus coexists with the larger H. atropileus, and, in the absence of Hemispingus sp, this species pair ranges up to the limit of trees. The ecological evidence and morphological similarity would suggest that superciliaris and trifasciatus may be conspecific, but they appear to be sympatric in southeastern Perú, where field study should be undertaken to clarify their elevational and ecological relationships.

Sporophila (Fringillidae).--Four seedeaters inhabit matorral and cultivated areas in the lowlands. Along with Volatinia jacarina they form mixed flocks. How they avoid extensive niche overlap is by no means entirely clear, but they differ somewhat in size and structure. The bill of S. obscura has a straighter culmen than that of the other Sporophilas.

P. A. Schwartz, Jr. (pers. comm.) feels that this species may properly belong in Tiaris, a genus of grassquits with wide tropical distribution but unrepresented in the valley. There are modest differences in average weight between the other three species: S. luctuosa, S. nigricollis, and S. castaneiventris (listed from largest to smallest). The weight ratios are 1.51: 1.15: 1.00. In addition, S. luctuosa is uncommon in the lowlands and is probably marginal there. It appears to be primarily a species of

middle elevations--we were surprised to capture three in cloud forest at 2600 m on the west side. S. castaneiventris and S. nigricollis are strictly lowland species in the valley.

Atlapetes (Fringillidae).--The four members of this genus of forest understory finches segregate by size and elevational distribution. Below about 2400 m, a larger, white-bellied species (A. brunneinucha) and a smaller, yellow-bellied one (A. tricolor) occur together. Above that elevation, the coexisting pair consists of A. torquatus (large and white-bellied) and A. rufinucha (small and yellow-bellied). The situation is analagous to that which prevails in the cotinga genus Pipreola. The coexisting species sort out by size, with a weight ratio of 1.58 for brunneinucha / tricolor and of 1.52 for torquatus / rufinucha. Elevational replacement in both the white-bellied and yellow-bellied species pairs occurs without overlap in ranges.

#### Ecological Specialists

Defining the niches and explaining the ecological relationships of all the species of birds which coexist in a given habitat is a far greater problem than dealing with the niches of congeners. The sorting mechanisms operating among closely related species are probably those which apply to the members of entire avian communities, but a greater variety in physiological, structural, and behavioral adaptations leads to less clear-cut differences in spatial relationships like vertical and elevational distribution or habitat preference. Characterizing the niches of even a part of the community, such as the canopy flock members, becomes very complex. In this section I discuss some species for which a certain

ecological factor seems to be of overriding importance. In that sense such a species is a specialist, but a narrow dimension for one feature often leads to a broad tolerance in another, such as elevational distribution. Foremost among these species are habitat specialists. Along with Basileuterus rivularis and Serpophaga cinerea, which were mentioned above, there are other species which are always or usually found along streams. These include the dipper Cinclus leucocephalus, the phoebe Sayornis nigricans, the furnariid Lochmias nematura, and the hummingbird Heliothryx aurita. The antbird Percnostola leucostigma inhabits dense leafy undergrowth which surrounds and sometimes covers small woodland brooks in the lowlands.

Other bird species are seldom found far from a particular sort of vegetation. Both species of Dryophila favor stands of bamboo of the genus Chusquea. The relative scarcity of D. caudata in the west slope seems directly attributable to the scarcity of Chusquea in the lower cloud forest. On the Vilcabamba side both the plant and the bird are common at these elevations. The antbirds Cymbilaimus lineatus and Cercomacra nigrescens are normally found in hanging tangles of lianas and vines in the lowland and hill forest subcanopy. The antbird Cercomacra nigrescens and the furnariid Synallaxis azarae are common understory species in "brights" in the cloud forest where blowdowns or landslides have removed part of the forest vegetation and where second-growth has taken hold. Both of these species are occasionally encountered in forest understory; their occurrence there seems related to the transitory nature of second-growth habitat and the consequent evolutionary necessity that they wander

widely and thus increase the possibility of stumbling on newly created areas that are suitable for them. Also associated with cloud forest clearings are the flycatchers Pyrrhomyias cinnamomea and Contopus fumigatus which sally out for insects in the open area from perches in trees at the clearings' edge.

Another group of specialists are the ant-followers. Several species of formicariids occasionally join ant-following flocks, but Pithys albifrons and Rhegmatorhina melanosticta are habitual ant-followers (Willis, 1969). Also feeding mainly on insects flushed by army ant swarms are three species of woodcreepers--Dendrocincla fuliginosa, Dendrocolaptes certhia, and Dendrocolaptes picumnus. The adaptation to perching on vertical surfaces which is essential to the bark-foraging habits of other dendrocolaptids is equally useful for these ant-followers. They can sally out from perches on tree trunks in the forest understory to capture flying insects.

Several other species possess distinctive structural features which may provide a competitive advantage while leading, in some cases, to a rather specialized niche. The most obvious example is Eutoxeres condensini, a hummingbird with a sickle-bill. This species is never very common but has an elevational range of over 2000 m. Its low abundance would reflect a relative scarcity of its probable food source, flowers with curved corollas, but its broad range would result from an absence of other species having the structural adaptations to compete effectively for this resource. Another hummingbird, Doryfera ludoviciae, which has an unusually straight, long bill, is also present but uncommon over a wide

range. It may also be adapted to feeding at flowers of a particular shape and may illustrate a situation paralleling that for Eutoxeres. Not every wide-ranging species can be accounted for in this manner, however. The hummingbird Amazilia chionogaster is found over a span of 3000 m from the deciduous forest of the Río Ene to the crest of the Vilcabamba, yet morphologically it is a "typical" hummingbird, with no apparent structural or behavioral specializations.

Other than the Trochilidae, there are at least two species whose wide ranges may be attributed to unique features. One is the flycatcher Mionectes striaticollis, which is present from the valley floor to tree-line and is probably the most common bird in the valley. From field observation of it and from its characteristically reddish or purplish excrement we know this species feeds on fruit as well as insects, a habit which gives it great ecological versatility compared to most other tyrannids. The Squirrel Cuckoo, Piaya cayana, is another highly successful species which is distinctive in both morphology and behavior. Aside from its congener, P. minuta, whose niche differences were already discussed, there would seem to be no species in the valley which is even potentially a close competitor.

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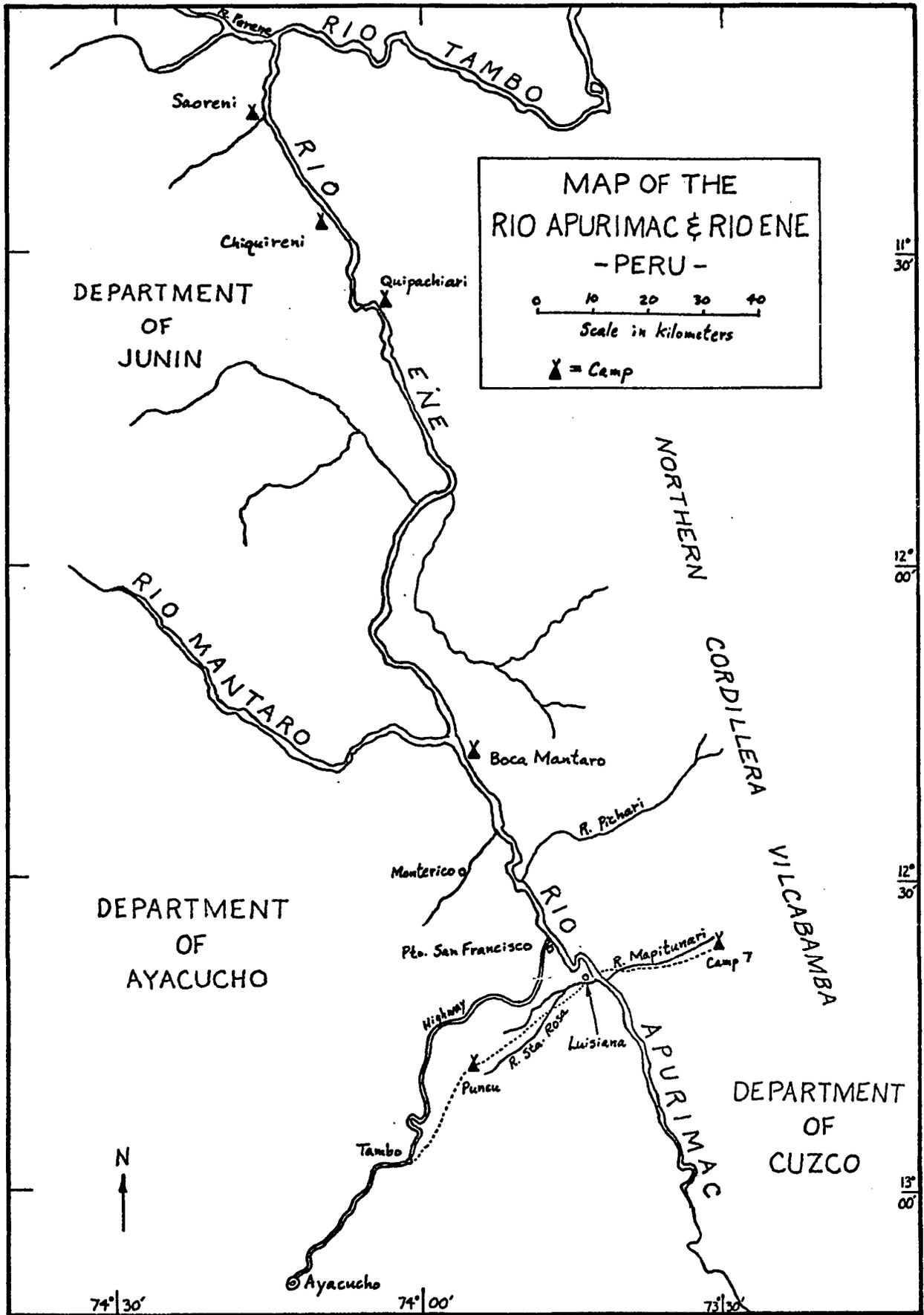
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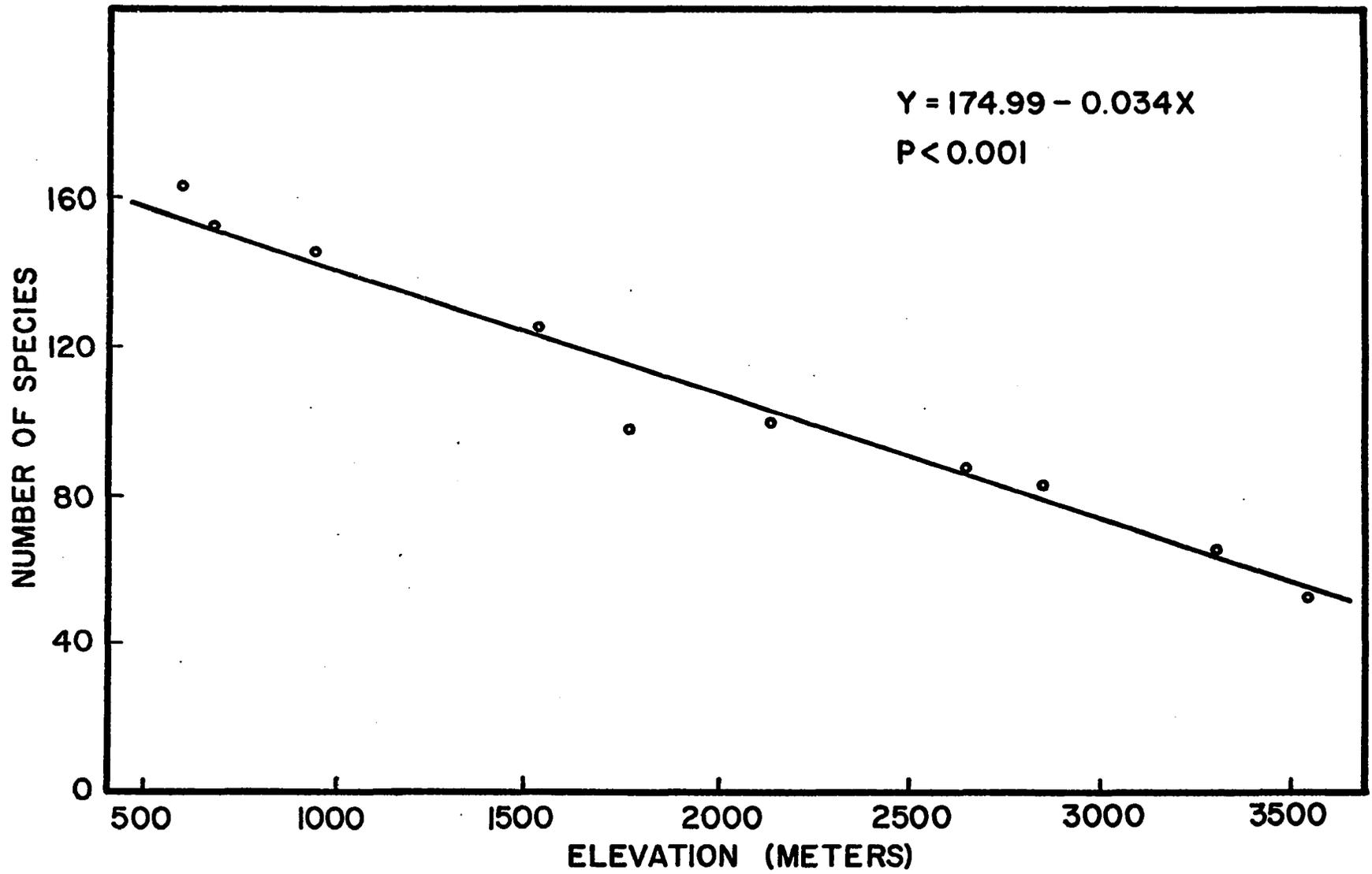
**Figure 1. Map of the Río Apurímac and Río Ene, Peru.**



**Figure 2. Schematic cross-section of the Apurímac Valley.**



**Figure 3. Number of forest species present at stations on the  
Vilcabamba gradient. Linear regression on elevation explains  
96.99% of the variation in species number.**



**Figure 4. Elevational ranges in forest of canopy flock species on the Vilcabamba gradient.**

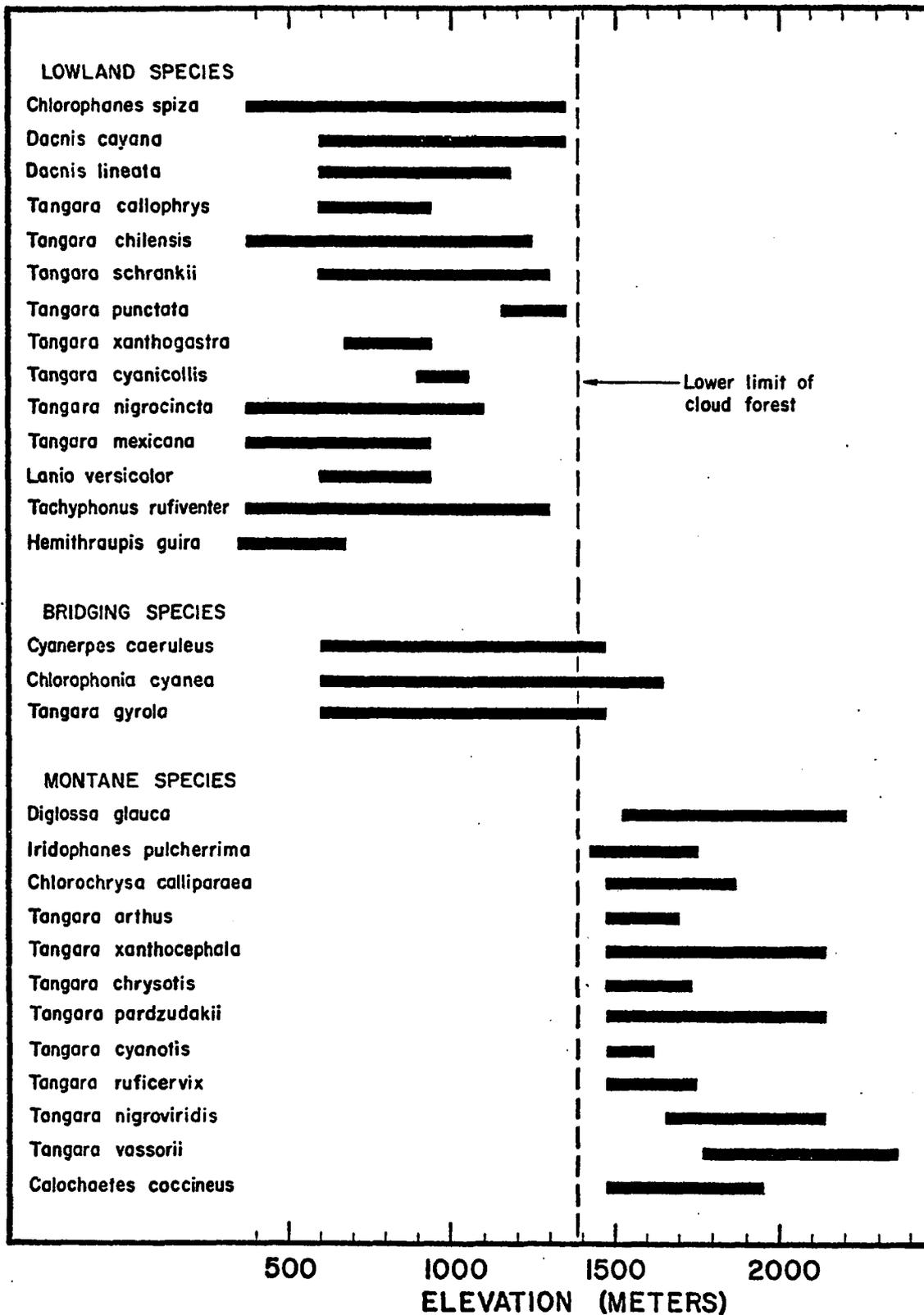


Figure 5. Number of sub-oscine species and New World nine-primaried  
oscine species as a percent of the total forest avifauna on  
the Vilcabamba gradient.

