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RESEARCH LETTER

Latitudinal extent and natural history characteristics of birds in Nicaragua

THOMAS W. GILLESPIE

Department of Geography, University of California Los Angeles, Los Angeles, CA. 90095–1524, U.S.A., E-mail: tg@geog.ucla.edu

ABSTRACT

This paper assesses the latitudinal extent of terrestrial breeding birds in Nicaragua. In particular, associations among latitudinal midpoint, body mass, and latitudinal extent are examined; significant differences between natural history characteristics (trophic guild, forest dependence, number of forest types) and latitudinal extent are identified; and a test is undertaken of Rapoport's rule for birds at the edge of their northern or southern range in Nicaragua. Birds in Nicaragua were classified into four categories based on latitudinal extent: birds generally restricted to Central America (20%); birds near the edge of their range within Nicaragua (34%); Neotropical birds (42%); and Pan-American birds (4%). Latitudinal midpoint had a significant negative correlation with latitudinal extent over different taxonomic scales. Natural history characteristics of trophic guild, forest dependence and number of forest types can account for significant differences in species latitudinal extent. Carnivores had greater latitudinal extents than most other trophic guilds, non-forest birds had greater latitudinal extents than birds that require patchy forest, and birds that occur in four or more forest types had greater latitudinal extents than birds restricted to one or two forest types. Contrary to Rapoport's rule, birds with a northern affinity or latitudinal midpoint north of Nicaragua had significantly smaller latitudinal extents than birds with a southern affinity or latitudinal midpoint south of Nicaragua. A comparison of natural history characteristics of birds with northern and southern affinities found no difference between trophic guild or forest dependence but a significant difference among the number of forest types used by forest birds. Birds with a southern affinity were restricted to fewer forest types than birds with a northern affinity.

Key words birds, geographical range, latitudinal extent, macroecology, natural history characteristics, Neotropics, Nicaragua, Rapoport's rule.

INTRODUCTION

The resident avifauna of Nicaragua is composed of species that have dispersed from the Nearctic and Neotropic realms and species that evolved within Central America (Sclater, 1858; Howell, 1969). The geographical range size and range boundaries of species that occur in Nicaragua are determined by a combination of complex interacting abiotic, biotic and anthropogenic factors (Root, 1988; Wiens, 1989; Brown, 1995). However, a number of natural history characteristics may account for differences in species range size at a regional spatial scale (Blackburn & Gaston, 1996a; Harcourt, 2000). Body mass is a commonly used natural history characteristic in macroecology, and a positive correlation between geographical range size and body size has been shown for North American terrestrial avifauna (Brown & Maurer, 1987; Brown, 1995). Others have shown that this pattern becomes less predictable when range sizes are examined over a smaller spatial scale or for subsets of taxa (Blackburn & Gaston, 1996a; Blackburn *et al.*, 1998). Brown & Maurer (1987) examined the trophic guilds of terrestrial birds of North America and found trophic guilds overlapped extensively in comparison with geographical range sizes. It is not known if this pattern occurs in Central or South America where trophic guilds may be more specialized than temperate regions (Stiles, 1983; Karr, 1989). Habitat specificity and number of habitat types used by a species has been identified as associated with the geographical range size (Brown, 1995; Gaston, 1996). Species with a wide geographical range tend to have broad habitat specificity and occur in a variety of habitat types (Kattan, 1992; Brown, 1995; Harcourt, 2000).

A number of studies have examined Rapoport's rule, which states that a species' geographical extent decreases from higher to lower latitudes (Stevens, 1989; Gaston *et al.*, 1998). Although the pattern has been established for a number of diverse taxa, there have been few studies from lower or southern latitudes, which hampers understanding of the pattern and process associated with Rapoport's rule (Gaston *et al.*, 1998). One way to test Rapoport's rule is to select an arbitrary band of latitude on the globe and identify species that are at their northern or southern range limits within this band. According to the pattern predicted by Rapoport's rule, birds with a northern affinity or latitudinal midpoints at higher latitudes should have greater latitudinal extent than birds with a southern affinity or latitudinal midpoints at a lower latitude. An examination of natural history characteristics between species with a northern or southern affinity may help explain the process associated with Rapoport's rule. In particular, species at lower latitudes are hypothesized to be more specialized in diet, habitat dependency and number of habitat types than species at higher latitudes (Stevens, 1989; Harcourt, 2000).

