ELEVATIONAL CORRELATES OF SPECIATION AND INTRASPECIFIC GEOGRAPHIC VARIATION IN PLUMAGE IN ANDEAN FOREST BIRDS

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ABSTRACT.—Intraspecific variation in plumage was used to test the null hypotheses that geographic variation in 280 species of elevationally restricted Andean forest birds is independent of elevation and is not a function of patchy geographic distribution. Both null hypotheses were rejected.

At most taxonomic levels, geographic variation in plumage was correlated positively with both the mean of its elevational distribution and the size of its geographic range. Vertical amplitude of elevational distribution was not a significant predictor of geographic variation in plumage in most taxa. Independent of these elevational correlates, patchily distributed species showed significantly more geographic variation than continuously distributed species.

These results show that geographic variation and presumably ongoing speciation phenomena are greater at higher elevations. The decreased species richness at high elevations may be attributable to a higher rate of extinction from catastrophic disturbance as well as to ecological factors that limit sympatry in newly formed species. *Received 6 August 1984, accepted 26 December 1984.*

IN this paper I examine the relationship between elevational distribution and possible speciation phenomena in Andean forest birds. Two initial observations are pertinent. First, on an elevational gradient in Peru, Terborgh (1977) found a negative correlation between elevation and bird species richness, canopy structure, and number of plant strata. Second, geographic barriers to dispersal and gene flow increase with elevation. Catastrophic vicariant events (e.g. glaciation, landslides, vulcanism, forest fragmentation by climatic events) are more prevalent in the physiographically complex Andean highlands than in the adjacent foothills and Amazonian lowlands.

I propose a simple model of speciation (see Mayr 1963, Pielou 1979) that incorporates these observations, predicts a pattern of geographic variation correlated with elevation, and accounts for the decrease in species richness with elevation. Two factors control the number of potential species along the elevational gradient. First, parent species are fragmented by vicariant events into a number of mutually isolated demes. The more fine-grained the fragmentation pattern, the greater the number of potential new species. Second, there are adaptive peaks; the more numerous these peaks, the greater the number of potential new species.

Predictions—(1) The frequency of fragmented populations and incipient speciation increases with elevation. (2) Intraspecific geographic variation increases with elevation. (3) Extinction rates of isolated populations are greater at higher elevations. (4) The range of species morphologies and the diversity of foraging behavior within ecological assemblages decreases with increasing elevation in correspondence with the decrease in resources and habitat complexity.

I investigated the first two predictions by examining geographic variation in plumage characters in Andean birds. I began with two basic assumptions: bird speciation is largely allopatric, and plumage differentiation is related to speciation. I tested the null hypothesis that geographic variation is independent of elevation and a subsidiary hypothesis that geographic variation is not a function of patchy geographic distribution.

STUDY AREA AND METHODS

Study area.—Humid Andean forest extends nearly uninterrupted from Venezuela southward along the eastern slope of the Andes to central Bolivia. My study area included the portion of the eastern slope of these mountains from the Río Marañón in northern Peru

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south to the Bolivian border (Fig. 1). This region was chosen because of the relative homogeneity and even distribution of humid Andean forests (ONERN 1976); the linear distribution of Andean forest bordered by *páramo* and *puna* on the west and lowland rain forest on the east, which facilitated mapping geographic ranges and locating contact zones and gaps in the distribution of montane bird species; and the availability of specimens from a series of mostly unpublished post-1965 expeditions [Louisiana State University Museum of Zoology (LSUMZ), Princeton University (specimens deposited in the American Museum of Natural History, AMNH), and the Field Museum of Natural History (FMNH)] to the eastern slope of the Peruvian Andes. Although the study area spans ca. 10° latitude, there is little regional difference in forest physiognomy correlated with latitude. Except for outlying spurs of the Eastern Cordillera, the undulating ribbon of humid Andean forest is backed by high-elevation *páramo* or *puna*. The entire elevational slope measured from the Amazonian lowlands (<500 m elevation) to timberline is rarely more than 30–50 km. The area and quality of present-day montane forest at any contour interval is unknown because of heavy cloud cover and inaccessibility. Large-scale maps indicate that the area between the 500-m and 1,500-m contour lines is perhaps twice as large as the area in the 1,500-m to 4,000-m contour interval. Humid Andean forest above 1,500 m elevation often is restricted to narrow corridors or is patchy at the heads of several deeply convoluted, dry intermontane valleys (e.g. upper Río Huallaga, upper Río Apurímac, Río Huari Huari). Humid forest of the Andean foothills (600–1,200 m elevation) is continuously distributed. Precipitation data from Andean forest in Peru are incomplete, but annual precipitation ranges from 2 to 16 m (ONERN 1976, Simpson and Haffer 1978). A distinct wet season occurs from November to May, but rainless periods of more than a few days are rare year-round. Four distinct vegetation zones (lowland rain forest, montane rain forest, cloud forest, and elfin forest), usually are present along the continuous physical gradient from the Amazonian lowlands to timberline (see Terborgh 1971). The term "Andean forest" (ca. 600–3,500 m elevation) refers collectively to montane rain forest, cloud forest, and elfin forest (*sensu* Terborgh 1971). Excellent descriptions of the humid forest of the Peruvian Andes can be found elsewhere (Tosi 1960; Terborgh 1971, 1977; Terborgh and Dudley 1973; Terborgh and Weske 1975; ONERN 1976).

Species list.—Of the 1,678 species recorded from Peru (Parker et al. 1982), about 320 exclusively inhabit Andean forest on the Amazonian side of the continental divide. The habitat fidelity of this heterogeneous assemblage (30 families) is supported by literally thousands of observations spanning 70 yr (e.g. Chapman 1917, 1926; Weske 1972). Although fossil evidence is not yet available, the large number of endemic species
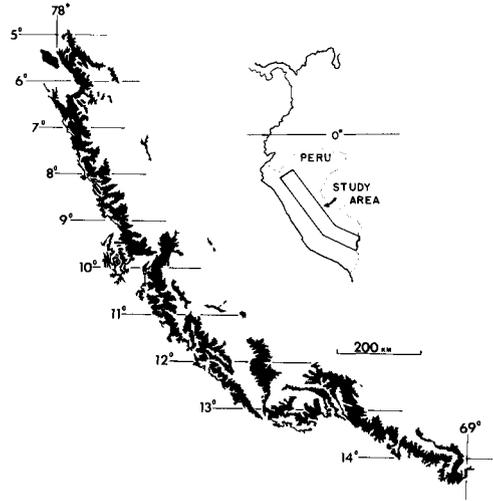
Fig. 1. Distribution of middle- to high-elevation humid Andean forest (ca. 1,200–3,400 m) along the eastern slope of the Peruvian Andes (adapted from ONERN 1976). Note the deeply dissected contours associated with river canyons and timberline. Forest on the lower slopes (600–1,200 m) is continuous and more evenly distributed.

and genera suggests a long occupancy in the region and an autochthonous origin of the Andean forest avifauna. Species residing in other habitats have different evolutionary histories (Haffer 1969, 1974). For this reason, species not restricted to humid Andean forest are excluded here. Examples of excluded habitats and species are: (1) *puna-páramo* grassland (e.g. *Asthenes flammulata, Phrygilus unicolor*); (2) *Polylepis* woodlands above timberline (e.g. *Oreomanes fraseri, Xenodacnis parina*); (3) intermontane deciduous forest (e.g. *Pachyramphus albogriseus, Tangara viridicollis*); (4) montane streams (e.g. *Cinclus leucocephalus*); (5) agricultural areas and scrub (e.g. *Troglodytes aedon*); and (6) lowland forest (primarily <500 m elevation; e.g. *Piaya cayana*).

I also excluded several species recorded from only one transect block (see Geographic range), represented by insufficient specimen material (e.g. *Accipiter collaris, Gallinago imperialis, Aegolius harrisii*), or taxonomically problematic (*Scytalopus, Elaenia*). The remaining 280 species and superspecies occurring in the study area and included in the analyses are listed in the Appendix. The composition of families follows Morony et al. (1975).

Geographic range.—To facilitate the measurement of geographic range, the study area was partitioned into 15 blocks (Fig. 2). This was an attempt to reduce the effects of coarse sampling (Pielou 1979) without sacrificing accuracy by excessive subdivision of the study area. Each block was delineated to include at least one major collecting locale (>250 specimens), and
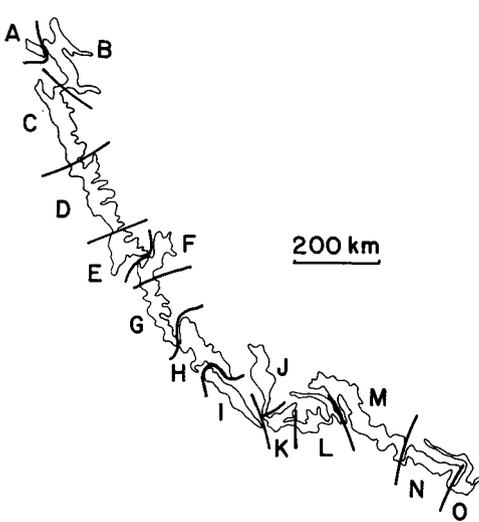
Fig. 2. Division of the study area into 15 transect blocks.

Fig. 3. Histogram of geographic range values for all species ($n = 280$). Species occurring in only one block were omitted.

representative collecting stations above 2,500 m and below 2,000 m elevation. The principal collecting stations in each transect block are listed in Graves (1983). A full complement of gradient habitats from lowland forest to timberline was present in each transect block. There was no significant correlation between the area of montane forest in a block and either the number of recorded species or specimens collected within a block. The boundaries between blocks were established, whenever possible, at discontinuities or narrow corridors in montane forest distribution. Certain transect blocks (e.g. Cordillera Colán, Block A) enclose isolated populations of high-elevation species.

Geographic range was based primarily on specimen label data in the LSUMZ, AMNH, and FMNH, and on published records (e.g. Zimmer 1931–1955). A species was considered to occur in a transect block if it was represented by a specimen or, in some cases, by sight records of easily recognized species (e.g. *Oroaetus isidori*). Terminal range boundaries were confirmed by published records or specimens. Species were considered to be patchily distributed and absent from a transect block only if they were not recorded by intensive post-1970 fieldwork in suitable habitat for the species (e.g. *Atlapetes rufinucha* in Block E). Otherwise, ranges were extrapolated to include intermediate transect blocks. If one judges by the discovery of many secretive, local, and sibling species (e.g. O'Neill and Graves 1977, Weske and Terborgh 1981), systematic collecting has been distributed uniformly along the eastern slope of the Peruvian Andes.

