

AVIFAUNA OF THE RÍO CORONA, TAMAULIPAS,
MEXICO: NORTHEASTERN LIMIT
OF THE TROPICS

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WE believe that the northeastern extent of tropical avifaunas in the Western Hemisphere is in the Río Soto la Marina drainage basin, Tamaulipas, Mexico. Specifically we refer to the breeding bird community of climax evergreen forest in the floodplain of the Río Corona, 50 km north of the Tropic of Cancer. As a working definition of a tropical lowland avifauna, we suggest that (1) breeding species diversity is significantly higher than in comparable avifaunas of the temperate zone, including that of the Río Grande Valley, Texas, and (2) such species diversity is seasonally stable (cf. MacArthur 1969, 1971). Howell (1969) mentioned the desirability of locating northernmost tropical avifaunas in Mexico. We concur and present our views in lieu of his statement that such northern limits are impossible to define.

Tropical avifaunas in northern Latin America are endangered; and because this is particularly true in Mexico (Hernández Corzo 1970, Phillips 1970), we call special attention to the avifauna of the Río Corona floodplain forests. Not only is this a unique scientific resource in need of description, but it is threatened by lumbering, gravel dredging, and downstream flooding by a newly constructed reservoir. Indeed, the tropical forest and birds of the Río Corona are worthy of protection, as this major American biome (Tamaulipan Dry Forest) is not represented in any planned or existing preserve (Dasmann 1972).

STUDY AREA AND METHODS

The Río Corona drains a small portion of the Sierra Madre Oriental in west central Tamaulipas, Mexico, and flows ca. 900 km east to the Río Purificación, a tributary of the Río Soto la Marina. Downstream from the present crossing of Mexico Highway 101, riparian environments of the Río Corona are or soon will be impacted by the reservoir, Presa Las Adjuntas. Upstream floodplain communities, including our study site, will be less affected. The major climatic feature of the region is the May–October wet season (monsoon) in which 80% of the 90 cm mean annual precipitation falls (Shreve 1944, Martin 1958). Monsoon temperatures average 26°C. Dry season temperatures average 19°C, and light freezes are occasional at this time.

The study site is a 16-ha area on the south bank of the Río Corona 30 km northeast of Ciudad Victoria at 250 m elevation (23° 55' N, 99° 00' W). Each of two 8-ha linear study plots includes the river (to 15 m in width), a lower river terrace (to 7 m), and an upper terrace of evergreen forest (to 340 m, Fig. 1). River



Fig. 1. Climax evergreen forest on the upper river terrace (floodplain) of the Río Corona, Tamaulipas, Mexico, 11 April 1974. Ebony (*Pithecellobium flexicaule*) in right foreground is 80 cm dbh and ca. 15 m tall. This tree and others of the superior stratum show the gradual leaf fall characteristic of the end of the dry season. Photograph taken in man-made clearing (foreground) in which shrub strata are 1–2 m in height.

space is included, because the crowns of *Taxodium mucronatum* on the lower terrace completely cross it at some points and are used for nesting by species (e.g. Rose-throated Becard, Black-throated Oriole) that forage in the forest. The north bank of the river is a natural border of each plot as is the abrupt ecotone between forest and grassland on the south side. Short east and west ends of each plot are arbitrary. A 1-ha primitive campground, in which inferior strata of the forest are cleared, is included in one plot; and a 2-ha gravel road and disturbed zone separates the plots.

We define the major vegetational structure of the Río Corona floodplain as climax evergreen forest, because it is dominated by evergreen trees averaging 15 m in height and 47 cm in diameter (dbh) and is characterized by a continuous tree canopy where undisturbed (cf. Fig. 1, Beard 1944). We calculate an average of 132 trees per ha in the superior stratum. Ebony (*Pithecellobium flexicaule*) is dominant with an importance value of 198 (relative density + dominance + frequency in 10

randomly placed, 100 m, point-quarter transects). Species of *Ehretia*, *Bumelia*, and *Condalia* are subdominant with combined importance values of 194. Because vegetational diversity does not explain bird species diversity in tropical forests (Howell 1971, Karr and Roth 1971) or avifaunal differences between temperate and tropical regions (see below), we did not analyze vegetative structure further.

