

## References and Notes

1. A. Arimura, *Biomed. Res.* **2**, 233 (1981).
2. P. Hobart, R. Crawford, L. P. Shen, R. Pictet, W. J. Rutter, *Nature (London)* **288**, 137 (1980).
3. R. H. Goodman, J. W. Jacobs, W. W. Chin, P. K. Lund, P. C. Dee, J. F. Habener, *Proc. Natl. Acad. Sci. U.S.A.* **77**, 5869 (1980).
4. L.-P. Shen, R. L. Pictet, W. J. Rutter, *ibid.* **79**, 4575 (1982).
5. W. L. Taylor, K. J. Collier, R. J. Deschenes, H. L. Weith, J. E. Dixon, *ibid.* **78**, 6694 (1981).
6. M. Magazin, C. D. Minth, C. L. Funckes, R. Deschenes, M. A. Tavianini, J. E. Dixon, *ibid.* **79**, 5152 (1982).
7. C. D. Minth *et al.*, *J. Biol. Chem.* **257**, 10372 (1982).
8. P. C. Andrews and J. E. Dixon, *ibid.* **256**, 8267 (1981).
9. R. H. Goodman, J. W. Jacobs, P. C. Dee, J. F. Habener, *ibid.* **257**, 1156 (1982).
10. J. E. Shields, M. A. Root, W. J. Rutter, unpublished data.
11. H. Oyama, R. A. Bradshaw, O. J. Bates, A. Permutt, *J. Biol. Chem.* **255**, 2251 (1980).
12. A. V. Schally *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **77**, 4489 (1980).
13. F. Esch, P. Bohlén, N. Ling, R. Benoit, P. Brazeau, R. Guilleman, *ibid.*, p. 6827.
14. L. Pradayrol, H. Jornavall, V. Mutt, A. Ribert, *FEBS Lett.* **109**, 5558 (1980).
15. S. L. Naylor, A. Y. Sakaguchi, L.-P. Shen, G. I. Bell, W. J. Rutter, T. B. Shows, *Proc. Natl. Acad. Sci. U.S.A.* **80**, 2686 (1983).
16. R. C. Crawford, P. Hobart, W. J. Rutter, in preparation.
17. R. F. Weaver and C. Weissmann, *Nucleic Acids Res.* **7**, 1175 (1979).
18. R. Breathnach and P. Chambon, *Annu. Rev. Biochem.* **50**, 349 (1981).
19. I. Sures, J. Lowry, L. H. Kedes, *Cell* **15**, 1033 (1978).
20. G. L. Slightom, A. E. Blechl, O. Smithies, *ibid.* **21**, 627 (1980).
21. C. S. Craik, W. J. Rutter, R. Fletterick, *Science* **220**, 1125 (1983).
22. G. I. Bell, J. H. Karam, W. J. Rutter, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 5759 (1981).
23. F. R. Blattner *et al.*, *Science* **202**, 1279 (1978).
24. A. Maxam and W. Gilbert, *Methods Enzymol.* **65**, 499 (1980).
25. J. L. Manley, A. Fire, A. Cano, P. A. Sharp, M. L. Gefter, *Proc. Natl. Acad. Sci. U.S.A.* **77**, 2855 (1980).
26. P. A. Weil, D. S. Luce, J. Segall, R. G. Roeder, *Cell* **18**, 469 (1979).
27. T. Matsui, J. Segall, P. A. Weil, R. G. Roeder, *J. Biol. Chem.* **255**, 11992 (1980).
28. D. N. Standring, A. Venegas, W. J. Rutter, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 5963 (1981).
29. We thank G. Bell and D. Standring for their contributions to this research and for their help in the preparation of the manuscript, V. Watt for aid in determining the restriction map of  $\lambda$ HSI-1 and  $\lambda$ HSI-2, and R. Crawford, W. Swain, and P. Hobart for valuable advice during this work. We also thank L. Spector for manuscript preparation. Supported by NIH grant AM 21344.

\* Present address: Institute of Biochemistry, Shanghai, People's Republic of China.

23 February 1983; accepted 16 February 1984

## 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 pat-

tern, 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 assem-

bled 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

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

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).

