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DISTRIBUTION AND CONSERVATION OF BIRDS OF NORTHERN CENTRAL AMERICA

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ABSTRACT.—Patterns of distribution, diversity, and endemism in the birds of northern Central America were analyzed based on 541 avian species in 24 biotic regions. Many contrasts were apparent. For example, whereas species richness was concentrated in the Atlantic lowlands, with the Pacific lowlands, interior valleys, montane areas, and the Yucatan Peninsula less diverse; species endemic to the entire region were concentrated in the mountains and in the Yucatan Peninsula. Geographic patterns of endemism presented contrasts depending on the spatial scale of analysis. In contrast to overall patterns, species narrowly endemic to single geographic units were concentrated along the Pacific Coast of Chiapas and in southern Veracruz. Conservation implications of these results were explored using complementarity algorithms, producing ordered regional priority lists for the creation of optimal reserve systems. Finally, a plan of action for the study and conservation of avian diversity in northern Central America is outlined, including elements of basic inventory, systematics, and geographic analysis.

Some of the earliest studies of New World tropical birds were in Central America, including the impressive summary produced by Salvin and Godman (1879–1904). These early studies, in combination with subsequent investigations, led to treatments for each country and region: Chiapas (Álvarez del Toro 1971), southern Veracruz (Lowery and Dahlquest 1951), the Yucatan Peninsula (Paynter 1955), Guatemala (Griscom 1932, Land 1970), Belize (Russell 1964), Honduras (Monroe 1968), El Salvador (Dickey and van Rossem 1930, Thurber et al. 1987), and Nicaragua (Howell, unpubl. ms.). Hence, at first glance the region seems well known ornithologically, and not in need of intensive study.

Ornithological research has been sporadic and superficial, with no comprehensive survey of the entire region. Although wars and political conflicts that have characterized the last thirty years have largely ended, ornithological attention (apart from the other contributions to this symposium) has been slow to focus on the region. Hence, our purpose in this paper is to synthesize a distributional overview of the birds of northern Central America, which, although based on imprecise and incomplete information, is intended to detect general patterns in the region's avifauna. Our hope is that this preliminary summary will stimulate renewed attention to the region, especially by workers employing new techniques such as molecular genetics, phylogenetic systematics, and geographic information systems. We also make suggestions regarding the direction and context of new efforts of study and conserve the birds of northern Central America.

METHODS

For the purposes of this study, we defined northern Central America as extending from the Isthmus of Tehuantepec and southern Veracruz south and east through the Yucatan Peninsula, Chiapas, Guatemala, Belize, El Salvador, and Honduras, to western Nicaragua. This region forms a biogeographic unit (Dinerstein et al. 1995) clearly related to the historical sea channels that eventually closed to form the Central American isthmus (Stehli and Webb 1985, Mann 1995). We divided the region into 24 geographic regions that were homogeneous in terms of habitat makeup and biotic continuity (Fig. 1). For a few regions, such as the pine savannas and rain forests of the Mosquitia region of northern Honduras and Nicaragua, potentially distinct regions and habitat types were lumped because we lacked precise data.

We created a data base summarizing distributions of 541 bird species in the regions. Because our intent was to focus on distributional patterns of terrestrial bird species, only resident, breeding land bird species were included. Sources included the regional treatments cited above, surveys of museum specimens (for Mexico principally, see Acknowledgments), Hernández-Baños and coworkers (1995) and Howell and Webb (1995). We scored species as present or absent in each region; species' distributions beyond the limits of the study area were indicated as extending farther north or far-

