AVIAN DISTRIBUTION IN CENTRAL AMERICA

THOMAS R. HOWELL

As Central America is not a naturally delimited geographic entity, I define it arbitrarily for present purposes as the area from the United States-Mexico border and the lower Rio Grande valley southward through Panama and including a small section of Colombian territory southwest of the Gulf of Urabá. A more exact demarcation of both boundaries is given below. For the sake of simplicity, Baja California and all offshore islands are excluded from consideration.

However one defines Central America, the analysis of the distribution of its avifauna remains an intriguing problem. During most of the Tertiary, part of the region was crossed by seaways that blocked the spread of many organisms and interrupted the ranges of others. The long physical isolation of North and South America permitted the evolution of distinctive biotas on those continents. The partly submerged and sometimes fragmented portions of Central America were for some individuals or groups an absolute barrier to northward or southward dispersal; for others they were a filter bridge; for still others, an obstacle that was nevertheless crossed in both directions, perhaps repeatedly. Around the end of the Pliocene an isthmus linking the northern and southern continents developed. This resulted in new and extensive invasions of previously separated sections of the Central American region by the biotas of North and South America, a process that is still continuing. Climatic changes in the Pleistocene influenced the extent and direction of these movements, and the last glacial period in particular brought about a strong southward thrust of the northern biota into what is now the tropical zone and doubtless caused halts and retreats in the dispersal of many northward-expanding forms of southern derivation.

This rough outline of historical events is well-known to all students of biogeography, and it has proved especially challenging to zoologists concerned with the distribution of vertebrates from the Cenozoic era to the Recent. The importance of Central America has been emphasized by Simpson (1965) in a collection of his writings on mammalian distribution, and an extensive symposium on the distribution of cold-blooded vertebrates in Central America was recently published in Copeia (1966, No. 4). Many ornithologists have dealt with problems of Central American bird distribution, and the most important of these up until the last decade were reviewed and discussed by Darlington (1957: 236–319), who also contributed new interpretations. The most recent treatment is that of Mayr (1964a) who dealt broadly with the entire Tertiary history of the avifauna

293 The Auk, 86: 293–326. April, 1969

of the Americas. Mayr commented succinctly on the difficulties and sources of error in attempting to sort out the various components in the American avifauna—old and recent colonizers, primary and secondary North and South American elements, expanding, relict, and unanalyzable groups—and stressed the need for developing more information from the analysis of contemporary bird distribution, particularly at the level of genera and species. It should indeed prove advantageous to analyze the avifauna of any Central American area in terms of the distribution of genera and species within each family that occurs there; the data obtained can then be tested for extrapolation to a broader scale.

I have gathered distributional data on the avifauna of Nicaragua, as I consider this area to be critical in understanding bird distribution in all of Central America. It is virtually traditional for each worker to consider his area of special interest to be the key to such understanding (Griscom, 1932: 3–4; Wetmore, 1965: 1; Haffer, 1967a), and I am no exception; my reasons are both historical and ecological.

GEOLOGIC HISTORY

The interpretation of the geologic history of Central America has undergone considerable change (or at least proposed change) in the past decade, and a brief review should be helpful. The following account discusses areas in terms of their contemporary names and boundaries in order to avoid cumbersome circumlocutions.

For many years the most widely accepted versions of the geography of Central America in the Tertiary were largely derived from Schuchert (1935). He designated an area extending from Chiapas, Mexico, to northern Nicaragua as "Nuclear Central America"; this was believed to have been separated from the rest of Mexico and North America by a seaway across the Isthmus of Tehuantepec and from South America by a seaway across southern Nicaragua, Costa Rica, and western Panama. The maps of Tertiary Central America given by Mayr (1946: 8) and Darlington (1957: 280) represent basically this same picture. Durham et al. (1955), after a careful geological and paleontological field investigation, concluded that no Tertiary or Quaternary Tehuantepec seaway existed; none of the alleged evidence for it could be substantiated. Dr. Durham informs me (pers. comm.) that his subsequent investigations support his earlier conclusion that such a seaway did not exist. With no water gap across Tehuantepec, then a continuous Tertiary land connection must have extended from North America at least to the southern boundary of Nuclear Central America, which is northern Nicaragua (Lloyd, 1963: 88).

Mayr (1964a, 1964b) reconsidered the Tertiary history of the American avifauna in the light of new data since his 1946 paper and excluded mention of a Tehuantepec seaway. He stated (1964a: 280) that the ocean gap separating the two continents "was apparently largest in the Cretaceous and early Tertiary. . . . At its widest, the gap ranged from Guatemala or Honduras southwards and included much of northwestern Colombia." Dr. Mayr has kindly informed me (in litt.) that he has no disagreement with the view that northern Nicaragua was above the sea and joined with the North American land mass in the Tertiary; in suggesting Guatemala or Honduras as the southern limit of this mass, he was merely indicating the general area without specific concern for the sometimes shifting political boundaries.

Woodring (1954) and Lloyd (1963) envisioned the area between the southern boundary of Nuclear Central America and South America as a seaway broken by various archipelagoes from at least early Eocene until late Pliocene, at which time an isthmian link was formed that connected the two areas for the first time since the evolution of modern orders of birds and mammals.

The recent discovery in the Canal Zone of Panama of a Miocene mammal fauna including large herbivores of North American affinity necessitates a further reassessment of the entire picture. The detailed account by Whitmore and Stewart (1965) leaves no doubt that the fauna of Miocene ungulates in the Canal Zone included members of several families (Equidae, Rhinoceratidae, Merycoidodontidae, Protoceratidae), all closely related to North American forms of the same age, that could only have reached Panama by way of a land connection to the west and north. On the basis of this evidence Whitmore and Stewart suggest that a Tertiary land mass not only extended continuously from North America through Nuclear Central America, but that by early middle Miocene land reached continuously as far south as the Canal Zone; that intermittent seaways may have crossed southern Nicaragua and parts of Costa Rica and Panama during the Miocene; that most of eastern Panama was separated from Colombia from the Oligocene to the Pliocene by the Bolivar Trough and was intermittently connected with western Panama; and that the last seaway to be closed, effecting the complete connection between North, Central, and South America at the end of the Pliocene, was the Bolivar Trough across northwest Colombia.

The sum of the current evidence indicates with reasonable certainty that: (1) at least from the early Tertiary to the present, continuous land has extended from North America to northern Nicaragua; (2) at least by early middle Miocene time, land was continuous as far south as the Panama Canal Zone; (3) no land connection existed between Central and South America until the end of the Pliocene. Less well-known is the extent and duration of seaways across the expanse between northern Nicaragua and northwest Colombia, but it seems certain that some existed. The Nicaraguan depression that forms the lowlands of southeastern Nicaragua (including the two great lakes) was the northernmost probable site of a Tertiary seaway. Even if the Pacific and the Caribbean were never actually connected in that region, at least an extensive embayment greatly narrowed the isthmus and must have thereby influenced the north-south movements of many animal groups. Post-Pliocene events included important orogenic activity and climatic changes, which contemporary ecological conditions and animal distributions strongly reflect.

DISTRIBUTIONAL SIGNIFICANCE OF NICARAGUA

As a result of the configuration and history of Central America as an archipelago-isthmus linking North and South America, its avifauna consists essentially of three components—one of northern derivation, one of southern derivation, and an endemic component; many taxa of the latter group are probably derived relatively recently from ancestors of northern or southern derivation. Sorting out the members of these components is a difficult zoogeographic problem. One approach would be to choose an appropriate reference point or region in Central America and to analyze the geographical affinities of its avifauna—that is to identify, if possible, those taxa that have reached the reference region from the north or from the south. For purposes of such analysis, the ideal reference region should be: (1) the site of a former major geologic discontinuity between northern and southern land masses; (2) a site of the termination of major types of habitat; (3) an area that includes the northern or southern limits of the ranges of many species; and (4) an area that has no taxa confined exclusively within its boundaries.

The region enclosed within the boundaries of Nicaragua fits these four categories rather closely. It is the site of the juncture of an ancient elevated northern land mass with a transient lowland area to the south that was sometimes covered by the sea. Northern Nicaragua marks the southern extent of naturally occurring pine forests in the western hemisphere, and no evidence suggests that pines ever extended south of the present limits (Mirov, 1967). These forests constitute a characteristically northern habitat, and many species of birds with wide northern distributions reach their southern limit in the Nicaraguan pines. Another habitat and its associated avifauna that is presently characteristic of northern Central America—the arid scrub and thorn forest of the Pacific slope—reaches its southern limit not far beyond the Nicaraguan border in the northwest quadrant of Costa Rica. On the Caribbean slope, lowland tropical rain forest covers much of eastern Nicaragua, including the former Nicaraguan depression, and then becomes much dissected among the complex highlands of Honduras and attenuated as the coast line changes from a north-south to an east-west direction. Correspondingly a number of lowland rain forest birds reach the northern limit of their range in Caribbean Nicaragua, or in the Olancho region of Honduras just to the north.

Despite its large area and its variety of habitats, Nicaragua has no strictly endemic species of birds although two were formerly thought to be so. The grackle *Cassidix nicaraguensis*, found primarily in the vicinity of the two large Nicaraguan lakes, has extended its range into northeastern Costa Rica, probably recently in association with deforestation and livestock-raising. The seed-finch *Oryzoborus nuttingi*, which some students consider conspecific with *O. crassirostris* of South America, has recently been collected in Costa Rica and western Panama. Other forms found only in Nicaragua and discontinuously in areas farther to the south (*Gampsonyx swainsonii*, *Nyctiphrynus ocellatus*, *Lurocalis semitorquatus*, *Myrmornis torquata*) are only subspecifically differentiated, it at all, from the more southern populations. With these few exceptions, all species found in Nicaragua also range into areas immediately to the north or south or both. Thus, to paraphrase G. Evelyn Hutchinson rather outrageously, I propose that Nicaragua is a particularly good historico-ecological theater in which to study the Central American distributional play.

It is at once evident that the simple theoretical ideal of categorizing Nicaraguan birds as northern or southern (or as Central American endemics of northern or southern affinity) can only be approached and not fulfilled. Widespread forms such as many water birds, raptors, and aerial feeders may never be designated with a high degree of probability as derived from a particular region. Climatic changes associated with glacial and interglacial periods in the Pleistocene must have caused alternate southward and northward extensions of range of many groups, and the fossil record relevant to Central American bird distribution is discouragingly meager. Nevertheless with appropriate caution and restraint, useful data should be obtainable from analysis of contemporary patterns of distribution.