The calculated geographic ranges have possible values from 1 to 15; however, the distribution is highly skewed toward maximum coverage of the study area (Fig. 3). This results from estimating range from a segment of the Andes that restricts the upper value to 15 (equivalent to 15 or more) transect blocks. Geographic range values indicate only the number of blocks in the study area in which a species is believed to occur. Range 15 values imply that a species is found throughout the study area; values less than 15 can have continuous or discontinuous distributions. The true distribution of range of Andean montane-forest species probably would be more normally distributed, with fewer extremely small or large ranges. Species with very small continuous ranges are unlikely to exhibit marked geographic variation. Other factors being equal, geographic range is correlated with the potential for geographic character variation. However, species with small but geographically distinct populations often are highly variable or polytypic. Therefore, the presence and location of all putative distribution gaps were noted.
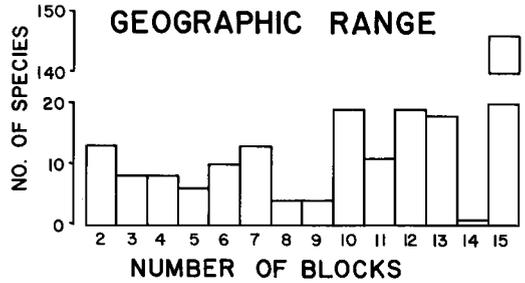
Elevational distributions.—The most complete distributional survey of bird species along an elevational transect in the Andes was conducted in the Cordillera Vilcabamba, Department of Cuzco, Peru (Terborgh and Weske 1969, 1975; Terborgh 1971, 1977; Weske 1972). Despite its thoroughness, the recorded distributional limits, relative species abundance, and degree of overlap or segregation of congeners along a transect incorporate several possible sources of error that must be recognized in comparative analyses. These are summarized briefly and apply to all Andean transects. First, irregularities in local topography (e.g. landslides, canyons, rock faces) often prevent adequate determination of elevational limits along portions of the transect. Experienced "trail cutters" follow the path of least resistance and purposefully avoid impenetrable habitat formations. In many cases, mist nets unavoidably are placed on trails, and observations are restricted to within a few meters of them. Species that occur in dense or patchily distributed habitats are missed for this reason. Field camps and mist-netting efforts usually are spaced at intervals along the elevational transect [e.g. 9 camps along the 40-km Vilcabamba trail (ca. 3,000-m elevational

range), Terborgh 1977]. Resolution of elevational limits between field camps is difficult, stemming in part from the burden of maintaining and checking mist nets up to several hundred meters above or below camp. Inclement weather, particularly prevalent above 1,500 m elevation, often fouls mist nets, hinders specimen preparation, and reduces bird activity during the time allotted for sampling at a particular elevation [e.g. LSUMZ field parties (1977–1980) recorded moderate to heavy rains and high winds on 79 of 83 camp days in the Divisoria de Huancabamba, Departments of Cajamarca and Piura, Peru].

Although many distributional limits are documented by voucher specimens, observer experience is an important source of sampling error. Local montane-forest avifaunas cannot be evaluated fully in a few weeks of fieldwork. Distinguishing between breeding residents and elevational wanderers is difficult. Despite many confounding variables, the elevational limits of humid Andean forest birds are relatively consistent along the eastern slope of Peru. However, because the type of data (sight record or specimen) and the number of observations differ from species to species, confidence bands of elevational limits cannot be reliably determined for between-species comparisons. To minimize error in this study, I used the maximum and minimum elevations recorded for each species along the eastern slope of Peru. These were converted to elevational means and vertical amplitudes (Fig. 4, Appendix). I compiled elevational ranges from several sources that used calibrated altimeters: (1) my own fieldwork, July–November 1976, May–November 1977, June–July 1978; (2) unpublished field notes of Theodore A. Parker III, Thomas S. Schulenberg, Mark B. Robbins, J. W. Eley, and John P. O'Neill; and (3) post-1965 elevational data on museum labels in LSUMZ, AMNH, and FMNH.

Museum studies.—The relationship of size and shape characters to speciation and race formation is unclear. Preliminary studies of Andean montane-forest birds reveal a chaotic pattern in geographic size variation at the community level unlike the smooth parallel clines observed in Northern Hemisphere studies (Remsen in prep., Graves in prep.). Consequently, size and shape characters are probably of less value in the study of comparative speciation than discrete plumage characters, especially for poorly known tropical avifaunas.

In contrast to size and shape, plumage pattern and color are relatively conservative. In some cases there is no apparent correlation of environmental clines with color pattern (Graves 1982). Predation, sexual selection (see review by Baker and Parker 1979), intraspecific competition (Rohwer 1982), interspecific interactions (Moynihan 1963, 1968; Cody 1974), and environmental abrasion (Burtt 1981) influence the evolution of plumage pattern and color in birds. Noncryptic plumages also may arise by selectively
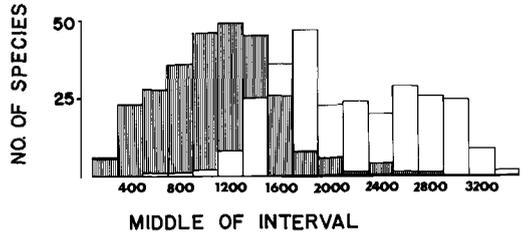
Fig. 4. The cumulative distribution of amplitude (open bars) and mean elevation (shaded bars) values for all species ($n = 280$). Elevation intervals are 200 m.

neutral random mutations or through pleiotropic effects.

For this reason, I took an operational approach to comparative systematics and classified and compared species in terms of presence (continuous and discontinuous variation) and absence of geographic variation in plumage (Graves 1983). In this study I treated plumage variation among populations rather than variation within single geographic localities. Thus, species occurring in only one transect block were excluded. All plumage surfaces on museum study skins were scrutinized, including some not normally visible (e.g. interscapular patches). Specimens in unworn adult plumage were examined in geographically arranged series under natural light. Color determinations (Ridgway 1912) and Kodachrome slides of unique specimens were taken in certain museums for later comparison with standard specimen series. Specimen series were examined at the LSUMZ, AMNH, and FMNH. Faded or "foxed" specimens were examined for plumage pattern but not for color comparison. My vision is normal with respect to red-green color-blindness (Ichikawa et al. 1978).

Classification of plumage differentiation.—Initially, all population samples of a given species were examined for geographic variation in plumage. Those species not displaying between-population variation within the study area in either plumage color or pattern (i.e. uniform along the eastern slope of the Peruvian Andes) were classified as having "no variation." If variation was observed, a second diagnostic procedure was conducted. To determine whether variation was continuous or discontinuous, each plumage character or character complex was evaluated independently. For species with large geographic distributions within the study area, variable characters were compared primarily with serially adjacent Peruvian populations. Widespread Andean species with limited distributions in the Peruvian Andes were compared with populations north (Ecuador, Colombia) or south (Bolivia) of the study area. However, classification here was based only on variation within the study area. Character states that appeared to vary continuously between populations in series were noted. This pro-

cess was repeated for all taxonomically applicable characters of each species.

I mapped range boundaries, distributional gaps, and steepening character gradients. Careful attention was given to all zones of contact. Without specific knowledge of the evolutionary history of the populations under examination, primary vs. secondary contact is impossible to determine in a general overview (Endler 1977). However, uniform, geographically widespread populations connected by relatively narrow zones of intergradation are probably in secondary contact (Mayr 1963). Species lacking discretely variable characters and differing only through clines were classified in the "continuous variation" category. These species were subdivided into those with only smooth clinal variation (= continuous smooth clines; see Huxley 1939) and those with clines containing distinct steps (=continuous obliquely stepped clines). In this paper, I refer to these as "smooth clinal" (II) and "step-clinal" (III). As measured by transect blocks, the area occupied by the steepened character gradient ranges from 7 to 29% of the species' geographical range within the study area. Presumably, all local populations differ from others genetically and perhaps phenotypically. This method, however, detects only conspicuous phenotypic differences among populations and is biased against the distinction of microgeographic variation.

When population samples were compared serially, the disappearance, appearance, or abrupt change in a conspicuous character between two adjacent populations was classified as "discontinuous" variation. In many cases, suites of characters were involved, and enumerating the specific changes was often difficult. As this process is largely descriptive, saying, for example, that "this species' plumage is entirely gray in population A but is glossy black in adjacent populations B and C" may be just as useful as detailed diagnosis of every feather tract. To paraphrase Mayr (1942), the number of plumage characters examined and quantified is limited only by the patience of the investigator. The presence of discontinuous variation is of greater interest than what feathers or feather tracts differ. As a rule, to qualify as discontinuous variation for the character in question, all specimens from one population had to differ from all specimens from the adjacent population. In addition to the conservative criteria of population distinctiveness, populations from two or more transect blocks, on one or both sides of the zone of discontinuity, had to be uniform for these characters. Species classified as having continuous and discontinuous variation might exhibit variable characters in one or both sexes. If at least one conspicuous character showed discontinuous variation, as defined here, the species was classified as possessing "discontinuous" variation (including "continuous horizontally stepped clines," "discontinuous obliquely stepped clines," and "discontinuous horizontally stepped clines" of Huxley

1939). Species with "continuous horizontally stepped clines" were tentatively categorized as having discontinuous variation if the zone of clinal continuum between geographically uniform populations was less than 5% of the species' range within the study area. In many cases, discontinuous variation was correlated with the presence of a geographical barrier or a gap in the distribution of a species. The discontinuous-variation category included species with populations thought to be below the allospecific level ("discrete variation," IV) and superspecies having two or more allospecies ("allospecies," V) within the study area (e.g. Metallura, Schizoeaca). Single allospecific populations within the study area (e.g. Buthraupis aureodorsalis) were examined for geographic variation without regard to allospecies occurring outside the study area.

In summary, the following categorical levels (I < II < III < IV < V) accounted for all possible geographic variation in plumage pattern and color:

I. "no variation"
   "continuous" variation
II. smooth clines
III. step clines
   "discontinuous" variation
IV. discrete variation
V. allospecies.

