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PREDICTING DISTRIBUTIONS OF MEXICAN MAMMALS USING ECOLOGICAL NICHE MODELING

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Given the uneven and biased nature of present understanding of geographic distributions of mammal species, tools for extrapolating from what is known to a more general prediction would be most useful. We used the genetic algorithm for rule-set prediction (GARP) to generate ecological niche models that were then projected onto geography to predict potential geographic distributions for 17 mammal species of Insectivora, Chiroptera, Rodentia, and Artiodactyla in Oaxaca, Mexico. GARP depends on point occurrence localities from museum records of species, along with electronic maps describing features of climate, topography, and vegetation type. Point localities were divided in 2 sets: one of localities from museum records dated before 1960, which was used to generate the predicted distributions, and the other of localities of museum records resulting from recent inventories (post-1960), which was used to test model accuracy. Predicted distributions for 11 of 17 species were statistically significantly more coincident with independent test points than random expectations; tests for the remaining 6 species would have required larger numbers of test localities to establish significance. GARP is a robust tool for modeling species' geographic distributions, with excellent potential for applicability to strategies for conservation of mammals in Oaxaca and elsewhere.

Key words: biogeography, ecological niche, GARP, genetic algorithm, Geographic Information Systems, potential geographic distribution

Modeling geographic distributions of species has received increasing attention for its wide applicability in diverse disciplines, such as biogeography, ecology, and conservation, among others (Carpenter et al. 1993; Godown and Peterson 2000; Karl et al. 2002; Peterson et al. 1999, 2000; Sánchez-Cordero et al. 2001; Schaeffer and Krohn 2002; Walker 1990). Traditional methods of depicting species' distributions connected marginal collecting localities (e.g., Hall 1981), assuming that species are uniformly distributed within this area. A strength of this method is that it defines limits of species' distributions clearly, although it may overestimate interior areas occupied by a species or underestimate inhabited areas outside known points.

Recent efforts have emphasized the approach of modeling species' ecological niches (Grinnell 1917; MacArthur 1972), which are then projected onto geographic maps to produce potential distributions. Qualitative approaches involve relating habitat types to known extents of species' occurrence to predict presence in areas in which the species has not yet been recorded (Scott et al. 2002). More robust statistical approaches relate biotic and abiotic factors (Austin et al. 1990; Fielding and Haworth 1995; Nix 1986) in a multivariate statistical environment to reconstruct species' distributions. Potential shortcomings to these efforts include lack of sufficiently large data sets on occurrence localities, biases and gaps in existing locality data, and tenuous assumptions that species' distributions will track land cover types (Stockwell and Peters 1999).

The genetic algorithm for rule-set prediction (GARP—Stockwell and Peters 1999) is one of several approaches available for generating ecological niche models and has been applied to diverse taxonomic groups (Peterson et al. 1999). GARP relates diverse ecological–environmental characteristics of known occurrence points to those of points sampled randomly from the rest of the study region, seeking to develop a series of decision rules that best summarizes factors associated with the species' presence (see "Materials and Methods"—Anderson et al. 2003; Peterson and Cohoon 1999; Peterson et al. 2002a, 2002b). Nonetheless, these ecological niche models do not consider the role of biotic interactions or history in shaping species' present-day ranges (Anderson et al. 2003; Feria and Peterson 2002; Peterson et al. 1999).

In this contribution, we tested the accuracy of predictions of ecological niche models drawn from GARP for mammalian

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species in the state of Oaxaca, Mexico. To provide an independent test of model validity, we used records of mammal occurrences in Oaxaca from prior to the publication of the detailed monographic summary of Goodwin (1969) to construct models and tested model validity using records accumulated subsequent to that date. Oaxaca holds an exceptionally rich mammalian fauna, so use of predictive models to complete its geographic understanding is essential for identifying priority regions for development of effective conservation strategies.

MATERIALS AND METHODS

Occurrence data.—We compiled a database of 7,500 point localities based on historical museum specimens and recent collections and inventories of mammal species occurring in the state of Oaxaca, Mexico (Appendix I). Each locality was georeferenced to the nearest 0.01° of latitude and longitude using 1:250,000 topographic maps (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad 1998; http://www.conabio.gob.mx).