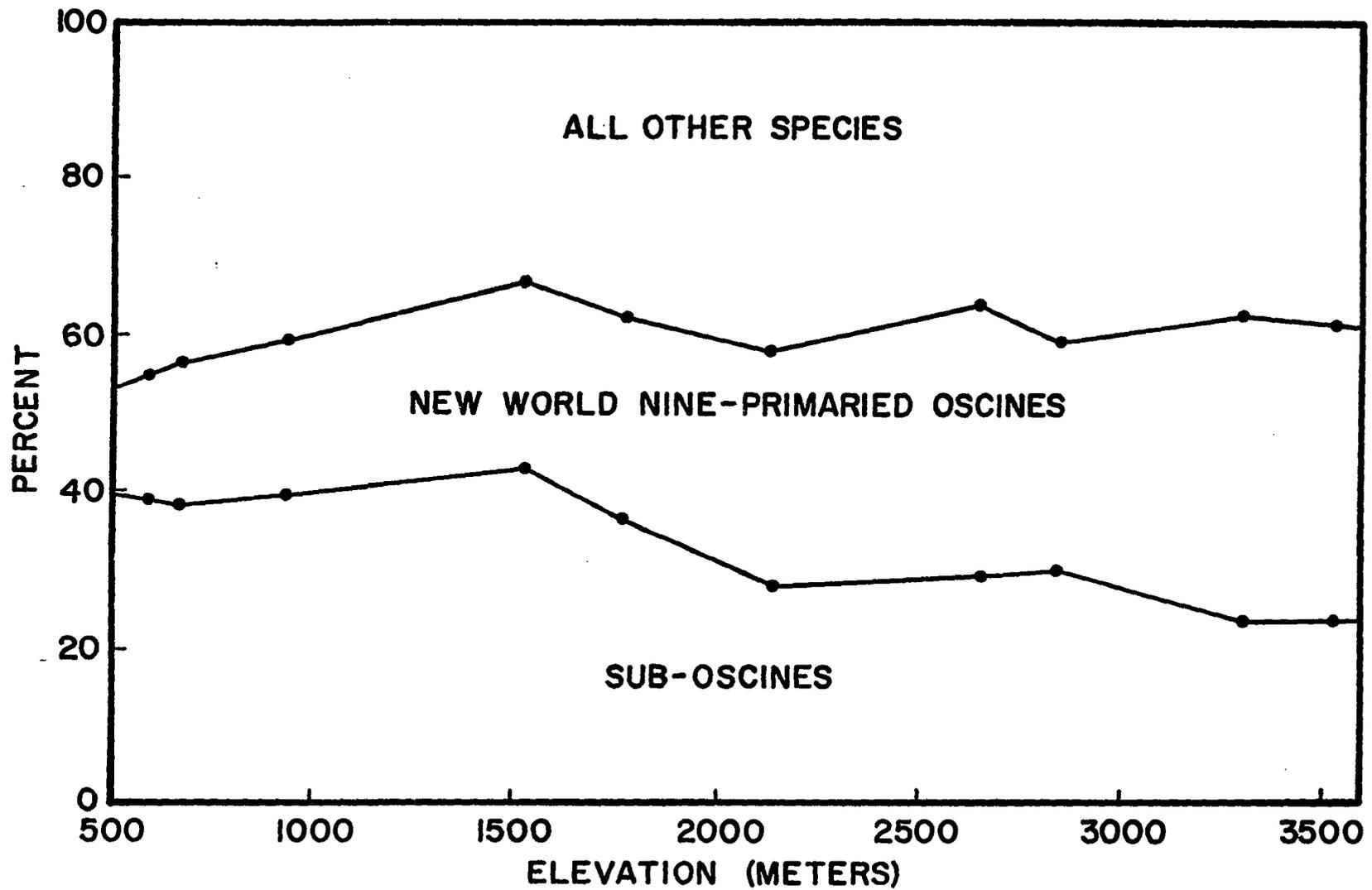
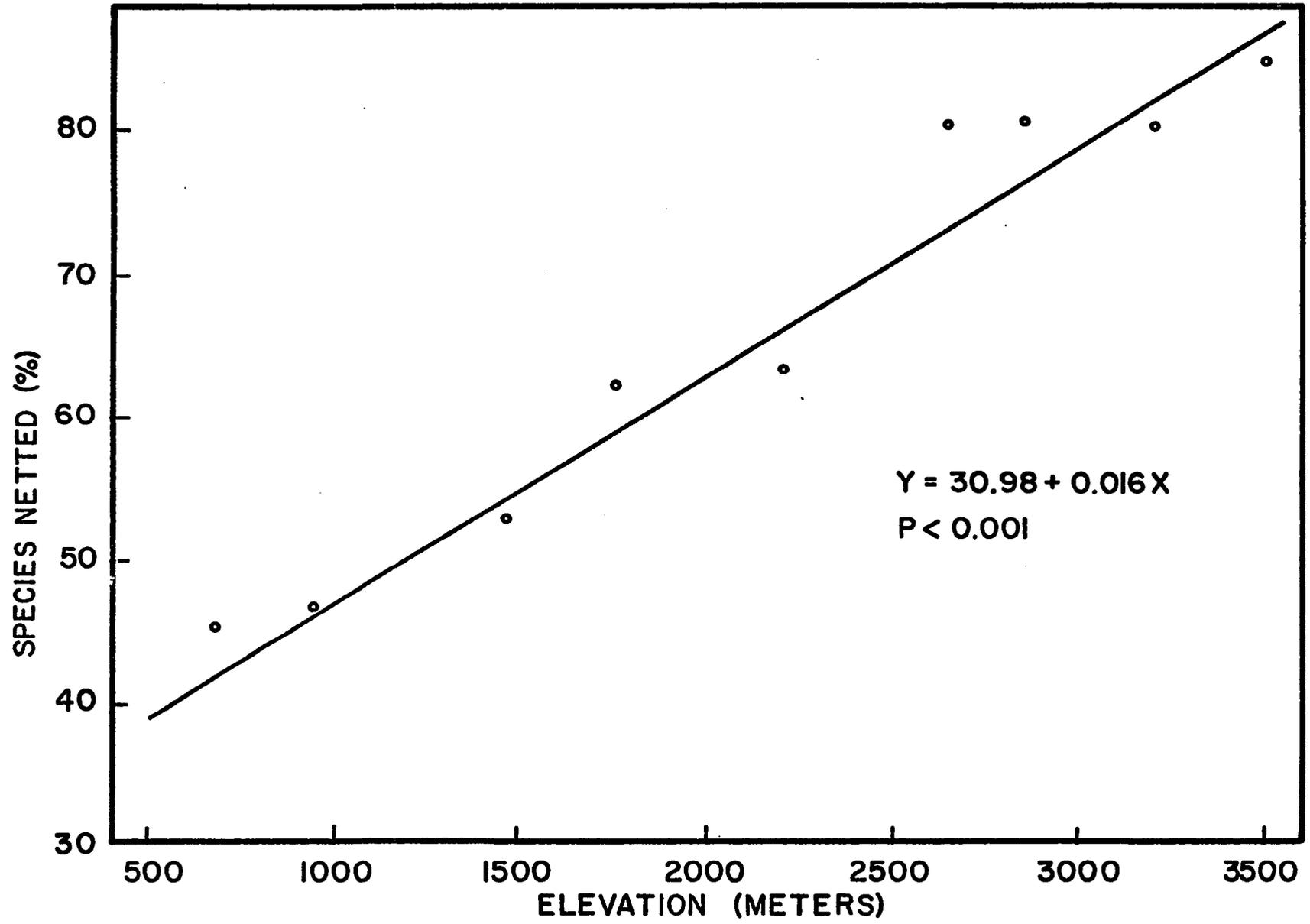


Figure 6. Number of forest species captured in nets at stations on the Vilcabamba gradient as a percentage of the total forest avifauna. Linear regression on elevation explains 93.35% of the variation in percent of species netted.



**Figure 7. Elevational ranges in forest of canopy flock species on the West Side gradient.**

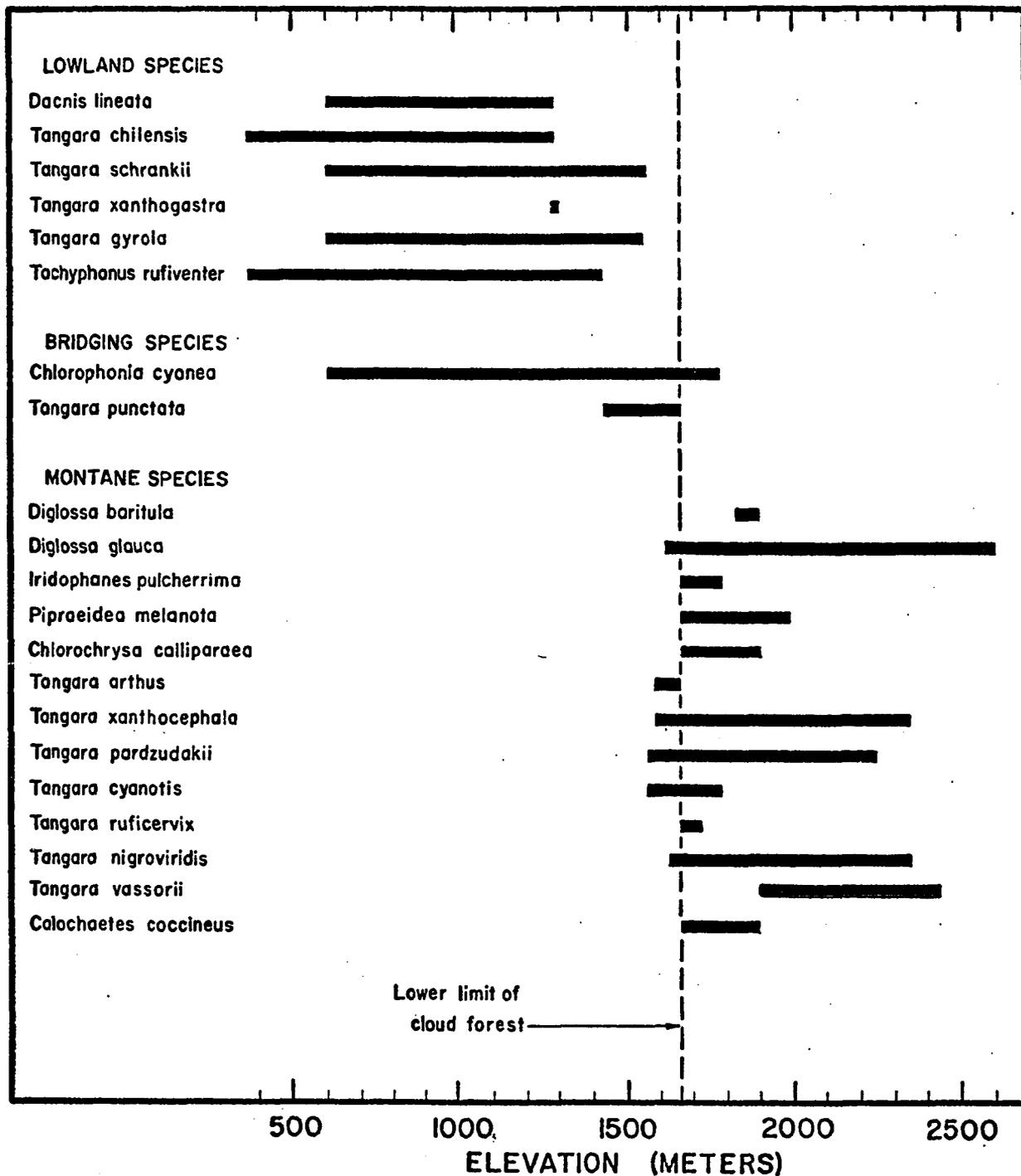


Figure 8. Elevational ranges of selected understory and subcanopy species on two elevational gradients. The range of each species on the Vilcabamba gradient is given by the upper bar and on the West Side gradient, by the lower bar. A tendency for higher distributional limits on the West side is evident. "S" and "U" following names of species denote subcanopy and understory species, respectively.

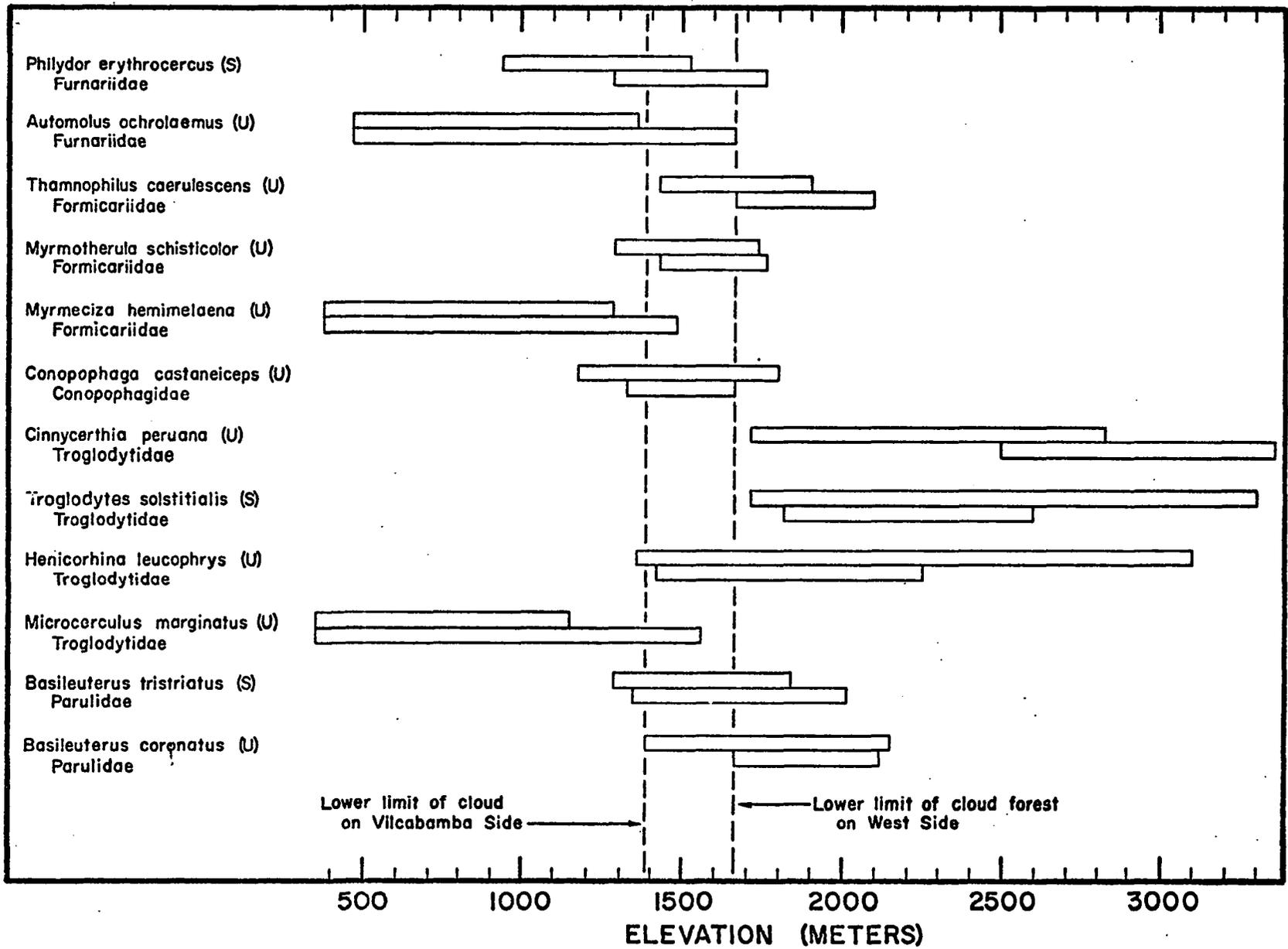


Figure 9. Relative abundance curves for flycatchers of the genus Pseudotriccus. The proportional occurrence of each species in net samples is plotted along the ordinate (see Appendix 2).