Definitions and Premises

Terms must be defined before continuation of the discussion. Unless otherwise stated, by "distribution" I refer to post-Pliocene distribution; by "northern" and "southern" I refer to areas north or south of Nicaragua; by "affinity" I refer to a geographical relationship of a contemporary population with the region from which its present distribution was derived. Thus in stating that a taxon is of northern or southern affinity, I mean to suggest that its post-Pliocene distribution stems from populations that formerly were or still are found only north or south of Nicaragua, respectively. In the subsequent distributional analysis, the following three premises are adopted as reasonable and valid except in cases where there is specific evidence to the contrary:

1. Any taxon found *exclusively* in the area from Nicaragua northward is of northern affinity. The only alternative explanation for such a distributional pattern would be that a taxon of originally southern distribution extended its range north of Nicaragua, maintained itself there, and failed to survive in more southern areas. This seems highly improbable. It is possible that the taxon in question may formerly have had a more extended distribution southward and that the populations south of Nicaragua have not survived; if so, the contraction of the range northward suggests that the taxon is indeed of northern affinity and thus supports the original premise. Some representatives of more southern areas have undoubtedly colonized areas north of Nicaragua, but most of these still exist as southern populations also. Other originally "southern" colonizers have differentiated into distinct taxa in the north—in which case the latter may be considered forms of northern affinity (see example below). It should be emphasized that these premises apply only to the particular taxon under consideration and not necessarily to the higher categories to which it belongs. For example a species may be of northern affinity (*Synallaxis erythrothorax*; Furnariidae; southern Mexico to Honduras) although the family and the genus are of southern derivation.

2. Any taxon found *exclusively* in the area from Nicaragua southward is of southern affinity. The reasoning is the same as in the previous premise, including the provision that a species may be of southern affinity (*Vermivora gutturalis*; Parulidae; mountains of Costa Rica and western Panama) although the genus and probably the family are of northern affinity. This premise may seem less secure than the first one as it is easier to imagine a northern taxon shifting its range southward during a Pleistocene glacial period and then remaining only in the southern area as an isolated relict population. However it is improbable that the entire population of a taxon would shift its range and leave no remnants in the northern area. For example there is an isolated population of the Acorn Woodpecker (*Melanerpes formicivorus*) in Colombia but the species also occurs from Oregon south to western Panama. Even if an entire population did shift southward during a glacial period without leaving remnants in the north, it is unlikely that none would expand back into the northern part of the original range under ameliorated conditions. For example it could possibly be argued that a species with a range such as that of *Ramphastos swainsonii* (Ramphastidae: northwestern South America to

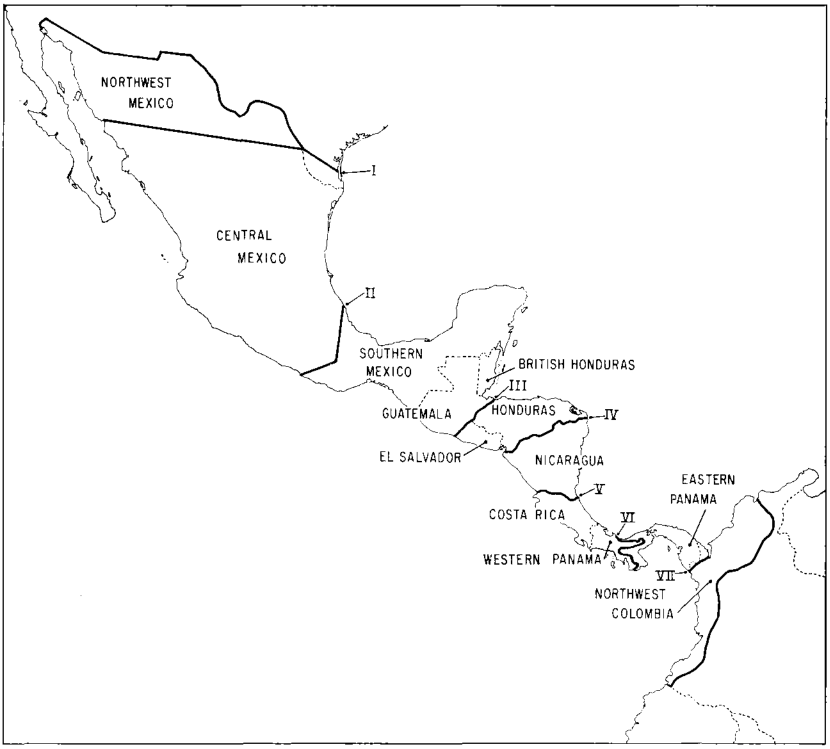
eastern Honduras) is actually of northern affinity, that its range shifted far to the south during a glacial period, and that it is still extending its range northward toward its area of origin but has not yet reached it. Those northern tropical populations that moved south during periods of glaciation would probably be the first to reoccupy the northernmost areas that again became habitable for tropical forms in postglacial times. The thousands of years since the last glacial period constitute ample time for such range expansion to the present northern limits of tropical habitat. Other reasons why a species may not have reoccupied its surmised former range—that the more northern tropical areas are in some way unsuitable, or that they are already occupied by competitors—are arguments in favor of the hypothesis of southern affinity. In general, a form that has moved south and north with a particular habitat would be expected to occupy the existing area of that habitat to the fullest extent possible at any given time.

3. The extent to which a taxon ranges south or north of Nicaragua is a rough indication of the probability of northern or southern affinity, respectively. This premise applies to those forms that are not confined to the northern or southern sections of Central America, and it follows from the first two premises. For example, species such as *Dendrortyx leucophrys* (Phasianidae; southern Mexico to northern Costa Rica) is probably of northern affinity; species such as *Ramphastos swainsonii* (see above) and *Myrmotherula fulviventris* (Formicariidae; Ecuador to eastern Honduras) are probably of southern affinity. The farther the "short end" of the range extends beyond Nicaragua, the greater the possibility of error in designating northern or southern affinity. Wide-ranging forms are unanalyzable in this manner unless additional evidence relevant to the problem is available.

METHODS

In order to test the above premises and the suggested importance of the Nicaraguan region for consistency with the available evidence on Central American bird distribution, I have devised a diagrammatic method of representing distributional data that utilizes Nicaragua as the reference region with which the rest of Central America may be compared. Hopefully this distributional model has relevance for all of Central America and, as the method may be applicable to other isthmian areas or to island chains extending between continents, it is presented here despite its still tentative form.

As bird distribution in Central America tends to fall into gradients following the long axis of the land mass, a plot of the avifaunas of sequential segments of the entire area should reflect distributional trends. Ideally Central America could be divided into such segments at points representing major avifaunal discontinuities that would correspond to important contemporary geographic and ecological interruptions. Unfortunately such concordance of discontinuities is never perfect except on a limited scale, and divisions must therefore be at least partly arbitrary. I have attempted to divide Central America into segments with lines that approximate zoogeographically significant terminations in the ranges of at least some birds. The segments are not



Map 1. Central America and Northwest Colombia as herein defined, divided into sequential segments (see text for explanation).

proposed as centers of origin or as refugia; they are simply portions of a distributional spectrum. Broad boundaries are drawn, as with a wide brush on a small scale map, in order to accommodate those inevitable instances in which a species' range is entirely on one side of a particular line except for a few recorded occurrences slightly beyond it. The division into segments is shown in Map 1.

Line I. It would be desirable to have the northernmost line drawn across the exact northern limits of the tropical avifauna in Mexico, but these limits prove impossible to define. No matter where the line is drawn, always a few widespread species of probable tropical derivation range slightly farther north. I have arbitrarily drawn a slightly bent line from latitude 28° N on the west side to 27° N on the Gulf coast of Texas. The line extends from the vicinity of Guaymas, Sonora, to the northern borders of Nuevo Leon and Tamaulipas at about 27° 30′ N (vicinity of Laredo, Texas), and then southeast to the intersection of 27° N with the Texas coast; the lower Rio Grande delta thus lies south of this boundary. This line approximates the northern limits of such presently tropical families as the Cracidae, Momotidae, and Dendrocolaptidae, and only two species in the Trogonidae (*Trogon elegans* and *Euptilotis neoxenus*) and one species in the Cotingidae (*Platypsaris aglaiae*) extend beyond it. Many other tropical genera and species extend only as far north as the

Alamos-Rio Mayo region of Sonora in the west (van Rossem, 1945) and the lower Rio Grande valley in the east. (Friedmann et al. 1950; Miller et al. 1957; A.O.U., 1957; Bennett, 1966), and the 28°–27° N line is just north of these areas. Also some northern species that reach extreme northwestern Mexico do not extend south beyond this line.

Line II is drawn from the intersection of latitude 20° N with the coast of central Veracruz south to the city of Oaxaca and then westward to the Oaxaca-Guerrero border on the Pacific Coast. This line approximates the northern limit of the range of many birds of the tropical lowlands and also the southern limit for some highland forms found on the central plateau of Mexico. The area delimited between this line and Line I is herein called Central Mexico, and it includes the lower Rio Grande valley in Texas.

Line III is the border between Guatemala and Honduras-El Salvador (the latter two republics are treated as a unit so that each segment spans the isthmus from coast to coast). It approximates the southern limit of most of the forms characteristic of the Yucatan peninsula (including British Honduras) as well as others not found south of the highest peaks in the Guatemalan highlands. Some forms found in the Caribbean lowlands farther south do not extend north of this line. This area is collectively referred to as Southern Mexico-Guatemala-British Honduras.

Line IV is the boundary between Honduras-El Salvador and Nicaragua. The highlands of northern Nicaragua are almost entirely below 6,000 feet in elevation, and a number of montane forms reach their southern limit in El Salvador and Honduras very near the Nicaraguan border. As previously mentioned, many Caribbean lowland species do not range north of Nicaragua, and the Honduras-El Salvador area is thus a useful zoogeographic unit.

Line V is the boundary between Nicaragua and Costa Rica and sets off Nicaragua as the reference region.

Line VI is drawn irregularly across Panama from the eastern edge of Chiriquí Lagoon on the Caribbean slope of the continental divide, east to the vicinity of Cerro Campana in western Panama Province, then back to the west along the Pacific slope of the divide to about 81° 30′ W near the Chiriquí-Veraguas boundary, then east and south to run slightly east of the eastern boundary of Veraguas Province in the Azuero Peninsula. I am indebted to Eugene Eisenmann for suggesting this line of demarcation, which includes the highlands of western Panama with those of Costa Rica and places appropriate sections of lowlands with those of eastern Panama.

