



# Prioritisation of Mexican lowland rain forests for conservation using modelled geographic distributions of birds

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## Summary

Mexican humid lowland tropical forests have seen extensive perturbation and deforestation in recent decades, and, as such, effective conservation planning is crucial. We developed ecological niche models and predicted geographic distributions for 89 species of birds ecologically restricted to Mexican rain forests, and used heuristic complementarity algorithms to identify priority areas for conservation. Our results focused on a single contiguous region of northern Chiapas as a key area – all species except three were predicted to co-occur in this area, which is made up of three highly complementary sub-areas. The relationship between this area and existing protected areas was explored, and concrete recommendations made for modification of existing protected areas.

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## Introduction

Lowland rain forest consistently ranks among the most species-rich habitats in Mexico (Ramamoorthy et al., 1993). Although endemism in Mexican rain forests is generally low (Escalante-Pliego et al., 1993), many efforts have nevertheless focused on effective biodiversity conservation in this habitat (Gómez-Pompa and Dirzo, 1995; Vales et al., 2000). This focus is important given that vast areas of this

habitat have already been disturbed – much of southern Veracruz, Tabasco, northern Oaxaca, and northern Chiapas has already been completely denuded of rain forest, reducing the habitat's extent in Mexico to a small fraction of its original extent (Ramamoorthy et al., 1993).

In the present investigation, we provide a worked example of melding two approaches – species' geographic distributions are interpolated and summarised using ecological niche modelling, and areas are prioritised for conservation using place prioritisation algorithms (Peterson et al., 2000; Sánchez-Cordero et al., 2005). We bring these

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relatively new tools from biodiversity informatics and quantitative geography to bear on the challenge of prioritising lowland areas in southeastern Mexico for conservation action. Species' geographic distributions are modelled based on data associated with natural history museum specimens, and priority areas identified based on the principle of complementarity among areas. This approach produces objective, quantitative prioritisations, and offers a unique perspective on conservation strategies in the region.

## Methods

This study concentrates on the 89 bird species that are ecologically restricted to lowland rain forests and that occur in Mexico. We chose species for inclusion based on previous literature (AOU, 1998; Howell & Webb, 1995) and personal experience (A. Townsend Peterson), limiting the study to those species geographically and ecologically restricted to lowland rain forest (i.e., not occurring in tropical dry forest, tropical semi-deciduous forest, etc.) and associated habitats (e.g., swampy areas, second growth). We assembled sets of occurrence points from natural history museum specimen records already organised in a large-scale database *Atlas of the Distribution of Mexican Birds* (Navarro-Siguenza et al., 2002, 2003; Peterson et al., 1998) (museums contributing data are listed in the Acknowledgements), and extracted latitude–longitude co-ordinates for further analysis.

Ecological/environmental maps used to develop distributional models in this study consisted of raster grids with 243,200 grid squares (pixels) of  $0.05^\circ \times 0.05^\circ$ . The four thematic coverages were provided by the Comisión Nacional para el Uso y Conocimiento de la Biodiversidad (<http://www.conabio.gob.mx>), and included elevation, mean annual precipitation, mean annual temperature, and potential vegetation type (Rzedowski, 1978). Developed originally at a spatial resolution of  $0.01^\circ$ , these coverages were generalised 25-fold to permit more rapid analysis.

The ecological niche of a species – defined here as the conjunction of ecological conditions within which it is able to maintain populations without immigration (Grinnell, 1917, 1924) – can be depicted as a polyhedron or polyhedrons in multidimensional ecological/environmental space (MacArthur, 1972). Several approaches have been used to approximate species' ecological niches, including range-based rules, logistic multiple regression, and generalised linear modelling (Austin et al., 1990; Carpenter et al., 1993; Nix, 1986). We

used the Genetic Algorithm for Rule-set Prediction (GARP), which includes several such methods (range rules, logistic multiple regression, etc.) in an iterative, machine-learning approach (Stockwell, 1999; Stockwell & Noble, 1992; Stockwell & Peters, 1999). Individual algorithms are used to produce component 'rules' in a broader rule-set, and hence portions of the landscape may be identified as inside or outside of the niche based on different algorithms. Extensive testing of GARP has indicated excellent predictive ability for species' geographic distributions (Anderson et al., 2003; Anderson et al., 2002; Fera & Peterson, 2002; Peterson, 2003; Peterson et al., 1999; Peterson et al., 2004a; Peterson et al., 2004b; Peterson et al., 2002). Recent sensitivity analyses of precisely the same data sets used here indicate that GARP is able to provide statistically robust distributional predictions based on 10–20 occurrence points, which are generally sufficient to achieve 90% of maximum predictive accuracy (Stockwell & Peterson, 2002a, 2002b, 2003).