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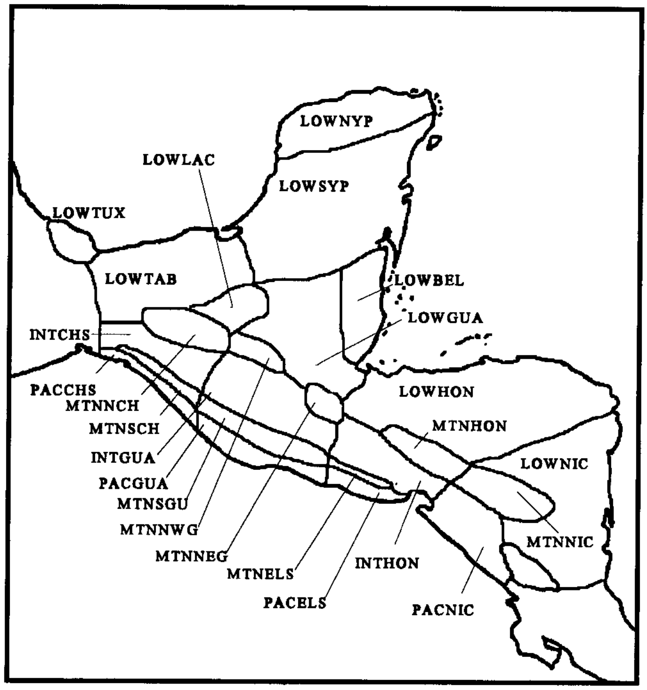

FIG 1. Map showing the 24 biotic regions employed in this study, with abbreviations used for reference in other figures.

ther south, based on the taxonomy and range descriptions in AOU (1983).

Subsequent analyses included UPGMA clustering of simple matching coefficient distances among regions derived from presence-absence matrices (Rohlf 1988). Near-optimal reserve combinations were obtained by means of a complementarity algorithm, implemented as follows: (1) series of criteria (e.g., species richness, endemism) were chosen and set in a specific order of importance; (2) a reserve was chosen based on the first criterion; (3) a second reserve was added based on the cumulative total for the first criterion (i.e., based on new species added to the total); (4) additional reserves were added one by one based on their effect on the cumulative species total. In case of a tie, the second criterion was used to decide among tied possibilities; further criteria were used in the event of ties in the second criterion. Because of the large numbers of species involved, globally optimal approaches (e.g., Church et al. 1996) were impractical to implement (Pressey et al. 1996).

RESULTS

Overall bird species richness was unevenly and nonrandomly distributed in northern Central America (Fig. 2A). Highest numbers of species were found in the Atlantic lowlands from southern Mexico south to Nicaragua, and species richness was lower on the Yucatan Peninsula and in the interior and Pacific portions of the region. Lowest species richness was found in the interior valleys, probably reflecting isolation or paucity of microhabitats in their arid habitats, as well as in the mountains and Pacific lowlands of Nicaragua.

Cluster analyses of the overall data set revealed five principal groupings of areas (Fig. 3): (1) the Atlantic lowlands exclusive of the Yucatan Peninsula, (2) Pacific lowlands, (3) interior valleys, (4) the Yucatan Peninsula, and (5) montane areas. The montane areas were most distinct from the remaining four clusters. Within the latter grouping, the Atlantic lowlands were most distinctive, followed by the Yucatan Peninsula; the Pacific lowlands, and interior valleys grouped closely together. The only geographically disparate areas that grouped together were the Yucatan Peninsula, the Pacific lowlands and interior valleys, reflecting their common semiarid tropical faunal elements. Hence, patterns of faunal similarity among regions appear to correspond to geographic proximity and/or habitat similarity.

