

## DISTRIBUTION OF OVERWINTERING NEARCTIC MIGRANTS IN THE YUCATAN PENINSULA, I: GENERAL PATTERNS OF OCCURRENCE<sup>1</sup>

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**Abstract.** Point counts and mist-net surveys were employed to study the winter distribution of nearctic migratory landbirds in Mexico's Yucatan Peninsula. Overwintering migrants comprised 42 regularly occurring species, and accounted for 30-58% (mean = 41%) of the individual birds encountered in surveys of a wide range of natural and disturbed habitats. Some migratory species were encountered most frequently in pastures, agricultural fields, or brushy second growth, but the main habitat for many migrants was tropical forest.

Migratory and resident species showed similar degrees of specialization with respect to the successional maturity of their habitats, but residents were more likely to specialize on particular types of mature forest. After mist-net capture data were standardized by rarefaction, there were no statistically significant differences in the ratio of migrants to permanent residents in habitats that ranged from pasture, through brushy old fields, to mature semievergreen forest. For any given number of captures, species richness of both migrants and residents was substantially higher in mist-net samples from pastures and brushy old fields than in those from mature semievergreen forest.

With few exceptions, nearctic migratory species that breed in mature temperate-zone forest occurred both in forest and in brushy second growth during winter, although some species were substantially less frequent in the latter habitat. In contrast, overwintering migrants that breed in edge or field habitats tended to avoid tropical forest in the Yucatan.

**Key words:** *Parulinae; migratory birds; distribution; habitat use; Yucatan Peninsula.*

### INTRODUCTION

In recent years, biologists and conservationists have expressed increasing concern over the status of nearctic migratory birds, species that breed in arctic or temperate North America, but spend the nonbreeding season south of the Tropic of Cancer (e.g., Keast and Morton 1980, Rappole et al. 1983, Wilcove and Whitcomb 1983, Powell and Rappole 1986). Since the 1950s, breeding populations of some nearctic migrants that breed in forest have undergone alarming local declines, particularly in regions where remaining woodlands are highly fragmented (e.g., Lynch and Whitcomb 1978, Morse 1980). Studies in eastern North America have shown that the area, isolation, physiognomy, and floristic composition of remnant forest patches all influence the occurrence and density of breeding birds, particularly nearctic migrants (e.g., Robbins 1980, Whitcomb et al. 1981, Lynch and Whigham 1984, Askins et al. 1987). For these long-distance migrants, it has also been suggested that population declines in local portions of the breeding grounds

reflect species-wide reductions that are causally related to the destruction of overwintering habitat in the neotropical region (Briggs and Criswell 1979, Morse 1980, Terborgh 1980, Rappole et al. 1983, Wilcove and Terborgh 1984, Powell and Rappole 1986). Certainly, there can be no doubt as to the rapid pace of deforestation in Middle America and the Caribbean islands (Myers 1980), areas where the majority of migratory species and individuals overwinter (Keast and Morton 1980).

While a link between tropical deforestation and declining populations of migratory landbirds in North America is both plausible and a cause for great concern, there is surprisingly little direct evidence for such a connection. Indeed, the existence of a pattern of global decline in migrant populations, as opposed to purely local perturbations, has yet to be unequivocally demonstrated. The only published continent-wide data set on population trends, the Breeding Bird Survey (BBS), indicates that breeding populations of most forest-associated migratory species were stable, or actually increased, between 1966 and 1979, the only period for which data have been published (Robbins et al. 1986). This latter finding, which has struck some biologists as counter-in-

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tuitive, seems to harken back to an earlier, and largely discredited, view (e.g., Slud 1960, Willis 1966, Leck 1972) that moderate levels of tropical forest disturbance might actually benefit the considerable number of nearctic migrant species that utilize edge habitats and successional vegetation on their tropical wintering grounds.

Analysis of more recent BBS data indicates that many of the increases observed between 1966 and 1979 have levelled off, or even have been reversed (Robbins et al., in press), but most migrant populations still appear to be as high or higher than they were in the late 1960s, according to BBS data. In large part, current uncertainties as to the specific threats posed to nearctic migrants by tropical deforestation reflect our ignorance of the winter ecology of even the commoner migrant species (Keast and Morton 1980, Rappole et al. 1983).

Within the northern neotropical region, the 240,000-km<sup>2</sup> Yucatan Peninsula stands out as an important overwintering center for nearctic migratory landbirds. Previous studies (e.g., Paynter 1955, Tramer 1974, Waide 1980, Waide et al. 1980) had shown that overwintering migrants are both diverse and abundant in the northern Yucatan Peninsula, but a comprehensive, quantitative survey of migrant numbers and habitat associations has not previously been attempted. In 1982 I undertook such a survey in order to address the following questions: (1) What are the relative densities of individual migratory species, and of migrants as a group, in the most widespread categories of natural and disturbed vegetation? (2) Are migrants as a group more tolerant of human-related habitat disturbance than are resident species? (3) What will be the likely impact of future land-use changes on migratory landbirds in the Yucatan?

## STUDY AREA AND METHODS

Fieldwork was concentrated in the Mexican states of Quintana Roo and Yucatan, but migrants were also surveyed in the states of Campeche and Chiapas, and in neighboring Belize and Guatemala (Fig. 1). The vegetation, climate, and geology of the Yucatan Peninsula have been well described from a zoogeographical viewpoint by Lee (1980), and only a brief account is presented here.

## CLIMATE AND NATIVE VEGETATION

The Yucatan Peninsula is fairly uniform in geology and topography. With the exception of the

Maya Mountains of Belize, essentially the entire peninsula is a low-lying shelf of Tertiary to Quaternary marine limestone. The present-day Yucatan gradually emerged from the sea floor, beginning at the southern end during the Oligocene-Miocene epoch, and continuing northward into Pleistocene and Recent times (Flores 1952, Hatt et al. 1953, West 1964).

The northern half of the peninsula lacks rivers and streams, and surface water is restricted to scattered shallow seasonal pools and a few lakes. Rainfall, which is strongly concentrated in a May–November wet season, increases markedly from north to south, and, in the northern half of the region, from west to east (Garcia 1965). At Progreso, on the northwestern coast of Yucatan state, the annual rainfall is 450 mm, and the native vegetation is low thorn scrub. Merida, only 30 km inland, receives about twice as much precipitation, and the native vegetation there is low deciduous forest, termed “selva baja caducifolia” (Miranda 1958). Between Merida and the Caribbean coast, some 300 km to the east, annual precipitation increases to about 1,200 mm, and low deciduous forest gives way to moderately tall semideciduous forest (“selva mediana subcaducifolia”), then to moderately tall semievergreen forest (“selva mediana subperennifolia”) in northern and central Quintana Roo. According to the Holdridge system of life zone classification (Holdridge et al. 1971), this west–east gradient corresponds to a transition from thorn woodland, through arid tropical forest, to dry tropical forest (Thien et al. 1982).

In southernmost Quintana Roo and Campeche, rainfall increases to 1,500 mm, streams and rivers are common, and taller, floristically richer semievergreen forest (“selva alta subperennifolia”) appears. This forest, which is intermediate between “tropical dry forest” and “tropical moist forest” according to the Holdridge system, is inhabited by a number of resident bird species that do not range farther northward into the drier portions of the peninsula (Paynter 1955). The wettest climate in the Yucatan Peninsula occurs along the Caribbean-facing slope of the Maya Mountains in southern Belize. Here, annual rainfall approaches 4,000 mm (Russell 1964), and the climax vegetation is “tropical wet forest” according to the Holdridge classification.

A number of distinctive natural vegetation types (e.g., mangrove swamp, sawgrass-palmetto savanna, dune scrub) occur along the Yucatan coast (see Lynch et al. 1985: fig. 2). For migratory

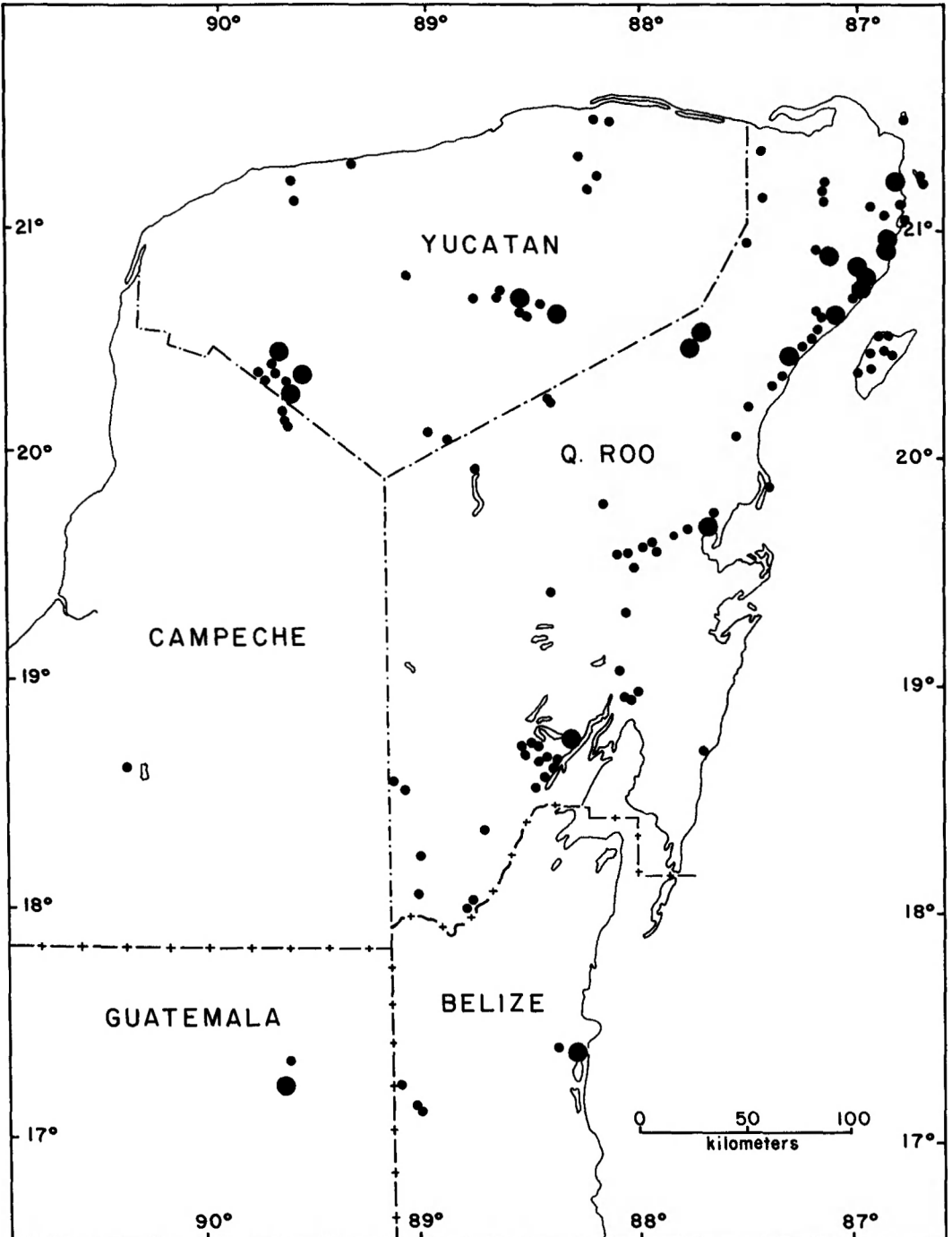


FIGURE 1. Map of the Yucatan Peninsula showing sites where point counts were made 1982–1987. Large symbols represent >12 counts; small symbols represent 4–12 counts. Several localities in northern Chiapas (just southwest of the area mapped) are not indicated.

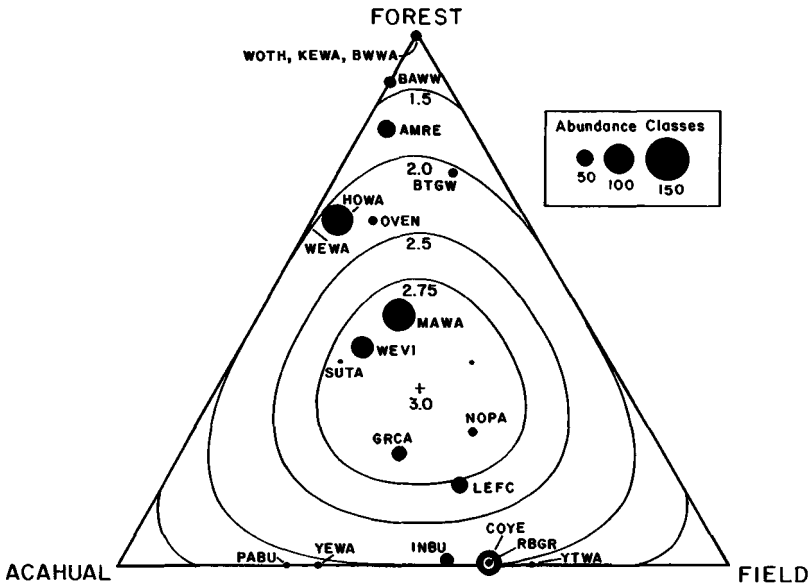


FIGURE 2. Diagram indicating relative rates of occurrence in three major habitats for 21 common migratory species, based on point-count data. Contours delimit zones of equal habitat diversity, based on  $\exp(H)$ . Species that plot near the center of the diagram, where  $\exp(H) = 3.0$ , are habitat generalists (i.e., they use all three successional stages in proportion to their availability); species that plot near a given corner are extreme specialists on that successional stage. Size of each symbol is proportional to overall rate of occurrence in all habitats. Species represented are Least Flycatcher (LEFC), Wood Thrush (WOTH), White-eyed Vireo (WEVI), Gray Catbird (GRCA), American Redstart (AMRE), Black-throated Green Warbler (BTGW), Black-and-white Warbler (BAWW), Blue-winged Warbler (BWWA), Common Yellowthroat (COYE), Hooded Warbler (HOWA), Kentucky Warbler (KEWA), Magnolia Warbler (MAWA), Northern Parula Warbler (NOPA), Ovenbird (OVEN), Worm-eating Warbler (WEWA), Yellow Warbler (YEWA), Yellow-throated Warbler (YTWA), Summer Tanager (SUTA), Indigo Bunting (INBU), Painted Bunting (PABU), and Rose-breasted Grosbeak (RBGR).

landbirds, the most important of these formations probably is dune scrub, remnants of which form a narrow, discontinuous fringe along the shores of both the Caribbean and the Gulf of Mexico (Moreno-Casasola and Espejel 1986). This vegetation exhibits strong floristic affinities with the islands of the northern Caribbean, and is the sole or major mainland habitat for several resident and migratory bird species that are otherwise restricted to the Antilles (Lopez-Ornat et al. 1989).

