Anales del Instituto de Biología, Universidad Nacional Autónoma de México,
Serie Zoología 74(2): 203-210. 2003

Geographic scale effects on ecological distributions of Mexican birds

Miguel A. Ortega-Huerta*
A. Townsend Peterson**

Resumen. Se estudio la influencia que tiene la escala espacial en la distribución ecológica y geográfica de 20 especies de aves en México, mediante variaciones en el área circundante de sus localidades de presencia. Se utilizó información categórica de cuatro variables ecológicas (vegetación potencial, temperatura media anual, precipitación media anual y elevación) a 10 diferentes tamaños de áreas vecinas (9-10 000 km2) para evaluar las asociaciones entre los sitios de presencia de las especies y los ambientes regionales. La distribución de las especies dependió de diferentes atributos ecológicos a diferentes escalas espaciales y las escalas de respuesta a los ambientes varió entre las especies. Por ello, utilizar enfoques de múltiple escala es clave para entender los patrones de distribución de las especies y para identificar las variables ambientales críticas en las distribuciones ecológicas de las especies.

Palabras clave: escala espacial, distribución, aves, México.

Abstract. The role of spatial scale in influencing ecological and geographic distributions of 20 bird species in Mexico was explored by varying the extent of spatial averaging around known occurrence sites. Categorical data for four ecological characteristics (potential vegetation, mean annual temperature, mean annual precipitation, and elevation) were used to assess associations between species' occurrences and regional environments, at 10 neighborhood sizes (9-10 000 km^2). Species' distributions depended on different environmental attributes at distinct spatial scales, and species differed in their scales of response to environments. A multi-scale approach is thus key to understanding distribu-

* Department of Geography, The University of Kansas, Lawrence, Kansas 66045 USA; present address, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado postal 70-153, México, D.F. 04510 México. maoh@ibiologia.unam.mx

**Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, Kansas 66045 USA

tional patterns of species, and for identification of critical environmental factors in species' ecological distributions.

Key words: spatial scale, distribution, birds, Mexico.

Introduction

Understanding factors that determine ecological and geographic distributions of species has been a fertile field for biogeographic research (Scott *et al.* 2002). Early approaches focused on discovering specific and critical environmental conditions limiting geographic distributions (Grinnell 1917, Root 1988): for example, Grinnell (1917) suggested that examination of a species' habitat should be carried out "...at as many points in the general range of the species as possible with the object of determining the elements common to all these points, and of these the ones not in evidence beyond the limits of the bird's range." Subsequent conceptualizations of species ecological niches focused mainly at more local scales: for example, MacArthur (1972) outlined a view in which geographic distributions are determined by a combination of physical environmental characteristics (*e.g.* temperature, humidity) and biotic interactions (*e.g.* predation, competition); this view has been elaborated into a body of theory explaining factors determining avian distributions (James 1971, Terborgh 1971, May & MacArthur 1972).

Micro and geographic scales can be considered the extremes of resolution for analyzing patterns of species distributions (Huggett 1998). Studies of associations between distribution of species and habitat types at local scales are abundant in the literature; studies at geographic scales, however, are much more scarce (Root 1988, Maurer 1994, Tucker *et al.* 1997). Nevertheless, cross-scale effects are frequent: micro-scale local habitat relationships may be key in understanding geographic distributions, and, conversely, general geographic patterns may suggest local habitat relationships. Species' distributions can thus be viewed as nested hierarchies of spatial inclusiveness beginning with the territory or home range of individuals, and ending with geographic ranges of species (Kolasa 1989, Allen & Hoekstra 1991).

This study focuses on associations between species' occurrences and ecological and environmental factors as a function of the scale at which those factors are considered. We assess the spatial scales at which distributions of bird species show strongest associations with environmental attributes across Mexico. By understanding variation in the strength of these associations across spatial scales, we hope to lay a foundation for incorporation of spatial scale as an integral element in species-habitat models.