Some comments on vegetational dynamics are appropriate, as they bear on a hypothesis advanced later regarding community productivity and stability. The forest is ca. 80% evergreen, including inferior strata, with a gradual leaf fall toward the end of the dry season (April). At no time in our experience in December, January, April, June, July, and August were trees or shrubs bare except locally when denuded by insects in April. Dry season insects and abundant fruit, especially *Ehretia* berries and *Pithecellobium* beans, invite foraging by a variety of breeding birds (e.g. Brown Jay, Red-crowned Parrot) and migrants, often together in a single tree. Although insects and fruits were more evident and presumably more abundant in June–August, we did not observe any obvious bird food shortage in the dry season.

Species of birds in each plot were recorded by the senior author in August 1956, July 1960, and by all of us in December 1973. Individuals per species were counted by F. R. and N. Y. Gehlbach 19–21 June 1973 (20 man-hours), and by all of us 9–11 January (35 man-hours) and 8–11 April (50 man-hours) in 1974. Each plot was censused separately and simultaneously with the other by one to three persons until we found no additional breeding species or increases in their densities. One to five mist nets per plot per day were operated during the January and April censuses for a total of 50 net-hours each month.

For analytical purposes the data were reduced to average number of breeding males (based on territorial, courtship, and/or nesting behavior), visitors (breeding species from nearby areas), and migrants (wintering or transient temperate zone species) per 8 ha per month. We reject the customary abstraction of plot census data to 100 acre (40 ha) units, because our experience with paired study plots in the present study and elsewhere (Gehlbach MS) indicates that unequal territory sizes and patchy distributions lead to erroneous assumptions of abundance with such abstractions (cf. Howell 1971).

For comparative purposes we used quantitative data on breeding birds in 15–49 acre (6–20 ha) plots in temperate floodplain forests on the Atlantic Coastal Plain of the U.S. and similar data from 15–30 acre (6–12 ha) plots in the tropical lowland forests of Mexico, Central America, and the highland forests of Mexico. Data were taken from Audubon Field Notes (American Birds) and grouped as (1) northeastern U.S., (2) southeastern U.S., (3) Mexico-Central American lowlands, 5–1600 m; and (4) Mexican highlands, 1000–2500 m (Appendix). Also used was a breeding bird study in an 8-ha floodplain forest dominated by *Pithecellobium flexicaule* in the lower Río Grande Valley, Texas (Shifflett and Gehlbach MS).

Data from the Río Corona, the Río Grande, and the literature were reduced to diversity or number of species (S) and equitability (Shannon-Weiner H' , using \log_2) as defined by Whittaker (1971). We also used number of individuals per species (I/S) as an informative feature of tropical versus temperate avifaunas (Howell 1971). Equitability, diversity, and individuals per species of the breeding bird component in each sample group and the Río Corona (means for January, April, June) were subjected to five-way analysis of variance. The results were significant ($F = 9.4\text{--}14.2$, $P < 0.01$), so Tukey's test of significance among means was applied. We accepted the $P < 0.05$ level of significance in this test.

