Habitat use, abundance, and persistence of Neotropical migrant birds in a habitat matrix in northeast Belize

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ABSTRACT. To ensure adequate protection of nonbreeding habitats used by Neotropical migratory landbirds, we must first address questions about habitat use and quality. On the Yucatan peninsula, migrants use many habitats, several of which remain unstudied, and methodological differences preclude interhabitat comparisons based on studies to date. We used distance sampling along line transects in six habitats in northeast Belize to examine use of previously unstudied habitats (e.g., salt marsh) by Neotropical migrants and to permit comparison across habitats. We calculated unadjusted and adjusted (for detectability) density estimates for individual migrant species and for all species combined to generate hypotheses about habitat quality based on the assumption that density and quality are positively correlated. Adjusted density estimates for all migrants were highest in black mangrove habitat (1799 ± 110 ind/km²), intermediate in three forest types and milpa (range 598–802 ind/km²), and lowest in salt marsh (207 ± 32.3 ind/km²). By combining density estimates with habitat availability in our study region, we estimated that evergreen forest and black mangrove supported 70% and 9% of the region's migrant population, respectively. At the species level, five of the 10 most common species had habitat preferences (>50% detections in one habitat). Given the diversity of habitat preferences among species and apparent seasonal movements, our results indicate that Neotropical migrants in northeast Belize are dependent on a matrix of interconnected habitats.

RESUMEN. **Uso de hábitat, abundancia y persistencia de un migratorio Neotropical en una matriz de hábitat en el noreste de Belize**

Para asegurar la protección adecuada del hábitat no- reproductivo utilizado por aves migratorias Neotropicales terrestres, debemos responder preguntas sobre el uso y la calidad del hábitat. En la península de Yucatán, lasaves migratorias utilizan muchos hábitats, varios de los cuales aún continúan sin ser estudiados. Además las diferencias metodológicas evitan hacer comparaciones inter-hábitat basadas en los estudios que se han hecho hasta ahora. Utilizamos unmuestreo a lo largo de transectos de distancia variable, en seis hábitats, algunos previamente no estudiados (ej. ciénagas salobres), en el noreste de Belize para examinar y comparar el uso por parte de las migratorias Neotropicales, Calculamos estimados de densidad, ajustados y no ajustados (para detectabilidad), para especies particulares de migratorias y para todas las especies combinadas para generar una hipótesis sobre la calidad del hábitat basándonos en la presunción que la densidad estaría positivamente correlacionada con la calidad del hábitat. Los estimados de densidad ajustados para todos los migratorios fueron más altos en mangle negro (1799 ± 100 ind/km²), intermedios en tres tipos de bosque y milpa rango 598–802 ind/km²) y menores en ciénagas salobres (207 ± 32.3 ind/km²). Combinando los estimados de densidad con la disponibilidad de hábitats en nuestra región de estudio, estimamos que el bosque siempreverde y el mangle negro sostienen el 70% y 9% de los migratorios en la región, respectivamente. A nivel de especies, cinco de las 10 especies más comunes tienen preferencias de hábitat (>50% de las detecciones en un hábitat). Dada la diversidad de preferencias de hábitat entre especies y el aparente movimiento estacional, nuestros resultados indican que las aves migratorias Neotropicales en el noreste de Belize dependen de una matriz de hábitats interconectados.

During the nonbreeding period, Neotropical migrants are known to occupy a wide variety of habitats, both natural and human-modified (Conway et al. 1995, Johnson et al. 2006), and appear to be more resilient to habitat modification than resident species (Wallace et al. 1996, Reid et al. 2008). Certain modifications, such as small cultivated clearings within forests, may even enhance habitat quality for species adapted to open or edge habitats (Lynch 1992, Morton 1992, Saab and Petit 1992). For some species, however, modified habitats may be lower in quality than natural habitats, as demonstrated by lower-survival rates and reduced reproductive success through carryover effects (Norris et al. 2003, Bearhop et al. 2004, Johnson et al. 2006).