It should be noted that the population structure categories are hierarchical but not mutually exclusive. For example, a species with discontinuous variation among populations (and classified as having "discontinuous" variation) also has nonvariable and can have clinally variable characters. A species in the "no variation" category, however, does not have continuously or discontinuously varying characters. Accordingly, the categories represent qualitative levels rather than quantitative measures of geographic variation.

RESULTS

Sexual dichromatism and geographic variation.— About 25% (72 of 280) of the species included in this study (see Appendix) are moderately sexually dichromatic. These include birds that are easily sexed by visual inspection of plumage but exclude those that differ only in the color of concealed crown patches (e.g. flycatchers) or other inconspicuous characters.

Sexual dichromatism appeared in 14 of the 30 families included in this study. A majority (43 of 72, 59.7%) of the dichromatic species occurred in 4 families: the Trochilidae (19 of 29, 65.5%), Picidae (6 of 6, 100%), Formicariidae (10 of 22, 45.5%), and Cotingidae (8 of 12, 66.7%). Although sexually dichromatic species were unevenly distributed taxonomically, there was
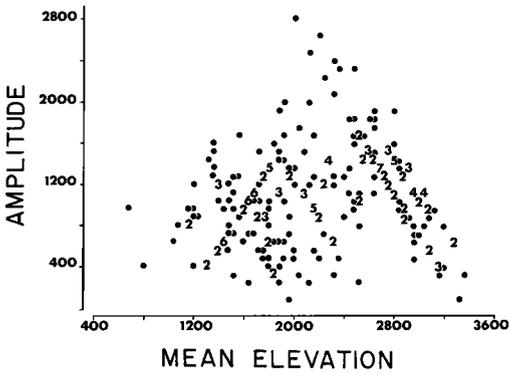
Fig. 5. Plot of amplitude and mean elevation values (m) for all species ($n = 280$).

Fig. 6. Pairwise Mann-Whitney U-tests for differences in mean elevation between species with different levels of plumage differentiation (I–V). Mann-Whitney U counts are given at the top of each cell. The mean ranks of elevation for each plumage comparison are shown at the bottom of each cell (column ranks on left, row ranks on right). A triangle indicates that the difference is significant (two-tailed; one triangle = $P < 0.10$, two triangles = $P < 0.05$).

no significant difference between them and sexually monochromatic species in geographic variation (plumage I–V) within the study area (Mann-Whitney U-test, $P > 0.05$). Additionally, there was no significant difference between the two groups either in extent of geographic range within the study area or in mean elevation and amplitude (Mann-Whitney U-test, $P > 0.05$). This indicates that any relationship between plumage differentiation and elevation or geographic range is unlikely to be biased by possible differential assessment of variation in sexually dichromatic and monochromatic species.

Elevational distribution and geographic variation.—Two important components of elevational distribution are the location (here estimated by mean elevation) and vertical amplitude of a species' distribution along an elevational gradient. Both variables may be correlated with geographic variation in Andean birds. Species that occur at extreme elevations (i.e. with high or low mean elevations) have restricted amplitude values. Those with intermediate mean elevations may have large or small vertical amplitudes. Thus, mean elevation and amplitude are not completely independent (Fig. 5), nor is their relationship linear. Because there was no clear choice of statistical test for these data, I used several statistical methods to examine the relationship between elevational distribution, general geographic distribution, and geographic variation in plumage.

Mean elevation and differentiation.—Because the underlying distribution of elevational parameters was unknown and measures of geographic range were skewed toward higher values,

the use of parametric statistics that assume normal distributions was ill advised.

A nonparametric test of the data from the total species list indicated there was a significant difference in mean elevation between species with different levels (I–V) of plumage differentiation (Kruskal-Wallis one-way test; $\chi^2 = 16.75$, $P = 0.002$). My expectation that plumage levels are ordered with respect to elevational parameters was examined with the Mann-Whitney U-test (Fig. 6). Mann-Whitney counts from 6 of the 10 cells were statistically significant; only 1 of these differed unexpectedly (II > III). The alternative hypothesis in the form H_a: I < II < III < IV < V, where one of the inequalities is strict, was tested by the large-scale approximation of Jonckheere ordered alternatives test (Hollander and Wolfe 1973):

$$J^* = \frac{J - \left(N^2 - \sum_{j=1}^{k} n_j^2\right)\bigg/ 4}{\left\{\left[N^2(2N + 3) - \sum_{j=1}^{k} n_j^2(2n_j + 3)\right]\bigg/72\right\}^{\frac{1}{2}}},$$

where J is the sum of the $k(k - 1)/2$ Mann-
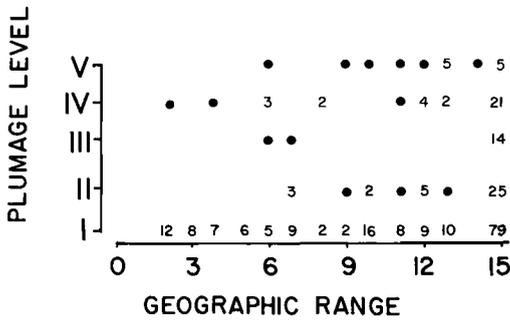
Fig. 7. Plot of the relationship between level of plumage differentiation and size of geographic range in transect blocks for all species ($n = 280$). Dots indicate one species, and numbers indicate total species.

TABLE 1. Spearman's rank correlation coefficients for the relationship between plumage level and mean elevation at each range value using different numbers of plumage levels.

Range value	n^b	Number of plumage levels[a]		
		2	3	5
15	146	0.24**	0.29***	0.28***
13	18	0.50*	0.43*	0.43*
12	19	−0.25	−0.47*	−0.46*
11	11	0.58*	0.57*	0.55*
10	19	0.04	0.04	0.04
7	13	0.05	0.05	−0.03
6	10	0.24	0.24	0.31
5	6	0.00[c]	0.00[c]	0.00[c]
4	8	0.41	0.41	0.41
3	8	0.00[c]	0.00[c]	0.00[c]
2	13	0.39	0.39	0.39
Fisher's test		$\chi^2 = 45.15$	$\chi^2 = 47.38$	$\chi^2 = 46.02$
		$P < 0.003$	$P < 0.002$	$P < 0.002$

[a] $* P < 0.05$, $** P < 0.01$, $*** P < 0.001$.
[b] Sample size.
[c] All plumage values were equal.

Whitney U counts and J^* is normally distributed.

The null hypothesis that plumage levels are not ordered with respect to mean elevation can be rejected ($J^* = -4.02$, $P < 0.00003$). These results imply that plumage differentiation is positively correlated with mean elevation; however, they do not account for variation due to the size of geographic range (Fig. 7). All other factors being equal, the larger a species' geographic range is, the higher the probability it will be dissected by some barrier to gene flow. In this study, "equal range" values were judged to be roughly proportional when used as an independent variable.

The outcome of any tests may be biased by misclassification of species in plumage groups. For statistical tests, I assumed that plumage levels were ordered (e.g. plumage level IV species are more geographically variable than plumage level III species). Ambiguities in interpretation of clines or degrees of specific distinctiveness (IV vs. V) could blur the division between adjacent plumage categories.

I examined the possible effects of misclassification by making a priori contrasts of 2 (I vs. II, III, IV, V), 3 (I vs. II, III, vs. IV, V), and 5 plumage categories. The relationship between plumage level and mean elevation of species with equal range values then was assessed with Spearman's rank correlation test. I used Fisher's test of combined probabilities (Sokal and Rohlf 1969) with a Chi-square distribution [$-2\Sigma \ln(p) = \chi^2$, $df = 2n$] to evaluate the probabilities across range values. The combined tail

probabilities from the correlation coefficients showed that plumage differentiation of species was positively correlated with mean elevation (Table 1). These results indicate that the relationship was robust to minor changes in plumage classification. Of particular interest are the highly significant coefficients for species that occurred throughout the study area (range = 15). Because the contrast results were similar, 5 plumage categories were used in the remaining tests. The constraint of "equal" ranges reduced the number of species combinations available for comparison at lower range values. I relaxed the range constraints by reducing the number of range increments from 15 to 7 (e.g. 10–11, 12–13, 14–15) and recalculated the correlation coefficients from the new range categories. The combined probabilities were highly significant (Fisher's test, $\chi^2 = 32.6$, $df = 12$, $P < 0.004$) and again indicate that the results were robust to minor changes in data organization. In other words, slight expansion of the geographic range categories did not substantially affect the correlation between plumage differentiation and mean elevation. However, none of the correlation coefficients for range classes below 15 was significant at $P = 0.05$. A further relaxation of range constraints yielded still lower significance values. For this reason, conclusions based

TABLE 2. Spearman's rank correlation coefficients for the relationship between plumage level and mean elevation at each range value, omitting different levels of plumage. Sample sizes appear in the left-hand column under each data category. Missing data values indicate a sample size less than 5.

Range value	Plumage level omitted[a]									
	I		II		III		IV		V	
15	67	0.25*	119	0.30***	132	0.35***	125	0.18*	141	0.21**
13	8	−0.29	17	0.43*	18	0.43*	13	0.42	13	0.51*
12	10	−0.78**	14	−0.71**	19	−0.46*	15	0.01	18	−0.40*
11	5	0.22	10	0.49	11	0.55*	10	0.42	10	0.62*
10	—	—	17	0.05	19	0.04	19	0.04	19	0.04
7	—	—	10	−0.41	12	0.25	13	−0.03	13	−0.03
6	—	—	10	0.31	9	0.34	7	0.54	10	0.31
5	—	—	6	0.00[b]	6	0.00[b]	6	0.00[b]	6	0.00[b]
4	—	—	8	0.41	8	0.41	7	0.00[b]	8	0.41
3	—	—	8	0.00[b]	8	0.00[b]	8	0.00[b]	8	0.00[b]
2	—	—	13	0.39	13	0.39	12	0.00[b]	13	0.39
Fisher's test	$\chi^2 = 10.38$		$\chi^2 = 43.40$		$\chi^2 = 53.49$		$\chi^2 = 32.47$		$\chi^2 = 41.66$	
	$P < 0.25$		$P < 0.005$		$P < 0.0005$		$P < 0.07$		$P < 0.009$	

[a] $* P < 0.05$, $** P < 0.01$, $*** P < 0.001$.
[b] All plumage values were identical.

on analyses using expanded range classes are suspect. I assumed that plumage categories represented divisions of a continuum of geographic variation (I < II < III < IV < V). The possibility that one plumage class might bias the analysis was examined by sequentially deleting species from each plumage category and recalculating the correlation coefficients (5 groups: I < II < III < IV; I < II < III < V; I < II < IV < V; I < III < IV < V; II < III < IV < V). The results from these subsets were similar (Fisher's test, $P < 0.25$ to $P < 0.0005$) to those from the total species pool (Table 2). When species with plumage category I were omitted, a sufficient number of species (≥ 5) for rank correlation was present only for range values 11, 12, 13, and 15, thus producing the large tail probability of the combined test ($P < 0.25$). The correlation coefficients for species that occurred throughout the study area (range = 15) were significant for all 5 groups. This indicates that the highly significant correlation between plumage differentiation and elevational distribution in Andean birds does not depend on species data from a particular plumage category.