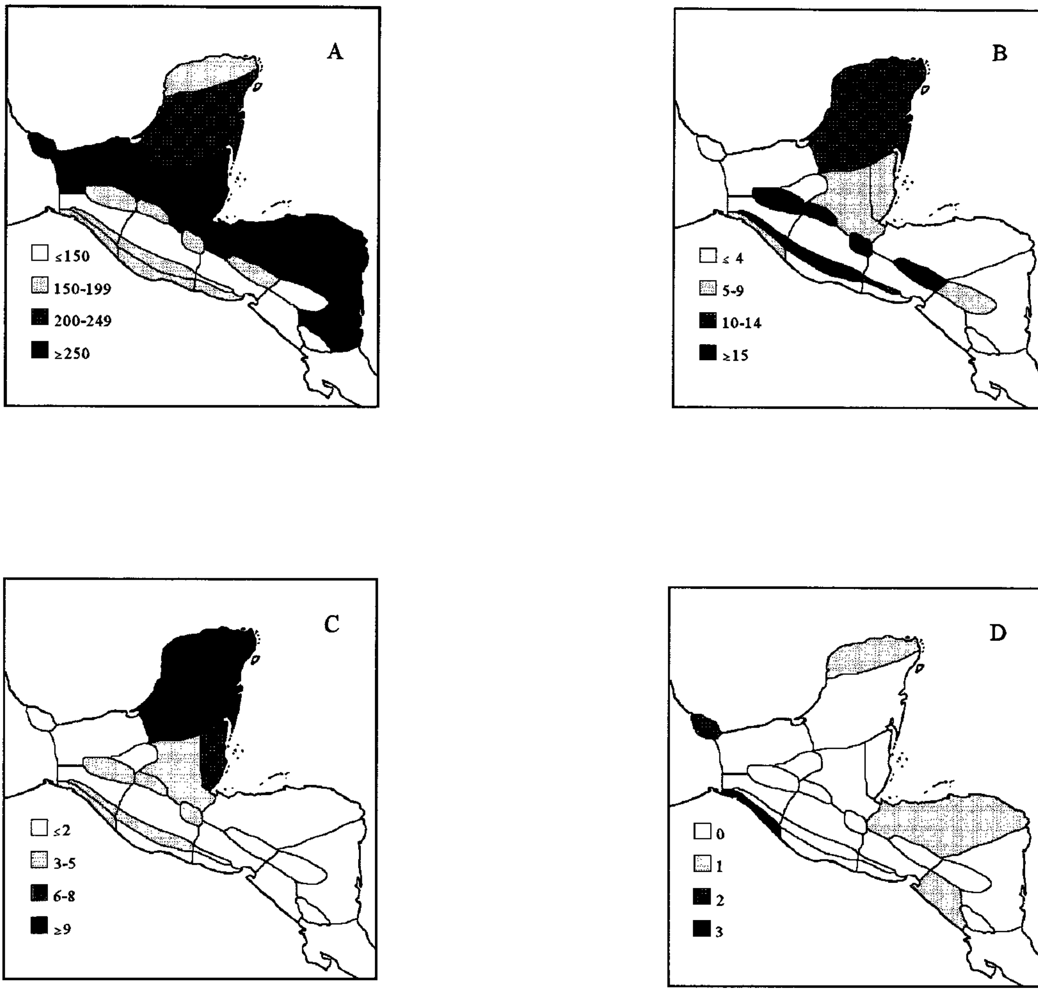

FIG. 2. Maps showing the geographic distribution of diversity of birds in northern Central America. Shown are (A) total numbers of species, (B) species endemic to northern Central America, (C) species restricted to five or fewer regions, and (D) species restricted to a single region.

Of the 541 species included in the data set, 150 (27.7%) ranged farther south than the study area, 138 (25.5%) ranged farther north, and 208 (38.4%) ranged both to the south and to the north. The remaining 45 (8.3%) occurred nowhere but in northern Central America (Table 1). The geographic distribution of these endemic species was highly localized (Fig. 2B): montane regions were major foci, and the Yucatan Peninsula contained a secondary concentration. Hence, patterns of endemism contrasted sharply with patterns of species richness.

Five avian genera were endemic to the region. The guans *Penelopina* and *Oreophasis* are both restricted to montane portions of the region. The motmot *Aspatha* is widely distributed; the turkey *Agriocharis* occurs throughout the Petén region (although submerged in *Meleagris* by AOU 1995); and the mimid *Melanoptila* is found only on the Yucatan Peninsula. Because all five are monotypic genera, no secondary speciation within the region appears to have taken place.

Clustering regions based on the distribution of endemic species revealed patterns similar to those recovered from analysis of all species (Fig. 3). Again, montane regions were most

