LINEARITY OF GEOGRAPHIC RANGE AND ITS POSSIBLE EFFECT ON THE POPULATION STRUCTURE OF ANDEAN BIRDS

GARY R. GRAVES

Department of Vertebrate Zoology, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560 USA

ABSTRACT.—Geographic ranges of widespread Andean forest bird species are linear, averaging over 300 times longer than they are wide. Among congeneric species, geographic variation in plumage was negatively correlated to the width (*W*) of their elevational distributions, presumably because narrower distributions are more easily fragmented by barriers to gene flow. The amplitude of a species' elevational distribution may be limited by zonation of resources and by genetic factors that prevent populations from adapting to local environments. Minimum amplitudes may be dictated by demographic consequences. *Received 13 April 1987, accepted 28 August 1987.*

ANDEAN forest birds have sinuous, narrow geographic ranges that correspond to narrow elevational bands of habitat. Most species are believed to be sedentary and to have short dispersal distances (Graves 1985). The pattern of range linearity in Andean birds seems to exemplify a one-dimensional case of population distribution.

There have been few attempts to identify linear communities in nature (e.g. Pielou 1977) and, surprisingly, no explicit examination of the consequences of linearity on the population structure of species. Theoretical and simulation studies (Wright 1943, Kimura and Weiss 1964, Rohlf and Schnell 1971) have predicted that populations in two-dimensional arrays will exhibit less geographic variation than those in linear or one-dimensional sequences, when migration between adjacent demes is fixed, and the number of generations is finite.

Previously, I examined relationships between elevational distribution and geographic variation in plumage among 280 species and superspecies of Andean forest birds (Graves 1985). Geographic variation was correlated positively with elevation and length of geographic range. I was unable to reject the null hypothesis of no relationship between variation and the amplitude of a species' elevational distribution. Here I pursue this hypothesis with a refined analysis. Specifically, I transform elevational range data to a direct measure of the surface distance occupied by a species (width of distribution) along an elevational gradient, estimate the degree of linearity (length-to-width ratio of geographic range) of ranges of Andean forest birds, test the hypothesis that patterns of geo-

graphic variation in congeneric species are related to range linearity, and discuss factors that may regulate elevational distributions of Andean forest birds.

METHODS

Species sample.—I standardized comparisons by restricting the analysis to a subset of species that have large, apparently continuous geographic ranges that span the latitudinal range of the Peruvian Andes (Fig. 1) and that occur primarily above 900 m elevation (Graves 1985: appendix). These species have similar latitudinal distributions within the study area. Elevational distributions of species from a single elevational transect in the Cordillera Vilcabamba (Weske 1972, Terborgh and Weske 1975) were compared with their cumulative distributions recorded from the Peruvian Andes (Graves 1985) (Fig. 2). Vilcabamba data were limited to species recorded at two or more stations along the transect.

Transformation of elevational amplitude to distributional width.—Amplitude is defined as the elevational range of a species from a specified region, such as a mountain range or a single elevational transect. Because the angle of slope in the Andes varies with elevation, amplitude measurements cannot be converted directly to "distributional width." Estimates of local and regional variation of slope in the Peruvian Andes are not available.

I obtained fractional estimates of slope across three contour intervals (1,000–2,000 m, 2,000–3,000 m, 3,000–4,000 m) of the eastern slope of the Peruvian Andes from a 1:1,000,000 topographic map (1973 Instituto Geographico Militar del Peru). The distance across contour intervals was measured along 100 transects drafted perpendicularly between the 1,000 m and 4,000 m (or 3,000 m when necessary) contour lines. The origin of those transects was determined by a random-numbers table. Because slope angle was low, differ-
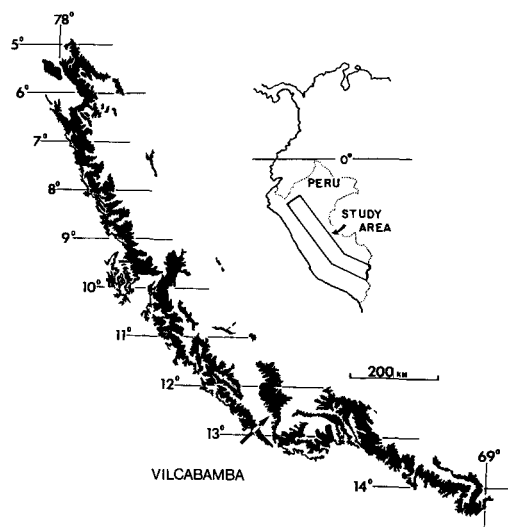
Fig. 1. Distribution of humid Andean forest (ca. 1,200–3,400 m) along the eastern slope of the Peruvian Andes (adapted from Graves 1985). Location of the transect in the Cordillera Vilcabamba (Weske 1972, Terborgh and Weske 1975) is indicated by an arrow.