Geographic variation in higher taxonomic categories.—Vuilleumier (1972) investigated speciation in 288 species (~60 genera) of South American birds. His emphasis was on Andean species living in open habitat (*páramo* and *puna*

steppes), montane forest, and dry intermontane basins and a few genera from other regions in South America. The sample was subdivided into higher taxonomic and ecological groups whose species were compared within groups. He concluded that the percentages of species with geographic variation and of species with isolates in the non-Passeriformes and Passeriformes were more or less equal and that no obvious reason explained the lack of difference.

I compared a set of species that partly overlapped his and found no significant difference (Mann-Whitney U, $P > 0.05$) in the size of geographic range or geographic variation (plumage levels I–V) between nonpasserine ($n = 71$) and passerine ($n = 209$) species.

Similarly, Vuilleumier (1972) concluded that the frequencies of species having geographic variation and of species having isolates are about equal in the suboscine and oscine families of the order Passeriformes. In my study there was no significant difference in geographic variation in plumage between taxa (Mann-Whitney U, $P > 0.05$); however, the size of geographic range in the study area was significantly larger (Mann-Whitney U, $P < 0.05$) in oscines. To check for possible area effects of range size on geographic variation, I compared a sample of oscine ($n = 53$) and suboscine ($n = 51$) species with equal-size ranges (=15) and

TABLE 3. Spearman's rank correlation coefficients for the relationship between plumage level and mean elevation at each range value for higher taxonomic categories. Missing data values indicate a sample size less than 5.

	Higher taxonomic categories[a]							
	Nonpasserines		Passerines		Suboscines		Oscines	
Range value	n[b]	r_s	n	r_s	n	r_s	n	r_s
15	42	0.24	104	0.32***	51	0.31*	53	0.32*
13	6	0.06	12	0.59*	6	0.14	6	0.74*
12	—	—	17	−0.46*	10	−0.65*	7	−0.31
11	—	—	8	0.48	—	—	5	0.35
10	—	—	15	0.02	9	−0.41	6	0.53
7	—	—	9	−0.64*	5	−0.89	—	—
6	—	—	7	0.71*	—	—	—	—
5	—	—	6	0.00[c]	—	—	—	—
4	—	—	6	0.66	—	—	—	—
3	—	—	7	0.00[c]	—	—	—	—
2	—	—	11	0.40	10	0.41	—	—
Fisher's test	$\chi^2 = 7.08$ $P < 0.136$		$\chi^2 = 47.13$ $P < 0.002$		$\chi^2 = 15.32$ $P < 0.230$		$\chi^2 = 23.48$ $P < 0.010$	

[a] * $P < 0.05$, *** $P < 0.001$.
[b] Sample size.
[c] All plumage levels were identical.

found no significant difference between the two taxonomic groups. This suggests that at present there are no *major* differences in the amount of differentiation between higher taxonomic categories of Andean birds.

Species from nonpasserine orders (tinamous through woodpeckers) showed only a margin-ally positive correlation (Fisher's test, $\chi^2 = 7.08$, $P < 0.136$) between plumage level and mean elevation (Table 3). Passerine species showed a highly significant correlation between plumage differentiation and mean elevation. Analysis of the two principal subdivisions of the Passeriformes gave somewhat different results.

TABLE 4. Spearman's rank correlation coefficients for the relationship between plumage level and mean elevation for specified range values at the family level.

Family	Range values	n[a]	r_s[b]	Fisher's test for individual families
Trochilidae	15	18	0.13	$\chi^2 = 7.98, P < 0.24$
	10–13	5	0.71	
	2–9	6	−0.34	
Furnariidae	15	11	0.57*	
Formicariidae	15	8	0.35	$\chi^2 = 4.69, P < 0.59$
	10–13	6	−0.09	
	2–9	8	−0.58	
Cotingidae	2–9	6	0.27	
Tyrannidae	15	25	0.38*	$\chi^2 = 12.52, P < 0.052$
	10–13	15	0.00	
	2–9	12	0.36	
Troglodytidae	15	5	0.67	
Turdidae	15	6	0.66	
Parulidae	15	8	0.30	
Emberizidae	15	30	0.29	$\chi^2 = 14.46, P < 0.025$
	10–13	20	0.46*	
	2–9	15	0.00	
Fisher's test over all families				$\chi^2 = 62.05, P < 0.001$

[a] Sample size.
[b] * $P < 0.05$.
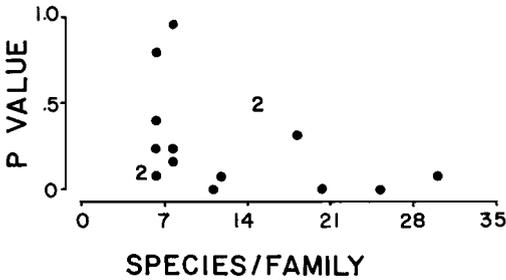
Fig. 8. Plot of *P*-values from Spearman's rank correlation coefficients and sample size from family-level comparisons (see Table 4).

Fig. 9. The elevational distribution of species occurring throughout the study area (range = 15 blocks) from the five most species-rich families in the Andes. The elevational gradient is divided into 200-m intervals. Sympatric species occurring within a particular interval are subdivided by magnitude of plumage variation for comparison; unmarked area = no geographic variation (I) in plumage, hatched area = clinal variation (II, III), and black area = discontinuous variation (IV, V).

Suboscines showed a weak positive correlation ($P < 0.23$) between plumage level and mean elevation, while oscines showed a significant positive correlation ($P < 0.01$). When species with discontinuous (patchy) geographic ranges (see Appendix) were omitted from the analyses, the significance levels of correlation coefficients and the combined probabilities across range values generally were higher for all higher categories. These results reinforce the conclusion that plumage differentiation was positively correlated with mean elevation. Significant values across higher taxonomic categories strongly suggest that this relationship is not limited to a small but influential taxonomic subset.

Family-level comparisons.—At the family level, only 8 of 30 families had 5 or more species for any range value. Over 66% (186 of 280) of the total species list occurs in the 5 most species-rich families (Trochilidae, Furnariidae, Formicariidae, Tyrannidae, Emberizidae). To increase the sample size, I relaxed the "equal range" constraint and grouped species from each family into three range classes (i.e. range values 2–9, 10–13, 14–15). Only 1 additional family (Cotingidae) with 5 or more species per range class was added. The correlation coefficients for the relationship of plumage differentiation and mean elevation across range classes and families were highly significant (Table 4; Fisher's test, $\chi^2 = 62.05$, df = 34, $P < 0.001$), although the probabilities of 5 families (Trochilidae, Cotingidae, Troglodytidae, Turdidae, Parulidae) were only marginally unusual ($0.07 < P < 0.28$), and 1 was not significant (Formicariidae, $P = 0.59$). Levels of significance in this test at the family level were inversely proportional to sample size (Fig. 8). Five of the 6 nonsignificant families

had less than 10 species from every range class. For higher taxonomic categories, the significance level of combined probabilities across families was higher when patchily distributed species were omitted (Fisher's test, $\chi^2 = 62.84$, df = 30, $P < 0.001$).

The elevational distributions of continuously distributed species (range = 15) from the 5 most species-rich families are shown in Fig. 9. With the exception of the Formicariidae, the proportion of species with discontinuous plumage variation (IV and V) increased with elevation. Only a few species with discontinuous variation occurred below 1,100 m. Although species with no variation (I) occurred along the entire elevational gradient in each family, most were found at lower elevations. The elevational distributions of species with continuous plumage variation (II and III) were somewhat intermediate between the no-variation and discontinuous-variation groups.

TABLE 5. Positive and negative scores from comparisons of congeneric species pairs with equal geographic ranges. Figures in parentheses represent the number of scores in genera when range restrictions were relaxed (to increments of two blocks, i.e. 2–3, 4–5, etc.). The P-value is the binomial probability (for $n > 25$, the large-sample approximation of Hollander and Wolfe 1973) of finding this many positive scores in n trials, omitting ties. P-values in parentheses represent the binomial probability when ties are partitioned and added to positive and negative categories.

Genus	Positive	Negative	Tie	
Pionus	1	0	0	
Coeligena	2	0	1	
Metallura	1	0	0	
Grallaria	2	1	0 (2)	
Pipreola	0	1	0	
Mionectes	1	0	0	
Ochthoeca	2	1	3	
Catharus	1	0	0	
Cacicus	0	1	0	
Basileuterus	1	1	1	
Diglossa	3	1	2	
Tangara	12	6	4	
Chlorospingus	1	1	1	
Hemispingus	0 (4)	1 (2)	1 (2)	
Atlapetes	1 (2)	0	0	
Total	28	14	13	$P < 0.02$ (<0.03)
Minus *Tangara*	16	8	9	$P < 0.08$ (<0.09)

Comparisons of congeneric species.—I used a modified binomial test of variable comparison for pairwise combinations of congeneric species. For each genus, all pairwise combinations were generated with the constraint that species pairs have equal geographic ranges (occur in the same number of transect blocks). For each species pair I asked the question: Does the species with the higher level of plumage differentiation also have the higher mean elevation? If the answer was "yes," I scored a "+1" for that species pair; if "no," I scored a "−1." When plumage levels were identical (tied), a "0" was scored for that species pair. The +1's and −1's were totaled for each genus.

It is worth noting that "0" values probably do not represent identical levels of plumage differentiation but rather an inability to distinguish finer levels of differentiation. For these data, the frequency of identical values was a function of the number of plumage levels discriminated. The more plumage levels recognized, the less likely it was that a pair of species would be identical. For example, from the total list there were 146 species with ranges of 15. Of the $\binom{146}{2} = 10{,}585$ pairwise combinations, there were 5,292 plumage ties (50%) when only 2 plumage categories were distinguished. The number of ties decreased to 4,234 (40%) when

3 plumage levels were used and to 3,747 (35.4%) when 5 were used. If more categories were used, the proportion of ties would continue to drop.