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Within habitats, quality may also vary over time and thus it is important to examine habitat use during different stages of the nonbreeding period (Lefebvre et al. 1994, Latta and Faaborg 2002). For example, in many areas in the Neotropics, the end of the nonbreeding period coincides with the dry season and differential drying of habitats may influence their importance to migrants (Lefebvre and Poulin 1996, Marra and Holmes 2001, Latta and Faaborg 2002). Habitat availability during the nonbreeding period is increasingly considered a limiting factor for Neotropical migrants (Sherry and Holmes 1996, Marra and Holmes 2001, Latta and Faaborg 2002) and, in a number of species, competition between individuals over territories has been shown to result in saturation of high-quality habitats (Wunderle and Latta 2000, Johnson et al. 2006). It follows that by measuring migrant density in different habitats, we can better understand habitat preferences and quality.

In Belize and the wider Yucatan region, a number of studies have provided baseline information about the use of nonbreeding habitats by Neotropical migrants (Lloyd-Evans 1984, Lynch 1989, 1992, Greenberg 1992, Kricher and Davis 1992, Mills and Rogers 1992, Petit et al. 1992, Piaskowski et al. 2005, 2006). However, widely occurring habitats in the Yucatan region, such as salt marsh, remain unstudied and density estimates corrected for detectability are not available for any habitat or migratory species on the Yucatan peninsula. Further, methodological differences (e.g., mist-nets vs. observations) preclude comparisons of habitat use across studies. Our objective was to compare habitat use by Neotropical migrants in six habitats in northeast Belize, three of which had not been studied previously (salt marsh, black mangrove, and tropical semideciduous broadleaf forest). To assess habitat use, we calculated density estimates by habitat for individual species, the entire migrant community, and for different stages of the nonbreeding season. Using these estimates, we made inferences about habitat quality to migrants and examine the degree to which habitat conservation priorities based on migratory birds overlap with overall species richness and the presence of threatened and endemic species.

METHODS

Our study was conducted in the Corozal district of Belize, primarily near the village of Sarteneja, from 21 November 2007 to 1 March 2008 (hereafter referred to as the winter months or season). The study area has largely escaped human modification and was therefore selected as an example of naturally occurring habitat. In our study area, we selected four study sites (Fig. 1): (1) La Isla (18°20'5.02"N, 88°07'35.76"W), an area south of Sarteneja on the northeast shore of Shipstern Lagoon that consisted of a habitat matrix of salt marsh, black mangrove, semideciduous disturbed forest, and Milpa, (2) Sarteneja Community Lands (18°19'49.07"N, 88°09'11.33"W), an area southwest of Sarteneja village that consisted of Milpas bordering on unbroken semideciduous undisturbed forest and contiguous with Shipstern Nature Reserve, (3) Shipstern Nature Reserve, a private nature reserve located west of Sarteneja where three areas containing both semideciduous undisturbed forest and evergreen forest were surveyed, including an eastern transect (18°19'05.48" N, 88°10'39.44W), western transect (18°17'52.28"N, 88°13'06.80"W), and a "main trail" (18°18'04.19"N, 88°12'44.52"W), and (4) Balam (18°06'24.41"N, 88°16'11.50"W), including the Balam Na private nature reserve and the privately owned Balam Jungle Estate that is located south of the Shipstern Lagoon within the largest contiguous forest block in northeast Belize. The area consisted primarily of evergreen forest.

