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THE DISTRIBUTION OF NEOTROPICAL MIGRANT BIRDS WINTERING IN THE EL CIELO BIOSPHERE RESERVE, TAMAULIPAS, MEXICO[1]

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Abstract. We documented the distribution of Neotropical migrant species wintering in four habitats in the Sierra Madre Oriental mountains in northeastern Mexico. We used point-count surveys and mist nets to determine the presence and relative abundance of migrant species in tropical semi-deciduous forest (300 m elevation), cloud forest (1,100 m elevation), humid oak-pine forest (1,200 m elevation), and dry pine-oak forest (1,800 m elevation) in the El Cielo Biosphere Reserve in Tamaulipas, Mexico. Thirty-two species of migrants were observed during the winters of 1993–1995; migrant species represented from 17% to 33% of the species detected in point counts and captured in mist nets in each habitat. Nearly half of the migrant species in El Cielo were habitat specialists; other species were found in a variety of habitats across their wintering ranges. Ruby-crowned Kinglet (*Regulus calendula*), Wilson's Warbler (*Wilsonia pusilla*), Blue-gray Gnatcatcher (*Polioptila caerulea*), and Hermit Thrush (*Catharus guttatus*) were the most frequently detected migrant species in El Cielo. Northern Mexico is an important wintering area for a diverse group of migrant species. Habitats at higher elevations with temperate-like forests and at lower elevations with tropical forests had the greatest species richness and supported the highest abundance of migrant species.

Resumen. Registramos la distribución de las especies de aves migratorias neotropicales invernando en cuatro hábitats de la cordillera de la Sierra Madre Oriental en el noreste de México. Se utilizaron los métodos de puntos de conteo y redes de captura para determinar la presencia y abundancia relativa de las especies migratorias en bosque tropical subcaducifolio (300 msnm), bosque mesófilo de montaña (1100 msnm), bosque húmedo encino-pino de (1,200 msnm) y en bosque seco de pino-encino (1,800 msnm), dendro de la reserva de la biosfera El Cielo en Tamaulipas, México. Treinta y dos especies de aves migratorias se observaron durante los inviernos de 1993 a 1995; las especies migratorias representaron entre el 17 y 33 % del total de las especies detectadas en los puntos de conteo y capturadas en las redes en cada tipo de hábitat. Cerca de la mitad de las especies migratorias presentes en El Cielo son espec'ficas a un tipo de hábitat mientras que otras se encontraron en vários hábitats a lo largo de su distribución invernal. Las especies migratorias más frecuentemente detectadas fueron el Reyezuelo Sencillo (*Regulus calendula*), el Chipe de Wilson (*Wilsonia pusilla*), Perlita Grisilla (*Polioptila caerulea*) y el Zorzalito Colirrufo (*Catharus guttatus*). La región norte de México es un área importante durante el invierno para un grupo diverso de especies migratorias. Los hábitats que tuvieron la mayor riqueza de especies y soportan la más alta abundancia de especies migratorias fueron los bosques templados y las selvas tropicales.

Key words: Neotropical migratory birds, Mexico, point counts, mist nets, nonbreeding season, abundance, habitat use.

INTRODUCTION

Neither the impact of migrants on Neotropical bird communities nor the causes of migrant bird decline can be assessed without documentation of where migrants occur during the nonbreeding season. Neotropical avian communities experience a large influx of migratory birds as species move south for the temperate winter. The competitive inter- and intraspecific interactions among migrants and residents during this nonbreeding season, and the consequences of these potential interactions on both population demographics and community structure, have been discussed frequently in the community ecology and migration literature (Leck 1972, Greenberg 1984, 1986).

Declines in North American Neotropical migrant birds have focused attention on studies of migrants on their wintering grounds (Terborgh

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1989, Finch 1991, Hagan and Johnston 1992). Habitat loss and fragmentation on the breeding grounds can lead to regional declines (Askins et al. 1990, Robinson et al. 1995), but how local declines and wintering events influence broad-range declines is not clear. Loss of suitable wintering habitat is a potential cause for the decline of some species (Rappole and Morton 1985, Rappole and McDonald 1994), but few studies document long-term trends in wintering habitats. The greatest diversity and abundance of migrant birds is found in the northern Neotropics, including Mexico and the Greater Antilles (Greenberg 1992), yet studies that have examined migrant species distribution and relative abundance across a variety of habitats are limited to western Mexico (Hutto 1980, 1989, 1992), southern Mexico (Lynch 1989, 1992), and the West Indies (Askins et al. 1992, Wunderle and Waide 1993, Wallace et al. 1996).

We examined the winter bird community in four habitats in the mountains of northeastern Mexico, with an emphasis on the distribution and relative abundance of migrant species among habitats in one geographical area. Our objectives were to (1) measure and compare the relative abundance of migrant and resident birds among the different habitats available in northeastern Mexico during the nonbreeding season, (2) determine how migrant species are distributed among the available habitats, (3) evaluate the use of mist nets and point-count surveys to detect migrant species in different habitats during the nonbreeding season, and (4) determine the mist net recapture patterns of migrant species during the winter.