The cumulative scores of pairwise combinations were used to examine the relationship between plumage differentiation and elevation. If there were no elevational differences among plumage categories, the pairwise scores should follow a binomial distribution with $P = 0.5$. For the binomial test, the probability of finding that many successes (positive or negative categories) in a given number of trials was calculated with the large sample approximation ($n > 25$) of Hollander and Wolfe (1973). Nontie scores could be calculated for species pairs from only 15 (9.0%) of 166 genera included in this study. Only 1 genus had 5 or more nontie scores (*Tangara*, 18). When range constraints were relaxed by reducing the number of range increments from 15 to 7 (e.g. 12–13, 14–15), only 6 additional nontie scores were obtained (5 positive, 1 negative). A binomial test of the cumulative scores over all genera showed a significant correlation between plumage differentiation and mean elevation (Table 5).

In summary, there was a significant correlation between plumage differentiation and mean elevation at the generic, familial, ordinal, and avifaunal levels in Andean forest birds.

Vertical amplitude and differentiation.—A pre-

TABLE 6. Spearman's rank correlation coefficients for the relationship between plumage level and vertical amplitude for the total species pool and for all species with continuous ranges (omitting species with distributional gaps ≥1 transect block).[a]

Mean elevation (m)	Species	Range values					
		2–9		10–13		14–15	
		n[b]	r_s	n	r_s	n	r_s
<1,850	Total	18	0.65**	27	0.40*	59	−0.06
	Continuous	15	0.44	21	0.04	59	−0.06
1,850–2,500	Total	26	0.37*	18	−0.22	43	−0.04
	Continuous	24	0.24	13	−0.29	43	−0.04
>2,500	Total	22	0.48*	22	−0.29	45	−0.06
	Continuous	17	0.33	18	−0.05	45	−0.06

[a] * $P < 0.05$, ** $P < 0.01$.
[b] Sample size.

liminary test of the data on the relationship between plumage differentiation and amplitude indicated that there was a significant difference in amplitude between species with different levels (I–V) of plumage differentiation (Kruskal-Wallis one-way test, $\chi^2 = 14.74$, $P < 0.005$). The vertical amplitude of a species may be viewed as a rough indicator of the breadth of habitat occupied in the face of environmental gradients and interspecific competitors. However, because of differences in slope angle, topographic heterogeneity, structural complexity of habitat, and available area between any two elevational contours, the amplitude measurement may not be directly comparable. For instance, an amplitude of 500 m centered at 750 m elevation may encompass 2 or 3 times as much area as an "equal" amplitude centered at 2,500 m elevation. In allopatric speciation, a narrow band of habitat is more easily fragmented by vicariant events than a wider band. It follows that species with specific habitat needs met only in a narrow elevational zone may be expected to show more geographic variation. Generalist species or other birds that require specific habitats or foraging substrates that occur in a wide elevational zone (e.g. bamboo) are less likely to vary geographically. An appropriate null hypothesis might be that given two species with equal geographic ranges and mean elevations, *ceteris paribus*, there is no relationship between plumage differentiation and amplitude. An alternative hypothesis suggests that narrow "amplitudes" are more easily fragmented by barriers to gene flow; thus, species with narrower amplitudes at any given elevation should show more geographic variation.

To examine this hypothesis I divided the elevational gradient into three subequal sections: (1) <1,850 m, (2) 1,850–2,500 m, and (3) >2,500 m. The mean elevation measures for 104, 87, and 89 species, respectively, fall in the three gradient sections. The possible values of geographic range were divided in a similar fashion (i.e. 2–9, 10–13, 14–15). The relationship between plumage differentiation and amplitude of species in each elevation/geographic range cell was examined. Overall, species with small geographic ranges (values 2–9) showed a significant positive correlation between plumage differentiation and amplitude across all elevational subdivisions (Table 6). This may be an artifact of data collection. The number of locations where elevational data were recorded was roughly proportional to the extent of a species' geographic range (i.e. the amplitude measurement tended to increase asymptotically with geographic range). As a point indicator, mean elevation is less sensitive to the effects of extreme values. Species with very small continuous geographic ranges (<5 transect blocks) showed no geographic variation in plumage; however, some species with slightly larger ranges showed clinal variation (see Appendix). These species with wider amplitudes by virtue of larger ranges will influence the rank correlation tests (Table 6). Unfortunately, partitioning these range categories dilutes the sample size. Species with small, discontinuous ranges often are differentiated. Isolated populations that have experienced some shift in niche expressed in vertical amplitude would increase the amplitude measurement for the species. This also produces a positive relationship between plumage differentiation and amplitude. When

TABLE 7.   Spearman's rank correlation coefficients for the relationship between plumage level and vertical amplitude for higher taxonomic categories.[a] Missing data values indicate a sample size less than 5.

Mean elevation (m)	Species	Range values					
		2–9		10–13		14–15	
		n[b]	r_s	n	r_s	n	r_s
<1,850	Nonpasserines	—	—	5	0.35	12	0.04
	Passerines	15	0.64**	22	0.36*	47	−0.09
	Suboscines	12	0.00	13	0.49*	29	0.24
	Oscines	—	—	9	0.27	18	−0.50*
1,850–2,500	Nonpasserines	6	0.66	6	−0.45	16	−0.13
	Passerines	20	0.26	12	−0.21	27	0.00
	Suboscines	12	0.59*	8	0.08	11	−0.04
	Oscines	8	0.00	—	—	16	−0.02
>2,500	Nonpasserines	5	0.00	—	—	14	−0.10
	Passerines	17	0.50*	18	−0.24	31	−0.03
	Suboscines	10	0.35	7	−0.41	12	0.11
	Oscines	7	0.72*	11	−0.25	19	−0.09

[a] * $P < 0.05$, ** $P < 0.01$.
[b] Sample size.

these species were omitted, the correlation coefficients were nonsignificant (Table 6) and showed a trend toward the predicted negative correlation between differentiation and amplitude. Species with medium-size geographic ranges (values 10–13) showed a significant positive correlation at low elevations but a negative relationship at medium and high elevations. Species with large geographic ranges showed a slightly negative, but nonsignificant, correlation between plumage differentiation and amplitude at all elevations.

The significance levels of the correlation coefficients from taxonomic subsets mirrored those from the total species pool (Table 7). Species with small geographic ranges showed a positive correlation between levels of plumage differentiation and amplitude, while no correlation or a slightly negative correlation typified species with relatively large geographic ranges. The only significantly negative correlation was found in oscines with large geographic ranges and low mean elevations.

Mean elevation, amplitude, and geographic range as predictors of plumage differentiation.—A nonparametric multiple regression was run, with the ranks of mean elevation, geographic range, and vertical amplitude as independent variables and plumage level as the dependent variable. Each variable was ranked separately, with average ranks assigned to ties; the rank of the dependent variable was predicted using the

ranks of the independent variables (Conover and Iman 1981).

At the faunal level, the partial correlation coefficients for mean elevation and geographic range were highly significant (Table 8). Amplitude generally was not a significant predictor of plumage differentiation, and mean elevation was a significant predictor of plumage differentiation in non-Passeriformes and Passeriformes. However, a dichotomy occurred between suboscines and oscines in the significance of this variable and between geographic range and amplitude as predictors of plumage differentiation. *P*-values of the partial correlation coefficients for geographic range and mean elevation generally were smaller when species with discontinuous (patchy) ranges were omitted from the analyses. Despite the small amount of variance (total R^2, adjusted for degrees of freedom) in plumage differentiation explained by these parameters, it is surprising that the simple measurement of elevational distribution had any predictive power.

At the family level there were marked differences in the relationship between plumage differentiation and vertical amplitude, mean elevation, and geographic range. Overall, plumage variation in hummingbirds (Trochilidae) showed little correlation with any independent variable. This is due in part to several high-elevation taxa that showed no significant variation in plumage in the study area (e.g.

TABLE 8. Significant correlations (all positive) from nonparametric multiple regression using the ranks of independent variables to predict the ranks of the dependent variable (plumage level) for various taxonomic assemblages.

Taxon	n^a	Independent variables[b]			Total R^{2c}
		Vertical amplitude	Mean elevation	Geographic range	
Total species list	A 280	NS	***	**	6.9
	B 255	NS	***	***	15.1
Nonpasserines	A 71	NS	*	NS	0.4
	B 64	NS	*	*	9.4
Passerines	A 209	NS	*	*	5.1
	B 191	NS	***	***	20.3
Suboscines	A 114	*	NS	NS	11.7
	B 104	NS	NS	**	20.6
Oscines	A 95	NS	***	*	9.8
	B 87	NS	***	**	22.7
Trochilidae	A 29	NS	NS	NS	−4.2
	B 27	NS	NS	NS	6.5
Furnariidae	A 18	NS	*	**	28.4
	B 17	NS	*	***	46.7
Formicariidae	A 22	*	NS	NS	24.8
	B 19	NS	NS	NS	29.9
Tryannidae	A 52	NS	NS	NS	13.1
	B 48	NS	NS	*	20.6
Emberizidae	A 65	NS	**	*	6.7
	B 58	NS	**	**	20.9

[a] Sample size. A = continuously and discontinuously distributed species, B = only continuously distributed species.

[b] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[c] Adjusted for degrees of freedom.

Pterophanes, Ensifera). Of the 5 largest families, the Trochilidae is the most heterogeneous (1.31 species/genus). This suggests that significance levels within families are related to some index of taxonomic diversity. Although species: genus ratios correlated significantly with number of species/family (omitting families with 3 or fewer species; $n = 15$, $R^2 = 19.2\%$, $P < 0.05$), the significance of independent variables as predictors of plumage differentiation in the 5 largest families was not correlated with the species: genus ratio.

The Furnariidae and Emberizidae conformed best to the predictions of the models at the family level (i.e. differentiation was greater in high-elevation birds with narrow amplitudes). When species with discontinuous ranges (1–7 per family) were omitted, the total R^2 increased and the partial correlation coefficients for amplitude were closer to the predicted negative correlation. In continuously distributed species, mean elevation (in 2 of 5 families) and geo-

graphic range (3 of 5) were significant predictors of plumage differentiation, whereas vertical amplitude was a nonsignificant predictor in all 5 families.