Developing potential distributions.—Ecological niche models were developed using the genetic algorithm for rule-set prediction (GARP—Stockwell and Peters 1999). Primary occurrence points refer to georeferenced (latitude and longitude) point localities where a species has been collected, information that can be obtained from voucher natural history museum specimens (Soberón 1999).

In GARP, occurrence points are divided evenly into training and intrinsic test data sets, and GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection. Choosing a method from a set of possibilities (e.g., logistic regression, bioclimatic rules), that method is applied to the training data, and a rule is developed. Predictive accuracy is then evaluated on the basis of 1,250 points resampled from the intrinsic test data and 1,250 points sampled randomly from the study region as a whole. Rules may then be evolved according to a variety of random perturbations to rule structure, or additional rules may be produced. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model, and the algorithm runs either 1,000 iterations or until convergence. More detailed descriptions of the method are provided elsewhere (Stockwell and Peters 1999).

Ecological niche models were developed on a desktop-computer implementation of GARP (http://www.lifemapper.org/desktopgarp; 20 March 2003). This implementation offers flexibility in choice of Geographic Information System data coverages by which the ecological landscape is described. We used 10 data coverages (0.04 × 0.04° pixel resolution) that summarized potential vegetation type (Rzedowski 1986; elevation, slope, and aspect [from the U.S. Geological Survey's Hydro-1K data set; http://www.usgs.gov, 24 February 2004]) and aspects of climate including mean annual precipitation, mean daily precipitation, maximum daily precipitation, minimum and maximum daily temperature, and mean annual temperature (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad 1998; http://www.conabio.gob.mx).

We selected 17 species from among the 191 mammal species recorded from Oaxaca for testing based on numbers of occurrence points available from before 1960 (minimum 10 unique point localities, range 10–22 localities) and from after 1960 (minimum 5 unique point localities, range 5–60 localities). Historical mammal inventories were conducted largely before 1960 (see summary in Goodwin 1969), providing a typical level of sampling as might be found in many regions of South America. Post-1960 data came mostly from the 1990s (e.g., Briones et al., in press; Briones-Salas 2000; Briones-Salas et al. 2001; Sánchez-Cordero 2001), a period in which the state saw intensive modern surveys. Given this natural break in survey effort, data were divided into 2 independent sets: pre-1960 localities for building models and post-1960 localities for testing model accuracy. Occurrence points varied from species widely distributed (e.g., *Odocoileus virginianus*) to species geographically restricted (e.g., *Cryptotis magna*) within Oaxaca.

With the pre-1960 data for each species, we developed 100 replicate ecological niche models using GARP: half of the pre-1960 points were used for model building, and the other half were used for selecting a best subset of 20 models containing low levels of omission (i.e., when predicting habitable areas as uninhabitable) and moderate indices of commission (i.e., when predicting uninhabitable areas as habitable—Anderson et al. 2003). Best-subset models were summed to produce a final composite model for each species.

A chi-square test was used to compare observed success in predicting post-1960 test localities with that expected under random models (Anderson et al. 2003; Peterson et al. 1999). Numbers of point localities post-1960 correctly and incorrectly predicted by GARP models were used as observed values; expected values were drawn from the product of the test sample size and the proportional area within Oaxaca predicted present in the model.