METHODS

STUDY AREAS

We surveyed the winter bird community in four habitats in the El Cielo Biosphere Reserve, located in the southern part of Tamaulipas, Mexico (23°15′ N, 99°50′ W), along the slopes of the Sierra Madre Oriental. El Cielo was designated as an ecological protected area by the state of Tamaulipas in 1985, prior to which time the area had been used for logging and agriculture. The 144,530-ha Reserve consists of a variety of natural and disturbed habitats ranging in elevation from 100 m to 2,300 m. Most of the logging activity ended by the early 1970s, but small cooperative villages ("ejidos") remain in areas that once supported large logging towns. The ejidos usually occupy a large clearing with small buildings and a variety of livestock, some of which graze in the surrounding forest. The best description of the region, including topography, climate and vegetation, is found in Martin (1958). We selected a specific study site in each of the four natural habitats in the proximity of field stations in the Reserve. The study sites are described below.

(1) Semi-deciduous tropical forest (300 m elevation) was sampled in the vicinity of Gómez Farias and the Los Cedros field station (23°03′N, 99°09′W), operated by the Universidad Autónoma de Tamaulipas. The canopy is 11–15 m high, with a dense understory of lower trees and shrubs. Common tree species include *Bursera simaruba, Brosimum alicastrum, Enterolobium cyclocarpum, Pseudobombax ellipticum, Phoebe tampicensis, Cedrela mexicana,* and *Savia sessiliflora.*

(2) Cloud forest (1,100 m elevation) was studied at Rancho del Cielo (23°06′N, 99°11′W), a field station operated by the University of Texas at Brownsville/Texas Southmost College. Rancho del Cielo is situated on the east-facing slopes of the Sierra de Guatemala, a disjunct portion of the Sierra Madre Oriental (Webster 1974), and it receives moisture laden air from the easterly trade winds. Mean annual rainfall is 2,000-2,500 mm (Martin 1958), and visibility is often confined to 30 m because of fog. The dense, semi-evergreen vegetation reaches a canopy height of 20–30 m and is covered with a variety of epiphytes. The dominant tree species are *Quercus sartotii, Q. germana, Liquidambar styraciflua, Acer skutchii, Magnolia tamaulipana, Fagus mexicana,* and *Podocarpus reichei* (Lonard 1975).

(3) Humid oak-pine forest (1,200 m elevation) was sampled near San José and the Canindo field station (23°03′N, 99°14′W), operated by the State of Tamaulipas. Canindo is located on the eastern flank of the second slope of the Sierra Madre Oriental and does not receive as much moisture and rainfall as the cloud forest. The vegetation in the humid oak-pine differs from the cloud forest both structurally and floristically. The humid oak-pine forest is more open, contains fewer understory trees and tall shrubs, and epiphytes are less abundant than in the cloud forest (Martin 1958). Mean canopy height is 20 m. Dominant tree species include

Quercus affinis, Q. mexicana, Pinus montezumae, P. patula, Liquidambar styraciflua, and *Acer skutchii.*

(4) Dry pine-oak forest (1,800 m elevation) was studied at Joya de Salas (23°10′N, 99°18′W), a small village on the western slopes of the Sierra Madre Oriental. Canopy height ranges from 12 m to 20 m, with some emergent junipers (*Juniperus flaccida*) reaching 25 m. The dry pine-oak forest is characterized by an open canopy, interspersed grassland, a mixture of evergreen and deciduous trees, and an abundance of moss-draped round-crowned oaks with gnarled trunks (Robbins and Heed 1951, Martin 1958). The dominant tree species are *Juniperus flaccida, Pinus teocote, P. montezumae, Quercus crassipes, Q. polymorpha,* and *Q. grisea* (Johnston et al. 1989).

SAMPLING METHODS

We used two techniques to survey birds in the four habitat types: point-count surveys and mist-net captures. Point counts were used to detect visible or calling species using all levels of the vegetation. We developed a series of 10 point-count stations within each of the four habitats, following the guidelines of Hutto et al. (1986). This technique involved a count of all birds seen or heard both within and outside a 25-m-radius area. Points were at least 200 m apart and each point was sampled for 10 min early in the day; each point count was repeated monthly, varying the order of points sampled, for a total of four times during the winters of 1994 and 1995. Point counts based on this protocol have been used successfully in recent years in Mexico and many Caribbean islands and seem to be the preferred technique for point-count surveys of species presence during the nonbreeding season (Hutto 1992, Robbins et al. 1992). Point-count data are presented as (mean detections per point) × 10 to facilitate comparisons.

Because some quiet and secretive species are poorly detected using point-count surveys, we supplemented the point-count data by capturing birds with mist nets. The mist nets were located along the same transects as the point count stations, but the mist nets and point counts were not sampled at the same time. We established four to five net lines within each of the four habitat types during the winters of 1993–1995; each net line consisted of sixteen 12-m nets (36-mm mesh) placed approximately end-to-end. Two of these net lines were operated for three consecutive days approximately monthly for 7 hr starting at dawn; preliminary mist-net samples revealed that most species were captured before 14:00. In addition, we operated two net lines in tropical semi-deciduous forest and three net lines in the other three habitats once each winter for three consecutive days from dawn to dusk; these net lines provided data that were directly comparable to previous studies done elsewhere in the tropics (Faaborg and Arendt 1989, Robbins et al. 1992). We were unable to use mist nets in the humid oak-pine forest in February 1994 or 1995 because of interference from neighboring livestock. Net lines were located at least 100 m from other net lines. Mist-net data were expressed as numbers of birds captured per 100 mist-net hr (mnh = 1 mist net open for 1 hr). We constructed species-effort curves to compare the number of migrants among sites because mist-netting effort was not equal at all sites.