GARP results were output as binary predictions of presence and absence across the southeastern Mexican landscape. In a few cases (four species), areas of over prediction apparently resulting from historical effects limiting species' geographic distributions (Peterson et al., 1999), were eliminated by intersecting the crude GARP prediction with a polygon developed by hand based on the known geographic distribution of the species (AOU, 1998; Howell & Webb, 1995).

To seek optimal combinations of areas for species representation on a pixel-by-pixel basis, we used a heuristic complementarity approach based on maximising species richness. Because the results were exceedingly simple, use of complex computer algorithms (Csuti et al., 1997; Kelley et al., 2002; Margules & Pressey, 2000; Pressey, 1994; Williams et al., 1996a; Williams et al., 1996b) to achieve these prioritisations proved unnecessary (Chen & Peterson, 2002). We summed predicted distributions across species to create a surface of predicted species richness, and chose a first priority area by identifying pixels with highest numbers of species co-occurring in this summed map. After eliminating species represented in this first area, we summed the remaining species, and chose a second area as the area of maximum species richness based on this reduced set of species. We continued this procedure of summing distributional maps of remaining species until the maximum species richness across the region was of single species.

We considered the position of six existing protected areas in southeastern Mexico, to place our 'optimal' areas in a more practical context: Cascadas

de Agua Azul; Montes Azules; Bonampak; Lacan-Tun; Chan-kin; and, Yaxchilan (size range 2580–331,200 ha) (Gómez-Pompa & Dirzo, 1995; Vales et al., 2000). We evaluated them similarly to the pixel-based analyses to determine their effectiveness; after tallying species predicted to occur in each area in ArcView, we chose the protected area richest in bird species as the first one to enter the heuristic system, eliminated those species from consideration, and identified further priority areas based on the species that they added to the overall total.

## Results

The 89 species in this study (listed in Table 1) showed a diversity of distributional patterns, ranging from broadly to narrowly distributed (Figure 1). For example, *Pipra mentalis* was predicted to be broadly distributed across much of the study region, and likely would occur in any significant forest patch in the region. In contrast, *Myrmotherula schisticolor* was predicted to occur in a few restricted areas only, a conclusion borne out by its minuscule distribution in Mexico. Two species presented special situations distributionally, both apparently restricted to karstic areas (Gómez de Silva Garza, 1997a, 1997b): *Hylorchilus sumichrasti* was predicted as restricted to central Veracruz and northern Oaxaca; and, *H. navai* was predicted to be distributed in extreme western Chiapas and eastern Oaxaca, although it also occurs in extreme southern Veracruz (Howell & Webb, 1995).

Distributional data were in general too scarce to permit model validation (Peterson, 2001, 2002). Therefore, we used published inventory information for two areas [Montes Azules (González-García, 1993) and Yaxchilan (Puebla-Olivares et al., 2002)] to assess the biological reality of our models. Of the 89 species that were the focus of this study, five (*Hylorchilus navai*, *H. sumichrasti*, *Terentriacus erythrurus*, *Falco deiroleucus*, and *Caprimulgus maculicaudus*) were predicted absent from the entirety of Montes Azules in our models, and the remaining 84 were predicted present; in the published inventory (González-García, 1993), 77 of the 84 predicted present were detected, and three of the five predicted absences were not detected. Hence, most of our model predictions were borne out by available information. For Yaxchilan, 10 of 14 predicted absences were supported, but only 44 of 75 predicted presences were supported, but predictions were significantly better than random ( $\chi^2 = 4.30$ ,  $df = 1$ ,  $P < 0.05$ ); overall, the indication is that the inventory remains incomplete or that

model results include some error (Puebla-Olivares et al., 2002). More generally, we checked all predictions of presence and absence for general correspondence with known distributional patterns (Howell & Webb, 1995), and found good general agreement.