This research on the latitudinal distribution of terrestrial breeding birds in Nicaragua has three primary objectives. First, this research examines the latitudinal extent of birds in Nicaragua. Secondly, this research undertakes hypothesis tests to identify if there are significant differences between natural history characteristics and latitudinal extent. Thirdly, this research tests for the pattern of Rapoport's rule by examining the latitudinal extent of species at the edge of their range in Nicaragua.

METHODS

Study area

Nicaragua is the largest country in Central America and has been identified recently as a biodiversity hotspot (Myers *et al.*, 2000). Nicaragua has eight habitat types that are used by terrestrial breeding birds (Gillespie, 2001): tropical dry forest, gallery forest and savanna occur on the western side of Nicaragua; upland pine–oak forest, montane or cloud forest and elfin forest occur on the tops of mountain ranges and volcanoes in central Nicaragua; pine savanna and lowland rain forest occur in eastern Nicaragua. Howell (1969) identified Nicaragua as an appropriate region to analyse the zoogeography of Central American avifauna because: (1) it is a former major geological discontinuity between northern and southern landmasses; (2) it contains major habitat types that terminate within Nicaraguan borders (i.e. upland pine–oak forest, pine savanna); and (3) it is an area that includes northern and southern limits of many species, with no taxa confined exclusively within its boundaries.

Data collection

Latitudinal extent and latitudinal midpoint were calculated for all terrestrial breeding birds in Nicaragua. Latitudinal extents were calculated as the straight-line distance between the northern and southern extremes of a species' breeding range with migratory ranges excluded (Gaston, 1996). It is expressed in the number of degrees within which a species is known historically to breed and was determined using a variety of range maps and breeding records from North, Central and South America. Latitudinal midpoint is the central point between a species' northern and southern extent. A complete list of sources for the Nicaraguan bird species list and for the calculation of latitudinal extent is available at www.geog.ucla.edu/birdrange/ref_nicar_birds.html.

Data on body mass, trophic guild, forest dependence and number of forest types were collected for all recorded terrestrial breeding birds in Nicaragua. Body masses were given in grams and were averages from mistnet data from Stiles & Skutch (1989) and Dunning (1992). Trophic guild classification followed Karr *et al.* (1990) and Stiles & Skutch (1989). Trophic guilds were classified as carnivores, frugivores, granivores, insectivores, nectarivores and omnivores. Forest dependence was based on a species' need for forest following the classification system of Stiles (1985). Species are classified as requiring almost solid forest, patchy forest or not needing forest. Seven forest types used by terrestrial breeding birds occur in Nicaragua: lowland rain forest, montane or cloud forest, elfin forest, tropical dry forest, gallery forest, lowland pine savanna and upland pine–oak forest. All forest birds were classified as occurring in one, two, three or four or more forest types (Stotz *et al.*, 1996; Gillespie, 2001). The majority of these data came from unpublished data from T.R. Howell, Stotz *et al.* (1996) and 17 months of field surveys within Nicaragua. All latitudinal and natural history data are available at www.geog.ucla.edu/birdrange ref_nicar_birds_data.html.

Data analysis

Associations among latitudinal midpoint, body mass and latitudinal extent were examined over three taxonomic scales: (1) all terrestrial breeding birds recorded in Nicaragua; (2) order and suborder (non-passerines, suboscines passerines, oscines passerines); and (3) eight large families and subfamilies with over 13 species: hawks (Accipitridae), pigeons (Columbidae), parrots (Psittacidae), hummingbirds (Trochilidae), antbirds (Formicariidae), flycatchers (Tyrannidae), tanagers (Thraupinae) and finches (Emberizinae). A Spearman's rank correlation was used to identify associations among latitudinal extent and latitudinal midpoint or body mass over the three taxonomic scales. Bonferroni corrections were employed for significance levels (Sokal & Rohlf, 1995).

Kruskal–Wallis tests and Mann–Whitney *U*-tests were used to test hypotheses of no differences between latitudinal extent and natural history characteristics of birds. Natural history characteristics included trophic guild, forest dependence and number of forest types. Significance levels from Mann–Whitney

U-tests are reported along with significance levels with Bonferroni corrections.