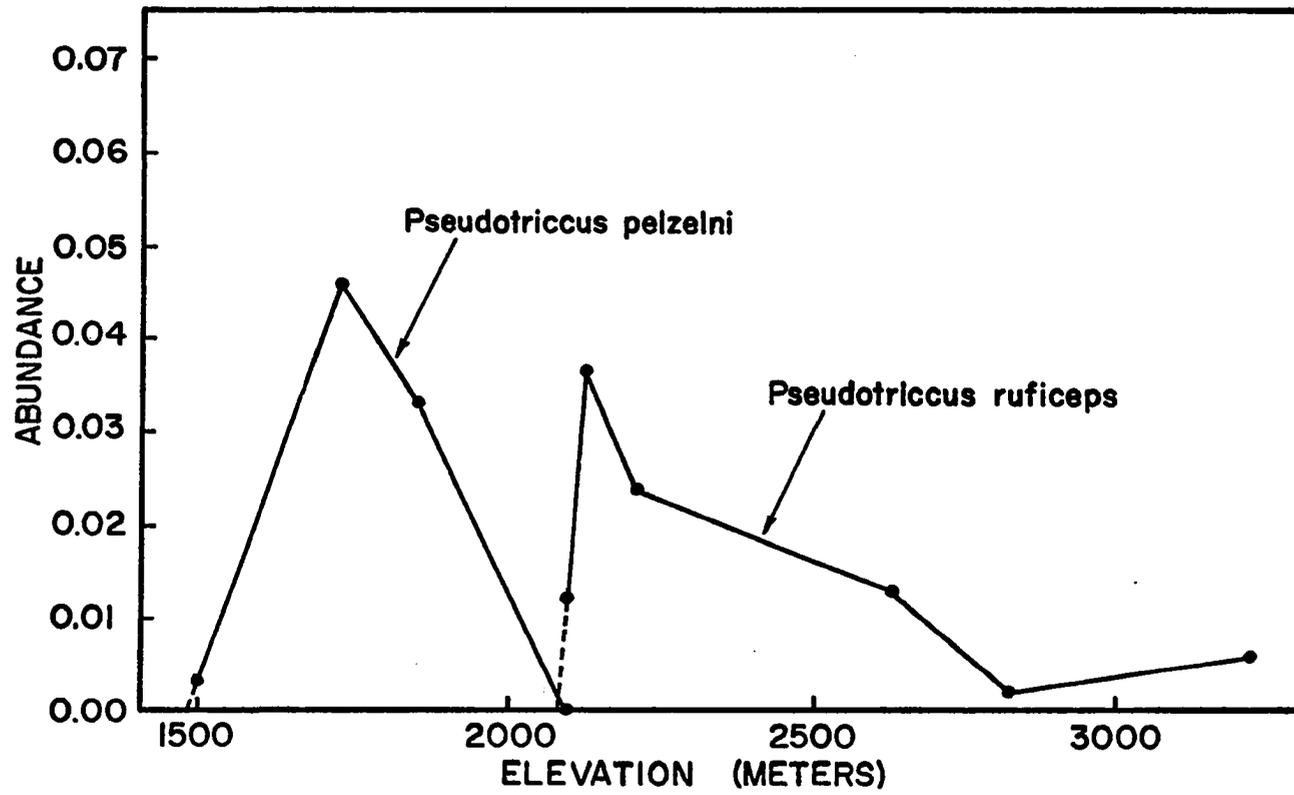


Figure 10. Relative abundance curves for the woodcreeper genus  
Xiphorhynchus.

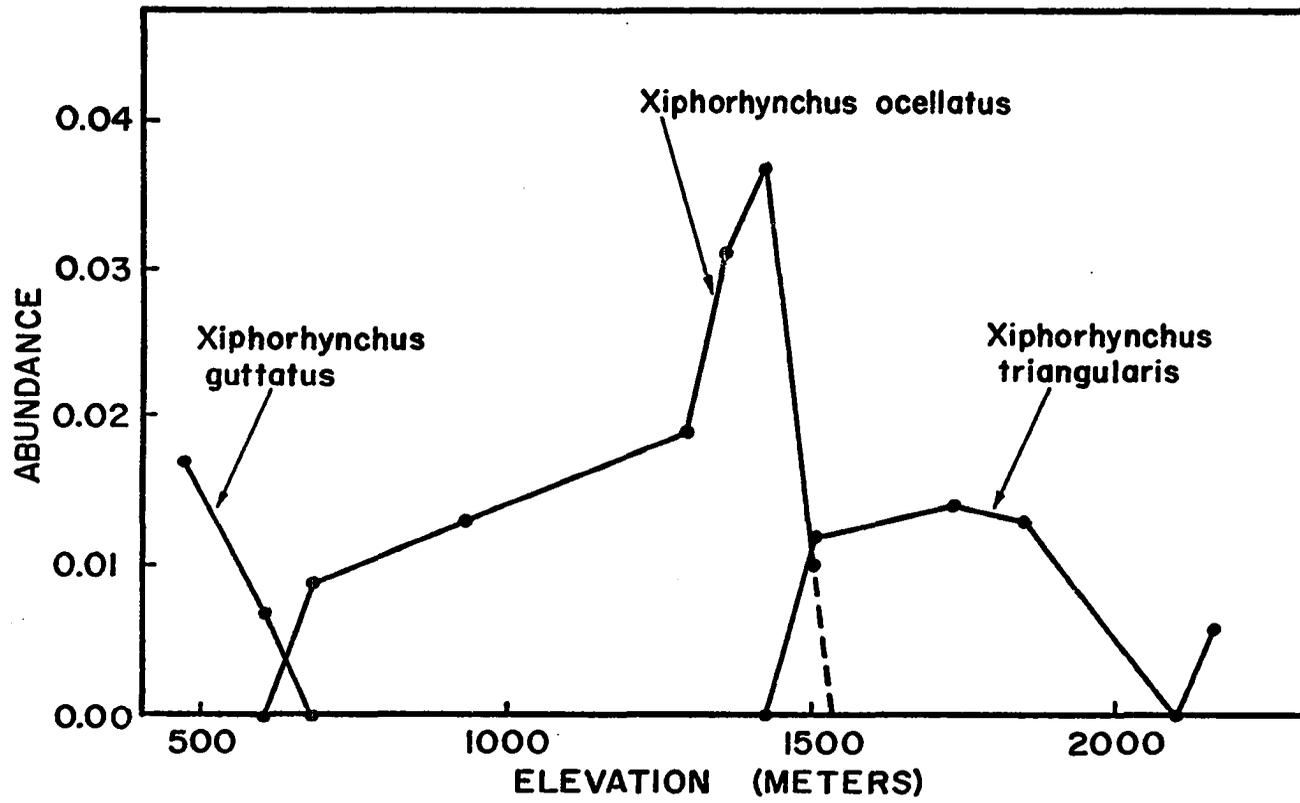


Figure 11. Relative abundance curves for two Ochthoeca flycatchers.

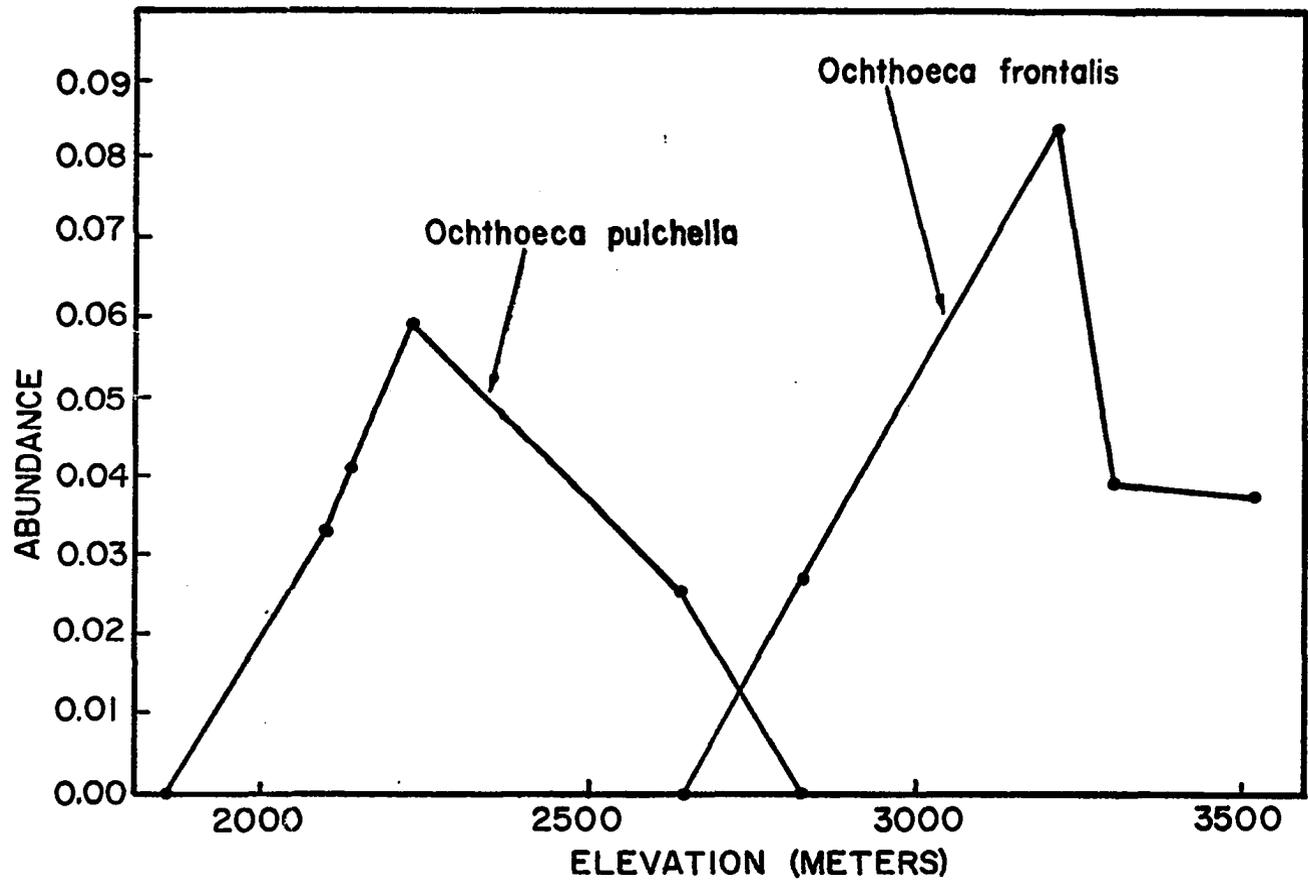


Figure 12. Relative abundance curves for Coeligena hummingbirds.

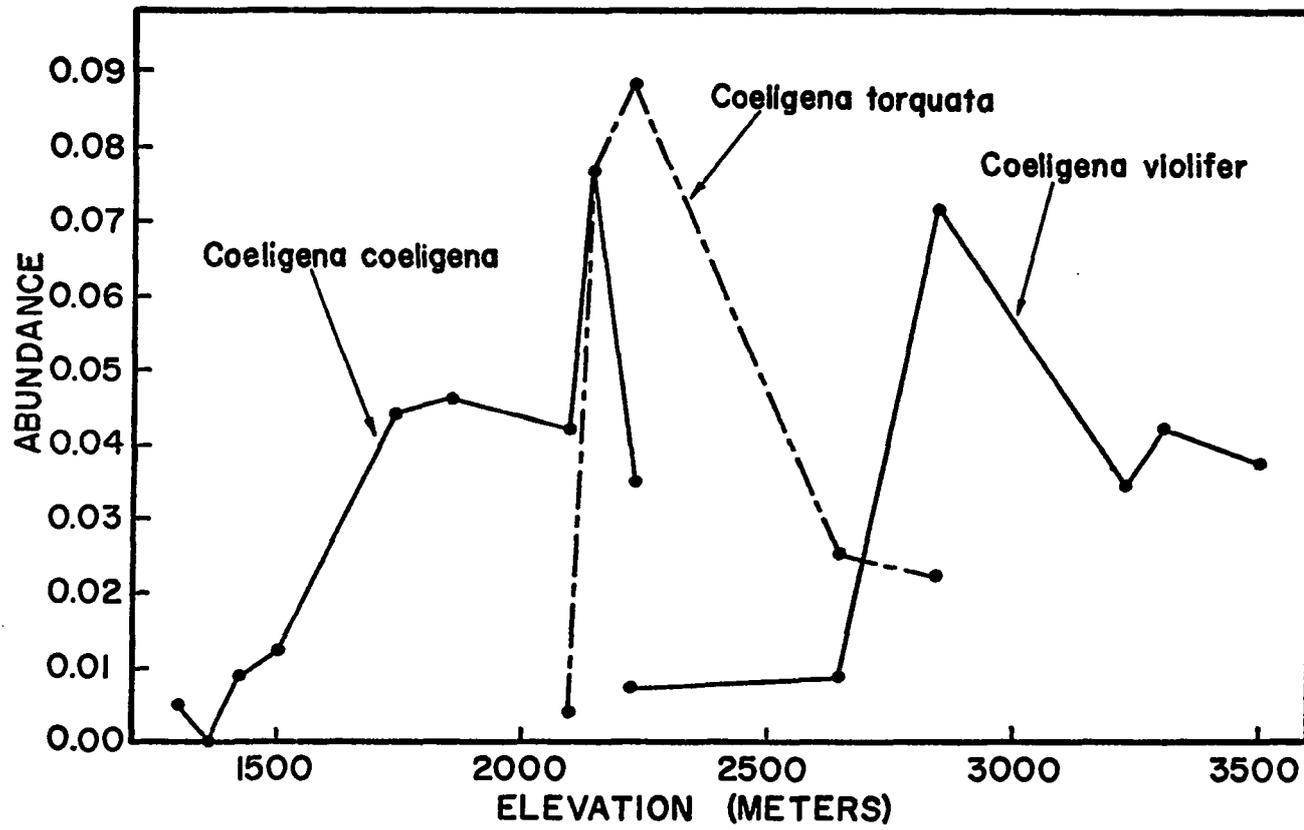


Figure 13. Relative abundance curves for wood-warblers of the genus  
Basileuterus.

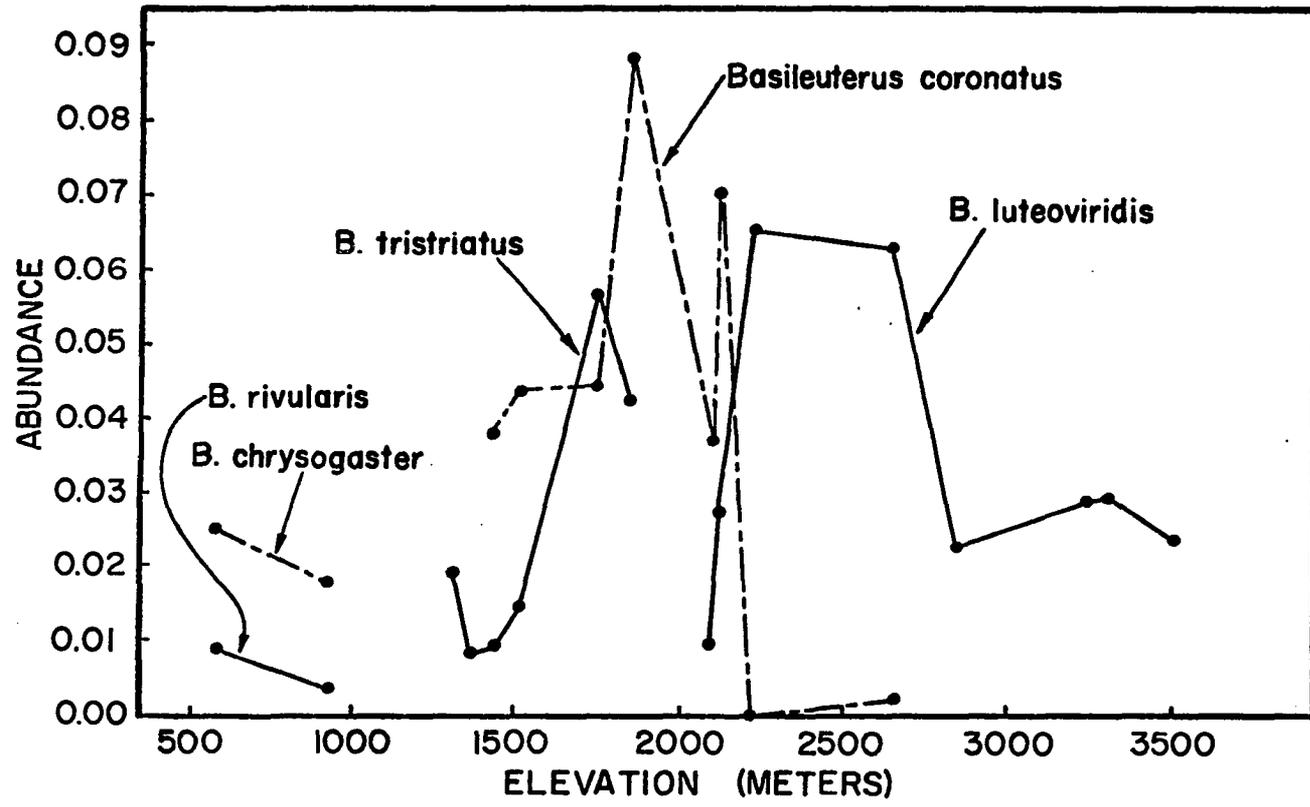


Table 1. Familial composition of the forest avifauna on the Vilcabamba elevational gradient. The number of forest species of each family is given for each of the stations on the gradient. Percentage figures give the proportion of the total forest avifauna comprised by certain major assemblages of families.

