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VENEZUELAN PÁRAMOS

FRANÇOIS VUILLEUMIER AND DAVID N. EWERT

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ABSTRACT

Páramos are insular in distribution and thus of interest to biogeographers. In the present paper new data are given on geographical distribution, ecological preferences, relative abundance, general behavior, and breeding of 47 species of birds studied on nine Venezuelan páramos in March-April 1975. Some data obtained in March 1968 and in May 1970 are also included.

Páramo vegetation is defined as the open formation growing above the upper limit of continuous montane forest in the Andes of Venezuela, Colombia, Ecuador, and northern Perú. This vegetation consists of grasses, herbs, low shrubs, cushion and rosette plants. *Polylepis* woodlands constitute true islands of a vegetation type distinct from, but growing within, páramo vegetation. A páramo species is a bird inhabiting one of six ecological categories distinguished within the páramo vegetation.

The result of six censuses, carried out at altitudes

from 3100 m. to 4430 m. suggest that bird species are unevenly distributed altitudinally in Venezuelan páramos. The way birds utilize four major features of the páramo (*Espeletia* spp., shrubs, water, and barren ground) is discussed. Geographical patchiness in birds of Venezuelan páramos is analyzed in terms of six variables: (1) incomplete sampling; (2) differences in dispersal ability; (3) lack of suitable ecological requirements; (4) exclusion by interspecific competition; (5) historical reasons associated with human modifications of habitats, and (6) historical reasons associated with Pleistocene fluctuations of climate and vegetation. Three major source areas can be postulated for colonization of páramos (North and Central America, adjacent areas of northern South America, and southern South America). Several species may have colonized the páramos of Venezuela from two or three source areas.

RESUMEN

Por su distribución discontinua los páramos ofrecen gran interés para estudios de biogeografía. En este artículo presentamos datos nuevos sobre distribución geográfica, biótupos, abundancia, comportamiento y nidificación de 47 especies de aves estudiadas en nueve páramos de Venezuela en marzo-abril de 1975. Algunos datos obtenidos en marzo de 1968 y mayo de 1970 son también incluidos aquí.

La vegetación de páramo esta definida como una formación vegetal abierta encontrada por encima del límite superior de la ceja de la montaña en los Andes de Venezuela, Colombia, Ecuador y del norte del Perú. Esta vegetación incluye gramineas, arbustos, plantas almohadillas y plantas en rosetas. Bosques de *Polylepis* se parecen a islotes de un tipo de vegetación distinto de la vegetación paramuña abierta, y además incluido adentro de ella. Las especies de aves del páramo pueden pertenecer ecológicamente a unas seis categorías ecológicas distintas en la formación de páramo.

Los resultados de seis censos hechos a alturas desde 3100 m. a 4430 m. sugieren que la distribución altitudinal de las especies de aves es irregular. Discutimos como las aves usan cuatro biótupos importantes del páramo: las *Espeletias*, los arbustos, el agua, y el suelo desnudo. La discontinuidad en la distribución geográfica de las aves de los páramos venezolanos esta analizada por medio de seis hipótesis: (1) Falta de datos, (2) diferencias en la capacidad de dispersión, (3) falta de biótupos preferenciales, (4) exclusión por competencia ecológica, (5) factores históricos debidos a la influencia humana, y (6) factores históricos debidos a las variaciones del clima y de la vegetación durante el Pleistoceno. Tres fuentes mayores de colonización de los páramos pueden ser identificadas: (1) América del Norte y Centro-América, (2) zonas adjacentes al páramo del norte de Sur América, y (3) el sur de Suramérica. Para algunas especies de aves podemos sugerir dos o tres fuentes posibles para su origen, pero no podemos decidir cual es la más probable.

INTRODUCTION¹

The distribution of bird species in Andean páramos is of interest to biogeographers because páramos are insular, and can serve as a model of island biogeography in continents (see the analysis of Vuilleumier, 1970, and subsequent discussions in MacArthur, 1972, pp. 105-106; Carlquist, 1974, pp. 576-594; Simpson, 1975, pp. 277-285; and Lack, 1976, p. 219). Distributional and ecological notes on páramo birds are included in the works of Phelps and Phelps (1958, 1963) for Venezuela; Chapman (1917), Todd and Carriker (1922), Meyer de Schauensee (1948-1952), Bourlière (1957), Olivares (1973), and Norton (1975) for Colombia; and those of Rhoads (1912), Chapman (1926), Moore (1934), Corley Smith (1969), and Vuilleumier (1976) for Ecuador. In spite of these publications, data on geographical distribution, ecological preferences, behavior, breeding seasons, and other aspects of the biology of many páramo species are still uneven, anecdotal, or lacking.

In the present report we give new information on páramo birds and point out areas where further research is needed.

We describe the results of observations carried out in March-April 1975 during a trip to several Venezuelan páramos.

Some notes from an earlier trip by Vuilleumier in March 1968, and another by David Ewert in late May 1970 are also included. Our observations supplement information in Phelps and Phelps (1958, 1963) on the distribution of páramo birds in Venezuela, except the Cendé area and the Perijá range, which we did not visit.

After we define páramo vegetation and what constitutes a páramo species of bird, we list the páramos visited by us in Venezuela, and describe the methods of observation. The results of our field work are presented in a summary of our census results, and in an annotated list of species.

¹We dedicate this paper to the founders of Venezuelan ornithology, the late William H. Phelps, Sr., and William H. Phelps, Jr.

Finally, we discuss habitat use by birds in the páramo, analyze the varying degrees of geographical patchiness in páramo birds of Venezuela, and the factors that affect the distribution of birds in páramos, and speculate on the possible origins of páramo birds.

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MATERIALS AND METHODS

DEFINITION OF PÁRAMO VEGETATION

The term "páramo" is used in several ways. Thus, it is necessary to define three terms: páramo vegetation, páramo, and Páramo Zone.

1. Páramo vegetation is the vegetation formation growing above the upper limit of continuous montane forest in the Andes of Venezuela, Colombia, Ecuador, and northern Perú. Páramo vegetation consists of grasses, herbs, low shrubs, cushion and rosette plants. In Venezuela, this formation is dominated physiognomically or in numbers of species by the genera *Lachemilla* and *Hesperomeles* (Rosaceae), *Pernetia* (Ericaceae), *Hypericum* (Guttiferae), *Espeletia* and *Senecio* (Compositae), *Puya* (Bromeliaceae), *Agrostis* and

Calamagrostis (Gramineae), and others (see Azocar, 1974, p. 3; Vareschi, 1970).

Azocar (1974) distinguished three communities within the páramo vegetation of Venezuela: the *Espeletia*-dominated community, the marsh and bog community, and the *Polylepis* woodland community. These communities are illustrated in figures 1 and 2.

Woodlands of *Polylepis sericea* Wedd. (Rosaceae) grow within the nonforested páramo communities on rocky slopes or in sheltered valleys on some mountains, and in Venezuela are restricted to the Andes in the State of Mérida at altitudes of 3400 to 4200 m. These woodlands seem to be isolated from montane forests lower down by either of the first two



FIG. 1. Two of the three communities distinguished by Azocar (1974) in the páramo vegetation of Venezuela. In the foreground, the marsh and bog community; in the background on the morainic ridge, the *Espeletia*-dominated community (Páramo de Mucubají).



FIG. 2. Left. Close-up of *Espeletia*-dominated community (Páramo del Aguila), showing two species of *Espeletia*. Right. *Polylepis sericea* woodland community (Páramo de Piedras Blancas).

communities cited by Azocar. Ecologically, therefore, the *Polylepis* woodlands of the Mérida Andes constitute true islands of a vegetation type distinct from the *Espeletia*, or the marsh and bog communities; consequently, some of the bird species inhabiting *Polylepis* woodlands occur only here and in montane forests, but not in the intervening open páramo vegetation. Thus, we do not consider these as páramo species. However, we discuss the ecological preferences of these species, as well as those of several other species found in *Polylepis* woodland and in open páramo.

Our discussion of the ecology of birds in relation to páramo vegetation is therefore slightly more restrictive than if we had treated equally all three communities of the páramo recognized by Azocar (1974).

2. When we use the word páramo in a geo-

graphical context, as in "Venezuelan páramos," or in "Páramo de Tamá," we mean a high montane locality or landscape type in the Andes characterized by páramo vegetation. Thus, the term Venezuelan páramos refers to the entire set of páramo localities of that country, or to the set of páramo localities that we visited; and Páramo de Tamá means the highest altitudinal zone of that mountain, where páramo vegetation is encountered.

In Venezuela (and in Colombia) páramo often means a montane locality or a farm in the Andes, even if it is not in páramo vegetation. As a result of this usage, many localities cited in the ornithological literature as "Páramo X" may not be in páramo vegetation, but may simply designate a high altitude area. Thus, Páramo Zumbador could refer to only those areas where páramo vegetation grows, or could

be used more generally to include high areas of the mountain, with or without páramo vegetation. Some confusion may arise because of a difference between vernacular usage and a more restricted botanical definition of páramo.

3. Páramo Zone is used by Phelps and Phelps (1963, p. 7) to specify the altitudinal zonation of high altitude birds in Venezuela. They followed Chapman (1917), who wrote that "the true Páramo Zone extends from the upper limit of trees to the lower limit of snow." In this paper we refer to Páramo Zone (or other Zones) only when citing Phelps and Phelps (1958, 1963).

DEFINITION OF A PÁRAMO SPECIES

In his 1970 analysis Vuilleumier included as páramo species: (1) "land birds occurring in one of the following ecological categories: (a) grassland only, (b) grassland and open scrub, (c) grassland, scrub, and upper edge of the

montane forests (ceja forests), and (d) edge only" and (2) "freshwater birds living on lakes and ponds within the páramo vegetation."

In the present paper we classify as páramo species 25 species of birds which belong to one of the following six categories (see table 1):

a) Open páramo vegetation (Azocar's *Espeletia*-dominated and marsh and bog communities).

b) The ecotone between open páramo vegetation and *Polylepis* woodlands growing above the upper level of continuous forest.

c) Open páramo vegetation, *Polylepis* woodland, and open and/or scrubby vegetation below páramo vegetation (such as shrubs, copses of small trees, edges of second-growth woods, and cultivated fields).

d) Open and scrubby vegetation up to and including open páramo vegetation.

e) Water habitats such as lakes and ponds within páramo vegetation.

TABLE 1
Species of Birds Included in an Analysis
of Altitudinal and Geographical Distribution of Páramo Birds in Venezuela

1. Species living in habitats of open páramo vegetation (rarely below)	<i>Buteo fuscescens</i> <i>Capella nobilis</i> <i>Chubbia jamesoni</i> <i>Chalcostigma heteropogon</i> <i>Cinclodes fuscus</i> <i>Leptasthenura andicola</i> <i>Schizoeaca fuliginosa</i> <i>Asthenes wyatti</i> <i>Cistothorus meridae</i> <i>Anthus bogotensis</i> <i>Catamenia inornata</i> <i>Phrygilus unicolor</i>
2. Species living in open páramo/ <i>Polylepis</i> woodland ecotone	<i>Oxygogon guerinii</i>
3. Species living in open páramo, <i>Polylepis</i> woodland and open and/or open scrubby vegetation below páramo vegetation such as shrubs, copses of small trees, and edges of second growth woods and of cultivated fields	<i>Schizoeaca coryi</i> <i>Ochthoeca fumicolor</i> <i>Turdus fuscater</i> <i>Spinus spinescens</i>
4. Species living in open and scrubby vegetation up to and including open páramo vegetation	<i>Falco sparverius</i> <i>Caprimulgus longirostris</i> <i>Notiochelidon murina</i> <i>Cistothorus platensis</i> <i>Sturnella magna</i> <i>Zonotrichia capensis</i>
5. Species found in water habitats such as lakes and ponds within open páramo vegetation	<i>Anas flavirostris</i>
6. Species found in water habitats such as fast-flowing streams within and below páramo vegetation	<i>Cinclus leucocephalus</i>

f) Water habitats such as fast-flowing streams within and below páramo vegetation.

Although we now include more habitat categories than Vuilleumier did in 1970, our definition of a páramo species is more restricted than his because we exclude species restricted to the upper edge of the montane forests (his category "d") and species found in montane forests and *Polylepis* woodlands.

Because we use a narrow definition of páramo species, we exclude from the list six species that were part of the 1970 study: *Eriocnemis vestitus*, *Metallura tyrianthina*, *Myiotheretes striaticollis*, *Mecocerculus leucophrys*, *Diglossa carbonaria*, and *Hemispingus verticalis*. On the other hand, we include two species not considered in 1970: *Caprimulgus longirostris* and *Cinclus leucocephalus*. Reasons for deletion or inclusion are given for each species in the annotated list.

We do not discuss in this paper seven species listed from Venezuelan páramos by Phelps and Phelps (1958, 1963) because we did not observe them in Venezuela. These species, which were included by Vuilleumier (1970) as páramo species are: *Vultur gryphus*, *Glauc-*

cidium jardinii, *Ramphomicron micro-rhynchum*, *Piculus rivolii*, *Grallaria squamigera*, *Myiotheretes fumigatus*, and *Catamenia homochroa*.

Vultur gryphus has recently been observed in Venezuela (Zonfrillo, 1977). Schwartz (in lett.) stated that *Glaucidium jardinii*, *Piculus rivolii*, *Grallaria squamigera* and *Myiotheretes fumigatus* are woodland birds. He has also found an additional species, *Colibri coruscans*, at Mucubají, where they were singing and displaying.

We exclude 22 species from the list of páramo species (table 2). Four are migrants from North America, seven occur at lower altitudes and do not, or probably do not, breed in the páramo (four are aquatic and three aerial), seven occur in temperate forest and/or temperate scrub up to timberline, and four occur in temperate forest and/or temperate scrub and in isolated *Polylepis* woodlands within páramo vegetation.

PÁRAMOS VISITED

We visited the following nine páramos,

TABLE 2
Species Excluded from a Distributional Analysis of Páramo Birds

1. Species occurring as migrants on the páramo	<i>Anas discors</i> <i>Tringa solitaria</i> <i>Capella gallinago</i> <i>Hirundo rustica</i>
2. Aquatic species occasionally found in the páramo but principally found below páramo	<i>Podiceps dominicus</i> <i>Podilymbus podiceps</i> <i>Phalacrocorax olivaceus</i> <i>Phaetusa simplex</i>
3. Aerial species occasionally found in the páramo but principally found below páramo	<i>Cathartes aura</i> <i>Streptoprocne zonaris</i> <i>Notiochelidon cyanoleuca</i>
4. Species found in temperate forests and/or temperate scrub up to timberline	<i>Oroaetus isidori</i> <i>Columba fasciata</i> <i>Ensifera ensifera</i> <i>Eriocnemis vestitus</i> <i>Myiotheretes striaticollis</i> <i>Diglossa lafresnayii</i> <i>Hemispingus verticalis</i>
5. Species found in temperate forests and/or temperate scrub, and in isolated <i>Polylepis</i> woodlands within páramo vegetation	<i>Metallura tyrianthina</i> <i>Margarornis squamigera</i> <i>Mecocerculus leucophrys</i> <i>Diglossa carbonaria</i>

listed roughly from northeast to southwest (see fig. 3).