Line VII is drawn to include with eastern Panama that portion of Colombia directly west of the Gulf of Urabá. The line follows the Rio Atrato from its delta to the center of the isthmus and then swings west to join the Panama border; the spur of Colombian territory that encompasses the Alturas de Nique (just south of Cerro Pirrí) is also included. Although this segment of Central America is a small one with many similarities to northwest Colombia, it is sufficiently distinctive distributionally to warrant separation. Several genera and species of birds are endemic to this region, and for many others it constitutes an interruption of their range between western Panama and Colombia (Eisenmann, 1955; Meyer de Schauensee, 1964; Haffer, 1967a, 1967b). This area is designated as Eastern Panama-Rio Atrato.

The entire series of segments of Central America is then bracketed by two additional sections—Mexico ("Northwest Mexico") north of Line I, and Colombia ("Northwest Colombia") west of the Santa Marta Mountains and the Sierra de Perijá; north of the Central and Western Andes; and the west slope of the Western Andes and the Pacific lowlands south into Nariño, where the three Andean ranges merge (Map 1). The bracketing regions are selected on the grounds that virtually all genera and species that breed in some part of Central America and also in either North or South America are found in either Northwest Mexico or Northwest Colombia, respectively. With rare exceptions no Central American form skips over Northwest Mexico or Northwest Colombia and reappears in other parts of the continental areas. On the other hand these bracketing regions usually include taxa that do not extend into Nicaragua or other parts of Central America, although there may be no obvious physical or ecologic barriers to their distribution. Thus consideration of the avifauna of these bracketing regions often indicates the variety and abundance of taxa that do not reach most of Central America and also calls attention to those forms that do not extend beyond the limits of Central America as herein defined. Areas north and south of the bracketing regions have probably not contributed to the contemporary avifauna of Central America except by way of Northwest Mexico and Northwest Colombia, respectively—in which case they are included in the diagrammatic model.

In some cases I have used arbitrary judgment in including or excluding certain taxa from the bracketing areas. For example *Corvus brachyrhynchos* and *Gymnorhinus cyanocephalus* are not included in Northwest Mexico as neither is known to breed there; *Nucifraga* is included as questionable. In Colombia all forms restricted to the temperate and páramo zones of the mountains are excluded as most of these have little or no relevance to Central America (*Eremophila* is a well-known exception), and certain forms that reach "Northwest Colombia" only in Nariño (such as *Capito squamatus*: western Ecuador to southwestern Nariño) are excluded for the same reason.

If the range of a genus or species that breeds in Central America does not extend into either of the bracketing regions, a Central American origin is suggested; if its range extends into only one of the bracketing regions, the possibility of derivation from that continent should be considered; if its range extends into both bracketing regions, the chances of determining its earlier geographical affinities (northern, southern, or Central American endemic) are slight.

PREPARATION OF THE DIAGRAMS

Following the premises and methods described above, the diagrams are prepared through the following steps:

1. A horizontal base line representing the number of genera and species in a given family that are found in Nicaragua is drawn.
2. This line is divided into segments representing the different regions discussed above, except that Nicaragua is represented as a point and not as a segment as it is the reference region with which the others are compared.
3. Genera are represented by squares and species by circles. Only known or probable breeding forms are included, and subspecies are not considered.
4. All genera and species in the given family that are found in one or more regions but *not* in Nicaragua are plotted in vertical columns *above* the segment of the base line representing that region or regions.
5. All genera and species in the given family that are found *within* Nicaragua but *not* in one or more of the other regions are plotted *below* the segment of the base line representing the region of absence.
6. Taxa found throughout all the regions (including Northwest Mexico and Northwest Colombia) are not plotted but are listed by name and indicated by a "x" adjacent to the diagram. Thus only those taxa with distributions that terminate at

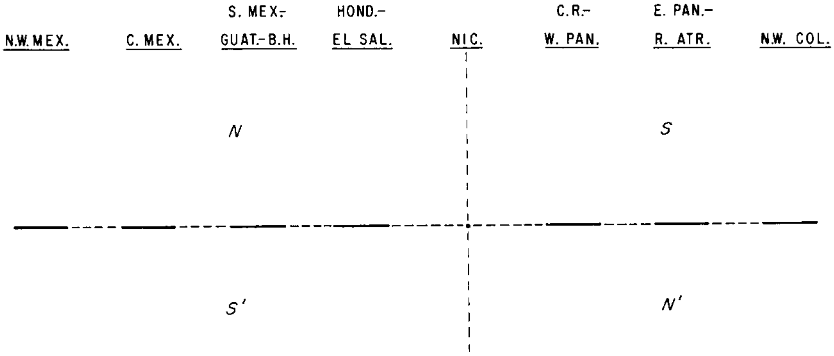


Figure 1. Base line of distributional diagram, divided into quadrants.

some point in Central America or Northwest Colombia are plotted; the others are listed only.

7. Genera in each family are numbered in the sequence given in Eisenmann's (1955) and Meyer de Schauensee's (1966) lists of Middle American and South American birds. Species take the number of the genus with the addition of a letter (1a, 1b, 1c, if the genus contains more than one species) following in general the sequence of the above-mentioned lists. Fortunately no Central American genus includes more than 26 species! All species that are known (or reasonably presumed) to breed in Central America and Northwest Colombia are listed, with their numbers, for each family.

8. Discontinuously distributed taxa that skip one or more entire region(s) are marked in the lists by an asterisk. Central American endemics that include or bracket Nicaragua within their range are marked in the diagram with a dagger at each end of the range. Further refinements of notation to incorporate additional information are discussed below.

Examples and Interpretations

Figure 1 shows the simplest possible diagram—a base line on which nothing is plotted. This would represent the distribution of a family in which all taxa were found throughout all the regions; however no such family exists.

Suppose that a family is represented by several taxa in Northwest Mexico and that the number of taxa declines progressively to the south, with none at all reaching Nicaragua. Plotting only solid columns for simplicity's sake, the resulting pattern is given in Figure 2. The diagram visually suggests a group of northern affinity, the distribution of which is attenuated as it ranges southward into Central America and terminates north of Nicaragua. Figure 3 diagrams the actual distribution of the family Paridae, a group of northern affinity that closely fits the hypothetical model. A group of southern affinity extending northward without reaching Nicaragua would yield a diagram approximating a mirror image of Figure 2; the family Capitonidae fits this model (Figure 4).

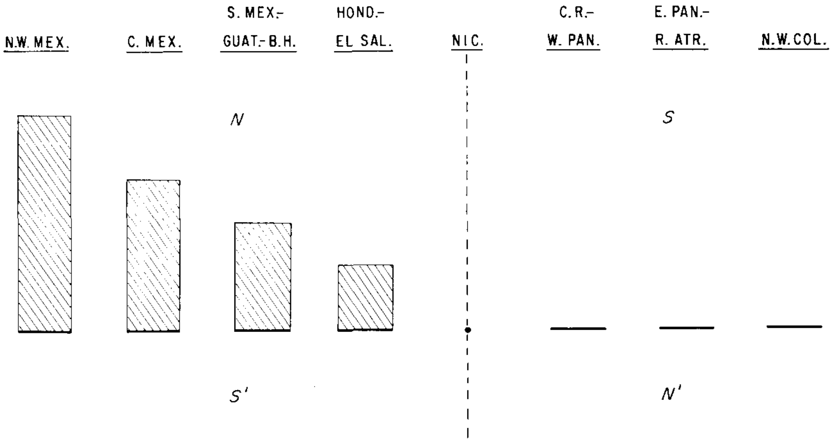


Figure 2. Hypothetical distributional pattern of taxa in a family of northern affinity, none of which range southward into Nicaragua.

Suppose now that a family has a distribution similar to that of the Capitonidae except that some taxa reach Nicaragua and a diminishing number of these extend into areas farther north. The resulting pattern is shown in Figure 5, and it suggests a group of southern affinity but a rather expansive one; if no taxon extends beyond Line I, the case for complete southern affinity is strengthened. Figure 6 illustrates the combined pattern for the families Galbulidae, Bucconidae, and Ramphastidae, all of which are similar in distribution with none extending north of Line I. Note that nothing is plotted *above* the line north of Nicaragua and nothing *below* the line south of Nicaragua; this indicates that no genus or species in these families is endemic to the areas north of Nicaragua and

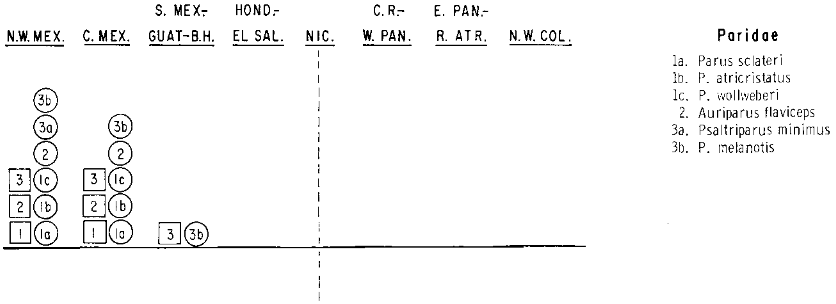


Figure 3. Distribution of the Paridae in Central America. (Raitt (1967) has recently shown that *P. minimus* and *melanotis*, although well-marked forms, are conspecific.)