RESULTS

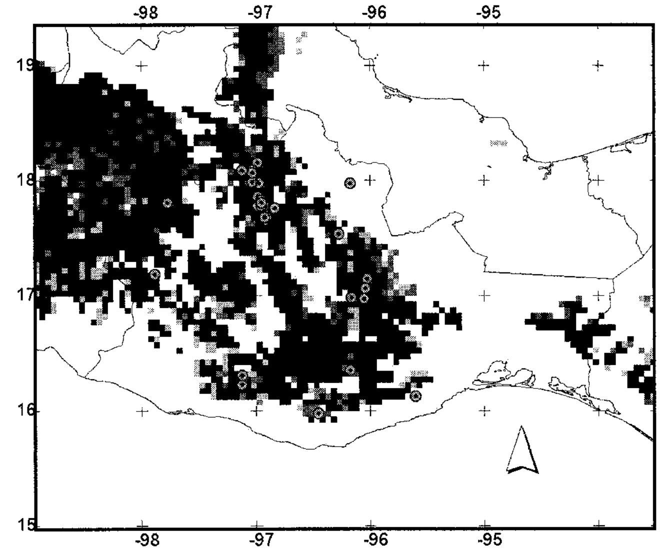
Models of ecological niche and the potential geographic distributional areas associated with them were obtained for the 17 species that met sample size criteria (Appendix II). Post-1960 localities were overlain on the species predictions to visualize correspondence with the prediction (Fig. 1). Predicted geographic distributions for 11 of the 17 species coincided with test points significantly better than random expectations ($P < 0.05$; Appendix II). For example, 27 of 33 post-1960 localities for *Liomys irroratus* were correctly predicted, even though only 30% of Oaxaca's area was predicted present; only 10 point localities would have been predicted by a random model ($\chi^2 = 41.8$, $d.f. = 1$, $P < 10^{-9}$; Fig. 1).

The remaining 6 species fell into 2 contrasting scenarios. Three species (*C. magna*, *Peromyscus mexicanus*, *Sciurus aureogaster*) were predicted to occur in >70% of Oaxaca; all had test sample sizes of >18 localities. The other 2 species (*P. melanophrys* and *Reithrodontomys megalotis*) had predicted areas of <40% of Oaxaca but also had small sample sizes (<13 localities). The only exception to this pattern was *Desmodus rotundus*, for which relatively small area predicted (27% of Oaxaca) combined with reasonable post-1960 sample size ($N = 41$). Hence, in 5 of 6 cases, the combination of area predicted and sample size made for low statistical power: a larger data set with better geographic spread of post-1960 localities would be necessary for an adequate test of model predictions (Appendix II—Peterson et al. 2002a).

DISCUSSION

Species' geographic distributions were predicted on the basis of independent temporal subsamples with statistical significance for 11 of 17 species tested: *Liomys irroratus*, *Microtus mexicanus*, *P. levipes*, *Glossophaga soricina*, *Carollia perspicillata*, *Artibeus jamaicensis*, *Balantiopteryx plicata*,

A. *Liomys irroratus*



B. *Peromyscus melanophrys*

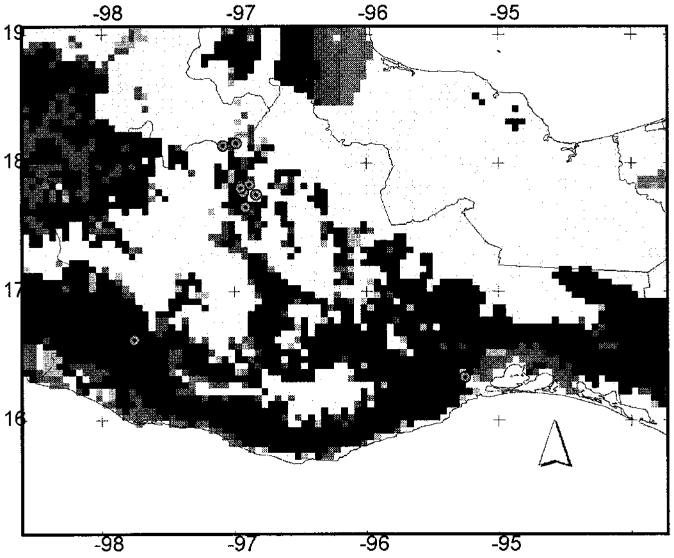


Fig. 1.—Ecological niches modeled using the genetic algorithm for rule-set prediction (GARP) and projected as potential distributions for A) *Liomys irroratus* and B) *Peromyscus melanophrys* in southeastern Mexico in the state of Oaxaca. A set of pre-1960 localities were used to generate the model (areas with darker shading indicate greater agreement among best-subsets models); point localities (dots) are post-1960 localities used to test model accuracy. *L. irroratus* potential distribution produced the best fit, where most post-1960 point localities coincided with the best-subsets models. *P. melanophrys* potential distribution produced the least fit since most post-1960 point localities lay in the same area, thus requiring a larger number of such test data for a robust test of the distributional prediction. See Appendix II.