According to the pattern predicted by Rapoport's rule, birds with a northern affinity or latitudinal midpoints at high latitudes should have a greater latitudinal extent than birds with a southern affinity or a latitudinal midpoint at a low latitude. Nicaragua's political boundaries are located between 15°N and 11°N. Birds that have a southern latitudinal extent or range limit between 15°N and 11°N were considered to have a northern affinity, while birds with a northern latitudinal extent or range limit between 15°N and 11°N were considered to have a southern affinity. Mann–Whitney *U*-tests were used to identify if there were significant differences between latitudinal extent and latitudinal midpoint for species with a northern and southern affinity. Chi-square tests were used to identify if there were significant differences among natural history characteristics (trophic guild, forest dependence, number of forest types) for species with a northern or southern affinity. Some trophic guilds (i.e. frugivores and granivores) and number of forest types (three forest types and four or more) were combined for the chi-square test to obtain an expected value greater than five.

RESULTS

Distributional patterns of Nicaraguan birds

There were 424 terrestrial breeding birds recorded in Nicaragua with latitudinal extents ranging from 2° to 121° (Fig. 1). Birds in Nicaragua were classified into four general categories based on latitudinal extent and affinity: birds generally restricted to Central America, birds near the edge of their range within Nicaragua, Neotropical birds and Pan-American birds. There are 84 species (20%) with a latitudinal extent of 12° or less that are generally restricted to Central America and southern Mexico. There are 143 species (34%) with a latitudinal extent between 13° and 29° that have either a Nearctic or Neotropical affinity and are at or near the edge of their latitudinal distribution in Nicaragua. There are 177 species (42%) that have a Neotropical distribution with a latitudinal extent between 30° and 68°. These species latitudinal extents are slightly greater in the southern hemisphere than in the northern hemisphere with the exception of 14 birds with a Nearctic affinity. Twenty 20 species (4%) have latitudinal extents of 70° or greater and have breeding ranges higher than 20° north and south latitude.