Methods

Distributional data for bird species were accumulated from specimens in natural history museums (see Acknowledgments) via the *Atlas of Mexican bird distributions*, a database that includes more than 180 000 geo-referenced site records of more than 1000 species, and represents the sum of Mexican bird specimens held in North American and European natural history museum collections (see Acknowledgments) (Peterson *et al.* 1998, Navarro-Siguenza *et al.* 2002). Twenty resident land bird species were selected at random from the 151 species for which more than 500 specimen records were available.

Environmental information describing the ecological landscape were drawn from Mexico's National Biodiversity Commission (http://www.conabio.gob.mx), including categorical vector coverages summarizing mean annual temperature, mean annual rainfall, potential vegetation and elevation; all coverages were ordinal except potential vegetation, which was unordered. Vector coverages and point data were transformed into grid format at a cell resolution of 0.01 x 0.01° (about 1 km²). ArcView (ESRI, version 3.0) was used for all spatial analyses.

Geographic scale was manipulated across about two orders of magnitude (3-100 km pixels) to assess sensitivity of species to different environmental characteristics at different spatial scales, as follows. We identified the most frequent value of each environmental characteristic in square neighborhoods of different sizes (3 x 3 km, 5 x 5 km, 10 x 10 km, 15 x 15 km, 20 x 20 km, 30 x 30 km, 40 x 40 km, 50 x 50 km, 60 x 60 km, and 100 x 10 km) centered on pixels in which species were known to occur. To provide a test of discrimination levels between observed occurrences and availability, 500 random points were obtained within a 30 km radius buffer surrounding known occurrences of each species, and were characterized at each neighborhood size as above.

Chi-square tests were used to compare observed and expected occurrences of species with respect to each environmental characteristic and neighborhood size. Expected occurrences of a species within an environmental attribute interval were calculated by multiplying the proportional occurrence of that interval in random points by the total number of observed occurrences for the species. Chi-square statistics comparing expected and observed values were calculated; these values were plotted against neighborhood size to visualize scale associations for each environmental characteristic. To visualize trends, a second order polynomial curve was fitted to the chi-square values across neighborhood sizes for each environmental attribute and species.

Results

The neighborhood analysis enabled us to assess variation in associations between species' occurrences and environmental attributes as a function of geographic scale.

Species differed widely in overall degree of association, and responded to particular environmental dimensions at different spatial scales (Fig. 1). For most species, use of environmental attribute intervals differed significantly from surrounding areas (i.e., compared with the 500 random points) at all neighborhood sizes (all $P < 0.01$).

Only a few species x spatial scale x environmental characteristic combinations failed to show significant associations (Table 1). To provide some examples, occurrences of *Atlapetes pileatus* and *Callipepla douglasii* were significantly associated with the most frequent value of each of the four environmental attributes at every neighborhood extent. Occurrences of *Aratinga canicularis*, *Chlorospingus ophthalmicus*, and *Momotus momota* differed significantly from random at all neighborhood sizes except the largest (100 x 100 pixels). On the other hand, occurrences of *Catherpes mexicanus* were not significantly associated with any environmental attribute at any neighborhood extent; other species showed significant discrimination for some environmental attributes only: for example, *Melanerpes uropygialis* and *Sitta carolinensis* were not significantly associated with precipitation at any neighborhood size.

Examining trends across spatial scales, species varied in the spatial scale at which their occurrences differed most significantly for each environmental parameter (Fig. 1). For example, *Callipepla douglasii* discriminated potential vegeta-

Table 1. Neighborhood sizes at which particular species were not significantly different from random use of environmental dimensions, based on chi-square values ($P > 0.01$).