(1) *Páramo de Santo Domingo*

State of Mérida, Distrito Rangel; May 1970 and March 16-17, 1975; 3000 to 3400 m.; vegetation characterized by relatively high density of *Espeletia* spp. on ridges, grassland and *Sphag-*

num-like mosses in boggy depressions, and scattered groves of trees and shrubs at the base of small cliffs and in other protected areas (see fig. 4 upper).

(2) *Páramo del Aguila*

State of Mérida, Distrito Miranda; March 12 and 30, 1975; 3600 to 3700 m.; vegetation

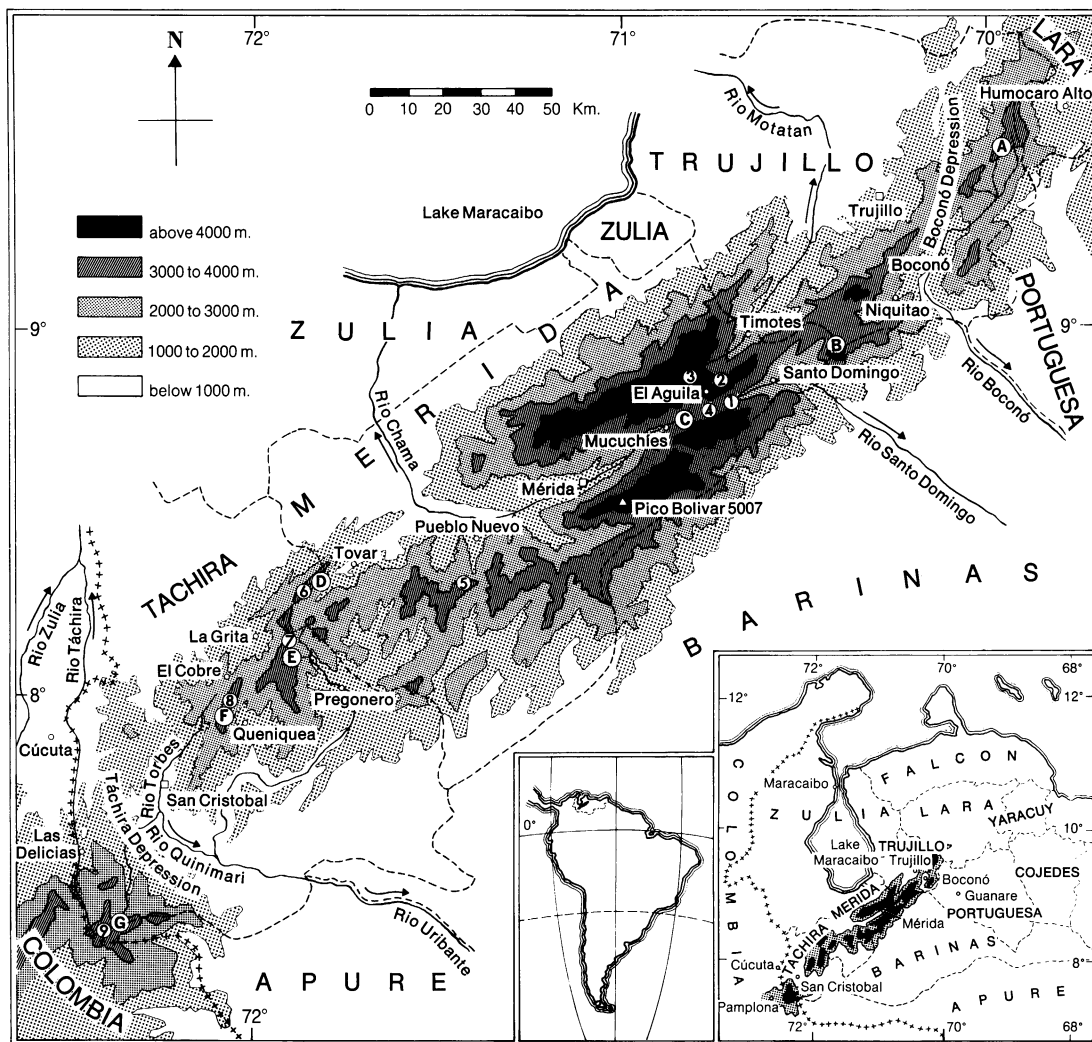


FIG. 3. Schematic map of the Venezuelan Andes showing the location of the nine páramos visited (1-9; see text and figs. 4-9 for descriptions and illustrations of vegetation), and of the seven páramo "blocks" (see table 5 for a list of bird species in each block). The blocks are: A = Cendé; B = Niquitao; C = Mérida; D = La Negra; E = Batallón; F = Zumbador; G = Tamá. Note: (1) the great isolation of blocks F and G by the Táchira depression; (2) the moderate isolation of blocks A and B by the Boconó depression, and of blocks C and D through páramo no. 5 (Quirorá); (3) the narrow isolation of blocks D, E, and F; (4) the very narrow isolation of blocks B and C.

similar to that at Páramo de Mucubají (see number 4) but distinctly drier, heavily grazed, and lacking boggy meadows; a patch of low *Polylepis-Hesperomeles* shrubs (see fig. 2 left and fig. 4 lower).

(3) *Páramo de Piedras Blancas*

State of Mérida, border of Distritos Rangel and Justo Briceño; March 14 and 18, 1975; 4000 to 4400 m.; vegetation consisting of scattered *Espeletia* spp. (some arborescent forms up to 4 m.), and scattered cushion plants, interspersed with boulders and barren ground marked by frost heave in some areas (see fig. 5); one stand of *Polylepis sericea* at about 4100 m. on steep slope covered with large boulders (see fig. 2 right).

(4) *Páramo de Mucubají*

State of Mérida, Distrito Rangel; March 1968, late May 1970, March 12-17, 1975; 3500 to 3700 m.; vegetation characterized by high density of *Espeletia* spp. interspersed with patches of low scrub (where *Hypericum* spp. was conspicuous) and grassland; isolated woodlands of *Polylepis sericea*; this area has been described in detail by Azocar (1974) (see fig. 1 and fig. 6 upper).

(5) *Páramo de Quirorá*

State of Mérida, Distrito Campo Elias; April 1, 1975; 2800 to 2900 m.; vegetation on steep slopes consisting chiefly of grasses with few *Espeletia* spp. and many *Pteridium* sp. ferns (Pteridaceae), the latter growing apparently after burning; sharp forest/páramo ecotone (see fig. 6 lower).

(6) *Páramo La Negra*

Border of the States of Mérida (Distrito Rivas Dávila) and Táchira (Distrito Jauregui); March 26, 1975; 3000 to 3100 m.; vegetation characterized by a relatively homogeneous mixture of grass, *Espeletia* spp., *Hypericum* spp. scrub, and numerous *Jamesonia* spp. ferns (Pteridaceae) (see fig. 7).

(7) *Páramo del Batallón*

State of Táchira, border of Distritos Jáuregui and Uribante; March 26, 1975; 3000 to 3300 m.; vegetation consisting of a mixture of grasses and *Espeletia* spp., and of tussock-grassland in moist areas; indistinct páramo/forest ecotone at 2900-3000 m. (see fig. 8).

(8) *Páramo Zumbador* (also called Páramo Almorzadero or Páramo de los Colorados) State of Táchira, border of Distritos Jáuregui and Cárdenas; March 25, 1975; 3000 to 3250 m.; vegetation consisting of a mixture of grasses, *Puya* (? *venezuelana* L.B. Smith), and *Espeletia* spp., and of some patches of homogeneous tussock-grassland (no illustrations: fog prevented taking photographs during our visit).

(9) *Páramo de Tamá*

State of Táchira, Distrito Junín; March 21-24, 1975; 2900 to 3250 m.; vegetation grazed, and regrowing after burning in places; vegetation dominated by a dense growth of grasses with *Puya* (? *venezuelana*), *Chusquea spencei* Ernst (Gramineae), scattered *Espeletia* spp. (up to 1.5 m. tall), and patches of dense shrubbery around boulders; ecotone between páramo and forest on steep slopes formed by thick shrubbery of *Chusquea spencei*, shrubs, ground-dwelling bromeliads, ferns, and herbs (see fig. 9).

METHODS OF OBSERVATION

At each páramo we studied all bird species by means of a combination of field observations through binoculars and collection of selected species. We sought to obtain data on altitudinal distribution, relative abundance, habitat selection, general behavior, and breeding behavior of each species. We concentrated our work in páramo vegetation as defined above, in *Polylepis* woodlands, and in the ecotone between páramo vegetation and montane forests.

All altitudes noted in 1968 and 1975 were obtained in the field with a Thommen 19 jewels pocket altimeter, which has an altitudinal range of 0 to 7000 m., and an accuracy of ± 50 m.

CENSUS METHODS

In order to supplement general observations we carried out seven censuses of bird abundance in open páramo vegetation at five páramos: Páramo de Santo Domingo (two sites), Páramo del Aguila, Páramo de Piedras Blancas, Páramo de Mucubají (two sites) (all in the Mérida Andes), and Páramo de Tamá (Táchira). Unfortunately, the census taken at Páramo de Tamá is not comparable with those from the Mérida Andes because light fog at Tamá reduced visibility.



FIG. 4. Upper: view of Páramo de Santo Domingo. Lower: view of Páramo del Aguila.



FIG. 5. Views of Páramo de Piedras Blancas. Upper: general landscape and vegetation. Lower: arborescent forms of *Espeletia* sp.

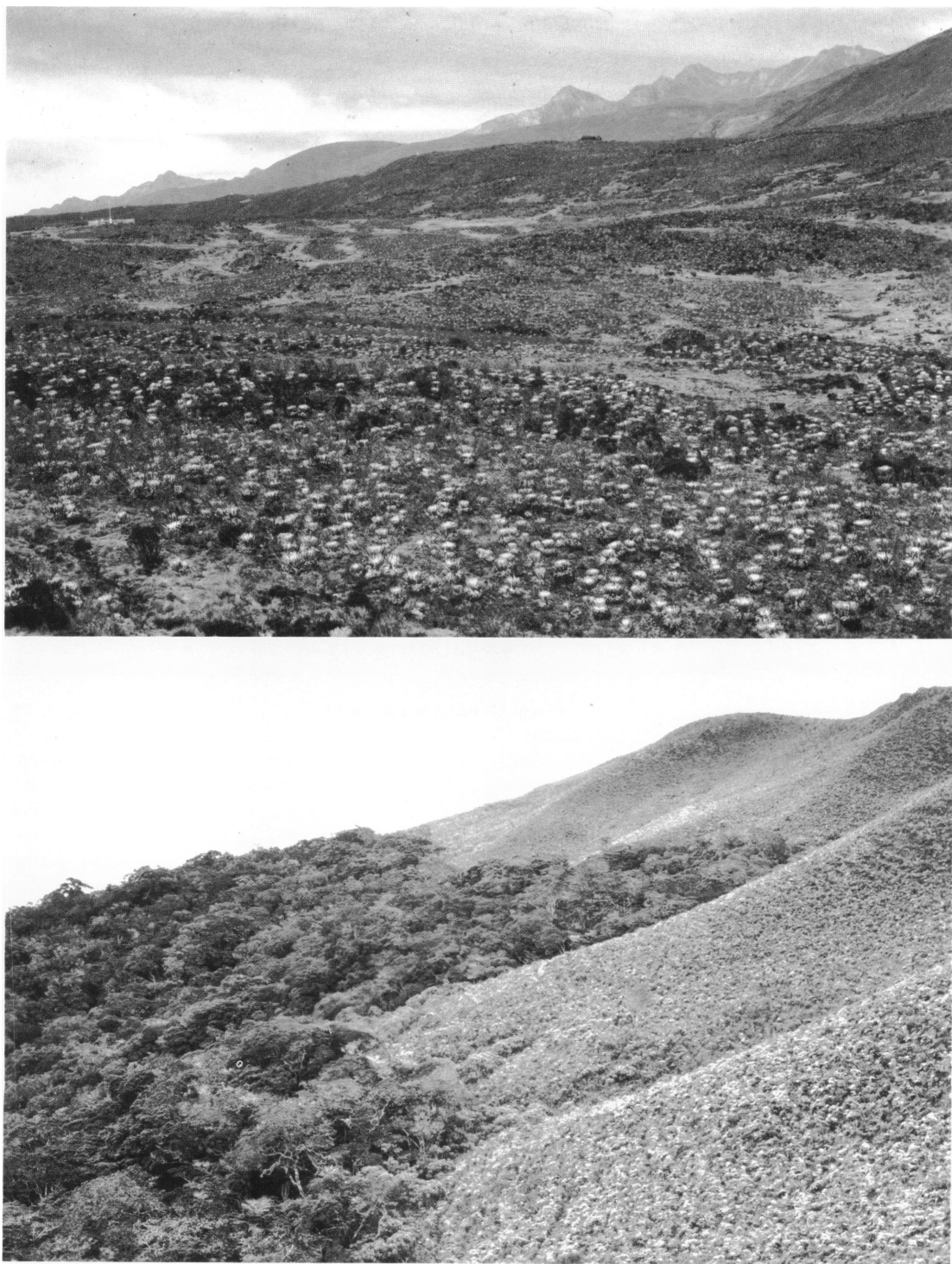


FIG. 6. Upper: view of Páramo de Mucubají. Lower: view of Páramo de Quirorá showing the sharp forest/páramo ecotone.



FIG. 7. View of Páramo La Negra.

Of the six remaining censuses, five were conducted between 0800 and 1100, and a sixth was completed by 1300. At each census site we recorded weather conditions, slope, exposure, and topography (see Appendix), and the vegetation structure along the transect.

During each census, we ran a 1 km. transect, stopping every 200 m. for two periods of five minutes, at each of the six stations on each transect. We counted all birds heard and observed at each station. Counts were made for two five-minute periods to see if comparable data would be collected each time. The highest

count of each species during the two five-minute periods was used as an estimate of the abundance of each species at each station. For example, at station 2 of Mucubají Census number 1, we counted two *Asthenes wyatti* during the first five minutes and three during the second five minutes. Thus, the total number of *Asthenes wyatti* was estimated to be three at that station. The total number of individuals estimated from each census site is the sum of individuals counted at each of the six stations at that census site.

RESULTS

CENSUS RESULTS

The results of six censuses, taken at Páramo de Santo Domingo (two censuses), Páramo de Mucubají (two), Páramo del Aguila (one), and Páramo de Piedras Blancas (one) are given in table 3. Table 4 gives for each census the total number of individuals and of species, the species diversity calculated from the Shannon-

Weaver index of diversity ($H' = -\sum p_i \log p_i$), the evenness, and the number of individuals per species.