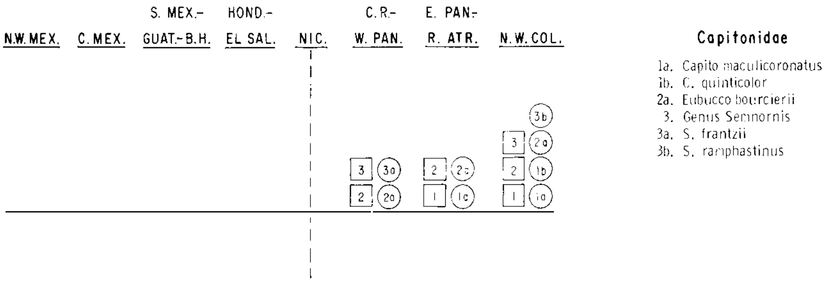


Figure 4. Distribution of the Capitonidae in Central America and Northwest Colombia.

that all genera and species found in Nicaragua are also found at least as far as Northwest Colombia. Nothing is plotted above or below the segment representing Honduras-El Salvador, which indicates that this region includes exactly the same taxa in these families as does Nicaragua. The total pattern strongly suggests a group of southern affinity, probably of South American derivation, some members of which range northward from South

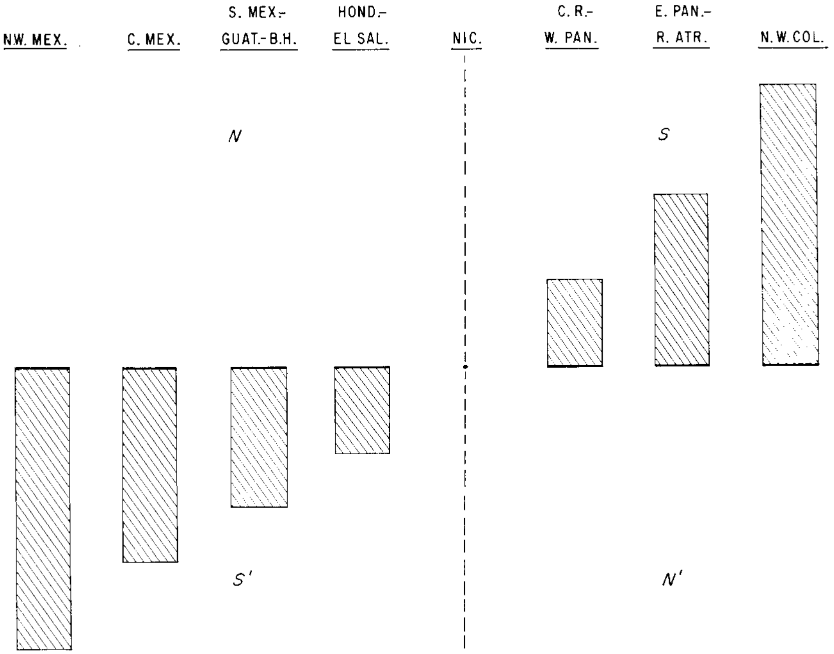


Figure 5. Hypothetical distributional pattern of an expansive family of southern affinity.

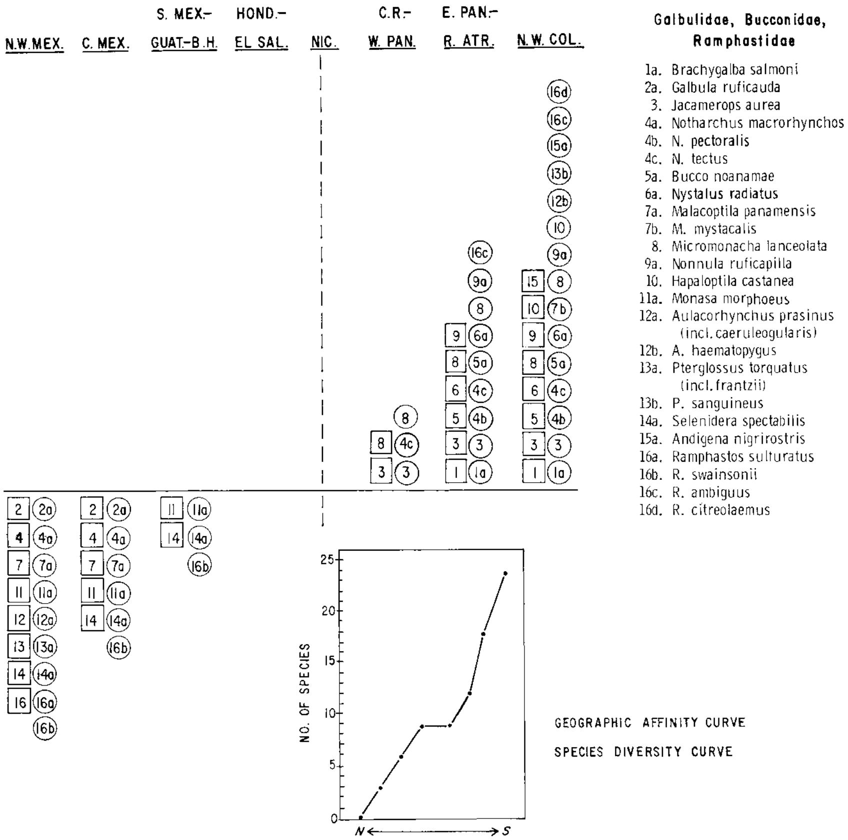


Figure 6. Distribution of the Galbulidae-Bucconidae-Ramphastidae in Central America and Northwest Colombia, including geographic affinity and species diversity curve (see text for explanation).

America for various distances but none beyond the tropical zone in Central America. This interpretation is consistent with generally accepted views about the distributional history of the three families (Mayr, 1964b). A mirror image of this pattern, with taxa above the line *only* north of Nicaragua and below the line *only* south of it, would suggest the converse interpretation—a group of northern affinity, probably of North American derivation, some taxa of which had ranges extending far south into Central America. However no family fits such a model without exceptions.

It is convenient to consider the diagrams as divided into quadrants north and south of Nicaragua and above and below the line. These are designated N and N′, S and S′ (Figure 1). Reasoning from the preceding premises and examples, I suggest that all taxa included exclusively in N

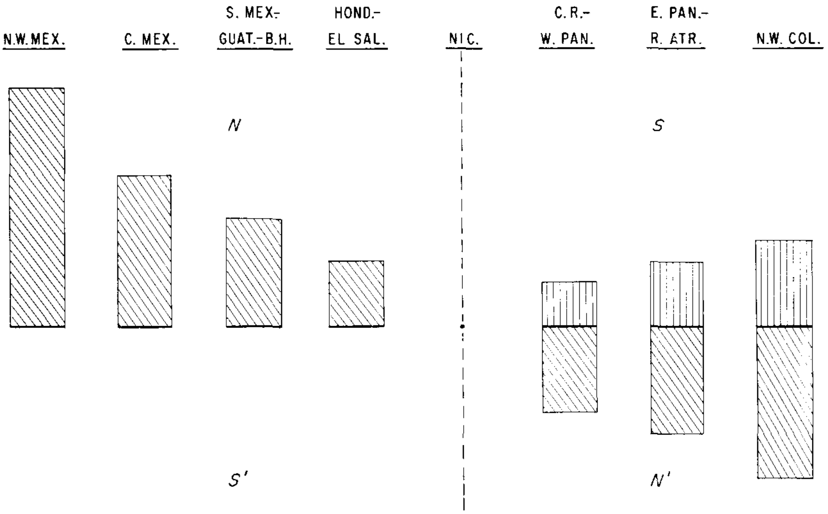


Figure 7. Hypothetical distribution pattern of a family of northern affinity with secondary radiation south of Nicaragua.

or N′ are of northern affinity and all taxa included exclusively in S and S′ are of southern affinity. If a taxon is plotted in both N′ and S′ (not exclusively in one or the other), its distribution is confined to some part of Central America including Nicaragua, and suggesting northern or southern affinity may not be admissible.

The families considered so far have distributions that fall into simple diagrammatic patterns; most families, of course, have more complex distributions with taxa appearing in three or usually all four quadrants of the diagram. Figure 7 illustrates a hypothetical pattern suggestive of a group of northern affinity that has reached Nicaragua and beyond with some secondary radiation of taxa south of Nicaragua (N, N′, and S). Note the absence of an S′ component. If this family were primarily of southern affinity and had expanded northward extensively, one would surely expect an S′ component, indicating some progressive dropping out of taxa north of Nicaragua (see Figure 6). The pattern suggests instead an expansive northern component (N and N′) and a less expansive southern one (S only). Figure 8 diagrams the distribution of the family Corvidae, which fits the hypothetical model moderately well with some additional complexities (if fewer genera are recognized, the complexities are lessened, cf. Amadon, 1944, Hardy, 1961). The genera *Cyanocorax* and *Cyanolyca* do not occur in Nicaragua and the relevant species that appear in both N and S are marked in the species list with an asterisk. There is a small

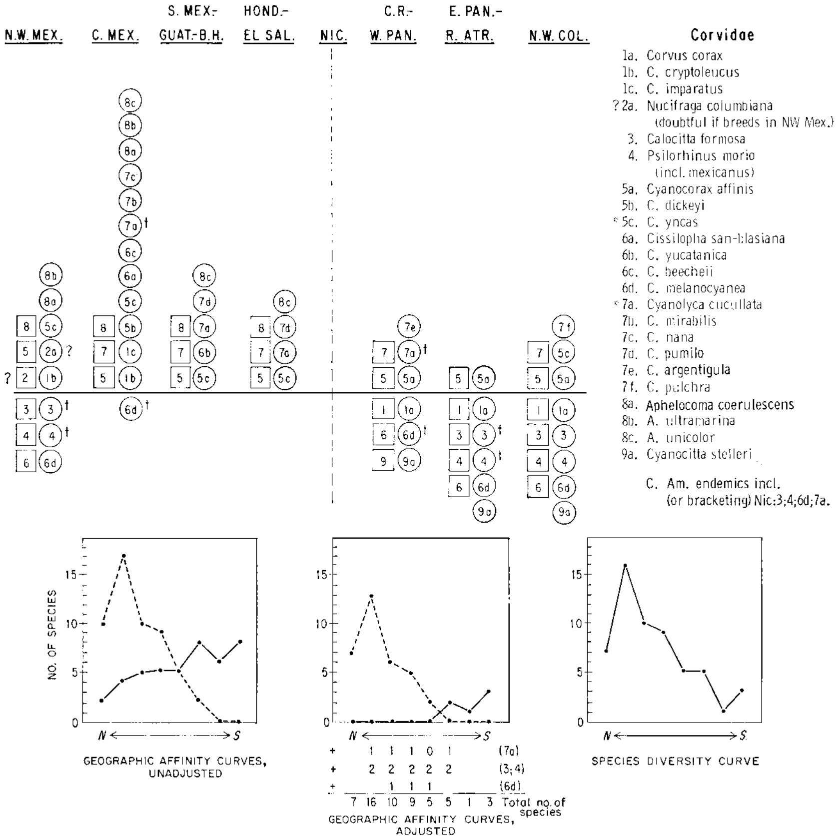


Figure 8. Distribution of the Corvidae in Central America and Northwest Colombia, with geographic affinity curves and species diversity curve. The points on the curves represent the same regions, in the same sequence, as in the distributional diagram (see text for further explanation).