Species	Potential vegetation	Temperature	Precipitation	Elevation
Aratinga canicularis	100	—	—	—
Atlapetes pileatus	—	—	—	—
Callipepla douglasii	—	—	—	—
Catharus aurantiirostris		50, 60, 100	—	15, 100
Catherpes mexicanus	All	All	All	All
Chlorospingus ophthalmicus	100	100	100	100
Columbina inca	—	3, 5, 10, 15, 30	—	50, 60, 100
Crotophaga sulcirostris	—	—	40, 50, 60, 100	—
Habia fuscicauda	—	—	40, 50, 60, 100	—
Leptotila verreauxi	3, 5, 100	—	—	—
Melanerpes formicivorus	—	50, 60	—	—
Melanerpes uropygialis	15, 30, 40	—	All	—
Molothrus aeneus	—	3, 5, 10, 15, 20, 30	—	30, 40, 50, 60
Momotus momota	100	—	—	—
Pipilo erythrophthalmus	—	100	—	—
Pipilo fuscus	—	3, 5, 10, 15, 40, 50, 60, 100	—	—
Quiscalus mexicanus	—	—	—	—
Sitta carolinensis	40, 50, 60, 100	100	All	60, 100
Thamnophilus doliatus	50, 60, 100	—	—	—
Tyrannus melancholicus	—	—	—	—

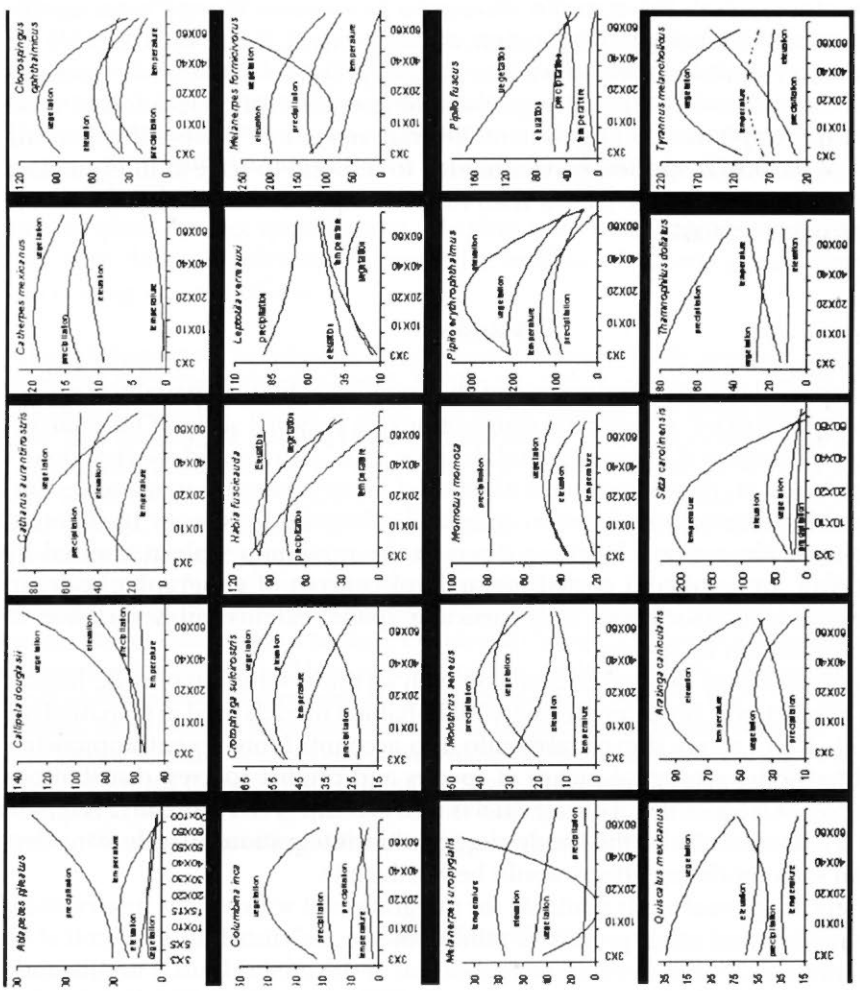

Fig. 1. Second-order polynomial curves fitted to chi-square values associated with species' responses to four environmental characteristics across different neighborhood sizes for each of 20 bird species in Mexico.