Family	Elevation on gradient (meters)										Family	Elevation on gradient (meters)									
	600	685	930	1520	1760	2130	2640	2830	3300	3520		600	685	930	1520	1760	2130	2640	2830	3300	3520
Tinamidae	3	2	2	1							Dendrocolaptidae	6	6	5	2	2	5	1	1		
Cathartidae	4	3	1	1	1	1					Furnariidae	6	6	6	12	10	4	5	6	5	3
Accipitridae	6	4	4	3	3	3	1	3	2	2	Formicariidae	21	17	14	9	5	6	2	1	1	
Falconidae	3	2	1	1							Conopophagidae		1	1	1	1					
Cracidae	2	2	3	1	1	1					Rhynocryptidae				1		1	1	1	1	1
Phasianidae		1			1	1					Cotingidae	7	6	4	5	2		3	2	2	2
Scolopacidae									1	1	Rupicolidae		1	1	1	1					
Columbidae	4	3	3	2	1	2	1	1	1	1	Pipridae	3	5	7	6	3	2				
Psittacidae	9	3	3	2		1	2	3	2	1	Tyrannidae	17	16	21	18	13	10	14	14	7	6
Cuculidae	1	1	1	1	1	1					All suboscines	60	58	59	55	37	28	26	25	16	12
Tytonidae	1	1	1	1	1							38%	38%	40%	44%	38%	29%	30%	30%	24%	23%
Strigidae	1	1	2	3	1	2	2	2	2	2	Hirundinidae			1				1	1	1	1
Steatornithidae									1		Corvidae				1	1	2				
Caprimulgidae							2	2			Troglodytidae	1	1	1	2	4	3	3	4	1	
Apodidae	2	2	2	2	2	2	2	2	2	2	Turdidae		1	1	1	3	3	3	3	2	2
Trochilidae	12	12	11	9	7	11	12	11	9	8	Vireonidae	4	4	4	1	1					
Trogonidae	2	1	2	1	2	3					Icteridae	3	4	3	2	2	3	1	1	1	1
Momotidae	1	1	1								Parulidae	1	2	4	4	3	3	2	2	2	1
Galbulidae	1	1	1		1						Coerebidae	5	4	4	3	4	4	5	5	5	5
Bucconidae	3	5	2	2	1						Thraupidae	15	15	16	19	14	15	14	11	12	6
Capitonidae	2	2	2	1	1						Catamblyrhynchidae						1	1	1	1	1
Ramphastidae	5	6	4	2	1	2	1				Fringillidae	3	4	3	1	2	4	5	3	4	5
Picidae	6	5	4	3	3	2	2	2	1	1	All New World	31	33	34	30	26	30	28	23	25	19
All non-passerines	68	58	50	36	27	32	25	26	21	18	9-primr. oscines	19%	22%	23%	24%	27%	31%	33%	28%	38%	37%
	43%	38%	34%	29%	28%	33%	29%	32%	32%	35%	Total species	160	151	146	125	98	98	86	82	66	52

Table 2. Weight ratios of elevationally replacing congeneric pairs. In each case, the congener with the higher elevational range is listed first, and the weight ratio given is that of the higher to the lower.

Species pair	Ave. wt.	Ratio	Species pair	Ave. wt.	Ratio
<i>Geotrygon frenata</i> <i>montana</i>	326.25 128.67	2.540	<i>Thripadectes holostictus</i> <i>melanorhynchus</i>	43.9 48.8	0.899
<i>Otus albigularis</i> sp	185.0 148.0	1.250	<i>Sclerurus mexicanus</i> <i>caudacutus</i>	28.3 41.8	0.677
<i>Otus</i> sp <i>ingens</i>	148.0 152.0	0.973	<i>Dysithamnus mentalis</i> <i>ardesiacus</i>	16.5 19.0	0.821
<i>Otus ingens</i> <i>watsoni</i>	152.0 120.8	1.258	<i>Drymophila caudata</i> <i>devillei</i>	11.92 10.3	1.157
<i>Momotus aequatorialis</i> <i>momota</i>	167.0 108.07	1.550	<i>Grallaricula ferrugineipectus</i> <i>flavirostris</i>	18.0 17.13	1.051
<i>Aulacorhynchus coeruleicinctis</i> <i>derbianus</i>	208.5 194.0	1.075	<i>Scytalopus unicolor</i> <i>femorialis</i>	17.6 22.58	0.779
<i>Aulacorhynchus derbianus</i> <i>prasinus</i>	194.0 146.25	1.326	<i>Myiobius villosus</i> <i>atricaudus</i>	14.03 10.10	1.389
<i>Picus rivolii</i> <i>rubiginosus</i>	86.0 76.75	1.120	<i>Rhynchocyclus fulvipectus</i> <i>olivaceus</i>	25.5 23.88	1.068
<i>Veniliornis nigriceps</i> <i>dignus</i>	45.3 45.8	0.989	<i>Pseudotriccus ruficeps</i> <i>pelzelni</i>	11.96 10.86	1.101
<i>Dendrocincia tyrannina</i> <i>fuliginosa</i>	60.17 47.15	1.280	<i>Pogonotriccus poecilotis</i> <i>orbitalis</i>	7.0 7.93	0.883
<i>Xiphorhynchus triangularis</i> <i>ocellatus</i>	46.78 35.07	1.333	<i>Troglodytes solstitialis</i> <i>aedon</i>	11.81 11.1	1.064
<i>Xiphorhynchus ocellatus</i> <i>guttatus</i>	35.07 62.39	0.562	<i>Vireo gilvus</i> <i>olivaceus</i>	12.0 12.82	0.936
<i>Lepidocolaptes affinis</i> <i>albolineatus</i>	31.5 28.9	1.090	<i>Myioborus melanocephalus</i> <i>miniatus</i>	10.75 10.53	1.021
<i>Cranioleuca albiceps</i> <i>curtata</i>	20.44 16.8	1.220	<i>Iridosornis reinhardti</i> <i>analis</i>	23.98 27.42	0.875
<i>Thripadectes scrutator</i> <i>holostictus</i>	66.3 43.9	1.510			

Table 3. Familial composition of the forest avifauna at stations on the humidity gradient. Figures for each station give the number of species present and the percentage of the species total comprised by each family.

Family	Station			Family	Station		
	Saoreni and Chiquireni: Dry forest	Quipachiari: Transitional forest	Luisiana: Humid forest		Saoreni and Chiquireni: Dry forest	Quipachiari: Transitional forest	Luisiana: Humid forest
Tinamidae	2 (3%)	1 (2%)	3 (2%)	Dendrocolaptidae	3 (4%)	5 (8%)	6 (4%)
Cathartidae	1 (1%)		4 (2%)	Furnariidae	1 (1%)	1 (2%)	6 (4%)
Accipitridae	2 (3%)		6 (4%)	Formicariidae	11 (14%)	8 (13%)	21 (13%)
Falconidae		1 (2%)	3 (2%)	Cotingidae	4 (5%)	6 (9%)	7 (4%)
Cracidae	2 (3%)		2 (1%)	Pipridae	1 (1%)	1 (2%)	3 (2%)
Columbidae	1 (1%)	2 (3%)	4 (2%)	Tyrannidae	14 (18%)	5 (8%)	17 (10%)
Psittacidae	2 (3%)	2 (3%)	9 (6%)	All suboscines	34 (44%)	26 (41%)	60 (38%)
Cuculidae	2 (3%)	2 (3%)	1 (1%)	Corvidae	1 (1%)		
Tytonidae			1 (1%)	Troglodytidae	2 (3%)	1 (2%)	1 (1%)
Strigidae	2 (3%)	3 (5%)	1 (1%)	Sylviidae	1 (1%)	1 (2%)	
Caprimulgidae	2 (3%)			Vireonidae	2 (3%)	3 (5%)	4 (2%)
Apodidae	1 (1%)		2 (1%)	Icteridae	2 (3%)		3 (2%)
Trochilidae	7 (9%)	5 (8%)	12 (7%)	Parulidae			1 (1%)
Trogonidae	1 (1%)	1 (2%)	2 (1%)	Coerebidae	1 (1%)	2 (3%)	5 (3%)
Momotidae	2 (3%)	1 (2%)	1 (1%)	Thraupidae	3 (4%)	7 (11%)	15 (9%)
Galbulidae			1 (1%)	Fringillidae	2 (3%)	1 (2%)	3 (2%)
Bucconidae	1 (1%)	1 (2%)	3 (2%)	All New World 9-prim. oscines	10 (13%)	13 (20%)	31 (19%)
Capitonidae		1 (2%)	2 (1%)	Total species	78 (100%)	64 (100%)	160 (100%)
Ramphastidae		2 (3%)	5 (3%)				
Picidae	2 (3%)	1 (2%)	6 (4%)				
All non-passerines	30 (38%)	23 (36%)	68 (43%)				

Appendix 1. List of Apurímac Valley species with their elevational ranges and average body weights. (1/17)

All species known to occur in the valley are listed. A number assigned to each species for reference purposes precedes its name. Species whose names are followed by a plus sign (+) are included on the basis of sight records only. Specimens from the Apurímac - Ene Valley of all other species have been deposited in the American Museum of Natural History or, when collected by H.-W. Koepcke, in the Museo de Historia Natural "Javier Prado" in Lima. The column headings are explained as follows:

Elevational range (meters)

Vilcabamba side: Species' elevational range on the Vilcabamba (= east) side of the valley, including its range on the valley floor, if any. The figures give lower and upper elevational limits in meters.

Valley floor: Species' elevational range, if limited to the valley floor. (The column is marked "x" if the species occurs on the valley floor and on one or both of the valley slopes.)

West side: Species' elevational range on the west side of the valley, including its range on the valley floor, if any.

Body weight (grams)

$\bar{X}$  = average weight of all birds, unsexed

$\bar{X}_m$  = average weight of males

$\bar{X}_f$  = average weight of females

$\bar{X}_c = (\bar{X}_m + \bar{X}_f) / 2$  = average of male and female averages

S.D. = standard deviation

n = number of individuals in the sample for that column

## Appendix 1 (2/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
1 Tinamus tao	685-1050		--1660--				
2 Tinamus major +		--600--					
3 Crypturellus soui	370-685	x		220.0 (--, 1)			
4 Crypturellus obsoletus	750-1520						
5 Crypturellus atrocapillus		x	340-1200				
6 Crypturellus tataupa		340-600				206.0 (--, 1)	
7 Podiceps occipitalis +			3660-3750				
8 Phalacrocorax olivaceus +		--600--					
9 Ardea cocoi +		500-600					
10 Casmerodius albus +		--600--					
11 Egretta thula +		--600--					
12 Florida caerulea +		--600--					
13 Butorides striatus +		--600--					
14 Tigrisoma fasciatum +	550-860	x					
15 Mesembrinibis cayennensis +		--600--					
16 Anas flavirostris +			--3370--				
17 Merganetta armata +	--860--						
18 Cairina moschata +		--600--					
19 Oxyura jamaicensis +			3370-3750				
20 Sarcoramphus papa +	500-2130	x					
21 Coragyps atratus +	500-685	x					
22 Cathartes aura +		340-600					
23 Cathartes melambrotos	600-685	x					
24 Elanoides forficatus +	600-2130	x					
25 Harpagus bidentatus	600-950	x					
26 Ictinia plumbea +		--600--					
27 Accipiter poliogaster +		--600--					
28 Accipiter striatus	1320-3520		1900-2350				
29 Buteo magnirostris	340-930	x	340-1600	265.0 (--, 1)			
30 Buteo albigula	--2100--						
31 Leucopternis albigollis +		--600--					
32 Oroaetus isidori +	2830-3520						
33 Spizastur melanoleucus +	--2830--						
34 Spizaetus tyrannus +	350-1760	x	350-1865				
35 Circus cinereus +			--3600--				
36 Pandion haliaetus +		370-470					
37 Herpetotheres cachinnans +		--600--					
38 Micrastur ruficollis	685-1710		--1660--				
39 Daptrius ater +		500-600					

## Appendix 1 (3/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
40 <i>Daptrius americanus</i>	370-685	x	370-800				
41 <i>Milvago chimachima</i> +		--600--					
42 <i>Phalcobaenus megalopterus</i> +			3370-3750				
43 <i>Falco deiroleucus</i> +		--600--					
44 <i>Falco ruficularis</i> +		340-600					
45 <i>Falco sparverius</i> +		--600--					
46 <i>Ortalis guttata</i>		x	340-1620				
47 <i>Penelope jacquacu</i>	685-1415				460.0 (--, 1)		
48 <i>Penelope montagnii</i>	1990-2415		2500-3370				
49 <i>Pipile cumanensis</i> +		470-600					
50 <i>Aburria aburri</i>	1450-1760*		1490-1760				
51 <i>Mitu mitu</i>	350-1240	x	350-1360				
52 <i>Odontophorus stellatus</i> +		--470--					
53 <i>Odontophorus gujanensis</i>	685-750						
54 <i>Odontophorus speciosus</i>	--1790--		--1630--				
55 <i>Odontophorus balliviani</i>	1940-2260						
56 <i>Rallus nigricans</i> +		--600--					
57 <i>Aramides cajanea</i>		x	600-800				
58 <i>Eurypyga helias</i> +	650-860						
59 <i>Hoploxypterus cayanus</i>		500-600					
60 <i>Charadrius collaris</i>		500-600					
61 <i>Tringa flavipes</i> +	--2830--	--430--					
62 <i>Tringa melanoleuca</i>		--600--					
63 <i>Actitis macularia</i> +		340-600					
64 <i>Gallinago gallinago</i> +			--3480--				
65 <i>Gallinago stricklandii</i> +			--3600--				
66 <i>Gallinago imperialis</i>	3300-3520						
67 <i>Sterna superciliaris</i>		470-600					
68 <i>Columba fasciata</i>	2620-3520		--2850--				
69 <i>Columba speciosa</i>		--600--					
70 <i>Columba cayennensis</i>		x	600-800				
71 <i>Columba plumbea</i>	370-2170	x	370-2300				
72 <i>Columbina talpacoti</i>		350-600					
73 <i>Claravis pretiosa</i> +		x	350-800				
74 <i>Claravis mondetoura</i>	--2190--		--1660--		100.25 (--, 2)		
75 <i>Leptotila verreauxi</i>		340-600		145.75 (16.62, 4)			
76 <i>Leptotila rufaxilla</i>	470-1070	x	470-1660	161.29 (12.42, 7)			

\* also once at 840 m

## Appendix 1 (4/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
77 Geotrygon montana	370-1070	x		128.67 (--, 3)			
78 Geotrygon frenata	1360-1730		--1630--*	326.25 (15.46, 4)			
79 Ara militaris		x	360-1660				
80 Ara macao +		470-600					
81 Ara severa		470-600					
82 Ara couloni		x	600-800				
83 Aratinga leucophthalmus +		x	350-800				
84 Aratinga weddellii	600-930	x	600-800				
85 Pyrrhura picta	370-1620	x	370-1660			67.0 (--, 1)	
86 Bolborhynchus lincola	1940-3300		--1660--		52.0 (--, 1)		
87 Bolborhynchus orbyngesius	--2830--						
88 Forpus xanthopterygius		--600--					
89 Hapalopsittaca melanotis +	--1970--						
90 Pionus menstruus	340-1480	x					
91 Pionus tumultuosus +			--3370--				
92 Amazona ochrocephala +		370-600					
93 Amazona mercenaria	2640-3520		2000-3370			340.0 (--, 1)	
94 Amazona farinosa +		--600--					
95 Piaya cayana	340-2515	x	340-1750				
96 Piaya minuta		x	600-800	48.40 (--, 2)			
97 Crotophaga ani		x	600-800				
98 Dremococcyx phasianellus		340-470		76.15 (--, 2)			
99 Tyto alba	600-1760	x					
100 Otus ingens	1370-1520		1660-1900		152.0 (--, 1)		
101 Otus watsonii		340-600		120.80 (7.19, 5)			
102 Otus albobularis	2650-3520		2600-3380			185.0 (--, 1)	
103 Otus sp	1730-2240			148.0 (--, 1)			
104 Pulsatrix perspicillata +	685-1500		--1660--				
105 Glaucidium minutissimum		x	370-1660		64.0 (--, 1)		
106 Glaucidium jardinii	2100-3520		3370-3520	60.50 (2.16, 4)			
107 Glaucidium brasilianum		340-600		67.33 (--, 3)			
108 Ciccaba virgata +	--900--						
109 Ciccaba huhula +	--1480--						
110 Steatornis caripensis	--3300--						
111 Nyctibius griseus +		x	550-1660				
112 Chordeiles rupestris		400-600					
113 Nyctidromus albicollis	350-685	x	350-800		60.0 (--, 1)		