From these analyses I conclude that plumage differentiation was related to elevational distribution. This differentiation generally is correlated positively with mean elevation. For most taxa amplitude did not appear to be a statistically significant predictor of differentiation.

Patchiness and geographic variation.—Few attempts have been made to analyze the role of patchiness in differentiation of populations and speciation in tropical avifaunas. Yet, distributional patchiness is a commonly reported phenomenon in tropical avifaunas (Diamond 1972, 1981). Most discussions are case-by-case accounts of range disjunctions and the possible cause-and-effect relationship between various ecological and historical factors and patchiness. From a sample of 19 patchy and 16 nonpatchy Andean species (plus "8 ?patchy, 4 ?nonpatchy,
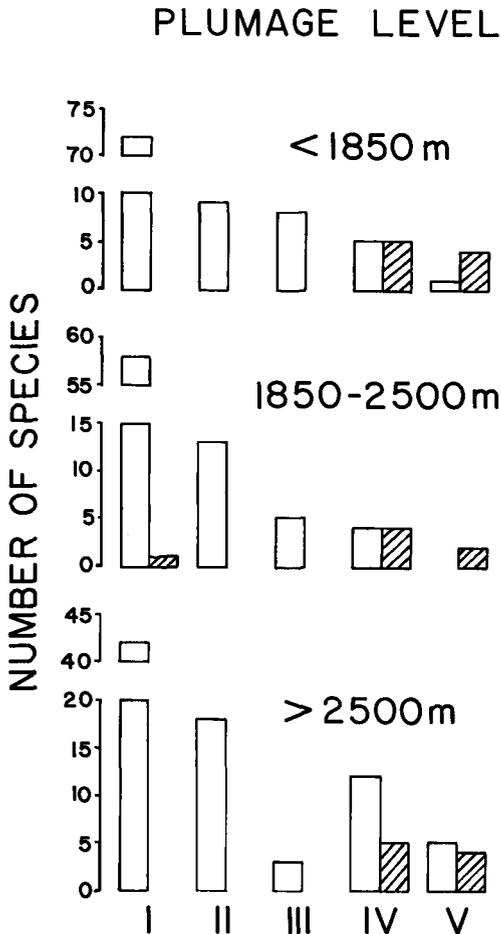
PLUMAGE LEVEL

Fig. 10. Histogram of plumage levels (I–V) for patchy and nonpatchy species with mean elevation values falling in three intervals, <1,850 m, 1,850–2,500 m, and >2,500 m. Species with continuous (nonpatchy) ranges are represented by open bars; species with discontinuous (patchy) ranges are represented by hatched bars.

and 1 uncertain species"), Vuilleumier (1980) concluded that patchily distributed species have more geographical variation than nonpatchily distributed species.

I reanalyzed Vuilleumier's (1980) data. The reported trend toward increased geographic variation with patchiness was not statistically significant (absent vs. present, lines 1 and 2, $\chi^2 = 1.80$, $P > 0.10$; lines 5 and 6, $\chi^2 = 1.58$, $P > 0.20$). Likewise, the proportions of patchy and nonpatchy species with morphologically differentiated isolates, secondary contact phenomena, or belonging to superspecies were not

significantly different. This suggests either that there is little difference in speciation rates between patchy and nonpatchy species of *páramo* and *puna* habitats or that some species were misclassified as patchy or nonpatchy.

To test whether patchiness in montane forest species is correlated with plumage differentiation and presumably speciation, I scored the geographic range of each species for discontinuities or "gaps." On small-scale maps (1: 5,000,000) most Andean forest species appear to have continuous ranges punctuated only by narrow river valleys or canyons. However, 25 (9%) species had range gaps that spanned one or more transect blocks and were considered to be patchy (see Appendix). This definition of patchiness is particularly cautious because a species was considered to be absent only if it has not been found in appropriate habitats and elevations since 1965. Several of these "patchy" species (e.g. *Pipreola frontalis*) eventually may be found to have continuous distributions. It should be noted that most tropical species (91% in this study) were not patchy, perhaps no more than Temperate Zone species.

Only three patchy species [*Chamaepetes goudotii*, *Haplophaedia aureliae* (one of two gaps), *Ampelion rufaxilla*] exhibited no variation in plumage across gaps. For the remaining patchy species, the range gap separated distinctive populations or allospecies.

In contrast to Vuilleumier's data for high Andean birds, patchy montane-forest species ($n = 25$) in this study had significantly more geographic variation than nonpatchy species ($n = 225$; Mann-Whitney U-test, $P < 0.00001$; Fig. 10). There was no significant difference between the groups in mean elevation or amplitude.

Because patchy species (24 of 25 showed geographic variation) may unduly influence the results of rank correlation tests, all species with discontinuous (patchy) ranges were omitted from Table 1 (5 plumage levels), and the Spearman's rank correlation coefficients were recalculated for nonpatchy species. The correlation between plumage level and mean elevation from this test was significant (Fisher's test, $\chi^2 = 38.58$, df = 22, $P < 0.018$).

Despite the lack of statistical difference between the groups in elevational parameters, patchy species may differ fundamentally in their abilities to disperse, colonize, use resources, or compete.

Diamond (1981) suggested four explanations for patchiness that may act singly or in combination: (1) undetected patchiness of habitat, (2) historical effects, (3) immigration-extinction equilibria, and (4) "lockouts" by established populations of competitors. As in most avifaunas, it is not certain what factors are responsible for patchiness in Andean montane bird distributions. In this case, however, three of Diamond's proposed explanations for patchiness do seem unlikely.

Most patchy species identified in this study have wide elevational distributions, and all are known to occur in the array of habitats present in the unoccupied gaps. It is highly unlikely that undetected habitat patchiness is responsible for large disjunctions (>800 km) in geographic range.

Immigration-extinction equilibria probably are not an important factor in the production of large, long-lived gaps in otherwise continuous populations. Repeated collections from many of the range discontinuities confirm the absence of many species whose absence from the region was first noted over 60 yr ago (Chapman 1921). This indicates that patchiness in these cases almost surely is not an artifact of incomplete sampling. Additionally, the sizeable proportion of species with well-differentiated taxa separated by gaps indicates a long-term genetic separation of populations (Mayr 1963).

To determine if the pattern of range gaps was nonrandom, the expected distribution of gaps in blocks B–N was calculated (by N. Gotelli) for each patchy species ($n = 25$). All possible distributions of gaps were enumerated and assumed to be equiprobable: (1) the expected values over all blocks are equal to the number of blocks in the gap(s), (2) range-gap blocks must be contiguous, and (3) multiple gaps for species cannot overlap. The expected number over all species was summed to a cumulative expected number for each block (Table 9). The difference between the observed and expected distribution was marginally significant ($0.05 < P < 0.10$). The immigration-extinction model predicts a uniform distribution of range gaps along the eastern Andean slope, proportional to regional species richness. That is, the number of species absent from a transect block, but having populations north and south of it in the study area, should be positively correlated to the number of species recorded from the block.

TABLE 9. The observed and expected number of range gaps for transect blocks B–N.

Block	Range gaps observed	Range gaps expected	Total species/ block
B	0	2.62	241
C	2	5.09	237
D	5	6.28	242
E	7	7.13	239
F	4	8.22	237
G	3	8.75	240
H	9	9.18	219
I	10	8.88	217
J	8	8.15	224
K	13	8.18	199
L	13	7.10	196
M	10	5.91	186
N	4	3.53	183
	$\chi^2 = 19.68$, df $= 12$, $0.05 < P < 0.10$		

The distribution of range gaps, however, was nonrandom. Moreover, there was a negative correlation between the number of species with range gaps at any single transect block and the total number of species recorded from that block.

Competition at the interspecific or "guild" level is unlikely to have produced the gaps. Evidence of "lockouts" by established populations of competitors, such as checkerboard distributions of congeners or geographic replacement of "guild" members, was not present. The competition model predicts an increase in "lockouts" with increasing species richness of the community (Gilpin and Case 1976). As noted previously, the number of gaps per transect block actually decreased with increasing species richness.

I conclude that the most likely factor influencing the location of gaps is the historical alteration of montane forest habitats during the Pleistocene. The nonrandom distribution of gaps along a uniform or imperceptibly grading environment supports a vicariant mode of isolation and differentiation. Range gaps probably were produced by the elimination of intermediate populations by climatic shifts (Graves 1982).

Discussion

Terborgh and Weske (1975) concluded that direct and diffuse competition accounts for more than two-thirds of the distributional lim-

its of Andean birds whose elevational ranges terminate between the lowlands and timberline. Most evidence of direct and diffuse competition is anecdotal in nature or derived from "natural experiments." Many examples of nonoverlapping congeneric species cited as evidence of competition on the Vilcabamba transect (e.g. *Coeligena, Thripadectes, Grallaria, Cacicus*) overlap at some other Peruvian Andean locations. Less frequently mentioned are the dozens of cases in which congeners overlap on the Andean elevational gradient.

Nonetheless, competition remains one plausible factor in limiting elevational distributions. If diffuse competition is a function of species richness, dispersing individuals may face increased competition when they move downslope and pass below a barrier extending downward from timberline. This would be especially important if the colonization took more than one generation to complete (e.g. breeding and molt may be difficult or impossible). Conversely, low-elevation barriers could be circumvented by species passing through continuous forest either above or below the barrier. Consequently, a low-elevation barrier may be less effective in preventing dispersal than high-elevation barriers. If diffuse competition is operative along the gradient, wandering individuals of low-elevation species should be encountered above their customary breeding elevation more often than vice versa. Data are not yet available to test this hypothesis. Predation would not seem to be a relevant factor as diurnal bird-eating predators are present at all elevations.

Model.—The concordant results from a variety of statistical tests indicate that plumage differentiation and ongoing speciation phenomena are positively correlated with mean elevation and strongly suggest that barriers to gene flow are more effective or more prevalent at higher elevations in the Andes. This supports the first two predictions of the proposed model. The lower productivity, smaller resource base, and decreasing stature of vegetation at higher elevations probably limit the number of adaptive peaks and thus the number of coexisting species. Adaptation to a narrow climatic regime, habitat selection, strong territoriality, interspecific competition, and a psychological reluctance to cross alien habitats may prevent some species from crossing even small barriers. High-elevation populations that have

acquired reproductive isolating mechanisms in allopatry may be less able to reinvade the geographic range of their sister species because of ecological factors. As evidence of this, geographically replacing allospecies (plumage level V) are mainly high-elevation taxa (e.g. *Metallura, Schizoeaca, Diglossa*). The increased number of adaptive peaks at lower elevations may facilitate sympatry in newly formed species.

