

Bergmann's rule near the equator: Latitudinal clines in body size of an Andean passerine bird

(clinal variation/temperature seasonality/*Diglossa*/flower piercer)

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ABSTRACT Critical correlative support for Bergmann's ecogeographic rule is provided by symmetrical patterns of size variation in *Diglossa carbonaria*, a tropical passerine bird whose geographic range in the Andes Mountains of South America straddles the equator. Body size is positively correlated with latitude both north and south of the equator. Moreover, parapatric taxa that exhibit either partial (northwestern Bolivia) or complete (northern Peru) reproductive isolation converge in body size. Relative uniformity in the length of the highly modified flower-piercing bill among populations of *D. carbonaria* that differ significantly in body size suggests that character displacement or interspecific competition is not responsible for these patterns. These findings support the hypothesis that climate, particularly temperature seasonality, is an important environmental determinant of geographic size variation in homeotherms. In addition they demonstrate that clinal variation correlated with subtle climatic gradients can occur in tropical environments.

Bergmann's ecogeographic rule, the tendency for body size in homeotherms to be positively correlated with latitude and colder climates, has been recognized for nearly 150 years (1). Although Bergmann's rule usually refers to intraspecific variation in body size in recent literature (2), Bergmann's paper emphasized interspecific variation as well (3).

The generality and cause of Bergmannian size variation have been debated (4–9), but parallel patterns among bird species from North America, Asia, Europe, and Australia implicate climate as a determinant of body size (3, 10–16) and suggest that larger size may be a thermoregulatory adaptation to severe or seasonal climates. As an example, much of the intracontinental size variation in introduced and native populations of the house sparrow (*Passer domesticus*) is correlated with geographic variation in temperature and humidity (17–19). Seasonality of temperature, however, is the only climatic variable studied thus far that is significantly correlated with sparrow body size in both Europe and North America (20). Collectively, these and other data (20–24) suggest larger body size may be a thermoregulatory adaptation to severe, seasonal, or unpredictable climates.

Most empirical evidence of Bergmann's rule comes from temperate latitudes (>20°). Several studies of size variation in tropical homeotherms have shown clinal patterns (25–27), but with the notable exception of Moreau's work on African *Zosterops* (28), statistical analyses of the relationship of body size with climatic variables have not been reported. Turning the focus to the neotropics, the primary difficulties facing investigators of size variation are the paucity of documented specimens, patchy distribution of collections, and lack of long-term weather data from key regions, along

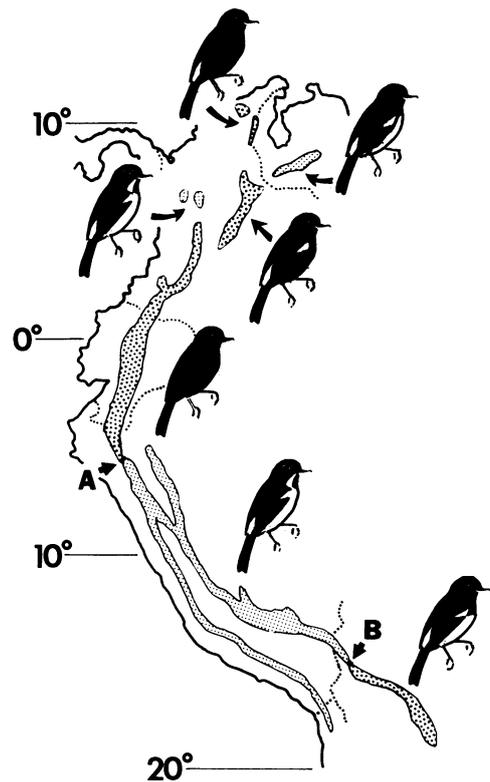


FIG. 1. Geographic distribution of *D. carbonaria* taxa in the Andes Mountains of South America (from top to bottom): *nocticolor*, *gloriosa*, *uilleumieri*, *humeralis*, *aterrima*, *brunneiventris*, and *carbonaria* (32). The similarly plumaged *brunneiventris* and *uilleumieri* are thought to resemble the ancestral stock because they occur in widely separated areas some 1500 km apart. This distributional hiatus is occupied by the black-plumaged taxa (*aterrima*, *humeralis*, *nocticolor*). Breast colors are rufous (*brunneiventris*), chestnut (*gloriosa*), gray (*carbonaria*), and black (*aterrima*, *humeralis*, *nocticolor*). Zones of secondary contact occur in northern Peru (A) and northwestern Bolivia (B).