Because the census taken at Páramo de Tamá was carried out in poor weather, unlike the six censuses completed in the Andes of Mérida, we did not include it in tables 3 and 4. However, the Tamá census yielded four *Schiz-*

oeaca fuliginosa, one *Cistothorus platensis*, one *Diglossa lafresnayii*, and five unidentified birds.

Tables 3 and 4 show several trends in distribution. As far as we know, these data represent the first attempt to estimate the relative abundance of birds at different altitudes in any Venezuelan páramo. Although the number of transects is small we present the data so that

the trends described below can serve as the basis for hypotheses concerning the altitudinal distribution and the relative abundance of certain species. Future work must include, besides more censuses, factors such as vegetation, food resources, soil, and climate, as they change with altitude.

(1) The first trend seems to be a marked drop in species numbers and in numbers of



FIG. 8. View of Páramo del Batallón at the indistinct forest/páramo ecotone.



FIG. 9. View of Páramo de Tamá.

individuals between about 3600 m. (census nos. 3, 4, and 5) and 4430 m. (census no. 6). Since we did not conduct censuses at intermediate altitudes, we cannot say whether this decrease is gradual or abrupt at a particular altitude. Future census work should be aimed at determining the precise relationship between altitude and species diversity and the related aspects of species numbers and numbers of individuals.

(2) Only two species, *Ochthoeca fumicolor* and *Phrygilus unicolor*, were found throughout the altitudinal range of our censuses, from 3100 m. to 4430 m.

(3) Six species were neither censused, nor observed, above about 3700 m.: *Anas flavivirostris*, *Schizoeaca coryi*, *Asthenes wyatti*, *Sturnella magna*, *Diglossa carbonaria*, and *Zonotrichia capensis*. Five other species were not censused above 3700 m. but were observed above that altitude: *Oxypogon guerinii*, *Turdus fuscater*, *Anthus bogotensis*, *Catamenia inornata*, and *Spinus pinescens*.

(4) The following four species were censused only at or above 3500 m.: *Cinclodes fuscus*, *Leptasthenura andicola*, *Anthus bogo-*

tensis, and *Catamenia inornata*. However, *Leptasthenura* was observed as low as 3300 m., and *Anthus* down to 2800 m. at Páramo de Quirorá.

(5) The following species may have their highest density at about 3600 m.: *Leptasthenura andicola*, *Asthenes wyatti*, *Anthus bogotensis*, *Catamenia inornata*, *Phrygilus unicolor*, and *Zonotrichia capensis*.

The above trends, although they need better documentation, suggest that bird species are not evenly distributed altitudinally in Venezuelan páramos. This uneven altitudinal distribution, coupled with geographical distribution, contributes to the patchy distribution of birds in the Venezuelan páramos. The environmental factors that govern the altitudinal and/or latitudinal distribution of páramo birds remain to be determined. We present in the Discussion some notes on habitat use as a preliminary contribution toward this study.

ANNOTATED LIST OF SPECIES

We mention in this list all the species seen or collected by us in 1968, 1970, and 1975 on Venezuelan páramos. We follow the nomencla-

ture and sequence used by Phelps and Phelps (1958, 1963) in their list of Venezuelan birds.

For each species we mention:

—the páramo(s) where it was observed or collected, its relative abundance, and the date and altitude of observations;

—whether our observations modify or extend the information in Phelps and Phelps;

—whether the species was included by Vuilleumier (1970) in his analysis of the páramo avifauna, and whether our view differs from his allocation; we feel that this information is useful because species lists were not included in the 1970 paper;

—any data on distribution, habitat preference, behavior, and/or breeding;

—any information on specimens collected.

FAMILY PODICIPEDIDAE

Podiceps dominicus

Páramo de Santo Domingo (one in May 1970 at about 3200 m.). This grebe is not reported from the Páramo Zone by Phelps and Phelps (1958), and was not considered part of the páramo avifauna by Vuilleumier (1970).

Podiceps dominicus is probably only a rare visitor to lakes in páramos.

Podilymbus podiceps

Páramo de Santo Domingo (two in May 1970 at about 3200 m.). *Podilymbus* is not recorded by Phelps and Phelps (1958) from the Páramo Zone, nor is it considered a páramo species by Vuilleumier (1970).

Like the preceding species, *Podilymbus*

TABLE 3
Results of Census Data from Six Sites in the Andes of Mérida
(For details on sites, see Appendix)

	Census Site							
Census number	1	2		3	4	5		6
Locality and Site	Santo Domingo			Mucubají		Aguila		Piedras Blancas
Species	No. 1 3100 m.	No. 2 3250 m.	Pooled ^(a)	No. 1 3560 m.	No. 2 3600 m.	3630 m.	Pooled ^(b)	4430 m.
<i>Anas flavirostris</i>	1	—	0.5	—	—	—	0.0	—
<i>Oxygogon guerinii</i>	1	—	0.5	—	—	—	0.0	—
<i>Cinclodes fuscus</i>	—	—	0.0	2	1	2	1.7	3
<i>Leptasthenura andicola</i>	—	—	0.0	4	—	7	3.7	1
<i>Schizoeaca coryi</i>	5	3	4.0	—	—	2	0.7	—
<i>Asthenes wyatti</i>	1	1	1.0	23	17	2	14.0	—
<i>Ochthoeca fumicolor</i>	7	1	4.0	1	2	3	2.0	1
<i>Turdus fuscater</i>	2	4	3.0	—	—	1	0.3	—
<i>Anthus bogotensis</i>	—	—	0.0	2	7	+(c)	3.0	—
<i>Sturnella magna</i>	5	3	4.0	+(c)	—	—	0.0	—
<i>Diglossa carbonaria</i>	—	—	0.0	—	1	—	0.3	—
<i>Catamenia inornata</i>	—	—	0.0	+(c)	6	+(c)	2.0	—
<i>Phrygilus unicolor</i>	1	—	0.5	6	2	6	4.7	1
<i>Zonotrichia capensis</i>	+(c)	—	0.0	1	8	+(c)	3.0	—
<i>Spinus spinescens</i>	20	—	10.0	—	—	3	1.0	—
Unidentified	6	2	4.0	1	2	—	1.0	—
Total number of species ^(d)	9	5	9	7	8	8	12	4
Total number of individuals (grand total)	49	14	31.5	40	46	26	37.4	6

(a) Pooled is the average number of individuals observed at Santo Domingo (sites No. 1 and No. 2).

(b) Pooled is the average number of individuals observed at Mucubají (sites No. 1 and No. 2) and at Aguila.

(c) A plus (+) indicates that the species was observed at the census site but not during the census period.

(d) Unidentified species are not counted as a species in the total number.

TABLE 4
Summarized Data and Diversity Index from Six Sites in the Andes of Mérida

Census Number	Census Site	Altitude	Vegetation ^a	Total No. of				
				Sp.	Ind.	Diversity	Evenness	Ind/Sp.
1	Santo Domingo-1	3100 m.	Dense, heterogeneous	9	43	2.37	0.75	5.44
2	Santo Domingo-2	3250 m.	Dense, homogeneous	5	12	2.13	0.92	2.80
3	Mucubají-1	3560 m.	Dense, heterogeneous	7	39	1.92	0.68	5.71
4	Mucubají-2	3600 m.	Dense, homogeneous	8	44	2.44	0.81	5.75
5	Aguila	3630 m.	Dense, homogeneous	8	26	2.75	0.92	3.25
6	Piedras Blancas	4430 m.	Sparse, homogeneous	4	6	1.79	0.90	1.50

^aFor more details on vegetation and habitat see Materials and Methods; for other details see Appendix.

podiceps is probably only a straggler to lakes in the páramos.

FAMILY PHALACROCORACIDAE

Phalacrocorax olivaceus

Páramo de Mucubají (one on March 12, 1975 at Laguna Grande at 3500 m.; two on March 13, 1975 at Laguna Negra at 3500 m.). This species was not noted by Phelps and Phelps (1958) from the Páramo Zone, nor was it included by Vuilleumier (1970) in his analysis of the distribution of páramo species.

This cormorant is probably only a visitor to the páramos, although it might breed occasionally around some páramo lakes.

FAMILY ANATIDAE

Anas discors

Páramo de Mucubají (two on March 17, 1975 at Laguna Grande at 3500 m.). This teal has been collected at Laguna Grande according to Phelps and Phelps (1958). This species was not included by Vuilleumier (1970) because migrants were excluded from his analysis of páramo species.

Anas flavirostris

Páramo de Santo Domingo (three on March 17,

1975 at 3100 m.). Páramo de Mucubají (two pairs and one other bird on March 12, 1975 at Laguna Grande at 3500 m.; three on March 17, 1975 at Laguna Grande). *Anas flavirostris* is cited only from the Páramo Zone by Phelps and Phelps (1958). Vuilleumier (1970) included the species in his analysis.

The birds at Páramo de Santo Domingo were pursuing each other in flight while calling before they landed on a narrow stream within a boggy meadow.

Schwartz (in lett.) reported seeing apparently post-breeding flocks of 10 to 20 teal in December and January at Laguna Grande, and smaller numbers during the rainy season when they were probably breeding. A large, flightless young bird was seen by Schwartz August 29, 1970 in the Mucubají region. It was accompanied by an adult.

FAMILY CATHARTIDAE

Cathartes aura

Páramo de Quirorá (several soaring birds on April 1, 1975 at 2800 m. near timberline). Phelps and Phelps (1958) indicated this species occurred from the Tropical to the Páramo Zone, but Vuilleumier (1970) did not consider it part of the páramo avifauna.

Apparently *C. aura* is probably only a visitor to páramos, reaching this vegetation where favorable thermals occur.

Schwartz (in lett.) suggested that *Cathartes aura* seen at high elevations could be migrants, but we did not determine whether these individuals were of the Venezuelan subspecies *ruficollis* or of a migratory North American subspecies.

FAMILY ACCIPITRIDAE

Buteo fuscescens (= *Geranoaetus melano-leucus*, see Meyer de Schauensee, 1966, p. 52)

Páramo del Aguila (five on March 12, 1975, one on March 30, 1975 at about 4000 m.). Páramo de Mucubají (two on March 19, 1968; in 1975 one on March 13, pair on March 14, and two landing near edge of small stream on March 15 at 3500 m.). Phelps and Phelps (1958) stated that this species is known only from the Páramo Zone of Mérida. This species was considered to be a páramo species by Vuilleumier (1970).

Oroaetus isidori

Páramo de Mucubají (a possible observation of one bird soaring with two *Buteo fuscescens* above a *Polylepis* woodland on March 19, 1968 at about 3600 m.). Páramo de Quirorá (one flying on April 1, 1975 at about 2800 m. at timberline). Phelps and Phelps (1958) reported this species in forests from the Subtropical Zone up to the Páramo Zone. Vuilleumier (1970) did not include *Oroaetus* in the páramo avifauna.

This eagle is probably only a visitor to páramos.

FAMILY FALCONIDAE

Falco sparverius

Páramo de Santo Domingo (one on March 16, 1975 at 2900 m.). Páramo de Mucubají (one on March 12, 1975 at 3600 m.). This falcon was reported by Phelps and Phelps (1958) from Páramos Santo Domingo and Mucuchíes, and was cited as a páramo species by Vuilleumier (1970).

FAMILY SCOLOPACIDAE

Tringa solitaria

Páramo de Mucubají (one on March 16, 1975 at 3500 m.). According to Phelps and Phelps (1958) this species occurs up to 3600 m. Because migrants were excluded from his analysis, Vuilleumier (1970) did not consider this sandpiper a páramo species.

The only individual seen was foraging in a boggy meadow.

Capella gallinago

Páramo de Mucubají (10 on March 16, 1975 at about 3500 m.). This species is known from the Páramo Zone (Phelps and Phelps, 1958), but was not considered part of the páramo avifauna by Vuilleumier (1970) because it is a migrant.

The group of snipes was seen with *Chubbia jamesoni* foraging in a boggy meadow.

Capella nobilis

Páramo de Tamá (one on March 21, 1975 at 2400 m.). Phelps and Phelps (1958) recorded *C. nobilis* only from the Páramo Zone of the Páramo de Tamá. Vuilleumier (1970) treated this snipe as a páramo species.

We observed one bird in a sedge bog surrounded by montane forest near a clearing, but we did not see this species in páramo vegetation above the timberline.

The precise habitat requirements of this species in Venezuela and elsewhere remain to be worked out. A downy young was collected on September 16, 1932 at Chin Blas, Sangay, Ecuador (Moore Laboratory Collection no. 4634), but unfortunately the altitude is not given on the label. Other specimens of *C. nobilis* and of *Chubbia jamesoni* in the Moore Collection from the Guayama Valley, between Mocha and Chimborazo, Ecuador (again, no altitude given), indicate that the two species are sympatric. At Malvasá, Cauca, Colombia, altitude 3200 m., M. A. Carriker, Jr. collected a male of *C. nobilis* with enlarged testes on January 24, 1958 (Los Angeles County Museum no. 33069). At the same locality another *nobilis* specimen was collected on January 27 (female, no gonad data, LACM 33070), and females of *Chubbia jamesoni* (no gonad data, LACM

33067 and 33068) on January 23 and January 31, respectively. These specimens suggest, again, sympatry of the two species. As *Chubbia jamesoni* appears to be a bird living chiefly, if not only, in páramo vegetation, these specimens imply that *C. nobilis* breeds in páramo vegetation also. Our Venezuelan observation at a lower altitude suggests the possibility of altitudinal movements in *C. nobilis*.

Chubbia jamesoni

Páramo de Mucubají (one seen on March 13, 1975 and two-three seen on March 16, 1975 at about 3500 m.). Páramo del Batallón (one on March 26, 1975 at 3200 m.). *Chubbia* is not cited from Batallón by Phelps and Phelps (1958), who called the species locally distributed and mentioned localities in the Andes of Trujillo, Mérida, and Táchira (only Tamá in the last state). Vuilleumier (1970) considered this species a member of the páramo avifauna.

At Mucubají *C. jamesoni* were flushed from a boggy meadow, where they were apparently feeding. At Batallón, the bird was flushed several times from a moist grassy area with scattered *Espeletia* spp.

FAMILY LARIDAE

Phaetusa simplex

Páramo de Mucubají (two on March 16, 1975 at Laguna Grande at 3500 m.). *Phaetusa* was not cited by Phelps and Phelps (1958) from the Páramo Zone, and was not included by Vuilleumier (1970) in his analysis. It has been reported from a high altitude at Riobamba on the Ecuadorian tableland by Taczanowski and Berlepsch (see Chapman, 1926, p. 185).

The two birds seen at Laguna Grande were undoubtedly strays from lower altitudes.

FAMILY COLUMBIDAE

Columba fasciata

Páramo de Quirorá (several on April 1, 1975 at 2850 m.). Páramo Zumbador (several on March 25, 1975 at 2900 m.). This species is not cited from the Páramo Zone by Phelps and Phelps (1958), nor was it considered a páramo species by Vuilleumier (1970). We do not consider it a páramo species in this paper.

At both Quirorá and Zumbador *C. fasciata* was seen in the ecotone between páramo and upper montane forest, at or near timberline.