An alternate but related idea is that high-elevation populations may not be able to resist extinction from vicariant events long enough to acquire reproductive isolating mechanisms and ecological adaptations sufficient for sympatry. Thus, higher extinction rates and limited ecological opportunities may work in concert to depress species richness at high elevations.

Clearly, more autecological data are needed before the causal mechanisms of bird speciation in the Andes can be understood. Here I emphasize a widespread pattern of geographic variation. I tentatively conclude that, although higher-elevation birds at present may be speciating more rapidly than low-elevation taxa, the accumulation of species is limited by extinction through disturbance and the inability of newly formed species to reinvade the range of sister species. Development of this model must await additional information on climate, physiography, and the history of major forest disturbance along the Andean elevational gradient. I predict that similar patterns of geographic variation will be found in other terrestrial animals (e.g. small mammals, frogs, nonvolant insects) that are elevationally restricted in humid Andean forest.

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APPENDIX.   (A) Mean elevation; (B) vertical amplitude; (C) geographic range (number of transect blocks); (D) range continuity [0 = continuous (unpatchy); 1 = discontinuous (patchy), one range gap; 2 = patchy, two range gaps]; (E) 0 = sexually monochromatic, 1 = dichromatic; (F) level of plumage differentiation (I = no variation, II = smooth clinal, III = step clinal, IV = discrete variation, V = allospecies).

	A	B	C	D	E	F
Tinamidae (tinamous)						
Nothocercus julius	2,987	725	7	0	0	II
N. nigrocapillus	2,500	1,000	15	0	0	II
Accipitridae (hawks and eagles)						
Accipiter striatus	2,330	2,040	15	0	0	I
Buteo leucorrhous	2,235	1,170	11	0	0	I
Oroaetus isidori	2,630	1,780	15	0	0	I
Cracidae (guans and curassows)						
Penelope montagnii	2,680	1,380	15	0	0	IV
Aburria aburri	1,442	635	13	0	0	I
Chamaepetes goudotii	2,262	1,475	8	1	0	IV
Phasianidae (partridges and quail)						
Odontophorus balliviani	2,470	1,060	6	0	1	I
Columbidae (pigeons and doves)						
Columba fasciata	2,375	2,350	15	0	0	I
Claravis mondetoura	1,790	800	15	0	1	I
Geotrygon frenata	2,025	1,750	15	0	0	I
Psittacidae (parrots)						
Leptosittaca branickii	2,875	950	12	0	0	I
Bolborhynchus lineola	2,480	1,640	10	0	0	I
Hapalopsittaca melanotis	2,535	1,130	6	0	0	I
Pionus sordidus	1,785	1,320	15	0	0	I
P. tumultuosus (supersp.)	2,735	1,270	15	0	0	V
Amazona mercenaria	2,322	2,395	15	0	0	I
Strigidae (owls)						
Otus ingens	1,722	1,005	15	0	0	I
O. marshalli	1,985	510	4	0	0	I
O. albogularis	2,950	1,140	15	0	0	I
Glaucidium jardinii	2,825	1,450	15	0	0	I
Xenoglaux loweryi	2,167	555	2	0	0	I
Ciccaba albitarsus	2,262	1,475	15	0	0	I

Appendix.   Continued.

	A	B	C	D	E	F
Caprimulgidae (nightjars)						
Uropsalis segmentata	2,810	1,120	15	0	1	I
U. lyra	1,465	730	15	0	1	I
Trochilidae (hummingbirds)						
Doryfera ludoviciae	1,865	1,930	15	0	1	I
Phaethornis guy	1,172	975	15	0	0	I
P. syrmatophorus	1,835	330	2	0	0	I
Colibri thalassinus	2,262	1,475	15	0	0	I
Adelomyia melanogenys	2,462	2,325	15	0	0	IV
Heliodoxa rubinoides	2,182	885	12	0	0	I
H. leadbeateri	1,577	1,295	15	0	1	II
H. branickii	1,160	820	11	0	1	I
Lafresnaya lafresnayi	2,865	970	9	0	1	II
Pterophanes cyanopterus	3,267	665	15	0	1	I
Coeligena coeligena	1,877	1,495	15	0	0	II
C. torquata	2,440	1,320	15	0	1	IV
C. violifer	2,925	1,350	15	0	1	IV
Ensifera ensifera	2,922	1,355	15	0	1	I
Boissonneaua matthewsii	2,245	1,170	13	0	0	I
Heliangelus amethysticollis	2,810	1,420	15	0	1	II
Eriocnemis luciani	3,215	770	11	1	1	IV
E. alinae	2,257	735	7	0	0	I
Haplophaedia aureliae	1,755	890	6	2	0	IV
Ocreatus underwoodii	1,875	1,500	15	0	1	III
Ramphomicron microrhynchum	2,975	750	13	0	1	I
Metallurra aeneocauda (supersp.)	3,267	665	15	0	1	V
M. tyrianthina	3,022	1,155	15	0	1	I
Chalcostigma ruficeps	2,675	1,350	15	0	1	I
Opisthoprora euryptera	3,142	415	4	0	0	I
Aglaiocercus kingi	1,875	1,500	15	0	1	I
Schistes geoffroyi	1,675	1,100	15	0	1	III
Loddigesia mirabilis	2,345	490	3	0	1	I
Acestrura mulsant	2,162	925	15	0	1	I
Trogonidae (trogons)						
Pharomachrus antisianus	1,875	1,500	15	0	1	I
P. auriceps	1,827	1,595	15	0	1	I
Trogon personatus	2,438	1,825	15	0	1	III
Momotidae (motmots)						
Momotus aequatorialis	1,707	855	15	0	0	I
Bucconidae (puffbirds)						
Malacoptila fulvogularis	1,585	610	15	0	0	I
Capitonidae (barbets)						
Eubucco versicolor	1,575	850	15	0	1	IV
Ramphastidae (toucans)						
Aulacorhynchus derbianus	1,350	1,600	15	0	0	I
A. coeruleicinctus (supersp.)	2,142	965	10	1	0	V
Andigena hypoglauca (supersp.)	2,750	1,200	13	1	0	V
Ramphastos ambiguus	1,325	400	7	0	0	I
Picidae (woodpeckers)						
Picumnus dorbygnianus (supersp.)	1,630	1,010	13	1	1	V
Piculus rivolii	2,445	1,110	13	1	1	IV
Veniliornis dignus	1,807	655	10	0	1	I
V. nigriceps	2,880	1,280	15	0	1	IV
Phloeoceastes pollens	2,897	905	7	0	1	II
P. haematogaster	1,637	1,025	10	0	1	I

APPENDIX. Continued.

	A	B	C	D	E	F
Dendrocolaptidae (woodcreepers)						
Dendrocincla tyrannina	1,877	1,135	12	0	0	II
Xiphorhynchus triangularis	1,675	1,100	15	0	0	III
Lepidocolaptes affinis	2,150	1,250	15	0	0	I
Campylorhamphus pucherani	2,532	805	13	0	0	I
C. pusillus	1,902	465	2	0	0	I
Furnariidae (ovenbirds)						
Synallaxis unirufa	2,620	1,460	10	0	0	I
Hellmayrea gularis[a]	3,063	575	7	0	0	I
Cranioleuca curtata	1,565	875	15	0	0	II
C. marcapatae	2,840	920	2	0	0	I
C. albiceps	3,020	760	2	1	0	IV
Schizoeaca fuliginosa (supersp.)	3,070	960	15	0	0	V
Thripophaga berlepschi	2,897	905	4	0	0	I
Margarornis squamiger	2,800	1,600	15	0	0	IV
Premnornis guttuligera	1,880	1,140	15	0	0	I
Premnoplex brunnescens	1,677	1,105	15	0	0	III
Pseudocolaptes boissonneautii	2,462	1,875	15	0	0	II
Syndactyla rufosuperciliata	2,150	1,700	15	0	0	I
S. subalaris	1,612	975	10	0	0	I
Anabacerthia striaticollis	1,647	1,035	15	0	0	I
Thripadectes scrutator	2,810	1,420	15	0	0	II
T. holostictus	2,147	955	15	0	0	II
T. melanorhynchus	1,432	615	13	0	0	I
Lochmias nematura	1,542	1,715	15	0	0	I
Formicariidae (antbirds)						
Thamnophilus unicolor	2,015	550	6	0	1	I
T. caerulescens	1,767	915	15	0	1	II
Myrmotherula schisticolor	1,647	1,045	13	0	1	I
Herpsilochmus pileatus	1,680	740	6	0	1	I
H. axillaris	1,432	615	15	0	1	I
Drymophila caudata	1,917	1,055	15	0	1	I
Terenura callinota (supersp.)	1,563	875	9	1	1	V
Pyriglena leuconota	1,525	1,150	15	0	1	IV
Chamaeza campanisona	1,230	860	10	0	0	II
Formicarius rufipectus	1,470	540	13	0	0	I
Grallaria squamigera	2,590	1,520	15	0	0	III
G. guatimalensis	1,072	775	15	0	0	I
G. carrikeri	2,502	245	4	0	0	I
G. albigula	1,862	675	3	0	0	I
G. hypoleuca (supersp.)	2,135	1,220	10	1	0	V
G. rufula	3,125	950	15	0	0	II
G. sp. n.	2,302	335	7	0	0	I
G. quitensis	3,300	100	2	0	0	I
Grallaricula flavirostris	1,657	1,065	15	0	0	II
G. ferrugineipectus	2,675	1,350	10	0	0	I
G. ochraceifrons	1,945	110	2	0	1	I
Conopophaga castaneiceps (supersp.)	1,565	870	13	1	1	V
Rhinocryptidae (tapaculos)						
Myornis senilis	2,787	1,125	4	0	0	I
Scytalopus macropus	2,962	675	3	0	0	I
Cotingidae (cotingas)						
Ampelion rufaxilla	2,112	225	8	1	0	I
Doliornis sclateri	3,063	575	5	0	0	I
Pipreola riefferii	2,147	955	6	0	1	III
P. intermedia	2,465	930	12	0	1	II
P. arcuata	2,872	1,295	15	0	1	II
P. pulchra	1,845	640	9	0	1	I

APPENDIX.   Continued.