We are aware that capture rates of nets are higher on first days of netting than third days (Faaborg, in press). All of our sites had similar proportions of first and third days, such that converting to captures per 100 mnh should present no between-site biases. All species except hummingbirds and birds greater than 100 g in mass were banded with numbered aluminum bands (U.S. National Biological Service bands for appropriate species, specialty bands for Mexican species).

RELATIVE ABUNDANCE AND DISTRIBUTION OF MIGRANT SPECIES

For purposes of this study, we considered the mean number of individuals per point (averaged over the four visits) to be an independent sample of a habitat because points were located far enough apart (200 m) to avoid counting the same birds at multiple points (Hutto 1992). We also considered each three-day operation of a net line to be an independent sample because the few individual birds that were captured in more than one net line were counted only once per visit to a habitat and there were at least 30 days between visits. Although true replicates require the comparison of species abundance among habitats at multiple sites, the scope of this study was limited to a single geographical area and multiple sites of each habitat type were not available.

We independently computed an index of migrant abundance for each site from the point-count data (detection rate) and the mist-net data (capture rate). We tested all data for normality (Wilk-Shapiro test) and homogeneity of variance (Bartlett's test). We transformed data as necessary or used nonparametric tests. For the point-count data, we compared birds per point from the within 25-m radius point counts among habitats using a one-way ANOVA for number of migrant species, migrant individuals, total species, and total individuals. We examined the relationship between number of species and individuals per point across habitats with a Spearman rank order correlation coefficient.

We compared migrant capture rates (birds captured per 100 mnh) among habitats with a one-way ANOVA, and between years using two-tailed paired *t*-tests. All capture numbers, except recapture data, were based on new captures and returns (birds recaptured the first time each year after migration to and from the breeding grounds); recapture data included returns and repeats (birds captured during the same netting period or winter season). We compared the distribution of repeats and returns among the four habitats with a series of *G*-tests of independence (Sokal and Rohlf 1995).

We evaluated the differential distribution of migrant species among the habitats in which a species was present with a one-way ANOVA with Tukey multiple comparisons for point-count data (after log transforming data with unequal variances) and a Kruskal-Wallis nonparametric ANOVA for mist-net data. Detections of migrant species did not differ significantly among the four point-count visits (as tested with a nested ANOVA by habitat and visit); we used the mean detection rate over four visits as the best estimate of bird abundance at each point. We found no significant effects of year or visit in a repeated measures ANOVA of mist-net data, so we calculated species' capture rates for each habitat by averaging the capture rates of all the net line samples over three years. By examining the frequency and location of mist-net recaptures, we determined some patterns of recapture probability and territoriality for select migrant species.

RESULTS

RELATIVE ABUNDANCE OF MIGRANT SPECIES

In total, we observed 134 landbird species, including 32 Neotropical migrants, in the natural habitats of El Cielo during the winters of 1993–1995. We detected 89 species in the point-count surveys, 22% (20 species) of which were migrants, and captured 100 species in mist nets, 26% of which were migrants. Four migrant species only were detected in point-count surveys, and eight migrant species only were detected with mist nets. Migrant species represented 17% (11/64) of the total species detected in the humid oak-pine forest, 22% (15/69) of the total in the cloud forest, 24% (21/88) of the total in the tropical semi-deciduous forest, and 33% (19/57) of the total in the dry pine-oak forest. Three migrant species, including Williamson's Sapsucker (*Sphyrapicus thyroideus*), Red-naped Sapsucker (*S. nuchalis*), and Yellow-rumped "Myrtle" Warbler (*Dendroica coronata*), were seen occasionally in the dry pine-oak forest, but they were not detected with point counts or mist nets.

We detected the greatest numbers of total individuals and migrant individuals per point in the tropical semi-deciduous forest (both $F_{3,36} > 6.1$, $P < 0.01$); the numbers of total and migrant species per point were not significantly different among habitats (both $F_{3,36} < 2.6$, Fig. 1). The mean number of migrant species per point was correlated with the mean number of migrant individuals per point ($r_s = 0.76$, $n = 77$, $P < 0.001$).

A total of 1,251 birds (new and returns only) were captured in 24,368 mist-net hours (mnh) during the winters of 1993–1995. Migrant individuals accounted for 39% of the captures, with Hermit Thrush (*Catharus guttatus*), Ruby-crowned Kinglet (*Regulus calendula*), Wilson's Warbler (*Wilsonia pusilla*), and Swainson's Thrush (*Catharus ustulatus*) representing 65% of the migrant captures. Although we captured the greatest number of migrant species in the tropical semi-deciduous forest, the dry pine-oak forest had the highest migrant capture rate and the largest absolute number of migrant birds captured (Table 1). In addition, 42% of the species captured in the dry pine-oak forest were migrants and only 27%, 29% and 26% of the captured species in the cloud forest, tropical semi-deciduous forest, and humid oak-pine forest, respectively, were migrants. Migrant capture rates varied significantly among habitats when based on capture rates over all seasons ($F_{3,56} = 2.77$, $P < 0.05$; Table 1). Although mist-netting effort was different among habitats, the absolute number of migrant species captured in a habitat ap-