With this set of 89 predicted geographic distributions, we used the heuristic complementarity approach to identify key areas as conservation priorities. Among existing protected areas, Montes Azules was predicted to hold 84 of the 89 species; Lacan-Tun followed with 81 species, of which 80 were included in the list from Montes Azules. Next, Bonampak held 80 species, and Chan-kin and Yaxchilan 75 species each, but all were already included in Montes Azules and Lacan-Tun; Cascadas de Agua Azul, however, with only 71 species, contributed one additional species to the system. Therefore, the optimised reserve system based on existing protected areas held 86 species in three reserves, leaving three species unprotected (Figures 2 and 3).

Assessing the region's avifauna without considering existing protected areas (Figure 2), a first area between northeastern Chiapas and southeastern Tabasco was predicted to hold 79 of the 89 species. A second area, in east-central Chiapas, held four additional species, and a third area, in eastern Chiapas, added three more. The optimisation ended in the third iteration, in which the three remaining species did not co-occur (*Falco deiroleucus*, *Hylorchilus navai*, and *Hylorchilus sumichrasti*). Hence, six areas were identified that included all 89 species, the first three of which equalled the ability of existing reserves to protect species.

## Discussion

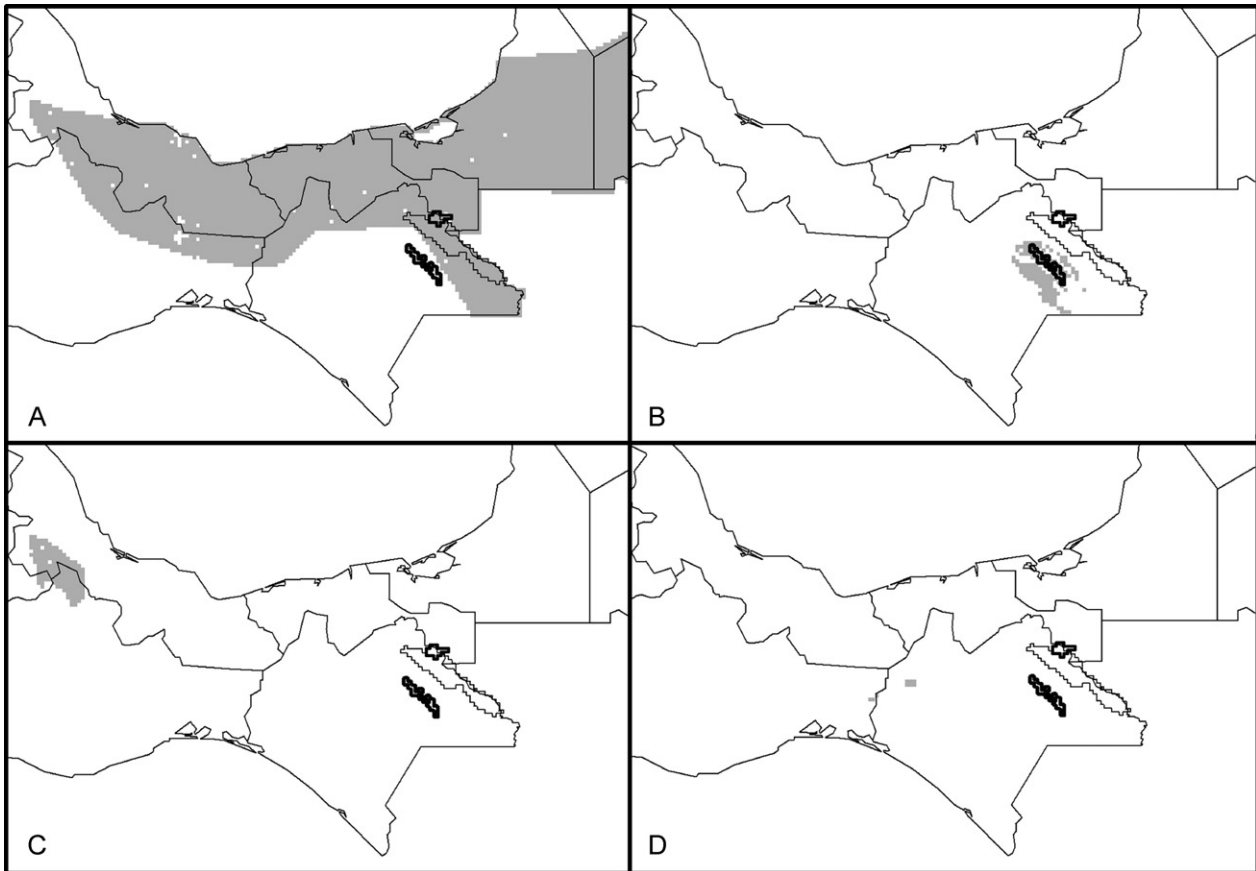
Obviously, the conclusions of this study are only as good as the distributional predictions on which they are based – for lack of better information, this study used older distributional information to characterise distributions of rain forest bird species, and so distributional predictions may be somewhat crude. However, the ecological niche modelling approach has seen considerable testing (see citations in Methods), and indeed tests in Mexico with exactly the same distributional and environmental data sets have indicated excellent predictive ability (Peterson et al., 1999; Peterson et al., 1999; Peterson et al., 1999, 2002; Stockwell & Peterson, 2002a). We therefore expect that most of the models developed and used herein would be highly predictive.