Baiomys musculus, *Oryzomys couesi*, *Odocoileus virginianus*, and *Liomys pictus*. Hence, GARP appears to predict potential distributions robustly based on independent test data for these species in Oaxaca. The remaining 6 species that were not predicted significantly better than random models (*C. magna*, *S. aureogaster*, *P. mexicanus*, *P. melanophrys*, *D. rotundus*, and *R. megalotis*) were predicted to occur broadly across Oaxaca, thus requiring larger numbers of post-1960 test data for a robust test of the distributional predictions (Anderson et al. 2002a; Peterson et al. 2002a; Fig. 1; Appendix II).

For example, all but 2 post-1960 point localities for *P. melanophrys* lie essentially in the same area, limiting the robustness of any statistical tests (Fig. 1). Furthermore, comparing models and tests for *G. soricina* (highly significant) and *D. rotundus* (not significant) both showed similar test sample sizes and proportional area that were predicted to be present in Oaxaca (Appendix II). The contrasting results for the 2 species are thus results of 1 of several factors: particulars of the geographic spread of the test data points (broader in *G. soricina* than in *D. rotundus*); effects of biotic interactions, history, or other nonecological factors in shaping *D. rotundus* distribution; or GARP failure to model accurately the species' ecological niche.

The remaining 5 species for which statistical significance was not achieved are probably plagued by insufficient statistical power for a robust test. In general, evidence of model failure was observed in a maximum of 1 of 12 species. It should be borne in mind that ecological niche models do not take into account either biotic interactions or effects of history, so not all the predicted distributional area is necessarily occupied by a species (Anderson 2002a, 2002b; Peterson et al. 1999).

Although the species tested represent only a small fraction of the mammal fauna of Oaxaca (17 of 191 species), most species were excluded from analysis owing to small sample sizes. Nonetheless, ecological niche models can still be developed for many more species if our temporal subsetting criteria are relaxed; such models would predict potential areas for species for further testing. For example, results of recent inventories (Briones et al., in press; Briones-Salas 2000; Briones-Salas et al. 2001; Sánchez-Cordero 2001) include new localities for *L. irroratus*, *L. pictus*, *P. levipes*, and *P. melanophrys*; these new sites were used herein to test models, and all such new tests localities fell within predicted distributions (Fig. 1). This exercise could be expanded for many more species, with ongoing inventory results used to validate and improve predicted distributions (Sánchez-Cordero 1993; Sánchez-Cordero et al. 2001).

Attempts to test the robustness of such GARP-based ecological niche models and resulting distributional hypotheses generated in GARP have proven successful for diverse taxa in several geographic regions (Anderson et al. 2002a, 2002b; Feria and Peterson 2002; Peterson 2001; Peterson and Kluza 2003; Peterson et al. 2002a, 2002c). Hence, GARP appears to be a robust tool for predicting species' distributions, with many potential uses in studies of mammals and other taxonomic groups. Ecological niche modeling has become an indispensable tool in disciplines as diverse as biogeography (Anderson et al.

2002a; Peterson et al. 1999), ecology (Anderson et al. 2002b; Peterson et al. 2002a, 2002b, 2002c), emerging diseases (Peterson et al. 2002d), agricultural pests (Sánchez-Cordero and Martínez-Meyer 2000), and conservation (Feria and Peterson 2002; Godown and Peterson 2000; Peterson et al. 2000; Sánchez-Cordero et al. 2001). As regards this study, modeling species' distributions can be especially relevant to conservation since Oaxaca has the second-largest mammalian fauna in the country and rampant deforestation threatens species' survival. A robust understanding of species' distributions can help identify priority regions having high species richness and endemism (Peterson et al. 2000), as is the case in many areas in Oaxaca.