Six habitat types were present at our four study sites: (1) Milpa agriculture, consisted of a matrix of forest in various stages of succession (see habitat 4) and active cultivated plots (<1 ha). (2) Salt marsh, an open habitat with patches of red mangrove scrub (*Rhizophora mangle*) and littoral forest associated with estuarine lagoons and subject to seasonal flooding. (3) Black mangrove (*Avicenia germinans*), treated separately from other mangrove habitat types (see above) due to a different vegetation structure and avian community. (4) Tropical semideciduous broadleaf forest (disturbed variant), characterized by a low canopy (8–12 m), a greater deciduous component than other forest types in Belize, and was subject to recent or ongoing disturbance mainly
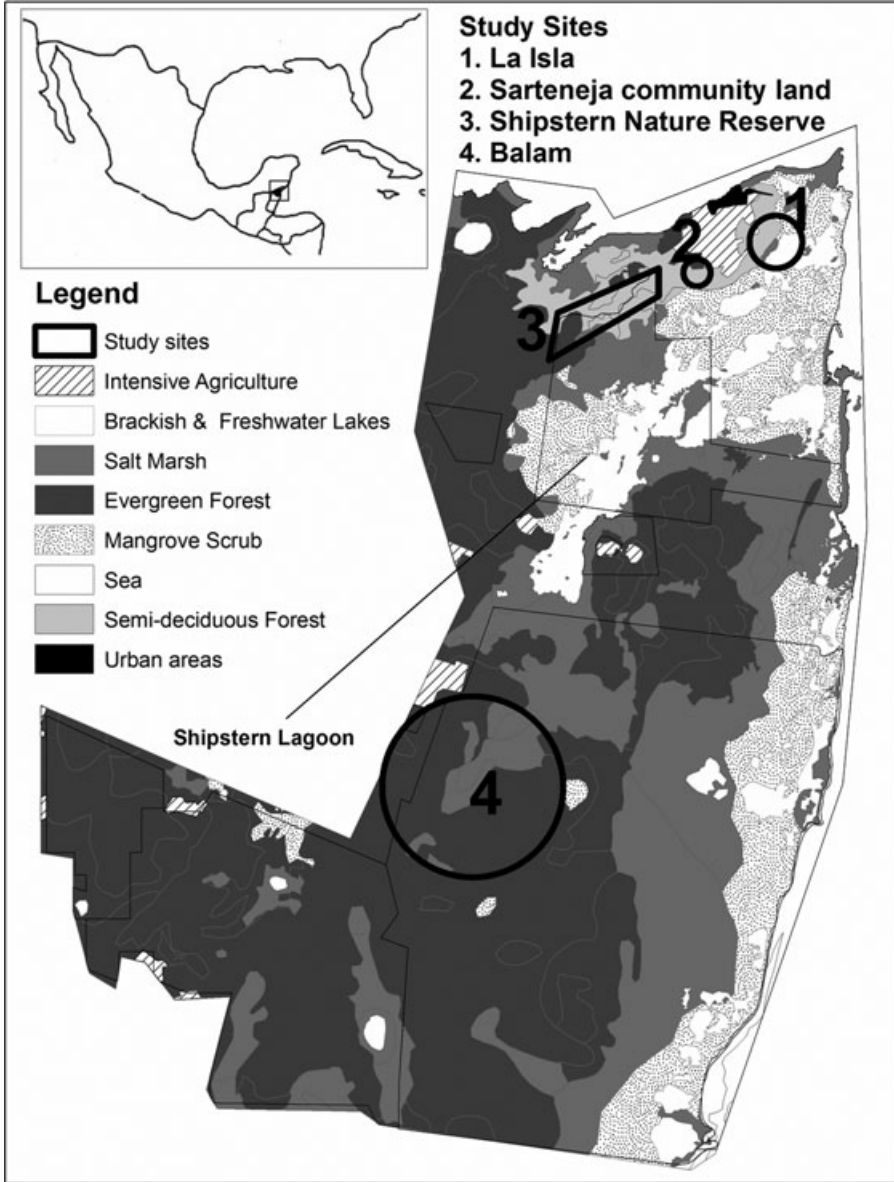
Fig. 1. Location of the study area in Central America and of the study sites (outlined in black and numbered) and habitat types in northeast Belize.

through selective logging and small-scale clearing for agriculture (hereafter, semideciduous disturbed forest). (5) Tropical semideciduous broadleaf forest (undisturbed variant), characterized by a higher canopy and different tree species than habitat 4 due to limited disturbance over the last 20 yrs (hereafter, semideciduous undisturbed forest). (6) Evergreen forest, char-

acterized by having a higher canopy (15–20 m) and greater annual rainfall than habitat types 4 and 5. A more detailed description of these habitats is provided by Meerman and Sabido (2001).

All study sites were affected to some degree by Hurricane Dean that passed north of Belize on 21 August 2007. Our observations indicated

a decreasing gradient of damage from north to south, although the edges of open areas in the south were damaged to the same degree as areas further north. The hurricane caused severe damage to the canopy in some places and this is considered in the evaluation of our data. Hurricanes regularly affect this region and the natural state of these forests is one of recovery.