**Table 1.** Summary of predicted presences and absences of bird species in six protected areas in southeastern Mexico, as well as in three 'optimal' areas selected based on our complementarity analyses

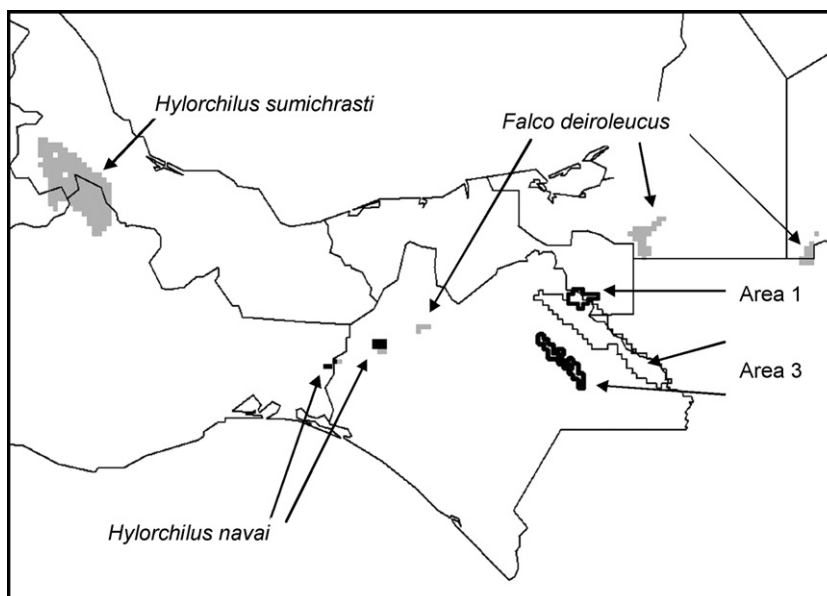
Area	Area (ha)	1	11	21	31	41	51	61	71	81
<i>Existing areas</i>										
Bonampak	4357	1111110111	0111111111	1101111011	1111111011	1111111100	1111111111	1101101111	1111111111	1111111111
Cascadas de Agua Azul	2580	1111111111	1111110111	1101001010	1111111100	1111111100	1111101110	1101101111	1111101111	1111010111
Chan-kin	12,185	1111110111	0111111111	1101111011	1101111011	1101111100	1011101101	1101101111	1011111011	1111111111
Lacan-Tun	61,874	1111110111	0111111111	1101111011	1101111011	1111111100	1111111111	1101101111	1111111111	1111111111
Montes Azules	331,200	1111111111	0111111111	1111111011	1111111011	1111111100	1111111111	1111111111	1111111111	1111011111
Yaxchilan	2621	1111110111	0111111111	1101111011	1101111011	1101111100	1011101101	1101101111	1111111111	1111111111
<i>Potential areas</i>										
Area 1	-	1111111111	1111111111	1101111011	1111111011	1111111100	1111111111	1101101111	1111111111	1111011111
Area 2	-	1001110101	0110110111	1011001000	1010111000	1111101100	1111101110	1111111111	1001101001	1111010111
Area 3	-	1111111111	1111111111	1101111011	1101111011	1101111100	1011101101	1101101111	1111111011	1111111111

Species are numbered, and names are provided in the footnote<sup>a</sup>.