RESUMEN

Dada la naturaleza sesgada de las distribuciones geográficas conocidas de especies de mamíferos, es necesario contar con herramientas para extrapolar el conocimiento actual a predicciones más robustas y completas. Se usó un algoritmo genético de cómputo (GARP) para modelar el nicho ecológico proyectado como distribuciones potenciales de especies de Insectivora, Chiroptera, Rodentia y Artiodactyla en el Estado de Oaxaca, México. Se conjuntó una base de datos de las localidades de colecta de ejemplares de colecciones científicas y mapas digitales de coberturas ambientales. Las localidades de colecta se dividieron en dos grupos: el primero, incluyó localidades de colecta fechadas antes de 1960, con las que se generaron los modelos de distribución potencial y, el segundo, incluyó localidades de colecta de inventarios recientes fechadas después de 1960; éstas fueron usadas para probar la precisión de las predicciones de los modelos. Los modelos de distribución potencial de once de 17 especies fueron significativamente mejores que modelos al azar; las restantes seis especies mostraron una combinación de amplia área de distribución predicha en Oaxaca y un número reducido de localidades fechadas después de 1960, por lo que nuestro poder estadístico no fue adecuado para probar los modelos rigurosamente. GARP parece ser una herramienta útil para modelar la distribución de los mamíferos y con gran potencial de ser usado con fines de conservación de la diversa mastofauna estatal.

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Appendix I

Specimen data were obtained from the following museum collections: Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México (CNMA-IBUNAM); University of Kansas Natural History Museum (KUNHM); Centro Interdisciplinario de Investigación y Desarrollo Regional de Oaxaca (CIIDIR-Oaxaca); American Museum of Natural History, New York (AMNH); National Museum of Natural History, Washington, D.C. (NMNH); Field Museum of Natural History, Chicago, Illinois (FMNH); Museum of Zoology, University of Michigan, Ann Arbor, Michigan (UMMZ); Michigan State University Museum, East Lansing, Michigan (MSU); Museum of Vertebrate Zoology, University of California, Berkeley, California (MVZ); Texas Tech University Museum, Lubbock, Texas (TTU); Texas Cooperative Wildlife Collections, Texas A&M University, College Station, Texas (TCWC).

Appendix II

Accuracy of the distributional predictions generated using the genetic algorithm for rule-set prediction (GARP) for 17 species of mammals from Oaxaca, Mexico. Observed refers to number of localities that did (= Yes) or did not (= No) match predicted locations for the species. Expected indicates number of locations expected to match (= Yes) or not match (= No), based on proportional area and sample size, if species were distributed randomly throughout the state. Chi-square test indicates the probability that observed differs from expected matching of localities.

Species	Proportion of area	Observed		Expected		χ^2	*P*
		Yes	No	Yes	No		
Liomys irroratus	0.301	27	3	9.9	20.0	41.8	1×10^{-10}
Glossophaga soricina	0.270	25	14	10.6	28.4	27.1	1×10^{-07}
Microtus mexicanus	0.083	7	11	1.5	16.5	21.9	2×10^{-06}
Carollia perspicillata	0.036	4	15	0.7	18.3	16.1	5×10^{-05}
Artibeus jamaicensis	0.041	6	31	1.5	35.5	13.5	2×10^{-04}
Peromyscus levipes	0.048	4	14	0.9	17.1	11.9	5×10^{-04}
Balantiopteryx plicata	0.461	22	9	14.3	16.7	7.6	5×10^{-03}
Baiomys musculus	0.221	10	14	5.3	18.7	5.3	0.021
Oryzomys couesi	0.314	15	15	9.4	20.6	4.8	0.028
Odocoileus virginianus	0.172	4	5	1.6	7.4	4.6	0.031
L. pictus	0.100	6	24	3	27	3.3	0.067
Desmodus rotundus	0.274	8	33	11.2	29.8	0.9	>0.10
Reithrodontomys megalotis	0.378	3	2	1.9	3.1	0.6	>0.10
Cryptotis magna	0.835	16	2	15	2.9	0.1	>0.10
P. mexicanus	0.718	41	19	43.1	16.9	0.1	>0.10
Sciurus aureogaster	0.788	22	3	19.7	5.3	0.3	>0.10
P. melanophrys	0.353	5	7	4.2	7.8	0.1	>0.10