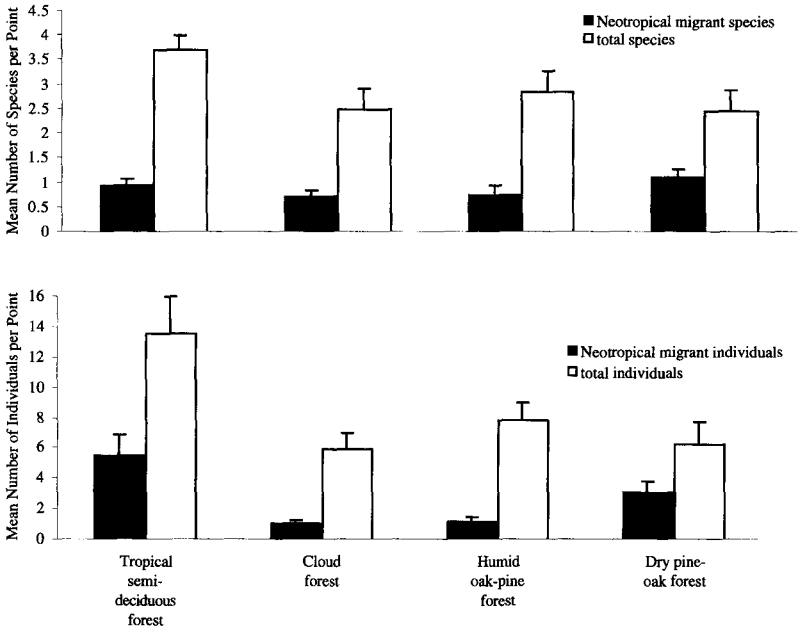

FIGURE 1. Mean (+ SE) numbers of Neotropical migrant species and individuals per point in four habitats in El Cielo during winter.

TABLE 1. Summary of migrant and total (migrant + resident) species and individuals captured in mist nets and detected in point-count surveys. Relative abundance (mean ± SE) is birds per 100 mnh (mist net hours) for mist-net captures and birds per point for point-count surveys.

Habitat	Mist-net captures	Point-count detections
Tropical semi-deciduous forest		
Number of migrant species	20	10
Total number of species	70	44
Number of migrant individuals	164	222
Total number of individuals	430	614
Relative abundance of migrant individuals	4.00 ± 0.83	5.48 ± 1.40
Cloud forest		
Number of migrant species	12	10
Total number of species	44	47
Number of migrant individuals	52	48
Total number of individuals	351	414
Relative abundance of migrant individuals	1.15 ± 0.23	1.02 ± 0.25
Humid oak-pine forest		
Number of migrant species	11	8
Total number of species	42	35
Number of migrant individuals	81	49
Total number of individuals	213	443
Relative abundance of migrant individuals	2.14 ± 0.36	1.13 ± 0.31
Dry pine-oak forest		
Number of migrant species	16	11
Total number of species	38	37
Number of migrant individuals	191	139
Total number of individuals	257	375
Relative abundance of migrant individuals	15.30 ± 6.84	3.03 ± 0.77

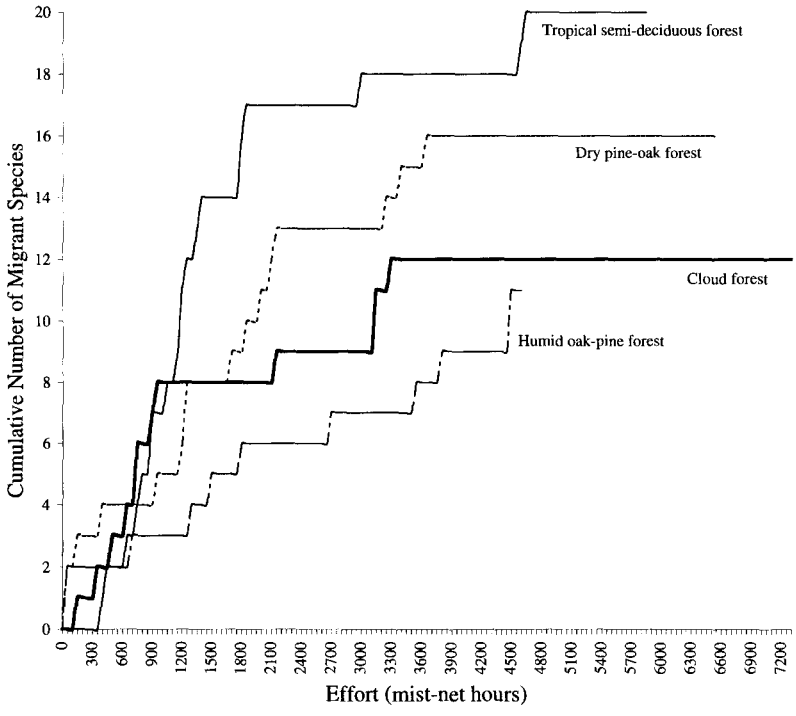

FIGURE 2. Relationship between mist-netting effort and species richness for migrant species found in four habitats in northeastern Mexico during winter.

peared to plateau between 3,500 and 4,500 mnh in three habitats (Fig. 2). In the humid oak-pine forest, additional mist netting may have yielded more species, but we did not detect any additional migrant species in the point-count surveys in this habitat.