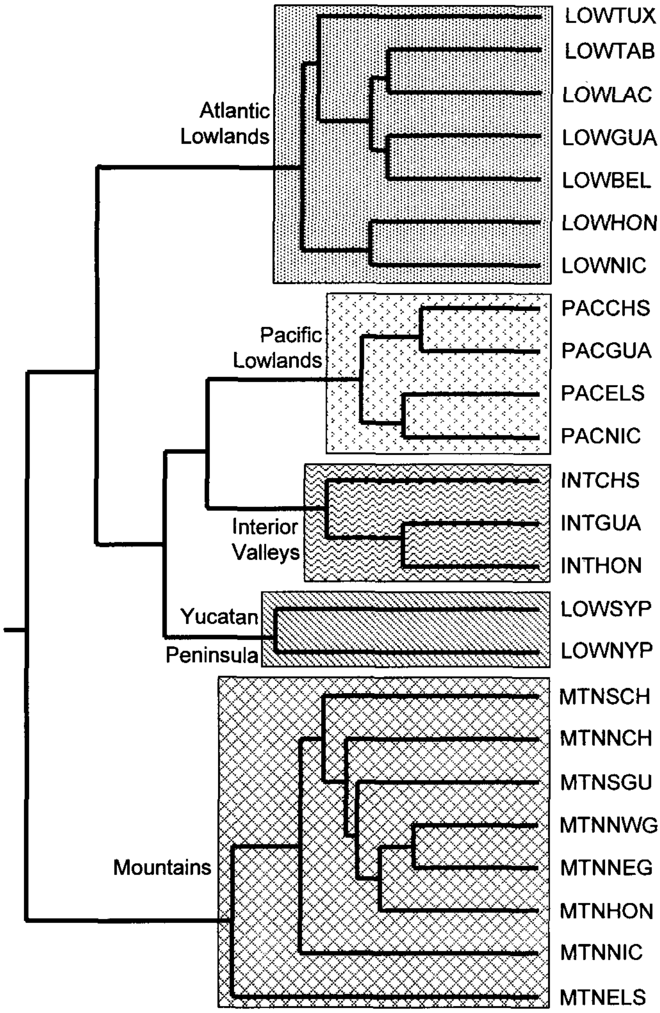

FIG. 3. Cluster analysis showing patterns of avifaunal similarity among regions based on all species. Abbreviations for regions given in Fig. 1.

distinctive, and clusters were recognizable for the Yucatan Peninsula and other lowland areas, although patterns were not as well defined as for the overall analysis. Hence, the fewer species involved in the endemic cluster analysis probably led to less clear overall resolution.

Examination of the spatial scale of endemism showed that endemic species' ranges included as few as one region (8 spp.), up to a maximum of 10 regions (1 spp.; Table 1). Regional endemics were concentrated in montane areas and in the Yucatan Peninsula (Fig. 2B). When only species found in five regions or fewer were considered, the Yucatan Peninsula had a higher concentration (Fig. 2C). The eight species restricted to single regions ("narrow endemics"), were found in the Pacific lowlands of Chiapas (*Passerina rositae, Aimophila sumichrasti, Campylorhynchus chiapensis*), the Los Tuxtlas region of southern Veracruz (*Campylopterus excellens, Geotrygon carrikeri*) and include 3 species in 3 other regions (Fig. 2D). Hence, foci of endemism vary strikingly depending on the spatial scale of the analysis.

TABLE 1. List of bird species endemic to northern Central America, with number of regions in which the species occurs.

Species	Number of regions
Agriocharis ocellata	5
Aimophila sumichrasti	1
Amazilia luciae	1
Amazona xantholora	2
Aratinga strenua	6
Arremonops chloronotus	6
Aspatha gularis	6
Atthis ellioti	7
Campylopterus excellens	1
Campylopterus rufus	5
Campylorhynchus chiapensis	1
Campylorhynchus yucatanicus	1
Caprimulgus badius	2
Carduelis atriceps	4
Colinus nigrogularis	4
Cyanocorax melanocyaneus	10
Cyanocorax yucatanicus	6
Cyanolyca pumilo	6
Cyrtonyx ocellatus	7
Doricha enicura	7
Ergaticus versicolor	5
Geotrygon carrikeri	1
Granatellus sallaei	6
Icterus auratus	2
Icterus maculialatus	4
Lampornis sybillae	2
Lampornis viridipallens	7
Melanerpes hoffmannii	1
Melanerpes pygmaeus	2
Melanoptila glabrirostris	4
Melanotis hypoleucus	7
Myiarchus yucatanensis	4
Notiochelidon pileata	7
Nyctiphrynus yucatanicus	3
Oreophasis derbianus	5
Ortalis leucogastra	4
Otus barbarus	3
Passerina rositae	1
Penelopina nigra	7
Piranga roseogularis	3
Strix fulvescens	7
Tangara cabanisi	2
Troglodytes rufociliatus	8
Turdus rufitorques	7
Xenotriccus callizonus	3

DISCUSSION

Conservation priorities.—The analyses presented above, although preliminary, have interesting implications for the conservation of avian diversity in northern Central America. Most importantly, overall patterns of avian species richness and endemism contrasted sharply, leading to a quandary for conservation prioritization: species richness was highest in the Atlantic lowlands, whereas endemism was greatest in montane regions and in the Yucatan Peninsula (Fig. 2A, B). Similar results have been encountered elsewhere and at other scales of analysis, making the generality of the result convincing (Escalante-Pliego et al. 1993, Peterson et al. 1993, Hernández-Baños et al. 1995, Peterson and Salazar, in press).