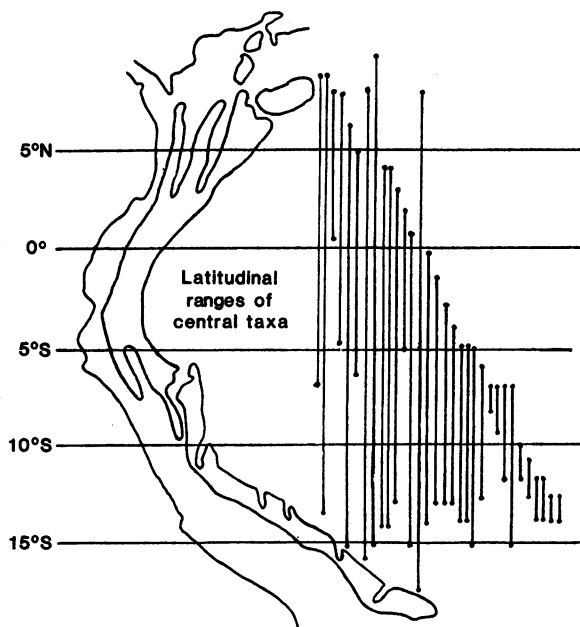


Fig. 1. Latitudinal ranges of central, intervening taxa in the leapfrog pattern are plotted adjacent to a schematic representation of the Andes (above 1500 m). Included are four cases in which more than one leapfrog pattern occurs within a species or subspecies.

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 transience (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.

J. V. REMSEN, JR.

Museum of Zoology,  
Louisiana State University,  
Baton Rouge 70893-3216

#### References and Notes

1. B. Rensch, *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung* (Borntraeger, Berlin, 1929); E. Mayr, *Systematics and the Origin of Species* (Columbia Univ. Press, New York, 1942); *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, Mass., 1963); J. A. Endler, *Geographic Variation, Speciation, and Clines* (Princeton Univ. Press, Princeton, N.J., 1977); F. Vuilleumier, *Proc. Int. Ornithol. Congr.* 17, 1296 (1980); in *Ecología y genética de la especiación animal*, O. A. Reig, Ed. (Universidad Simón Bolívar, Caracas, 1982), pp. 101-148.
2. W. L. Brown, Jr., *Quart. Rev. Biol.* 32, 247 (1957).
3. F. M. Chapman, *Bull. Am. Mus. Nat. Hist.* 48, 243 (1923); J. T. Zimmer, *Auk* 46, 21 (1929); F. Vuilleumier, *Am. Mus. Novit.* (No. 2381) (1969); G. R. Graves, *Condor* 84, 1 (1982).
4. F. M. Chapman, *Bull. Am. Mus. Nat. Hist.* 55, 90 (1926).
5. E. O. Wilson and W. L. Brown, Jr., *Syst. Zool.* 2, 97 (1953); F. C. James, *Ecology* 51, 365 (1970); R. K. Selander, in *Avian Biology*, D. S. Farner and J. R. King, Eds. (Academic Press, New York, 1971), vol. 1, pp. 57-147.
6. C. E. Hellmayr, C. B. Cory, B. Conover, *Catalogue of Birds of the Americas*, parts I to XI (Zoological Series, vol. 13, Field Museum of Natural History Chicago, 1918 to 1948); J. T. Zimmer, "Studies of Peruvian birds," Nos. 1 to 66 (published in *American Museum Novitates* from 1931 to 1955); E. R. Blake, *Manual of Neotropical Birds* (Univ. of Chicago Press, Chicago, 1977), vol. 1.
7. D. Amadon, *Condor* 51, 250 (1949).
8. *Chamaepetes goudotii*, *Eriocnemis luciani*, *Synallaxis azarae*, *Myrmotherula longicauda*, *Ochthoeca cinnamomeiventris*, *O. frontalis*, *O. fumicolor*, *Pseudotriccus ruficeps*, *Mecocerculus leucophrys*, *Hemitriccus granadensis*, *Rupicola peruviana*, *Turdus fuscater*, *Atlapetes rufinucha*, *A. schistaceus*, *A. torquatus*, *Chlorospingus ophthalmicus*, *Hemispingus superci-*

- 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. Schlenker, 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)].
12. J. M. Diamond, Science 179, 759 (1973).
  13. *Haplospiza rustica* (T. A. Parker III and J. V. Remsen, in preparation).
  14. The term "polytypic 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 polytypic 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.
  16. F. M. Chapman, Bull. Am. Mus. Nat. Hist. 48, 243 (1923).
  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.