TABLE 1
 AVIFAUNA OF EVERGREEN FOREST IN THE FLOODPLAIN OF THE
 RÍO CORONA, TAMAULIPAS, MEXICO¹

Species	9-11 Jan. 1974	8-11 April 1974	19-21 June 1973
Least Grebe (<i>Podiceps dominicus</i>) V		1	
Neotropic Cormorant (<i>Phalacrocorax olivaceus</i>) V		2	
Anhinga (<i>Anhinga anhinga</i>) V	1	1	
Great Blue Heron (<i>Ardea herodias</i>) V	1	1	
Little Blue Heron (<i>Florida caerulea</i>) V	1	1	
Muscovy (<i>Cairina moschata</i>) B ²		1	1
Turkey Vulture (<i>Cathartes aura</i>) V		2	2
Black Vulture (<i>Coragyps atratus</i>) V		5	5
Hook-billed Kite (<i>Chondrohierax uncinatus</i>) V ³	1	1	
Crane Hawk (<i>Geranospiza caerulescens</i>) V ²		1	
Common Black Hawk (<i>Buteogallus anthracinus</i>) V ²	1		
Bay-winged Hawk (<i>Parabuteo unicinctus</i>) V	1		
Gray Hawk (<i>Buteo nitidus</i>) B ²	1	1	1*
Roadside Hawk (<i>Buteo magirostris</i>) V ²		1	
Red-shouldered Hawk (<i>Buteo lineatus</i>) M	1		
Crested Caracara (<i>Polyborus plancus</i>) V	1	1	
Collared Forest-Falcon (<i>Micrastur semitorquatus</i>) B ²		1	1
Plain Chachalaca (<i>Ortalis vetula</i>) B ^{3, 4}	3	4	5
Common Turkey (<i>Meleagris gallopavo</i>) B	1	1	
Spotted Sandpiper (<i>Actitis macularia</i>) M	1	1	
Red-billed Pigeon (<i>Columba flavirostris</i>) B ^{3, 4}	5	3*	2
White-winged Dove (<i>Zenaida asiatica</i>) B ^{3, 4}			3*
Common Ground-Dove (<i>Columbina passerina</i>) B	3	1	1
White-tipped Dove (<i>Leptotila verreauxi</i>) B ^{3, 4}	3	3*	2
Green Parakeet (<i>Aratinga holochlora</i>) B ²		2*	5
Olive-throated Parakeet (<i>Aratinga astec</i>) V ²			2
Red-crowned Parrot (<i>Amazona viridigenalis</i>) B ²	4	5*	5
Yellow-headed Parrot (<i>Amazona ochrocephala</i>) B ²	1	2	2
Groove-billed Ani (<i>Crotophaga sulcirostris</i>) B ^{3, 4}		1	2
Great Horned Owl (<i>Bubo virginianus</i>) V	1	1	1
Ferruginous Pygmy-Owl (<i>Glaucidium brasilianum</i>) B ³	1	1	1
Mottled Owl (<i>Ciccaba virgata</i>) B ²	1	1	1
Common Nighthawk (<i>Chordeiles minor</i>) M		8	
Pauraque (<i>Nyctidromus albicollis</i>) B ^{3, 4}	1	1	1
Fawn-breasted Hummingbird (<i>Amazilia yucatanensis</i>) B ^{3, 4}		2	2
Elegant Trogon (<i>Trogon elegans</i>) B ²	1	1	1*
Ringed Kingfisher (<i>Ceryle torquata</i>) B ³	2*	1	1
Belted Kingfisher (<i>Ceryle alcyon</i>) M	1		
Green Kingfisher (<i>Chloroceryle americana</i>) B	2*	2	1
Blue-crowned Motmot (<i>Momotus momota</i>) B ²	1	1*	1
Bronze-winged Woodpecker (<i>Piculus aeruginosus</i>) B ²	1	1	
Lineated Woodpecker (<i>Dryocopus lineatus</i>) B ²	1	1	1*
Golden-fronted Woodpecker (<i>Centurus aurifrons</i>) B	2	2	2*
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>) M	3	1	
Ladder-backed Woodpecker (<i>Dendrocopos scalaris</i>) V		1	
Rose-throated Becard (<i>Platypharis aglaiae</i>) B ³	2	3*	2*

¹ Mean number of males of breeding species (B), and mean number of nonbreeding visitors (V) and migrants (M) per 8 ha per census period. When sex was impossible to determine morphologically or behaviorally (e.g. Plain Chachalaca in January) a 50/50 sex ratio was assumed. An asterisk indicates that nesting was observed. If a breeding species was not present in January, it is assumed to be migratory.

² Species reaches its northeastern breeding limit in the Río Soto la Marina drainage basin of Tamaulipas.

³ Species reaches its northeastern breeding limit in the Río Grande Valley or south coastal region of Texas.

⁴ Species also breeds in a 8-ha floodplain forest plot dominated by *Pithecellobium flexicaule* in the Río Grande Valley, Texas (Shifflett and Gehlbach MS).