ences between actual and observed map distances are <1%. Estimates of the average width (km) of contour intervals along the eastern slope of the Peruvian Andes were: 1,000–2,000 m interval, 7.7 ± 5.2 km; 2,000–3,000 m interval, 6.9 ± 5.0 km; 3,000–4,000 m interval, 5.6 ± 4.0 km. I calculated the width of elevational distributions by dividing amplitude into fractions corresponding to contour intervals. The average width (W) of a species' elevational distribution was estimated by:

$$W = \sum_{i=1}^{i} pd,$$

where p was the percentage of elevational overlap with contour interval i, and d was the average width of interval i in kilometers. Fractions of amplitudes occurring below 1,000 m were multiplied by the average width of the 1–2,000 m interval. Correlation between amplitude and W was determined with a Spearman rank correlation coefficient.

   Length of geographic range.—Map scale and step length influence the measurement of geographic range (Pennycuick and Kline 1986). When outlying ridges and satellite ranges are connected at the 3,000-m contour line, the length of the Peruvian Andes varies roughly from 2,750 to 3,300 km, depending on the choice of step length or reference points. Species capable of traversing valleys or nonforest habitats above treeline (a possible example is the hummingbird *Pterophanes cyanoptera*) may have markedly reduced dispersal distances between reference points. In this study I chose 3,000 km as a conservative measure of

the range length. Length-to-width ratios (LWR) of ranges were estimated by: LWR = 3,000 km/W.

   Linearity hypothesis.—I used congeneric species to test the hypothesis that linearity, as a function of W, was correlated with intraspecific geographic variation. Comparisons at the generic level should provide results that are least encumbered by phylogenetic variation in morphology and life-history traits. I determined geographic variation in plumage characters from detailed study of museum specimens. Variation was scored qualitatively, with hierarchical values ranging from 1 for species exhibiting no variation along the eastern slope of Peruvian Andes to 5 for superspecies composed of strongly differentiated allopatric or parapatric populations at or near the species level. Data and a complete description of methods are given by Graves (1985).

   For all possible pairs of congeneric species, I noted the relationship of W with geographic variation. If variation was negatively correlated to linearity, within each pair, species that exhibited the most geographic variation should have the narrowest elevational distribution. Summed scores of pairwise combinations were analyzed with a binomial test (for $n > 25$, large sample approximation of Hollander and Wolfe 1973).

RESULTS

   Amplitude and distributional width (W) of species ($n = 129$), based on cumulative records from the Peruvian Andes, was positively correlated (Spearman rank $r = 0.96$). The mismatch between amplitude and W was due to elevational variation in the slope angle. Observed amplitudes of species along the Vilcabamba transect averaged 61% of cumulative amplitudes from all Peruvian localities (Fig. 2), indicating that elevational distributions vary regionally.

   Linearity.—Length-to-width ratios of geographic ranges of Andean forest birds attained values from 164 to 804 ($n = 129$, $\bar{x} = 333$) (Fig. 3). Because ranges of all species extend beyond the study area, those are minimal estimates. Rohlf and Schnell (1971: 320) suggested that LWRs of 100 were about as linear "as one could expect to observe in nature." This is clearly an underestimate; LWRs of some Andean species or superspecies may exceed 2,000. Other measures of "linearity" of Andean bird distributions, such as perimeter/area, should be highly correlated to length-to-width ratios. Although comparative data from other highland (e.g. New Guinea, Himalayas) or lowland regions (e.g. *varzea*-inhabiting species in Amazonia) have not
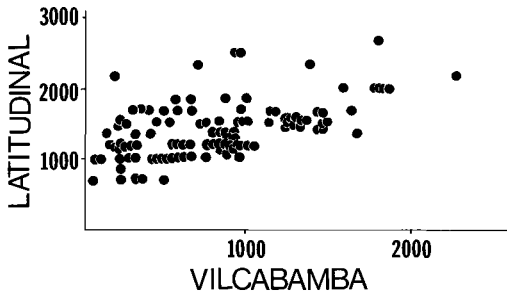
Fig. 2. Plot of species' amplitude ($n = 109$) based on cumulative elevational distribution along the latitudinal gradient (Graves 1985) and local amplitude recorded along the Vilcabamba transect. X- and y-axes are in meters.
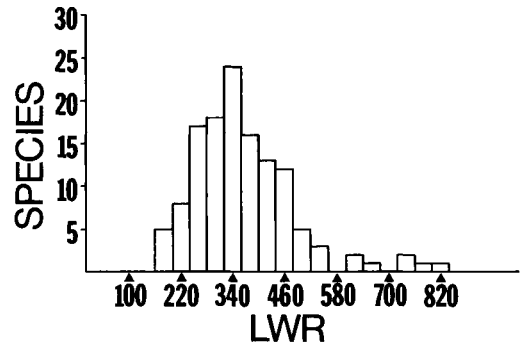