#### HUMAN MODIFICATION OF NATIVE VEGETATION

For thousands of years natural vegetation gradients in the Yucatan Peninsula have been altered, sometimes virtually beyond recognition, by human land-use. In the semiarid northwest, a century and a half of intensive cultivation of henequen (the source of sisal fiber) has compounded the effects of more than two millennia of slash-and-burn maize agriculture. As a result,

primary forest has been eliminated from the state of Yucatan and from northern Campeche (Bequaert 1935), although there are sizeable areas of secondary forest. To the east, the transition from semideciduous to semievergreen forest corresponds approximately to the political border between the states of Yucatan and Quintana Roo, and between a landscape that has been profoundly altered by human activities and one that retains extensive tracts of old-growth forest (Lynch et al. 1985: fig. 3). Even in forested areas, the presence of literally hundreds of Maya ruins testifies to the fact that virtually the entire peninsula has been subjected to human disturbance in the past.

At least since the collapse of the Classic phase of Maya culture (ca. 900 A.D.), human settlement has been concentrated in the dry northwestern portion of the Yucatan (the present Yucatan state and adjacent northern Campeche). The remainder of the peninsula had retained extensive areas of native forest until recent decades, when con-

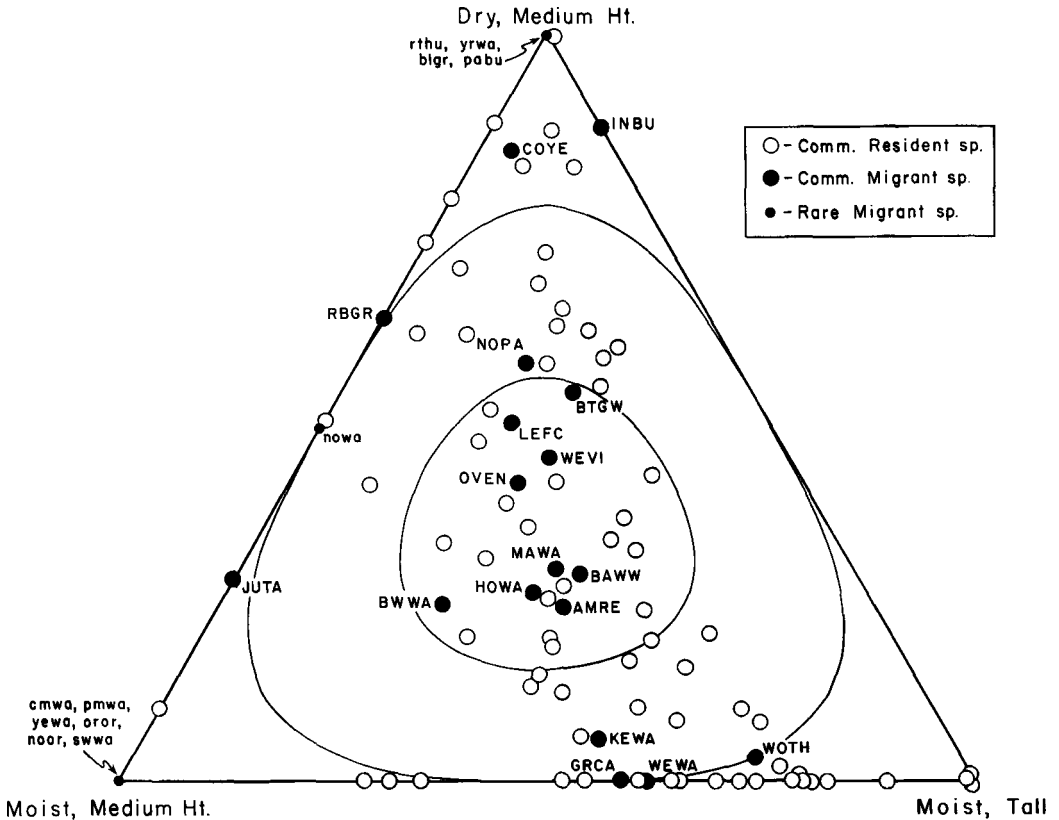


FIGURE 3. Diagram indicating occurrence rates in three widely distributed forest types by frequently encountered migrants (large closed symbols) and residents (open symbols). See legend to Figure 2 for explanation of contours and mnemonic abbreviations for migratory species. Infrequently encountered migrants (small closed symbols) that are not represented in Figure 2 are Ruby-throated Hummingbird (rthu), Northern Waterthrush (nowa), Cape May Warbler (cmwa), Palm Warbler (pmwa), Swainson's Warbler (swwa), Yellow-rumped Warbler (yrwa), Blue Grosbeak (blgr), Northern Oriole (noor), and Orchard Oriole (oror).

struction of new roads began to allow large-scale agricultural and ranching development in central and southern Campeche, southern Quintana Roo, and northern Belize. The largest remaining blocks of essentially intact tropical forest occur in the northern two-thirds of Quintana Roo, and in an irregular area that extends eastward from the northern Peten of Guatemala and southern Campeche, through southernmost Quintana Roo, and into Belize. The remainder of the peninsula is now mostly a patchwork of pastures, permanent fields and orchards, shifting agricultural plots (locally termed "milpas"), brushy old fields ("acahuales"), and secondary forest.

There is less mature forest in the Yucatan today than at any time since the 16th century Spanish conquest, a period of catastrophic depopulation for the area's Maya inhabitants (Thompson

1970). However, the area that is presently forested may actually exceed the extent of forest at the height of the Classic Maya civilization, 1,000-1,500 years ago. Clearly, migratory birds, like other elements of the Yucatan's biota, have had to accommodate a long history of human disturbance.

HABITAT CLASSIFICATION

For purposes of analysis nine major classes of vegetation were recognized: (1) active pasture (potrero) or cornfield (milpa), (2) brushy old field (acahual), (3) native coastal scrub, (4) semideciduous forest, (5) semievergreen forest, (6) evergreen forest, (7) mangrove swamp forest, (8) riverine floodplain forest, and (9) seasonally inundated low woodland (tintal). Some forest types (categories 4-9) were further subdivided into two

TABLE 1. Number of point counts performed in 19 habitats in the Yucatan Peninsula, 1982–1987.

Major habitat group	Stature of vegetation				Total counts
	Low ( $\leq 3$ m)	Medium (4–10 m)	Tall (11–20 m)	Very tall ( $> 20$ m)	
Open field	92				92
Native coastal scrub	60				60
Savanna	4				4
Brushy old field	72				72
Semideciduous forest	60	116	8		184
Semievergreen forest	20	196	208		424
Moist forest	4	12	36	12	64
Tall floodplain forest			16		16
Mangrove forest	20	8			28
Seasonally inundated forest	24	8			32
Grand total					976

to four height intervals, such that the total number of defined habitat categories was 19 (Appendix I). Each bird survey point was assigned to one of these 19 habitat types (Table 1). Details of vegetation structure and floristic composition were documented at several hundred 0.04-ha plots located within 20 m of survey points. The results of the latter study will be presented elsewhere (J. F. Lynch, D. F. Whigham, and E. S. Morton, unpubl.).

#### POINT SURVEYS

Migrant and resident birds were surveyed in the Yucatan Peninsula during the winters of 1982–1987 (Fig. 1). Our point-count technique combined aspects of the I.P.A. (“Index Ponctuel d’Abondance”) and E.F.P. (“Echantillonnage Fréquentiel Progressif”) methods developed by Blondel, Ferry and coworkers (Blondel et al. 1970, 1981; Ferry 1974; Blondel 1975, 1977), and previously applied to North American breeding bird communities (e.g., Whitcomb et al. 1981, Lynch and Whigham 1984). In each tract of vegetation we counted all birds that were seen or heard (regardless of distance) on a single visit to each of four survey points. We used a 10- to 12-min observation period per point, rather than the 20 min specified for both the I.P.A. and the E.F.P. methods. However, counts of 10–12 min should give acceptable coverage, according to the results of comparative studies of count efficiency (Scott and Ramsey 1981, Pyke and Recher 1985, Verner 1985, Hutto et al. 1986).

Variants of the unlimited point-count method (e.g., the variable circular-plot method, the fixed-radius point count method) have been used to estimate absolute densities of birds (e.g., Reyn-

olds et al. 1980, DeSante 1981). However, comparisons with the results of intensive spot-mapping indicate that the methods based on point counts may yield misleading absolute (or even relative) densities for most of the species in some bird communities, particularly in forested ecosystems (DeSante 1986, Hutto et al. 1986). We therefore interpret our point counts as indices of relative abundance (Verner 1985) that are best suited for comparisons of the prevalence of a given species across habitats or geographic regions.

Within a given tract, each of the four survey points were located at least 150 m apart, and were no closer than 100 m to habitat boundaries, except where the linear form of the habitat (e.g., mangrove fringe) made this impossible. In practice, we were able to achieve the desired spacing between four survey points in most stands that were larger than ca. 15 ha. Where single tracts of this extent were unavailable (e.g., small slash-and-burn agricultural plots), we divided the required four points between two nearby tracts of a given vegetation type. Stands of less than 2 ha were not included in our study.

The procedure was for two observers (occasionally more) to walk 100–150 m into a designated tract, wait a few moments for bird activity to equilibrate, and begin the count. Surveys were continued for 10–12 min, the shorter interval being used only if no new birds had been detected between min 8 and min 10. Because the primary focus of this study was the status of nearctic migrant landbirds, many of which respond to generalized distress calls and other stimuli, we employed several techniques to increase the likelihood of detecting migrants at close range

within the count period. First, territorial *chip* notes of two common overwintering migratory species (Hooded Warbler and Kentucky Warbler) were played back for 3–5 min, using a Uher 4000 Report Monitor tape recorder. Imitations of the distress *squeak* call of a small passerine and the *poip-poip-poip* whistle of the Ferruginous Pygmy-Owl were then used to elicit responses. To quantify the effects of these stimuli, a series of paired comparisons were made between counts using aural stimuli counts where no active attempt to elicit responses was made. The results of these comparisons, which will be presented elsewhere (J. Lynch, unpubl.), indicated that migratory warblers and vireos showed minor, but a statistically significant, positive response to our aural stimuli, but resident species as a group were unaffected. The main benefit to this study of using aural stimuli was that they tended to cause migrants to approach the observer more closely, thereby allowing more accurate sex/age determination, reading of color bands, etc.

Aerial foragers that did not make use of the vegetation were not counted, as they could not be unambiguously assigned to particular habitats. Thus, many common species (e.g., vultures, soaring hawks, swifts, swallows) did not appear on our survey lists unless they were observed perched or otherwise associated with terrestrial vegetation.

#### MIST NETTING

Because many previous studies of nearctic migrants in the Yucatan and elsewhere in the neotropics have employed mist netting to estimate patterns of relative abundance (e.g., Tramer 1974; Waide 1980; Waide et al. 1980; Karr 1981a, 1981b), and because mark-recapture data arising from netting studies can provide valuable information on home-range size and survivorship in some species (e.g., Karr 1981a), we supplemented our point counts with mist netting. We recognize that the latter technique is strongly biased against species that are mainly active in the forest canopy, or that are too large or too small to be efficiently captured by nets of a given mesh size. Nevertheless, mist-net capture rates can be meaningful indices of abundance for species of appropriate size that are active mainly in the ground and shrub strata. In addition, we believed it was important to compare the results of mist-netting studies directly with those of the point-count method.