TABLE 1—Continued

Species	9-11	8-11	19-21
	Jan. 1974	April 1974	June 1973
Eastern Phoebe (<i>Sayornis phoebe</i>) M	1		
Tropical Kingbird (<i>Tyrannus melancholicus</i>) B ^{3, 4}	1	1*	1*
Sulphur-bellied Flycatcher (<i>Myiodynastes luteiventris</i>) B ²			1*
Great Kiskadee (<i>Pitangus sulphuratus</i>) B ^{3, 4}	2	2*	2
Brown-crested Flycatcher (<i>Myiarchus tyrannulus</i>) B ^{3, 4}		1	
Least Flycatcher (<i>Empidonax minimus</i>) M	1	1	
Northern Beardless Tyrannulet (<i>Camptostoma imberbe</i>) B ^{3, 4}			1*
Rough-winged Swallow (<i>Stelgidopteryx ruficollis</i>) B		1	1
White-necked Raven (<i>Corvus cryptoleucus</i>) V	1	1	
Mexican Crow (<i>Corvus imparatus</i>) B ²	4	3*	3
Brown Jay (<i>Psilorhinus morio</i>) B ²	5	5*	5
Green Jay (<i>Cyanocorax yncas</i>) B ^{3, 4}	3	1*	1
Black-crested Titmouse (<i>Parus atricristatus</i>) B	2	2	2
Spot-breasted Wren (<i>Thryothorus maculipectus</i>) B ²	3	3	3
Northern House-Wren (<i>Troglodytes aedon</i>) M	1	1	
American Robin (<i>Turdus migratorius</i>) M	3		
Clay-colored Robin (<i>Turdus grayi</i>) B ²	1	1	
Hermit Thrush (<i>Catharus guttatus</i>) M	1		
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>) M	5	1	
Ruby-crowned Kinglet (<i>Regulus calendula</i>) M	5	1	
Cedar Waxwing (<i>Bombycilla cedrorum</i>) M	4		
White-eyed Vireo (<i>Vireo griseus</i>) B			1
Yellow-throated Vireo (<i>Vireo flavifrons</i>) M		1	
Solitary Vireo (<i>Vireo solitarius</i>) M	1	1	
Yellow-green Vireo (<i>Vireo flavoviridis</i>) B ³			1*
Black-and-white Warbler (<i>Mniotilta varia</i>) M	2	1	
Orange-crowned Warbler (<i>Vermivora celata</i>) M	5	1	
Nashville Warbler (<i>Vermivora ruficapilla</i>) M	1	1	
Northern Parula Warbler (<i>Parula americana</i>) M		1	
Tropical Parula Warbler (<i>Parula pitiayumi</i>) B ²	1	2	2*
Yellow-rumped Warbler (<i>Dendroica coronata</i>) M	6		
Black-throated Green Warbler (<i>Dendroica virens</i>) M	1	1	
Yellow-throated Warbler (<i>Dendroica dominica</i>) M	1		
Yellow-breasted Chat (<i>Icteria virens</i>) M		1	
Wilson's Warbler (<i>Wilsonia pusilla</i>) M	3	1	
Bronzed Cowbird (<i>Tanagavius aeneus</i>) B ^{3, 4}			2
Great-tailed Grackle (<i>Cassidix mexicanus</i>) V		1	
Hooded Oriole (<i>Icterus cucullatus</i>) B ³	1	1*	1*
Black-headed Oriole (<i>Icterus graduacauda</i>) B ³	1	1	
Black-throated Oriole (<i>Icterus gularis</i>) B ^{3, 4}	3	3*	3*
Summer Tanager (<i>Piranga rubra</i>) B	1	1	
Western Tanager (<i>Piranga ludoviciana</i>) M	1		
Crimson-collared Grosbeak (<i>Rhodothraupis celaeno</i>) B ²		1	1
Blue Bunting (<i>Cyanocompsa parellina</i>) B ²	1	1	
Painted Bunting (<i>Passerina ciris</i>) M		1	
Olive Sparrow (<i>Arremonops rufivirgatus</i>) B ^{3, 4}	3	4	3
Lincoln's Sparrow (<i>Melospiza lincolni</i>) M	1		

AVIFAUNAL STRUCTURE

In four field seasons on the Río Corona we found at least 48 breeding species (Table 1). About half of these (48%) reach their northeastern breeding limits in the Rio Grande Valley or south coastal region of Texas and so provide a definite tropical aspect to that regional avifauna;