To add further complication, "endemism" can be defined in several ways. Although the simplest version is "found nowhere else," a case can be made for the importance of considering range size as well to identify endemic species (ICBP 1992). Unfortunately, geographic concentrations of endemism may differ based on spatial scale and definition used (Figure 2B–D), making identification of priorities complex.

Another complication for implementation of conservation policies is the lack of information on available habitat. The spatial extent and geographic distribution of patches of primary habitat remaining in northern Central America remain unassessed. Without this critical information, design of adequate strategies for conservation at a fine scale is all but impossible. Hence, evaluation of geographic patterns of land use and habitat distribution would represent an important advance in biodiversity conservation in the region.

A variety of approaches can be used to establish priorities for creating references. If geographic patterns in species richness and endemism were coincident, an optimal strategy would be to represent each of the principal assemblages in the cluster analysis in a reserve system (Peterson and Salazar, in press). Because such coincidence is lacking in the present case, we have taken a more quantitative approach based on the principle of complementarity among reserves in the system.

Under the assumption that a reserve within a particular region should hold the important components of the region's biodiversity, we performed two complementarity analyses based on different criteria. The first maximized representation of single-region endemics. In cases where this criterion was equivocal, we used representation of endemic species with ranges of five or fewer regions; succeeding criteria were overall endemism and species richness (Fig. 4). Under this approach, the optimal reserve system included (in order of decreasing importance) the following areas: Pacific lowlands of Chiapas, Los Tuxtlas, northern Yucatan Peninsula, Atlantic lowlands of Honduras, Pacific lowlands of Nicaragua, Sierra Norte of Chiapas, interior valley of Chiapas, mountains of Nicaragua, southern Yucatan Peninsula, and mountains of southern Guatemala. This prioritization therefore represents a near-optimal combination of reserves in regions of Central America for the preservation of avian diversity, emphasizing restricted-range endemics.

An alternative approach emphasized species richness, followed by overall endemism, five-region endemics, and single-region endemics (Fig. 4). Under this prioritization, first in importance were the Atlantic lowlands of Honduras, followed by the Sierra Norte of Chiapas, southern Yucatan Peninsula, Pacific lowlands of Chiapas, interior valley of Chiapas, mountains of southern Guatemala, Los Tuxtlas, northern Yucatan Peninsula, mountains of Nicaragua, and Tabasco. This list therefore represents a near-optimal reserve scheme for preserving bird diversity by emphasizing species richness.

The two complementarity implementations yielded highly noncoincident results, suggesting that hard decisions may be required for conservation efforts to proceed. Comparing rankings for areas included in both systems yielded an r^2 of 0.001 (Spearman rank correlation), indicating little or no association. Hence, conservation efforts must begin by choosing an order of importance for the different dimensions of biodiversity to make prioritization of different areas possible. We suggest that the restricted-range endemics are at much greater risk of extinction and that their prioritization should be accorded precedence.

Spatial scale of endemism.—An additional consideration for the use of endemism in conservation planning springs from the examination of distribution of endemism at different spatial scales, pointing out the danger of areal definitions of endemism in biodiversity studies. Fig. 2 illustrates the changing nature of foci of endemism based on different spatial definitions; whereas regional endemism is focused in montane regions and the Yucatan Peninsula, narrow endemics are concentrated along the Pacific lowlands of Chiapas and in Los Tuxtlas. Similar results have been obtained in studies of other avian assemblages (Hernández-Baños et al. 1995), suggesting that endemism defined at different spatial scales may not always yield coincident results.