\* also a juvenal once at 800 m

## Appendix 1 (5/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
114 <i>Caprimulgus rufus</i> +		350-420					
115 <i>Caprimulgus longirostris</i>	2640-2900					36.4 (---, 1)	
116 <i>Hydropsalis climacocerca</i>		--600--					
117 <i>Uropsalis segmentata</i>	2250-2830		2600-3370		42.0 (---, 1)	43.35 (---, 2)	42.68
118 <i>Streptoprocne zonaris</i>	600-3520	x	600-800				
119 <i>Cypseloides rutilus</i>	600-3520	x	600-800				
120 <i>Chaetura</i> sp. +		--340--					
121 <i>Doryfera ludovicae</i>	1280-2830		1700-1900	5.90 (0.35, 6)			
122 <i>Glaucis hirsuta</i>		350-370		5.80 (---, 2)			
123 <i>Threnetes leucurus</i>	470-685	x		5.77 (0.42, 9)			
124 <i>Phaethornis guy</i>	685-1520		1425-1660	5.01 (0.29, 8)			
125 <i>Phaethornis superciliosus</i>	340-930	x	340-800	5.74 (0.48, 23)			
126 <i>Phaethornis hispidus</i>		340-600		4.90 (0.47, 22)			
127 <i>Phaethornis stuarti</i>	340-930	x	340-800	2.90 (---, 2)			
128 <i>Eutoxeres condamini</i>	470-2640	x	470-1660	9.12 (0.94, 11)			
129 <i>Campylopterus largipennis</i>	350-685	x		8.49 (0.75, 7)			
130 <i>Florisuga mellivora</i>	600-930	x					
131 <i>Colibri thalassinus</i>	2100-3300			5.0 (---, 1)			
132 <i>Colibri coruscans</i>	600-3520	x	600-3370	8.8 (---, 1)			
133 <i>Lophornis delattrei</i>		--600--					
134 <i>Chlorostilbon mellisugus</i>		x	600-800		2.5 (---, 1)		
135 <i>Thalurania furcata</i>	370-1435	x			4.50 (---, 2)	3.95 (0.34, 5)	4.22
136 <i>Hylocharis cyanus</i>		--600--					
137 <i>Chrysuronia oenone</i>	600-930	x					
138 <i>Amazilia chionogaster</i>	350-3520	x	350-1790	5.00 (---, 3)			
139 <i>Amazilia lactea</i>		340-600		4.72 (0.37, 10)			
140 <i>Adelomyia melanogenys</i>	1520-2160		1660-2350	3.46 (0.29, 15)			
141 <i>Heliodoxa rubinoides</i>	2100-2160						
142 <i>Heliodoxa leadbeateri</i>	930-1735		1620-1780		9.0 (---, 1)	7.23 (0.60, 8)	8.12
143 <i>Heliodoxa branickii</i>	910-1290			5.10 (---, 3)			
144 <i>Pterophanes cyanopterus</i>			3370-3600		10.60 (---, 2)	9.8 (---, 1)	10.20
145 <i>Coeligena coeligena</i>	1290-2220		1660-1900	6.70 (0.60, 18)			
146 <i>Coeligena torquata</i>	2100-2830		1780-3100	6.72 (0.36, 12)			
147 <i>Coeligena violifer</i>	2250-3520		3270-3600		7.78 (0.21, 4)	6.55 (---, 2)	7.17
148 <i>Ensifera ensifera</i>	3300-3520		--3600--				
149 <i>Boissonneaua matthewsii</i>	1960-2830		1760-2090		8.3 (---, 1)		
150 <i>Heliangelus amethysticollis</i>	2230-3520		2100-3380		5.78 (0.26, 11)	4.83 (0.25, 13)	5.31
151 <i>Eriocnemis luciani</i>	2830-3520		3370-3600	6.21 (0.34, 7)			
152 <i>Ocreatus underwoodii</i>	1480-1950		1500-2090		2.8 (---, 1)	3.03 (---, 3)	2.92

## Appendix 1 (6/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
153 Metallura aeneocauda	3190-3520						
154 Metallura eupogon			3370-3600	4.56 (0.34, 10)			
155 Metallura tyrianthina	2640-3520		3370-3600	3.58 (0.41, 9)			
156 Chalcostigma ruficeps	2640-2830			3.8 (--, 2)			
157 Chalcostigma stanleyi			--3750--				
158 Aglaiocercus kingi	1830-2210		2100-2240				
159 Schistes geoffroyi	--1390--		--1660--	3.58 (0.47, 5)			
160 Heliiothryx aurita	685-900			5.70 (--, 3)			
161 Heliomaster longirostris		--600--					
162 Calliphlox amethystina		--600--					
163 Acestrura mulsant	--2620--					3.2 (--, 1)	
164 Pharomachus antisianus +	--2130--						
165 Pharomachus auriceps	1630-2160		1680-2010				
166 Trogon melanurus +		340-470					
167 Trogon viridis		470-600					
168 Trogon collaris	700-1520		1610-1780				
169 Trogon personatus	1630-2230		1660-3350			60.3 (--, 1)	
170 Trogon curucui	600-1260	x					
171 Ceryle torquata +		340-500					
172 Chloroceryle amazona +		470-600					
173 Chloroceryle americana		470-600					
174 Electron platyrhynchum		--350--		63.15 (--, 2)			
175 Baryphthengus ruficapillus	685-1430		1360-1660	160.0 (--, 1)			
176 Momotus momota		340-600		108.07 (7.06, 7)			
177 Momotus aquatorialis			1660-1940			167.0 (--, 1)	
178 Galbula cyanescens	470-1290	x	470-1720	25.28 (1.60, 6)			
179 Malacoptila fusca	600-930	x					
180 Malacoptila fulvogularis	1400-1840		--1790--			65.0 (--, 1)	
181 Micromonacha lanceolata	685-800		--1660--			22.0 (--, 1)	
182 Nonnula ruficapilla	470-1520	x					
183 Monasa nigrifrons	340-860	x	340-890	80.71 (5.05, 15)			
184 Monasa morphoeus +	--685--						
185 Chelidoptera tenebrosa		340-600					
186 Capito niger	600-1100	x					
187 Eubucco richardsoni	370-940	x					
188 Eubucco versicolor	1150-1760		1300-1760		37.80 (--, 3)	33.0 (--, 1)	35.40
189 Aulacorhynchus derbianus	1520-1735		1620-2150	194.00 (29.00, 5)			
190 Aulacorhynchus prasinus	370-1520	x	370-1660	146.25 (2.06, 4)			
191 Aulacorhynchus coeruleicinctis	1680-2160		1900-2050	208.5 (--, 2)			

## Appendix 1 (7/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
192 <i>Pteroglossus castanotis</i>	370-920	x	370-800	165.13 (--, 3)			
193 <i>Pteroglossus mariae</i>	600-1370	x	--1660--				
194 <i>Pteroglossus beauharnaesii</i> +	--685--						
195 <i>Selenidera reinwardtii</i>	470-1390	x					
196 <i>Andigena hypoglauca</i>	2150-2640		--2600--		330.0 (--, 1)	300.5 (--, 2)	315.25
197 <i>Ramphastos cucicri</i> +	470-685	x		10.3 (--, 1)			
198 <i>Picumnus aurifrons</i>	600-930	x					
199 <i>Picumnus cirrhatus</i> +			--1660--				
200 <i>Colaptes rupicola</i> +			--3530--				
201 <i>Piculus rivolii</i>	2100-2830		2350-2700			86.0 (--, 1)	
202 <i>Piculus rubiginosus</i>	1285-1940		1580-2300			76.75 (--, 2)	
203 <i>Piculus leucolacmus</i>	600-930	x					
204 <i>Coleus granmicus</i> +	--800--						
205 <i>Dryocopus lineatus</i>		--600--					
206 <i>Melanerpes cruentatus</i>	340-685	x	340-1100				
207 <i>Veniliornis passerinus</i>		x	600-800	32.45 (--, 2)			
208 <i>Veniliornis affinis</i>	600-930	x					
209 <i>Veniliornis dignus</i>	1480-2100		1660-1980		45.8 (--, 1)		
210 <i>Veniliornis nigriceps</i>	2640-3520		--3370--		45.3 (--, 1)		
211 <i>Phloeoceastes melanoleucos</i>		x	350-1085				
212 <i>Phloeoceastes rubricollis</i>	685-910			216.0 (--, 1)			
213 <i>Phloeoceastes haematogaster</i>	1425-2150		1425-1660				
214 <i>Dendrocincla tyrannina</i>	1850-2150		--2270--	60.17 (--, 3)			
215 <i>Dendrocincla fuliginosa</i>	370-930	x		47.15 (2.07, 15)			
216 <i>Deconychura longicauda</i>	--685--		--1660--		28.9 (--, 1)	28.0 (--, 1)	28.45
217 <i>Sittasomus griseicapillus</i>	350-1390	x	350-1660	16.23 (1.24, 6)			
218 <i>Glyphorhynchus spirurus</i>	470-1300*	x	470-1290	15.13 (0.63, 4)			
219 <i>Dendrexetastes rufigula</i>		--370--			76.5 (--, 1)		
220 <i>Xiphocolaptes prumeripirhynchus</i>	1720-2230		--1780--			114.0 (--, 1)	
221 <i>Xiphocolaptes orenocensis</i>	--930--						
222 <i>Dendrocolaptes certhia</i>		--370--		66.65 (--, 2)			
223 <i>Dendrocolaptes picumnus</i>		340-600		79.30 (4.29, 4)			
224 <i>Xiphorhynchus ocellatus</i>	685-1520		1420-1660	35.06 (1.92, 7)			
225 <i>Xiphorhynchus guttatus</i>		470-600		62.39 (3.46, 19)			
226 <i>Xiphorhynchus triangularis</i>	1520-2160		1660-2140	46.78 (2.62, 6)			
227 <i>Lepidocolaptes affinis</i>	2100-2230		1660-2240		31.5 (--, 1)		
228 <i>Lepidocolaptes albolineatus</i>	600-685	x		28.90 (--, 2)			

\* also once at 1425 m

## Appendix 1 (8/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
229 <i>Campylorhamphus pucheranii</i>	2130-2830		--2600--		70.5 (--, 1)		
230 <i>Synallaxis azarae</i>	1300-1990		--1660--	16.35 (--, 2)			
231 <i>Synallaxis cabanisi</i>	470-685	x	470-800	22.67 (1.49, 22)			
232 <i>Synallaxis albigularis</i>		x	470-800	16.55 (1.00, 4)			
233 <i>Synallaxis gujanensis</i>	350-685	x	350-800*	18.08 (1.28, 12)			
234 <i>Synallaxis unirufa</i>	2200-3230			17.61 (0.76, 7)			
235 <i>Synallaxis cherrieri</i>	470-600	x			16.8 (--, 1)	19.8 (--, 1)	
236 <i>Cranioleuca curtata</i>	--1520--		1660-1810				
237 <i>Cranioleuca albiceps</i>	2640-3400			20.44 (1.34, 9)			
238 <i>Schizoeca fuliginosa</i>	2830-3520		3370-3600	18.23 (1.47, 7)			
239 <i>Asthenes flammulata</i>			3500-3780			26.2 (--, 1)	
240 <i>Margarornis squamiger</i>	2100-3520		2600-3600	17.26 (1.40, 17)			
241 <i>Premnornis guttuligera</i>	1290-1830		1660-2100	15.89 (1.12, 15)			
242 <i>Premnoplex brunescens</i>	1290-2230		--1660--	16.28 (0.98, 18)			
243 <i>Pseudocolaptes boissonneautii</i>	1720-3400		2295-3370	47.67 (2.01, 6)			
244 <i>Hylocistis subulatus</i>	600-685	x		31.00 (--, 2)			
245 <i>Syndactyla rufosuperciliata</i>	1300-1830		1660-1900	27.72 (1.11, 9)			
246 <i>Syndactyla subalaris</i>	1360-1830		1660-2100	28.94 (1.25, 14)			
247 <i>Anabacerthia striaticollis</i>	1420-1735‡		1660-1900	24.78 (1.26, 18)			
248 <i>Philydor erythrocerus</i>	930-1520		1290-1760				
249 <i>Philydor ruficaudatus</i>	600-1050	x					
250 <i>Automolus dorsalis</i>		--600--		35.37 (5.02, 7)			
251 <i>Automolus ochrolaemus</i>	470-1360	x	470-1660	34.99 (2.11, 13)			
252 <i>Thripadectes holostictus</i>	1735-1830			43.90 (--, 2)			
253 <i>Thripadectes melanorhynchus</i>	1290-1520		--1660--	48.80 (2.24, 5)			
254 <i>Thripadectes scrutator</i>	2100-3520		--2600--		66.3 (--, 1)		
255 <i>Xenops rufus</i>	1480-1780		1560-1790				
256 <i>Xenops minutus</i>	470-1400	x	470-1420	12.94 (0.68, 8)			
257 <i>Sclerurus caudatus</i>	1290-1830		1660-1900	28.30 (0.88, 4)			
258 <i>Sclerurus caudatus</i>		--370--				41.8 (--, 1)	
259 <i>Lochmias nematura</i>	685-1740			29.33 (--, 3)			
260 <i>Cymbilaimus lineatus</i>	470-1000	x			60.50 (2.14, 4)	60.10 (3.24, 5)	60.30
261 <i>Taraba major</i>		x	340-800		31.5 (--, 1)	27.83 (--, 3)	29.67
262 <i>Thamnophilus doliatus</i>		x	340-1250		25.7 (--, 1)	29.50 (--, 3)	27.60
263 <i>Thamnophilus aethiops</i>		340-370					
264 <i>Thamnophilus schistaceus</i>	370-685	x			21.60 (--, 3)	20.60 (--, 2)	21.20

\* once also at 1660 m in second-growth

‡ once also at 930 m

## Appendix 1 (9/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_F$ (S.D., n)	$\bar{X}_c$
265 <i>Thamnophilus murinus</i>		340-600			18.00 (---, 3)	16.58 (1.09, 4)	17.29
266 <i>Thamnophilus caerulescens</i>	1420-1900		1660-2100		22.40 (0.96, 4)	22.45 (0.86, 4)	22.43
267 <i>Thamnistes anabatinus</i>	980-1420		1340-1660				
268 <i>Dysithamnus mentalis</i>	930-1480		1660-1790		15.6 (---, 1)	14.0 (---, 1)	14.80
269 <i>Thamnomanes ardesiacus</i>	600-685	x			19.0 (---, 1)		
270 <i>Thamnomanes schistogynus</i>		--470--			20.20 (---, 3)	17.8 (---, 1)	19.00
271 <i>Myrmotherula brachyura</i>	350-685	x		7.0 (---, 1)			
272 <i>Myrmotherula haematonota</i>	600-930	x			10.0 (---, 1)		
273 <i>Myrmotherula ornata</i>		470-600			10.5 (---, 1)		
274 <i>Myrmotherula axillaris</i>	340-930	x			8.46 (0.73, 12)	8.33 (0.79, 13)	8.40
275 <i>Myrmotherula schisticolor</i>	1290-1735*		1425-1760		9.8 (---, 2)	9.9 (---, 1)	9.85
276 <i>Myrmotherula menetriesii</i>	470-685	x					
277 <i>Dichrozona cincta</i>	--930--						
278 <i>Herpsilochmus pileatus</i>	1480-1620		1420-1670				
279 <i>Herpsilochmus rufimarginatus</i>		--600--					
280 <i>Drymophila devillei</i>		--350--			10.3 (---, 1)		
281 <i>Drymophila caudata</i>	1390-2230*		1660-2110		12.40 (---, 2)	11.60 (---, 3)	12.00
282 <i>Cercomacra cinerascens</i>	350-1150	x					
283 <i>Cercomacra nigrescens</i>	685-1740		1660-1790		19.60 (---, 3)	19.74 (1.63, 5)	19.67
284 <i>Pyriglena leuconota</i>	1290-2100		--1660--		35.55 (---, 2)		
285 <i>Myrmoborus leucophrys</i>		x	350-800		22.05 (1.32, 11)	20.52 (1.44, 12)	21.29
286 <i>Myrmoborus myotherinus</i>		--600--					
287 <i>Hypocnemis cantator</i>		x	340-800		13.44 (0.92, 5)	12.61 (0.87, 7)	13.03
288 <i>Perenostola leucostigma</i>	685-930#		--1660--	24.25 (1.17, 4)			
289 <i>Myrmeciza hemimelaena</i>	370-1290	x	370-1480		15.97 (0.69, 9)	16.03 (1.25, 9)	16.00
290 <i>Pithys albifrons</i>	470-930	x	470-800	20.82 (1.17, 19)			
291 <i>Rhegmatorhina melanosticta</i>		470-600		36.60 (---, 2)			
292 <i>Hylophylax naevia</i>	470-930	x			14.27 (0.71, 18)	14.02 (1.28, 6)	14.15
293 <i>Hylophylax poecilonota</i>	470-930	x			19.30 (1.23, 7)	20.14 (0.85, 8)	19.72
294 <i>Chamaeza campanisona</i>	1330-1520		--1660--	91.32 (2.28, 5)			
295 <i>Chamaeza mollissima</i>	1830-2230						
296 <i>Formicarius analis</i>	350-1170	x		60.39 (4.07, 14)			
297 <i>Formicarius rufipectus</i>	1630-1700		--1660--				
298 <i>Gallaricula flavirostris</i>	1455-2190		1660-2110	17.13 (2.16, 9)			
299 <i>Gallaricula ferrugineipectus</i>	2260-2640				18.0 (---, 1)		
300 <i>Myrmothera campanisona</i>		--600--					