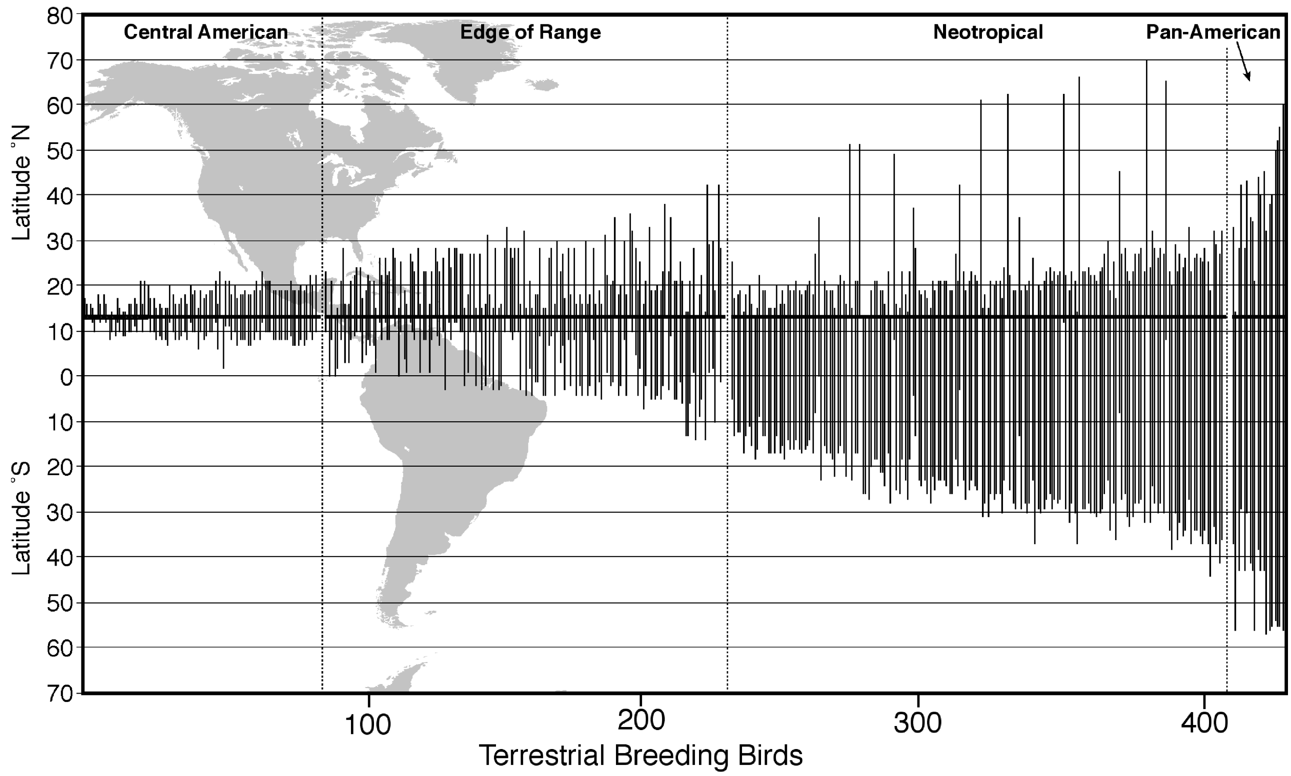

Fig. 1 The latitudinal extent of 424 terrestrial breeding birds in Nicaragua ranked by increasing latitudinal extent from smallest to largest latitudinal extent. A line is drawn at the latitudinal centre of Nicaragua at 13°N for reference. Birds can be divided into four general categories based on northern or southern affinity and latitudinal extent.

Table 1 Latitudinal extent in degrees for birds of Nicaragua and associations between latitudinal extent and latitudinal midpoint or body mass for birds in Nicaragua over three taxonomic scales

Taxonomic levelss	*n*	Latitudinal extent mean (std. dev.)	Latitudinal midpoint	Body mass
Terrestrial breeding birds	424	31.2 (21.1)	–0.586**	0.208**
Orders and suborders				
Non-passerines	189	33.7 (23.8)	–0.692**	0.343**
Suboscine passerines	100	30.9 (17.1)	–0.581**	0.116
Oscine passerines	135	28.3 (19.5)	–0.308**	–0.099
Family and subfamilies				
Accipitridae	25	51.6 (15.6)	–0.166	0.232
Columbidae	19	43.2 (27.4)	–0.758**	–0.029
Psittacidae	14	17.3 (11.7)	–0.441	0.557
Trochilidae	33	16.8 (9.4)	–0.558*	0.272
Formicariidae	21	28.0 (12.0)	–0.668*	0.088
Tyrannidae	49	35.7 (19.6)	–0.602**	0.368
Thraupinae	29	26.8 (17.2)	–0.649**	0.045
Emberizinae	23	26.0 (14.9)	–0.472	–0.389

Bonferroni adjusted significance levels * $P < 0.05$, ** $P < 0.01$.

Natural history characteristics and latitudinal extent

Latitudinal extents, latitudinal midpoints and body mass were examined over different taxonomic levels (Table 1). There was a significant negative association between latitudinal extent and the latitudinal midpoint for all terrestrial breeding birds and for major orders and suborders. Five families or subfamilies had significant negative associations between latitudinal extent and latitudinal midpoint. There was a significant positive correlation between the latitudinal extent of terrestrial breeding birds and body mass. When orders and suborders were examined, there was a significant positive correlation between latitudinal extent and body mass of non-passerines. An analysis of the eight largest families or subfamilies in Nicaragua resulted in no significant correlation between body mass and latitudinal extent.

A Kruskal–Wallis test revealed that there were significant differences ($P = < 0.0001$) among natural history characteristics within trophic guilds, forest dependence classes, number of forest types and latitudinal extent. Natural history characteristics were compared with species latitudinal extent (Table 2). Carnivores and granivores had the greatest latitudinal extent of all trophic guilds while nectarivores and frugivores had the smallest latitudinal extent. There were significant differences among a majority of the trophic guilds. In particular, carnivores had significantly greater latitudinal extents than all other trophic guilds except granivores. There was no significant difference among the latitudinal extent and solid and patchy forest preference, but species that do not require forest had significantly larger ranges than patchy forest birds. Birds that occurred in only one or two habitat types in Nicaragua had a significantly smaller latitudinal extent than birds that occurred in three or more forest types.

Rapoport's rule

One hundred (24%) terrestrial breeding birds reach their range limits at the same latitude as Nicaragua's political boundaries. There were 46 birds with a northern affinity that reached the end of their southern extent in Nicaragua and 54 birds with a southern affinity that had their northern extent in Nicaragua. Birds with a northern affinity (mean latitudinal midpoint 21.8, standard deviation 7.6) had significantly (Mann–Whitney U, $P = < 0.0001$) higher latitudinal midpoints than birds with a southern affinity (mean latitudinal midpoint 7, standard deviation 4.2). However, species with a southern affinity (mean latitudinal extent 23.8, standard deviation 15.7) had significantly greater latitudinal extents (Mann–Whitney U, $P = 0.034$) than species with a northern affinity (mean latitudinal extent 17.2, standard deviation 14.4).