FAMILY CAPRIMULGIDAE

Caprimulgus longirostris

Páramo de Tamá (one heard singing on March 22, 1975 after sunset just above timberline at 3000 m.). This species was previously known from Páramo de Tamá, but Phelps and Phelps (1958) indicated only the Subtropical and Temperate Zones. Vuilleumier (1970) did not include *C. longirostris* in the páramo avifauna. In this paper, however, we consider this species to be part of the páramo avifauna on the basis of this observation and of another recent observation by Vuilleumier of the species at 4200 m. in páramo vegetation in Colombia (Páramo del Ruiz, October 8, 1975).

FAMILY APODIDAE

Streptoprocne zonaris

Páramo de Quirorá (several on April 1, 1975 at timberline at about 2800 m.). Phelps and Phelps (1958) cited this species from the Tropical and Subtropical Zones. Vuilleumier (1970) did not include *S. zonaris* as a páramo species. This swift appears to be a straggler to páramos.

FAMILY TROCHILIDAE

Ensifera ensifera

Páramo de Tamá (one on March 24, 1975 just below timberline at 2850 m.). Phelps and Phelps (1958) reported this species from a few localities in the Andes of Mérida, in thickets of the Temperate Zone at 3000 m., but not from Tamá. Vuilleumier (1970) did not consider *Ensifera ensifera* to be a páramo species.

Eriocnemis vestitus

Páramo de Tamá (common on March 21 to 24, 1975 at 2850-3000 m.). Phelps and Phelps (1958) reported this species from Tamá and from the Mérida Andes in thickets of the Páramo and Temperate Zones (2800 to 3600 m.). Vuilleumier (1970) included *Eriocnemis vestitus* in his list of páramo species.

Eriocnemis vestitus appears to be a common hummingbird at Tamá at, and slightly below,

timberline. We did not observe it in open páramo vegetation, but only in ecotonal areas between páramo and upper montane forest below. Thus, we would not include *E. vestitus* in the avifauna of páramo vegetation as defined in this paper (see Definition of a Páramo Species).

Two specimens collected on March 21, 1975 at 2950 m. were prepared as skins. The male (AMNH 811971) weighed 5 g., was molting, had an unossified skull, and small testes. The female (AMNH 811970) weighed 5 g., had no molt, an unossified skull, and small ova.

Metallura tyrianthina

Páramo del Aguila (one on March 30, 1975 at 3700 m.). Páramo de Quirorá (common on April 1, 1975 at 2820 m.). Páramo del Batallón (several on March 26, 1975 at 2980 m.). Phelps and Phelps (1958) noted that this species occurs in the Páramo Zone up to 3800 m.; they do not record it from Páramo del Batallón. Vuilleumier (1970) included *M. tyrianthina* in his list of páramo birds, but we do not do so now because it appears to be restricted to ecotonal habitats.

Metallura tyrianthina does not seem to inhabit open páramo vegetation as defined in this paper, except where it is adjacent to *Polylepis sericea* woodlands, and to patches of tall shrubs and short trees at the lower altitudes of the open páramo vegetation. The one bird seen at Aguila fed at flowers of *Hesperomeles pernettyoides* Wedd. (Rosaceae) in scrub consisting of *Hesperomeles* and *Polylepis sericea*. We observed several birds at timberline at Quirorá, and at Batallón several individuals were seen in dense, patchy shrubbery adjacent to forest.

Four specimens were collected: one (AMNH 4639, spirit) is from Aguila, one (AMNH 4640, spirit) is from Quirorá, and two (AMNH 811969, skin; AMNH 4641, spirit) are from Batallón. Three of the birds (AMNH 4640, 4641, and 811969) are males, weighed 3.0 g., and had no molt. Small gonads were noted in AMNH 4640 (Quirorá) and 4641 (Batallón), and the skull of AMNH 4641 (Quirorá) was unossified.

Chalcostigma heteropogon

Páramo de Tamá (several on March 22-23,

1975 at 3000 to 3200 m.). This species was cited from Tamá by Phelps and Phelps (1958) from 3000 to 3275 m. It was included by Vuilleumier (1970) as a páramo species.

Chalcostigma heteropogon was the only hummingbird species observed in páramo vegetation at Tamá; it occurred from timberline up through páramo vegetation, especially near small cliffs and tall boulders.

Oxypogon guerinii

Páramo de Santo Domingo (one female or immature on March 17, 1975 at 3100 m.). Páramo del Aguila (one immature male and one female on March 30, 1975 at 3700 m.). Páramo de Piedras Blancas (one adult male on March 18, 1975 at 4100 m.). Páramo de Mucubají (one immature male on March 13, 1975 at 3520 m.; one immature in March 1968). *Oxypogon* occurs from 3500 to 4100 m. in shrubby areas of the Páramo Zone according to Phelps and Phelps (1958), and is considered a member of the páramo avifauna by Vuilleumier (1970).

At Páramo de Santo Domingo the one individual seen was perched on a tree in a copse. At Páramos del Aguila, de Piedras Blancas and de Mucubají the birds occurred in *Polylepis* scrub or at the edge of *Polylepis* woodland. At Aguila two birds fed at the flowers of *Hesperomeles pernettyoides*, and at Piedras Blancas one bird foraged near the top of a *Polylepis* tree. Our observations indicate that, at least in the dry season, *Oxypogon* does not inhabit open páramo vegetation but is more or less restricted to ecotonal areas between *Polylepis* woodlands or other shrubbery and the more open páramo vegetation. Our observations are in agreement with those of Schwartz (in lett.), who stated that *Oxypogon* is seldom, if ever, seen in open páramo vegetation outside the main flowering season. Schwartz (in lett.) reported that *Oxypogon* is constantly present in the open páramo vegetation during the main flowering season of the páramo flora, perhaps from August to November. He located a young bird just out of the nest in mid-December near Laguna Grande. The nest was under the overhang of a stream bank.

One female of *Oxypogon* (AMNH 9500, skeleton) was taken March 30, 1975 at 3700 m. near El Aguila in *Polylepis* scrub. She weighed 4.0 g., had no fat, tiny ova, and black irides.

FAMILY FURNARIIDAE

Cinclodes fuscus

Páramo del Aguila (two on March 30, 1975 during a census at 3610 m.). Páramo de Piedras Blancas (seen commonly on March 14 and 18, 1975 from 4000 to 4400 m.). Páramo de Mucubají (seen regularly between March 12 and 17, 1975 at 3500 to 3600 m.). Phelps and Phelps (1963) did not indicate that *Cinclodes* occurs below 3800 m., so our observations lower the known elevational range of this species in Venezuela to 3500 m. Vuilleumier (1970) included *C. fuscus* in his analysis of páramo birds.

At 3500 to 3600 m., *Cinclodes fuscus* appeared to be largely restricted to areas adjacent to water, usually small streams. At 4000 to 4400 m. at Páramo de Piedras Blancas, *C. fuscus* was probably the most common species. It occurred throughout a habitat composed of open, sparse stands of *Espeletia* spp. (up to 3 m. tall), *Hinterhubera imbricata* Cuatr. (Compositae), cushion plants, and open ground with rocky outcroppings and little grass cover. Most birds appeared to be paired, and many were singing a song that consisted of a trill. They were terrestrial and did not utilize shrubbery. These observations suggest that *C. fuscus* is more common at higher altitudes, where it is ecologically more widespread than at lower elevations, and occurs away from water. This may be because *C. fuscus* depends on poorly vegetated areas for foraging, so as the environment becomes more barren at higher elevations it can support greater numbers of *Cinclodes*.

Two males collected at Piedras Blancas were preserved in spirit. One (AMNH 4632) was obtained on March 14, 1975 at 4300 m. It weighed 33.0 g., had worn plumage, and a completely ossified skull; its testes were enlarged, and its gut contained one large caterpillar and a small amount of insect remains. The other (AMNH 4631) was taken on March 18, 1975 at 4250 m. It weighed 31.0 g., and had slightly worn plumage with some molt in the mystacial stripe area; its testes were enlarged, and its gut was empty.

Leptasthenura andicola

Páramo del Aguila (seen on March 12, 1975 at about 3600 m., seven on March 30, 1975 at

3610 m. during a census). Páramo de Piedras Blancas (seen on March 14 and 18, 1975 up to about 4400 m.). Páramo de Mucubají (seen regularly from March 12 to 17, 1975 between 3400 and 3600 m.). Our observations of *Leptasthenura* from 3400 to 4400 m. extend the known elevation range of the species in Venezuela which was given as 3500-4100 m. by Phelps and Phelps (1963). Vuilleumier (1970) included *Leptasthenura* as part of the páramo avifauna.

Leptasthenura andicola occurs in *Polylepis sericea* woodland and scrub, in copses of *Stevia lucida* Lag. (Compositae) and in open páramo vegetation where there is a mixture of *Espeletia* spp. and shrubs. *Leptasthenura* was observed to forage on small shrubs at heights ranging from just above ground level to at least 1.5 m. aboveground, and occasionally under the flaking bark of *Polylepis*, at the base of epiphytic bromeliads, and on *Espeletia* (in the foliage, and once in *Espeletia* seed heads). *Leptasthenura* seemed to spend relatively less time at each feeding site than other páramo birds, thus giving the impression of a restless species.

Schizoeaca fuliginosa

Páramo de Tamá (fairly common on March 21-24, 1975 from 3050 to 3200 m.). Phelps and Phelps (1963) noted the presence of *S. fuliginosa* from the "Temperate Zone" of Tamá. Vuilleumier (1970) included this species in his analysis of páramo birds.

This species occurs in areas covered by dense shrubbery and ferns. Birds seemed to be paired and were singing. The voice of *S. fuliginosa* is very reminiscent of that of *S. coryi*. Call notes, which are either contact or alarm calls can be transcribed as "vñh" or "pñh," just as in *S. coryi*. The song is a trill, consisting of a series of high-pitched notes, which increase in tempo and slightly in pitch. The trill resembles that of *Asthenes wyatti*, although it is longer.

One pair was collected and prepared as skins. The male (AMNH 811984) had large testes, was singing when collected, weighed 19 g., and had an incompletely ossified skull. The female (AMNH 811985) had ova about 1.5 mm. in diameter, weighed 18 g., and had an incompletely ossified skull. Both birds had insect

remains in their gut (the male had, in addition, some small seeds in the stomach), white irides, bluish gray legs with yellowish soles, and dark gray or blackish bill with the mandible paler at the base.

Schizoeaca coryi

Páramo de Santo Domingo (several on March 16 and 17, 1975 from 3100 to 3250 m.). Páramo del Aguila (at least two on March 30, 1975 at 3700 m.). Páramo de Mucubají (several seen from March 12 to 17, 1975 between 3400 and 3500 m.). Páramo de Quirorá (several on April 1, 1975 from 2800 to 2900 m.). Páramo La Negra (common on March 26, 1975 at 3000 to 3100 m.). Páramo Zumbador (one bird on March 25, 1975 at 3000 m.). We saw *Schizoeaca coryi* from 2800 to 3700 m., and possibly also heard it in a *Polylepis* woodland at Páramo de Piedras Blancas on March 18, 1975 at 4100 m. Our observations seem to constitute the first records of this species for Páramos Quirorá and Zumbador (see Phelps and Phelps, 1963). This species was included by Vuilleumier (1970) as part of the páramo avifauna.

Schizoeaca coryi was locally common but ecologically patchily distributed in vegetation of relatively dense, tall scrub at or above timberline, which includes *Hypericum* spp. scrub, the edges of *Polylepis sericea* woodlands, copses of *Stevia lucida*, and other shrubby types of vegetation. *Schizoeaca coryi* was near the ground at Laguna Negra much of the time, and remained inconspicuous in the vegetation. One bird was seen foraging along the limbs of *Polylepis* where there was dried lichen growth. We did not observe this species foraging on *Espeletia* spp. On two occasions we observed *coryi* simultaneously moving the tail up and down and flicking the wings open. Most birds seemed to be paired.

One pair was collected at Páramo La Negra in *Hypericum* spp. shrubbery at 3070 m. Both birds had a brood patch, with the female (AMNH 811982, skin) having a more developed brood patch than the male (AMNH 811983, skin). The gonads of both birds were moderately enlarged. The male had a completely unossified skull, the female had ossification only in the occipital region. The male weighed 17.5 g., the female 15.5 g. The gut of

the male contained mostly insects (including Coleoptera and Orthoptera) and seeds, that of the female was full of insect remains but had no seeds. Two birds, probably a pair (AMNH 4644 and 4645, spirit), were collected at Páramo de Quirorá on April 1, 1975 at 2830 m. in a copse of arborescent *Espeletia* sp. at timberline. Both birds weighed 17.0 g. The iris color was dark brown or grayish brown for the three birds in which we noted iris color, unlike the white iris color of *S. fuliginosa*. The leg color was bluish gray, as in *fuliginosa*. The bill color was dark grayish brown with the lower mandible having a pinkish brown base as in *fuliginosa*.

Asthenes wyatti

Páramo de Santo Domingo (at least one bird on March 17, 1975 at 3100 m., and another at 3250 m.). Páramo del Aguila (two on March 30, 1975 at 3620 m.). Páramo de Mucubají (common from March 12 to 17, 1975 between 3500 and about 3600 m.). We saw *A. wyatti* from 3100 m. to at least 3600 m., although it was not reported below 3500 m. by Phelps and Phelps (1963). Vuilleumier (1970) cited this species as a member of the páramo avifauna.

Asthenes wyatti has a patchy distribution but is locally common, especially around 3500 to 3600 m. It appeared to favor a vegetation consisting of a dense mixture of *Espeletia* spp. and shrubs, interspersed with more open, grassy areas, and was near the ground much of the time. *Asthenes* was seen to forage on *Espeletia* near the terminal bud and at the base of the rosette of living leaves. One bird was observed carrying nest material.

We heard two types of vocalizations. The first was a single, insect-like trill consisting of a series of notes, slightly modulated, and very slightly accelerated toward the end of the trill. It lasted less than one second. The second vocalization, which also lasts one second or less, is a repetition of three trills, all three being approximately equal in pitch and length. The frequency of delivery was about the same for the two song types. The two song types were alternately emitted by different birds, but with some temporal overlap. We do not know whether these vocalizations are given only by males, only females, or both, or whether this constitutes duetting. Songs were typically deliv-

ered from perches on *Espeletia* spp. At Mucubají, songs were heard frequently on the morning of March 14, when it was foggy, but not on March 13, when it was clear and frosty.

Margarornis squamigera

Páramo de Piedras Blancas (one possibly sighted on March 18, 1975 in *Polylepis sericea* woodland at 4100 m.). Páramo de Mucubají (at least four birds on March 13, 1975 at Laguna Negra at 3530 m.). Phelps and Phelps (1963) recorded 3200 m. as the highest elevation reached by this species in Venezuela, and Laguna Negra is not cited as one of the localities where it occurs. Vuilleumier (1970) did not include this species in his list of páramo birds. Our observations support his decision.