19 April 1983; accepted 24 August 1983

## Arctic Biostratigraphic Heterochroneity

Hickey *et al.* (1) described the magnetic stratigraphy (not magnetic anomaly profile) and biostratigraphy of Upper Cretaceous and Lower Cenozoic sediments of the Eureka Sound Formation (2, 3) of arctic Canada and claimed that there is substantial heterochroneity of biostratigraphic units. Their conclusions, if correct, have great ramifications with respect to the correlation and evolution of the North American biota and to the underlying bases for biostratigraphy in general. Although the conclusions rest almost entirely on the magnetostratigraphy of the sediments in question, the data as presented cannot be assessed; indeed, the paleomagnetic work (4) is essentially unpublished except in abstract (5). Nevertheless, the summary of numeric data (1, reference 14) leads us to believe that the magnetic stratigraphy is suspect and that the correlation of supposed magnetozones to the geomagnetic polarity time scale is very insecure.

A necessary criterion for assigning normal or reversed polarity to a sample direction is whether the calculated virtual geomagnetic pole (VGP) for the north-seeking magnetization falls, respectively, at high northern or high southern paleolatitudes with respect to the mean paleomagnetic pole; the polarity should be regarded as indeterminate if the VGP falls at intermediate latitudes—for example, within 45° of the paleoequator. Such intermediate positions can be records of

excursions or polarity transitions of the geomagnetic field but more frequently are indicative of poor data, the result of sample misorientation or mismeasurement, unresolved complex magnetizations, or other experimental errors and inadequacies in the magnetic record.

The poor internal consistency of the paleomagnetic data used by Hickey *et al.* compromises any precise interpretation of the stratigraphic polarity sequence. The parameter *K* (estimate of Fisher's precision parameter) is a measure of dispersion in the directional data; when *K* approaches zero the directions are uniformly distributed on a sphere and are random, whereas for large values of *K* the directions are confined to a small portion of the sphere near to the mean direction (6). The cited value for *K* is 2.4 for the 158 sample VGP's used to construct the magnetic polarity stratigraphy. It is useful to calculate from *K* the radii of the circles whose centers are the mean and which contain specified percentages of the sample VGP's (7). For the given value of *K* and a Fisherian distribution, 50 percent of the sample VGP's are expected to lie within about 44°, and 63 percent (the circular standard deviation, analogous to the standard deviation of the normal distribution) lie within about 52° of the estimated overall mean paleomagnetic pole position. In other words, the sense of polarity of more than a third to almost half the samples should be

considered indeterminate because their VGP positions are expected to fall in low paleolatitudes and farther than 45° from the paleomagnetic pole. This leaves no more than 100 and as few as 80 samples to determine the polarity sequence of about 3500 m of section.

The large dispersion in the paleomagnetic data strongly suggests the presence of pervasive spurious or secondary magnetizations and a low fidelity record of the geomagnetic field. Relevant evidence from laboratory or field tests was not presented to suggest otherwise. Although we cannot ascertain the stratigraphic distribution of the 80 to 100 samples that might provide interpretable polarity information, if they were uniformly distributed through the composite section spanning about 40 million years (Campanian to Early Eocene), then an average temporal resolution of no better than 0.4 million years is possible. Considering that polarity chrons and subchrons in the Late Cretaceous and Early Tertiary have durations of similar order (8–11) and that about 30 percent of the sections are unexposed, we believe that the polarity sequence of the Eureka Sound Formation sections must be considered poorly constrained. Since correlation to the geomagnetic polarity time scale depends critically on recognizing a characteristic pattern of normal and reverse polarity intervals, the inclusion of magnetozones on the basis of ambiguous or missing data will change the magnetic stratigraphy in significant ways.

The poor paleomagnetic data, the ambiguities in independent lithostratigraphic correlation between sections, and the lack of evidence concerning possible unconformities and time gaps within the Eureka Sound Formation (notably between informal members III and IV which contain the terrestrial vertebrates) are impediments to a meaningful discussion of alternative magnetostratigraphic correlations. It should suffice to mention that in general the correlation of a normal polarity magnetozon with chron C24N because it is "stuttered" (1) is not diagnostic on its own, since for example the younger chron C23N is also "stuttered" (8–12). Chron C33N was identified supposedly on the basis of the stratigraphic thickness of the normal polarity magnetozon, "corroborated" by fossils, but in fact the basis was mainly biostratigraphic, bringing the argument full circle.

Paleobotanical and other evidence indicates that polar climate in the Late Cretaceous and Early Tertiary, although seasonal, was more moderate than that of today. Therefore one might expect