Standard 12-m × 2-m nylon mist nets (mesh size 3.2 cm and 3.8 cm) were operated intermittently between 1984 and 1987 at 15 locations in northern and central Quintana Roo (Fig. 1). Each site was an essentially homogeneous stand of a major natural or secondary vegetation type, ranging from pastures and milpas, through old fields of varying ages, to mature semievergreen forest (Table 2). At each site 20–36 nets were set either in a single line or in two or three parallel lines of eight to 12 nets each. Net lines were separated by at least 50 m. In one intensively studied tract of semievergreen forest, two mist nets were placed in each of 12 40-m × 40-m plots that extended over an area of about 5.5 ha. A netting bout consisted of operating all the nets at a given site for 2–4 (usually 3) consecutive days. The number of bouts per site ranged from one to six, with most sites being sampled on two to four occasions (Table 1). Nets were opened at first light, and were closed at 11:30–12:30, by which time capture rates usually had declined and rising temperatures tended to stress netted birds, especially in the more open habitats. Captured birds were identified to species, sexed and aged (where possible), weighed, and color-banded for future recognition. “Captures” refer to the number of different individuals netted per net hour (or net morning) in a given bout. Thus, the same bird caught in two different years (or at two different seasons of the same year) was counted as two captures, but an individual captured repeatedly within the same bout was counted only once.

#### RESULTS

##### DIVERSITY OF THE AVIFAUNA

Fieldwork between the months of November and March revealed a total of 213 species of landbirds (excluding aerial foragers), of which 44 (21%) were overwintering nearctic migrants (Appendix II). Limited observations in October and April revealed the presence of several additional transient migratory species (Appendix II), but these are not included in our analysis of winter bird communities. Of the overwintering migratory species, one (Cedar Waxwing) was casually observed on a single occasion, but was not encountered during either the point counts or mist-netting surveys. The other 43 winter visitors were either recorded only in point surveys (10 species), only by mist netting (5 species), or by both sur-

TABLE 2. Localities and habitats where mist netting was conducted in the Mexican state of Quintana Roo in 1984–1987. Only data for the time of year when migrants were present (late August to late April) are presented. Localities labelled “Sian Ka’an” are within the Sian Ka’an Biosphere Reserve, east of Felipe Carillo Puerto, in central Quintana Roo; “Puerto Morelos” refers to a cluster of localities within 15 km of the village of Puerto Morelos, on the northeastern coast of Quintana Roo.

Major habitat type	Locality	Netting bouts	Net hours	Net mornings
Active field or pasture	Sian Ka’an	4	673	164
	Puerto Morelos	1	310	69
	Subtotal	5	983	173
Early acahual (1–3 years)	Puerto Morelos	1	144	32
	Sian Ka’an	1	528	96
	Puerto Morelos	1	459	34
Subtotal	3	1,131	162	
Mid-stage acahual (4–7 years)	Sian Ka’an	1	264	48
	Puerto Morelos	3	1,356	280
	Subtotal	4	1,620	328
Semievergreen forest (medium stature)	Puerto Morelos	6	2,826	576
	Puerto Morelos	4	1,920	336
	Sian Ka’an	1	240	48
	Sian Ka’an	1	384	72
	Puerto Morelos	2	598	120
Subtotal	14	5,968	1,152	
Semievergreen forest (tall)	Puerto Morelos	2	858	141
Native coastal scrub	Sian Ka’an	2	322	56
	Sian Ka’an	2	644	116
	Subtotal	4	1,824	172
Grand total		32	11,562	2,128

vey methods (28 species). A majority (28/43 = 65%) of the overwintering species of migratory landbirds belonged to the emberizid subfamily Parulinae (Appendix II).

#### POINT SURVEYS

A total of 976 point counts was made during the winters of 1982–1987. The following 12 habitat types were not censused frequently enough (<50 counts) to permit detailed statistical analysis (Table 1): tall semideciduous forest (8 points), low semievergreen forest (20), low (4), medium (12), tall (36), and very tall (12) moist forest, savanna (4), low mangrove forest (20), medium mangrove forest (8), tall floodplain forest (16), low inundated deciduous forest (24), and medium inundated deciduous forest (8). Results of surveys in these 12 habitat types are not included in the following statistical analysis, but some qualitative results are noted in our discussions of general habitat associations and geographic

patterns (see below—Results). The remaining seven habitat types were each sampled 60–208 times. Even for the commonest species of migrants, the mean number of individuals detected in point counts where the species was present was only slightly greater than unity ( $\bar{x} = 1.11$ ; range = 1.07–1.26;  $n = 12$  species). “Frequency” and “abundance” are assumed to be related, but statistical analyses are based on presence/absence data, not on absolute numbers. Absolute densities were not determined in this study, except for Hooded Warblers (Green et al. 1988).

*Successional patterns.* Major successional trends were summarized by comparing point survey data for three common habitat classes: (1) fields and pastures that were in active use or had been abandoned for less than a year, (2) brushy old fields (acahuales) 4–7 years into abandonment, and (3) mature medium-stature semievergreen forest (*selva mediana subperennifolia*), an extensive vegetation type in the eastern half



of the peninsula (Fig. 2). Most of our mist netting was conducted in this forest type and its seral stages.

Active and very recently abandoned fields (milpas) and pastures (potreros), which in Quintana Roo almost always contain at least a few living and dead trees and clumps of brush, appeared to support a rich bird community (Table 3), although it was not known whether or not birds observed in cleared areas also made use of adjacent forest. Nearctic migrants accounted for 17% (17/101) of the species encountered in 92 point counts within this habitat, and migrants were among the most frequently detected species: 10 of the 34 most commonly encountered field-associated species (29%) were winter visitors, which also accounted for 27% of all individual birds that were tallied. In order of decreasing frequency of occurrence, the main migratory species in potreros and milpas (hereafter termed "field/brush" communities) were Common Yellowthroat, Least Flycatcher, Magnolia Warbler, Indigo Bunting, Gray Catbird, White-eyed Vireo, Northern Parula Warbler, Yellow-throated Warbler, Rose-breasted Grosbeak, and Yellow Warbler (Table 3).

Four of the six most frequently detected permanent residents in the field-brush community (Golden-fronted Woodpecker, Tropical Mockingbird, Tropical Kingbird, Scrub Vireo) are ecologically similar to congeners that inhabit disturbed habitats in temperate North America. Thus, the winter bird community associated with field-brush vegetation appears to be numerically dominated by nearctic migrants and by resident species that have closely related counterparts in the North Temperate Zone.

The 72 point surveys conducted in acahuales (successional communities dominated by shrubs and young trees) revealed the presence of 80 species (Table 3). Although fewer acahuales than field-brush sites were sampled, both the total number of migratory species (19) and the proportion of migratory species (24%) that was detected were somewhat higher in acahuales. As was also true in field-brush communities, migrants were disproportionately represented among the most frequently encountered species: seven of the 10 most commonly detected species in acahuales were migrants (Table 3), and migrants accounted for 33% of all individual birds that were encountered. In decreasing order, the most frequently encountered migratory species

in acahuales were Magnolia Warbler, Common Yellowthroat, Hooded Warbler, White-eyed Vireo, Least Flycatcher, Gray Catbird, Indigo Bunting, and American Redstart. Four of these eight species are also associated with brushy and edge habitats on their breeding grounds, and all except the Hooded Warbler and American Redstart were frequent in field-brush communities as well as acahuales during winter (see above). The most frequently detected resident species in acahuales (Scrub Vireo, Melodious Blackbird, Tropical Kingbird, Golden-fronted Woodpecker, Hooded Oriole) were also commonly encountered in fields and pastures (Table 3).

The 404 point surveys conducted in late-successional and mature medium-stature semievergreen forest (*selva mediana subperennifolia*) revealed the presence of 99 bird species, of which 18 (18%) were nearctic migrants (Table 3). Five of the 10 most frequently encountered species in semievergreen forest were migrants, which also accounted for 40% of the total individuals encountered. In decreasing order, the most frequently detected migrants in semievergreen forest were the Hooded Warbler, Magnolia Warbler, American Redstart, White-eyed Vireo, Black-and-white Warbler, Wood Thrush, Black-throated Green Warbler, Kentucky Warbler, Gray Catbird, and Least Flycatcher. Whereas most of the migratory species that occurred in acahuales also were found, at least occasionally, in heavily disturbed open fields, only two typical acahual species (Magnolia Warbler, White-eyed Vireo) were also commonly encountered in mature forest. When the degree of specialization of migrant species on actively disturbed (Field), midsuccessional (Acahual), and late successional (6–20 m height) semievergreen forest (Forest) is summarized in a triangular diagram (Fig. 2), most species cluster along a line passing through the "Forest" apex, and bisecting the Field-Acachual axis.

Forest stature appeared to be a relatively unimportant determinant of migrant occurrence. There were virtually no statistically significant differences between the rates of occurrence of any migrant species in medium-stature (6–10 m) vs. taller (11–20 m) *selva mediana subperennifolia* (Table 4).

Of the 10 most frequent resident species in agricultural fields and pastures, only one (Brown Jay) also ranked among the 10 most frequent species in mature forest. Similarly, only one of

TABLE 3. Occurrence of nearctic migrants in three successional habitats, based on the percentage of point counts where each species was encountered (PP) and capture rate in mist nets (CR). CR =  $100 \times$  no. of individuals captured per net per morning. For each habitat, species are listed in decreasing order of their frequency in point counts.

Field/pasture		Acahual		Mature semievergreen forest	
Species	PP (CR)	Species	PP (CR)	Species	PP (CR)
1. Common Yellowthroat	54 (11)	1. Magnolia Warbler	36 (5)	1. Hooded Warbler	69 (4)
2. Least Flycatcher	28 (5)	2. Common Yellowthroat	35 (7)	2. Magnolia Warbler	57 (1)
3. Magnolia Warbler	28 (3)	3. Hooded Warbler	33 (6)	3. American Redstart	47 (0)
4. Indigo Bunting	22 (41)	4. White-eyed Vireo	29 (12)	4. White-eyed Vireo	31 (2)
5. Gray Catbird	17 (7)	5. Gray Catbird	21 (14)	5. Black-and-white Warbler	28 (2)
6. White-eyed Vireo	15 (6)	6. Least Flycatcher	21 (5)	6. Wood Thrush	17 (3)
7. Northern Parula Warbler	11 (0.9)	7. Indigo Bunting	18 (4)	7. Black-throated Green Warbler	16 (0)
8. Yellow-throated Warbler	9 (0.6)	8. Yellow Warbler	11 (2)	8. Kentucky Warbler	13 (2)
9. Rose-breasted Grosbeak	9 (0.3)	9. American Redstart	8 (1)	9. Gray Catbird	10 (0.1)
10. Yellow Warbler	5 (0.8)	10. Northern Parula Warbler	7 (2)	10. Least Flycatcher	9 (0.3)
11. Hooded Warbler	4 (3)	11. Rose-breasted Grosbeak	6 (0)	11. Ovenbird	7 (4)
12. Black-throated Green Warbler	4 (0)	12. Yellow-throated Warbler	4 (0)	12. Northern Parula Warbler	6 (0)
13. American Redstart	2 (2)	13. Ovenbird	3 (8)	13. Worm-eating Warbler	2 (0.5)
14. Painted Bunting	1 (4)	14. Painted Bunting	3 (2)	14. Summer Tanager	2 (0.1)
15. Ovenbird	1 (2)	15. Summer Tanager	3 (0.8)	15. Blue-winged Warbler	2 (0)
16. Summer Tanager	1 (2)	16. Black-and-white Warbler	3 (0.5)	16. Northern Waterthrush	1 (0.2)
17. Orchard Oriole	1 (1)	17. Worm-eating Warbler	1 (0.8)	17. Common Yellowthroat	0.5 (0)
18. Yellow-breasted Chat	0 (3)	18. Northern Waterthrush	1 (0)	18. Indigo Bunting	0.5 (0)
19. Northern Waterthrush	0 (2)	19. Black-throated Green Warbler	1 (0)	19. Black-throated Blue Warbler	0 (0.2)
20. Black-and-white Warbler	0 (0.6)	20. Wood Thrush	0 (8)	20. Swainson's Warbler	0 (0.1)
21. Blue Grosbeak	0 (0.6)	21. Kentucky Warbler	0 (2)		
		22. Yellow-breasted Chat	0 (2)		
		23. Blue-winged Warbler	0 (0.8)		
		24. Yellow-bellied Sapsucker	0 (0.5)		
		25. Swainson's Warbler	0 (0.5)		
		26. Orchard Oriole	0 (0.2)		

the 10 most frequent resident species in acaciales (Fawn-breasted Hummingbird) also ranked within the 10 most frequently detected species in forest. No resident species was frequent in all three seral stages, although a number of species occurred at least occasionally across the entire successional continuum (Table 3). At the level of the three successional stages that were compared, the 26 most frequent migratory species and the 52 most frequent residents did not differ significantly in their degree of specialization on one successional habitat (Mann-Whitney  $U = 778$ ;  $P > 0.14$ ). As was true for migrants, resident species occurred with similar frequency in medium-stature and tall selva mediana subperennifolia (Table 4).

*Comparisons between semievergreen and semideciduous forest.* Although the semideciduous woodland that occurs in the heavily populated northwestern portion of the Yucatan is entirely second growth, it commonly attains the same stature as mature semievergreen forest that is found to the east and south. With few exceptions, the same migratory species occurred in both the drier and more humid forest types, although the relative frequency of most species differed from one forest type to the other (Table 4). Black-throated Green Warblers and White-eyed Vireos were significantly more frequent in semideciduous forest, while the Wood Thrush, Gray Catbird, Hooded Warbler, Kentucky Warbler, Magnolia Warbler, and American Redstart were more frequent in semievergreen forest. Least Flycatcher, Ovenbird, Black-and-White Warbler, and Northern Parula Warbler occurred with similar frequency in both types of forest. The only two migratory species that were relatively frequent in one forest type but virtually absent from the other were the Wood Thrush and Kentucky Warbler, which occurred, respectively, in 11% and 13% of 408 point counts in semievergreen forest, but each of which occurred in only 1/101 (1%) of the counts in semideciduous forest ( $P < 0.01$ ; binomial test).