Fig. 3. Histogram of linearity (LWR) values for species that range throughout the eastern slope of the Peruvian Andes.

been compiled, the Andean avifauna may be unique in having a large percentage of species with LWRs exceeding 100.

Comparison of congeneric species pairs.—A majority of genera (7 of 12) with congeneric species contains only two species, so that comparison among such species pairs is mutually independent. Other genera contain up to 7 species and 21 species pairs that lack complete independence (Table 1). If we assume such pairwise comparisons are independent and that no relationship between variables existed, pairwise scores should follow a binomial distribution ($P = 0.5$). For each pair I asked the conditional question (yes/no): Does the species that exhibits the most geographic variation also have a narrower distribution (W or amplitude)? Based on raw scores, variation was uncorrelated with W ($P < 0.12$) or amplitude data. Eighteen of 34 (53%) of the nontie pairwise scores were from the genus *Tangara*, however; no other genus contributed more than 3 nontie scores. Those nonindependent data have a strong influence on statistics and, if viewed uncritically, may lead to misinterpretation of the results. Six of the 7 species of *Tangara* have highly overlapping distributions with nearly equivalent lower elevational limits (1,070–1,130 m). The seventh species (*T. vassorii*, 1,670–3,350 m) exhibits considerable geographic variation but barely overlaps its congeners. When this species was omitted, *P*-values were significant (W, $P < 0.03$). When all species of *Tangara* were omitted, scores were highly significant ($P < 0.001$).

To minimize the influence of speciose lineages (e.g. *Tangara*), I examined the predominant pattern ("average") of pairwise scores for each genus (Table 1). A binomial test of the cumulative yeses and noes indicated that geographic variation was negatively correlated to linearity (W, $P < 0.05$) and uncorrelated to raw amplitude.

As noted earlier, geographic variation was also correlated with elevation (Graves 1985). To examine the interaction of W with elevation as a determinant of variation, I sorted 33 congeneric species pairs, omitting ties, in a 2 × 2 table (Table 2). Species pairs would be distributed evenly ($P = 0.25$ of occurring in a given cell) if there were no relationship between linearity and elevation. In only 2 species pairs did species with the wider and lower elevational range exhibit a greater amount of geographic variation than its congener. The chance of finding as many as 15 or as few as 2 pairwise scores in any cell is remote (binomial test, $P < 0.006$). This indicated there was a strong tendency for species with marked intraspecific variation to have high and narrow geographic ranges. Considering the limited 3-fold range (3.8–12.8 km) of W for congeneric species pairs, those statistics suggest that linearity of geographic range is a determinant of population structure in birds. Those results may arise from an increase in fragmentation of populations with linear ranges rather than from "linearity" effects predicted by neutral genetic models (Felsenstein 1976, Slatkin 1985).

DISCUSSION

Regulation of elevational amplitude.—Elevational distributions of forest birds in the Andes vary regionally (Terborgh and Weske 1975, Graves 1985, Terborgh 1985). After two decades of work

TABLE 1. Comparison of geographic variation and elevational distribution parameters among congeneric pairs of species. Nontie scores for pairs in each genus are listed below. Generic "averages" are indicated by "yes" or "no." P-values are one-tailed.