S′ component, but the genera and the species also appear in N′ and are thus Central American endemics (*Calocitta formosa*, *Psilorhinus morio* and *Cissilopha melanocyanea*, marked with a dagger) and not necessarily or even probably of southern affinity. No genus (as currently recognized) or species occurs throughout the entire area. This pattern supports the hypothesis that the family is of Old World derivation, reaching the New World from the Palearctic region, and that the jays underwent considerable radiation in North and Central America with relatively few forms reaching South America, where further speciation occurred. (Amadon, 1944; Parkes, 1958; Mayr, 1964b). Possibly *Cyanocorax affinis* represents a species of subsequent South American derivation that has extended its

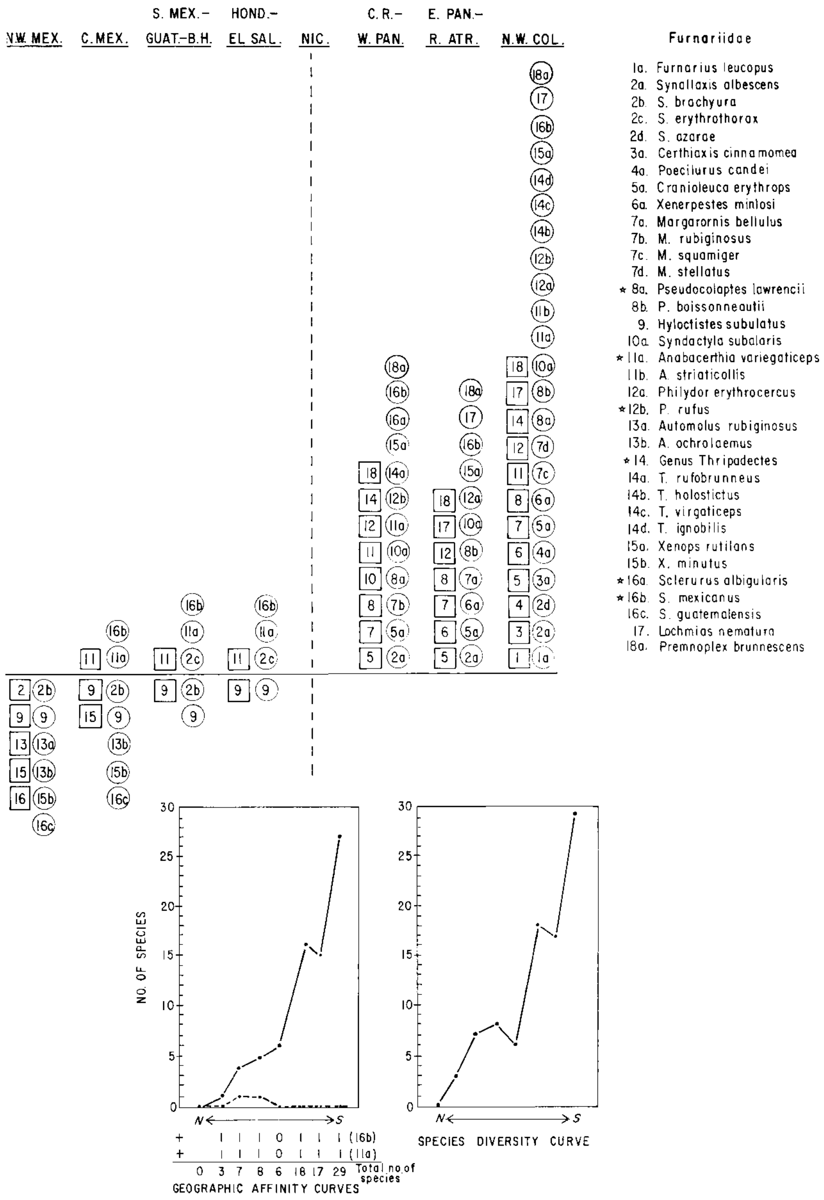


Figure 9. Distribution of the Furnariidae in Central America and Northwest Colombia, with geographic affinity and species diversity curves (see Figure 8 and text for explanation).

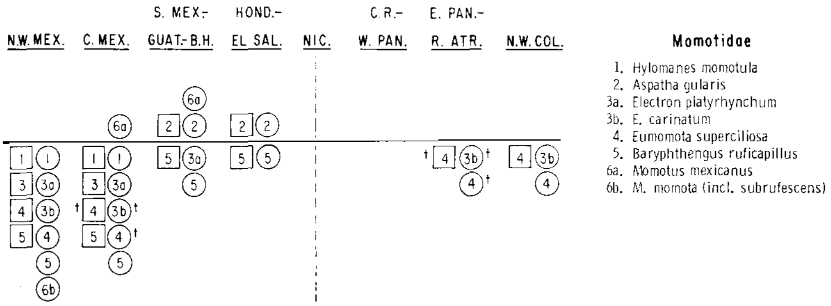


Figure 10. Distribution of the Momotidae in Central America and Northwest Colombia.

range northward through Panama into Costa Rica. Note that the S component includes no genera that do not also range widely throughout much of Central America; thus no genera are endemic to the region south of Nicaragua (*Uroleuca* is not recognized as distinct from *Cyanocorax*), but several genera either do not reach Nicaragua from the north or fail to extend beyond it. This situation further supports the suggestion that the family is primarily of northern affinity.

The distribution of the family Furnariidae provides a similar but converse pattern that is also more clear-cut (Figure 9). This is a group of southern affinity that has extended northward into Central America, with many taxa failing to reach or extend beyond Nicaragua. The small N component includes two forms that are unrecorded from Nicaragua but are otherwise found from Central Mexico into South America. Only a single species, *Synallaxis erythrothorax*, is endemic to the region north of Nicaragua and constitutes the only furnariid species of northern affinity; all other taxa found north of Nicaragua range all the way from Northwest Colombia, as shown by the absence of an N′ component.

Figure 10 shows the distribution of the Momotidae. This pattern is unique in having N, N′, and S′ components but no S, as no taxa within the family are found exclusively south of Nicaragua, which is not only unique, but remarkable for an entirely tropical family. Note that two genera and four species are restricted to Central America, and half of these are confined to areas north of Nicaragua. No genus or species is endemic to South America unless *M. subrufescens* is considered specifically distinct from *M. momota* or *Baryphthengus ruficapillus* distinct from *B. martii.* The total pattern strongly suggests a group of Central American derivation, some members of which have extended into South America. Only one form, *B. ruficapillus*, has a distribution strongly suggestive of southern affinity. The distributional diagram thus lends support to the

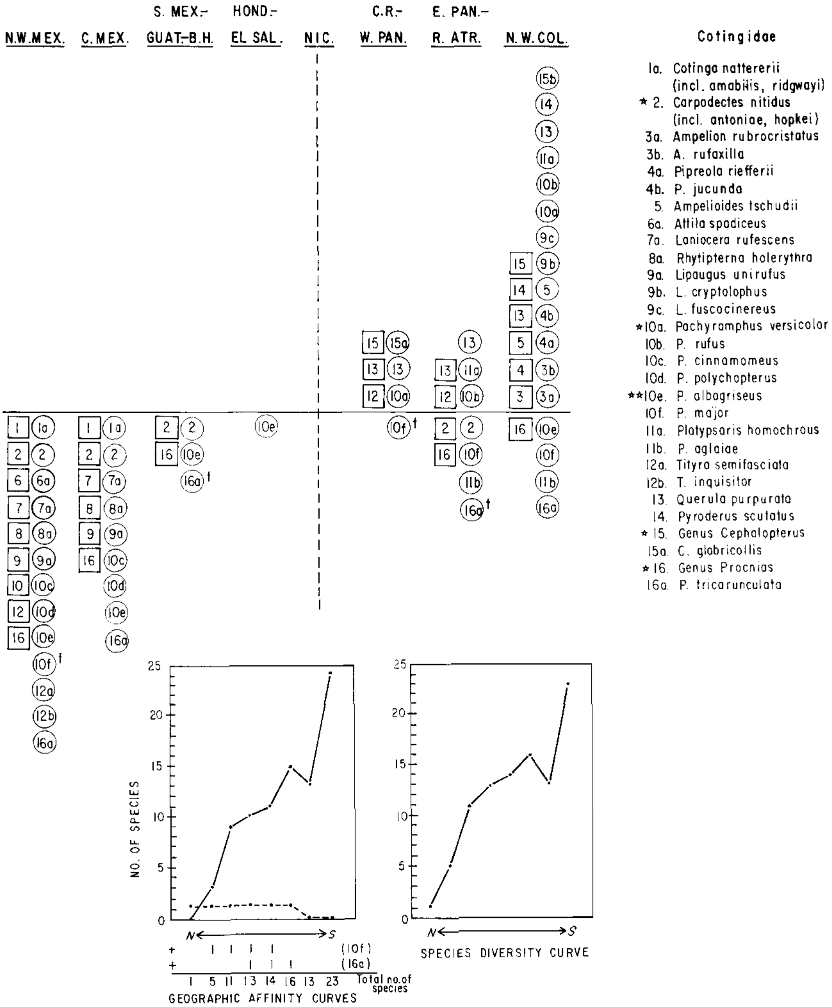


Figure 11. Distribution of the Cotingidae in Central America and Northwest Colombia, with geographic affinity and species diversity curves (see Figure 8 and text for explanation).

hypothesis that the motmots are a family of Central American origin, as Chapman (1923) postulated.

The family Cotingidae (Figure 11) presents still another three-quadrant pattern. The large S and S′ components suggest a group that is primarily of southern affinity; a relatively few forms are found in both N′ and S′, indicating a small Central American endemic component.

If *Cotinga amabilis, C. ridgwayi, and C. nattererii* are considered conspecific and *Carpodectes nitidus, C. antoniae,* and *C. hopkei* are likewise regarded as a single species, the distributional picture is simplified. There can be little doubt that the Central American populations of *Cotinga* are, at most, slightly differentiated species derived ultimately from South American ancestors. This seems less probable for *Carpodectes* as *hopkei* is the only form found in South America, and it occupies a relatively limited range on the Pacific coast of Colombia and northwestern Ecuador. It is possible that the genus *Carpodectes* evolved in southern Central America; if so, the genus and the species would still be of southern affinity as herein defined. Lumping each group of three species arranges them in the diagram with taxa of southern affinity, and as this seems reasonable I have combined them under the names *Cotinga nattererii* and *Carpodectes nitidus.*

Pachyramphus major seems clearly of northern affinity, and it is allopatric with the southern *P. albogriseus.* The latter is apparently absent from Northwest Colombia as herein delimited, although it occurs elsewhere in that country; I have placed it under the line in that area with a double asterisk to indicate its anomalous distribution.