TABLE 2
COMPARISONS OF TWO COMPONENTS OF THE RÍO CORONA AVIFAUNA,
TAMAULIPAS, MEXICO¹

	Breeding species	Visitors plus migrants
Equitability (H')	5.00 \pm 0.20 (0.14)	3.65 \pm 1.88 (1.33)
Diversity (S)	39.33 \pm 5.44 (3.86)	22.31 \pm 18.34 (12.97)
Individuals/species	1.92 \pm 0.12 (0.08)	1.92 \pm 0.64 (0.45)

¹Data are mean \pm 2 SE and (coefficient of variation) based on censuses in June, January, and April.

35% are at their northeastern breeding limits in the Río Soto la Marina basin, and 17% are widespread in North America. Thus the breeding avifauna of the Río Corona is a mixed assemblage zoogeographically, but the majority of species (83%) are distinctly tropical. In fact, certain species (e.g. Spot-breasted Wren) have been used as indicators of tropical forests in Mexico (Phillips 1970).

If one looks at the regional affinities of a breeding avifauna in the Río Grande Valley (the 8-ha plot in *Pithecellobium* forest), he finds that 15 (65%) of the 23 species are tropical (Table 1), but there are only 23 species in the same community type that supports twice as many species per unit area on the Río Corona. Equally instructive is the fact that all 15 tropical species on the Río Grande also nest in our Río Corona plots, yet 33 additional species coexist in that space. One reason why additional species occupy the Río Corona forest is that additional individuals do not. The mean I/S of the Río Corona breeding avifauna is 1.92, whereas mean I/S on the Río Grande is 2.43. Thus, we believe a tropical avifauna can only be understood, hence adequately defined, on ecologic grounds (e.g. low I/S MacArthur 1969, Howell 1971).

Number of individuals per species in the Río Corona avifauna is low indeed (Table 2) and most like that of Mexico and Central America, although I/S does not differ significantly between the southeastern U.S. and Mexico-Central America samples (cf. Table 3). I/S decreases latitudinally as diversity and equitability increase, but the decline is not coincident with the rise in S and H' . I/S drops most abruptly between the two U.S. samples, while S and H' rise most dramatically between the U.S. and Mexico-Central America. The S and H' indices of tropical lowland avifaunas are significantly higher than those of temperate avifaunas (U.S. floodplain samples), and the Río Corona S and H' values do not differ significantly from those of tropical America but do differ significantly from those of temperate America (the U.S. samples are statistically alike in S and H').

We submit that an abrupt shift to tropical avifaunal structure

TABLE 3

COMPARISONS OF BREEDING AVIFAUNAS IN FORESTS OF ATLANTIC COASTAL FLOODPLAIN (U.S.) AND MEXICAN-CENTRAL AMERICAN LOWLANDS¹

	Northeastern U.S. N = 10	Southeastern U.S. N = 8	Mexico-Central America N = 9
Equitability (H')	3.94 ± 0.12 (0.38)	4.03 ± 0.32 (0.90)	4.93 ± 0.48 (1.48)
Diversity (S)	22.10 ± 2.58 (8.14)	24.38 ± 3.86 (10.90)	40.56 ± 11.28 (33.86)
Individuals/species	3.81 ± 0.76 (2.28)	2.49 ± 0.68 (2.66)	1.74 ± 0.28 (0.76)

¹ Data are mean ± 2 SE and (2 SD).

(significantly high S and H') occurs at the Río Corona and perhaps elsewhere in the Río Soto la Marina system. The shift does not occur in the Rio Grande Valley, Texas, for our Rio Grande data (S = 23, H' = 4.10, I/S = 2.43) resemble those of the southeastern U.S. (cf. Table 3). The Río Corona is at least 400 km north of the temperate to tropical avifaunal shift indicated by Tramer (1974) and ca. 250 km north of the shift predicted by Klopfer and MacArthur (1961). The latter is the northernmost area in which there is no frost, rainfall variation is less than 20%, and mean daily temperature range exceeds mean annual temperature range (cf. Klopfer 1959, Pianka 1966). No such climatic stability characterizes our Río Corona study site.