tion, precipitation, and elevation at large extents, with no extent-effect of temperature. *Momotus momota* discriminated potential vegetation, temperature, and elevation at medium extents, with no extent-effect of precipitation. *Habia fuscicauda* discriminated vegetation, temperature, and precipitation at small extents, but showed no extent-effect of elevation. Intermingled neighborhood extents, however, were more typical: for example, *Melanerpes formicivorus* showed most significant associations with potential vegetation at a large extent, but at small extents for temperature, precipitation and elevation. Similarly, *Quiscalus mexicanus* discriminated more significantly potential vegetation, temperature, and elevation at small extents, and precipitation at large extent. Overall, in spite of these individualistic responses of particular species, species tended to respond to scale at intermediate extents significantly more frequently than random expectations (chi-square test, $?^2 = 13.1$, df = 1, $P < 0.01$).

Discussion

This study provides a first exploration of the complex role that spatial scale plays in determining species' geographic distributions on regional scales. Our analyses are based on categorical environmental data for all of Mexico and species' occurrence data based on data associated with natural history museum specimens, aiming to examine interactions between scale and selectivity by species in different environmental dimensions. Working down to the minimum scale permitted by available data, we applied a nested hierarchical concept of geographic scale, in which variations in associations with particular spatial extents imply variation in scale-discrimination by species.

Many applications depend critically on such an understanding of scale-habitat selection interactions. For example, the wildlife-habitat models used in Gap Analysis (Scott *et al.* 1996) rarely if ever take scale into account. More recent approaches designed to model ecological niches of species and predict species' distributions similarly do not frequently take scale effects into account (Peterson 2001, Peterson *et al.* 2002). The results of this study suggest that integration of scale considerations into such modeling effects would be worthwhile.

A variety of approaches is available for integration of scale effects into ecological niche models and other predictive models of species' distributions (Scott *et al.* 2002). A simplest approach would be replication of the methods used in this study for each species, and inclusion of each environmental variable at the appropriate scale of resolution. A second tactic might be inclusion of each environmental variable at several scales of resolution, and to employ some sort of selection or elimination procedure to reduce the dimensionality of the modeling challenge; for example, jackknife procedures can be used to identify critical coverages or to discard coverages that reduce predictivity (Peterson & Cohoon 1999). Finally, for approaches that involve a machine-learning step or other random-walk procedures (Stockwell

& Noble 1992, Stockwell 1999, Stockwell & Peters 1999), it is often feasible simply to allow the algorithm to choose from among multiple replicates of each environmental variable at different spatial resolutions, although strong costs are involved in terms of computational speed with the addition of numerous environmental layers to the analysis. Such steps are presently under testing, and inclusion of scale effects in ecological niche models should soon be feasible.

Many synthetic products based on such models, including inferences about species' niche evolution, predictions of species' invasions, will almost certainly come to be understood as strongly scale-dependent, once appropriate test are conducted. This analysis contributes to an appreciation of the complex nature of species' geographic distributions: not only are multiple factors involved in determination of species' distributional limits, but species may perceive and respond to those factors on quite-distinct spatial scales, ranging from microscopic to continental. Inclusion of these complexities in predictive models will clearly greatly improve the functioning of such efforts.

Acknowledgments. The following natural history museums kindly provided access to specimens and data that formed the basis for the occurrence information used in this study: American Museum of Natural History, New York; Academy of Natural Sciences, Philadelphia; Bell Museum of Natural History, Minneapolis; British Museum (Natural History), Tring; Carnegie Museum of Natural History, Pittsburg; Canadian Museum of Nature, Ottawa; Denver Museum of Natural History; Delaware Museum of Natural History; Fort Hays State College; Field Museum of Natural History, Chicago; Iowa State University, Ames; University of Kansas Natural History Museum, Lawrence; Los Angeles County Museum of Natural History; Natuurhistorische Museum, Amsterdam; Louisiana State University Museum of Zoology, Baton Rouge; Museum of Comparative Zoology, Harvard University, Cambridge; Moore Laboratory of Zoology, Occidental College, Los Angeles; Muséum nationale d'Histoire naturelle, Paris; Museum of Vertebrate Zoology, Berkeley; Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México; University of Nebraska, Lincoln; Royal Ontario Museum, Toronto; San Diego Natural History Museum; Southwestern College, Kansas; Texas Cooperative Wildlife Collections; University of Arizona; University of British Columbia Museum of Zoology; University of California at Los Angeles; Universidad Michoacana de San Nicolás de Hidalgo; U.S. National Museum of Natural History; Western Foundation of Vertebrate Zoology; and Peabody Museum, Yale University.