Resident species showed a significantly greater tendency than migrants to occur preferentially in either semideciduous or semievergreen forest, although most residents were found at least occasionally in both forest types (Table 4). Whereas 8 of 12 (67%) migratory species that occurred commonly in one or more of the three widespread forest types (short semideciduous, short semievergreen, and medium-stature semiever-

green) were classed as forest generalists (i.e.,  $\exp[H'] > 2.7$ ), only 19 of the 61 (31%) most frequently detected forest-dwelling resident species were so classed. At the other extreme, none of the 12 most frequent forest-dwelling migrants was classified as highly specialized on one forest type (i.e.,  $\exp[H'] < 1.6$ ), but 7 of 61 (12%) of the permanent residents fell into this category. A tendency for residents to specialize on tall, moist forest is evident in a triangular plot of the three forest types (Fig. 3).

*Occurrence of migrants in other habitats.* Consistent patterns of occurrence of some migratory species in some of the 12 less-studied habitat types (see above) suggested restricted habitat use in some instances (Tables 5 and 6). Although sample sizes are too small to permit reliable statistical analysis in all species, moist tropical forest (including selva alta subperennifolia), which was surveyed in southernmost Quintana Roo, Chiapas, Belize, and northern Guatemala, was the forest type with the highest occurrence rates for several migratory species, including the Wood Thrush, Gray Catbird, Kentucky Warbler, and Worm-eating Warbler. Conversely, the White-eyed Vireo, Northern Parula Warbler, Black-throated Green Warbler, Hooded Warbler, American Redstart, and Black-and-white Warbler were less frequent in the lush forests of the southern peninsula than in dry forests to the north. Yellow-throated Vireo, Magnolia Warbler, and Ovenbird showed no consistent differences in frequency of occurrence between wet and dry forest types.

The Cape May Warbler, Palm Warbler, Yellow-throated Warbler, Yellow-rumped Warbler, and Blue Grosbeak all occurred with highest frequency in coastal scrub, although none of these except the Blue Grosbeak was encountered at a sufficient number of survey points to allow the statistical significance of this pattern to be assessed. The primary tropical wintering areas for these species are the Bahamas and the Greater Antilles (Emlen 1977, Rappole et al. 1983), and except for the Cape May Warbler, these species also occurred regularly in pastures and milpas in the northern Yucatan, sometimes many kilometers from the coast. Other migratory species were relatively scarce in coastal scrub except during fall and spring, when large numbers of transient Tennessee Warblers, Red-eyed Vireos, and Eastern Kingbirds were present (A. Lopez, pers. comm.; pers. observ.). A few resident species (e.g.,

TABLE 4. Degree of specialization of the 88 most frequently encountered forest-dwelling species with respect to three types of forest, based on point-count data. Species marked with an asterisk (\*) were more frequently found in nonforest habitats, but also occurred in forest. Numbered codes for resident species are identified in Appendix II. Degree of specialization is based on the exponential of the Shannon-Weiner diversity statistic ( $H'$ ) calculated from the relative rates of occurrence in three forest types: (1) semideciduous, (2) medium height semievergreen, and (3) tall semievergreen.  $\text{Exp}(H')$ , which can be interpreted as the number of equally used habitats, can vary from a minimum of 1.0 (complete specialization on one forest type) to a maximum of 3.0 (equal use of all three forest types). Ignoring the 14 species whose main habitats were not forest, migrants show significantly less tendency toward habitat specialization than do permanent residents ( $\chi^2 = 37.3$ ;  $df = 7$ ;  $P < 0.005$ ).

Degree of specialization	Migrant species ( $n = 18$ )	Resident species ( $n = 70$ )
Generalists ( $\text{exp}[H'] > 2.7$ )	Least Flycatcher,* White-eyed Vireo, Black-throated Green Warbler, Magnolia Warbler, American Red- start (9 species = 50%)	14, 38, 42, 45, 63, 73, 77, 84, 86, 96, 102, 108, 109, 113, 115, 120, 138, 150, 151, 155* (20 species = 29%)
Moderate specialists ( $1.6 < \text{exp}[H'] < 2.7$ )		
Semideciduous forest	Northern Parula Warbler, Common Yellowthroat,* Rose-breasted Grosbeak* (3 species = 17%)	1, 28, 41, 53, 79, 82, 88, 89, 97,* 99, 112, 127,* 129, 148,* 165 (15 species = 21%)
Medium-stature semi- evergreen forest	Summer Tanager (1 species = 6%)	121,* 125, 128 (3 species = 4%)
Tall semievergreen forest	Wood Thrush, Gray Catbird,* Yel- low-throated Vireo, Kentucky Warbler (4 species = 22%)	32, 33,* 36, 39, 44, 49, 52, 60, 62, 74, 92, 107, 119, 139, 140, 141, 143 (17 species = 24%)
Equal occurrence rates in both semiever- green types	(none = 0%)	7, 67, 85, 94 (4 species = 6%)
Extreme specialists ( $\text{exp}[H'] < 1.6$ )		
Semideciduous forest	Indigo Bunting* (1 species = 6%)	116, 155, 164* (3 species = 4%)
Medium height semi- evergreen forest	(none = 0%)	162 (1 species = 1%)
Tall semievergreen forest	(none = 0%)	17, 19,* 58, 59, 75, 104, 161* (7 species = 10%)

Black Catbird, Tropical Mockingbird, Bananaquit) reached extraordinarily high densities (as measured by mist-net capture rates) in some areas of coastal scrub (A. Lopez and J. Lynch, unpubl.).

Coastal mangrove forest was inhabited by a wide variety of migrants, and point surveys in this habitat showed a higher percentage of migrant individuals (58%) than any other habitat that was sampled (Table 5). Nevertheless, only one migratory species (Northern Waterthrush) had its maximum rate of occurrence in mangrove forest (Table 6). Other migrants that were frequently detected in mangrove forest were the Common Yellowthroat, Northern Parula Warbler, Yellow Warbler (both migratory and

resident races), Yellow-throated Warbler, Black-and-white Warbler, American Redstart, and Worm-eating Warbler.

*Degrees of habitat specialization.* The method of contingency analysis described by Hobbs and Bowden (1982) helps to clarify the pattern of differential use of natural and disturbed habitats by overwintering migrants. Contingency analysis of the 23 species that were abundant enough for meaningful statistical analysis reveals distinctive patterns in the use of the nine most frequently sampled habitat categories (Table 6). Six species (Yellow Warbler, Yellow-throated Warbler, Yellow-rumped Warbler, Common Yellowthroat, Indigo Bunting, Rose-breasted Grosbeak) were

TABLE 5. Absolute and relative occurrence rates of nearctic migrants in major vegetation types in the Yucatan Peninsula. Tabled entries are mean numbers of species (S) and individuals (I) detected per cluster of four point counts within each contiguous tract of vegetation that was surveyed.

Habitat	No. tracts	All birds		Migrants		Percent migrants	
		S	I	S	I	S	I
Field/pasture	22	19.2	49.0	5.6	16.3	29.2	33.3
Brushy old field	16	20.6	40.0	6.2	12.4	30.1	30.1
Secondary drier forest	31	17.0	28.6	6.2	12.1	36.5	42.3
Inundated drier forest	7	13.7	23.3	6.7	11.6	48.9	49.8
Mature drier forest	9	18.9	28.4	7.4	13.3	39.2	46.8
Low moist forest	10	16.0	30.5	5.6	11.7	35.0	38.4
Secondary moist forest	48	19.1	37.0	7.0	15.1	36.6	40.8
Mature moist forest	58	21.1	39.2	6.9	15.1	32.7	38.5
Evergreen forest (all)	20	18.2	27.3	6.1	10.7	33.5	39.2
Coastal mangrove forest	7	13.1	27.3	7.1	15.9	54.2	58.2
Coastal scrub	14	19.2	49.0	3.1	10.4	29.2	33.3

TABLE 6. Patterns of habitat specialization in the 23 most common species of overwintering nearctic migrants in the Yucatan Peninsula, based on point counts. Overall  $\chi^2$  values and significance levels (\*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ , \*\*\*\* =  $P < 0.0001$ , ns =  $P > 0.05$ ) are given for the degree of heterogeneity shown by each species in its use of nine major habitats. Tabled entries indicate whether occurrence rate in each individual habitat was statistically different from random at  $P < 0.1$  (Hobbs and Bowden 1982); H = higher than expected occurrence rate, L = lower; a minus sign (-) indicates no significant difference from random; habitats: Fi = field and pasture; Ac = acahual; LD = low, semideciduous forest; MD = medium-height, semideciduous forest; MM = medium-height semievergreen forest; TM = tall semievergreen forest; Mo = moist tropical forest; Fl = mangrove and seasonally flooded forest; CS = native coastal scrub.

Species	Overall $\chi^2$	Habitat								
		Fi	Ac	LD	MD	MM	TM	Mo	Fl	CS
Early successional specialists										
Yellow Warbler	47.9****	-	-	-	L	L	L	L	-	-
Yellow-throated Warbler	37.4****	H	-	L	L	L	L	L	-	-
Yellow-rumped Warbler	23.3****	-	L	-	L	-	L	L	-	-
Common Yellowthroat	100.1****	H	-	-	-	L	L	L	-	-
Indigo Bunting	62.8****	H	H	-	-	L	L	-	L	-
Rose-breasted Grosbeak	24.4****	H	-	-	-	-	L	L	L	L
Generalists										
Least Flycatcher	15.4 (ns)	-	-	-	-	-	-	-	-	-
Gray Catbird	25.2****	-	-	-	L	-	-	-	-	-
White-eyed Vireo	31.0****	-	-	-	-	-	-	-	-	-
Northern Parula Warbler	8.7 (ns)	-	-	-	-	-	-	-	-	-
Magnolia Warbler	107.8****	-	-	L	-	H	H	-	L	L
Forest generalists										
Black-throated Green Warbler	48.1****	-	L	-	H	-	-	-	-	L
American Redstart	78.5****	L	-	-	-	-	-	-	-	L
Ovenbird	26.8****	L	-	-	-	-	-	-	-	L
Forest specialists										
Wood Thrush	65.0****	L	L	L	L	-	H	H	L	L
Yellow-throated Vireo	22.6****	L	L	L	-	-	H	L	L	L
Blue-winged Warbler	52.2****	L	L	L	-	-	-	-	-	L
Black-and-white Warbler	63.2****	L	L	-	-	-	H	-	L	L
Kentucky Warbler	52.6****	L	L	L	L	-	H	H	L	L
Hooded Warbler	228.3****	L	-	-	-	H	H	L	L	L
Extreme habitat specialists										
Wilson's Warbler	73.6****	L	L	L	L	L	L	H	L	L
Northern Waterthrush	86.8****	-	-	-	-	L	-	L	H	-
Blue Grosbeak	20.6**	L	L	L	-	L	L	L	L	H

significantly more frequently encountered in fields or pastures, or in early old fields, than in any of several types of forest. Another group of five species (Least Flycatcher, Gray Catbird, White-eyed Vireo, Northern Parula Warbler, Magnolia Warbler) occurred across essentially the entire successional spectrum, and were found in semi-deciduous, semievergreen, and evergreen forest. Although the habitat distribution of three of the five species with the weakest tendency to specialize in their habitat use is not completely random, occurrences in any one habitat type are not substantially higher or lower than would be expected by chance. These five migratory species may be termed "habitat generalists."

Three species (American Redstart, Black-throated Green Warbler, Ovenbird) tended not to occur in the highly disturbed vegetation of milpas and pastures, but were found with similar frequency across the entire remaining spectrum of wooded habitats, regardless of stature or moisture regime. Such species may be termed "forest generalists."

A sizeable group of migrants (six species: Wood Thrush, Yellow-throated Vireo, Blue-winged Warbler, Black-and-white Warbler, Kentucky Warbler, Hooded Warbler) can be categorized as "forest specialists." These species were detected with significantly higher frequency than expected in mature forest, and with significantly lower than expected frequency in early successional habitats (Table 6). All six species occurred more frequently in semievergreen and/or evergreen forest than in semideciduous forest.

Finally, three species (Northern Waterthrush, Blue Grosbeak, Wilson's Warbler) were closely associated with a single habitat type (inundated woodland, coastal scrub, and moist evergreen forest, respectively), within the portion of the Yucatan that was studied. Such species, which may be termed "extreme habitat specialists," rarely or never were encountered in any other habitat.

#### MIST-NETTING RESULTS

Mist nets were operated at 15 sites for a total of 2,128 net mornings (11,526 net hr). In all, 144 bird species were captured, of which 38 (26.4%) were nearctic migrants. The following discussion focusses on the use by migrants and resident species of the successional continuum of habitats typical of the zone of semievergreen forest in

northern and central Quintana Roo, where all of our mist netting was conducted.

*Active pastures and recently abandoned agricultural fields.* These brushy field habitats, which were sampled at five locations (Table 2), yielded 72 species, of which 20 (27.8%) were migrants. The total capture rate (CR =  $100 \times$  number of individuals captured/net/morning) was high in pastures and fields (CR = 247.7), but the sample was numerically dominated by only a few abundant species. The two most frequently captured species, the Indigo Bunting (a migrant) and White-collared Seedeater (a resident), together accounted for 30.4% of all captures in open habitats (Table 3a). Both species occur in flocks during winter. As was true for point counts, migrants made up a disproportionate number (9 of 24 = 37.5%) of the species that were most frequently netted in open habitats. In order of decreasing abundance the most frequently captured migrants in open fields were Indigo Bunting, Common Yellowthroat, Gray Catbird, White-eyed Vireo, Least Flycatcher, Painted Bunting, Magnolia Warbler, and Yellow-breasted Chat.