The genus *Procnias* is one of the very few found in Central America that skips Northwest Colombia and reappears farther east in South America.

Meyer de Schauensee (1966: 314) quotes Ames' and Warter's view that the Attilinae should be transferred to the Tyrannidae. I am inclined to agree, but prefer to follow current usage until publication of the relevant evidence. All the taxa in question are part of the southern component, and their deletion would make the south-to-north slope somewhat less steep.

When their distribution is plotted with Nicaragua as a reference point, most families are found to have taxa falling in all four quadrants, N, N′, S, S′. These patterns indicate, as expected, that the Nicaraguan representatives of these families include forms of both northern and southern affinities. The family Picidae exemplifies such a pattern (Figure 12). It will be seen that Nicaragua includes three Central American endemic forms (*Piculus simplex, Celeus castaneus,* and *Phloeoceastes guatemalensis*); other than these, it is reasonable to suggest that all taxa included in N and N′ are of northern affinity and all those included in S and S′ are of southern affinity.

Further information may be developed in the model if a symbol to indicate the principal habitat of each species is entered beside the species symbols (Figure 12). In designating habitat types I follow Monroe's (1969) adaptation of Carr's (1950) classification of animal habitats in

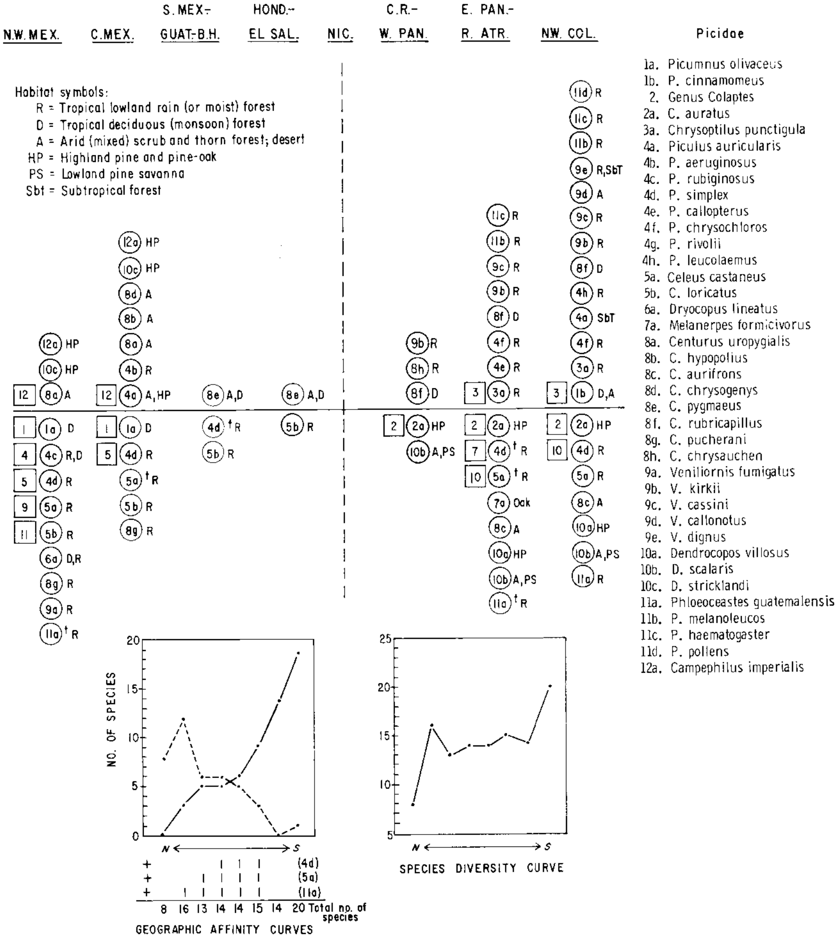


Figure 12. Distribution of the Picidae in Central America and Northwest Colombia (see text for discussion of habitat symbols), with geographic affinity and species diversity curves (see Figure 8 and text for explanation).

Honduras. In designating habitats by symbols it is impossible to indicate finer distinctions such as preference for edge situations, second growth, or lower or higher levels within forest. The symbols are meant to suggest in general, not in detail, the environment in which most of the species' range lies.

When the habitat symbols are added to the diagram for the family Picidae, it will be noted that most species in the N and N′ components are birds of the arid scrub or pine or pine-oak habitats; most species in the S

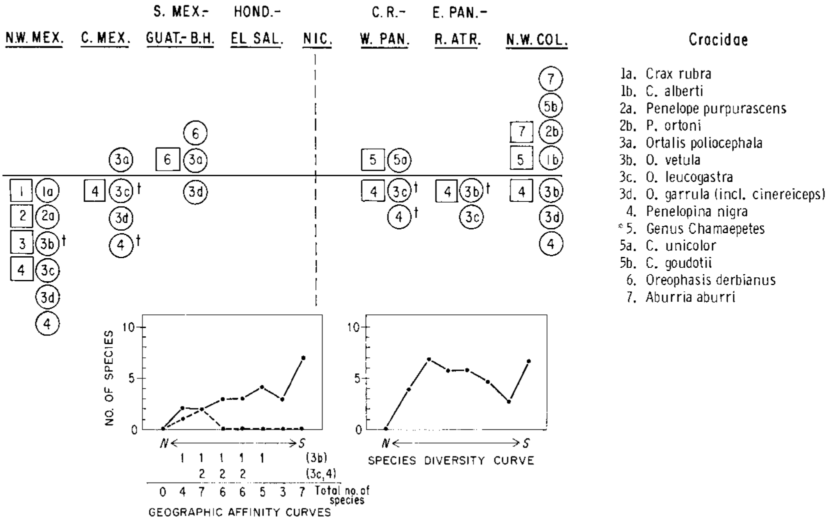


Figure 13. Distribution of the Cracidae in Central America and Northwest Colombia, with geographic affinity and species diversity curves (see Figure 8 and text for explanation).

and S′ components are birds of humid lowland broad-leafed forests. The habitat data are in accord with the distributional interpretation suggested by the pattern of the diagram, for arid scrub and pine associations occur in Central America largely or exclusively north of Nicaragua and humid lowland forests are most extensive and continuous from Nicaragua south. It is noteworthy that the four species in the N-N′ component that inhabit humid lowland forests are allopatric with closely related species farther south.

The family Cracidae has been cited as an example in which contemporary distribution could mislead the zoogeographer (Mayr, 1964a: 287). The range of Recent forms could suggest a group of South American origin that has spread northward relatively recently into Central America, whereas the fossil record shows that cracids were present in North America as far back as the Oligocene or even the Eocene (Brodkorb, 1964: 303). The diagram (Figure 13) utilizes the revisions of Vuilleumier (1965) and Vaurie (1965), following Moore and Medina (1957) with regard to *Ortalis* species of Mexico. Note the presence of a distinct component of northern affinity that includes two endemic genera. This contrasts with the patterns of groups such as the Galbulidae-Bucconidae-Ramphastidae, for which all available evidence indicates a South American center of dispersal, and is consistent with the fact that the cracids have a long history of occurrence in areas north of the present-day region of greatest abundance and diversity. The interpretation of contemporary cracid distribution based on the diagram is in general accord with that of Haffer (1967a: 361–362); the diagram also suggests that *Ortalis*, with three species of northern affinity in Central America, may have been an occupant of that area somewhat earlier than *Crax* and *Penelope*.

The Cathartidae are also known from the fossil record to have been an abundant and varied group in North America dating back at least to the Lower Oligocene (Brodkorb, 1964: 252), although the present distribution might suggest an origin in South America and a relatively recent invasion of the northern continent. The presence of *Gymnogyps*, a distinct genus now restricted to regions north of 28–27° N, suggests the existence of the once-important northern component that the fossil record reveals.

GEOGRAPHICAL AFFINITY AND SPECIES DIVERSITY

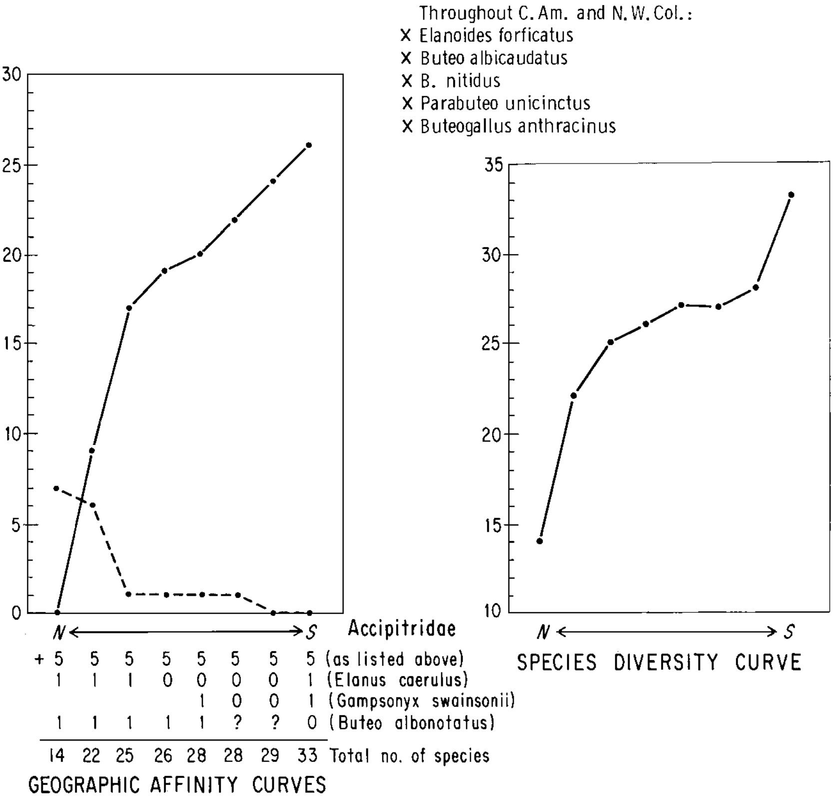
The examples that have been cited show some of the ways in which the model may be useful in interpreting the distribution of particular families, especially for the reference region (in this case, Nicaragua). Still other uses can be derived from the above-and-below the line form, which may at first appear more confusing than helpful.