Field methods. We censused birds along variable-distance transects at all study sites. Transect length was measured using a GPS unit and most transects were 500 m long; two transects in black mangrove were 100 m and 125 m in length, respectively, due to limited patch size. Due to the limitations of working in dense forest, most transects followed existing trails, tracks, or survey lines and were designed to follow as straight a line as possible. Transects were walked within the first 3 h after sunrise at an even pace (mean duration = 29.4 ± 9.1 [SD] min). All birds seen or heard were recorded and assigned to a distance band based on their perpendicular distance from transects. From 20 November 2007 to 28 January 2008, distance bands were: 0–25 m, 25–50 m, and 50–100 m. After 28 January, the number of bands was increased to five to improve the definition of detection curves used in density calculations: 0–5 m, 5–10 m, 10–25 m, 25–50 m, and 50–100 m. Each transect was walked at least 15 times during our study. Raw data are available through the Avian Knowledge Network (www.avianknowledge.net).

To reduce observer bias, we conducted practice surveys along several transects before initiating our study to compare detection abilities, standardize assignment of birds to distance bands, and ensure that both observers could identify the species present by song and call. Further, we each walked individual transects an approximately equal number of times to reduce observer bias. However, we acknowledge that data obtained through audio-visual surveys have inherent biases such as underestimation of secretive species and those that rarely vocalize (Buckland et al. 1992).

Each transect was assigned to one of the six habitat types. Black mangrove (three transects), salt marsh (four transects), and milpa (four transects) were relatively homogenous and easily identified habitats and transects were assigned to them subjectively. For transects in forest (five in semideciduous disturbed forest, four in semideciduous undisturbed forest, and eight in evergreen forest), a series of habitat variables were measured to allow habitat differentiation by cluster analyses. These included three 5 × 5 m plots located at evenly spaced intervals and on alternating sides along the transects. Within plots, habitat variables were measured following a modified version of the method described by James and Shugart (1970) for sampling vegetation in forest and shrub systems (see Martin et al. 1997). In each plot, we estimated mean canopy height and percentage canopy cover by measuring and averaging canopy height and cover at the four corners of the plot, number of snags >10 cm dbh, number of large (> 38 cm dbh), medium (23–37 cm dbh), and small trees (2–22 cm dbh), percent of ground covered by grass, forbs, shrubs, cactus, leaf litter, dead wood, rock, and water, and average leaf litter depth from measurements at the four corners of the plot. We also quantified hurricane damage as the number of recently fallen (whole trees uprooted recently) and broken trees (trees with major limbs or trunk broken by the wind) per plot. In addition, to assess tree composition, we placed three 15 × 5 m "tree strips" per transect where the number of trees (>10 cm dbh) of six common species were counted, including gumbo limbo (*Bursera simaruba*), chicle (*Manilkara sapote*), cotton tree (*Ceiba pentandra*), waree wood (*Caesalpina gaumeri*), black poisonwood (*Metopium browneii*), and salam (*Lysiloma latisilquum*).

Habitat differentiation by cluster analysis. To categorize forest transects by forest type, a matrix containing the habitat structure and tree strip data for each transect was standardized and analyzed with a cluster analysis in the program Minitab (settings: average-linkage between groups method and distance calculated through correlation). Dendrograms were generated to assess the resulting transect groupings by vegetation similarity. To determine if birds perceived and responded to vegetation differences, a cluster analysis using migrant species composition and abundance was also conducted for all transects.

Composition of the migrant community. Species presence was assessed from detections during transects. To determine if we had effectively surveyed the migrant community, we constructed species accumulation curves for

each habitat to see if new species detected reached an asymptote. The point of saturation was defined as the point in the curve where the slope increased less than one new species for every three transects. To assess the relative abundance of all landbird migrant species within the community and by habitat, we calculated unadjusted densities per km² for each species in each habitat. Here, unadjusted densities are the sum of all individuals detected within 25 m on either side of transects and corrected for transect length to give a density/km². A 25-m cut-off was selected for three reasons: (1) most individuals (83.3 ± 14.2%) were detected within 25 m in all habitats, (2) parameter estimates for detection curves and their 95% confidence intervals overlapped in all habitats (indicating comparability) except salt marsh, where detection rates were higher, and (3) the effective strip width for all habitats was greater than 10 m and less than 25 m in all habitats. Given that average detectability was higher in salt marsh, comparisons to salt marsh using unadjusted densities must be treated with caution.

Unadjusted densities underestimate true densities because detection rates are not 100% within 25 m of a transect. Further, because they do not account for differences in detectability among habitats and species, they should be treated cautiously when interpreting small differences between habitats and species. We calculated the average difference between unadjusted and detectability corrected density, hereafter referred to as adjusted density estimates (see below), for four species to determine if relative differences by habitat were reliable when considering unadjusted estimates.