*Brushy old fields (acahuales).* This structurally and floristically heterogeneous habitat was sampled at two sites (Table 2) that were 5–7 years into abandonment when netted. At this stage, regenerating pastures and old fields in central Quintana Roo typically contain patchy stands of *Cecropia* and other fast-growing trees, areas of shrubs and tall bracken fern (*Pteridium*), and remnant patches of the grasses and weeds typical of earlier successional stages. A total of 328 net mornings in acahuales yielded 87 bird species, of which 22 (25.3%) were nearctic migrants. The total capture rate was high (CR = 113.3), though lower than in open fields. Numerical dominance was also relatively high, and the two commonest species (the migratory Gray Catbird and the resident Blue Bunting) accounted for 23.0% of all individuals captured (Table 3b). Ten of the 27 most frequently captured species (35.2%) in brushy old fields were migrants. In order of decreasing abundance, the most frequently netted migratory species were the Gray Catbird, White-eyed Vireo, Wood Thrush, Common Yellowthroat, Hooded Warbler, Least Flycatcher, Magnolia Warbler, and Indigo Bunting.

*Medium-stature semievergreen forest.* This widely distributed forest type was sampled at five locations (Table 1). Interviews with local resi-

dents and comparisons with other stands of known age indicated that none of the forests we studied was less than 30 years old, and most were more than 50 years old. A netting effort of 1,096 net mornings in semievergreen forest yielded relatively few captures ( $CR = 40.5$ ), and revealed the presence of only 54 species. To a degree, the low capture rate in this habitat reflected the fact some sites were netted monthly or bimonthly for part of the study period. Net avoidance may have reduced the success rate per net per morning in such instances (Karr 1981a), but even if data for frequently sampled plots were disregarded, the capture rate for maturing forest was only a fraction of that in earlier successional stages.

Migrants made up a relatively high percentage (25.4%) of the species netted in semievergreen forest, and comprised an even higher proportion of the most frequently netted species: seven of the 18 commonest species in our samples (38.9%) were migrants. Dominance was unexpectedly high in this habitat, and the two most frequently netted species, both residents (Red-throated Ant-Tanager and Ruddy Woodcreeper), contributed 44.2% of all captures (Table 3c). The most frequently netted nearctic migrants in semievergreen forest were the Hooded Warbler, Ovenbird, Wood Thrush, Kentucky Warbler, Black-and-white Warbler, White-eyed Vireo, and Magnolia Warbler.

*Effect of total captures on apparent species richness.* Because different numbers of individuals were captured in each habitat, observed between-habitat differences in the total species richness of the nettable portion of the community, and in the relative abundance of migrant species, could be interpreted as artifacts of different sample size (Sanders 1968; Simberloff 1972, 1978). To test this possibility, the statistical technique of rarefaction was applied to the mist-net capture data, using the program SIM (Simberloff 1978). When mist-net capture data for open fields, early acahuals, mid-stage acahuals, and semievergreen forest were rarefied to a common number of captures per site ( $n = 100$ ), the predicted number of migratory species per sample of captures did not differ significantly ( $P > 0.05$ ) among the four successional stages ( $\bar{x} = 13.5$ ; range = 11.2–14.2).

A second rarefaction analysis helped to clarify the relationship between total species richness in the ground/shrub stratum and the successional

maturity of habitats. This analysis was restricted to three habitat categories: pastures and fields less than 1 year into abandonment (473 captures; 67 species), acahuals 5–7 years into abandonment (556 captures; 74 species), and medium-stature semievergreen forest (662 captures; 54 species). Rarefaction of these data (Table 7; Fig. 4) revealed that any given number of captures would be expected to include essentially the same number of species in pastures as in acahuals. However, for mature forest, the predicted number of species for a given number of captures was approximately 30% lower than in earlier successional stages. This result holds even for fairly large hypothetical samples (300–500 captures). As noted earlier, mist-net samples in forest inevitably under-sample species that are active mainly in the canopy, and the total number of species in a tropical forest might be substantially greater than in successional habitats. Nevertheless, the mist-netting data reinforce the point made earlier on the basis of point survey results: Secondary vegetation in the Yucatan is used by a diverse assemblage of both resident and migratory species.

## DISCUSSION

### DIVERSITY AND ABUNDANCE OF NEARCTIC MIGRANTS IN THE YUCATAN PENINSULA

Data from point counts and mist-net surveys agreed in showing that overwintering nearctic migrants were both diverse and common in most habitats throughout the Yucatan. Despite the very different sampling biases of the two methods, the proportion of migrant species and individuals was similar in point counts and mist-net samples of a given habitat type. However, the rank order of individual species abundances varied substantially between the two sampling methods (Table 3). Results from both survey methods suggest that in most habitats a disproportionately large fraction of the most frequently detected (or netted) species was migrants.

These results differ in some major respects from those reported by Tramer (1974), who surveyed migrants and residents in nine plots in the northwestern Yucatan. Although the proportion of migrant species recorded by Tramer (7–40%; median = 28%) was similar to the values determined in the present study, he reported that migrants made up only 3–36% (median = 14%) of the

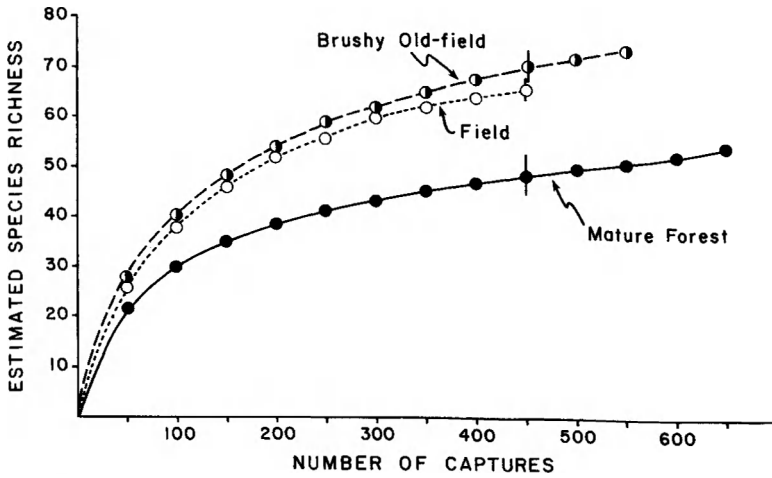


FIGURE 4. Rarefaction curves for mist-net data, showing the rate at which species richness increases as a function of the number of captures. The vertical lines at  $n = 450$  captures represent 2 standard deviations of the projected mean species richness.

individuals in the communities he surveyed. That is, Tramer concluded that the average migrant species was less abundant than the average resident. This disparity between Tramer's results and ours is difficult to reconcile, even allowing for the fact that our use of playbacks slightly increased the proportion of migrants to residents in our point surveys (see above). Tramer's conclusions were based on censuses of a limited number of plots, most of which were too small (<10 ha) to justify general conclusions on relative abundance (Waide et al. 1980). Apparently, numerous identification problems also confounded some of Tramer's (1974) results (Austin et al. 1981).

TABLE 7. Rarefaction analysis of mist-net capture data for three major successional habitats in Quintana Roo. Entries are predicted means (and standard deviations) of species as a function of the total number of captures ( $n$ ). For any given subsample size, species richness is significantly lower in mature forest than in fields or acahuales.

Individuals in subsample	Predicted species richness		
	Field ( $n = 473$ )	Acahual ( $n = 556$ )	Forest ( $n = 662$ )
50	25.9 (2.6)	27.8 (2.6)	21.6 (2.3)
100	38.4 (2.9)	40.1 (3.0)	29.6 (2.6)
200	52.2 (2.7)	54.0 (3.0)	38.2 (2.5)
300	59.7 (2.2)	62.3 (2.6)	43.4 (2.4)
400	64.5 (1.4)	67.9 (2.1)	47.2 (2.1)
500	—	72.1 (1.3)	50.3 (1.7)
600	—	—	51.6 (1.4)

The results of the present study are in closer accord with those reported by Waide (1980), based on his mist netting of six plots in southeastern Campeche. There, the median percentage of new captures contributed by migrants was 50% (range = 32–57%). When Waide's data for three early successional sites are pooled, migrants made up 20/65 (30.8%) of the species he captured, a proportion that is similar to the 20/72 (27.8%) we found for similar disturbed habitats in Quintana Roo. Waide's (1980) data indicate that in southeastern Campeche migratory species made up 14/43 (32.6%) of the species netted in two areas of maturing semievergreen forest, as compared with 14/55 (25.4%) for the same type of forest in Quintana Roo. The slightly lower proportion of migrant species in the two Quintana Roo habitats can reasonably be attributed to our greater sampling intensity in the latter state (189 net days vs. Waide's 141 net days in early successional fields; 1,096 net days vs. Waide's 136 net days in maturing semievergreen forest). With increasing netting effort, the number of resident species continues to increase as more and more rare species are added (Fig. 4), whereas the number of migrant species captured in a given habitat quickly approaches an asymptote.

In maturing semievergreen forest, the proportion of captured individuals that belonged to migratory species was similar in Quintana Roo (32.9%) and Campeche (36.7%), but in early successional habitats the proportion of migrants was much higher in Campeche (55.1% vs. 38.8%).



This difference is almost entirely due to the extraordinary abundance of one migratory species, the Indigo Bunting, in the three old fields sampled by Waide in Campeche. This patchily distributed (Rappole et al. 1983; pers. observ.), flocking species accounted for 60.5% of the migrants Waide (1980) captured at his three early successional sites. Although the Indigo Bunting was also the single most abundant migrant we netted in open fields in Quintana Roo, there the species accounted for only 124/287 (43.1%) of the total migrants captured. Migrants other than Indigo Buntings made up similar proportions of the total captures in the field community in Campeche (32.6%) and Quintana Roo (30.1%). Extreme seasonal dominance of tropical bird communities by a single migrant species is unusual, but not unique. As an example, Emlen (1977) reported that Palm Warblers made up 77% of the total winter bird community in open pine woodlands in the Bahamas.

Summarizing, the results of the present study are in basic agreement with those of Waide (1980) indicating that overwintering birds make up about one-third of the individuals from netted samples in Yucatan forests, and up to one-half or more of the individuals netted in secondary habitats. The migrants captured in secondary habitats are dominated by one species, the Indigo Bunting.

#### HABITAT ASSOCIATIONS OF MIGRANTS AND RESIDENTS

In the Yucatan Peninsula a few overwintering migrants (e.g., White-eyed Vireo, Magnolia Warbler) occurred across essentially the full range of successional habitats, although they were not encountered with equal frequency in all vegetation types. Other migrants occurred at much higher than expected frequencies in open fields and brushy successional habitats (e.g., Common Yellowthroat, Yellow-breasted Chat, Indigo Bunting, Rose-breasted Grosbeak), or in closed-canopy forest (e.g., Wood Thrush, Kentucky Warbler, Black-and-white Warbler, American Redstart). As a group, migrants were no more strongly associated with disturbed habitats than were residents, but this was not because migrants avoided secondary vegetation. Instead, both migrants and residents occurred at relatively high frequency in early successional vegetation (cf., Willis 1980). The co-occurrence of forest-adapted and field-adapted species in secondary vegetation produced very high local species richness and oc-

currence rates in samples from these disturbed habitats. However, many migratory species were more frequent in one or another class of tropical forest (or in forest generally) than in pastures and early old fields (Tables 3, 6). Despite this fact, no migratory species was restricted to old-growth forest.

In agreement with previous studies of breeding bird communities in eastern North America (Willson 1974, May 1982, Mehlhop and Lynch 1986) overwintering migrants appear to show a discontinuity in habitat use between the shrub stage of succession (when the tree canopy has not yet closed) and closed-canopy forest, regardless of its stature. As has also been documented during the breeding season (Kricher 1973, Mehlhop and Lynch 1986), some migrants whose main winter habitat is forest (e.g., Black-and-white Warbler, Black-throated Green Warbler, Ovenbird, Worm-eating Warbler, Magnolia Warbler) were also regularly encountered in early successional habitats. Although some of these species (e.g., Black-throated Green Warbler) tended to be restricted to hedge rows and remnant trees within areas of early secondary vegetation, most were also observed to forage in low, dense grasses and weedy vegetation. Whether some individuals of such species actually restrict their winter activity to early successional vegetation is an important question whose answer will require detailed studies of known individuals through the winter.

In the Yucatan, overwintering forest-associated migrant species also commonly made use of early successional habitats, but migratory species that were most frequent in old fields tended not to utilize closed-canopy forest. Of nine migrant species whose main winter habitat in the Yucatan was either natural scrub or early successional vegetation, six (Yellow-throated Warbler, Yellow Warbler, Common Yellowthroat, Indigo Bunting, Painted Bunting, Rose-breasted Grosbeak) were rarely or never observed in mature forest (Table 3, Fig. 2).