with the necessary weakness of the correlative method. Nevertheless, patterns of size variation in neotropical species whose ranges cross the equator offer a critical test of the temperature seasonality hypothesis. Other selective agents on body size such as interspecific competition, predator-prey relationships, and climatic variables such as humidity, cloudiness, and rainfall may exhibit little intratropical correlation with latitude. Temperature seasonality, however, is generally correlated with latitude in continental South America (29, 30). If the temperature seasonality hypothesis is correct, then symmetrical patterns of size variation in homeotherms should occur on either side of the equator. I report here a conclusive demonstration of Bergmannian size variation near the equator in an Andean passerine bird, the carbonated flower piercer (*Diglossa carbonaria*).

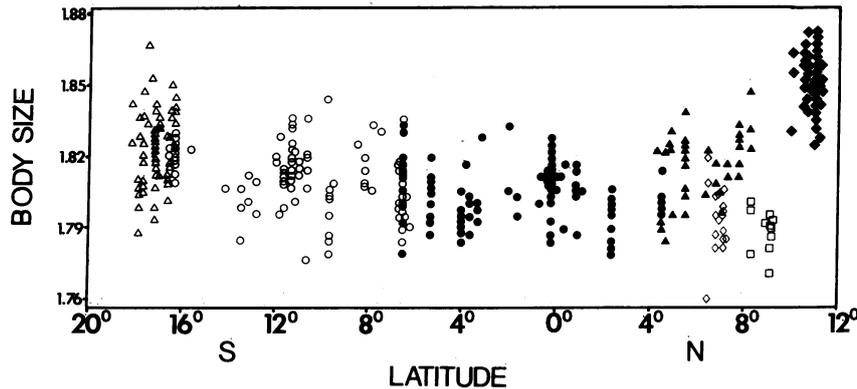


FIG. 2. Bergmannian size variation in body size (geometric mean of \log_{10} wing and \log_{10} tail lengths) of male specimens ($n = 356$) of *D. carbonaria* (see Fig. 1). Δ , *carbonaria*; \circ , *brunneiventris*; \bullet , *aterrima*; \blacktriangle , *humeralis*; \diamond , *vuilleumieri*; \square , *gloriosa*; \blacklozenge , *nocticolor*; \bullet , \blacktriangle , \blacklozenge , "black" taxa.

METHODS

Flower piercers are nine-primaried oscines restricted to the highland forest and shrub lands of the neotropics from Mexico south through Central America to northern Argentina (31). The genus *Diglossa* reaches its greatest diversity in the Andes where up to seven species occur on an elevational gradient. *D. carbonaria* is a polytypic species composed of a linear series of nonmigratory populations (Fig. 1) that inhabit a narrow elevational zone from 2300 to 3400 m above sea level (or rarely from 1800 to 4000 m) in the Andes from Colombia (11°10' N) and Venezuela south to northern Chile and Bolivia (18°30' S). In common with most other species in the genus, *D. carbonaria* has a highly modified, hooked bill that it uses to pierce tubular flower corollas in order to extract nectar. Recent field work (32, 33) indicates that some of the seven allopatric or parapatric taxa may be partially or totally reproductively isolated. Nomenclaturally, these form a superspecies (34) composed of allospecies, at or near the species level (to avoid confusion taxa are referred to in this paper by subspecific epithet). There appear to be no significant differences in elevational distributions among taxa; populations are similar in ecology and social behavior (35, 36) and seem to form a single "ecological" species.