<sup>a</sup>(1) *Accipiter bicolor*, (2) *Agamia agami*, (3) *Amaurilmnas concolor*, (4) *Amazilia candida*, (5) *A. tzacatl*, (6) *Amazona farinosa*, (7) *Ara macao*, (8) *Arremon aurantirostris*, (9) *Automolus ochrolaemus*, (10) *Campylopterus hemileucurus*, (11) *Caprimulgus maculicaudus*, (12) *Caryothraustes polioaster*, (13) *Celeus castaneus*, (14) *Cercomacra tyrannina*, (15) *Chlorophanes spiza*, (16) *Ciccaba nigrolineata*, (17) *Columba cayennensis*, (18) *C. nigrirostris*, (19) *C. speciosa*, (20) *Cotinga amabilis*, (21) *Crypturellus boucardi*, (22) *C. soui*, (23) *Cyanerpes lucidus*, (24) *Dendrocincla anabatina*, (25) *Dysithamnus mentalis*, (26) *Electron carinatum*, (27) *Euphonia gouldi*, (28) *Falco deiroleucus*, (29) *Florisuga mellivora*, (30) *Glaucidium griseiceps*, (31) *Glyphornychus spirurus*, (32) *Harpagus bidentatus*, (33) *Harpia harpyja*, (34) *Heiornis fulica*, (35) *Henicorhina leucosticta*, (36) *Hylomanes momotula*, (37) *Hylophilus decurtatus*, (38) *H. ochraceiceps*, (39) *Hylorchilus navai*, (40) *H. sumichrasti*, (41) *Lanio aurantius*, (42) *Laniocera rufescens*, (43) *Lepidocolaptes souleyetii*, (44) *Leptopogon amaurocephalus*, (45) *Leptotila plumbeiceps*, (46) *Leucopernis albicollis*, (47) *Lipaugus unirufus*, (48) *Lophornis helenae*, (49) *Lophostrix cristata*, (50) *Malacoptila panamensis*, (51) *Manacus candei*, (52) *Melanerpes pucherani*, (53) *Microcerculus philomela*, (54) *Microharpia quixensis*, (55) *Myiobius sulphureipygus*, (56) *Myrmotherula schisticolor*, (57) *Notharchus macrorhynchos*, (58) *Odontophorus guttatus*, (59) *Ornithion semiflavum*, (60) *Oryzoborus funereus*, (61) *Pachyrhamphus cinnamomeus*, (62) *Panyptila cayennensis*, (63) *Phaeochoera cuvierii*, (64) *Phaethornis longuemareus*, (65) *Pionopsitta haematotis*, (66) *Pipra mentalis*, (67) *Platyrinchus cancrinus*, (68) *Polioptila plumbea*, (69) *Psarocolius montezuma*, (70) *P. wagleri*, (71) *Pteroglossus torquatus*, (72) *Ramphastos sulfuratus*, (73) *Ramphocelus passerinii*, (74) *R. sanguinolentus*, (75) *Rhytipterna holerythra*, (76) *Salpator maximus*, (77) *Scaphidura oryzivora*, (78) *Schiffornis turdinus*, (79) *Sclerurus guatemalensis*, (80) *Spizaetus tyrannus*, (81) *Spizastur melanoleucus*, (82) *Tangara larvata*, (83) *Taraba major*, (84) *Terenotriccus erythrurus*, (85) *Thamnites anabatinus*, (86) *Tinamus major*, (87) *Trogon massena*, (88) *Vireolanius pulchellus*, (89) *Xenops minutus*.