Residents and migrants did not differ significantly in their tendency to specialize on a particular successional stage of vegetation, but forest-dwelling resident species were more likely than forest-dwelling migrants to occur at higher than expected frequency in a particular forest type (Fig. 3). Half of the 18 migratory species that occurred frequently in at least one of three widespread forest types (medium-stature semievergreen, tall

TABLE 8. Summary of correlation analysis of mist-net capture rates vs. occurrence rates in point counts. Tabled values are Spearman's rank correlation coefficients and the total number of species recorded in each habitat. Significance levels: \*\* =  $P < 0.01$ ; \* =  $P < 0.05$ ; ns =  $P > 0.05$ .

Habitat	Migrants	Residents
Fields and pastures	0.49* ( $n = 21$ )	0.20 ns ( $n = 79$ )
Brushy old fields	0.49** ( $n = 26$ )	-0.02 ns ( $n = 83$ )
Medium semievergreen forest	0.48* ( $n = 20$ )	0.21 ns ( $n = 88$ )

semievergreen, medium semideciduous) were classed as forest generalists, i.e., they occurred at approximately expected frequencies in all three forest types. Eight additional migratory species showed a moderate degree of concentration in one forest type, but only one species (Indigo Bunting) was categorized as highly specialized on one of the three forest types. The latter species is, in fact, mainly associated with brushy old fields (Table 3), but on a few occasions it was observed in semideciduous woodlands.

Forest-dwelling residents, on the other hand, tended to exhibit a well-defined tendency to occur at higher than expected frequency in medium-height or tall semievergreen forest. More than two-thirds (50 of 70) of the most common forest-associated resident species were classified as either moderately or markedly specialized on one of the three forest types. The proportion of forest specialists would have been higher if there had been sufficient census data to include the humid forests of the southern Yucatan in the formal analysis. This region harbors a number of resident species that do not range north of southernmost Quintana Roo and Campeche (Paynter 1955, Lopez-Ornat et al. 1989). The ranges of most such species are centered in the wet lowland forests of Middle America, and even semievergreen forest is probably suboptimal habitat for them; semideciduous forest is altogether avoided. Several nearctic migrants (Wood Thrush, Gray Catbird, Magnolia Warbler, Kentucky Warbler) occurred with higher frequency in the humid evergreen forests of the southern Yucatan than in the semievergreen or semideciduous forests to the north, although larger sample sizes are needed to confirm these trends.

#### COMPARISON OF POINT COUNTS AND MIST-NET SURVEYS

There was no significant correlation between the rank order of occurrence rates of individual resident species as estimated by point counts vs. mist-net surveys in any of the three successional habitats where comparisons could be made (Table 8). For migrants, Spearman's rank correlation coefficients for point-count data vs. mist-net survey results were statistically significant ( $r_s = 0.48-0.49$ ;  $P < 0.05$ ) but the coefficients of determination (0.23-0.24) were relatively small. For surveys of entire bird communities, point counts appear to be superior to mist-netting surveys, both because of the latter method's biases against species that are large, or that forage high in the canopy, and because mist netting is relatively costly in time and labor. As a concrete example, a 3-day bout of operating 20-30 mist nets in Quintana Roo, plus the additional time needed to cut lanes, and to set up and take down the nets, typically produced a strongly biased sample of 35-100 individual birds. By comparison, four mornings of point counts would be expected to yield 32-64 individual surveys, depending on logistics and weather. This translates to 280-560 individual bird contacts per 4-day period.

Even at the level of individual species, the results of point counts and mist-net surveys are not generally related by a constant proportionality factor across different habitats. For example, the Magnolia Warbler, a generalist species with respect to the successional maturity of vegetation, occurred in 28% of our point counts in fields and pastures, 36% of the counts in acahuales, and 57% of the points within forest (Table 3). The actual number of individual Magnolia Warblers per point count where the species was observed was 1.26 ( $n = 197$  occurrences for 1982 and 1983), a figure which did not vary significantly with habitat type. This suggests that the frequency of occurrence should be a good index to the actual abundance of this species. Assuming this to be the case, Magnolia Warblers were about twice as common in forest as in open fields. However, because the Magnolia Warbler tends to forage in the canopy of whatever type of vegetation it inhabits, the species is much less subject to capture by nets in tall forest than in low scrub; relative capture rates in fields, acahuales, and forest were 5, 5, and 1, respectively (Table 3). In the absence of other information, these mist-net-

ting data might cause one to conclude that Magnolia Warbler strongly "prefers" disturbed habitats to forest, which is precisely the reverse of the pattern revealed by point counts.

An even more extreme example of the inappropriateness of mist-netting data as an index of abundance for canopy species is provided by the American Redstart. This insect-hawking canopy specialist was detected at 45% of 408 survey points (mean number of individuals per occurrence = 1.17) in semievergreen forest. However, redstarts very rarely forage close to the forest floor, and they were never netted in nearly 6,000 net hours of mist netting in closed-canopy forest (Table 3). On the other hand, the American Redstart occurs uncommonly in brushy old fields (8% of point counts), and even in milpas (2% of point counts), and individuals that forage in the "canopy" of these low-stature habitats are occasionally captured by standard 2-m-high mist nets. Capture rates for redstarts in acahuales (CR = 2) and in fields (CR = 1), though quite low, were higher than in forest (CR = 0), where the species is one of the most frequently observed migrants.

One category of birds for which mist netting might be predicted a priori to yield better indices of abundance than point counts consists of small, flocking, ground-foraging species. Among the nearctic migrants in the Yucatan, the most obvious example is the Indigo Bunting, which had a capture rate almost four times as high as the next most frequently netted migrant in fields and pastures, but which ranked only fourth in the frequency of detection in point counts (Table 3). A reasonable interpretation of this result is that mist netting is more effective than point counts at tallying absolute numbers of flocking species within a designated area. However, as R. Greenberg has suggested (pers. comm.), the density of wide-ranging, nonterritorial, flocking species (e.g., Indigo Bunting) may be substantially overestimated by mist netting, because the number of flock members that eventually pass through a given small area (e.g., a grid of mist nets) will be higher than the number of equivalent territorial individuals that could permanently reside within the same area. In the present study, the only species for which mist-net data clearly appeared to provide better indices of abundance than point counts were fairly small, secretive, nonflocking taxa that inhabited dense low-stature plant com-

munities. Among the few nearctic migrants in this category were the Gray Catbird and Yellow-breasted Chat.

Point counts are also subject to bias, but few species were revealed by mist-netting that were not also detected in point counts. The reverse was not true, and many large species and canopy specialists were rarely or never netted. Interspecific differences in detectability exist (e.g., Whitcomb et al. 1981), and point counts do not necessarily provide a reliable basis for estimating absolute (as opposed to relative) densities, nor for comparing different communities whose constituent species differ greatly in detectability (DeSante 1981, Verner 1985, Hutto et al. 1986).

#### WITHIN-SPECIES HABITAT DIFFERENCES

Although each species has been analyzed as a single entity in the foregoing assessment of habitat use, at least some migratory species show important age- and sex-related differences in habitat occurrence during the nonbreeding season. In perhaps the best-documented case of this sort, Lynch et al. (1985) showed that in the Yucatan, overwintering male and female Hooded Warblers defend nonoverlapping feeding territories that differ dramatically in vegetation structure. Males were found to be most common in closed-canopy forest with relatively open understory; females tended to occur in lower, but more dense, woody vegetation, conditions that are most often seen in acahuales and young secondary forest. Subsequent field studies have confirmed this pattern for the Hooded Warbler, and have revealed similar, if less striking, modes of habitat separation based on age or sex, or both, in several other species of small, insectivorous migrants in the Yucatan region (R. Greenberg, A. Lopez-Ornat, and J. F. Lynch, unpubl.). Whether such local differentiation might in turn produce regional gradients in the distribution of sex and age classes has not yet been determined, although preliminary results suggest that the sex ratio of Hooded Warbler may be biased toward males in the heavily forested eastern portion of the Yucatan (Lynch et al. 1985).

#### FUTURE PROSPECTS FOR MIGRATORY BIRDS IN THE YUCATAN PENINSULA

Over the past two millennia, the Yucatan Peninsula has undergone several cycles of widespread human disturbance, followed by exten-

sive regeneration of native vegetation. Although Mexico's present rapid pace of population growth and economic development has thus far spared some parts of the peninsula, ever-increasing pressures for higher production of lumber, livestock, and food crops are threatening remaining extensive tracts of tropical forest. Which of the many possible scenarios for economic development actually come to pass in the Yucatan will have profound consequences for migratory birds. If, for example, future disturbance of the tropical forest resulting in a mosaic of remnant woodlands, small and temporary agricultural plots, and regenerating old fields, as has been the case historically in much of the area, prospects are relatively good for those migratory species that can make use of low-stature disturbed or native vegetation. Examples include species that actually appear to prefer such habitats (e.g., Common Yellowthroat, Yellow-breasted Chat, Indigo Bunting, Painted Bunting, Rose-breasted Grosbeak), as well as ecological generalists that occur with similar frequencies in both forest and shrub-field habitats (e.g., Gray Catbird, White-eyed Vireo, Magnolia Warbler, Northern Parula Warbler). However, this is not to say that some species in the latter category might not undergo substantial density reductions if most mature forest were to be replaced by brushy second growth. As an example, if one assumes that occurrence rates in point surveys are proportional to local densities for a given species, our data suggest that a landscape consisting of milpas and acahuals might support only one-half to two-thirds the number of Magnolia Warblers as a pristine forested landscape (Table 3). Still, fairly generalized migrants such as the Magnolia Warbler probably would maintain a wintering population in the Yucatan even if the area devoted to traditional slash-and-burn agriculture were to expand considerably.

At the other extreme, migrants that rely on (or at least occur most frequently in) moist, closed-canopy forest (e.g., Wood Thrush, Yellow-throated Vireo, Kentucky Warbler) would be expected to suffer severe setbacks if wholesale destruction or major disturbance of the peninsula's remaining forests were to take place, even if some landscape diversity were to be maintained in the form of hedgerows and successional woodlots. Again, basing an estimate on point survey data, the change from a forested landscape to one covered by milpas and early-stage

acahuals might reduce the regional population of a forest-dependent species such as the Kentucky Warbler by as much as 80–100%, depending mainly on how much the fallow cycle is shortened. Once secondary succession has produced a sapling-stage forest, which in the Yucatan requires 10–15 years (pers. observ.), most forest-dependent migrants are able to invade a tract and maintain reasonably high to very high densities. However, as the human population in a region increases, there is a tendency for the fallow period to become shortened, sometimes to less than 10 years. The latter pattern has already occurred in heavily settled portions of Yucatan and Campeche states.

For most overwintering migratory passerines, the single most critical feature of the Yucatan's future landscape will be the extent to which some form of woody vegetation, even if it is successional scrub or young woodland, persists or is allowed to regenerate. The present study has demonstrated that secondary habitats are routinely used by many overwintering migrants, including some species (e.g., Least Flycatcher, Hooded Warbler, Magnolia Warbler, Black-and-white Warbler, American Redstart) normally restricted as breeders to sizeable tracts of mature forest. Despite the fact that winter densities of some of these species appear to be substantially lower in successional scrub than in mature tropical forest (based on point-count data), secondary vegetation constitutes an important reservoir of winter habitat for the majority of nearctic migrants in the Yucatan and, one suspects, elsewhere in Middle America. The ability of most migratory species to utilize other vegetation types in addition to mature forest may help to explain the otherwise anomalous observation that most forest-associated migrants do not appear to have suffered global declines in abundance during the 1960s and 1970s (Robbins et al. 1986), even in the face of unprecedented destruction of primary forest in the northern neotropics. However, more recent continent-wide population data (Robbins et al., in press) suggest that these same migratory species have tended to decline over the last decade (1978–1987). Population trends in neotropical migrants, particularly species that overwinter in tropical forest, should be carefully monitored for evidence of continued decline.

The fact that many forest-associated migrants in the Yucatan region also occur in woody second growth does not, of course, mean that they are

immune to the negative effects of tropical deforestation. Where forest is permanently converted to overgrazed pasture or intensively farmed fields, as is now the case in much of Middle America (e.g., Sader and Joyce 1988), one would predict that populations of most species of migrants will experience local dislocations or overall population reductions, or both (cf., Rap-pole and Morton 1985). To the extent that the future economic development of Middle America and the northern Caribbean entails the complete suppression of native woody vegetation in favor of cattle pasture and food crops, species-wide declines are expected to occur in breeding populations of migratory birds, particularly in species that are (1) restricted (or nearly so) to forest during the nonbreeding season, and (2) limited in their winter distributions to Middle America and the Caribbean islands, where deforestation is proceeding at the most rapid rate. Should complete deforestation occur throughout the Yucatan (admittedly an unlikely prospect), only those few migratory species that under pristine conditions were associated with sparsely vegetated beach strands or savanna (e.g., Yellow-rumped Warbler, Palm Warbler, Blue Grosbeak, Indigo Bunting) would be expected to thrive. A combination of quantitative studies of bird densities in a range of natural and disturbed habitats, together with a regional assessment of vegetational cover, will be necessary if we are to track and project the impact of habitat change on individual migratory species in sufficient detail (e.g., Green et al. 1988).

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APPENDIX I. Characteristics of vegetation types that were surveyed in the Yucatan Peninsula. “Phases” are subcategories of a given vegetation type, based on canopy height (CHT). Categories are listed in order of increasing canopy height, with drier formations before inundated formations.

APPENDIX I. Continued.