Density and relative abundance by habitat. Overall densities of migrants may be an indication of the relative quality of habitats to wintering birds (Latta and Faaborg 2001, 2002). To examine this possible relationship, we calculated the density of all landbird migrants, regardless of species, by habitat using the program DISTANCE 5.0 (Laake et al. 2006), taking into account variation in detectability among habitats. To allow interhabitat comparisons, we calculated adjusted density estimates for species where we had at least 20 observations per habitat (because the accuracy of estimates increases with sample size) in at least three habitats. Species meeting these criteria included Magnolia Warblers (*Dendroica magnolia*), American

Redstarts (*Setophaga ruticilla*), Hooded Warblers (*Wilsonia citrina*), and Black-throated Green Warblers (*Dendroica virens*). For all adjusted density calculations in DISTANCE, we used detections of birds made after 28 January when distance bands were modified to improve calculation of detection curves and also to represent late-winter densities when habitats are expected to be at their most limiting due to the effects of the dry season (Lefebvre et al. 1994, Johnson et al 2006). Three model sets were tested with stratification by habitat and truncated at 50 m to avoid outlier intervention in function modeling (Buckland et al. 1992): (1) uniform with cosine and simple polynomial adjustment, (2) half normal with hermite polynomial adjustment, and (3) hazard rate with cosine adjustment. Model selection was carried out using Akaike Information Criteria (Buckland et al. 1992).

Because adjusted density estimates could not be calculated for all species, we used unadjusted density estimates (see methods above) to compare the relative abundance of the 10 most common migrant species by habitat. To examine relative abundance between habitats within species, we created a pie chart for each species by converting the unadjusted density estimates by habitat into a percentage of individuals, in a hypothetical population, occupying each of the six habitats. When considering relative habitat use, the reliability of unadjusted density estimates is expected to depend on the similarity of detectability between habitats (Thompson 2002, Johnson 2008) and thus comparisons between "forested" habitats are expected to be more reliable than those between open and forested habitats. To examine the reliability of our unadjusted density estimates, we converted the adjusted density estimates calculated for four species (see above) into percentages and compared them to those resulting from the unadjusted densities.

To determine the importance of each habitat in a landscape context, we converted adjusted density estimates for all migrants by habitat into an estimate of the total wintering population in each habitat within the study area (see Fig. 1). This involved multiplying densities by the estimated area of each habitat; the latter was calculated using ArcGIS and an ecosystem map of northeast Belize (Meerman and Sabido 2001).
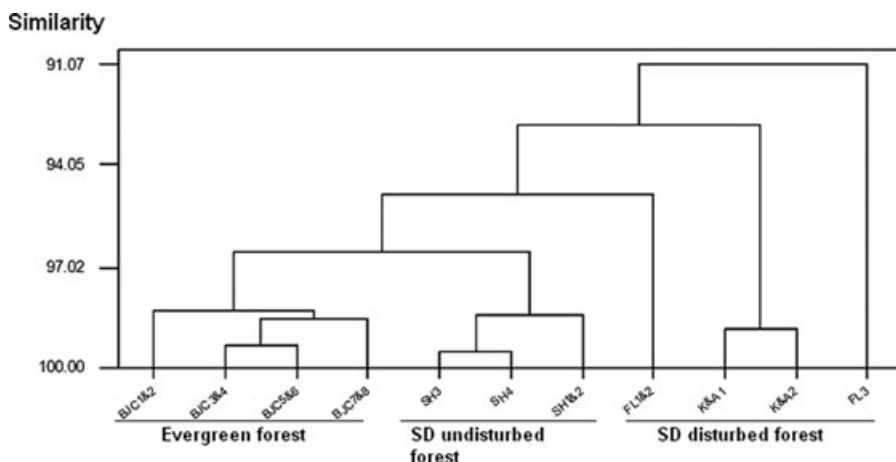
Fig. 2. Dendrogram resulting from a cluster analysis of forest transects by vegetation structure and common tree species composition. Assignment of a particular transect to a habitat type is indicated by three habitat labels, for example, evergreen forest. Individual transect labels correspond to study sites as follows: BJC—Balam, SH—Shipstern Nature Reserve, FL—La Isla (forest transects only), and K&A—Sarteneja Community Lands. SD = semideciduous.