Within the elevational range of *D. carbonaria*, annual temperature variation depends on seasonal differences in cloud cover, humidity, and the relative proximity of the

Humboldt current. Owing to the complex topography of the Andes, demes of flower piercers may be exposed to significant variation in temperature and precipitation over linear distances as short as a few kilometers. Long-term climatic data are available for only a few Andean localities. Thus, correlations between body size and temperature and humidity are not yet possible. Latitude, which is generally correlated with temperature seasonality in the Andes (29), was therefore used in this study as a surrogate variable.

RESULTS

Body size of 531 museum specimens was estimated by the geometric mean of log-transformed wing and tail lengths, which are highly correlated with one another ($\delta\delta$, $r^2 = 0.833$; ♀♀ , $r^2 = 0.825$). For specimens accompanied by mass data, wing length was significantly correlated with body mass ($n = 57$; $r^2 = 0.458$, $P < 0.0001$). Sexes were considered separately because body size of males was significantly larger than that of females ($F_{1,16} = 313.5$, $P < 0.0001$).

When all populations were pooled, body size in both sexes was highly correlated with latitude both north and south of the equator (Fig. 2 and Table 1). The "black" taxa (*nocticolor*, *humeralis*, *aterrima*), which differ from one another in the amount of gray on the rump and shoulders, are believed to form a monophyletic group within the radiating *D. carbonaria* superspecies (31, 32). They are flanked by the

Table 1. Relationship between body size and latitude in the carbonated flower piercer (*D. carbonaria*)

| Taxon | Range of latitude | Sex | <i>n</i> | <i>b</i> * | SE* | <i>r</i> | <i>P</i> |
|-----------------------|---------------------------------|--------|----------|------------|------|----------|----------|
| Pooled comparisons | | | | | | | |
| All taxa pooled | North of equator (0°–11°10') | Male | 141 | 5.31 | 0.53 | 0.42 | <0.0001 |
| | | Female | 87 | 4.94 | 0.55 | 0.48 | <0.0001 |
| | South of equator (0°–18°10') | Male | 215 | 1.08 | 0.17 | 0.16 | <0.0001 |
| | | Female | 87 | 1.29 | 0.24 | 0.25 | <0.0001 |
| Black taxa pooled | North (0°–11°10') | Male | 114 | 5.64 | 0.40 | 0.64 | <0.0001 |
| | | Female | 79 | 4.93 | 0.41 | 0.65 | <0.0001 |
| Individual taxa | | | | | | | |
| <i>humeralis</i> | North (4°24'–8°20') | Male | 35 | 3.61 | 1.76 | 0.09 | NS |
| | | Female | 19 | –3.78 | 2.36 | 0.08 | NS |
| <i>aterrima</i> | North (0°–4°35') | Male | 29 | –3.14 | 1.95 | 0.05 | NS |
| | | Female | 15 | –0.90 | 2.46 | 0.00 | NS |
| | South (0°–6°30') | Male | 65 | 0.40 | 0.63 | 0.00 | NS |
| | | Female | 28 | –1.92 | 0.75 | 0.17 | NS |
| <i>brunneiventris</i> | South (6°25'–16°30') | Male | 87 | 1.18 | 0.50 | 0.05 | NS |
| | | Female | 39 | –0.33 | 0.60 | 0.00 | NS |

Individual taxa have geographic ranges of $>3^\circ$ latitude. *b*, Regression coefficient; NS, not significant. Significance of *P* values is adjusted for number of simultaneous tests ($0.05 \times 14 = 0.007$).

*Multiple by 10^{-4} .

ornately plumaged geographic isolates, *gloriosa* (Venezuela) and *uilleumieri* (Colombia), in the northern Andes. Correlations of body size with north latitude within the black-plumaged clade were positive and highly significant. Body sizes of *gloriosa* and *uilleumieri* are smaller than predicted from regression of the black taxa. This divergence from prediction may be attributed to genetic differentiation in peripheral isolates as suggested by marked plumage differences (32).