Recaptured birds accounted for 25% to 27% of all captures (Table 2). Recaptures were separated into birds recaptured during the same winter (repeats), and birds captured during subsequent winters (returns). We recaptured a total of 449 birds (repeats and returns), 47% of which were migrants. Most recaptures in all habitats were repeats for all species and migrant species (69% to 89%). In total, 91 individuals (7% of the total captures) were recaptured between winters, including 7 birds that were captured repeatedly in 1993, 1994 and 1995. Migrants represented 28% of the returns after one winter and 43% of the returns after two winters (Table 2). The distribution of repeats and returns among the four habitats for migrants was not significantly different ($G_3 = 0.56$), indicating that migrants in each habitat exhibited similar recapture patterns both within a winter and between winters.

MIGRANT SPECIES DISTRIBUTION

We detected a total of 458 migrant individuals in the point-counts surveys; three species accounted for 63% of these observations including the Ruby-crowned Kinglet (32%), Blue-gray Gnatcatcher (*Polioptila caerulea,* 30%), and Wilson's Warbler (10%). Mean number of individuals per point for a given species was correlated with percent of points at which the same species was present at each site ($r_s = 0.87$, $n = 285$, $P < 0.001$); therefore, mean number of birds per point was used to compare relative abundance and frequency of occurrence among the four habitats for migrant species present in at least two habitat types. Of the 19 migrant species found in point counts, 10 species were detected at least one time per visit in at least two habitats (Table 3). There were significant differences in relative abundance among the habitats used by a species for four migrant species. Eastern Phoebe (*Sayornis phoebe*) and Hermit

TABLE 2. Total number of birds recaptured, number of birds recaptured during the same season (repeats) and number of birds recaptured between winters (returns) in each of four habitats. Numbers in parentheses are percent of total captures for Total recaptures, and percent of recaptures of Repeats and Returns.

Habitat/Species	Total recaptures	Repeats	Returns after 1 winter	Returns after >1 winter
Tropical semi-deciduous forest				
All species	162 (27)	130 (80)	32 (20)	0
Migrants	65 (29)	56 (86)	9 (14)	0
Swainson's Thrush	12 (23)	11 (92)	1 (8)	0
Wilson's Warbler	16 (33)	11 (69)	5 (31)	0
Ovenbird	8 (40)	7 (88)	1 (12)	0
Cloud forest				
All species	121 (26)	84 (69)	31 (26)	6 (5)
Migrants	26 (36)	21 (81)	3 (11)	2 (8)
Hermit Thrush	5 (42)	3 (60)	1 (20)	1 (20)
Hammond's Flycatcher	11 (48)	10 (91)	1 (9)	0
Ovenbird	5 (56)	2 (40)	2 (40)	1 (20)
Humid oak-pine forest				
All species	71 (25)	59 (83)	12 (17)	0
Migrants	29 (27)	25 (86)	4 (14)	0
Hermit Thrush	13 (57)	10 (77)	2 (15)	0
Hammond's Flycatcher	10 (45)	8 (80)	2 (20)	0
Dry pine-oak forest				
All species	95 (27)	78 (82)	16 (17)	1 (1)
Migrants	89 (33)	79 (89)	9 (11)	1 (1)
Hermit Thrush	77 (45)	69 (90)	8 (10)	1 (1)
Ruby-crowned Kinglet	12 (15)	11 (92)	1 (8)	0
Total				
All species	449 (26)	351 (78)	91 (20)	7 (2)
Migrants	209 (31)	181 (87)	25 (12)	3 (1)

Thrush were detected most frequently in dry pine-oak forest, Blue-gray Gnatcatcher was most abundant in tropical semi-deciduous forest, and Ruby-crowned Kinglet was detected most often in both tropical semi-deciduous forest and dry pine-oak forest (Tukey multiple comparisons).

Capture rates for six of the 26 migrant species captured in mist nets over three winters were significantly different among the four habitats (Table 3). We captured Yellow-bellied Flycatchers (*Empidonax flaviventris*), Ruby-crowned Kinglets, and Hermit Thrushes most frequently in the dry pine-oak forest, Swainson's Thrushes and Ovenbirds (*Seiurus aurocapillus*) most frequently in the tropical semi-deciduous forest, and Hammond's Flycatchers (*E. hammondii*) most frequently in the humid oak-pine forest. Eight species were captured in only one habitat type. Hermit Thrushes and Ruby-crowned Kinglets in the dry pine-oak forest exhibited relatively high capture rates among the migrant species.