Seasonal persistence by habitat. To examine variation among habitats in species presence and persistence during the winter, data were analyzed for two sampling periods: early winter (21 November–21 December) and late winter (28 January–29 February). We considered just three habitats (milpa, semideciduous disturbed forest, and black mangrove) where at least 5 km of transects had been completed in both periods and only those species where at least one individual was recorded per 500 m transect during one of the periods. Unadjusted density estimates (per km^2) for each period were then calculated using methods described above. To test the null hypothesis that there was no difference in abundance in early and late winter, we ran repeated measures General Linear Models with Poisson errors on the raw count data from transects (again including only birds recorded within 25 m) in Program R (www.r-project.org; package glmmML, model glmmboot).

Habitat prioritization. To assess the overlap between habitat priorities of migrants and those of the wider avian community, we compared species richness and a Priority Diversity Index (PDI):

$$PDI = \sum (E_i A_i)R,$$

where E_i = site endemism index (number of sites where the species i is present), A_i = abundance

score of the ith species, and R = species richness on the site (Bolton and Specht 1983). The PDI was calculated using all bird species (both migrant and resident), giving weight to those that were abundant at a site and restricted to fewer sites (i.e., unique species by habitat) and according to their relative frequency of occurrence in each habitat (Sutherland 2000). Values are presented as means ± 1 SD, except where stated otherwise.

RESULTS

Habitat differentiation through cluster analysis. Habitat clustering by vegetation structure and tree composition coincided with our subjective assignment of transects to habitat types. The grouping reflected both the degree of moisture and disturbance in the forest types, with evergreen forest at one end of the spectrum and semideciduous disturbed forest at the other (Fig. 2). The cluster analysis of all habitats by migrant species composition and abundance revealed a similar pattern. This indicated that the measured habitat differences were also perceived by migrants and thus we maintained the habitat designations from the cluster analysis for all subsequent analyses.

Composition of the migrant community. Along 84.7 km of transects, we recorded 2225

Table 1. Unadjusted densities[a] per km² for all species of migrant landbirds detected in six habitat types during the winter in northeast Belize. The mean represents the average density if all habitats were equally represented in the environment.

Common name	Scientific name	Black mangrove	Milpa	Semideciduous– undisturbed	Evergreen forest	Semideciduous– disturbed	Salt marsh	Mean
Yellow-bellied Flycatcher	*Empidonax flaviventris*	–	–	7.1	4.7	–	–	2.0
Least Flycatcher	*Empidonax minimus*	5.8	44.7	2.4	–	0.8	–	8.9
White-eyed Vireo	*Vireo griseus*	17.3	92.9	11.9	40.0	39.2	4.0	34.2
Yellow-throated Vireo	*Vireo flavifrons*	1.4	1.2	–	2.4	0.8	–	1.0
Wood Thrush	*Hylocichla mustelina*	–	–	2.4	18.8	4.7	–	4.3
Gray Catbird	*Dumetella carolinensis*	86.3	23.5	19.0	9.4	25.9	20.0	30.7
Blue-winged Warbler	*Vermivora pinus*	–	–	–	–	1.6	–	0.3
Northern Parula	*Parula americana*	116.5	10.6	–	4.7	2.4	8.0	23.7
Yellow Warbler	*Dendroica petechia*	–	1.2	–	–	0.8	–	0.3
Magnolia Warbler	*Dendroica magnolia*	92.1	120.0	97.6	96.5	114.5	10.0	88.4
Yellow-rumped Warbler	*Dendroica coronata*	8.6	1.2	–	2.4	–	44.0	9.4
Black-throated Green Warbler	*Dendroica virens*	67.6	65.9	33.3	9.4	51.8	–	38.0
Yellow-throated Warbler	*Dendroica dominica*	5.8	1.2	–	–	–	–	1.2
Black-and-White Warbler	*Mniotilta varia*	59.0	9.4	19.0	14.1	31.4	2.0	22.5
American Redstart	*Setophaga ruticilla*	89.2	24.7	83.3	82.4	56.5	4.0	56.7
Worm-eating Warbler	*Helmitheros vermivorus*	–	–	7.1	9.4	0.8	–	2.9
Ovenbird	*Seiurus auricapillus*	–	1.2	–	2.4	3.1	–	1.1
Northern Waterthrush	*Seiurus noveboracensis*	212.9	–	–	2.4	–	16.0	38.6
Kentucky Warbler	*Oporornis formosus*	–	–	–	11.8	1.6	–	2.2
Common Yellowthroat	*Geothlypis trichas*	73.4	8.2	–	–	–	60.0	23.6
Hooded Warbler	*Wilsonia citrina*	14.4	28.2	59.5	54.1	43.9	–	33.4
Yellow-breasted Chat	*Icteria virens*	5.8	–	–	–	–	–	1.0
Summer Tanager	*Piranga rubra*	5.8	2.4	–	–	–	–	1.4