It should be noted that body size within taxa was not significantly correlated with elevation ($P > 0.05$). This indicates that an altitudinal effect (3, 28, 37–39), if present, is obscured by error in altitude measurement or dispersal from the natal site in the narrow elevational range of carbonated flower piercers. The latter possibility is consistent with the field observation near the secondary contact zone in northern Peru of juvenile birds up to 21 km from the nearest breeding population (32).

Regression coefficients of body size–latitude correlations for individual taxa have mixed signs and were nonsignificant when family error rate was controlled. This is due, in part, to the reduced latitudinal range of taxa and small sample size. Latitudinal patterns of size variation appear to be nonlinear in some cases and contradictory to the expectations of a positive latitude–body size relationship. For example, population samples of *aterrima* from humid cloud forests of southern Colombia (2°–3° N) were smaller than those from the relatively drier intermontane region (ca. 0°) surrounding Quito in northern Ecuador. This size differentiation may reflect local variation in climate (3) as well as genetic differences among populations.

In comparisons of pooled taxa, the steepest gradient in body size occurs north of the equator. Although correlations between body size and latitude were lower south of the equator, some of the strongest evidence for climatic influence on flower-piercer phenotypes is found at zones of contact between phenotypically divergent populations in Peru and Bolivia. In northern Peru (6°25' S) (Fig. 1 location A), *brunneiventris* and *aterrima* exhibit complete reproductive isolation in a narrow zone of range overlap (32). A second contact zone occurs near La Paz, Bolivia (16°30' S) (Fig. 1 location B), where *brunneiventris* and *carbonaria* hybridize, at least occasionally (32, 33). Hybrids are readily distinguished by the mosaic pattern of plumage elements combining apomorphic characters from both of the parental forms (refs. 32 and 33; see methods in ref. 40). This strongly suggests that plumage pattern and color within the *D. carbonaria* superspecies are polygenically controlled. Thus, components of *Diglossa* plumage can be utilized as genetic markers. In both contact zones, measurements of wing, tail, tarsus, and bill of taxon pairs are statistically indistinguishable ($P > 0.05$) (32) and body size variation across contact zones appears to be clinal.

Although the cohesive effect of gene flow (2, 41) may be responsible for the size convergence (or absence of size divergence) of genetically differentiated but hybridizing taxa in Bolivia, alternative explanations must be sought for the remarkable size similarity of apparently reproductively isolated taxa in Peru. Contact between *aterrima* and *brunneiventris* probably occurred recently, mediated by several hundred years of human disturbance of habitat and cultivation (32). Character displacement (42, 43) has not had sufficient time to evolve and morphological convergence is most likely due to selection by climate and environmental resources, although nongenetic environmental induction (44) cannot be discounted.

Local populations of carbonated flower piercers compete with other species of flower piercers (from 0 to 6 sympatric *Diglossa* species), hummingbirds (6–20 sympatric species), and bees, for nectar and insects on flowers. The great

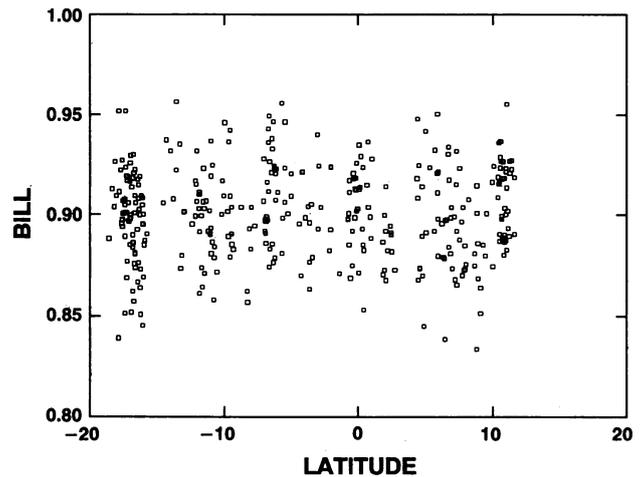


FIG. 3. Relationship of bill length (\log_{10}) of male carbonated flower piercers (*D. carbonaria*) ($n = 362$) and latitude. Negative latitudes are in the Southern hemisphere.