Several birds were observed in *Polylepis* woodland, where they frequently probed among lichens on the branches, and occasionally on the trunks of *Polylepis* trees; they were frequently seen hanging upside-down. They were foraging in groups of up to four individuals. Our observations indicate that *Margarornis squamigera* occurs in *Polylepis* woodland above the temperate forest timberline, but does not live in páramo vegetation as defined in this paper.

FAMILY TYRANNIDAE

Myiotheretes striaticollis

Páramo de Quirorá (one at timberline on April 1, 1975 at about 2800 m.). Phelps and Phelps (1963) recorded this species from 3000 and 3050 m. in Venezuela. Vuilleumier (1970) included *M. striaticollis* as part of the páramo avifauna, but he would not do so now (see Description of Habitats in Vuilleumier, 1971, p. 205).

The one individual observed was carrying a very large beetle (Scarabid?) which was subsequently dropped. The bird flew down toward timberline from the open páramo vegetation with the beetle in its bill, suggesting this prey was captured in páramo vegetation. It gave one melancholy whistle, described as "tiuuu," which carried over a long distance.

Ochthoeca fumicolor

Páramo de Santo Domingo (common on March 16 and 17, 1975 from 3070 to 3250 m.).

Páramo del Aguila (several on March 12 and 30, 1975 at 3600 to 3700 m.). Páramo de Piedras Blancas (several on March 14 and 18, 1975 from 4000 to 4400 m.). Páramo de Mucubají (common from March 12 to 17, 1975 at 3400 to 3600 m.). Páramo de Quirorá (pair on April 1, 1975 at 2820 m.). Páramo de Tamá (a few on March 21 to 24, 1975 at about 2950 m.). We observed this species from 2820 m. to 4400 m., but it was not reported above 4200 m. by Phelps and Phelps (1963). *Ochthoeca fumicolor* was included by Vuilleumier (1970) in his analysis of the páramo avifauna.

Ochthoeca fumicolor was recorded in all habitats we visited from upper temperate forest and timberline up to páramo vegetation, and including woodlands of *Polylepis sericea*. At Quirorá and Tamá, *fumicolor* was observed only at timberline, at 2820 and 2950 m., respectively, where they appeared to be less common than at other páramos. At these two sites *O. fumicolor* occupied a vegetation type similar to that of *O. rufipectoralis* in Perú and Bolivia. In the Andes of Mérida, *O. fumicolor* was present in timberline scrub, *Stevia lucida* copses, open páramo, and *Polylepis sericea* woodland from 3070 to 4400 m., where it was found in a wider range of vegetation communities than any other species. *Ochthoeca fumicolor* typically perched at the top of vegetation, which could be *Espeletia* spp. where it was the tallest vegetation, or *Stevia*, where it occurred in copses. In *Polylepis* it may forage more frequently at medium to low heights than near the canopy. Occasionally *fumicolor* would descend to the ground to pick up food.

In the Mérida Andes most *fumicolor* were paired. A nest of *O. fumicolor superciliosa*, apparently under construction, was found on March 18, 1975 at Páramo de Piedras Blancas at about 4000 m. in an open *Polylepis* woodland. The nest, a cup lined with rabbit fur, was in a cavity of an *Espeletia* sp. plant, 5 to 7 cm. deep, which opened where the dead leaves covered the stalk. The cavity opened 20 cm. above the ground and may have been dug out by the birds. From the presence of many rabbit feces and several burrows, we judged that rabbits were common, and their fur could easily be obtained. Schwartz (in lett.) located one nest,

apparently just completed, in a niche of a bank at 3000 m. between Santo Domingo and Mucubají. It was lined with plant (? *Espeletia*) material.

Four specimens were collected, three of the subspecies *superciliosa* Sclater and Salvin and one of the subspecies *fumicolor* Sclater.

All three specimens of *O. fumicolor superciliosa* appeared to be paired, had enlarged gonads, and had insect remains in the gut. One male (AMNH 4642, spirit) collected on March 13, 1975 at 3530 m. at Páramo de Mucubají had an incompletely ossified skull and weighed 14.0 g.; the other male (AMNH 9507, skeleton) collected March 30, 1975 at 3670 m. at Páramo del Aguila, had a fully ossified skull and weighed 15.0 g. One female, collected March 18 at 4050 m. at Páramo de Piedras Blancas (AMNH 4643, spirit), had a completely ossified skull, a brood patch, largest follicles 1.0 mm., and weighed 15.0 g.

One male of the subspecies *O. fumicolor fumicolor* (AMNH 9508, skeleton), collected March 21, 1975 at 2950 m. at Páramo de Tamá, had a completely ossified skull, small testes, and weighed 16.5 g.

Mecocerculus leucophrys

Páramo de Santo Domingo (one on March 16, 1975 at 2850 m., another at 2900 m., and two at 3200 m.). Páramo de Mucubají (fairly common on March 13, 1975 at Laguna Negra at 3530 m.). Páramo de Quirorá (present at timberline at 2800 m. on April 1, 1975). Vuilleumier (1970) considered this species to be a member of the páramo avifauna. However, *Mecocerculus* appears to require tall shrubs or short trees adjacent to more open areas, such as the nonforested páramo vegetation formation, and cannot, therefore, be considered a member of the páramo avifauna.

At Páramo de Santo Domingo at 2850 m. one bird was seen in second-growth woodland, another at 2900 m. in more open vegetation near boulders, and two birds occurred at 3200 m. in a copse of *Stevia lucida*. At Páramo de Mucubají two birds appeared to follow a group of *Margarornis squamigera* in *Polylepis* woodland, and at Páramo de Quirorá the species occurred at timberline.

FAMILY HIRUNDINIDAE

Notiochelidon murina

Páramo de Santo Domingo (several in late May 1970 at about 3250 m.). Páramo de Mucubají (several on March 19, 1968 at about 3500 m.; several on March 15, 1975 at about 3500 m.). Páramo de Tamá (many on March 21, 1975 at 2950 m.). Phelps and Phelps (1963) cited this species from three localities in the Mérida Andes (Llano Rucio, El Valle, and El Escorial), and one in Trujillo (Teta de Niquitao), at altitudes of 2200 m. to 2800 m. Our records extend the range of *N. murina* to Páramo de Tamá, and extend the upper altitudinal limit to 3500 m. Vuilleumier (1970) included the species in his analysis of páramo birds.

At all three páramos, *N. murina* was seen in flocks flying low over páramo vegetation.

Notiochelidon cyanoleuca

Páramo de Quirorá (several on April 1, 1975 at 2800 m. at timberline). Phelps and Phelps (1963) cited 2500 m. as the upper altitudinal limit of this species. It was not included by Vuilleumier (1970) in his analysis of páramo birds, a view with which we concur.

Hirundo rustica

Páramo de Mucubají (flocks on March 15 and 17, 1975 up to 3560 m.). *Hirundo* was not included in Vuilleumier's (1970) analysis of páramo birds, because it is a migrant in Venezuela.

FAMILY CINCLIDAE

Cinclus leucocephalus

Páramo de Santo Domingo (several on March 16 and 17, 1975 up to 3250 m.). Páramo del Aguila (one on March 12, 1975 at 3650 m.). Páramo de Piedras Blancas (one on March 18, 1975 at 4000 m.). This species was not reported above 3600 m. by Phelps and Phelps (1963). Vuilleumier (1970) did not include it in his analysis of páramo birds, but it does occur where páramo vegetation grows if fat flowing streams are present.

At Páramo de Santo Domingo two nests under construction were found. Both nests were domed, were made of moss, and were placed in mossy crevices among boulders on stream

banks about 1 m. above the surface of the water, facing downstream.

One nest, found about 1.5 m. above a stream on March 16, 1975 at 3200 m., was made entirely of moss. Both members of the pair flicked their wings while we observed the nest. When a third *Cinclus* appeared, both members of the pair extended their necks and pointed their bills up at a 45 degree angle.

The second nest, found about 0.5 m. above the surface of the stream, was under construction on March 17, 1975 when we saw both birds carrying moss to it. This nest was upstream from the one found the previous day, and was about 30 cm. from an old *Cinclus* nest. Both members of the pair wetted the moss in the stream before flying up to their nest.

FAMILY TROGLODYTIDAE

Cistothorus platensis tamae

Páramo de Tamá (common from March 21 to 24, 1975 from 2950 to about 3200 m.). Phelps and Phelps (1963) reported this species from the Subtropical and Temperate Zones and listed the elevational range as 2200 to 3275 m. *Cistothorus platensis* was included by Vuilleumier (1970) as a páramo species.

We found this species in dense, low shrubbery just above timberline and up to 3200 m., where it inhabited a vegetation of low grasses and scattered *Espeletia* spp. Many birds were singing.

Cistothorus meridae

Páramo de Santo Domingo (one on March 17, 1975 at 3300 m.). Vuilleumier (1970) included this species as part of the páramo avifauna. The one bird seen was in a moist spot with dense grass, moss, and low thicket cover.

Another *Cistothorus*, perhaps of this species, was observed in grassy páramo with scattered, low *Espeletia* spp. at 3200 m. at Páramo Batallón on March 26, 1975. Neither *C. meridae* nor *C. platensis* is cited by Phelps and Phelps (1963) from Batallón.

FAMILY TURDIDAE

Turdus fuscater

This species was observed primarily in three habitats. We observed *T. fuscater* in or near *Polylepis* woodland: Páramo del Aguila (several

on March 12 and 30, 1975 at 3650 m.), Páramo de Piedras Blancas (one pair on March 18, 1975 at 4100 m.), and Páramo de Mucubají (several on March 12 and 17, 1975 at about 3600 m.); in copses of *Stevia lucida* and other shrubs above timberline: Páramo de Santo Domingo (several on March 17, 1975 at 3100 and 3250 m.; several on March 16, 1975 at 3400 m.); and at or just below timberline: Páramo de Santo Domingo (one on March 16, 1975 at 2850 m. and another at 3070 m.), Páramo de Quirorá (common on April 1, 1975 at 2800 m.), Páramo del Batallón (common on March 26, 1975 at 3100 m.), Páramo Zumbador (several on March 25, 1975 at 3000 m.), and Páramo de Tamá (pair at 3000 m.). Vuilleumier (1970) cited this species as a member of the páramo avifauna.

This species appeared to be most common at the interface between open areas and tree and shrub growth but individuals were occasionally seen in open páramo vegetation. One nest, containing two incubated eggs, was found April 1, 1975 at 2800 m. at Páramo de Quirorá. The large bulky nest was placed about 1 m. above-ground in a shrub at timberline. We collected the eggs (AMNH 17918), and the nest (collection of the Estación Biológica de Rancho Grande).

Three birds were collected. One specimen from Páramo de Piedras Blancas (AMNH 4662, spirit) was collected on March 18, 1975 at 4100 m. It was a male with small gonads (although it appeared to be paired), weighed 154 g., had a completely ossified skull, and a gut full of insect and plant remains. Another specimen from Páramo de Mucubají (AMNH 4663, spirit) was taken at 3530 m. on March 13, 1975. It was a male with small gonads, a fully ossified skull, weighed 128 g., and had Orthoptera and a Hymenoptera in its stomach. The third specimen (AMNH 9497, skeleton) was collected at Páramo del Batallón at 3100 m. on March 26, 1975. It was a female weighing 133 g. It had an enlarged oviduct, brood patch, worn plumage, partially ossified skull, and the stomach contained green seeds.

FAMILY MOTACILLIDAE

Anthus bogotensis

Páramo de Santo Domingo (one or two on

March 16, 1975 at 3070 m.). Páramo del Aguila (two on March 30, 1975 at 3630 m.). Páramo de Piedras Blancas (two on March 18, 1975 at about 4200 m.). Páramo de Mucubají (common between March 12 and 17, 1975 at 3500 to 3700 m.). Páramo de Quirorá (one on April 1, 1975 at 2800 m.). Páramo La Negra (two on March 26, 1975 at 3000 m.). Páramo del Batallón (several on March 26, 1975 at 3150 to 3300 m.). Páramo Zumbador (two collected on March 25, 1975 at 3000 to 3200 m.). Phelps and Phelps (1963) did not record *A. bogotensis* from Páramos Quirorá, Batallón or Zumbador. Schwartz (in lett.) collected a male at 2700 m. on September 30, 1969 in open country on the road to Michelena near Puesto Zumbador. This specimen record of *bogotensis* lowers the known elevational range of this species in the Mérida and Trujillo Andes of Venezuela from 3100 m. (Phelps and Phelps, 1963) to 2700 m. Vuilleumier (1970) included this species in his analysis of the páramo fauna.

Most individuals of this species were seen in open grassy or boggy areas, irrespective of the slope of the ground. They foraged by walking on the ground. Many birds seemed to be paired and one male was heard singing at sunrise on March 16, 1975 from a song perch near the ground. Two males of *bogotensis* were collected March 25, 1975 at Páramo Zumbador at approximately 3000 m. and 3200 m. (AMNH 811977 and 811978, skins). The testes of one male were moderately enlarged. Both birds weighed 26 g., had fully ossified skulls, and their stomachs were full of insects.

FAMILY COEREBIDAE

Diglossa lafresnayii

Páramo Zumbador (three on March 25, 1975 at 3000 m.). Páramo de Tamá (several on March 21-24, 1975 from 2950 to 3000 m.). This *Diglossa* was not included by Vuilleumier in his 1970 analysis of the páramo avifauna.

In both localities *D. lafresnayii* was found only in the ecotone between páramo and temperate forest. At Zumbador this habitat consisted of very dense, low shrubs, trees, and tree ferns with a ground cover of moss and *Espeletia* spp. One or 2 m. tall ericaceous and composite shrubs, interspersed with *Chusquea*, and *Blechnum*-like ferns, with a ground cover

of moss dominated this transition at Tamá. A song, characterized as a warble, was heard from birds at Tamá.

Two birds were collected at Zumbador. One female weighed 15.5 g., had tiny gonads, and had a completely ossified skull (AMNH 811993, skin). One unsexed bird weighed 15.0 g. had a partly ossified skull (AMNH 9505, skeleton). One male and one female were collected at Tamá on March 23, 1975. The male (AMNH 811991, skin) had small testes, a fully ossified skull, and weighed 17.0 g. The female (AMNH 811992, skin) had very small ovaries, a fully ossified skull and weighed 15.0 g. Both birds had insect remains in the stomach, including one beetle which was in the male's stomach, and were in fresh plumage.

Diglossa carbonaria

Páramo del Aguila (one pair and possibly another bird on March 30, 1975 at 3700 m.). Páramo de Mucubají (one on March 16, 1975 at 3600 m.). Páramo de Quirorá (common on April 1, 1975 at 2800 m.). Páramo del Batallón (about three birds on March 26, 1975 at 2980 m.). This *Diglossa* was not listed by Phelps and Phelps (1963) from Páramos Quirorá and Batallón. It is cited by Vuilleumier (1970) as a páramo species, but we do not treat it as a páramo species here (see section Definition of a Páramo Species).