Because MacArthur (1971) suggested that montane avifaunas in the tropics resemble temperate avifaunas in structure, we restrict our discussion of tropical limits to lowland community types (below ca. 1600 m). Our synthesis of eight breeding bird censuses from the Mexican highlands reveals that H' = 4.45 ± 0.30 and S = 28.25 ± 4.52 (mean ± 2 SE). This H' value is not significantly different from that of the southeastern U.S. or Mexico-Central American lowlands, while the S value is not significantly different from either U.S. floodplain value, but is distinct from that of the tropical lowlands (cf. Table 3). Thus, Mexican highland avifaunas provide an equitability continuum between temperate and tropical lowland avifaunas but, based on diversity, are more aligned with the temperate zone.

Diversity or number of species seems to be the easiest means of differentiating a tropical lowland from a temperate lowland avifauna and, at the same time, is a reliable predictor of H' (r = 0.97 for the tropical lowlands, 0.93 for temperate floodplains, P < 0.001, cf. Tramer 1969). We present regressions of H' on S for temperate versus tropical lowland avifaunas, therefore (Fig. 2). The two predictive relationships are significantly different (t = 3.09, P < 0.01). Tropical avifaunas show less change in equitability with the addition or subtraction of species than temperate avifaunas. This, we suggest, reflects increased avifaunal

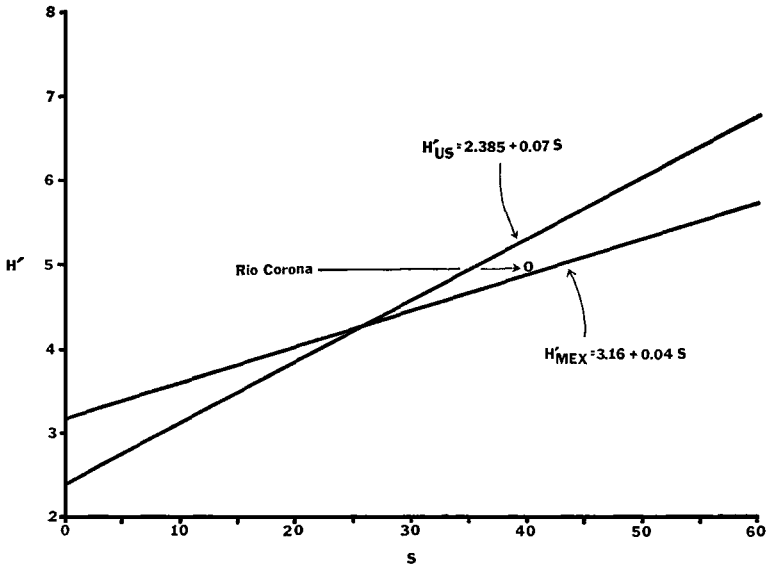


Fig. 2. Regression analysis of breeding species equitability (H') against species diversity (S) for 18 temperate floodplain forest avifaunas (H'_{US}) and 9 tropical lowland forest avifaunas (H'_{MEX}). Position of the Río Corona, Tamaulipas, Mexico, avifauna is indicated, based on mean H' and S from January, April, and June censuses.

stability in the tropical lowlands, an often stated but rarely demonstrated concept. If the Río Corona breeding bird community is truly tropical, then it should be relatively stable seasonally.

SEASONALITY

To encounter maximum potential seasonal flux, we attempted to census the dry season, including nonbreeding and breeding periods (January, April), and the wet breeding season (June), but we found kingfishers digging nest holes in January. Observed incidence of nesting increased from 4% of the breeding species to 27% in both April and June (Table 1). The long nesting season, spanning at least 6 months, half of them dry and half wet, may lower breeding intensity (cf. Ricklefs 1966). This, in turn, could lessen competition for the increased demands of food and space, especially during April nesting when visitors and migrants are prevalent (Table 1), and promote the higher and more stable S and H' indices of breeding species (Table 2).