Literature cited

ALLEN, T. F. H. & T. W. HOEKSTRA. 1991. *Toward a unified ecology*. Columbia University Press, New York, 384 p.

GRINNELL, J. 1917. Field tests of theories concerning distributional control. *American Naturalist 51*: 115-128.

HUGGETT, R. J. 1998. *Fundamentals of Biogeography*. Routledge, New York, 261 p.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bulletin 83*: 215-229, 235-236.

KOLASA, J. 1989. Ecological systems in hierarchical perspective: Breaks in community structure and other consequences. *Ecology 70*: 36-47.

MACARTHUR, R. 1972. *Geographical Ecology*. Princeton University Press, Princeton, N.J., 269p.

MAURER, B. A. 1994. *Geographic Population Analysis: Tools for the Analysis of Biodiversity*. Blackwell Scientific Publications, London, 130p.

MAY, R. M. & R. H. MACARTHUR. 1972. Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences USA 69*: 1109-1113.

NAVARRO-SIGUENZA, A. G., A. T. PETERSON & A. GORDILLO-MARTÍNEZ. 2002. A Mexican case study on a centralised database from world natural history museums. *CODATA Journal 1*: 45-53.

PETERSON, A. T. 2001. Predicting species' geographic distributions based on ecological niche modeling. *Condor 103*: 599-605.

PETERSON, A. T., L. G. BALL & K. C. COHOON. 2002. Predicting distributions of tropical birds. *Ibis 144*: 27-32.

PETERSON, A. T. & K. C. COHOON. 1999. Sensitivity of distributional prediction algorithms to geographic data completeness. *Ecological Modelling 117*: 159-164.

PETERSON, A. T., A. G. NAVARRO-SIGÜENZA & H. BENTIEZ-DÍAZ. 1998. The need for continued scientific collecting: A geographic analysis of Mexican bird specimens. *Ibis 140*: 288-294.

ROOT, T. 1988. Environmental factors associated with avian distributional boundaries. *Journal of Biogeography 15*: 489-505.

SCOTT, J. M., P. J. HEGLUND & M. L. MORRISON (eds.) 2002. *Predicting species occurrences: issues of accuracy and scale*. Island, Washington, D.C., 868 p.

SCOTT, J. M., T. H. TEAR & F. W. DAVIS (eds.) 1996. *Gap Analysis: A landscape approach to biodiversity planning*. American Society for Photogrammetry and Remote Sensing, Bethesda, Maryland.

STOCKWELL, D. R. B. 1999. Genetic algorithms II. *In:* A. H. Fielding (ed.) *Machine learning methods for ecological applications*. Kluwer Academic, Boston, pp. 123-144.

STOCKWELL, D. R. B. & I. R. NOBLE. 1992. Induction of sets of rules from animal distribution data: A robust and informative method of analysis. *Mathematics and Computers in Simulation 33*: 385-390.

STOCKWELL, D. R. B. & D. P. PETERS. 1999. The GARP modelling system: Problems and solutions to automated spatial prediction. *International Journal of Geographic Information Systems 13*: 143-158.

TERBORGH, J. W. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Perú. *Ecology 52*: 26-36.

TUCKER, K., S. P. RUSHTON, R. A. SANDERSON, E. B. MARTIN & J. BLAIKLOCK. 1997. Modeling bird distributions—a combined GIS and Bayesian rule-based approach. *Landscape Ecology 12*: 77-93.

Recibido: 1. IX. 2003
Aceptado: 10. X. 2003