High Incidence of "Leapfrog" Pattern of Geographic Variation in Andean Birds: Implications for the Speciation Process

Abstract. *Many species of birds in the humid forests of the Andes show a pattern of geographic variation in color that is virtually unknown in other regions of the world. This pattern, here termed "leapfrog," is one in which two populations very similar in appearance are geographically separated from each other by very different, intervening populations of the same species. Approximately 21 percent of all Andean bird species and superspecies with three or more differentiated populations show the leapfrog pattern, and several of these show multiple cases of leapfrogging color patterns. Lack of concordance in the geographic distribution of taxa showing the leapfrog pattern suggests that there is a strongly random component in phenotypic differentiation with respect to direction, geography, and timing.*

Patterns of geographic variation in birds have been documented and analyzed for a half-century or more, and the interpretation of these patterns has provided much of the basis for speciation theory (*1*). The clinal nature of most patterns of color variation has been interpreted as evidence for the importance of gene flow, environmentally induced selection, or both, in determining population structure (*1*). Syntheses of overall patterns of geographic variation produced "Gloger's rule"—the tendency for populations from more humid areas to be more heavily pigmented than conspecific populations from less humid areas—and what could be called "Mayr's rule"—the association between increasingly marked geographic isolation and increasingly marked phenotypic differentiation.

I now report a pattern of geographic variation in color in Andean birds, the generality of which has heretofore not been recognized. This counterclinal pattern, here labeled the "leapfrog" pattern, is one in which, within a single biotope, two phenotypically very similar populations are geographically separated from each other by very different intervening populations of the same species (see cover). Geographic variation of this type has been reported for a few bird species (*2*), and two cases from the Andes have been studied extensively (*3*); however, such cases have received little theoretical attention.

To quantify the frequency of occurrence of the leapfrog pattern in Andean birds, I analyzed geographic variation in color patterns of all bird species in humid forest and forest edge in the Andes from northern Colombia and Venezuela to northwestern Argentina, the southern limit of humid montane forest. This region was selected because of the relative homogeneity in habitats at any given elevation over a broad latitudinal range (*4*). The sample consisted of 386 species and an additional 30 superspecies assembled from a subset of the species sample.

Geographic variation in color pattern was analyzed within the framework of current subspecies limits. Although the subspecies concept has been attacked repeatedly on conceptual and practical grounds (*5*), subspecies were used as the unit of analysis simply because no alternative existed; a quantitative, comprehensive assessment of color variation in all 386 species would be a life-long task. The study skin collection of the Museum of Zoology, Louisiana State University, was the primary source of data for the analysis. These data were supplemented by compendiums of subspecies descriptions (*6*) and recent taxonomic revisions. A species or superspecies was considered to show the leapfrog pattern if two geographically nonadjacent taxa were more similar in plumage pattern and color to one another than either was to the intervening taxon.

A conservative bias in the analysis was that only major, conspicuous features of coloration and pattern were analyzed; potential leapfrog patterns in subtle, less obvious plumage characters were ignored. Another conservative bias was that many described subspecies from the Andes cannot be readily distinguished from adjacent populations with taxonomically acceptable (75 percent), much less statistically acceptable (95 percent) (*7*), certainty; inclusion of invalid subspecies artificially inflates the number of species in which a leapfrog pattern can be detected.

By definition, the leapfrog pattern can be detected only in species with three or more subspecies. Of the 386 species examined, 127 were monotypic, 45 had only one, and 85 had only two subspecies within the geographic limits of the study. Thus, 129 species (33.4 percent) remained for inclusion in the analysis. Of these, 25 (about 19 percent) (*8*) showed the leapfrog pattern. An additional nine species showed the leapfrog pattern when subspecies from outside the main Andes were included; for example, from the tepuis of southeastern Venezuela, coastal ranges of Venezuela, and the highlands of Middle America. As for superspecies, only six of the 30 examined contained the necessary minimum of three component allospecies. Of these, three superspecies (50 percent) displayed a leapfrog pattern of color variation (*9*). Thus, combining species and superspecies, of 135 taxa in which the leapfrog pattern is possible (that is, those with three or more component taxa), 28 (about 21 percent) displayed leapfrog color variation (Table 1). Furthermore, there are multiple cases of the leapfrog pattern within three species and one superspecies (*10*). Leapfrog patterns occur with disproportionately higher frequency in taxa with higher numbers of component taxa; more than 50 percent of the species or superspecies with six or more component taxa show the leapfrog pattern (Table 1).