We believe that most species concentrate their nesting in comparatively short-time intervals, staggered with or replacing ecologically similar

breeding species (Table 1). Species with similar nesting requirements do not nest at the same time unless their densities are dissimilar. For example White-winged and White-tipped Doves are similar in abundance and size, and both use dense thorny shrubs below about 4 m, but only the White-tipped Dove nests in April. Conversely, Green Parakeets and Red-crowned Parrots are quite unlike in abundance, size, and use of woodpecker-drilled versus natural cavities for nesting, but nest contemporaneously. Of the 24 species we observed nesting, only four (17%) seem to have individually prolonged nesting periods. Three of these (Rose-throated Becard, Black-throated and Hooded Orioles) may very well compete for nest space in the drooping branches of *Taxodium mucronatum*.

Among breeding birds, equitability is more stable than diversity (Table 2). The variation in diversity is caused by species that migrate south before the dry season (e.g. White-winged Dove, Sulphur-bellied Flycatcher, Yellow-green Vireo; 29% of the avifauna, Table 1). While seasonal flux in abundance of 69% of all breeding species is noted, offsetting trends among potential competitors may enhance the stability of H' in the nonbreeding season. For example when White-winged Doves are absent, the other columbids are most plentiful (Table 1). Nevertheless we cannot discount the possibility of competitive pressure from visitors and migrants as suggested by the seasonal relations of breeding vireos, warblers, and flycatchers versus migrants in these families.

Of particular interest is mean I/S of both breeding and nonbreeding groups, as they are equal but show unequal seasonal flux (Table 2). The I/S of breeding species exceeds that of visitors and migrants by a factor of 1.2 except in June when four visitors, particularly vultures, are relatively abundant (Table 1). By then there are 7.6 breeding individuals per visitor and no migrants in the community. We suggest that the higher and more stable density of breeding birds is a major factor enabling them to preempt resources and hence dominate the avifauna.

SUMMARY AND CONCLUSIONS

That tropical birds penetrate northward along the Atlantic and Pacific coasts of Mexico is well known, but prior to this study the northern limits of a tropical bird community were conjectural (Howell 1969). Baker and Fleming (1962) found tropical breeding species near La Pesca, Tamaulipas, in the Río Soto la Marina drainage 20 km south of our study site but did not provide data on avifaunal structure. Similarly, Martin et al. (1954) and Sutton and Pettingill (1942) noted tropical species in the lowlands of the Sierra de Tamaulipas and Río Sabinas, respectively, still farther south. Sutton and Pettingill's (1943) data on

birds of riparian forests near Linares, Nuevo León, 110 km northwest of our study site, are equally suggestive of a northern tropical avifauna as is Short's (1974) study on thorn forest birds near Álamos, Sonora, on the Pacific versant. Nevertheless, we emphasize that the avifaunal nature of the northern tropics is ecologically, not zoogeographically, distinguishable from that of the southernmost temperate zone.

Tramer (1974) proposed that species diversity (S) is stable between 50° and 20° N, but our comparison of Río Grande and Río Corona avifaunas indicates that number of breeding species per unit area doubles between 26° and 24° N. This is surprising, as the Río Grande and Río Corona study plots represent the same vegetation type (the evergreen forest dominated by *Pithecellobium flexicaule* is centered in this region). Yet avifaunas of the two floodplain areas are structurally temperate and tropical, respectively, with 33 additional breeding species at the Río Corona and significantly higher S and H'. The distinctive equitability, comparable to all tropical lowland avifaunas we assessed, contrasts with Tramer's (1974) statement that higher equitability in tropical avifaunas is largely a subjective impression.

We postulate that the abrupt shift to tropics at or near the Río Corona is a function of 1.5 times as much annual rainfall and 14% more in the monsoon season as compared with the Río Grande (Ciudad Victoria, Tamaulipas, vs. Brownsville, Texas; see Martin 1958). Because the annual temperature regime hardly changes between the two points, the added precipitation must enhance community productivity. Food resources must be increased thereby, especially into the dry season. This, we suggest, allows breeding birds to remain competitively less affected by migrants and visitors than in the Río Grande Valley and hence contributes to the higher diversity and equitability of the Río Corona avifauna.