RECAPTURES

We recaptured the highest number of migrant species in the dry pine-oak forest, including 77 recaptured Hermit Thrushes (Table 2). Most Hermit Thrushes were recaptured within the same winter (90%) and within 25 m of their original capture location (Gram, unpubl. data), suggesting that they possess winter territories. Only 9% (8/95) of the banded Hermit Thrushes were recaptured between years, but there were 18 individual repeats in 1993, 15 in 1994, and 8 in 1995. Returns after one winter for Hermit Thrush represented from 11% to 20% of all recaptures at three sites. More than 60 Ruby-crowned Kinglets were captured in the dry pine-oak forest, but there were only 12 total recaptures, with only one return. Returns after more than one winter may have been limited by the relatively short field season and fewer mist-net hours in 1995. Swainson's Thrushes and Wilson's Warblers were the most commonly cap-

tured and recaptured migrants in the tropical semi-deciduous forest. In the cloud forest and humid oak-pine forest, we frequently recaptured Hammond's Flycatchers and Hermit Thrushes (Table 2).

DISCUSSION

RELATIVE ABUNDANCE OF MIGRANT SPECIES

Our results show that the number and relative abundance of migrant species differ among the habitats examined; habitats at higher elevations with temperate-like forests and at lower elevations with tropical forests support the greatest numbers and proportions of migrant species. Most migrant species are present in small numbers, and a few species are relatively abundant, such as Blue-gray Gnatcatcher, Hermit Thrush, Swainson's Thrush, and Ruby-crowned Kinglet.

Migrant species represented 24% of the winter bird community in El Cielo. Studies in western Mexico and Central America found that migrants comprised from 19% to 25% of the species detected in a variety of habitats (Kricher and Davis 1992, Robbins et al. 1992). In tropical semi-deciduous and dry pine-oak forests, we detected more migrants per point than did Askins et al. (1992) in the Virgin Islands, or Hutto (1992) in western Mexico, who detected less than two migrants per point in a variety of habitats similar to those in El Cielo. Lynch (1989) and Blake and Loiselle (1992) reported a mean detection rate of one bird per point for the most common migrant species in the Yucatan and central Costa Rica, whereas we detected a mean of 3.4 Blue-gray Gnatcatchers per point in tropical semi-deciduous forest and 1.9 Ruby-crowned Kinglets per point in dry pine-oak forest. Our migrant capture rates were similar to those found in Belize (Petit et al. 1992) and higher than those found in Costa Rica (capture rates were 0.7 to 8.8 migrant birds per 100 mnh; Blake and Loiselle 1992). Wood Thrush, Swainson's Thrush, and Ovenbird, the most frequently captured migrant species in Costa Rica, had lower capture rates (0.5 to 1.6 birds per 100 mnh) than Hermit Thrush or Ruby-crowned Kinglet in El Cielo (3.4 and 2.6 captures per 100 mnh, respectively, in dry pine-oak forest). In general, the mist-net and point-count data from El Cielo suggest that there are relatively more wintering migrants in the northern Neotropics than further south.

In western Mexico, Hutto (1992) reported many of the same patterns of migrant distribution as this study despite differences in scale and sampling design. Hutto conducted point counts in three habitats comparable to those in El Cielo, and 15% to 31% of his species detections per point were migrants (compared with 23% to 30% in El Cielo). Migrants shared similar habitat breadth estimates, with 59% of western migrants and 47% of eastern migrants restricted to one habitat type. Furthermore, 63% of the migrant individuals detected by Hutto were from five species, including the Ruby-crowned Kinglet which accounted for 24% of the migrant individuals detected in western Mexico and 32% in El Cielo. Northern Mexico is certainly an important wintering area for many migrant species, with some species present in high densities and other species only detected occasionally in specific habitats.

MIGRANT SPECIES DISTRIBUTION

The group of migrant species wintering in El Cielo is diverse both taxonomically and behaviorally. Ten migrant species were found in three or four of the habitats we sampled, whereas 15 species were restricted to one habitat type (Table 3). Of the species found in only one habitat, seven of them were found in the dry pine-oak forest; Hutto (1992) detected 14 migrants (47% of habitat specialists) exclusively in the pine-oak-fir forests of western Mexico. In El Cielo, the dry pine-oak forest at Joya de Salas is distinctly different from the other sites by its heavily coniferous forest, interspersed overgrazed pastures, and western location; these characteristics may account for the high proportion of habitat specialists. Williamson's Sapsucker and Red-naped Sapsucker were found exclusively in dry pine-oak forest in El Cielo and pine-oak-fir forest in western Mexico (Hutto 1992), suggesting that some migrant species may seek out winter habitats that have a vegetation structure similar to that of their breeding habitats (Petit et al. 1992).

At a local and regional scale, some migrant species use a wide range of habitats with equal frequency. Black-and-white Warblers were found in all forested habitats in El Cielo (Table 3), as in western Mexico (Hutto 1992), the Yucatan Peninsula (Lynch 1989), and Greater Antilles (Wunderle and Waide 1993). In contrast, the Hermit Warbler was found in only dry pine-oak forest in El Cielo and only in cloud

TABLE 3. Mist-net capture rates (birds per 100 mnh ± SE) and point-count detection rates (birds per point × 10 ± SE) for Neotropical migrant species in the habitats sampled in El Clelo. Comparisons of mist-net data among habitats based on Kruskal-Wallis ANOVA (*H*) and comparisons of point-count data among habitats based on one-way ANOVA with log-transformed data.