Diglossa carbonaria was found most commonly at timberline at Páramo de Quirorá and less commonly at Páramo del Batallón. This species was seen occasionally in scrubby woodland, which included *Polylepis*, at Páramo del Aguila. Once one individual was seen moving rapidly in open páramo consisting of *Espeletia* spp. It is possible that the bird was traveling from one woodland to another.

The pair of birds at Páramo del Aguila was engaged in flight pursuits and song which suggested that the pair was courting. This species was very common at Páramo de Quirorá where many individuals were singing, giving flight songs, and appeared to be defending their territories. Other birds at Quirorá seemed to be feeding young, and at least one pair was feeding a fledgling out of the nest in a grove of arborescent *Espeletia* sp. just above timberline. The female of that pair was collected (AMNH 4628, spirit) and had a regressing brood patch,

large ova 1.5 by 1.5 mm., an enlarged oviduct, a completely ossified skull, and weighed 11.5 g.

One nest, most likely of this species, was found at timberline at Quirorá. The nest was placed in a clump of grass at ground level at the upper edge of an embankment which was 1.2 m. tall. The nest, only slightly protected from above by a few stems of grass, was a deep cup of grasses and moss lined with the whitish pubescent growth of *Espeletia*. A recently killed, beheaded nestling was found below the nest. The nest and fledgling are now in the collection of the Estación Biológica de Rancho Grande.

The one specimen collected at Batallón (AMNH 811994, skin) was a male with moderately enlarged gonads, had a completely ossified skull, and weighed 11.0 g.

FAMILY ICTERIDAE

Sturnella magna meridionalis

Páramo de Santo Domingo (common on March 16 and 17, 1975 at 3000 to 3300 m.). Páramo de Mucubají (one singing male on March 13, 1975 at 3600 m.). Páramo La Negra (several on March 26, 1975 at 3000 to 3100 m.). Páramo del Batallón (one pair on March 26, 1975 at 3000 to 3100 m.). Phelps and Phelps (1963) did not cite this species from Batallón, and did not record it above 3000 m. *Sturnella* was listed as a páramo species by Vuilleumier (1970).

Sturnella appears to be more or less restricted to the lower altitudes of the páramo and occurs down to approximately 1700 m. where there are open areas (Phelps and Phelps, 1963). In the past, *Sturnella magna meridionalis* may have been restricted to the lower edge of páramo vegetation, but with clearing of the forests below it moved to lower altitudes. It now occupies the edges of cultivated fields, meadows, and open areas with *Espeletia* spp., especially where patches of grass occur. We observed this species only once above 3300 m. when one male appeared at a study site for part of the morning. Why *Sturnella* does not occur regularly above 3300 m. is not clear.

Most *Sturnella* appeared to be paired and males were singing frequently. Flight songs were heard and observed. The song had some

of the rich qualities of that of the Western Meadowlark, *Sturnella neglecta*. This species was observed by Lanyon and Ewert at Páramo de Santo Domingo in late May 1970 up to 3200 m., when they were found in pairs and males were singing.

FAMILY THRAUPIDAE

Hemispingus verticalis

Páramo de Tamá (several on March 23 and 24, 1975 from 2600 to 2950 m.). Our observations suggest that this species is not so rare at Tamá as collection records in Phelps and Phelps (1963) indicate. This species was included by Vuilleumier (1970) in his analysis of the páramo avifauna for Colombia but not for Venezuela. Our observations indicate that this *Hemispingus* is indeed a temperate forest and páramo/temperate forest ecotonal species in Venezuela and that it should not be considered part of the Venezuelan páramo avifauna. Reports of this species from Colombia suggest, however, that it may inhabit páramo vegetation there (Meyer de Schauensee, 1951, p. 1066), but it seems to occur in temperate forest in Ecuador (Chapman, 1926, p. 869).

Hemispingus verticalis was observed singly and in pairs at timberline and in montane forest down to 2600 m. At least one pair fed on berries of *Ternstroemia meridionalis* Mutis (Theaceae), when they appeared to walk from one fruit to another over the thick foliage. They were often associated with flocks of tanagers and flycatchers, when they fed at mid to upper heights in the canopy.

FAMILY FRINGILLIDAE

Catamenia inornata

Páramo del Aguila (one pair on March 30, 1975 at 3620 m.). Páramo de Mucubají (fairly common from March 12 to 17, 1975 at 3500 to 3600 m.). Phelps and Phelps (1963) reported *Catamenia inornata mucuchiesi* from only two páramos in the Mérida Andes (Páramos de Mucuchíes and San Antonio) from 3700 m. to 4200 m., and *C. i. minor* only from Páramo de Tamá at 3275 m. This species is cited by Vuilleumier (1970) as a member of the páramo avifauna.

Catamenia inornata appears to be uncommon in the Mérida Andes and found only in open páramo vegetation above 3500 m. It was less frequently seen than *Phrygilus unicolor* and when observed could be found singly, in pairs, and once in a flock with *Phrygilus unicolor* and *Zonotrichia capensis*. We usually flushed them from open páramo with *Espeletia* spp., where they foraged on the ground. Once several birds were seen picking seeds from flower heads of *Espeletia* spp.

Spinus spinescens

Páramo de Santo Domingo (flocks on March 16 and 17, 1975 at 3100 to 3200 m.). Páramo del Aguila (flocks, singing males on March 12 and 30, 1975 at 3600 to 3700 m.). Páramo de Mucubají (common in flocks on March 12-17, 1975 at 3500 to 3600 m.). Páramo del Batallón (two on March 26, 1975 at 3150 to 3300 m.). This species was included by Vuilleumier (1970) in his analysis of páramo birds.

Several scattered flocks of *Spinus* having up to 20 individuals were found feeding on the seeds of *Espeletia* spp. Members of a flock would usually be feeding at several *Espeletia* within 50 feet of each other. One singing male which did not appear to be a member of a flock was heard at Páramo del Aguila on March 30, 1975. Two other birds were heard singing from *Polylepis* shrubs at Aguila. In contrast to these individuals, another flock of 20 adult males, adult females, and immatures, was observed at Páramo de Santo Domingo in thick shrubbery, actively moving from perch to perch, often near lichens, and only some singing was heard.

Spinus spinescens also occurs in open fields in the Temperate Zone below the páramo (Phelps and Phelps, 1963). Thus, while this species is of regular occurrence and common in páramo vegetation, it is not restricted to páramo.

Phrygilus unicolor

Páramo de Santo Domingo (one on March 17, 1975 at 3100 m.). Páramo del Aguila (several on March 12 and 30, 1975 at 3500 to 3700 m.). Páramo de Piedras Blancas (common on March 14 and 18, 1975 up to 4400 m.). Páramo de Mucubají (common from March 12-17, 1975 at 3500 to 3600 m.). Páramo Zumbador (one on

March 25, 1975 at 3250 m.). Páramo del Batallón (several on March 26, 1975 at 3150 to 3300 m.). Páramo de Tamá (a few on March 22, 1975 at 3150 to 3250 m.). *Phrygilus* was cited by Vuilleumier (1970) as a páramo species.

This species occurred commonly throughout the open páramo from 3100 to 4400 m., in habitats ranging from grassland to barren areas with low cushion plants and scattered tall *Espeletia* spp. but it did not occur in or at the edge of *Polylepis* woodland. Frequently flushed from the ground, the birds flew a short distance, and after landing ran rapidly between the plants. They foraged on the ground in the vicinity of *Espeletia* spp., or on the matted turf, as well as at the edge of small streams where they plucked food from the water, and occasionally near the top of *Espeletia* spp. where they fed on seeds. While feeding along streams, *Phrygilus* would hop from rock to rock while going upstream or downstream in a manner similar to that of *Cinclodes*. *Phrygilus* was less common than *Cinclodes* at 4000 m. and above. At least some birds may have been paired and one bird was singing on the morning of March 13 at Mucubají.

Five specimens were collected, and none showed evidence of breeding. One bird, sexed as a male by plumage, was collected at Aguila on March 30, 1975 at 3620 m. (AMNH 9509, skeleton) and had a completely ossified skull, weighed 21.5 g., had the esophagus full of seeds, at least one pupa, and grains of quartzite sand. Three birds were collected at Piedras Blancas. One bird (AMNH 4633, spirit), sexed as a male by its plumage, was collected on March 14, 1975 at 4300 m. and weighed 20.0 g., had an entirely ossified skull, moderately worn plumage, no fat, and the gut was full of minute seeds. Another male (AMNH 4634, spirit) was collected on March 18, 1975 at 4270 m. It had small testes, weighed 22.0 g., had a nearly fully ossified skull, generally worn plumage, no fat, and the gut was full of seeds of different sizes and colors. A bird, sexed as a female by plumage (AMNH 4635, spirit), was collected on March 18, 1975 at 4280 m. It weighed 22.0 g., had a partially ossified skull, was molting its remiges and rectrices, had no

fat, and the gut had seeds and small bits of pebbles. One male collected at Zumbador (AMNH 811989, skin) on March 25, 1975 at 3250 m., had very small testes, an unossified skull except for a small part at the base of the parietals, weighed 20.0 g., and had some molt of body coverts.

Zonotrichia capensis

Páramo de Santo Domingo (two on March 16, 1975 at 3100 and 3400 m.). Páramo del Aguila (one on March 30, 1975 at 3620 m.). Páramo de Mucubají (local from March 12-17, 1975 at

3500-3600 m.). Páramo de Quirorá (present on April 1, 1975 at 2800 m.). Páramo La Negra (present on March 26, 1975 at 3000 to 3100 m.). *Zonotrichia* was cited by Vuilleumier (1970) as part of the páramo avifauna.

This species, widely distributed in the Subtropical and Temperate Zones, occurred only locally in the páramo, usually near human habitations, around stone walls, and in small copses. At such places it foraged primarily on the ground, but once was seen feeding on the seeds of *Espeletia* sp. Some individuals were singing.

DISCUSSION

HABITAT USE BY BIRDS IN THE PÁRAMO

In this section we consider how birds utilize four major features of the páramo: *Espeletia* spp., shrubs other than *Espeletia*, water, and barren or open ground. These notes are based on a small number of observations taken at the end of the dry season and serve only to outline how birds of the páramo interact with the gross features of the environment.

Dorst (1955) and Koepcke (1954) described how birds utilize the various habitats of the Peruvian puna, and later Dorst (1957) outlined the way birds use stands of *Puya raimondii* (Bromeliaceae) in southern Peru, and Dorst and Roux (1972) briefly discussed the alpine zone of Ethiopian mountains in relation to the Peruvian puna. There are however, no similar studies for the páramo.

ESPELETIA spp: Our observations failed to reveal use of these plants for roosting, unlike Dorst's (1957) and Vuilleumier's (unpubl.) observations for *Puya raimondii* in the puna of Perú and Bolivia. Similarly, we did not observe birds feeding at flowers of *Espeletia* spp. although some plants were in bloom. Observations should be made during the main period of flowering, in October-December, to ascertain whether flowers are a major source of food.

In the East African afro-alpine zone, *Nectarinia johnstoni* does not seem to feed as much at flowers of *Senecio* spp., which are

physiognomically equivalent to *Espeletia* spp. in the high Andes, as they do at flowers of *Lobelia* spp. (Coe, 1961, 1967). In the high Andes of Perú and Bolivia, the only birds seen feeding at flowers of *Puya raimondii* were *Oreotrochilus estella*, a hummingbird; *Asthenes dorbignyi*, a spinetail; and *Phrygilus gayi*, an emberizid finch (Vuilleumier, unpubl.). Ruschi (1961) did not mention observing *Oxyopogon guerinii* feeding at flowers of *Espeletia*.

Both *Asthenes wyatti* and *Leptasthenura andicola* forage on *Espeletia*. *Asthenes* was seen foraging near the terminal bud and at the base of the rosette of living leaves. *Leptasthenura* occasionally foraged on the foliage, and once foraged among the seeds of the seed head where it seemed to search for arthropods. Large numbers of arthropods are harbored at the base of leaves of *Espeletia*.

We observed *Catamenia inornata*, *Spinus spinescens*, and *Phrygilus unicolor* feeding on seeds of *Espeletia*.

Espeletia spp. were used as nest sites, and parts of these plants were also used for nesting material. We found one nest of *Ochthoeca fumicolor* in an *Espeletia*, and found woolly material from *Espeletia* lining a nest of *Diglossa carbonaria*, and lining a domed nest of an unidentified Furnariidae (either *Schizoeaca coryi*, *Leptasthenura andicola*, or *Asthenes wyatti*). Ruschi (1961) collected five nests of *Oxyopogon guerinii* on the Venezuelan Andes. The one nest illustrated is said to be made of mate-

rial from *Espeletia schultzei*. We did not find concentrations of several nests on one plant of *Espeletia*, unlike what can be found on single plants of *Puya raimondii*.

In summary, *Espeletia* is used in at least four ways by birds: two species of insectivores forage on the plant, three species of granivores eat the seeds, several species (a hummingbird, a furnariid, a tyrannid, and a coerebid) use *Espeletia* for nest material, and the plant is used as a nest site by at least one species.

SHRUBS OTHER THAN ESPELETIA: Shrubs other than *Espeletia*, such as *Senecio* sp., *Hypericum* sp., *Hesperomeles* sp., etc. did not seem to be used extensively by páramo birds, except *Leptasthenura andicola* and *Schizoeaca coryi*, which foraged in them regularly. *Asthenes* might also forage in these shrubs. We also found one nest of an unidentified Furnariidae in a low shrub.

Elsewhere in the high Andes, shrubs of the genus *Chuquiraga* (Compositae) are used by hummingbirds of the genus *Oreotrochilus* in Ecuador (Corley Smith, 1969) and in Perú (Dorst, 1956; Carpenter, 1976) for feeding. The nectar of *Chuquiraga* spp. seems to be important in the diet of *Oreotrochilus* (Carpenter, 1976). We saw *Oxypogon guerinii* feeding at flowers of *Hesperomeles pernettyoides*, and it would be interesting to find out what the nutritive value of these plants is compared with *Chuquiraga*.

WATER: Páramo birds that characteristically forage in or near water appear to utilize these habitats (ponds, rushing streams) differently. Birds that foraged in or at the edge of ponds include *Anas flavirostris* and *Cinclodes fuscus*. These two species showed no spatial overlap since *Anas* foraged in ponds, whereas *Cinclodes* was restricted to the shore lines of ponds, that occurred at altitudes at or above 3500 m.

At least three species used rushing streams for foraging: *Cinclus leucocephalus*, *Cinclodes fuscus*, and *Phrygilus unicolor*. *Cinclus* inhabited wider streams, whereas narrower ones were used by *Cinclodes* and *Phrygilus*. Although *Cinclodes* and *Phrygilus* foraged along the same stretches of streams, we observed no interactions between them. *Cinclus* occurs far-

ther downstream than *Cinclodes* and *Phrygilus*, and no interactions were observed between any of these species.