| | | | | Untransformed amplitude | | | | | |
| | W | | | Latitudinal maxima | | | Vilcabamba transect | | |
Genus	Yes	No	Average	Yes	No	Average	Yes	No	Average
Pionus	1	0	Yes	1	0	Yes	—	—	—
Coeligena	2	0	Yes	2	0	Yes	1	1	—
Metallura	1	0	Yes	1	0	Yes	1	0	Yes
Grallaria	1	0	Yes	1	0	Yes	0	1	No
Ochthoeca	3	0	Yes	3	0	Yes	2	1	Yes
Catharus	0	1	No	0	1	No	—	—	—
Myioborus	1	0	Yes	0	1	No	0	1	No
Basileuterus	2	0	Yes	2	0	Yes	1	1	—
Diglossa	3	0	Yes	3	0	Yes	2	1	Yes
Tangara	6	12	No	6	12	No	6	12	No
Chlorospingus	0	1	No	0	1	No	0	1	No
Atlapetes	1	0	Yes	1	0	Yes	1	0	Yes
Totals	21	14		20	15		14	19	
		($P < 0.12$)			($P < 0.20$)			($P > 0.20$)	
Minus all *Tangara* species	15	2		14	3		8	7	
		($P < 0.001$)			($P < 0.006$)			($P > 0.19$)	
Generic averages		Yes = 9			Yes = 8			Yes = 4	
		No = 3			No = 4			No = 4	

in the Andes, Terborgh (1985) concluded, "direct and diffuse competitive exclusion account for about two-thirds of the distributional limits of Andean birds, ecotones for about one-sixth, and unspecified factors that vary in parallel with the environmental gradient for the remaining one-sixth. Competitive exclusion emerges as the factor of overriding importance in the exceedingly diverse Andean fauna."

Although interspecific competition may be common in Andean bird communities, there is little compelling evidence to suggest that the occurrence of a species is significantly affected by competitors in the core of its elevational range. For example, Weske's (1972) data showed that the peak relative abundance of many species occurred within the elevational range of one or more congeners. In discussing other factors, Terborgh (1985) pointed out, "the farther an ecotone falls from the center of a species' range, the more likely it is to act as a proximate barrier to distribution." I suggest that competition acts similarly as a proximate barrier. Species may be excluded by competitors in regions where they are poorly adapted—at the margins of their optimal range.

Ultimately, elevational distributions are a reflection of natural selection for adaptations re-

lated to food, habitat resources, and life-history traits (e.g. social systems, dispersal) (see Diamond 1973). Elevational zonation of habitat, foraging substrates, and food, in themselves, may prevent species from becoming too elevationally generalized, as few suites of resources are found throughout the gradient (cf. Janzen 1966, Huey 1978). Conversely, altitudinal gene flow may prevent demes from adapting to local conditions along an elevational transect. Genetic adaptation in montane forest birds is thus likely to be primarily latitudinal rather than elevational. Together, elevational zonation of resources and the cohesive effects of gene flow may ultimately influence the tails of distribution along elevational transects. If true, latitudinal variation in elevational distribution (Terborgh and Weske 1975, Terborgh 1985) may be due more to genetic adaptation of populations to the gradient of resources than to competition—a hypothesis that has neither been addressed nor tested.

Consequences of amplitude compression.—How narrow can the amplitude of a widespread species be? In theory, the minimal value that W may attain would be the diameter of a single territory. Data on territory or home-range size are not available for any Andean forest species.

Estimates are needed, however, to evaluate the demographic effects of amplitude compression. Territory size for Andean species may be similar to that for species in lowland Amazonian forest. Munn (1985) estimated population densities of 77 species of passerines that accompany mixed-species flocks at Cocha Cashu in southeastern Peru. His maximum estimate of density ranged from 1 to 90 ($\bar{x} = 19$) individuals·species^{-1}·km^{-2}. Territories may overlap one another and are irregularly shaped, but assuming they were mutually exclusive and completely packed, home-range size of pairs would range from 0.02 to 2.0 km^2 ($\bar{x} = 0.11$). Home-range size of many non-passerine species, especially large raptors and parrots, may exceed the maximum value for passerines by an order of magnitude. Exclusive of such species, estimates of W for most Andean birds (W, 3.7–18.3 km) are several times larger than the diameter of the largest expected territory, but are probably less than 100 territory diameters for any species. This conclusion makes it quite clear that, on average, global populations of Andean forest birds are much smaller than those of lowland Amazonian species with planar two-dimensional ranges. Based on maximal estimates and complete saturation of habitat (90 individuals/km^2; $W = 20$ km), populations of widespread forest species along the eastern slope of the Peruvian Andes do not exceed 5,500,000 individuals, with the average being less than 520,000.