Species		Mist nets		
Common name	Latin name	Tropical semi-deciduous forest	Cloud forest	Humid oak-pine forest
Yellow-bellied Sapsucker	*Sphyrapicus varius*			
Yellow-bellied Flycatcher	*Empidonax flaviventris*	0.05 ± 0.02		
Least Flycatcher	*E. minimus*	0.05 ± 0.03		0.05 ± 0.03
Hammond's Flycatcher	*E. hammondii*	0.02 ± 0.01	0.12 ± 0.05	0.23 ± 0.07
Dusky Flycatcher	*E. oberholseri*		0.02 ± 0.02	
Gray Flycatcher	*E. wrightii*		0.01 ± 0.01	
Empidonax spp.	*Empidonax* sp.			
Eastern Phoebe	*Sayornis phoebe*			0.02 ± 0.02
House Wren	*Troglodytes aedon*	0.01 ± 0.01		
Ruby-crowned Kinglet	*Regulus calendula*	0.12 ± 0.04	0.01 ± 0.01	0.04 ± 0.03
Blue-gray Gnatcatcher	*Polioptila caerulea*	0.10 ± 0.05		
Swainson's Thrush	*Catharus ustulatus*	0.42 ± 0.11	0.01 ± 0.01	0.01 ± 0.01
Hermit Thrush	*C. guttatus*	0.08 ± 0.04	0.08 ± 0.04	0.24 ± 0.07
Wood Thrush	*Hylocichla mustelina*	0.06 ± 0.03	0.05 ± 0.02	
Gray Catbird	*Dumetella carolinensis*	0.09 ± 0.03		
Solitary Vireo	*Vireo solitarius*	0.02 ± 0.01	0.02 ± 0.01	0.07 ± 0.05
Orange-crowned Warbler	*Vermivora celata*	0.03 ± 0.01		
Nashville Warbler	*V. ruficapilla*	0.02 ± 0.01		
Northern Parula	*Parula americana*			
Yellow-rumped "Audubon's" Warbler	*Dendroica coronata*			
Townsend's Warbler	*D. townsendi*	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.02
Hermit Warbler	*D. occidentalis*			
Black-throated Green Warbler	*D. virens*	0.03 ± 0.01		0.01 ± 0.01
Yellow-throated Warbler	*D. dominica*			
Black-and-white Warbler	*Mniotilta varia*	0.08 ± 0.03	0.02 ± 0.01	0.01 ± 0.01
Ovenbird	*Seiurus aurocapillus*	0.25 ± 0.08	0.05 ± 0.03	
Wilson's Warbler	*Wilsonia pusilla*	0.41 ± 0.14	0.05 ± 0.02	0.20 ± 0.01
Yellow-breasted Chat	*Icteria virens*	0.06 ± 0.03		
Summer Tanager	*Piranga rubra*			
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	0.09 ± 0.06		
Lincoln's Sparrow	*Melospiza lincolnii*			

* = $P < 0.05$, ** = $P < 0.01$.

forest and pine-oak-fir forest in western Mexico. Black-throated Green Warbler was detected in all habitats in El Cielo, but it was a habitat specialist in cloud forest in western Mexico. It is possible that the Hermit Warbler in dry pine-oak forest is occupying the eastern edge of its wintering range and is rarely found in cloud forest in El Cielo because it is too far east; the reverse situation may hold for the Black-throated Green Warbler, an eastern species. These species' distribution patterns suggest that the same species may use different habitats throughout its wintering range.

The abundance (frequency of detection/capture rate) of some migrant species varied among habitats (Tables 3), suggesting a potential disparity in perceived resource availability among habitats, either due to fewer preferred resources or increased competition for those resources. In addition, factors such as amount of available habitat, abundance of predators, similarity of wintering habitat to breeding habitat, and sex/age distribution may influence the abundance of a species in a habitat type within a single geographical area (Holmes et al. 1989, Blake and Loiselle 1992). Habitats with a greater abundance of a species are not necessarily the preferred habitat type of a species for an area (Van Horne 1983); survival rates also are an important component of determining preferred habitat

TABLE 3. Extended.

Mist nets			Point counts					
Dry pine-oak forest	*n*	*H*	Tropical semi-deciduous forest	Cloud forest	Humid oak-pine forest	Dry pine-oak forest	*n*	*F*
0.18 ± 0.18	3					1.25 ± 0.55	6	
0.09 ± 0.09	6	3.66*						
0.01 ± 0.01	11	0.01						
0.02 ± 0.01	50	3.10*				0.75 ± 0.38	4	
0.01 ± 0.01	4	0						
0.09 ± 0.09	2	0						
			0.50 ± 0.33	1.00 ± 0.76	0.75 ± 0.38	0.50 ± 0.33	26	0.64
0.03 ± 0.02	6	0			0.25 ± 0.25	0.50 ± 0.25	7	6.82*
0.01 ± 0.01	2	0						
2.60 ± 1.45	98	4.63*	12.75 ± 3.54	2.00 + 0.97	2.25 ± 0.87	19.25 ± 3.54	145	9.56**
	11		34.25 ± 8.33	0.25 ± 0.25			138	49.00**
0.01 ± 0.01	56	10.83**						
3.39 ± 1.49	215	2.75*	0.50 ± 0.33	1.50 ± 0.55	0.50 ± 0.33	4.50 ± 1.30	35	13.74**
	14	0.47	0.25 ± 0.25				1	
	10			0.25 ± 0.25			1	
0.04 ± 0.02	18	0.14	1.25 ± 0.67	0.75 ± 0.53	2.00 ± 1.04	1.25 ± 0.56	21	0.44
0.02 ± 0.01	6	0.06						
	2							
			0.50 ± 0.33				2	
0.03 ± 0.03	4					0.25 ± 0.25	1	
	4	0.07		1.00 ± 0.76	1.50 ± 0.67	1.75 ± 0.75	17	0.34
						0.75 ± 0.53	3	
	4	0.56	1.25 ± 0.78	1.00 ± 0.55	0.75 ± 0.38	0.50 ± 0.38	16	0.72
				0.25 ± 0.25			1	
0.01 ± 0.01	17	2.22	1.00 ± 0.55	0.25 ± 0.25	0.75 ± 0.38	0.75 ± 0.38	11	0.60
	35	6.09**						
	74	2.62	3.50 ± 0.75	3.25 ± 0.75	4.25 ± 0.92		44	0.31
	7							
			0.25 ± 0.25				1	
	9			0.25 ± 0.25			1	
0.01 ± 0.01	1							