These results raise two questions: (i) Why does the leapfrog pattern appear with such high frequency in the Andes in comparison with other areas of the world (*11*)? and (ii) How is leapfrog variation produced?

The answer to the first question seems straightforward. Any pattern of geographic variation should be amplified in the Andes for the following reasons. (i) The tremendous topographic relief of the Andes, with its extremely high cordilleras transected by very deep river canyons, is matched by no other mountain range over such a broad latitudinal range. (ii) The linearity of the Andes and the resulting long and narrow, north-south distribution of taxa greatly reduces the potential area of contact between parapatric forms; thus the area across which gene flow could occur is greatly reduced in comparison to the less linear distributions of taxa in other areas. (iii) The richness of the avifauna relative to other montane regions increases the number of taxa in which any potential pattern may be detected.

How is the leapfrog pattern produced? Hypotheses that involve long-distance dispersal from source areas, such as Diamond's (*12*) "checkerboard" pattern in montane New Guinea, would be extremely unlikely to apply to the sedentary Andean birds that exhibit the leapfrog pattern; long-distance migration or movement is not known for any bird species of the humid slope of the Andes and is suspected for only one species (*13*). Thus, it is improbable that more distant populations would colonize an area more readily than populations adjacent to the same area. Other hypotheses—such as (i) convergent evolution in the phenotypically similar but geographically separated taxa (*14*); (ii) more rapid, divergent evolution in the central, intervening taxa in evolutionary "hot spots"; (iii) centrifugal speciation (*4*); or (iv) ancient corridors connecting the currently separated but phenotypically similar taxa—would all predict a moderate to high degree of concordance in the geographic distributions of the central taxa. This is not the case; the ranges of the central taxa are scattered throughout the Andes with many falling either entirely north or entirely south of the equator (Fig. 1).

Table 1. Frequency of leapfrog patterns with respect to number of component taxa (subspecies in the case of species level examples, allospecies in the case of superspecies examples).

Component taxa (No.)	Examples (No.)	Examples in which leapfrog pattern occurs	
		No.	%
3	53	6	11.3
4	35	3	8.5
5	15	2	13.3
6	17	9	52.9
7	10	4	40.0
8	2	1	50.0
9	2	2	100.0
14	1	1	100.0
Total	135	28	20.7

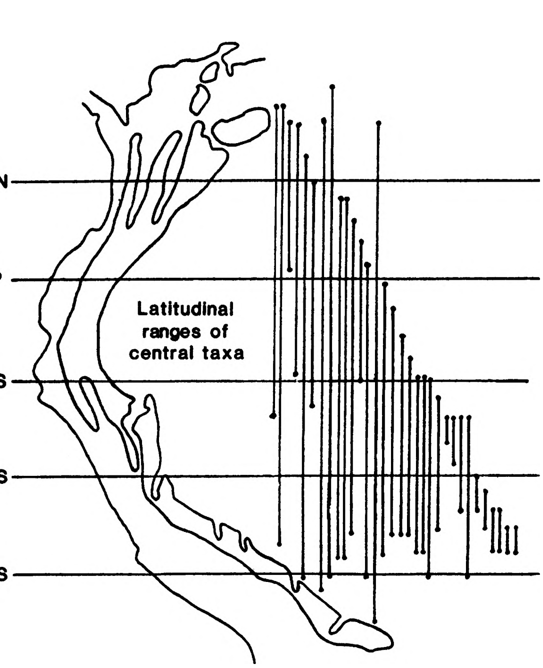

Fig. 1. Latitudinal ranges of central, intervening taxa in the leapfrog pattern are plotted adjacent to a schematic representation of the Andes (above 1500 m). Included are four cases in which more than one leapfrog pattern occurs within a species or subspecies.

This rather chaotic geographic distribution of central and peripheral taxa (*15*) suggests that many phenotypic changes may appear at random with respect to geography and are not induced by the environment in any predictable way. Once a taxon is fragmented into geographically isolated populations, phenotypic change may occur at different times and rates in any of the isolates; some of the time, by chance alone, the central taxon will differentiate first, producing the leapfrog pattern. This is essentially the same hypothesis formulated long ago by Chapman (*16*). If this hypothesis is correct, much of the phenotypic differentiation involved in the speciation process may be due to stochastic factors, absence of gene flow, and transilience (*17*), rather than to more predictable, environmentally induced factors. Rigorous tests of these hypotheses will be reported (*18*).