\* once also at 2170 m

\* once also at 1295 m

# once also at 1500 m

## Appendix 1 (10/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
301 Grallaria squamigera	1830-2140						
302 Grallaria guatemalensis	685-1460						
303 Grallaria erythroleuca	2150-2200						
304 Grallaria rufula	2640-3175		3000-3600			38.0 (--, 1)	
305 Grallaria andecola			--3750--				
306 Conopophaga castaneiceps	1170-1800		1315-1660		27.57 (--, 3)	27.55 (2.45, 4)	27.56
307 Corythopsis torquata	685-1350			17.25 (--, 2)			
308 Scytalopus unicolor	1960-3520		2600-3600	17.60 (1.66, 4)			
309 Scytalopus femoralis	1290-1735		1250-2160	22.58 (1.27, 6)			
310 Lanisoma elegans		--370--				47.0 (--, 1)	
311 Ampelion rubrocristatus	2830-3520		2850-3600				
312 Pipreola intermedia	--2660--		2140-2930		50.0 (--, 1)		
313 Pipreola pulchra	--1710--		1660-2150		51.2 (--, 1)	57.5 (--, 1)	54.35
314 Pipreola frontalis	1520-1630		1630-1790		41.80 (--, 3)	41.84 (1.81, 5)	41.82
315 Pipreola arcuata	2640-3520		2850-3370		95.5 (--, 1)	103.00 (--, 2)	99.25
316 Attila spadiceus		--600--					
317 Casinornis rufa		340-350		24.76 (2.70, 15)			
318 Rhytipterna simplex		470-600*		36.80 (3.61, 5)			
319 Lipaugus vociferans +		350-600					
320 Pachyramphus versicolor	--2640--		--1660--				
321 Pachyramphus polychopterus		340-600			20.70 (1.17, 5)	21.78 (1.58, 4)	21.24
322 Pachyramphus marginatus +	470-685	x					
323 Pachyramphus albogriseus	1520-1780		1660-1860				
324 Platypsaris rufus	685-1710		--1760--				
325 Platypsaris minor		--370--			40.2 (--, 1)		
326 Tityra semifasciata	370-1620	x	370-1660				
327 Tityra inquisitor		370-600					
328 Quercula purpurata +	600-685	x					
329 Cephalopterus ornatus	685-970						
330 Gymnoderus foetidus		--600--					
331 Rupicola peruviana	685-1950		1610-1920				
332 Pipra fasciicauda	340-685	x		15.91 (0.82, 106)	16.02 (0.90, 24 <sup>@</sup> )		
333 Pipra chloromeros	685-1360*	x	800-1340 <sup>#</sup>	15.32 (0.77, 9)	15.73 (--, 3 <sup>@</sup> )		
334 Pipra pipra	930-1730 <sup>!</sup>		1590-1900	13.43 (0.65, 12)	13.15 (0.66, 4 <sup>@</sup> )		
335 Pipra caeruleicapilla	930-1730		1660-1900	9.15 (0.78, 19)	8.55 (0.43, 6 <sup>@</sup> )		

\* also once at 930 m and once at 1520 m  
 \* also once each at 470 m, 600 m, and 2120 m  
 # also once each at 470 m, 600 m, and 1660 m  
 ! also once each at 2130 m and 2160 m

@ sample comprised of fully adult males only

## Appendix 1 (11/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{x}$ (S.D., n)	$\bar{x}_m$ (S.D., n)	$\bar{x}_f$ (S.D., n)	$\bar{x}_c$
336 <i>Machaeropterus pyrocephalus</i>		x	600-1260*		9.9 (--, 1)		
337 <i>Chloropipo unicolor</i>	930-1830*		1660-1900	15.49 (0.91, 27)			
338 <i>Chloropipo holochlora</i>	685-930						
339 <i>Piprites chloris</i>	470-1520	x	470-1760				
340 <i>Schiffornis turdinus</i>	685-1520			28.40 (--, 2)			
341 <i>Muscisaxicola fluviatilis</i>		x	470-800		64.0 (--, 1)		
342 <i>Myiotheretes striaticollis</i>			--3600--				
343 <i>Myiotheretes fumigatus</i>	2640-3520				32.2 (--, 1)		
344 <i>Myiotheretes fusciorufus</i>			2350-2540				
345 <i>Myiotheretes erythrogygius</i> +			3370-3600				
346 <i>Ochthoeca fumicolor</i>	3300-3520		3370-3750		17.8 (--, 1)	14.0 (--, 1)	15.90
347 <i>Ochthoeca rufipectoralis</i>	2620-3520		3370-3520	10.83 (0.45, 6)			
348 <i>Ochthoeca cinnamomeiventris</i>	2100-2830			11.9 (--, 1)			
349 <i>Ochthoeca frontalis</i>	2830-3520		--3370--	10.72 (0.58, 5)			
350 <i>Ochthoeca pulchella</i>	2100-2670		--2600--	12.27 (0.89, 6)			
351 <i>Sayornis nigricans</i>	600-900	x		20.67 (--, 3)			
352 <i>Colonia colonus</i>		500-600					
353 <i>Pyrocephalus rubinus</i> +		--340--					
354 <i>Ochthornis littoralis</i>		--600--					
355 <i>Tyrannus melancholicus</i>	470-930	x	470-1660				
356 <i>Legatus leucophaeus</i>		--600--					
357 <i>Conopias cinchoneti</i>	860-940		--1660--				
358 <i>Megarhynchus pitangua</i> +		340-370					
359 <i>Myiodynastes maculatus</i>	600-930	x					
360 <i>Myiodynastes chrysocephalus</i>	930-1480						
361 <i>Myiozetetes granadensis</i>		x	600-800				
362 <i>Myiozetetes similis</i>	470-700	x	470-800				
363 <i>Pitangus sulphuratus</i> +		330-600					
364 <i>Myiarchus ferox</i>		x	600-800	27.8 (--, 1)			
365 <i>Myiarchus cephalotes</i>	1480-1675		--1660--	26.95 (--, 2)			
366 <i>Myiarchus tuberculifer</i>	1520-2170	350-600	1650-2600	21.0 (--, 1)			
367 <i>Contopus fumigatus</i>	1520-2130		1550-1660				
368 <i>Empidonax euleri</i>	470-1350	x	470-800	9.7 (--, 1)			
369 <i>Cnemotriccus fuscatus</i>	470-685	x		15.00 (--, 2)			
370 <i>Mitrephanes phaeocercus</i>	1480-1760		1660-1780	9.85 (--, 2)			
371 <i>Terenotriccus erythrurus</i>	350-930	x		7.04 (0.27, 8)			
372 <i>Myiobius villosus</i>	930-1400		--1660--		15.05 (--, 2)	12.0 (--, 1)	13.53

\* also once at 1900 m

\* also three times between 2200 m and 2250 m

Appendix 1 (12/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
373 <i>Myiobius atricaudus</i>		x	600-800	10.11 (1.25, 7)			
374 <i>Myiotriccus ornatus</i>	910-1730			13.5 (--, 1)			
375 <i>Pyrrhomias cinnamomea</i>	1480-2830		1620-2130	10.50 (--, 2)			
376 <i>Myiophobus flavicans</i>	1730-1830		1660-2270	12.70 (0.94, 15)			
377 <i>Myiophobus inornatus</i>	1520-1620						
378 <i>Myiophobus ochraceiventris</i>	2830-2930						
379 <i>Myiophobus fasciatus</i>		x	600-800				
380 <i>Myiophobus roraimae</i>	1320-1520		1560-1900	13.60 (--, 2)			
381 <i>Onychorhynchus coronatus</i>		350-370		14.98 (1.65, 4)			
382 <i>Platyrinchus platyrhynchos</i>	685-930						
383 <i>Platyrinchus mystaceus</i>	930-1830		1660-1900	11.33 (--, 3)			
384 <i>Platyrinchus flavigularis</i>	--1520--						
385 <i>Tolmomyias assimilis</i>	470-930	x	470-1230	17.8 (--, 1)			
386 <i>Tolmomyias poliocephalus</i>		340-600		11.04 (0.69, 5)			
387 <i>Tolmomyias flaviventris</i>	340-725	x	340-1000	13.67 (--, 3)			
388 <i>Rhynchocyclus olivaceus</i>	685-1080			23.88 (3.52, 4)			
389 <i>Rhynchocyclus fulvipectus</i>	1420-1840			25.50 (--, 2)			
390 <i>Ramphotrigon fuscicauda</i>		--350--		19.52 (0.95, 5)			
391 <i>Todirostrum chrysocrotaphum</i>	370-1285	x	370-1430				
392 <i>Todirostrum cinereum</i>		x	600-800	7.0 (--, 1)			
393 <i>Todirostrum latirostre</i>		x	350-800	8.09 (0.71, 22)			
394 <i>Idioptilon granadense</i>	2100-2830		2280-2600	7.87 (0.42, 9)			
395 <i>Lophotriccus pileatus</i>	870-1830		1310-1660	8.23 (0.60, 9)			
396 <i>Myiornis auricularis</i>		340-600		5.30 (0.36, 9)			
397 <i>Myiornis ecaudatus</i>	370-980	x					
398 <i>Pseudotriccus pelzelni</i>	1520-1880		1660-1900	10.86 (0.82, 22)			
399 <i>Pseudotriccus ruficeps</i>	2100-3190		2600-3370	11.96 (--, 3)			
400 <i>Pogonotriccus poecilotis</i>			1560-1900	7.0 (--, 1)			
401 <i>Pogonotriccus orbitalis</i>	685-930		--1425--	7.93 (--, 3)			
402 <i>Phylloscartes ventralis</i>	1480-1760		1560-2150	7.85 (--, 2)			
403 <i>Pseudocolopteryx acutipennis</i>		x	600-800				
404 <i>Anairetes</i> sp. +			--3600--				
405 <i>Uromyias agraphia</i>	2640-3520				9.9 (--, 1)	9.9 (--, 1)	9.85
406 <i>Serpophaga hypoleuca</i>		--600--					
407 <i>Serpophaga cinerea</i>	600-900	x	600-700				
408 <i>Mecocerculus leucophrys</i>	2830-3520		3370-3600	13.93 (1.34, 6)			
409 <i>Mecocerculus stictopterus</i>	2660-2830		--3600--				
410 <i>Elaenia flavogaster</i>		x	600-800				
411 <i>Elaenia spectabilis</i>		--600--					
412 <i>Elaenia albiceps</i>		x	340-1780	15.89 (2.54, 9)			

## Appendix 1 (13/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
413 Elaenia gigas		x	470-800		31.0 (--, 1)		
414 Elaenia pallatangae	--2640--		--1660--				
415 Myiopagis galmardii	340-1150	x		11.95 (0.88, 8)			
416 Phacomyias murina		x	600-800				
417 Camptostoma obsoletum		--600--					
418 Phylomyias griseiceps		--350--			7.4 (--, 1)		
419 Tyranniscus uropygialis	2640-2830		--2500--			8.7 (--, 1)	
420 Tyranniscus nigrocapillus	1830-1920		2300-2350				
421 Tyranniscus bolivianus	1390-2830		1610-1860		11.9 (--, 1)	10.0 (--, 1)	10.95
422 Tyrannulus elatus		400-600				8.1 (--, 1)	
423 Ornithion inermis	470-940	x			7.0 (--, 1)		
424 Leptopogon superciliaris	685-1620		1340-1660	13.84 (0.92, 5)			
425 Leptopogon amaurocephalus	340-930	x	340-800	11.68 (0.87, 27)			
426 Leptopogon taczanowskii	1735-2640						
427 Mionectes striaticollis	600-3300	x	1660-3370	15.01 (1.69, 89)			
428 Mionectes olivaceus	470-1430	x	1290-1660	13.78 (1.13, 28)			
429 Pipromorpha macconnellii	470-685	x	470-800	12.53 (0.98, 22)			
430 Tachycineta albiventer		400-600					
431 Phacoprogne tapera		--470--			34.5 (--, 1)		
432 Notiochelidon murina			--3370--				
433 Notiochelidon cyanoleuca		x	600-890				
434 Notiochelidon flavipes	2640-3520						
435 Atticora fasciata		500-600					
436 Neochelidon tibialis	+ 700-900					15.8 (--, 1)	
437 Stelgidopteryx ruficollis			470-800				
438 Cyanolyca viridicyana	2075-2200		2600-2900		127.0 (--, 1)	113.0 (--, 1)	120.00
439 Cyanocorax violaceus	+ 1270-2150	340-350					
440 Cyanocorax yncas	1270-2150		1625-1760				
441 Cinclus leucocephalus	685-890						
442 Odontorchilus branickii	1300-1760		1560-1760			10.2 (--, 1)	
443 Cinnycerthia peruana	1710-2830		2500-3370	19.61 (1.77, 8)			
444 Cistothorus platensis	--3500--		3530-3600			11.0 (--, 1)	
445 Thryothorus euophrys	--2830--						
446 Thryothorus coraya	350-1600	x	350-1660	23.85 (2.52, 10)			
447 Troglodytes aedon		x	470-1100*			11.1 (--, 1)	
448 Troglodytes solstitialis	1710-3300		1815-2600	11.81 (0.74, 9)			
449 Henicorhina leucophrys	1360-3100		1410-2250	15.73 (1.23, 26)			
450 Microcerculus marginatus	340-1150	x	340-1560	17.32 (0.81, 17)			

\* also once at 1660 m in second-growth

## Appendix 1 (14/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
451 <i>Cyphorhinus thoracicus</i>	1300-1410		--1660--				
452 <i>Donacobius atricapillus</i>		--600--					
453 <i>Myadestes ralloides</i>	1735-2230*		1660-2600	27.73 (1.66, 17)			
454 <i>Entomodostes leucotis</i>	2100-2830		1660-3370	57.93 (2.05, 6)			
455 <i>Catharus dryas</i>			--1660--	35.90 (2.50, 7)			
456 <i>Platycichla leucops</i>	--1400--		1660-1900	61.48 (4.39, 5)			
457 <i>Turdus fuscater</i>	2620-3520		2600-3750	146.50 (--, 2)			
458 <i>Turdus serranus</i>	1750-3520		--3370--	82.3 (--, 1)			
459 <i>Turdus nigriceps</i>	685-930*		--1660--		54.15 (--, 2)	50.41 (2.46, 7)	52.28
460 <i>Turdus ignobilis</i>		x	470-800	59.62 (4.12, 12)			
461 <i>Polioptila plumbea</i>		340-370				6.5 (--, 1)	
462 <i>Cyclarhis gujanensis</i>		x	600-900#				
463 <i>Sraragdolanus leucotis</i>	600-1150	x					
464 <i>Vireo olivaceus</i>	340-1300	x	340-1290#	12.82 (0.62, 27)			
465 <i>Vireo gilvus</i>	1480-1760		1560-2040		12.0 (--, 1)		
466 <i>Hylophilus hypoxanthus</i>	600-1100	x	600-1460				
467 <i>Hylophilus ochraceiceps</i>	600-930	x		13.20 (--, 3)			
468 <i>Scaphidura oryzivora</i>		x	600-800				
469 <i>Psarocolius decumanus</i>	600-1100	x	600-1250#				
470 <i>Psarocolius atrovirens</i>	1480-2150		1625-1900				
471 <i>Psarocolius angustifrons</i>	600-950	x	600-800#			188.0 (--, 1)	
472 <i>Cacicus cela</i>	340-930	x	340-800				
473 <i>Cacicus uropygialis</i>	1270-1840		1660-1900	89.7 (--, 1)			
474 <i>Cacicus leucoramphus</i>	1810-2160		--2500--				
475 <i>Cacicus solitarius</i>		--600--			94.5 (--, 1)	67.5 (--, 1)	81.00
476 <i>Cacicus holosericeus</i>	2100-3520			47.75 (--, 2)			
477 <i>Icterus cayanensis</i>	600-685	x					
478 <i>Parula pitiaiyumi</i>	940-1620		1410-1900				
479 <i>Myioborus miniatus</i>	930-1780		1290-2020	10.53 (0.57, 4)			
480 <i>Myioborus melanocephalus</i>	1990-3300		2350-2600	10.75 (--, 2)			
481 <i>Basileuterus luteoviridis</i>	2100-3520		2500-3370	16.47 (1.40, 19)			
482 <i>Basileuterus chrysogaster</i>	685-940			12.10 (0.80, 6)			
483 <i>Basileuterus tristriatus</i>	1290-1830		1340-2010	12.74 (1.22, 22)			
484 <i>Basileuterus coronatus</i>	1390-2150@		1660-2110	16.04 (1.25, 23)			

\* also once each at 600 m, 930 m, and 1285 m

\* also once at 2120 m

# also once at 1660 m in second-growth

@ also once at 2640 m

## Appendix 1 (15/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
485 Basileuterus rivularis	600-930	x	600-800*	16.08 (0.65, 4)			
486 Coereba flaveola		x	470-800	10.58 (0.69, 4)			
487 Conirostrum speciosum		340-600			10.1 (--, 1)	9.0 (--, 1)	9.55
488 Conirostrum cinereum			3520-3600			13.0 (--, 1)	
489 Conirostrum ferrugineiventre	--3520--		3370-3750				
490 Conirostrum sitticolor	2640-3520		3370-3600	10.35 (--, 2)			
491 Conirostrum albifrons	1950-2200		--2140--			10.0 (--, 1)	
492 Diglossa caerulea	1735-2100		1850-1900	14.96 (--, 5)			
493 Diglossa baritula			1820-1900				
494 Diglossa lafresnayii	2500-3520		3370-3600	15.84 (1.26, 26)			
495 Diglossa carbonaria	3300-3520		3370-3750		13.1 (--, 1)	11.85 (--, 2)	12.48
496 Diglossa albilatera	2140-3300		2110-2150		12.60 (0.49, 5)	11.50 (--, 2)	12.05
497 Diglossa glauca	1520-2200*		1610-2600	13.02 (0.81, 17)			
498 Diglossa cyanea	1735-3520		1660-3580	18.19 (1.25, 43)			
499 Cyanerpes caeruleus	600-1480	x	600-1660				
500 Chlorophanes spiza	370-1360	x	370-1660	18.15 (--, 2)			
501 Iridophanes pulcherrima	1425-1760		1660-1780				
502 Dacnis cayana	600-1360	x					
503 Dacnis lineata	600-1180	x	600-1290				
504 Xenodacnis parina			--3750--		13.0 (--, 1)	12.0 (--, 1)	12.50
505 Tersina viridis		x	600-1660				
506 Chlorophonia cyanea	600-1630	x	600-1790				
507 Euphonia xanthogaster	600-2130	x	600-1990		14.36 (0.54, 5)	13.34 (0.79, 5)	13.85
508 Euphonia minuta		--600--					
509 Euphonia chlorotica		x	600-800				
510 Euphonia lanirostris		340-600			15.8 (--, 1)	15.2 (--, 1)	15.50
511 Euphonia rufiventris	370-980	x					
512 Euphonia mesochrysa	1100-1760		1290-1800				
513 Euphonia chrysopasta	470-930	x					
514 Pipraeidea melanota			1660-1990	21.0 (--, 1)			
515 Chlorochrysa calliparaea	1480-1875		1660-1900				
516 Tangara callophrys	600-930	x					
517 Tangara chilensis	370-1250	x	370-1290				
518 Tangara schrankii	600-1300	x	600-1560	21.5 (--, 1)			
519 Tangara punctata	1150-1350		1425-1660				
520 Tangara xanthogastra	685-930		--1290--				