Considering species only, a simple graph may be constructed by using the number of species in each region above and below the line as points and connecting them sequentially. This produces two curves running from N to N′ (dashed line) and S to S′ (solid line), intersecting through Nicaragua. Figure 8 shows such a graph for the Corvidae; it is merely a simplified representation of the diagram, and the slopes of the two curves suggest the rate of change (in relation to Nicaragua) in numbers of species of presumed northern and southern affinity throughout Central America. Recall that, according to the premises proposed, all taxa in one or the other of the terminal columns in N′ and S′ (below the line, in Northwest Mexico, Northwest Colombia) are of northern and southern affinity, respectively, as indicated by the fact that they have "dropped out" south or north of Nicaragua. (Any that have not dropped out at either end are not plotted but listed with an "x" symbol.) The relative contributions to the Central American avifauna of species of the northern and southern components may be clarified by shifting the curves vertically so that both terminal points fall on the same base line. The distance between this base line and a point on the N to N′ curve gives the number of species of northern affinity in that geographic region, and the distance to the corresponding point on the S to S′ curve gives the number of species of southern affinity. The sum of these (plus the number of species, if any, found throughout all of Central America) gives the total number of species found in the particular geographic region. One qualification is that Central American endemic species that include or bracket Nicaragua in their range must be deleted before plotting the curves, for these species appear in both terminal columns and will thus cause incorrect totals. The number of such endemics, if any, may then be added to the totals for the areas in which they occur.

The complete curves and totals for Corvidae (Figure 8) should clarify by example this complex explanation. Of the four Central American endemic species that include or bracket Nicaragua in their range (*Cyanolyca cucullata*, a high montane species, is absent from Nicaragua) *Calocitta formosa* and *Cissilopha melanocyanea* seem surely of northern affinity; the other two may be, but the distributional evidence is inconclusive. The curves show graphically the steep and regular decline in number of species of corvids of northern affinity from Central Mexico to Costa Rica, with none reaching Eastern Panama; two species of southern affinity occur in Costa Rica, but none of probable southern affinity ranges farther north. Thus the corvids of Central America are preponderantly of northern affinity, the mixture of northern and southern components becoming approximately equal (although small *in toto*) in Costa Rica–Western Panama.

The geographical affinity curves for the Galbulidae-Bucconidae-Ramphastidae (Figure 6) and for the Picidae (Figure 12) illustrate simple and complex situations respectively. The former shows a steep and regular decline from south to north (or a marked increase from north to south) with no evidence of a distinct northern component. The curves for the Picidae, as expected, show pronounced northern and southern components, with the northern predominating north of Southern Mexico, an approximately equal mixture south through Nicaragua, and a steep increase and predominance of species of southern affinity from Costa Rica southward.

The family Accipitridae is well represented in Central America, with five wide-ranging species found throughout the area but only one Central American endemic form that ranges into Nicaragua (*Accipiter chionogaster*; if this form is regarded as conspecific with *striatus* or *erythronemius*, or if all three are lumped, then this exception disappears). The geographical affinity curve (Figure 14; distributional diagram not given) shows that northern forms predominate in Northwest Mexico and decline sharply southward to Southern Mexico-Guatemala-British Honduras; they level off south into Nicaragua, and further decline to zero representation in Eastern Panama. Species of southern affinity predominate greatly, although in steadily declining numbers, from Northwest Colombia to South-



+5	5	5	5	5	5	5	5	(as listed above)
1	1	1	0	0	0	0	1	(Elanus caerulus)
				1	0	0	1	(Gampsonyx swainsonii)
1	1	1	1	1	?	?	0	(Buteo albonotatus)
14	22	25	26	28	28	29	33	Total no. of species

Figure 14. Geographic affinity and species diversity curves for the Accipitridae in Central America and Northwest Colombia (see Figure 8 and text for explanation).

ern Mexico; north of that area the decline is precipitous, with approximately equal representation of northern and southern species in Central Mexico. The five wide-ranging species are presently of largely tropical distribution, but evidence is insufficient for more than a guess about their earlier distribution and dispersal.

The geographical affinity curve for the Parulidae (Figure 15; distributional diagram not given) is somewhat similar to that of the Corvidae. Species of northern affinity predominate north of Nicaragua and decline steadily to a zero point in Eastern Panama (*Geothlypis semiflava* reappears in Colombia). Species of southern affinity predominate south of Nicaragua and decline rather steadily to the north. Two peaks in the curves are noticeable; one in Central Mexico results largely from the presence of five endemic species of *Geothlypis*, and the other, in Costa Rica–Western Panama, results from endemism in the high mountains of

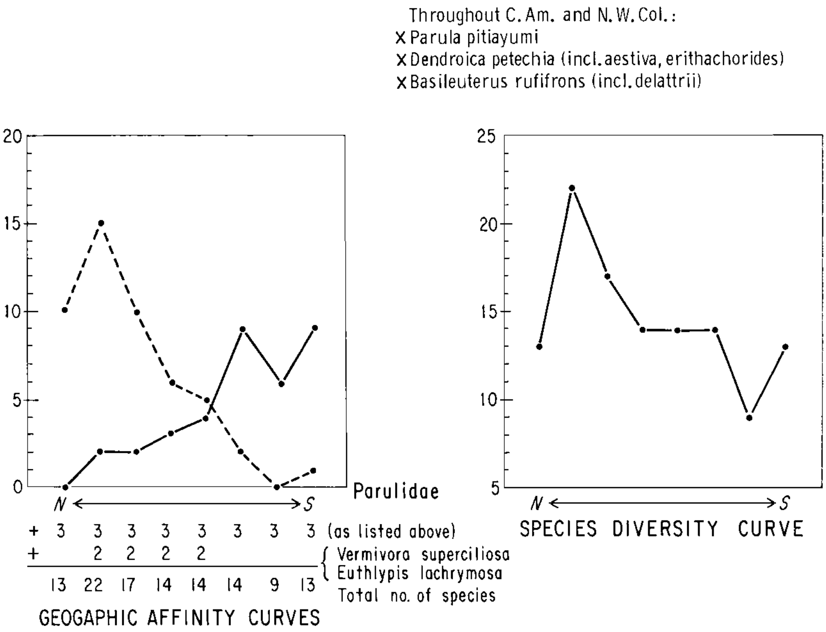


Figure 15. Geographic affinity and species diversity curves for the Parulidae in Central America and Northwest Colombia (see Figure 8 and text for explanation).

that region. Such peaks point up areas of endemism, and valleys of course indicate areas of impoverishment. Two Central American endemic species, *Euthlypis lachrymosa* and *Vermivora superciliosa*, reach their southern limits in Nicaragua and seem certainly of northern affinity.

With the total number of species in each region calculated from the geographical affinity curves, a "species diversity curve" for that family in Central America may be plotted using the simplest measure of diversity —the number of species. The curve is constructed by taking the lowest number of species as the approximate level of the base line and plotting the number of species found in the other regions as points above the line. This plot is of interest in several ways. It may point up distributional anomalies, as shown by the curve for the family Cotingidae (Figure 11) that dips sharply in Eastern Panama; it would be a smooth south-to-north slope otherwise, and one would predict that this area would have 19 or 20 species instead of only 13. The species diversity curve also suggests by the direction of the slope whether the representation of the family in Central America is preponderately of northern or southern affinity, and it shows whether species diversity within the family increases or decreases from north to south.

LATITUDINAL TRENDS IN SPECIES DIVERSITY

The measurement of species diversity and the significance of latitudinal trends in this parameter have received considerable attention in recent years; MacArthur (1965) and Pianka (1966) provide useful reviews, with extensive bibliographies, of current ideas in this field. Detailed discussion of this intriguing and still-controversial subject is outside the scope of this paper, but the data presented here may be useful and relevant. For example within the latitudes encompassed by Central America as herein defined (28°–27° N to about 7° N), bird species diversity may change in opposite directions depending on the family under consideration. Among those for which diversity curves are given, the Galbulidae-Bucconidae-Ramphastidae (Figure 6) show an unequivocal increase from higher to lower latitudes; the Picidae (Figure 12) and Accipitridae (Figure 15) show a similar trend but of composite origin (species of northern affinity decrease as those of southern affinity increase); the Corvidae (Figure 8) and Parulidae (Figure 16) show a decline from north to south, also of composite origin. The shape of the diversity curves for these latter two families is so similar as to suggest a similar New World distributional history. This raises the obvious point that discussions of the basis for latitudinal trends in species diversity should include consideration of trends within categories below the level of the Class, and that the history of these taxa should also be considered insofar as possible. Attention to the varying latitudinal trends in diversity in lower categories may reveal influential historical and ecological factors that are masked by consideration of large-scale phenomena only.

The distributional diagram-and-graph method may also aid in the interpretation of the history of pantropical groups in the New World. The Capitonidae (Figure 4) and the Trogonidae (Figure 16) have a similar contemporary distribution pattern, with representatives of each family in the Oriental, Ethiopian, and Neotropical regions. Both families are usually considered examples of groups with a formerly wide distribution over the northern hemisphere that have undergone contraction of their ranges with the southward retreat of tropical conditions, resulting in their presently discontinuous distribution (Mayr, 1946: 16; Darlington, 1957: 274; Austin, 1961: 185). The data presented for the Trogonidae support this hypothesis as there is a distinct northern component, including an endemic genus, although the genera are perhaps too finely split in this homogeneous family. Furthermore two forms extend north of the 28°–27° N line, with *Euptilotis* ranging up to 3,000 m in coniferous forest in Northwest Mexico (Miller et al., 1957). The fossil remains of *Archaeotrogon* and *Paratrogon* from the early to mid-Tertiary of Europe (Romer, 1966:

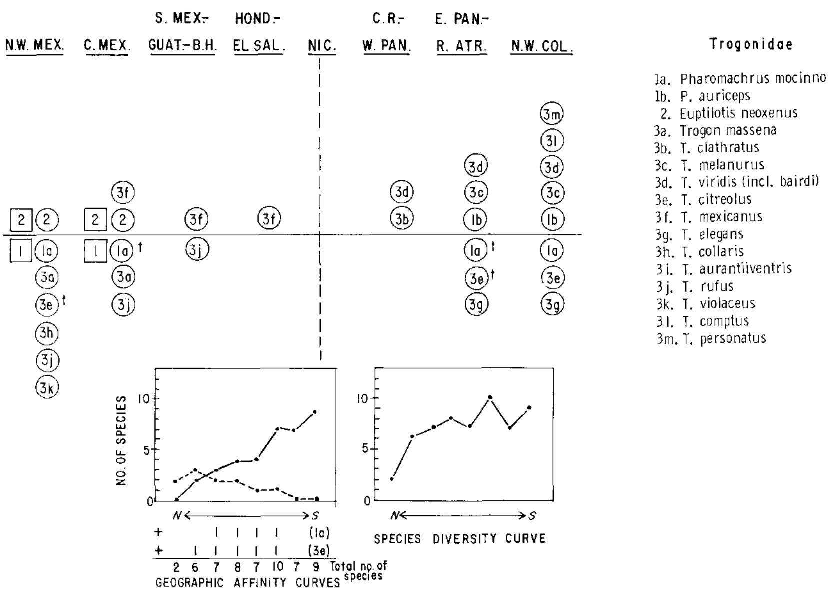


Figure 16. Distribution of the Trogonidae in Central America and Northwest Colombia, with geographic affinity and species diversity curves (see Figure 8 and text for explanation).