There is no reason to suspect that leapfrog patterns are restricted to color; perhaps other characters, such as vocal dialects, allele frequencies, and morphometrics, also show leapfrog variation. Examination of other Andean biota, especially butterflies, frogs, and plants with strongly patterned flowers, may also reveal this pattern.

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References and Notes

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liaris, *H. melanotis*, *Euphonia xanthogaster* (Andean foothill races), *Tangara arthus*, *Diglossa lafresnayii*, *Basileuterus tristriatus*, *B. coronatus*, *Conirostrum sitticolor*, and *Cyanolyca viridicyana*. R. A. Paynter, Jr. [*Bull. Mus. Comp. Zool.* **148**, 323 (1978)], pointed out the leapfrog pattern in *Atlapetes*. One of the leapfrog patterns rests on an undescribed new subspecies in *Pseudotriccus ruficeps* (T. S. Schulenberg, in preparation).
9. *Metallura aeneocauda* supersp., *Schizoeaca fuliginosa* supersp., and *Diglossa carbonaria* supersp.
10. *Chamaepetes goudotii*, *Atlapetes rufinucha*, *Chlorospingus ophthalmicus*; *Schizoeaca fuliginosa* supersp. For discussion of variation in *Schizoeaca*, see J. V. Remsen [*Proc. Biol. Soc. Wash.* **94**, 1068 (1981)].
11. It is assumed that the virtual absence of reports of such patterns in other areas reflects a low incidence rather than lack of thorough study. The likelihood of the latter seems remote because geographic variation in birds has been much more thoroughly studied in North America, Eurasia, Africa, and Australasia than in South America; scrutiny of syntheses of geographic variation in these regions reveals no clear cases of the leapfrog pattern within a given biotic region, although instances of presumed convergence, mostly interpretable as examples of Gloger's rule, can be identified where regions similar in climate or habitat are separated by a region differing in these respects [A. Keast, *Bull. Mus. Comp. Zool.* **123**, 305 (1961); B. P. Hall and R. E. Moreau, *An Atlas of Speciation in African Passerine Birds* (Trustees of the British Museum of Natural History, London, 1970); D. W. Snow, Ed., *An Atlas of Speciation in African Non-Passerine Birds* (Trustees of the British Museum of Natural History, London, 1978); C. Harrison, *An Atlas of the Birds of the Western Palearctic* (Princeton Univ. Press, Princeton, N.J., 1982)].
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14. The term "polytopic subspecies" has been applied to such cases by E. O. Wilson and W. L. Brown, Jr. [*Syst. Zool.* **2**, 97 (1953)]. Although climatological data are generally unavailable for forested regions of the humid eastern Andes, it seems highly unlikely that any subtle geographic differences that may exist would be sufficient to promote the radical and abrupt phenotypic changes that characterize geographic variation in Andean birds. Mayr's [*Ibis* **101**, 293 (1959)] broader definition of polytopic subspecies would encompass the leapfrog pattern.
15. Limits of geographic distribution in Fig. 1 often coincide with geographic barriers; for example, the Marañón, Apurímac, and Urubamba rivers in Peru.
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17. A. R. Templeton, *Evolution* **34**, 719 (1980).
18. J. V. Remsen, Jr., and S. M. Lanyon, in preparation.
19. The Andean bird collections at the Museum of Zoology of Louisiana State University have been generously supported by J. S. McIlhenny, B. M. Odom, H. Irving, and L. Schweppe. G. Barrowclough, G. Bejarano, R. Bleiweiss, B. S. Bowen, G. R. Graves, M. S. Hafner, N. K. Johnson, R. R. Koford, S. M. Lanyon, J. P. O'Neill, and F. Vuilleumier provided many constructive criticisms of the manuscript.

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Individuals from 3 populations of *Hemispingus superciliaris*, a small tanager of the Andes that illustrates the "leapfrog" pattern of geographic variation. Yellow populations of the northern and southern Andes are geographically separated by very differently colored gray populations in central Peru. This type of pattern is found in about 20% of all Andean birds with 3 or more subspecies.

Painting by John P. O'Neill, Museum of Natural Science, Louisiana State University, Baton Rouge 70803