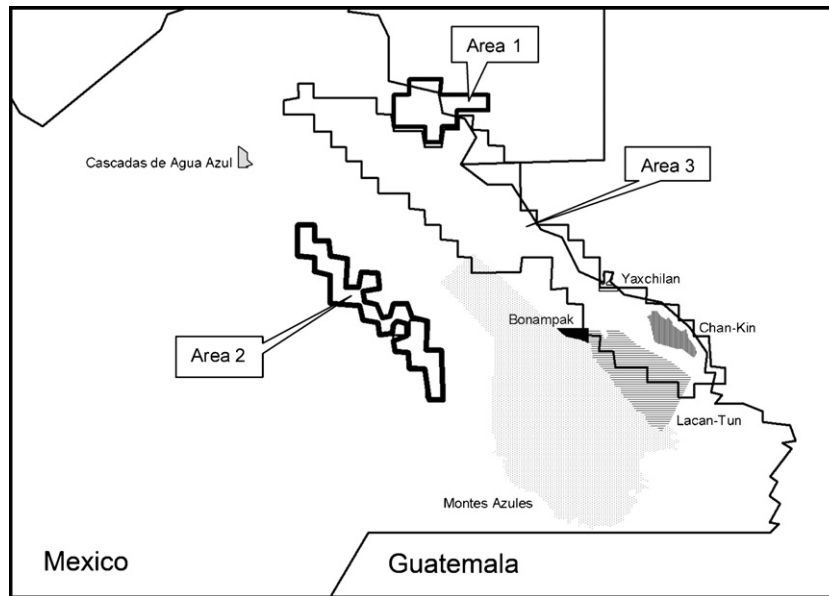


**Figure 1.** Example distributional models for four species developed in this study: (A) *Pipra mentalis*; (B) *Myrmotherula schisticolor*; (C) *Hylorchilus sumichrasti*; and (D) *H. navai*. Shown with black lines are the priority areas detected in this study.



**Figure 2.** First three areas identified by the pixel-based prioritisation analyses, which added 79, 4, and 3 species to the system, as well as the predicted distributions of the three species (*Falco deiroleucus*, *Hylorchilus sumichrasti*, *H. navai*) that did not fall in any of the three areas.





**Figure 3.** Areas identified in the prioritisation analyses in relation to existing protected areas in northern Chiapas.

The application of complementarity methods to predictive models is also subject to a number of concerns and limitations. Complementarity can introduce undesirable qualities (e.g., selecting peripheral or extreme areas) into prioritisations because of its clear emphasis on the most different faunal compositions; for that reason, several alternative and improved procedures have been developed (Csuti et al., 1997; Freitag et al., 1997; Lomolino, 1994; Williams et al., 1996a, 1996b). Application of those more complex methodologies in the present example, however, is made quite difficult by the enormous number of pixels under consideration in our analyses, in contrast to the usual applications of such methods; what is more, the very simple structure and distribution of the species under study made complex algorithms unnecessary.

Our comparison of pixel-based optimisations with optimisations of existing protected areas suffers somewhat from differences of scale. The protected areas range as large as  $3 \times 10^5$  ha, whereas the individual pixels are 4900 ha each, two orders of magnitude smaller. Hence, although both prioritisations arrive at 86 species in three areas, the pixel-based optimisation does it much more efficiently per unit area. Clearly, though, reserve areas must be developed with a view towards species' persistence, and not just representation, and so larger areas in reserves can be very important (Cowling et al., 1999).

The coincidence between our 'optimal,' pixel-based areas and the set of protected areas existing in the region is quite striking (Figure 3). In fact, the

existing protected areas form a cluster that is almost continuous and contiguous. Most of the area remaining unprotected in this area constitutes the three 'optimal' areas identified in this study. Hence, a clear recommendation emerging from our analyses is that of integrating the six protected areas in northeastern Chiapas (Cascadas de Agua Azul, Montes Azules, Bonampak, Lacan-Tun, Chan-Kin, and Yaxchilan) into a more inclusive reserve, and including the intervening area as part of land management efforts (Figure 3). In combination with protected areas more specific to the two karst-specific *Hylorchilus* wrens, and possibly the falcon *Falco deiroleucus* (which has a spotty, but broad, range south of Mexico), this system would be near-optimal for Mexican rain forest avifaunas.

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Museum of Natural History; Natuurhistorische Museum, Amsterdam; Louisiana State University Museum of Zoology; Museum of Comparative Zoology; Moore Laboratory of Zoology, Occidental College; Museum Nationale d'Histoire Naturelle, Paris; Museum of Vertebrate Zoology; Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México; University of Nebraska; Royal Ontario Museum; San Diego Natural History Museum; 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; US National Museum of Natural History; Western Foundation of Vertebrate Zoology; and Peabody Museum, Yale University. This study was supported by the National Science Foundation.

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