Seasonality is an important determinant of temperate avifaunas and, conversely, seasonal stability is indicative of tropical avifaunas (Fretwell 1972). However, climatic and avifaunal stability are not congruent in the northernmost tropics as indicated at the Río Corona. This area experiences a pronounced wet and dry seasonality and occasional light freezes, yet most (71%) of the breeding birds are residents. Those that leave apparently migrate before the dry season but are replaced, in part, by concomitant increases in resident species. This sustains breeding species density, hence confers numerical dominance of the tropical breeding component over visitors and migrants.

The long, presumably low intensity type breeding season, in which ecologically similar species replace each other as nesting species, reduces competition among the breeding species and between them and visitors

and migrants. Nesting activities on the Río Corona span the January–June period, certainly, and probably extend into July and August on the basis of the senior author's casual observations. This 6- to 8-month period closely resembles the 6.6- to 9.8-month nesting interval given by Ricklefs (1966, 1969) for the tropics and contrasts with the 3.1- to 4.2-month period he noted for the temperate zone. It is another feature indicative of the tropical nature of the Río Corona avifauna.

Our concept of a tropical lowland avifauna at its northern geographic limits rests primarily on equitability among breeding species. Such equitability reflects functional stability of the community, i.e. its "tropicality", because the evenness of species abundances facilitates within and between season replacements (theoretically, one species will replace another most readily if the two are similar in abundance as well as other niche parameters). Based on counts of males, we propose that (1) a seasonal variation of less than 20% in equitability of breeding species, and (2) a Shannon-Weiner index larger than 4.5 for breeding species will distinguish a tropical lowland from a temperate lowland avifauna. The significantly high correlation of H' with S and the significantly different slopes of tropical and temperate avifaunal regressions of H' on S (Fig. 2) mean that one can count number of species to predict equitability typical of a tropical lowland avifauna.

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RESUMEN

El límite noreste de las avifaunas tropicales en el Nuevo Mundo se encuentra en la cuenca del Río Soto la Marina, Tamaulipas, México. Nos referimos específicamente a las aves se reproducen en el bosque (selva veranera siempreverde) a lo largo del Río Corona. Un bosque similar en el valle del Río Bravo en Texas mantiene una avifauna ecológicamente templada, a pesar de que la mayoría de las especies han sido derivadas de los trópicos. Criterios ecológicos, y no zoogeográficos, determinan la naturaleza ya sea tropical o templada de las avifaunas en reproducción. Una avifauna tropical se distingue de una templada en (1) estar localizada bajo 1600 m, (2) en tener una variación estacional del índice Shannon-Weiner de menos del 20%, y (3) un índice Shannon-

Weiner mayor de 4.5 de las especies en anidación, basado en el número de machos. Un monzón veraniego y posiblemente un prolongado período de anidación de las aves caracterizan el área de estudio del Río Corona. El monzón teóricamente aumenta la productividad de la comunidad, y el régimen de reproducción reduce la competencia entre las aves. Estos factores promueven la diversidad y estabilidad de las avifaunas típicas de los trópicos.

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APPENDIX

Breeding bird censuses in Audubon Field Notes (American Birds) from which quantitative data on breeding species were used; listed by state, volume, and page number(s) within sample groups.

(1) Northeastern U.S.: Massachusetts 19: 589-590; New Jersey 7: 340-341, 8: 366, 20: 608; Maryland 7: 341, 20: 609, 22: 658, 24: 739, 25: 964-965, 27: 964-965.

(2) Southeastern U.S.: Georgia 20: 609-610; Alabama 14: 498; Louisiana 27: 974; Arkansas 12: 454-455, 14: 490, 15: 522; Oklahoma 16: 519; Texas (D. Wolf, MS).

(3) Mexico-Central American Lowlands: Veracruz 6: 314-315, 7: 352-353, 9: 425-426; Sinaloa 22: 686; Zacatecas 18: 561; Quintana Roo 13: 468; British Honduras 15: 510; Costa Rica 16: 525-526, 18: 554-555.

(4) Mexican Highlands: Tamaulipas 19: 599-600, 20: 648-649; Zacatecas 18: 560-561; Oaxaca 19: 598-599; Chiapas 7: 351-352, 8: 374, 10: 429, 11: 448.