BARREN OR OPEN GROUND: The only species regularly observed foraging in open or barren areas were *Cinclodes fuscus*, *Catamenia inornata*, *Phrygilus unicolor*, and to a lesser extent *Anthus bogotensis*. Both *Cinclodes fuscus* and *Phrygilus unicolor* occupied relatively barren areas, either wet or dry. *Cinclodes* occurred in the most open areas, where it appeared to probe in the soil and search the surface. *Catamenia* and *Phrygilus* foraged closer to vegetation, such as cushion plants, where they picked up food items from the surface. *Anthus*, on the other hand, usually occurred in wetter areas where it appeared to glean food items from the surface.

The Venezuelan páramos have relatively few species foraging on open ground compared with areas above timberline farther south in the Andes. For example, in the páramos of central Colombia *Muscisaxicola alpina* (Tyrannidae) is observed in addition to the three species discussed, and in Ecuadorian páramos, besides these four species, ground foragers would also include: *Nothoprocta curvirostris*, *Theristicus caudatus*, *Attagis gayi*, *Phalacrocorax carunculatus*, *Vanellus resplendens*, *Cinclodes excelsior*, and perhaps others. In the puna of Perú, occurrence of members of the genera *Colaptes*, *Geositta*, *Upucerthia*, *Diuca*, and *Sicalis* further increases the diversity of ground-foraging birds.

GEOGRAPHICAL PATCHINESS IN PÁRAMO BIRDS IN VENEZUELA

We consider that a species of bird has a "patchy distribution" (P) if it occurs in 50 percent or less of the seven Venezuelan páramo blocks in table 5. On the other hand, we consider that a bird species is "generally distributed" (G) if it occurs on more than 50 percent of the Venezuelan páramos of table 5.

An example of a patchily distributed species of the Venezuelan páramos is *Cinclodes fuscus*. It occurs only on páramos in the states of Lara, Trujillo, and Mérida (blocks A, B, and C), but it has not been collected or reported from any

TABLE 5
Distribution of Bird Species in the "Páramo Blocks" of Venezuela^a

Species	Páramo Blocks						
	A Cendé	B Niquitao	C Mérida	D La Negra	E Batallón	F Zumbador	G Tamá
<i>Anas flavirostris</i> (G)	—	+	+	—	+	—	+
<i>Buteo fuscescens</i> (P)	—	—	+	—	—	—	—
<i>Falco sparverius</i> (P)	+	—	+	—	—	—	+
<i>Capella nobilis</i> (T)	—	—	—	—	—	—	+
<i>Chubbia jamesoni</i> (G)	+	+	+	—	+	—	+
<i>Caprimulgus longirostris</i> (P)	—	—	+	—	—	+	+
<i>Chalcostigma heteropogon</i> (T)	—	—	—	—	—	—	+
<i>Oxygogon guerinii</i> (P)	—	+	+	—	—	—	—
<i>Cinclodes fuscus</i> (P)	+	+	+	—	—	—	—
<i>Leptasthenura andicola</i> (P)	—	+	+	—	—	—	—
<i>Schizoeaca coryi</i> (G)	+	+	+	+	+	+	—
<i>Schizoeaca fuliginosa</i> (T)	—	—	—	—	—	—	+
<i>Asthenes wyatti</i> (P)	—	+	+	—	—	—	—
<i>Ochthoeca fumicolor</i> (G)	+	—	+	+	+	+	+
<i>Notiochelidon murina</i> (P)	—	+	+	—	—	—	+
<i>Cinclus leucocephalus</i> (P)	+	—	+	—	+	—	—
<i>Cistothorus platensis tamae</i> (T)	—	—	—	—	—	—	+
<i>Cistothorus meridae</i> (P?)	—	+	+	+	?	—	—
<i>Turdus fuscater</i> (G)	+	?	+	+	+	+	+
<i>Anthus bogotensis</i> (G)	+	+	+	+	+	+	+
<i>Sturnella magna</i> (G)	+	—	+	+	+	—	+
<i>Catamenia inornata</i> (P)	—	—	+	—	—	—	+
<i>Spinus spinescens</i> (P)	+	—	+	—	+	—	—
<i>Phrygilus unicolor</i> (G)	+	+	+	+	+	+	+
<i>Zonotrichia capensis</i> (G)	+	?	+	?	+	+	+
Total number of species per block	12	11-13	21	7-8	11-12	7	16

^aData from Phelps and Phelps, 1958, 1963; and from personal observation by the authors in 1968, 1970, and 1975. See figure 3 for geographical location of blocks.

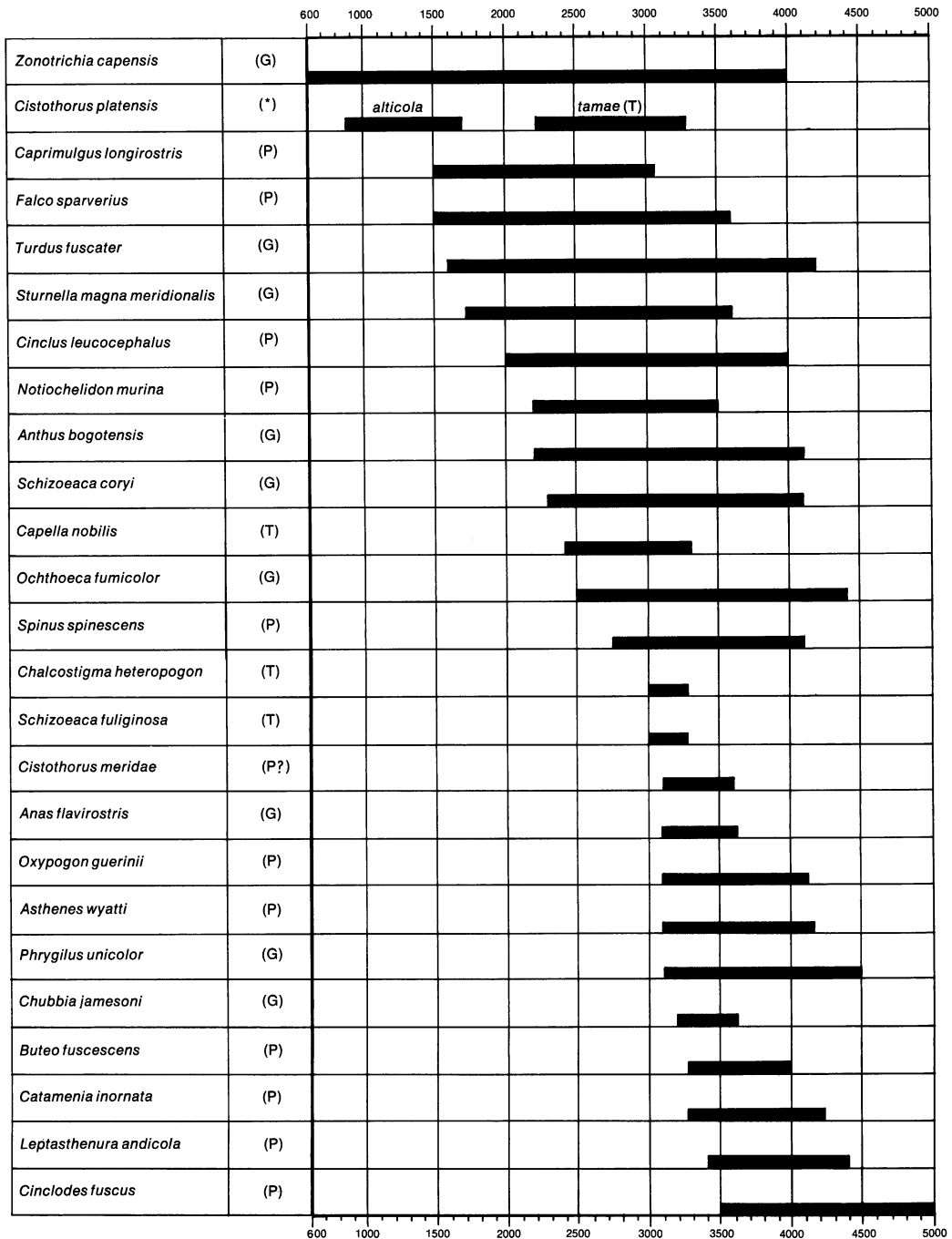
Note: G = generally distributed; P = patchily distributed; T = Tamá only.

páramo in the State of Táchira (blocks D-G). *Cinclodes fuscus* occurs in páramos of the Colombian Andes, however, and from there southward to Tierra del Fuego. An example of a generally distributed species is *Phrygilus unicolor*, which occurs on all the páramo blocks of the Venezuelan Andes.

The above definitions do not take into account the three species and one subspecies that occur in páramo vegetation of the Venezuelan Andes only at Páramo de Tamá (T): *Capella nobilis*, *Chalcostigma heteropogon*, *Schizoeaca fuliginosa*, and the subspecies *Cistothorus platensis tamae*. These have distribution patterns to which our definitions of "patchy distribution" and "general distribution" do not apply: these species are dealt with separately.

We used data from our observations as they are summarized in the annotated list of species and in the census results, and from Phelps and Phelps (1958, 1963), to analyze patchiness in the distribution of páramo birds in Venezuela. Table 5 gives the presence/absence of the 25 páramo species in "blocks" of páramo in Venezuela, and figure 10 indicates the altitudinal range of these species in Venezuela, arranged according to lowest altitudinal limit, from lowest to highest. On the basis of these data we examine factors that might affect relative patchiness. At the outset we must point out that our discussion concerning the distribution of páramo species applies only to Venezuelan birds, since we have not included data from Colombian or Ecuadorian páramos in this

ALTITUDE IN METERS



paper. A comprehensive analysis of patchiness in páramo birds has been prepared by Vuilleumier and Simberloff (MS).

FACTORS AFFECTING THE DISTRIBUTION OF BIRD SPECIES ON PÁRAMOS

At least six factors could affect the distribution of birds on the Venezuelan páramos. Thus a species may have a patchy distribution because of:

- (1) Incomplete sampling by ornithologists.
- (2) Differences in dispersal ability of different species.
- (3) Lack of suitable ecological conditions.
- (4) Exclusion by interspecific competition.
- (5) Human modification of habitat.
- (6) Pleistocene fluctuations of climate and vegetation which altered the size and proximity of presently isolated páramo blocks.

These six factors are not independent of each other, and the absence of a given species from one or more páramos in the Venezuelan Andes could be due to a combination of these factors. We nevertheless discuss them separately for ease in presentation.

(1) **INCOMPLETE SAMPLING:** The data on the geographical (table 5) and altitudinal (fig. 10) distribution of páramo species in Venezuela are largely a result of the collecting efforts of Phelps and Phelps (1958, 1963). Other collectors have visited páramos in Venezuela, and their specimens provide additional information concerning the distribution of páramo birds. Our data contribute additional information on the distribution of some species. Yet much remains to be learned through more systematic exploration of all Venezuelan páramos. Extended trips must be made throughout the year with the goal of obtaining a representative collection of all species at a given locality.

Some páramos, especially those in the Mérida Andes, are relatively well known ornithologically because of their accessibility. Other, more isolated páramos, such as Zumbador and Batallón, are probably less well studied. Hence, the distribution of several species may appear to be patchy because of incomplete sampling. This may be especially true of species having low population densities, and of

species living in relatively specialized habitats. For instance, we failed to observe *Catamenia homochroa*, a species known from only a few specimens in the Venezuelan Andes. This species may well be more widely distributed than is known, but it may escape detection during short visits because it is relatively rare. Since it is difficult to evaluate the effect of incomplete sampling it is possible that we consider some species to have a patchy distribution which are in fact generally distributed. Only further work will fill in apparent gaps in distribution due to insufficient collecting.

(2) **DISPERSAL ABILITY:** Some species may disperse more readily than others. A species capable of dispersing readily might therefore be present on more páramos, and be more generally distributed. Hence, a knowledge of the relative dispersal abilities of the páramo species in Venezuela could help us understand one facet of patchiness in the distribution of páramo birds.

Mayr (1965) postulated that birds which are good colonists usually have one or more of the following qualities: (1) they travel in small flocks; (2) are granivorous; (3) are associated ecologically with fresh water habitats; (4) are able to fly for long distances over inhospitable habitats; (5) are able to discover unoccupied habitat; and (6) are able to shift their habitat preferences. We tried to apply these criteria to the 25 species of birds considered by us to belong to the páramo avifauna in Venezuela. However, we cannot judge criteria 4, 5, and 6 without much guesswork. Therefore, we cannot objectively assess the colonizing ability of the páramo species, or how differences in dispersal ability have affected the distribution patterns of species found on Venezuelan páramos.

(3) **LACK OF SUITABLE ECOLOGICAL CONDITIONS:** The absence of suitable habitat for a given species on a given páramo may preclude this species from occurring there, even if it reaches that páramo. We believe that at least four and probably five species have distributions that may be limited by the availability of suitable habitat.

These species, and the habitat that apparently limits their distribution to only a few of the Venezuelan páramos, are the following: *Buteo fuscescens* (cliffs for nesting?), *Oxy-*

pogon guerinii (the interface between open páramo vegetation and woodland or shrubbery above timberline, especially *Polylepis*?), *Cinclus leucocephalus* (fast-flowing streams within páramo vegetation), and *Cistothorus meridae* (sedge bogs and wet areas with low, dense, shrubby growth?). To these four species may be added *Cinclodes fuscus*, whose patchy distribution may be due to a preference for open areas with sparse vegetation, a habitat apparently absent from several Venezuelan páramos. We believe that the specialized habitat preferences of these five species limits their geographical distribution in Venezuelan páramos.

(4) PATCHINESS DUE TO EXCLUSION BY COMPETITION: The concept of interspecific competition, recently formalized by MacArthur (e.g., 1972), is thought to be an extremely important factor in the distribution of bird species on islands (see Diamond, 1975; Lack, 1976), and in continental areas (see Terborgh, 1971; Cody, 1974). Competitive relationships between species may be a factor that contributes to four patterns of distribution that are observed among páramo birds of Venezuela. They can be classified under three categories: (a) allopatric distribution (one case), (b) altitudinal separation on the same páramo (one case), (c) broad altitudinal overlap with partial geographical overlap (two cases).

(a) ALLOPATRIC DISTRIBUTION: *Schizoeaca coryi* is generally distributed in Venezuelan páramos, except at Tamá, whereas *S. fuliginosa* occurs in Venezuela only at Tamá. However, the distribution of *fuliginosa* is not patchy in Colombia. The two species are differentiated morphologically, and are allopatric, being separated from each other by a low elevation barrier, the Táchira depression (see fig. 3).

In view of the nonpatchy distribution of both forms in their ranges, it is possible that the Táchira depression has prevented dispersal, or that competition between the two species prevented them from becoming sympatric. We believe that the barrier that presently separates the two species has been an obstacle to their dispersal, because of its width and its low elevation, and that proto-*coryi* diverged from proto-*fuliginosa* after they became isolated respectively northeast and southwest of the Táchira depression.