377) demonstrate a formerly more northern distribution of the family in the Old World.

The New World Capitonidae do not range north of Costa Rica (about 12° N) and no fossils are known. If this hardy group reached South America from the Old World by way of North and Central America, it is difficult to understand why no relict population remains in Nuclear Central America—i.e. in Nicaragua or farther north. If that route of immigration was not followed, then transoceanic colonization is the most logical alternative. I suggest rafting from Africa to South America as a reasonable possibility, basing this proposal on life history data compiled from Skutch (1944), Austin (1961), and Dorst (1964). Barbets are hole-nesting, hole-roosting birds that are weak-flying and sedentary and thus unlikely to undertake long-sustained flights. Many are omnivorous, opportunistic feeders. In at least some species both members of a pair roost together in the nest cavity, and in the nonbreeding season they may form dormitories with up to 16 birds roosting together in a single tree cavity. Birds with such habits might be carried great distances in a raft of trees; by utilizing the shelter of a nesting or roosting cavity, a pair or a group might survive a long journey that would be fatal to other birds with habits leading to greater exposure. With these characteristics, barbets would seem to be as capable of dispersion by rafting as any group among the land birds. Some of the above qualifications apply also to trogons and to many of the Psittacidae, but the evidence for a former more northern distribution of these groups is much stronger than for the Capitonidae.

Geographical affinity curves and diversity curves for genera may be plotted in exactly the same manner as the species curves. The curves for genera tend to parallel the species curves but not always consistently; sometimes the slopes are in opposite directions in one or more areas. Many neotropical genera are poorly defined and may be either too inclusive or too exclusive. This often necessitates such elaborate discussion of alternatives, with reference back to the distributional diagrams, that it seemed best not to include the possibly ambiguous generic curves in this preliminary paper.

Discussion

The conscientious zoogeographer must take into consideration all available and relevant historical and biological evidence in attempting to account for the distribution of animals. When such evidence is sparse, as it usually is, it is tempting to seize on correlations between old geological or environmental configurations and contemporary distribution patterns and give them a cause-and-effect interpretation. Central America offers abundant opportunities for interpretations of this kind, for the present distributional limits of many avian genera and species correspond to the boundaries of ancient land masses such as Nuclear Central America or the Talamanca Range (Lloyd, 1963) that now comprises part of Costa Rica and western Panama.

Any inferences drawn from such correlations should be subjected to careful scrutiny. Deevey (1949) correctly emphasized that the age of a species is not necessarily the same as the age of its distribution pattern, and the age of a distribution pattern (such as a particular vegetation association) is not necessarily the same as the age of the geologic formation to which it may correspond. Nevertheless, a land mass of long-continued existence is likely to develop orogenic features and edaphic conditions that have long-term ecologic consequenses, and these in turn may influence contemporary patterns of distribution. For example, as previously discussed, the southern boundary of the old Nuclear Central America in northern Nicaragua is approximated by the present southern limit of naturally-occurring pine forest, but the Nicaraguan pines are probably of relatively recent derivation and may date back only a few thousand years at most, possibly establishing themselves following aboriginal slash-and-burn agriculture (Denevan, 1961; Taylor, 1963). In any case the establishment of pines in this region required, among other things, a soil type favorable for their survival and the geographical proximity of a parent population from which they could be derived.

The highlands of northern Nicaragua include extensive areas of thin acidic soils formed by weathering of granitic rocks that have been exposed continuously since the Paleozoic; pines can tolerate the poor soils and periodic burning in this region that are detrimental to the survival of many other trees (Denevan, 1961). The continuity of land from North America to northern Nicaragua has provided a potential avenue of dispersal for pines throughout the Cenozoic and the Recent. The importance of the lowland gap in southern Nicaragua is shown by the absence of naturally distributed pines in areas farther south although suitable soils and climate are present and pines thrive there when introduced. Pine-adapted birds of northern origin such as *Dendroica graciae*, *Loxia curvirostra*, and *Spizella passerina* have extended their ranges south to the limit of pines in Nicaragua, but no farther. Thus although there may be no direct causal relationship between the geology of northern Central America and the ranges of these birds, their present distribution appears to reflect indirectly the influence of the geologic history of the region.

In attempting to analyze Central American bird distribution I have tried to show that study of present-day ranges may still yield useful information about the history and geographic affinities of the avifauna, and that examination of a critical distributional region (Nicaragua) provides data that may be extended and applied to the isthmus as a whole. The diagrammatic model was devised to illustrate graphically and in condensed form the distributional data on which my interpretation is based. In considering the various diagrams and graphs presented, it is of particular importance to remember that whatever validity they have is based entirely on the cogency of the premises outlined in the introductory and explanatory sections. Any neatness of pattern and clarity of line is an inherent property of the premises and method employed and does not necessarily confirm or validate either. This *caveat* is perhaps more necessary for the author than the reader, but neither will be harmed by stressing the point. It also emphasizes one of my intentions, which is to stimulate those with special knowledge of the relevant families and regions to test the present interpretations for accuracy and consistency with the weight of other evidence pertaining to bird distribution in Central America.

ACKNOWLEDGMENTS

Jürgen Haffer provided me with copies of his publications and helpful information in correspondence; his data and interpretations of neotropical bird distribution I find compatible with my own, and I regret that time did not permit revisions incorporating his contributions more fully. M. D. F. Udvardy also provided helpful information and called my attention to Croizat's "Panbiogeography" (1958). Croizat stresses the significance of Nuclear Central America in bird distribution (pp. 335–336) and seems to regard this region as an ancient "node" of differentiation; however, it is difficult to extract Croizat's basic ideas from the layers of polemic in which they are buried.

Field work in Nicaragua was supported by NSF grants GB 3683 and GB 3783. My field companions helped immeasurably in obtaining basic distributional data and in discussing zoogeographic concepts, and I am therefore particularly grateful to O. M. Buchanan, L. F. Kiff, F. G. Stiles, and J. E. Zoeger.

SUMMARY

Central America is defined for purposes of distributional discussion as the area from the United States–Mexico border and the lower Rio Grande valley south through Panama and including a small part of Colombia southwest of the Gulf of Urabá (Map 1). Baja California and all offshore islands are excluded from consideration.

Present geological and paleontological evidence indicates that land was continuous throughout the Cenozoic from North America to northern Nicaragua; land extended as far south as the Canal Zone in the middle Miocene; a seaway probably crossed southern Nicaragua for at least part of the Tertiary, perhaps intermittently; other Tertiary seaways were present farther south; the final land connection with South America was formed by the closure of the Bolivar Trough in northwest Colombia near the end of the Pliocene.

On the grounds of its geologic history and contemporary ecological and distributional considerations Nicaragua is selected as a key reference region, the avifauna of which reflects the major distributional trends in Central America.

Nicaragua is the site of an important Tertiary geologic discontinuity; major habitats and their associated avifaunas show attenuation or termination of their ranges there; it has no strictly endemic bird species; almost its entire avifauna appears to be derived from regions to the north or to the south. If the Nicaraguan avifauna could be sorted into components of northern and southern affinity, the method of sorting and the data derived would be highly relevant for analysis of the avifauna of Central America as a whole.

Only post-Pliocene distribution is considered unless otherwise mentioned. "Northern" and "southern" refer to the regions north or south of Nicaragua, and "affinity" refers to a geographical relationship of a contemporary population to the region (north or south of Nicaragua) from which its post-Pliocene distribution is derived. Taxa that are found ex-

clusively north of Nicaragua (sometimes including North America) are considered to be of northern affinity, and those ranging exclusively south of Nicaragua (sometimes including South America) are considered to be of southern affinity; i.e., their present distribution stems from populations that were found north or south of Nicaragua, respectively, by the end of the Pliocene.

Those taxa that range into or somewhat beyond Nicaragua from the north (or south) are probably of northern (or southern) affinity. The shorter the distance that one end of the range of such taxa extends beyond Nicaragua, the greater the probability of designating the geographical affinity correctly. Taxa with distributions confined to Central America (possibly including Nicaragua) are called Central American endemics; the possibility of determining their geographical affinity is uncertain and depends on the extent of their ranges. Wide-ranging forms found throughout Central America and into North and South America are of indeterminate affinity.

As Central America is an isthmus linking continents to the north and to the south from which much of its avifauna was derived, a distributional plot of the birds of sequential segments of the isthmus should reveal north-south or south-north gradients in distribution. Eight segments from Northwest Mexico to Northwest Colombia are delimited, and occurrence or absence of genera and species in a given family in each of these regions is determined. The eight regions are arbitrarily demarcated and are not proposed as centers of origin or distribution.

Nicaragua is utilized as the reference region with which the other segments (regions) of Central America are compared, and a distributional diagram is prepared by which all genera and species in a given family may be sorted into those of probable northern or southern affinity, or Central American endemics, or widespread forms of indeterminate affinity.

Using figures derived from the diagrams, the numbers of species of northern or southern affinity within each family may be plotted for each of the eight Central American regions and a graphic representation (geographic affinity curve) of increase or decrease in species of northern or southern affinity within Central America may be drawn. The data may also be used to plot a species diversity curve showing the latitudinal trend of increase or decrease in total number of species within a given family throughout Central America.

A sample of avian families of both simple and complex distribution patterns are plotted in this manner, and the interpretation of their affinities as suggested by the diagrams is compared with that suggested by other data.

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Department of Zoology, University of California, Los Angeles, California 90024.