\* also once at 1660 m in second-growth

\* also once at 2830 m

## Appendix 1 (16/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_F$ (S.D., n)	$\bar{X}_C$
521 Tangara arthus	1480-1700		1590-1660		23.3 (--, 1)		
522 Tangara xanthocephala	1480-2130		1590-2350				
523 Tangara chrysotis	1480-1730						
524 Tangara parduzdakii	1480-2130		1560-2240			28.00 (--, 2)	
525 Tangara cyanotis	1480-1620		1560-1780				
526 Tangara cyanicollis +	900-1050		--1660--				
527 Tangara nigrocincta	370-1100	x					
528 Tangara ruficervix	1480-1760		1660-1720		17.15 (--, 2)		
529 Tangara mexicana	370-930	x					
530 Tangara gyrola	600-1480	x	600-1550				
531 Tangara nigroviridis	1650-2130		1620-2350	16.55 (--, 2)			
532 Tangara vassorii	1770-2360		1900-2430				
533 Iridosornis analis	1320-2100		1660-1900	27.43 (1.07, 15)			
534 Iridosornis reinhardti	2080-3520		2430-3520	23.98 (1.72, 23)			
535 Anisognathus igniventris	2620-3520		2850-3600	35.78 (2.54, 14)			
536 Anisognathus lacrymosus	2200-3520		2280-2600	31.84 (1.67, 17)			
537 Anisognathus flavinucha	1370-1950		1640-2150	44.27 (--, 3)			
538 Buthraupis montana	2100-3300		2300-3520	99.50 (--, 2)			
539 Dubusia castaneoventris	2130-3520		2130-2600	28.30 (--, 3)			
540 Dubusia taeniata	2170-3300			40.73 (--, 3)			
541 Thraupis virens		x	600-1660	39.5 (--, 1)			
542 Thraupis palmarum		x	600-1230				
543 Thraupis cyanocephala	1950-2720		2300-2350	40.35 (3.72, 4)			
544 Thraupis bonariensis			1660-3600		35.0 (--, 1)		
545 Ramphocelus carbo	470-685	x	470-1290		28.47 (1.21, 20)	27.63 (1.87, 17)	28.05
546 Ramphocelus nigrogularis		--600--					
547 Calochaetes coccineus	1480-1950		1660-1900				
548 Piranga leucoptera	1480-1540		1575-1660				
549 Haëia rubica	600-950	x			35.2 (--, 1)	35.7 (--, 1)	35.45
550 Ianio versicolor	600-930				18.5 (--, 1)		
551 Tachyphonus rufus			--800--				
552 Tachyphonus rufiventer	370-1300	x	370-1425		18.0 (--, 1)	17.5 (--, 1)	17.75
553 Creurgops dentata	1480-2150				19.60 (--, 2)		
554 Trichothraupis melanops	1150-1520		--1660--				
555 Hemithraupis guira	350-685	x			12.3 (--, 1)		
556 Thlypopsis sordida		470-600		15.95 (1.30, 6)			
557 Thlypopsis ornata	--3320--						
558 Thlypopsis ruficeps	--2620--		--3600--		10.6 (--, 1)		
559 Chlorospingus ophthalmicus	1735-2640		1760-2430	24.51 (2.54, 7)			

## Appendix 1 (17/17)

Species	Elevational range (meters)			Body weight (grams)			
	Vilcabamba side	Valley floor	West side	$\bar{X}$ (S.D., n)	$\bar{X}_m$ (S.D., n)	$\bar{X}_f$ (S.D., n)	$\bar{X}_c$
560 <i>Chlorospingus flavigularis</i>	880-1520						
561 <i>Chlorospingus parvirostris</i>	1500-1740						
562 <i>Chlorospingus canigularis</i>			1630-1660				
563 <i>Cnemoscopus rubirostris</i>	2100-2830		2130-2600		21.50 (0.41, 4)	16.35 (0.90, 4)	18.93
564 <i>Hemispingus atropileus</i>	2640-3300		2600-3370	22.45 (3.23, 4)			
565 <i>Hemispingus superciliaris</i>	2100-3300			13.85 (--, 2)			
566 <i>Hemispingus frontalis</i>	1460-1790		1660-1900	18.06 (1.52, 14)			
567 <i>Hemispingus melanotis</i>	1710-2230		--1660--			14.6 (--, 1)	
568 <i>Hemispingus sp</i>	3190-3520						
569 <i>Hemispingus xanthophthalmus</i>	2640-3520		2500-2580				
570 <i>Hemispingus trifasciatus</i>			--3370--				
571 <i>Chlorornis riefferii</i>	2100-3300		2140-2600	55.13 (--, 3)			
572 <i>Cissopis leveriana</i>	350-685	x	350-800	73.77 (--, 3)			
573 <i>Catamblyrhynchus diadema</i>	2100-3520		--3370--	16.4 (--, 2)			
574 <i>Saltator maximus</i>	600-930	x	600-1250	45.00 (1.92, 6)			
575 <i>Saltator coerulescens</i>		x	600-800	61.7 (--, 1)			
576 <i>Pitylus grossus</i>	370-930	x		53.3 (--, 1)			
577 <i>Paroaria gularis</i>		--600--					
578 <i>Pheucticus chrysopeplus</i>	2100-2640		1660-3520			56.5 (--, 1)	
579 <i>Pheucticus aureoventris</i>	--2140--		1660-2430			65.5 (--, 1)	
580 <i>Cyanocompsa cyanoides</i>	470-1290	x	470-800		27.93 (2.11, 4)	24.43 (--, 3)	26.18
581 <i>Volatinia jacarina</i>	340-600	x	340-800	9.80 (--, 3)			
582 <i>Sporophila luctuosa</i>	600-2830	x	600-2600	12.48 (0.55, 4)			
583 <i>Sporophila nigricollis</i>		x	600-800	9.50 (--, 2)			
584 <i>Sporophila obscura</i>	350-2100	x	350-1660	11.16 (0.84, 29)			
585 <i>Sporophila castaneiventris</i>		x	470-800	8.27 (--, 3)			
586 <i>Oryzoborus angolensis</i>	--685--			13.47 (--, 3)			
587 <i>Catamenia inornata</i>	--3520--		--3600--	15.5 (--, 2)			
588 <i>Catamenia homochroa</i>	3230-3520						
589 <i>Phrygilus unicolor</i>			3370-3750	21.80 (--, 2)			
590 <i>Haplospiza rustica</i>	1740-3520		1660-2600	15.65 (1.02, 13)			
591 <i>Atlapetes rufinucha</i>	2520-3520			25.7 (--, 1)			
592 <i>Atlapetes tricolor</i>	--2100--		--1660--			29.5 (--, 1)	
593 <i>Atlapetes brunneinucha</i>	1320-2250		1660-1900	46.62 (3.29, 14)			
594 <i>Atlapetes torquatus</i>	2640-2830		2600-3370	38.95 (2.14, 4)			
595 <i>Lysurus castaneiceps</i>	--1410--						
596 <i>Myospiza aurifrons</i>	470-685	x	470-800				
597 <i>Zonotrichia capensis</i>	3300-3520		3370-3600				
598 <i>Spinus magellanicus</i>	2650-3180	x	600-1660				

Appendix 2. List of Apurímac Valley species with figures for relative abundance based on netted samples. (1/12)

Part A gives information on the net-lines and associates each net-line with a column in Part B. The total number of species and individuals in each sample is noted.

Part B gives relative abundance figures. Only those species of birds which were netted are listed. The reference number assigned to each species in Appendix 1 precedes the species' name on this list. The proportional occurrence of a species in a sample is expressed as a decimal fraction. The decimal in front of the three-digit figure has been omitted. The actual number of individuals of a given species which were caught in any sample can be calculated by multiplying the figure for proportional occurrence by the sample size given in Part A.

Appendix 2 (2/12). Part A: Net-line information. The net-lines preceded by numbers 2 through 17 were located on the Vilcabamba transect, 19 through 26 were on the West Side transect, and 27 through 31 were on the Apurimac - Ene transect.

Column on Part B	Net-line	No. of species caught	Total indiv. caught	Elevation (meters)	Max. no. nets	Dates	Vegetation
1	Luisiana forest	51	284	600	15	11 Aug - 2 Sep 1965 20-22 Aug 1966	Lowland humid forest
2	Vb-0	69	442	685	27	30 July - 7 Aug 1968 10-16 June 1970	Lowland humid forest
3	Vb-1	68	605	910-950	20	28 June - 14 July 1966 11-16 June 1967 12-20 June 1968	Hill forest
4	Vb-2: lower lower	57	207	1270-1330	11	28 July - 9 Aug 1966	Hill forest
5	Vb-2: middle lower	42	130	1330-1390	11	28 July - 9 Aug 1966	Hill forest / cloud forest transition
6	Vb-2: upper lower	42	109	1390-1470	12	1-9 Aug 1966	Hill forest / cloud forest transition
7	Vb-2: upper upper	67	419	1480-1540	15	16-31 July 1966 23-27 June 1967	Cloud forest
8	Vb-2½: lower	72	498	1700-1760	12	12-21 Aug 1967 22-30 June 1968 20-27 June 1970	Cloud forest
9	Vb-2½: upper	56	307	1770-1930	18	12-21 Aug 1967 22-30 June 1968 20-27 June 1970	Cloud forest
10	Vb-3: lower	73	337	2070-2120	12	8-19 July 1967 3-5 Aug 1968	Cloud forest
11	Vb-3: middle	53	328	2130-2190	13	11-17 Aug 1966 28 June - 19 July 1967	Cloud forest

## Appendix 2 (3/12). Part A

Column on Part B	Net-line	No. of species caught	Total indiv. caught	Elevation (meters)	Max. no. nets	Dates	Vegetation
12	Vb-3: upper	47	170	2190-2260	13	29 June - 19 July 1967	Cloud forest
13	Vb-4	69	630	2620-2660	16	16-23 July 1967 3-10 July 1968 25-30 June 1970	Elfin forest
14	Vb-5	66	451	2820-2840	14	21-31 July 1967 9-13 July 1968	Elfin forest
15	Vb-6: lower	35	178	3170-3300	12	31 July - 11 Aug 1967 12-25 July 1968	Elfin forest
16	Vb-6: upper	49	311	3290-3340	16	31 July - 11 Aug 1967 12-25 July 1968	Mixed elfin forest and grassland
17	Vb-7	44	219	3450-3525	27	16-31 July 1968	Mixed elfin forest and grassland
18	Luisiana matorral	41	231	600	16	8 Aug - 2 Sep 1965 15-19 June 1970	Matorral
19	Santa Rosa	39	204	800	21	13-18 Aug 1968 8-12 July 1970	Second-growth
20	Huanhuachayo coffee	41	100	1660	5	18-22 Aug 1968 12-18 July 1970	Overgrown coffee plantation
21	Huanhuachayo purma	41	97	1660	6	18-22 Aug 1968 12-18 July 1970	Tall second-growth
22	Huanhuachayo forest	67	368	1660	12	18-22 Aug 1968 12-18 July 1970	Cloud forest
23	Estera Rohuana	40	143	1900	20	14-18 July 1970	Cloud forest
24	Yuraccyacu	24	93	2600	22	19-23 July 1970	Cloud forest

## Appendix 2 (4/12). Part A

Column on Part B	Net-line	No. of species caught	Total indiv. caught	Elevation (meters)	Max. no. nets	Dates	Vegetation
25	Puncu	40	231	3370-3390	21	23-28 Aug 1968 25-29 July 1970	Mixed elfin forest and cloud forest
26	Uchuy Monte	16	90*	3600	8	28-29 July 1970	Mixed elfin forest and puna grassland
27	Boca Mantaro matorral	24	65	460	10	6-11 Aug 1970	Matorral
28	Boca Mantaro forest	31	124	470-480	35	6-11 Aug 1970	Lowland humid forest
29	Quipachiari	32	151	370	51	13-18 Aug 1970	Transitional forest
30	Chiquireni	40	143	350-370	51	20-23 Aug 1970	Dry deciduous forest
31	Saoreni	31	99	340-400	51	24-28 Aug 1970	Dry deciduous forest

\* Birds netted at Uchuy Monte were not banded, and no exact count of individuals was kept. The listed total of 90 is approximate. Species captured in this net-line are indicated in Part B by "X".



Appendix 2 (6/12). Part B

Sp. no.	Species	Column																																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31							
145	<i>Coeligena coeligena</i>				005		009	012	044	046	042	076	035								020	031	011	028															
146	<i>Coeligena torquata</i>										003	076	088	025	022									028	022														
147	<i>Coeligena violifer</i>												006	008	071	034	042	037									026	X											
148	<i>Ensifera ensifera</i>																010	018										X											
149	<i>Boissonneaua matthewsii</i>										009				002	007																							
150	<i>Helianthus amethysticollis</i>												006	048	064	006	029	014							097	022													
151	<i>Eriocnemis luciani</i>														004		023	018								013	X												
152	<i>Ocreatus underwoodii</i>						002	008	003															021															
153	<i>Metallura aeneocauda</i>															006		014																					
154	<i>Metallura eupogon</i>																									043	X												
155	<i>Metallura tyrrhina</i>													002	018	090	084	073								056	X												
156	<i>Chalcostigma ruficeps</i>													005	009																								
158	<i>Aglaiocercus kingi</i>									015			006																										
159	<i>Schistes geoffroyi</i>																					040	010	008															
160	<i>Heliothryx aurita</i>		009																																				
163	<i>Acestrura mulsant</i>														002																								
168	<i>Trogon collaris</i>							002																															
169	<i>Trogon personatus</i>									010	003		006										010		007														
174	<i>Electron platyrhynchum</i>																																		014				
175	<i>Baryphthengus ruficapillus</i>		005	005	014	008																	010																
176	<i>Momotus momotus</i>	007																																	015	008	007	021	010
177	<i>Momotus aequatorialis</i>																								003														
178	<i>Callula cyaneus</i>		007	007	014																	026	005																
179	<i>Malacoptila fusca</i>		004		013																																		
180	<i>Malacoptila fulvogularis</i>						018			003																													
181	<i>Micromonacha lanceolata</i>		002																																				
182	<i>Nonnula ruficapilla</i>		014			005	008			002																													
183	<i>Nonnula nigrifrons</i>																																				013	028	091
188	<i>Eubucco versicolor</i>					005																			003														
189	<i>Aulacorhynchus derbianus</i>									002															011														
190	<i>Aulacorhynchus prasinus</i>					010																	015			008													
191	<i>Aulacorhynchus coerulescinctis</i>									002	010	015	015																										
193	<i>Pterodroma mariae</i>			005																																			
195	<i>Selenidera reinwardtii</i>		004			002	005																																
198	<i>Picumnus aurifrons</i>																																						
201	<i>Piculus rivolii</i>											006				002	002																						
202	<i>Piculus rubiginosus</i>									002																													
207	<i>Veniliornis passerinus</i>																																						
210	<i>Veniliornis nigriceps</i>																																						
213	<i>Phloeocoastes haematogaster</i>																																						
214	<i>Dendrocincila tyrannina</i>																																						
215	<i>Dendrocincila fuliginosa</i>		021	014	005																																056	033	
216	<i>Deconychura longicauda</i>				002																																		
217	<i>Sittasomus griseicapillus</i>		004	002	015	014																															007	021	
218	<i>Glyphorhynchus spirurus</i>		007	009	046	024			002																											008			
219	<i>Dendrozetastes rufigula</i>																																				007		
220	<i>Xiphocolaptes promeripirhynchus</i>									007			006	006																									
222	<i>Dendrocolaptes certhia</i>																																				013		
223	<i>Dendrocolaptes picumnus</i>																																				007	020	