Natural history characteristics were examined for species with northern and southern affinities (Table 3). There were no significant differences between trophic guilds ($\chi^2 = 3.5$, d.f. = 4, $P = 0.485$) or forest dependence ($\chi^2 = 4.0$, d.f. = 2, $P = 0.133$) for species with a southern and northern affinity. There was a significant difference among the number of forest types used by forest birds and affinity ($\chi^2 = 13.4$, d.f. = 2, $P = 0.001$); birds with a southern affinity were restricted to fewer forest types than birds with a northern affinity.

Table 2 Latitudinal extent in degrees for birds in Nicaragua and a comparison among natural history characteristics and latitudinal extent based on Mann–Whitney *U*-tests with Bonferroni corrections

Natural history characteristics	*n*	Latitudinal extent mean (SD)	Mann–Whitney significance levels				
Trophic guild			Frugivores	Granivores	Insectivores	Nectarivores	Omnivores
Carnivores	29	58.4 (23.0)	< 0.001**	0.005	< 0.001**	< 0.001**	< 0.001**
Frugivores	48	19.8 (15.4)		0.001*	< 0.001**	0.715	< 0.001**
Granivores	18	36.2 (20.9)			0.391	0.001*	0.229
Insectivores	152	31.8 (18.8)				< 0.001**	0.805
Nectarivores	33	16.8 (9.5)					< 0.001**
Omnivores	144	31.8 (21.2)					
Forest dependence			Patchy forest	Non-forest			
Solid forest	56	29.6 (16.5)	0.453	0.021			
Patchy forest	271	28.4 (18.8)		< 0.001**			
Non-forest	97	40.5 (26.6)					
Forest types			2 types	3 types	4 or more		
1 type	60	23.6 (15.12)	0.506	0.007	0.002*		
2 types	128	24.9 (15.16)		0.006	0.001*		
3 types	82	32.2 (18.70)			0.280		
4 or more types	55	35.3 (20.82)					

Bonferroni adjusted significance levels * $P < 0.05$, ** $P < 0.01$.

Table 3 Natural history characteristics of birds at the edge of their northern and southern range in Nicaragua

Natural history characteristics	Southern affinity *n* (%)	Northern affinity *n* (%)
Trophic guild		
Carnivores	2 (4)	1 (2)
Frugivores	6 (11)	6 (13)
Granivores	1 (2)	3 (7)
Insectivores	25 (46)	14 (30)
Nectarivores	7 (13)	6 (13)
Omnivores	13 (24)	16 (35)
Forest dependence		
Solid forest	11 (20)	3 (7)
Patchy forest	34 (63)	35 (76)
Non-forest	9 (17)	8 (17)
Forest types		
1 type	17 (38)	3 (8)
2 types	20 (44)	17 (45)
3 types	8 (18)	11 (29)
4 or more	0 (0)	7 (18)

DISCUSSION

Latitudinal distribution of Nicaraguan birds

Birds generally restricted to Central America have latitudinal extents between 20°N and 8°N. The 8°N southern limit of these species is associated with the southern Panama isthmus, although one species extends into Colombia. The northern extent of Central American birds occurs in southern Mexico. This region contains one of the few east–west mountain ranges in the Neotropics and the region is located near the northernmost extent of cloud forest and lowland rain forest (Howell, 1969; Watson & Peterson, 1999). Although there are no endemic birds in Nicaragua, there are 24 birds restricted to Central America that do not extend into Mexico or South America. These species may be of global conservation importance (Long *et al.*, 1996). However, only two species were included on the threatened birds of the world list and none received an urgent or high conservation priority from the list of threatened birds of the Neotropics (Stotz *et al.*, 1996; BirdLife International, 2000). This suggests that Nicaragua may deserve a relatively low conservation priority compared to other Neotropical countries, but little quantitative abundance data exist in Nicaragua to assess the accuracy of these global conservation priority lists.

It is interesting to note that as total latitudinal extent increases, there is a great deal of fluctuation between the northern and southern affinities of species. Species with a northern affinity generally require pine or cloud forests while species with a southern affinity generally require lowland tropical forest. Species at the edge of their distributional or elevational ranges have been hypothesized to be more susceptible to local extinction as a result of habitat fragmentation (Terborgh & Winter, 1980; Christiansen & Pitter, 1997). If this is the case, the high proportion (24%) of species at their range limit within Nicaragua may suggest that many forest birds are vulnerable to local extinction. Yet, there has been evidence that species ranges contract to the edge not to the centre of their ranges (Channell & Lomolino, 2000).