types. Wood Thrushes were captured more frequently in moist lowland forest than in surrounding second-growth vegetation in Veracruz, Mexico (Winker et al. 1990); individuals in the forest usually defended territories, whereas those in the second-growth were nonterritorial wanderers. Territorial birds showed relatively high site-fidelity within and among winters and a low mortality rate in comparison to wanderers (Rappole et al. 1989, Winker et al. 1990, Conway et al. 1995).

In El Cielo, Hermit Thrushes and Swainson's Thrushes were detected in all habitats but showed significantly higher capture rates and point-count detections in the dry pine-oak and tropical semi-deciduous forests, respectively. Some individuals of both species appear to defend winter territories in the habitat in which they were found most frequently, as suggested by relatively high recapture rates and within-season site persistence (Table 2). Hermit Thrush in dry pine-oak forest exhibited a similar return rate as Wood Thrush in Veracruz (7%; Winker et al. 1990) and also may have a similar social system with territorial sedentary individuals in higher quality habitat and nonterritorial wanderers in less productive habitat. A winter limitation hypothesis for the decline of some Neotropical migrant species' populations suggests that individuals defending a winter territory in higher quality habitat have a lower mortality rate than individuals without a territory (floaters) in lower

quality habitat (Rappole and McDonald 1994); thrushes wintering in El Cielo may fit this pattern.

EFFECTIVENESS OF MIST NETS AND POINT COUNTS

For a nonbreeding season study in diverse habitats, we found that both mist nets and point counts were necessary sampling methods to detect the array of migrant species wintering in El Cielo. Our results from the mist-net and point-count data suggested similar conclusions about both the abundance of migrant species in each habitat and the distribution of individual species among habitats. The combination of both mist-net and point-count data provided more information on migrant species in El Cielo than did the data from either single sampling method.

In general, the mist nets were most effective at capturing ground and shrub dwelling species, such as thrushes and understory warblers, and in habitats with high densities of short understory plants, such as the tropical semi-deciduous forest at Los Cedros. Mist netting also enabled us to detect many *Empidonax* flycatchers that were difficult to distinguish visually and rarely vocalized. By capturing and marking individual birds, we determined the body condition and recapture probabilities of some species, leading to hypotheses about the winter social systems of select species. Mist netting, however, was time and labor intensive, required specialized equipment that was difficult to transport to remote sites, and only sampled the lower 2 m of a habitat.

Point counts were most effective at detecting both vocal and actively moving species, such as warblers and woodpeckers. Many migrant species in El Cielo participated in mixed-species foraging flocks that rarely moved below the forest canopy (Gram 1996) and, thus, were not effectively sampled with mist nets. Point counts were easy to standardize and provided comparisons of detections per point among habitats, assuming a species could be detected. Many secretive species that did not vocalize in the winter or inhabited dense vegetation were difficult to detect with point counts; we could not reliably determine indices of abundance for these species with point counts alone. Once an observer knew the vocalizations and visual characteristics of the species present in a habitat, point counts required no special equipment or set-up after the route was identified, took relatively little time (4–5 hr per morning), and sampled the entire habitat.

CONCLUSIONS

Northeastern Mexico supports a large, diverse group of wintering migrant species in a variety of habitats. We found higher numbers and relative abundances of migrant species in El Cielo than most other studies found in southern Mexico, the West Indies, or Central America. Some migrants are habitat specialists, whereas other species are found in different habitats across their wintering ranges. Recaptures within and between winters indicate that some species are faithful to a specific site both within a season and between subsequent winters.

Differential abundances among habitats for a species may suggest habitat preferences, but the interpretation of observed distributional patterns can be both complicated and misleading without information on resource use and availability, survivorship, and social system characteristics. The next step is to determine whether there is a survival advantage for individuals occupying particular habitats or microhabitats. Hermit Thrushes in dry pine-oak forest may very well be defending territories but, until we can show differential survival rates among individuals in different habitats, we do not know if Hermit Thrushes prefer dry pine-oak forest or if they are simply in dry pine-oak forest because their preferred habitat is not available. A series of multi-year studies designed to examine species-specific habitat relationships and differential survival rates across the wintering range of a single species would help us to better understand the mechanisms responsible for structuring winter bird communities.

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