Narrowness of amplitude could point to a highly specialized, successful adaptation to a specific fraction of a resource gradient or, conversely, to a competitively inferior species. Nevertheless, the width of a species' amplitude must be above a minimum threshold, a value below which local populations would eventually become extinct. In my data the minimum value of W was 3.7 km (latitudinal elevational range, 1,560–2,050 m). Could a distinctive species with a very narrow cumulative amplitude (ca. $W = 1.0$ km) inhabit the *entire* eastern slope of the Peruvian Andes without being detected? Mist-net sampling has been conducted in too many localities along the Peruvian Andes between 1,000 and 3,500 m for this to be a reasonable possibility (Graves 1985).

When the amplitude for a species is compressed for whatever reason, the perimeter/area ratio of its geographic range becomes larger, and demographic and environmental stochasticity (Shaffer 1981, Soulé and Simberloff 1986)

TABLE 2. Independently sorted scores for relationship within each congeneric species pair.

		Geographic variation negatively correlated to linearity (W)?	
		Yes	No
Geographic variation positively correlated to elevation (latitudinal minimum)?	Yes	15	10
	No	6	2

becomes increasingly important in determining the longevity and fate of populations. As elevational boundaries recede and local density decreases, individuals near the edge of the range may have difficulty finding mates or flocking associates and solitary individuals may become more susceptible to predation. In addition, effective dispersal would become exclusively horizontal; individuals dispersing elevationally would become "lost" in habitats lacking conspecifics. Unless immigration from adjacent populations occurs, local populations subjected to the cascading effects of population decrease, under intense selection, may become extinct in a few generations. For isolated populations that persist, inbreeding and loss of heterozygosity pose serious obstacles to survival. Compression below the species-specific "threshold" amplitude and subsequent dissolution of continuous geographic range might explain the patchy distribution of some forest species in the Andes (e.g. *Atlapetes rufinucha*). The apparent lack of widespread species with extremely narrow, but continuous, distributions ($W < 3$ km) suggests that this process is either rare or one that occurs rapidly. In either case, this process may drive speciation by producing geographical isolates (Mayr 1963).

LITERATURE CITED

DIAMOND, J. M. 1973. Distributional ecology of New Guinea birds. Science 179: 759–769.

FELSENSTEIN, J. 1976. The theoretical population genetics of variable selection and migration. Ann. Rev. Genet. 10: 253–280.

GRAVES, G. R. 1985. Elevational correlates of speciation and intraspecific geographic variation in plumage in Andean forest birds. Auk 102: 556–579.

HOLLANDER, M., & D. A. WOLFE. 1973. Nonparametric statistical methods. New York, Wiley.

HUEY, R. B. 1978. Latitudinal pattern of between-altitude faunal similarity: mountains might be "higher" in the tropics. Am. Nat. 112: 225–229.

JANZEN, D. H. 1966. Why mountain passes are higher in the tropics. Am. Nat. 100: 233–249.

KIMURA, M., & G. H. WEISS. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49: 561–576.

MAYR, E. 1963. Animal species and evolution. Cambridge, Massachusetts, Harvard Univ. Press.

MUNN, C. A. 1985. Permanent canopy and understory flocks in Amazonia: species composition and population density. Pp. 683–712 in Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. No. 36.

PENNYCUICK, C. J., & N. C. KLINE. 1986. Units of measurement for fractal extent, applied to the coastal distribution of Bald Eagle nests in the Aleutian Islands, Alaska. Oecologia 68: 254–258.

PIELOU, E. C. 1977. The latitudinal spans of seaweed species and their patterns of overlap. J. Biogeogr. 4: 299–311.

ROHLF, F. J., & G. D. SCHNELL. 1971. An investigation of the isolation-by-distance model. Am. Nat. 105: 295–324.

SHAFFER, M. L. 1981. Minimum population sizes for species conservation. BioScience 31: 131–134.

SLATKIN, M. 1985. Gene flow in natural populations. Ann. Rev. Ecol. Syst. 16: 393–430.

SOULÉ, M. E., & D. SIMBERLOFF. 1986. What do genetics and ecology tell us about the design of nature reserves? Biol. Conserv. 35: 19–40.

TERBORGH, J. 1985. The role of ecotones in the distribution of Andean birds. Ecology 66: 1237–1246.

———, & J. S. WESKE. 1975. The role of competition in the distribution of Andean birds. Ecology 56: 562–576.

WESKE, J. S. 1972. The distribution of the avifauna in the Apurimac Valley of Peru with respect to environmental gradients, habitat, and related species. Ph.D. dissertation, Norman, Univ. Oklahoma.

WRIGHT, S. 1943. Isolation by distance. Genetics 28: 114–138.