- but which almost always contained abundant native grasses, herbs, shrubs, and regenerating trees. In most areas of the Yucatan that were studied, at least a few living and dead canopy trees were present in open fields as scattered emergents. One phase was distinguished: Open field (CHT 0–2 m).
2. *Brushy old-field* (“*acahual*”). Dense secondary scrub that develops within 2–3 years of abandonment of pasture or cropland. The canopy tended to be highly patchy and irregular in stature, but its height was generally less than 3 m. Scattered emergent clumps of fast-growing pioneer trees (e.g., *Cecropia obtusifolia*) or stump sprouts of previous canopy trees were typically present. Acahuales taller than about 3 m graded into the young serial stages of various forest types, depending on the regional climate and on local edaphic conditions. One phase was distinguished: Brushy old field (CHT 1–3 m).
  3. *Native coastal scrub*. A heterogeneous natural assemblage that was restricted to a narrow, discontinuous strip along the coast of the peninsula. Major components were salt-tolerant grasses, herbs, and shrubs, together with emergent palms (e.g., *Coco nucifera*, *Thrinax radiata*) and stunted individuals of certain species of trees from the neighboring forest communities (e.g., *Bursera simaruba*, *Metopium brownei*). Substrate was typically loose calcareous sand, occasionally with outcrops of limestone. The canopy was low and uneven, and was commonly interrupted by areas of grass and herbs, or by areas of exposed substrate. Along the dry northern coast of the peninsula, the native scrub featured emergent cacti (Cactaceae spp.) and agaves (*Agave* spp.). One phase was distinguished: Native coastal scrub (CHT 1–3 m).
  4. *Savanna*. A frequently inundated grassland that typically featured combinations of sawgrass (*Cladium jamaicense*) and other grasses, cattail (*Typha domingensis*), and sedges, with scattered clumps or individuals of emergent shrubs, palms, and trees. Extensive savannas flanked freshwater wetlands in east-central Quintana Roo. One phase was distinguished: Savanna (CHT 1–3 m).
  5. *Seasonally inundated forest*. This low, patchily distributed forest type typically occurred at the fringes of savannas and within shallow, seasonally flooded depressions. Surface conditions varied from flooded to extremely dry, depending on season and year. The canopy trees tended to be deciduous, and were dominated by Leguminosae. Characteristic species included *Bucida buceras*, *Haematoxylon campechianum*, *Dalbergia glabra*, and *Pithecellobium albicans*. Two phases were distinguished: Low (2–3 m), Medium-stature (4–10 m).
  6. *Mangrove forest*. A specialized association that occurred in permanently inundated or mucky soils in a narrow, discontinuous fringe along the Gulf and Caribbean coasts. Canopy height and tree density varied markedly in response to local conditions, especially in the most widespread species, red mangrove (*Rhizophora mangle*). Other characteristic trees included black mangrove (*Avicennia germinans*) and buttonwood (*Conocarpus erectus*).

1. *Agricultural fields and pastures*. Highly disturbed, low-stature communities that were often dominated by exotic cultivated crops and forage grasses,

APPENDIX I. Continued.

- tus*). Two phases were recognized: Low (1–3 m), Medium-stature (4–10 m).
7. *Semideciduous forest*. Included various forms of the “Selva Subcaducifolia” of Miranda (1958). Characterized by the presence of 50–75% deciduous species, this diverse forest type was widespread in areas of Yucatan, Campeche, and western Quintana Roo that received 700–1,100 mm of annual rainfall. Characteristic trees included *Bursera simaruba*, *Lonchocarpus* spp., *Lysiloma latisiliqua*, *Metopium brownei*, *Senna racemosa*, and *Vitex gaumeri*. Three phases were distinguished: Low (CHT 2–3 m), Medium-stature (CHT 4–10 m), Tall (CHT 11–20 m).
  8. *Semievergreen forest*. Included all but the tallest phases of the “Selva Subperennifolia” of Miranda (1958). In this diverse association, which occurred in areas of Quintana Roo and Campeche where annual precipitation was 1,100–1,400 mm, about 50–75% of the plant species were evergreen. Characteristic tree species included *Brosimum alicastrum*, *Manilkara zapota*, *Metopium brownei*, *Psidium sartorianum*, *Swietenia macrophylla*, and *Vitex gaumeri*. Three phases were distinguished: Low (CHT 2–3 m), Medium-stature (CHT 4–10 m), Tall (CHT 11–20 m).

APPENDIX I. Continued.

9. *Moist forest*. Includes the tallest, floristically richest phase of the “Selva Perennifolia” (Miranda 1958), which occurred in southern Quintana Roo and adjacent Campeche, as well as the tall, essentially evergreen forests of central Belize, northern Guatemala, and northern Chiapas. Dominant tree species were similar to those in semievergreen forest, but they attained greater stature in moist forest. Rainfall in areas supporting moist forest ranged from about 1,200–2,000 mm. Four phases were distinguished: Low (CHT 2–3 m), Medium-stature (CHT 4–10 m), Tall (CHT 11–20 m), Very tall (CHT 21–30 m).
10. *Floodplain forest*. This association occurred in wet alluvial soils along permanent river systems in Belize and northern Chiapas. The understory was typically species-poor and was structurally modified due to frequent scouring by flood waters, but canopy trees attained considerable stature. Although various height classes of floodplain forest occurred in the study region, only one phase was censused: Tall floodplain forest (CHT 11–20 m).

APPENDIX II. List of migratory and resident landbirds encountered in point counts (PC) and mist-net surveys (MN) on the Yucatan Peninsula 1982–1987. Scientific and common names, and the order of families follow the AOU (1983) check-list. Within families, genera are arranged alphabetically, as are common names within genera. List does not include aquatic species, aerial foragers not seen using vegetation, species casually observed outside of formal point counts, or species observed only during summer. Migratory species marked with an asterisk (\*) were transients observed only during fall and/or spring migration.

Species	How detected	
	PC	MN
A. Nearctic migrants		
Falconidae		
1. American Kestrel ( <i>Falco sparverius</i> )	X	
Trochilidae		
2. Ruby-throated Hummingbird ( <i>Archilochus colubris</i> )	X	
Picidae		
3. Yellow-bellied Sapsucker ( <i>Sphyrapicus varius</i> )		X
Tyrannidae		
Tyranninae		
4. Least Flycatcher ( <i>Empidonax minimus</i> )	X	X
5. <i>Empidonax</i> sp.		X
6. Great Crested Flycatcher ( <i>Myiarchus crinitus</i> )	X	X
Muscicapidae		
Turdinae		
*7. Gray-cheeked Thrush ( <i>Catharus minimus</i> )		X
8. Swainson's Thrush ( <i>C. ustulatus</i> )		X
*9. Veery ( <i>C. fuscescens</i> )		X
10. Wood Thrush ( <i>Hylocichla mustelina</i> )	X	X



## APPENDIX II. Continued.

A. Nearctic migrants	Species	How detected	
		PC	MN
<b>Mimidae</b>			
	11. Gray Catbird ( <i>Dumatella carolinensis</i> )	X	X
<b>Vireonidae</b>			
	*12. Red-eyed Vireo ( <i>Vireo olivaceus</i> )		X
	13. White-eyed Vireo ( <i>V. griseus</i> )	X	X
	14. Yellow-throated Vireo ( <i>V. flavifrons</i> )	X	X
<b>Emberizidae</b>			
<b>Parulinae</b>			
	15. Black-throated Blue Warbler ( <i>Dendroica caerulescens</i> )		X
	16. Black-throated Green Warbler ( <i>D. virens</i> )	X	
	17. Cape May Warbler ( <i>D. tigrina</i> )	X	
	*18. Chestnut-sided Warbler ( <i>D. pensylvanica</i> )		X
	19. Magnolia Warbler ( <i>D. magnolia</i> )	X	X
	20. Palm Warbler ( <i>D. palmarum</i> )	X	X
	21. Prairie Warbler ( <i>D. discolor</i> )	X	
	22. Yellow Warbler ( <i>D. petechia</i> )—migratory races	X	X
	23. Yellow-throated Warbler ( <i>D. dominica</i> )	X	X
	24. Yellow-rumped Warbler ( <i>D. coronata</i> )	X	X
	25. Common Yellowthroat ( <i>Geothlypis trichas</i> )	X	X
	26. Worm-eating Warbler ( <i>Helmitheros vermivorus</i> )	X	X
	27. Yellow-breasted Chat ( <i>Icteria virens</i> )		X
	28. Swainson's Warbler ( <i>Limnothlypis swainsonii</i> )	X	X
	29. Black-and-white Warbler ( <i>Mniotilta varia</i> )	X	X
	30. Kentucky Warbler ( <i>Oporornis formosus</i> )	X	X
	31. Northern Parula Warbler ( <i>Parula americana</i> )	X	X
	*32. Prothonotary Warbler ( <i>Protonotaria citrea</i> )		X
	33. Louisiana Waterthrush ( <i>Seiurus motacilla</i> )	X	
	34. Northern Waterthrush ( <i>S. noveboracensis</i> )	X	X
	35. Ovenbird ( <i>S. aurocapillus</i> )	X	X
	36. American Redstart ( <i>Setophaga ruticilla</i> )	X	X
	37. Blue-winged Warbler ( <i>Vermivora pinus</i> )	X	X
	38. Golden-winged Warbler ( <i>V. chrysoptera</i> )	X	
	39. Nashville Warbler ( <i>V. ruficapilla</i> )	X	
	*40. Tennessee Warbler ( <i>V. peregrina</i> )		X
	41. Hooded Warbler ( <i>Wilsonia citrina</i> )	X	X
	42. Wilson's Warbler ( <i>W. pusilla</i> )	X	
<b>Thraupinae</b>			
	43. Summer Tanager ( <i>Piranga rubra</i> )	X	X
<b>Cardinalinae</b>			
	44. Blue Grosbeak ( <i>Guiraca caerulea</i> )	X	X
	45. Indigo Bunting ( <i>Passerina cyanea</i> )	X	X
	46. Painted Bunting ( <i>P. ciris</i> )	X	X
	47. Rose-breasted Grosbeak ( <i>Pheucticus ludovicianus</i> )	X	X
<b>Icterinae</b>			
	48. Northern Oriole ( <i>Icterus galbula</i> )	X	
	49. Orchard Oriole ( <i>I. spurius</i> )	X	X

## Summary:

Overwintering species: 43 species  
 Detected only in point surveys: 10 species (23.2%)  
 Detected only by mist-netting: 5 species (11.6%)  
 Detected by both methods: 28 species (65.1%)  
 Fall/spring transients: 6 species  
 Grand total: 49 nearctic migratory species

## APPENDIX II. Continued.

Species	How detected	
	PC	MN
B. Permanent residents		
Tinamidae		
1. Thicket Tinamou ( <i>Crypturellus cinnamomeus</i> )	X	
2. Great Tinamou ( <i>Tinamus major</i> )	X	
Ardeidae		
3. Cattle Egret ( <i>Bubulcus ibis</i> )	X	
4. Green-backed Heron ( <i>Butoroides striatus</i> )	X	
Acciptridae		
5. Bicolored Hawk ( <i>Accipiter bicolor</i> )	X	
6. Gray Hawk ( <i>Buteo nitidus</i> )	X	
7. Roadside Hawk ( <i>B. magnirostris</i> )	X	
8. Zone-tailed Hawk ( <i>B. albonotatus</i> )	X	
9. Common Black Hawk ( <i>Buteogallus anthracinus</i> )	X	
10. Black-shouldered Kite ( <i>Elanus leucurus</i> )	X	
11. Crane Hawk ( <i>Geranospiza caerulescens</i> )	X	
Falconidae		
12. Bat Falcon ( <i>Falco rufigularis</i> )	X	
13. Collared Forest-Falcon ( <i>Micrastur semitorquatus</i> )	X	X
Cuculidae		
14. Plain Chachalaca ( <i>Ortalis vetula</i> )	X	
15. Crested Guan ( <i>Penelope purpurascens</i> )	X	
Phasianidae		
16. Black-throated Bobwhite ( <i>Colinus nigrogularis</i> )	X	
Columbidae		
17. Blue Ground Dove ( <i>Claravis pretiosa</i> )	X	X
18. Pale-vented Pigeon ( <i>Columba cayennensis</i> )	X	
19. Red-billed Pigeon ( <i>C. flavirostris</i> )	X	
20. Scaled Pigeon ( <i>C. speciosa</i> )	X	
21. Short-billed Pigeon ( <i>C. nigrirostris</i> )		X
22. White-crowned Pigeon ( <i>C. leucocephala</i> )	X	
23. Common Ground-Dove ( <i>Columbina passerina</i> )	X	X
24. Ruddy Ground-Dove ( <i>C. tapacoti</i> )	X	X
25. Ruddy Quail-Dove ( <i>Geotrygon talpacoti</i> )	X	X
26. Caribbean Dove ( <i>Leptotila jamaicensis</i> )	X	X
27. Gray-chested Dove ( <i>L. cassinii</i> )	X	X
28. White-tipped Dove ( <i>L. verreauxi</i> )	X	X
29. White-winged Dove ( <i>Zenaida asiatica</i> )	X	
Psittacidae		
30. Red-ored Parrot ( <i>Amazona autumnalis</i> )	X	
31. White-fronted Parrot ( <i>A. albifrons</i> )	X	
32. Yellow-ored Parrot ( <i>A. xantholora</i> )	X	X
33. Olive-throated Parakeet ( <i>Aratinga nana</i> )	X	X
Cuculidae		
34. Groove-billed Ani ( <i>Crotophaga sulcirostris</i> )	X	X
35. Lesser Roadrunner ( <i>Geococcyx velox</i> )	X	
36. Squirrel Cuckoo ( <i>Piaya cayana</i> )	X	X
Strigidae		
37. Mottled Owl ( <i>Ciccaba virgata</i> )	X	
38. Ferruginous Pygmy-Owl ( <i>Glaucidium brasilianum</i> )	X	X
Trochilidae		
39. White-bellied Emerald ( <i>Amazilia candida</i> )	X	X
40. Rufous-tailed Hummingbird ( <i>A. tzacatl</i> )	X	