	A	B	C	D	E	F
P. frontalis	1,400	1,200	12	1	1	IV
Ampelioides tschudii	1,752	1,255	15	0	1	I
Lipaugus cryptolophus	1,750	900	8	0	0	I
Pyroderus scutatus	1,952	855	7	0	0	II
Rupicola peruviana	1,340	1,320	15	0	1	III
Pachyramphus versicolor[b]	1,938	1,675	15	0	1	I
Pipridae (manakins)						
Chloropipo unicolor	1,813	1,375	15	0	1	II
Masius chrysopterus	1,432	615	2	0	1	I
Pipra coeruleocapilla (supersp.)	1,400	1,000	14	0	1	V
Tyrannidae (flycatchers)						
Phyllomyias sclateri	1,762	475	5	0	0	I
P. plumbeiceps	1,840	320	11	0	0	I
P. nigrocapillus	2,590	1,520	10	0	0	I
P. cinereiceps	1,722	1,195	15	0	0	I
P. uropygialis	2,787	1,925	12	0	0	I
Zimmerius bolivianus	2,070	1,520	10	0	0	I
Z. viridiflavus	1,785	1,320	7	0	0	III
Mecocerculus poecilocercus	2,395	1,310	12	0	0	I
M. hellmayri	1,500	300	2	0	0	I
M. calopterus	1,432	615	4	0	0	I
M. minor	2,152	945	5	0	0	I
M. stictopterus	3,022	1,155	15	0	0	I
Anairetes agraphia	3,095	910	12	0	0	II
Mionectes striaticollis	1,985	2,770	15	0	0	II
M. olivaceus	670	920	15	0	0	I
Leptopogon taczanowskii	2,188	905	12	0	0	I
L. superciliaris	1,342	1,315	15	0	0	III
Phylloscartes poecilotis	1,805	490	15	0	0	I
P. ophthalmicus	1,563	875	12	1	0	IV
P. gualaquizae	1,800	400	2	0	0	I
P. orbitalis	800	400	15	0	0	I
P. ventralis	1,675	1,100	15	0	0	I
Pseudotriccus pelzelni (supersp.)	1,662	1,125	12	1	0	V
P. ruficeps	2,630	1,480	15	0	0	II
Lophotriccus pileatus	1,460	1,180	15	0	0	IV
Hemitriccus granadensis	2,500	1,000	13	1	0	IV
H. rufigularis	1,050	600	10	0	0	I
H. cinnamomeipectus	1,870	260	2	0	0	I
Rhynchocyclus fulvipectus	1,550	900	15	0	0	I
Platyrinchus mystaceus	1,563	875	15	0	0	III
P. flavigularis	1,630	220	10	0	0	I
Myiotriccus ornatus	1,397	1,205	15	0	0	I
Myiobius villosus	1,397	1,205	15	0	0	I
Myiophobus flavicans	1,945	750	10	0	0	I
M. phoenicomitra	1,313	375	2	0	0	I
M. inornatus	1,710	580	9	0	0	I
M. roraimae	1,425	950	15	0	0	I
M. pulcher	1,900	600	3	0	0	I
M. ochraceiventris	2,917	865	15	0	0	I
Pyrrhomyias cinnamomea	2,237	2,225	15	0	0	II
Mitrephanes olivaceus	1,740	520	15	0	0	I
Contopus fumigatus	1,875	1,500	15	0	0	III
Ochthoeca cinnamomeiventris	2,675	1,350	15	0	0	II
O. frontalis	2,982	1,075	15	0	0	IV
O. pulchella	2,395	850	15	0	0	IV
O. rufipectoralis	3,085	930	15	0	0	IV
Myiotheretes fumigatus	2,960	1,120	12	0	0	I
M. fuscorufus	2,960	1,120	6	1	0	IV

APPENDIX. Continued.

	A	B	C	D	E	F
Knipolegus signatus	2,215	470	7	0	1	I
Myiarchus cephalotes	1,675	1,100	15	0	0	I
Conopias cinchoneti	1,205	910	11	0	0	I
Myiodynastes chrysocephalus	1,465	1,070	15	0	0	I
Hirundinidae (swallows)						
Notiochelidon flavipes	2,982	1,075	15	0	0	I
Corvidae (jays)						
Cyanolyca viridicyana	2,637	1,125	15	0	0	IV
Troglodytidae (wrens)						
Odontorchilus branickii	1,563	875	15	0	0	II
Cinnycerthia peruana	2,540	1,660	15	0	0	IV
Thryothorus euophrys (supersp.)	2,540	1,420	6	1	0	V
Troglodytes solstitialis	2,530	1,640	15	0	0	III
Henicorhina leucophrys	2,112	1,975	15	0	0	I
H. leucoptera	2,045	310	4	0	0	I
Cyphorhinus thoracicus	1,875	1,500	15	0	0	II
Turdidae (thrushes)						
Myadestes ralloides	2,012	1,225	15	0	0	I
M. leucogenys	1,200	400	3	0	0	I
Entomodestes leucotis	2,135	2,470	12	0	0	I
Catharus fuscater	2,465	1,570	15	0	0	II
C. dryas	1,563	875	15	0	0	I
Platycichla leucops	1,900	2,000	15	0	1	I
Turdus serranus	2,210	2,620	15	0	1	I
T. nigriceps	1,367	1,535	15	0	1	I
Vireonidae (vireos)						
Vireo gilvus	1,752	1,255	15	0	0	I
Icteridae (oropendolas and caciques)						
Psarocolius atrovirens	1,715	870	11	0	0	I
Cacicus uropygialis	1,625	710	10	0	0	I
C. leucorhamphus (supersp.)	2,580	1,540	15	0	0	V
Amblycercus holosericeus	2,810	1,420	15	0	0	I
Parulidae (wood warblers)						
Myioborus miniatus	1,537	1,275	15	0	0	I
M. melanocephalus	2,670	1,360	15	0	0	III
Basileuterus luteoviridis	2,810	1,420	15	0	0	IV
B. signatus	2,565	1,470	11	0	0	II
B. tristriatus	1,567	885	15	0	0	IV
B. coronatus	2,005	1,390	15	0	0	II
Conirostrum sitticolor	3,022	1,155	15	0	0	II
C. albifrons	2,075	1,100	15	0	1	II
Emberizidae (tanagers and finches)						
Diglossa caerulescens	1,967	1,315	15	0	0	I
D. lafresnayii (supersp.)	3,050	1,100	15	0	0	V
D. albilatera	2,650	1,300	10	0	1	I
D. glauca	1,862	1,475	15	0	0	I
D. cyanea	2,620	1,920	15	0	0	I
Iridophanes pulcherrima	1,637	1,025	12	0	0	I
Nephelornis oneilli	3,170	360	3	0	0	I
Chlorophonia cyanea	1,300	1,400	15	0	1	I
C. pyrrhophrys	2,313	625	7	0	1	I
Euphonia musica	1,870	1,140	15	0	1	I
E. mesochrysa	1,200	1,200	15	0	1	I
Chlorochrysa calliparaea	1,563	875	15	0	1	IV
Tangara punctata	1,392	535	15	0	0	II
T. arthus	1,495	790	15	0	0	II

APPENDIX.   Continued.

	A	B	C	D	E	F
T. xanthocephala	1,875	1,500	15	0	0	III
T. chrysotis	1,535	930	15	0	0	I
T. parzudakii	1,875	1,500	11	0	0	I
T. cyanotis	1,500	750	11	0	0	I
T. labradorides	1,890	420	2	0	0	I
T. ruficervix	1,563	875	15	0	0	III
T. nigroviridis	1,877	1,495	15	0	0	I
T. vassorii	2,510	1,680	15	0	0	IV
T. argyrofenges	1,810	1,020	6	1	1	IV
Iridosornis analis	1,815	1,370	15	0	0	I
I. jelskii	3,175	350	13	0	0	II
I. rufivertex	2,760	1,520	10	0	0	I
Anisognathus igniventris	2,930	1,340	15	0	0	IV
A. lacrymosus	2,760	1,520	10	0	0	II
A. flavinuchus	1,785	950	12	1	0	IV
Buthraupis montana	2,810	1,420	15	0	0	II
B. aureodorsalis	3,170	360	3	0	0	I
Dubusia castaneoventris	2,825	1,390	12	0	0	II
D. taeniata	2,760	1,180	12	0	0	II
Thraupis cyanocephala	2,262	1,475	15	0	0	I
Calochaetes coccineus	1,587	925	10	0	0	I
Piranga leucoptera	1,432	615	15	0	1	I
P. rubriceps	2,313	625	5	0	1	I
Creurgops verticalis	1,875	1,500	7	0	1	I
C. dentata	1,800	600	6	0	1	I
Trichothraupis melanops	1,688	1,075	13	0	0	I
Sericossypha albocristata	2,340	1,195	7	0	0	I
Chlorospingus ophthalmicus	1,920	1,440	15	0	0	IV
C. flavigularis	1,160	820	15	0	0	I
C. parvirostris	2,063	1,125	15	0	0	I
C. canigularis	1,392	535	13	0	0	I
Cnemoscopus rubrirostris	2,620	1,460	10	0	0	I
Hemispingus atropileus (supersp.)	2,835	1,070	13	1	0	V
H. parodii	3,355	330	3	0	0	I
H. superciliaris (supersp.)	2,725	1,250	13	1	0	V
H. frontalis	1,967	1,315	12	0	0	I
H. melanotis	1,952	1,345	12	1	0	IV
H. rufosuperciliaris	2,955	790	5	0	0	I
H. xanthophthalmus	2,950	1,140	15	0	0	I
H. trifasciatus	3,185	370	11	0	0	I
Chlorornis riefferii	2,675	1,350	15	0	0	II
Catamblyrhynchus diadema	2,760	1,520	15	0	0	I
Saltator cinctus	2,305	1,270	5	0	0	I
Haplospiza rustica	2,590	1,860	15	0	1	I
Atlapetes rufinucha	2,645	1,810	8	2	0	IV
A. tricolor	2,075	1,100	7	0	0	I
A. schistaceus	2,975	450	4	1	0	IV
A. brunneinucha	1,725	1,550	15	0	0	I
A. torquatus	2,685	1,370	15	0	0	IV
Lysurus castaneiceps	1,215	930	13	0	0	I
Carduelis olivacea[c]	1,813	1,375	15	0	1	I

[a] Formerly in *Synallaxis*.
[b] Placed in the Tyrannidae (Traylor *in* Peters 1979).
[c] *Carduelis* (Fringillidae) placed in Emberizidae for comparison.