(b) ALTITUDINAL SEPARATION ON THE SAME PÁRAMO: Schwartz (in lett.) pointed out that the distribution of *Cistothorus meridae* and *C. platensis* is consistent with the hypothesis that competition limits the distribution of these two congeners. *C. meridae* is restricted to altitudes above 3000 m. in the Mérida Andes, whereas *C. platensis alticola* reaches up to only 1700 m. but at Tamá, where *C. meridae* is absent, *C. platensis tamae* ranges from 2200 to 3275 m. (see fig. 10). This suggests that the presence of *C. meridae* at high altitudes in Mérida may preclude *C. platensis alticola* from becoming established higher up there, since *C. platensis tamae*, in the absence of *C. meridae* at Tamá, occupies higher altitudes.

(c) BROAD ALTITUDINAL OVERLAP WITH PARTIAL GEOGRAPHICAL OVERLAP: (a) The distribution of *Asthenes wyatti* is patchy in the Andes of Venezuela, since it occurs only in blocks B and C. It also occurs at Perijá: Phelps (1977) recently described a new subspecies, *perijanus*, from that range. The most closely related competitor of *Asthenes wyatti* may be *Schizoeaca coryi*, which has a nonpatchy geographical distribution. The altitudinal range of *A. wyatti* is encompassed by that of *Schizoeaca coryi*, but the latter occurs down to 2300 m. (see fig. 10). It is possible that the patchy geographical distribution of *Asthenes wyatti* in Venezuelan páramos is due to competition with *Schizoeaca coryi*.

In Venezuela, *Asthenes wyatti* occurs in colonies where low páramo vegetation is interspersed with grassy areas, whereas *S. coryi* is widely distributed in shrubby areas. The absence of favorable habitat at a particular páramo for one of these two species may account for its absence. At Páramo La Negra, the lack of grassy areas interspersed with shrubby areas may prevent *Asthenes* from becoming established. Thus, the distribution of these two species may simply reflect their nonoverlapping ecological requirements irrespective of any competitive relationships between them.

Although the distribution of *Asthenes* and *Schizoeaca* may be consistent with the view that competition limits their occupation of available habitats, there are no data that can be used to determine whether competition between the species or habitat patchiness determines

their distribution. (See also, below, Historical Factors Associated with Pleistocene History.)

(b) The second case of broad altitudinal overlap with partial geographical overlap involves the finches *Catamenia inornata* and *Phrygilus unicolor*. *Catamenia* occurs on two páramo blocks (C and G), whereas *Phrygilus* occurs on all, and the altitudinal range of *Catamenia* is included within that of *Phrygilus* (fig. 10). *Catamenia* is also less common than *Phrygilus*. Both species forage on the ground in the same habitat. These observations suggest the possibility that the larger *Phrygilus* excludes *Catamenia* from certain páramos as a result of competition for similar resources, but what these resources are remains to be studied. Detailed work will be necessary to determine whether competition affects the distribution of *Catamenia* as suggested here, or whether the distribution of its preferred habitat is patchy.

In summary, interspecific competition might affect distribution patterns in these four cases, although other factors may be at least as important as competition in determining the distribution of these species.

(5) HUMAN MODIFICATION OF HABITAT: Two species, *Falco sparverius* and *Notiochelidon murina* occur in open areas at the lower edge of some páramos (A, C, G; and B, C, G, respectively), and have a patchy distribution. The distribution of these species suggests that páramo vegetation is marginally suitable habitat for them. Perhaps some populations of these species colonized páramo from nonforested habitats in the Subtropical and Temperate Zones at localities where the original forest habitat has been cleared by man. In some of these areas (A, B, C), the transition from montane forest to páramo has been replaced by open, scrubby vegetation, or by pastures alternating with wooded copses. However, at Tamá (G) where both *Falco sparverius* and *Notiochelidon murina* occur, there is an abrupt transition from montane forest to páramo. Thus, it may be that suitable habitats were always available for these species on some páramos such as Tamá but the presence of *Falco sparverius* and *Notiochelidon murina* on other páramos may be a result of the creation of new habitat by recent activities of man.

(6) PLEISTOCENE HISTORY: The work of Schubert and his colleagues (Schubert 1972, 1974, 1975; Schubert and Valastro, 1974; Salgado-Labouriau and Schubert, 1976) is providing biogeographers with geological and palynological data that will eventually be very useful in reconstructing the vegetational history associated with fluctuations in climate during the Plio-Pleistocene. It seems premature to us, and to Schubert (in lett.) to attempt to reconstruct a detailed history of the distribution of páramo birds in Venezuela based on these data. Nevertheless, it is obvious that changes in climate during the Pleistocene have resulted in altitudinal shifts of the zones of vegetation in the Venezuelan Andes.

These altitudinal shifts have been correlated with altitudinal movements of mountain glaciers, so that the presence of moraines and other geological traces of glaciation (roches moutonnées, etc.) at altitudes far below the present glacial line suggests that páramo vegetation once occurred at lower altitudes.

Biogeographically, the altitudinal movements of the glaciers have alternately increased and reduced the relative isolation of presently isolated páramo "islands." Vuilleumier (1969), and Haffer (1970, 1974) postulated that these movements have resulted in alternating periods of "passive dispersal" (glacials) and "passive isolation" (interglacials) of páramo birds. Several blocks of Venezuelan páramos, which are presently only barely isolated, were probably connected to each other during glacial advances by continuous páramo vegetation. Figure 3 shows the relative isolation of the páramo blocks.

The current proximity of some páramos in the Táchira Andes (the La Negra-Batallón-Zumbador complex, blocks D, E, and F) suggests that these páramos formed one continuous unit during glacial phases of the Pleistocene. Furthermore, this block must have been either continuous with, or at least more closely connected to, the main block of páramos in the Andes of Mérida (blocks B and C) through a series of páramos, including Quirorá (see fig. 3). And, blocks B and C (Niquitao and Mérida) were probably nearly continuous with block A (Cendé and neighboring páramos). But it is

doubtful whether Tamá and neighboring páramos (Cristo, Judío), forming block G, were connected to the La Negra-Batallón-Zumbador complex (blocks D, E, F), because of the low elevation of the Táchira depression, which constitutes a major physiographic and ecological barrier today, and surely acted as a barrier even during glacials. Even if timberline was lowered by about 1000 m., from about 3000 down to about 2000 m., the Táchira depression would have presented a *ca.* 20 km. broad expanse of non-páramo vegetation. However, the Tamá block was certainly connected with páramos in the Colombian Andes further south, perhaps all the way to the huge block near the Cocuy Range, for the barrier there is quite narrow.

In terms of patchiness in geographical distribution, it is possible that bird species found on the páramo that also occur below 3000 m. (lowest limit of either natural timberline as at Tamá, or man-induced timberline, as in the Mérida Andes) might have had continuous distributions from block A to block E during a glacial period. Even today the páramos do not constitute an insular environment for these species. Ecologically, these species (cat. 3, 4, 6 of table 1) seem to occur in more habitats than those restricted to altitudes above 3000 m. Thus some patchiness is expected, but not to the degree seen in the species found above 3000 m. today.

For the latter species (categories 1, 2, 5 of table 1), a depression of timberline down to 2000 m. would have meant less isolation, and hence less geographical patchiness, than today. But another increase in the altitude of timberline to about 3000 m. would have re-established a pattern of patchiness.

Furthermore, since the largest areas of páramo in Venezuela lie in blocks B and C, which also have the greatest altitudinal range and the greatest diversity of habitats, we expect that some species with a patchy distribution whose lower altitudinal limit is today 3000 m., would be restricted to these blocks. This is so because they became extinct elsewhere after an interglacial increase of the timberline, simply because these other blocks are not ecologically varied enough.

From data in table 5 and in figure 10, we

can establish whether there are correlations between geographical patchiness and occurrence at various altitudes.

First, of the three species restricted (as species or allospecies) to the Tamá block, none occurs below 2000 m., one has its lower altitudinal limit at 2400 m. (*Capella nobilis*, but this datum is difficult to interpret: we do not know whether the species breeds so low), and two occur only above about 3000 m. (*Chalcostigma heteropogon* and *Schizoeaca fuliginosa*). All three occur south in Colombia. And *Cistothorus platensis tamae* does not occur below 2200 m. Thus all these taxa are restricted to relatively high altitudes. The Táchira depression presumably acted as a barrier during glacial periods, even if these species occurred as low as 1200 m. It is also possible that *Schizoeaca* and *Cistothorus* have their distributions limited by competition.

Secondly, of the six species that occur below 2000 m. today, two (or 33.3%) have geographically patchy distributions. One is *Falco sparverius*, whose distribution may be patchy because of human activities on and below the páramo.

Of the six species (Tamá species excluded) which have their lower distributional limit between 2000 and 3000 m., three (or 50%) have patchy distributions. One of the three (*Cinclus leucocephalus*) may have a patchy distribution because its habitat is local in distribution. Another species (*Notiochelidon murina*) may have a patchy distribution because of past human disturbance (see above).

Thirdly, of 10 species (excluding Tamá species) occurring only above 3000 m., six or perhaps seven (or 66.6-70%) have patchy distributions. Of the six species that occur only above 3000 m. and have a patchy distribution, four (or 66.6%) occur in the Mérida Andes. One (*Buteo fuscescens*) occurs only in block C; and three (*Oxygogon guerinii*, *Leptasthenura andicola*, and *Asthenes wyatti*) occur only in blocks B and C. We suggested earlier that *Buteo* and *Oxygogon* are locally distributed because of habitat patchiness, and that *Asthenes wyatti* might have a patchy distribution because of competition with *Schizoeaca*.

Thus, there is a positive correlation between

altitudinal distribution and geographical patchiness so that species found at lower altitudes are more generally distributed than species restricted to higher altitudes. Some of this geographical patchiness may be due to factors other than the history of the Venezuelan Andes. These factors include the distribution of suitable habitat and competition between species. In some cases, at least, more than one factor may contribute to a given instance of patchiness, but we cannot determine the relative importance of these factors.

ORIGINS OF PÁRAMO BIRDS IN VENEZUELA

We assume, on the basis of geological and palynological work by Schubert (1972, 1974, 1975; Schubert and Valastro, 1974; Salgado-Labouriau and Schubert, 1976) that the Venezuelan páramos are a geologically young vegetation formation, probably dating back to the Pleistocene, or the Plio-Pleistocene. Thus, the páramo vegetation must have been colonized by birds in a geologically recent past. Where, then, did the birds come from that colonized the páramo?

We assume that colonizing birds came from three areas: North America, including Central America; adjacent areas of northern South America, including vegetation zones immediately below páramo; and southern South America, including the southern Andes and Patagonia.

Although the avifauna of Venezuelan páramos was not treated by Chapman, his views on the origin of páramo birds in Colombia (1917) and Ecuador (1926) clearly show that he believed that most species of páramo birds were either derived from species found in southern South America or moved up the Andean chain to northern South America from the southern Andes of Patagonia. In table 6 we indicate the possible origins of the 25 species that we consider the páramo avifauna in Venezuela.

We emphasize the uncertainty of determining the area(s) each species of páramo bird came from. Hence the geographical origin of each species from the three possible source areas is indicated in the table by one or more

question marks because we are not certain of the origin of that species.

We determined the possible area of origin by examining the present distribution of each species, together with the distribution of congeners, or, if the genus is monotypic, together with the distribution of genera thought to be closely related to it. This procedure is similar to that usually followed by zoogeographers concerned with the origins of species in a given fauna.

The uncertainties of such a procedure are obvious in table 6. For seventeen species, two (eight spp.) or even three (nine spp.) origins are possible. We cannot decide which origin is the most likely. We have nevertheless included table 6 in order to show that speculations on

TABLE 6
Possible Geographical Origins of Bird Species
Found in Páramos of Venezuela

Species	North America	South America	
		Northern (local)	Southern
<i>Anas flavirostris</i>	?	—	?
<i>Buteo fuscescens</i>	?	?	?
<i>Falco sparverius</i>	?	?	?
<i>Capella nobilis</i>	?	?	?
<i>Chubbia jamesoni</i>	—	—	?
<i>Caprimulgus longirostris</i>	?	?	?
<i>Chalcostigma heteropogon</i>	—	?	?
<i>Oxyopogon guerinii</i>	—	?	?
<i>Cinclodes fuscus</i>	—	—	?
<i>Leptasthenura andicola</i>	—	—	?
<i>Schizoeaca fuliginosa</i>	—	—	?
<i>Schizoeaca coryi</i>	—	—	?
<i>Asthenes wyatti</i>	—	—	?
<i>Ochthoeca fumicolor</i>	—	?	?
<i>Notiochelidon murina</i>	—	?	?
<i>Cinclus leucocephalus</i>	?	?	?
<i>Cistothorus platensis</i>	?	?	?
<i>Cistothorus meridae</i>	—	?	—
<i>Turdus fuscater</i>	?	?	?
<i>Anthus bogotensis</i>	?	—	?
<i>Sturnella magna</i>	?	?	—
<i>Catamenia inornata</i>	—	?	?
<i>Spinus spinescens</i>	?	?	?
<i>Phrygilus unicolor</i>	—	—	?
<i>Zonotrichia capensis</i>	?	?	?

the origins of species in a fauna, even in a vegetation type as recent as the páramos, is risky. There are, however, eight species that probably originated from one area (one ? in table 6).

The problem of determining the origin of a species stems largely from the fate of species after they have colonized the páramo. They could diverge there phyletically and eventually

become endemic taxa, perhaps endemic subspecies, the distribution of which is correlated with the isolation of blocks of páramo during the Pleistocene. Speciation (splitting) could take place, and be followed by secondary or "double" invasions.

Thus, determining the origins of páramo birds is difficult.

APPENDIX
THE SEVEN CENSUS SITES IN VENEZUELAN PÁRAMOS

Census Number	1	2	3	4	5	6	7
Locality and site	Santo Domingo-1	Santo Domingo-2	Mucubají-1	Mucubají-2	Aguila	Piedras Blancas	Tamá
Date	March 17, 1975	March 17, 1975	March 15, 1975	March 16, 1975	March 30, 1975	March 14, 1975	March 22, 1975
Altitude	3100 m.	3250 m.	3560 m.	3600 m.	3630 m.	4430 m.	3000-3200 m.
Time	08.20-10.45	08.00-09.40	08.50-10.45	08.30-10.10	11.10-12.55	09.00-10.30	08.15-09.45
Weather							
% cloud cover	75-80	20-50	50	70	20	60-70	100
wind direction							
and force	SE, weak	—	—	—	N, light to moderate	NW, light but variable	E, moderate
rain	none	none	none	none	none	none	none
fog	none	none	none	none	none	none	light
air temp.	4°-5° C	4°-7° C	6° C	3°-8° C	7°-8° C	4°-5° C	[not taken]
Topography							
slope	about 20°	5-10°	15°	20°	10°-15°	5°	35°-40°
exposure	N- SE	E	SE	SE	N	W	SW
Landscape features	varied: cirque with marshy bottom, barred by ridge	top of morainic ridge sloping to stream bank	grassy meadow down to outlet of Laguna Grande, and up a morainic ridge	morainic ridge	stream bed and slopes along ridge	gently sloping ground	steep slope up to a plateau

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