There is a latitudinal asymmetry for Neotropical birds that occur in Nicaragua. The northern breeding limits occur around 20° in the northern hemisphere and at slightly higher latitudes in the southern hemisphere. A similar pattern has been noted for birds in the New World, in which species richness is pear-shaped, with greater species richness at higher latitudes in the southern hemisphere than in the northern hemisphere (Blackburn & Gaston, 1996b). Although climate could be used to explain this pattern, the true meteorological equator is located 3°N of the cartographic equator, suggesting the opposite bias (France, 1998). A more plausible explanation is that tropical forests extend to higher latitudes in the southern hemisphere. The latitudinal limits of tropical dry forest, cloud forest and lowland rain forest in the northern hemisphere are located at 27°N, 22°N and 22°N, respectively, while the limits of these forest types in the southern hemisphere are located at 22°S, 28°S and 28°S, respectively (Dinerstein *et al*., 1995). This most probably accounts for the slight asymmetry in Neotropical bird ranges.

Natural history characteristics and range

There is a growing body of literature that examines how abiotic and biotic factors determine avian range boundaries and the relationship among geographical range, abundance and body size or mass (Wiens, 1989; Brown, 1995; Blackburn & Gaston, 1996a). However, besides body mass, there is significantly less information on how natural histories of species are associated with range size or latitudinal extent. Natural history characteristics of body mass, trophic guild, forest preference and number of habitat types are important in explaining the latitudinal extent of birds in Nicaragua.

Body mass has been associated with geographical range size when a large number of species that occur in a region are examined, but not when a subset of these species are examined (Blackburn & Gaston, 1996a; Blackburn *et al*., 1998). The same appears true in Nicaragua and will occur most probably for birds in other regions. Although there is a positive correlation between terrestrial breeding birds and body mass, the pattern is less pronounced when an analysis is undertaken at the order or family level. Certain trophic guilds have significantly larger range sizes than other trophic guilds. Carnivores have the greatest latitudinal extent followed by granivores, insectivores and omnivores, while frugivores and nectarivores have the smallest latitudinal extent. There appears to be less overlap in trophic guilds within the tropical bird communities than within temperate bird communities (Brown & Maurer, 1987). Although carnivores have greater geographical ranges than other trophic groups, the order in which other trophic guilds occur may be a region specific-pattern. Forest birds have smaller ranges than non-forest birds in Nicaragua. Most species that require forest have smaller ranges than non-forest species and this may be a region-specific pattern in the tropics, although ranges of forest birds will probably decrease as tropical forest cover continues to decrease in the Neotropics (Myers *et al*., 2000). Species that occur in one and two forest types have a significantly smaller range than species that occur in three or more. Number of forest or habitat types may be one of the best predictors of a species' latitudinal extent for birds in Nicaragua and for that matter in other regions.

Rapoport's rule?

Although species richness was greater for species with a southern affinity compared to species with a northern affinity, species with a southern affinity had significantly greater latitudinal extents. Furthermore, there was a significant negative relationship between latitudinal midpoint of terrestrial breeding birds and latitudinal extent over a number of taxonomic scales. Blackburn & Gaston (1996a) also noted that New World bird geographical range size was smallest at about 17°N. This study of latitudinal extent of Nicaraguan birds concurs with Gaston *et al.* (1998) and Harcourt (2000) in that Rapoport's rule is best referred to as Rapoport's effect, because there is too much variability in the pattern to be considered a rule.

Comparisons of natural history characteristics of birds with northern and southern affinities does not provide clear support for the argument that species' natural histories are more specialized toward the equator (Stevens, 1989). Birds with a southern affinity comprise an increased proportion of insectivores (i.e. ant followers), a decrease in the proportion of omnivores and increases in species with solid forest preference. However, there is only a statistically significant difference between number of forest types used by birds with a northern affinity and birds with a southern affinity. A similar variable pattern using habitat and diet breadth has been shown for primates in the tropics (Eeley & Foley, 1999; Harcourt, 2000). Future research on the causes of Rapoport's effect should include natural history characteristics of trophic guild, habitat specificity and number of habitat types to identify if this pattern occurs in other regions and for other taxa.

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BIOSKETCH

Tom Gillespie received his PhD in Geography from the University of California Los Angeles in 1998. His research interests are focused on predicting patterns of bird and plant species richness in fragments of tropical dry forest in the Caribbean, Central America, and South-east Asia. He is currently an assistant professor at the University of California Los Angeles.