A worrisome implication of this result regards recent studies of avian endemism on a worldwide scale. ICBP (1992) defined species with total ranges of 50,000 km^2 or less as endemics, and analyzed their geographic distribution to establish priority zones for conservation attention. These results suggest that such studies may yield pictures of endemism that are highly unstable and unpredictable depending on their position along some unknown spectrum as seen in Fig. 2. Hence, the conclusions reached by ICBP (1992) and other studies imposing single spatial definitions on endemism may prove to reflect only one dimension of endemism, rather than some single underlying pattern.

Future directions.—Based on the analyses presented above and on our understanding of present ornithological activity in northern Central America, we suggest three general research areas that need much more activity. These topics are inventory, systematics, and geographic analysis—thorough, synthetic studies in each realm would greatly improve the knowledge and understanding of the region's avifauna.

A first, and most critical, need is for basic avifaunal inventories. These studies document details of distribution for each species, and permit understanding community composition, inferring historical geographic patterns, determining conservation priorities, and many other important facets of the geography and ecology of bird species. Properly documented by voucher specimens (Remsen 1995), and other associated data, inventories can serve as the foundation for many systematic and geographic studies as well.

An example of the dire need for basic inventory studies can be taken from a two-week study in 1993 on Cerro Piedra Larga, Oaxaca, Mexico (Escalona-Segura et al., unpubl. data). This mountain, although in close proximity to well-known sites in a thoroughly documented