Appendix 2 (7/12). Part B

Sp. no.	Species	Column																																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31				
224	Xiphorhynchus ocellatus		009	013	019	031	037	010														093														
225	Xiphorhynchus guttatus	007																																		
226	Xiphorhynchus triangularis						012	014	013		006											021	003	014						016	073	007	071			
227	Lepidocolaptes affinis									012		006																								
229	Carpylorhamphus pucheranii											006		002											011											
230	Synallaxis azarae			005				002	003												010															
231	Synallaxis cabanisi		005																		113	039							046							
232	Synallaxis albigularis																				026	015							015							
233	Synallaxis gujanensis	004																			030	078	020						052		014					
234	Synallaxis unirufa											006	025	002	006																					
235	Synallaxis cherriei	021																																		
236	Cranioleuca curtata						002																003													
237	Cranioleuca albiceps													038	004	039	016																			
238	Schizoeca fuliginosa														027	073	032	059													043	X				
240	Margarornis squamiger									003	006	006	021	016	039	033	014																			
241	Premornis guttuligera			005			018	019	032	003													022	049												
242	Premoplex brunnescens				014	015	018	046	056	078	012	034	012									010	022													
243	Pseudocolaptes boissonneaui																																			
244	Hylactistis subulatus		005																																	
245	Syndactyla rufosuperciliata				005	008	018	048	040	007											010	021	011	014												
246	Syndactyla subalaris					008	018	024	024	020											010	052	008	028												
247	Anabacerthis striaticollis			002			018	012	020																											
248	Philydor erythrocerus			002	048	023		002																												
249	Philydor ruficaudatus		002	002																																
250	Automolus dorsalis																				030															
251	Automolus ochrolaemus	004	045	026	010	023																	003										016			
252	Thripadectes holostictus								008	010																										
253	Thripadectes melanorhynchus				014			017															010	014												
254	Thripadectes scrutator										003	006	006	002																						
256	Xenops minutus	018	016	025	024	015	009																											032		
257	Sclerurus mexicanus				005		012	004	003															008	007											
258	Sclerurus caudacutus																																	007		
259	Lochmias nematura		007						002																											
261	Taraba major																																014	020		
262	Thamnophilus dollatus																															015		010		
263	Thamnophilus aethiops																																020	010		
264	Thamnophilus schistaceus	014	005																													016	013			
265	Thamnophilus murinus	004																														020		040		
266	Thamnophilus caerulescens								012	020	036											040		014												
267	Thamnistes anabatinus				010		009																													
268	Dysithamus mentalis			036	019	077		005													020	010	008													
269	Thamnomanes ardesiacus	025	020																																	
270	Thamnomanes schistogynus																																032			
271	Myrmotherula brachyura																																	007		
272	Myrmotherula haematonota	007	007	025																																
273	Myrmotherula ornata	014																																		
274	Myrmotherula axillaris	035	018	002																												008				
275	Myrmotherula schisticolor				024	008	055	041	002		003												019									031	056	079	014	020
277	Dichrozona cineta			008																																

Appendix 2 (8/12). Part B

Sp. no.	Species	Column																																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31		
281	<i>Drymophila caudata</i>						012	028	042	036	073	065											014											
283	<i>Cercomacra nigrescens</i>		002		014	031		007	024											040	010	014												
284	<i>Pyriglena leuconota</i>				010	031		009	019	004	009									020		011												
285	<i>Myrmoborus leucophrys</i>	004																	074	034							154			035				
286	<i>Myrmoborus myotherinus</i>	014																																
287	<i>Hypocnemis cantator</i>	021																	013	005										049	081			
288	<i>Pernostola leucostigma</i>		018	005																		003												
289	<i>Myrmeciza hemimelaena</i>	102	025	026	024																								048	046				
290	<i>Pithys albifrons</i>	021	050	040																005								040						
291	<i>Rhegnatorhina melanosticta</i>	004																											016					
292	<i>Hylophylax naevia</i>	014	063	030																									097					
293	<i>Hylophylax poecilonota</i>	011	038	051																								048						
294	<i>Chamaeza campanisona</i>					008		009	007													016												
295	<i>Chamaeza mollissima</i>									003	003		012																					
296	<i>Formicarius analis</i>		025	003																								032	013	007				
297	<i>Formicarius rufipectus</i>								002													003												
298	<i>Grallaricula flavirostris</i>						009	014	024	046	003		006									008	007											
299	<i>Grallaricula ferrugineipectus</i>												006	002																				
300	<i>Myrmothera campanisona</i>	004																																
301	<i>Grallaria squamigera</i>									003		003																						
302	<i>Grallaria guatemalensis</i>		007	002			009																											
303	<i>Grallaria erythroleuca</i>											006	006																					
304	<i>Grallaria rufula</i>													002															009					
306	<i>Conopophaga castaneiceps</i>				068	085		074	029	022	003											020	021	014										
307	<i>Corythopsis torquata</i>		005	017		008																												
308	<i>Scytalopus unicolor</i>									009		018	041	008	007	022	003	005															017	
309	<i>Scytalopus femoralis</i>				010			002	006	003												020	010	008	007								007	
310	<i>Lanius elegans</i>																																	
311	<i>Ampelion rubrocristatus</i>												002			003														009				
312	<i>Pipreola intermedia</i>												002																					
313	<i>Pipreola pulchra</i>								002															008										
314	<i>Pipreola frontalis</i>																						010	010										
315	<i>Pipreola arcuata</i>												008	007	006	003													004					
316	<i>Attila spadiceus</i>	007																																
317	<i>Casiornis rufa</i>																																070	061
318	<i>Rhytipterna simplex</i>	004						002																					015	007	007	020		
320	<i>Pachyrhamphus versicolor</i>												003									010												
321	<i>Pachyrhamphus polychopterus</i>																																056	010
331	<i>Rupicola peruviana</i>			008		008				003													003											
332	<i>Pipra fasciicauda</i>	331	007																	017								185	169	358	126	040		
333	<i>Pipra chloromeros</i>		025	063	005	008					003									004	010													
334	<i>Pipra pipra</i>			005	029	046		055	062	002		003	006								030	062	019	028										
335	<i>Pipra caeruleicapilla</i>			021	019	038		018	029	002												010	041	063	007									
336	<i>Machaeropterus pyrocephalus</i>	035																			004			007										
337	<i>Chloropipo unicolor</i>			007	014	031		028	014	008	007		018									030	113	052	056									
338	<i>Chloropipo holochlora</i>		002	003																														
339	<i>Piprites chloris</i>		002		005			009	002														010											
340	<i>Schiffornis turdinus</i>		007	012					012																									
343	<i>Nyiotheretes fumigatus</i>												005						005															

Appendix 2 (9/12). Part B

Sp. no.	Species	Column																														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
346	Ochthoeca fumicolor																013	023								022	X					
347	Ochthoeca rufipectoralis													024	040	011	019	059								017						
348	Ochthoeca cinnamomeiventris									006			012	003	002																	
349	Ochthoeca frontalis														027	084	039	037								048						
350	Ochthoeca pulchella									033	040	059	025												032							
364	Myiarchus ferox																	004	010													
365	Myiarchus cephalotes							010													030											
366	Myiarchus tuberculifer								002	024	006											010								007		
368	Empidonax euleri			012	005	008															010							015				
369	Cnemotriccus fuscatus																											031				
370	Nitrephanus phaeocercus								002	003																						
371	Terentotriccus erythrurus	018		010																											033	021
372	Myiobius villosus			002	005	015	009																005									
373	Myiobius atricaudus																		026	015												
374	Myiotriccus ornatus					008		014	004																							
375	Pyrrhomyias cinnamomea						002	004	003	006	003	006		007								010	003									
376	Myiophobus flavicans								018	010														005	063							
377	Myiophobus inornatus							005																								
378	Myiophobus ochraceiventris														002																	
380	Myiophobus roraimae				005		037	007														010			007							
381	Cnycorhynchus coronatus																													013	014	
382	Platyrinchus platyrhynchus	004		002																												
383	Platyrinchus mystaceus			007	019	015	009	007	002	003														005	007							
384	Platyrinchus flavigularis								002																							
385	Tolmomyias assimilis			005	005																											
386	Tolmomyias poliocephalus																														028	010
387	Tolmomyias flaviventris																		004													020
388	Rhynchoeyclus olivaceus			023	017																											
389	Rhynchoeyclus fulvipectus						018	005	006	010																						
390	Ramphotricon fuscicauda																															042
392	Todirostrum cinereum																					005										
393	Todirostrum latirostre																					061	025						046	013	042	
394	Idioptilon granadense										003			029	016										054							
395	Lophotriccus pileatus			005	024	046	018	029	026	003												030	010	011								
396	Myiornis auricularis																													021	071	
398	Pseudotriccus pelzelni						002	046	033														010	030	007							
399	Pseudotriccus ruficeps									012	037	024	013	002	006											011	004					
400	Pogonotriccus poecilotis																									007						
401	Pogonotriccus orbitalis			020	015																											
402	Phylloscartes ventralis							002																								
405	Uromyias agraphia													024	002	039	003	027														
408	Mecocerculus leucophrys																002	022	029	018							048					
409	Mecocerculus stictopterus																															
412	Elaenia albiceps																														021	010
414	Elaenia pallatangae														003																	
415	Myiopagis gaimardii																														049	010
419	Tyranniscus uropygialis														003	002																
421	Tyranniscus bolivianus														006	002																
424	Leptopogon superciliosus			011	018	048	046		022														010									
																						030			008							

Appendix 2 (10/12). Part B

Sp. no.	Species	Column																														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
425	<i>Leptopogon amaurocephalus</i>		045	025															005									015	032	070	020	
426	<i>Leptopogon taczanowskii</i>							002	007	018	015	006	002																			
427	<i>Mionectes striaticollis</i>	004	005	045	135	185	193	076	062	059	060	046	065	086	062	006	026			160	082	155	119	011	004							
428	<i>Mionectes olivaceus</i>		136	081	014		009															010						008				
429	<i>Pipromorpha macconnellii</i>	035	014																052	098							008					
434	<i>Notiochelidon flavipes</i>												004			010	005															
437	<i>Stelgidopteryx ruficollis</i>																	004	005													
438	<i>Cyanolyca viridicyana</i>									018		012																				
440	<i>Cyanocorax yncas</i>							002		003	003																					
443	<i>Cinnycerthia peruana</i>							024	033	015	021	053	005	004										022								
445	<i>Thryothorus euophrys</i>													002																		
446	<i>Thryothorus coraya</i>			053	015		012											069	064								031		007			
447	<i>Troglodytes aedon</i>																			010												
448	<i>Troglodytes solstitialis</i>								006	006	009		013	004		003							028	022								
449	<i>Henicorhina leucophrys</i>				008		028	012	030	039	003	037	018								010		035	063								
450	<i>Microcerculus marginatus</i>	014	032	018																								031	040	020	010	
451	<i>Cyphorhinus thoracicus</i>				014	015	009															005										
453	<i>Myadestes ralloides</i>		002	010				034	072	021	027	006								010	031	011	007	011								
454	<i>Entomolestes leucotis</i>									003			002	004								005	007		004							
455	<i>Catharus dryas</i>																			010	021	035										
456	<i>Platycichla leucops</i>						009															011	007									
457	<i>Turdus fuscater</i>															003	009															
458	<i>Turdus serranus</i>								010	033	034	024	002	011		003	009									017						
459	<i>Turdus nigriceps</i>		002	003						003																						
460	<i>Turdus ignobilis</i>																	043	005			041	043					046				
462	<i>Cyclarhis gujanensis</i>																	004														
464	<i>Vireo olivaceus</i>																												070	162		
467	<i>Mylophilus ochraceiceps</i>	011	016	010																												
470	<i>Psarocolius atrovirens</i>						002																									
471	<i>Psarocolius angustifrons</i>		002																													
473	<i>Cacicus uropygialis</i>						002																003									
474	<i>Cacicus leucoramphus</i>								007	012	018																					
475	<i>Cacicus solitarius</i>																		009													
476	<i>Cacicus holosericeus</i>									006	015	024	008	006		005																
479	<i>Myioborus miniatus</i>		002				005	006													030		005									
480	<i>Myioborus melanocephalus</i>									042	006	018	016	002	003									022								
481	<i>Basiluterus luteoviridis</i>									009	027	065	062	022	022	029	023							075	052							
482	<i>Basiluterus chrysogaster</i>		025	018																												
483	<i>Basiluterus tristriatus</i>				019	008	009	014	056	042											020	010	022	049								
484	<i>Basiluterus coronatus</i>						037	043	044	088	036	070		002									008	084								
485	<i>Basiluterus rivularis</i>		009	003																005	010											
486	<i>Coereba flaveola</i>																		013													
488	<i>Conirostrum cinereum</i>																															
489	<i>Conirostrum ferrugineiventre</i>																018								004							
490	<i>Conirostrum sitticolor</i>													002	011	019	009								009							
492	<i>Diglossa caculescens</i>							002	007	009																						
494	<i>Diglossa lafresnayii</i>												035	075	084	077	078								134	X						
495	<i>Diglossa carbonaria</i>															003	014								004	X						
496	<i>Diglossa albilatera</i>										009	018	014	002		006																

Appendix 2 (11/12). Part B

Sp. no.	Species	Column																																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31		
497	<i>Diglossa glauca</i>						010	016	020	021				002							050		019	007	011									
498	<i>Diglossa cyanea</i>									002	024	021		057	080	017	042	018					003	049	161	048								
499	<i>Cyanerpes caeruleus</i>						002																											
500	<i>Chlorophanes spiza</i>					008																								013				
501	<i>Iridophanes pulcherrima</i>					008	009																											
502	<i>Dacnis cayana</i>					008																												
507	<i>Euphonia xanthogaster</i>		011	025	019	015	018	026	016	023	006										010		011											
510	<i>Euphonia laniirostris</i>																														013			
515	<i>Chlorochrysa calliparva</i>						002	002																										
518	<i>Tangara schrankii</i>		002																															
531	<i>Tangara nigroviridis</i>										015																							
532	<i>Tangara vassorii</i>										002																							
533	<i>Iridosornis analis</i>				005	008	018	069	024	020	003												005	042										
534	<i>Iridosornis reinhardti</i>										006	009		084	067	096	100	041							065	039								
535	<i>Anisognathus igniventris</i>													021	027	079	080	073							082								X	
536	<i>Anisognathus lacrymosus</i>													049	056	062	029	005							054									
537	<i>Anisognathus flavinucha</i>							006														010												
538	<i>Buthraupis montana</i>									015				003	011		003																	
539	<i>Dubusia castaneoventris</i>											003		008	016	006	006	005																
540	<i>Dubusia taciata</i>											003		014		006	006																	
541	<i>Thraupis virens</i>																				005													
543	<i>Thraupis cyanocephala</i>									003		003		006																				
544	<i>Thraupis bonariensis</i>																																	
545	<i>Ramphocelus carbo</i>		004																			104	182										X	
549	<i>Habia rubica</i>		018	011	017																												077	
550	<i>Lanio versicolor</i>																																	
552	<i>Tachyphonus rufiventer</i>		004	005																														
553	<i>Creurgops dentata</i>																																	
554	<i>Trichothraupis melanops</i>				029	008	009	026				006												005										
555	<i>Hemithraupis guira</i>																																007	
556	<i>Thlypopsis sordida</i>																				009												077	
557	<i>Thlypopsis ornata</i>																	003																
558	<i>Thlypopsis ruficeps</i>																																	
559	<i>Chlorospingus ophthalmicus</i>																									035								
560	<i>Chlorospingus flavigularis</i>				005		046	007				006																						
561	<i>Chlorospingus parvirostris</i>									002																								
562	<i>Chlorospingus canigularis</i>																																	
563	<i>Cnemoscopus rubirostris</i>										009	009	006	011	009									005			043							
564	<i>Hemispingus atropileus</i>																																	
565	<i>Hemispingus superciliaris</i>										012																							
566	<i>Hemispingus frontalis</i>						009	048	038	013																024	014							
567	<i>Hemispingus melanotis</i>									002	003																							
568	<i>Hemispingus sp</i>																																	
569	<i>Hemispingus xanthophthalmus</i>																																	
570	<i>Hemispingus trifasciatus</i>																																	043
571	<i>Chlorornis riefferii</i>										036	018	006	019	016	006	003																	
572	<i>Cissopsis leveriana</i>																																	
573	<i>Catanblyrhynchus diadema</i>											003	006		019	004	017					005											009	
574	<i>Saltator maximus</i>		004	014																														

Appendix 2 (12/12). Part B

Sp. no.	Species	Column																															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
575	<i>Saltator coerulescens</i>																	004	005														
576	<i>Pitylus grossus</i>	004																															
578	<i>Pheucticus chrysopeplus</i>									003														007							008		
579	<i>Pheucticus aureoventris</i>										003																						
580	<i>Cyanocorpsa cyanoides</i>	032	011	013	005															005										024			
581	<i>Volatinia jacarina</i>																			005											007	030	
582	<i>Sporophila luctuosa</i>																			005				032									
583	<i>Sporophila nigricollis</i>																			015													
584	<i>Sporophila obscura</i>								002		003									162			021	003							014		
585	<i>Sporophila castaneiventris</i>																		004	015													
586	<i>Oryzoborus angolensis</i>		005																														
587	<i>Catamania inornata</i>																		009													X	
588	<i>Catamania homochroa</i>													022		045	174																
589	<i>Phrygilus unicolor</i>																														009	X	
590	<i>Haplospiza rustica</i>								002	003	074	027	129	014	040	011	039	023					003		118								
591	<i>Atlapetes rufinucha</i>													011		003	005																
592	<i>Atlapetes tricolor</i>									003										020													
593	<i>Atlapetes brunneinucha</i>				005	023	018	014	030	036	021	030	012										021	022	007								
594	<i>Atlapetes torquatus</i>												008	002											011	004							
595	<i>Lysurus castaneiceps</i>						009																										
597	<i>Zonotrichia capensis</i>																003	005								004		X					