## APPENDIX II. Continued.

Species	How detected	
	PC	MN
<b>B. Permanent residents</b>		
41. Cinnamon Hummingbird ( <i>A. rutila</i> )	X	X
42. Buff-bellied Hummingbird ( <i>A. yucatanensis</i> )	X	X
43. Green-breasted Mango ( <i>Anthracothorax prevostii</i> )	X	X
44. Wedge-tailed Sabrewing ( <i>Campylopterus curvipennis</i> )	X	X
45. Fork-tailed Emerald ( <i>Chlorostilbon caniveti</i> )	X	X
46. Mexican Shearail ( <i>Doricha eliza</i> )	X	
47. Little Hermit ( <i>Phaethornis longuemareus</i> )	X	
48. Long-tailed Hermit ( <i>P. superciliosus</i> )	X	
<b>Trogonidae</b>		
49. Citreoline Trogon ( <i>Trogon citreolus</i> )	X	X
50. Collared Trogon ( <i>T. collaris</i> )	X	X
51. Slaty-tailed Trogon ( <i>T. massena</i> )	X	
52. Violaceous Trogon ( <i>T. violaceus</i> )	X	X
<b>Momotidae</b>		
53. Turquoise-browed Motmot ( <i>Eumomotus superciliosa</i> )	X	
54. Blue-crowned Motmot ( <i>Momotus momota</i> )	X	X
<b>Alcedinidae</b>		
55. Green Kingfisher ( <i>Chlorceryle americana</i> )	X	X
56. Pygmy Kingfisher ( <i>C. aenea</i> )	X	X
<b>Bucconidae</b>		
57. White-necked Puffbird ( <i>Bucco macrorhynchus</i> )	X	
<b>Ramphastidae</b>		
58. Collared Aracari ( <i>Pteroglossus torquatus</i> )	X	X
59. Keel-billed Toucan ( <i>Ramphastos sulfuratus</i> )	X	X
<b>Picidae</b>		
60. Pale-billed Woodpecker ( <i>Campephilus guatemalensis</i> )	X	
61. Chestnut-colored Woodpecker ( <i>Celeus castaneus</i> )	X	
62. Lineated Woodpecker ( <i>Dryocopus lineatus</i> )	X	
63. Golden-fronted Woodpecker ( <i>Melanerpes aurifrons</i> )	X	X
64. Yucatan Woodpecker ( <i>M. pygmaeus</i> )	X	X
65. Ladder-backed Woodpecker ( <i>Picoides scalaris</i> )	X	X
66. Golden-olive Woodpecker ( <i>Piculus rubiginosus</i> )	X	X
67. Smokey-brown Woodpecker ( <i>Veniliornis fumigatus</i> )	X	X
<b>Furnariidae</b>		
68. Rufous-breasted Spinetail ( <i>Synallaxis erythrothorax</i> )		X
69. Plain Xenops ( <i>Xenops minutus</i> )	X	X
<b>Dendrocolaptidae</b>		
70. Ruddy Woodcreeper ( <i>Dendrocincla homochroa</i> )	X	X
71. Tawny-winged Woodcreeper ( <i>D. anabatina</i> )	X	X
72. Barred Woodcreeper ( <i>Dendroclaptus certhia</i> )	X	X
73. Olivaceous Woodcreeper ( <i>Sittasomus griseicapillus</i> )	X	X
74. Ivory-billed Woodcreeper ( <i>Xiphorhynchus flavigaster</i> )	X	X
<b>Formicariidae</b>		
75. Black-faced Antthrush ( <i>Formicarius analis</i> )	X	X
76. Barred Antshrike ( <i>Thamnophilus doliatus</i> )	X	X
<b>Tyrannidae</b>		
<b>Tyranninae</b>		
77. Bright-rumped Attila ( <i>Attila spadaceus</i> )	X	X
78. Northern Beardless-Tyrannulet ( <i>Camptostoma imberbe</i> )	X	X
79. Tropical Pewee ( <i>Contopus cinereus</i> )	X	X
80. Caribbean Elaenia ( <i>Elaenia martinica</i> )	X	X
81. Yellow-bellied Elaenia ( <i>E. flavogaster</i> )	X	X

## APPENDIX II. Continued.

Species	How detected	
	PC	MN
B. Permanent residents		
82. Boat-billed Flycatcher ( <i>Megarhynchus pitangua</i> )	X	X
83. Ochre-bellied Flycatcher ( <i>Mionectes oleagineus</i> )	X	X
84. Dusky-capped Flycatcher ( <i>Myiarchus tuberculifer</i> )	X	X
85. Wied's Crested Flycatcher ( <i>M. tyrannulus</i> )	X	X
86. Yucatan Flycatcher ( <i>M. yucatanensis</i> )	X	X
87. Sulfur-rumped Flycatcher ( <i>Myiobius sulphureipygius</i> )	X	X
88. Greenish Elaenia ( <i>Myiopagis viridicata</i> )	X	X
89. Social Flycatcher ( <i>Myiozetetes similis</i> )	X	X
90. Royal Flycatcher ( <i>Onychorhynchus coronatus</i> )	X	X
91. Great Kiskadee ( <i>Pitangus sulphuratus</i> )	X	X
92. White-throated Spadebill ( <i>Platyrinchus mystaceus</i> )	X	X
93. Eye-ringed Flatbill ( <i>Rhynchocyclus brevirostris</i> )	X	X
94. Northern Bentbill ( <i>Oncostoma cinereigulare</i> )	X	X
95. Common Tody-Flycatcher ( <i>Todirostrum cinereum</i> )	X	
96. Yellow-olive Flycatcher ( <i>Tolmomyias sulphureus</i> )	X	X
97. Tropical Kingbird ( <i>Tyrannus melancholicus</i> )	X	X
Tityrinae		
98. Gray-collared Becard ( <i>Pachyrampus major</i> )	X	
99. Rose-throated Becard ( <i>P. aglaiae</i> )	X	X
100. Rufous Mourner ( <i>Rhytipterna holerythra</i> )	X	
101. Black-crowned Tityra ( <i>Tityra inquisitor</i> )	X	
102. Masked Tityra ( <i>T. semifasciata</i> )	X	X
Pipridae		
103. White-collared Manakin ( <i>Manacus candei</i> )	X	
104. Red-capped Manakin ( <i>Pipra mentalis</i> )	X	X
105. Thrushlike Manakin ( <i>Schiffornis turdinus</i> )	X	X
Hirundidae		
106. Gray-breasted Martin ( <i>Progne chalybea</i> )	X	
Corvidae		
107. Brown Jay ( <i>Cyanocorax morio</i> )	X	
108. Green Jay ( <i>C. yncas</i> )	X	
109. Yucatan Jay ( <i>C. yucatanicus</i> )	X	
Troglodytidae		
110. Band-backed Wren ( <i>Campylorhynchus zonatus</i> )	X	
111. White-breasted Wood-Wren ( <i>Henicorhina leucosticta</i> )	X	
112. Carolina Wren ( <i>Thryothorus ludovicianus</i> )	X	X
113. Spot-breasted Wren ( <i>T. maculipectus</i> )	X	X
114. House Wren ( <i>Troglodytes aedon</i> )	X	X
115. White-bellied Wren ( <i>Uropsila leucogastra</i> )	X	X
Muscicapidae		
Sylviinae		
116. Blue-gray Gnatcatcher ( <i>Poliophtila caerulea</i> )	X	X
117. Tropical Gnatcatcher ( <i>P. plumbea</i> )	X	
118. White-lored Gnatcatcher ( <i>P. albiloris</i> )	X	
119. Long-billed Gnatwren ( <i>Ramphocaenius melanurus</i> )	X	X
Turdinae		
120. Clay-colored Robin ( <i>Turdus grayii</i> )	X	X
Mimidae		
121. Black Catbird ( <i>Melanoptila glabirostris</i> )	X	X
122. Tropical Mockingbird ( <i>Mimus gilvus</i> )	X	X
123. Cozumel Thrasher ( <i>Toxostoma guttatum</i> )	X	

## APPENDIX II. Continued.

B. Permanent residents	Species	How detected	
		PC	MN
<b>Vireonidae</b>			
<b>Vireoninae</b>			
	124. Lesser Greenlet ( <i>Hylophilus decurtatus</i> )	X	X
	125. Tawny-crowned Greenlet ( <i>H. ochraceiceps</i> )	X	X
	126. Cozumel Vireo ( <i>Vireo bairdi</i> )	X	
	127. Mangrove Vireo ( <i>V. pallens</i> )	X	X
	128. Yucatan Vireo ( <i>V. magister</i> )	X	X
<b>Cyclarhinae</b>			
	129. Rufous-browed Peppershrike ( <i>Cyclarhis gujanensis</i> )	X	X
<b>Emberizidae</b>			
<b>Parulinae</b>			
	130. Golden-browed Warbler ( <i>Basileuterus belli</i> )	X	X
	131. Yellow Warbler ( <i>Dendroica petechia</i> )—resident race	X	X
	132. Gray-crowned Yellowthroat ( <i>Geothlypis poliocephala</i> )	X	X
	133. Gray-throated Chat ( <i>Granatellus sallaei</i> )	X	X
<b>Coeribinae</b>			
	134. Bananaquit ( <i>Coereba flaveola</i> )	X	X
<b>Thraupinae</b>			
	135. Red-legged Honeycreeper ( <i>Cyanerpes cyaneus</i> )	X	
	136. Gray-crowned Tanager ( <i>Eucometis penicillata</i> )	X	X
	137. Olive-backed Euphonia ( <i>Euphonia gouldi</i> )	X	
	138. Scrub Euphonia ( <i>E. affinis</i> )	X	X
	139. Yellow-throated Euphonia ( <i>E. hirundinacea</i> )	X	X
	140. Red-crowned Ant-Tanager ( <i>Habia rubica</i> )	X	X
	141. Red-throated Ant-Tanager ( <i>H. juscicauda</i> )	X	X
	142. Black-headed Shrike-Tanager ( <i>Lanio aurantius</i> )	X	
	143. Rose-throated Tanager ( <i>Piranga roseogularis</i> )	X	X
	144. Crimson-collared Tanager ( <i>Ramphocelus sanuginolentus</i> )	X	
	145. Scarlet-rumped Tanager ( <i>R. passerinii</i> )	X	
	146. Stripe-headed Tanager ( <i>Spindalis zena</i> )	X	X
	147. Yellow-winged Tanager ( <i>Thraupis abbas</i> )	X	
<b>Cardinalinae</b>			
	148. Northern Cardinal ( <i>Cardinalis cardinalis</i> )	X	X
	149. Black-faced Grosbeak ( <i>Caryothraustes poliogaster</i> )	X	
	150. Blue Bunting ( <i>Cyanocampsa parellina</i> )	X	X
	151. Black-headed Saltator ( <i>Saltator atriceps</i> )	X	X
	152. Buff-throated Saltator ( <i>S. maximus</i> )	X	
	153. Grayish Saltator ( <i>S. coerulescens</i> )	X	
<b>Emberizinae</b>			
	154. Orange-billed Sparrow ( <i>Arremon aurantiirostris</i> )	X	
	155. Green-backed Sparrow ( <i>Arremonops chloronotus</i> )	X	X
	156. Olive Sparrow ( <i>A. rufivirgatus</i> )	X	X
	157. White-collared Seedeater ( <i>Sporophila torqueola</i> )	X	X
	158. Yellow-faced Grassquit ( <i>Tiaris olivacea</i> )	X	X
	159. Blue-black Grassquit ( <i>Volatinia jacarina</i> )	X	X
<b>Icterinae</b>			
	160. Yellow-billed Cacique ( <i>Amblycercus holosericeus</i> )	X	X
	161. Melodious Blackbird ( <i>Dives dives</i> )	X	X
	162. Altamira Oriole ( <i>Icterus gularis</i> )	X	X
	163. Black-cowled Oriole ( <i>I. dominicensis</i> )	X	X
	164. Hooded Oriole ( <i>I. cucullatus</i> )	X	X
	165. Orange Oriole ( <i>I. auratus</i> )	X	X
	166. Yellow-backed Oriole ( <i>I. chrysater</i> )	X	X
	167. Yellow-tailed Oriole ( <i>I. mesomelas</i> )	X	X
	168. Montezuma Oropendula ( <i>Psarocolius montezuma</i> )	X	
	169. Great-tailed Grackle ( <i>Quiscalus mexicanus</i> )	X	

APPENDIX II. Continued.

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Summary:

Detected only in point surveys: 61 species (note: 21/61 do not occur in region of central Quintana Roo that was netted; 40 species were seen in central Quintana Roo, but not netted there)  
Detected only by mist netting: 2 species  
Detected by both methods: 106 species  
Grand total: 169 resident species

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