diversity of potential competitors (35) makes quantitative analysis of regional patterns of interspecific competition difficult. Because of the peculiar flower-piercing bill of *D. carbonaria*, congeneric species are their most likely avian competitors. Checkerboard distributions of flower-piercer species, however, do not explain patterns of size variation in *D. carbonaria*. Taxa in the glossy flower-piercer superspecies (*Diglossa lafresnayii*) are most similar to *D. carbonaria* in size, plumage pattern and color, and foraging ecology (31, 35, 45). *D. lafresnayii* has a more limited geographic range and a narrower elevational distribution and prefers cloud forest edge at timberline. Both species are locally syntopic over much of Amazonian slope of the Andes between 10° N and 17° S, but *D. lafresnayii* is absent from the Pacific slope of the Andes south of 6° S in northern Peru. The largest average body size in *D. carbonaria* occurs in Bolivia, where it is sympatric with *D. lafresnayii*, and in northern Colombia (*nocticolor* of Sierra Nevada de Santa Marta and Serrania Perija), where *D. lafresnayii* is absent. When *nocticolor* specimens are omitted, body size–latitude correlations of black taxa that are sympatric with *D. lafresnayii* north of the equator remain highly significant ($\delta\delta$, $r^2 = 0.23$, $P < 0.0001$; ♀♀ , $r^2 = 0.14$, $P < 0.03$). Thus, there is no evidence to suggest that character displacement or interspecific competition is responsible for latitudinal patterns of body size in *D. carbonaria*. This is supported by the relative uniformity of bill length among populations that differ significantly in body size along the latitudinal gradient (Fig. 3). Correlations of bill length and latitude are nonsignificant ($P > 0.05$) for both sexes, while bill length and body size correlations are nonsignificant for females ($r^2 = 0.01$, $P > 0.17$) and only marginally significant for males ($r^2 = 0.02$, $P > 0.01$).

Significant environmental influences on flower-piercer phenotypes are suggested by two observations: (i) positive correlations of body size with latitude north and south of the equator and (ii) convergence of body size in taxa exhibiting various amounts of reproductive incompatibility in zones of secondary contact. These data indicate that clinal patterns of variation in birds correlated with climatic variables are not restricted to temperate latitudes and may occur in relatively nonseasonal tropical environments.

DISCUSSION

The generality of Bergmannian size variation in Andean birds has yet to be investigated. Past studies (46, 47) have shown that differentiation in forest birds is positively correlated with

the mean of a species' elevational distribution. Species with high and narrow elevational ranges frequently exhibit complex latitudinal patterns of plumage and size variation (unpublished data), which are correlated with geographic barriers to gene flow. Dramatic variation among species having similar elevational distributions reflects differences in phenotypic plasticity and gene flow mediated by ecological and social behaviors. Impedance of gene flow combined with extreme variation in regional climatic gradients (e.g., arid intermontane rain shadows surrounded by cloud forest) facilitates adaptation to local environments and nonclinal patterns of size variation. The perception of Bergmannian size variation rests, in part, on clinal variation (3), which in turn depends on gene flow and spatial correlation of selective agents on body size including climate. Because of this, Bergmannian patterns of variation may increase with decreasing elevation in the Andes and be more common in the comparatively uniform Amazonian lowlands.