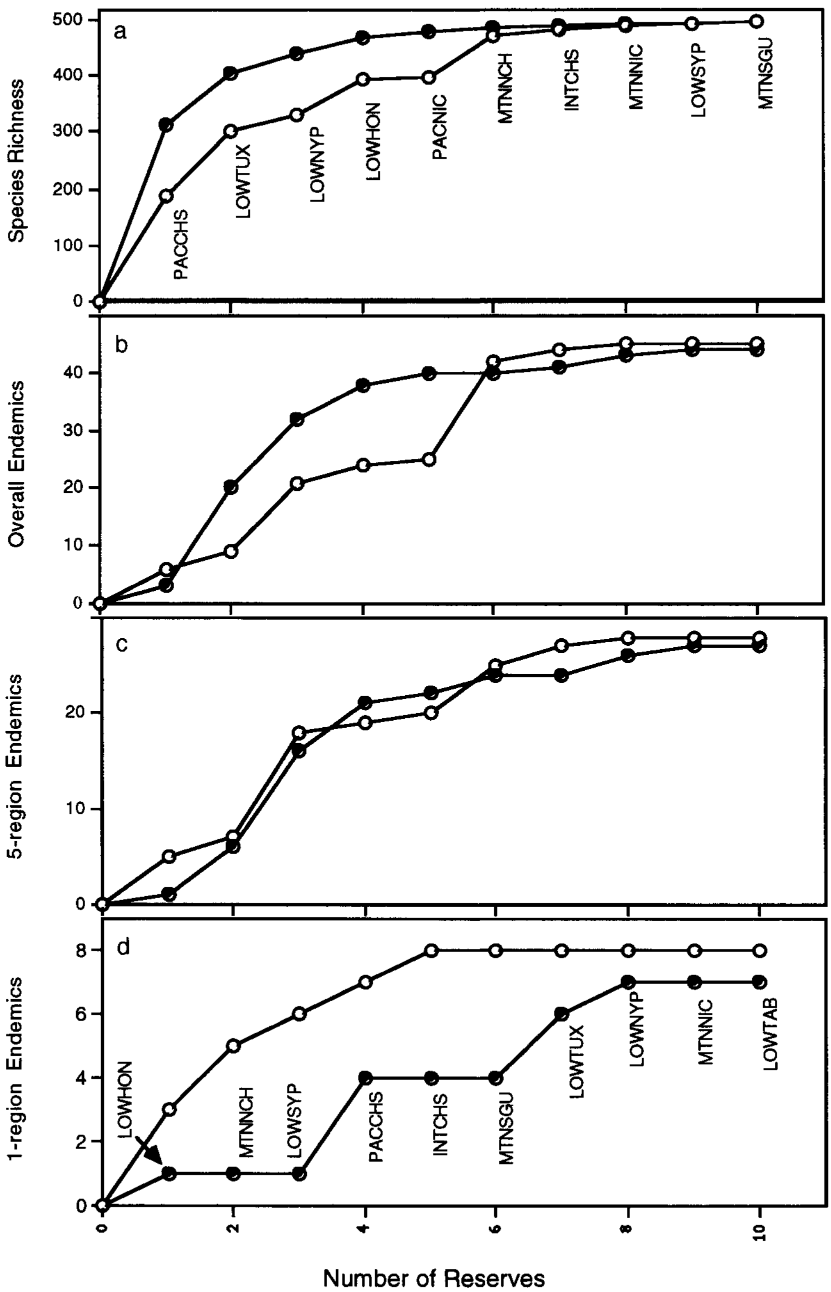

FIG. 4. Cumulative graphs of representation of species in reserve systems in northern Central America, based on criteria ranked as species richness, overall endemism, endemics to 5 or fewer regions, and endemics to single regions (closed symbols), and based on criteria ranked as endemics to single regions, endemics to five or fewer regions, overall endemism, and species richness (open symbols). A. Total species richness, B. Overall endemics, C. Endemics restricted to five regions, D. Endemics restricted to one region. Abbreviations for regions are from Fig. 1.

state (Binford 1989), is isolated between the southeastern termini of the Sierra de Miahuatlán and the Sierra de los Mixes. It had never been surveyed ornithologically—the expectation was that its fauna would be allied with that of one mountain range or the other (Hernández-Baños et al. 1995). After careful study, however, we found three forms of eastern affinity (Sierra de los Mixes), mixed with four of western affinity (Sierra de Miahuatlán), making the mountain a fascinating and unique mix of the distinct avifaunas of the neighboring mountain ranges. Other unexpected discoveries, such as the rare Maroon-fronted Ground-Dove (*Claravis mondetoura*) and the first-known sympatry of two differentiated populations of the Amethyst-throated Hummingbird (*Lampornis amethystinus*), further serve to illustrate the importance of these basic studies. Many other sites throughout northern Central America remain unsurveyed or inadequately sampled; hence, much remains to be learned about the birds of the region.

Systematic studies form an important second element in our proposed plan of action. Although the taxonomy, distribution, ecology, and variation of birds appear to be generally well documented (e.g., AOU 1983), in fact, much remains to be studied. Major methodological and theoretical advances in systematics in the past three decades have been applied to only a few species in Mesoamerica. As a result, most species' taxonomy has seen no recent systematic attention, making modern study imperative.

Much systematic work will prove necessary to delineate the species-level taxa of birds in northern Central America. With respect to Mexican birds, ongoing systematic studies have identified many species-level units that need to be recognized for a full appreciation of the dimensions of avian biodiversity—for example, multiple species are recognizable within all three currently recognized *Aphelocoma* jays (Peterson 1992), Acorn Woodpeckers (*Melanerpes formicivorus*; Benítez-Díaz 1992), *Cypseloides* swifts (Navarro-Sigüenza et al. 1992), *Geotrygon* quail-doves (Peterson 1993), Rosy-throated Thrush-Tanager (*Rhodinocichla rosea*; Peterson et al., unpubl. data), House Wren (*Troglodytes aedon*; Escalona-Segura 1995), and many others. More than 50 complexes remain in need of study, including newly recognized forms that would increase the number of species endemic to Mexico by at least 240% (Navarro-Sigüenza and Peterson, unpubl. data)! Although action in creation of reserves should not await these detailed examinations, these changes will influence the picture of biodiversity in Mexico and other northern Central American countries.

Thirdly, explorations of the application of synthetic geographic approaches to biodiversity questions in northern Central America are badly needed. The results presented above are the crudest of beginnings, based on imprecise data and a subjective regionalization. More sophisticated approaches would permit many improvements. For example, known occurrence points for species can be associated with thematic geographic factors to produce statistical models of the probability of species' occurrence across the landscape (e.g., Miller et al. 1989, Walker and Cocks 1991, Hollander et al. 1994). Remote sensing approaches can be used to characterize the distribution and limits of large extents of primary habitat (Skole and Tucker 1993). Finally, synthetic approaches can overlay predicted species' ranges to form "biodiversity maps," which can be compared with geographic features using landscape metrics (Van Dorp and Opdam 1987, Hejl 1992) and used to situate conservation areas (Harrison and Martinez 1995). Synthetic analyses will prove instructive and informative about many previously unappreciated details of biodiversity, especially in exceptionally diverse and little-studied tropical regions like northern Central America.

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