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1. Bergmann, C. (1847) *Gottinger Studien* 3, 595–708.
2. Mayr, E. (1963) *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, MA).
3. James, F. C. (1970) *Ecology* 51, 365–390.
4. Scholander, P. F. (1955) *Evolution* 9, 15–26.
5. Rosenzweig, M. L. (1968) *Am. Midl. Nat.* 80, 299–315.
6. McNab, B. K. (1971) *Ecology* 52, 845–854.
7. Zink, R. M. & Remsen, J. V. (1986) in *Current Ornithology*, ed. Johnston, R. F. (Plenum, New York), Vol. 4, pp. 1–69.
8. Geist, V. (1987) *Can. J. Zool.* 65, 1035–1040.
9. Patterson, J. D. (1990) *Can. J. Zool.* 68, 1610–1612.
10. Rensch, B. (1936) *Arch. Naturgeschi* 5, 317–363.
11. Meise, W. (1938) *Proc. Ninth Internat. Ornithol. Congr. (Internat. Ornithol. Congr., Berlin)*, pp. 233–255.
12. Ripley, S. D. (1950) *J. Bombay Nat. Hist. Soc.* 49, 355–417.
13. Snow, D. W. (1954) *Evolution* 8, 19–28.
14. Hamilton, T. H. (1961) *Evolution* 15, 180–195.
15. Power, D. M. (1969) *Syst. Zool.* 18, 363–373.
16. Tidemann, S. C. & Schodde, R. (1989) *Emu* 89, 79–82.
17. Johnston, R. F. (1969) *Syst. Zool.* 18, 206–231.
18. Johnston, R. F. & Selander, R. K. (1971) *Evolution* 25, 1–28.
19. Johnston, R. F. & Selander, R. K. (1973) *Am. Nat.* 107, 373–390.
20. Murphy, E. C. (1985) *Evolution* 39, 1327–1334.
21. Kendeigh, S. C. (1969) *Auk* 86, 13–25.
22. Calder, W. A. (1974) in *Avian Energetics*, ed. Paynter, R. A., Jr. (Nuttall Ornithol. Club, Cambridge, MA), No. 15, pp. 86–151.
23. Boyce, M. S. (1978) *Oecologia* 36, 1–19.
24. Searcy, W. A. (1980) *J. Theoret. Biol.* 83, 579–593.
25. Crowe, T. M. (1978) *Ann. S. Afr. Mus.* 76, 43–146.
26. Handford, P. (1983) *Evolution* 37, 920–930.
27. Haffer, J. & Fitzpatrick, J. W. (1985) in *Neotropical Ornithology*, eds. Buckley, P. A., Foster, M. S., Morton, E. S., Ridgely, R. S. & Buckley, F. G. (American Ornithol. Union, Washington) Monogr. 36, pp. 147–168.
28. Moreau, R. E. (1957) *Bull. Br. Mus. Nat. Hist. Zool.* 4, 311–433.
29. Schwerdtfeger, W., ed. (1976) *Climates of Central and South America, World Survey of Climatology Volume 12* (Elsevier, Amsterdam).
30. Muller, M. J. (1982) *Selected Climatic Data for a Global Set of Standard Stations for Vegetation Science* (Junk, The Hague, Netherlands).
31. Vuilleumier, F. (1969) *Am. Mus. Novit.* 2381, 1–44.
32. Graves, G. R. (1982) *Condor* 84, 1–14.
33. Vuilleumier, F. (1984) *Natl. Geogr. Res. Rep.* 16, 713–731.
34. Amadon, D. (1966) *Syst. Zool.* 15, 246–249.
35. Moynihan, M. (1974) *Geographic Variation in Social Behavior and in Adaptation to Competition Among Andean Birds* (Nuttall Ornithol. Club No. 18, Cambridge, MA).
36. Graves, G. R. (1982) *Biotropica* 14, 316–317.
37. Rand, A. (1936) *Am. Mus. Novit.* 890, 1–14.
38. Traylor, M. A. (1950) *Condor* 52, 123–126.
39. Koster, F. (1976) *J. Ornithol.* 117, 75–99.
40. Graves, G. R. (1990) *Proc. Biol. Soc. Wash.* 103, 6–25.
41. Barton, N. H. & Hewitt, G. M. (1989) *Nature (London)* 341, 497–503.
42. Brown, W. L. & Wilson, E. O. (1956) *Syst. Zool.* 4, 49–64.
43. Grant, P. R. (1972) *Biol. J. Linn. Soc.* 4, 39–68.
44. James, F. C. (1983) *Science* 221, 184–186.
45. Isler, M. L. & Isler, P. R. (1987) *The Tanagers: Natural History, Distribution, Identification* (Smithsonian Institution, Washington).
46. Graves, G. R. (1985) *Auk* 102, 556–579.
47. Graves, G. R. (1988) *Auk* 105, 47–52.