[a] Unadjusted density was calculated by summing all individuals detected within 25 m on either side of transects and correcting for transect length to give a density/km².

Table 2. Species diversity and adjusted densities by habitat for all Neotropical migrant landbirds recorded during late winter (28 January–29 February) in northeast Belize. In combination with estimates of available habitat in the study area, densities have been converted into estimates for the total number of migrants spending the nonbreeding season in each habitat. We accounted for differences in detectability among habitats.

Habitat	No. of migrant species	Migrants/ km² ± SE	N^a	Habitat area in study area (km²)	Estimated number of individuals in study area
Black mangrove	17	1799.6 ± 110.4	448	29.63	53,320
Milpa	16	802.2 ± 65.7	264	8.71	6983
Semideciduous undisturbed forest	11	674.9 ± 64.9	132	10.16	6856
Evergreen forest	17	609.6 ± 47.2	167	676.93	412,648
Semideciduous disturbed forest	17	598.3 ± 50.0	352	49.32	29,508
Salt marsh	10	207.2 ± 32.3	51	377.36	78,170
				TOTAL	**587,487**

[a]N = total number of individuals detected.

individuals of 23 landbird migrant species during the winter season in northeast Belize (Table 1). Although generally similar across habitats, species richness was lower in semideciduous undisturbed forest and salt marsh (Table 2). Species accumulation curves showed that detection rates of migrant species reached a point of saturation in all habitats after a maximum of 15 transects, with more open habitats apparently reaching saturation faster than closed-forest habitats (11 transects for milpa and salt marsh, 12 transects for black mangrove, 13 transects for semideciduous disturbed and undisturbed forest, and 15 transects for evergreen forest).

Of all birds detected along transects, regardless of habitat, 43.3 ± 13.2% were migratory. This percentage varied among habitats, with black mangrove having the highest percentage (62.4%), followed by semideciduous disturbed forest (45.8%), milpa (40.0%), salt marsh (32.6%), evergreen forest (28.6%), and semideciduous undisturbed forest (27.5%). Overall abundance across all habitats varied among species, with some being abundant, for example, Magnolia Warblers, and others found in lower numbers, for example, Blue-winged Warblers (*Vermivora pinus*; Table 1). Habitat use also varied considerably, with five of the 10 most common species occurring primarily (45–92% of detections) in black mangrove (Fig. 3). Other species either showed more uniform unadjusted densities across habitats or occurred more in forest habitats (Table 1, Fig. 3).

Density and relative abundance by habitat.   Our adjusted density estimates indicate that, regardless of species, the highest density of migrants was found in black mangrove, with densities more than two times greater than in any other habitat (Table 2). Milpa had higher densities than the other three forest habitats, and densities were markedly lower in salt marsh. Adjusted density estimates for Magnolia Warblers, American Redstarts, Hooded Warblers, and Black-throated Green Warblers were higher than the unadjusted density estimates, as would be expected when correcting for detectability (Table 3). For these species, differences averaged 3.5 ± 2.3%, with a maximum difference of 7%. Unadjusted density estimates were therefore assumed to be reliable indices of differential habitat use when variation was greater than 10% (Table 1, Fig. 3), whereas differences less than 10% were considered partly or wholly a result of differences in detectability.

Habitat area estimates and subsequent extrapolation from the density of migrants per habitat suggest that evergreen forest supported the greatest number of Neotropical migrants in our study area (Table 2). Our analysis also demonstrated that a large number of migrants are found in salt marsh, albeit at low densities.

Seasonal persistence by habitat.   Differences in abundance and persistence were evident between early and late winter and among different habitats (Table 4). Many of these differences were not significant, possibly in part because our analysis lacked the power to
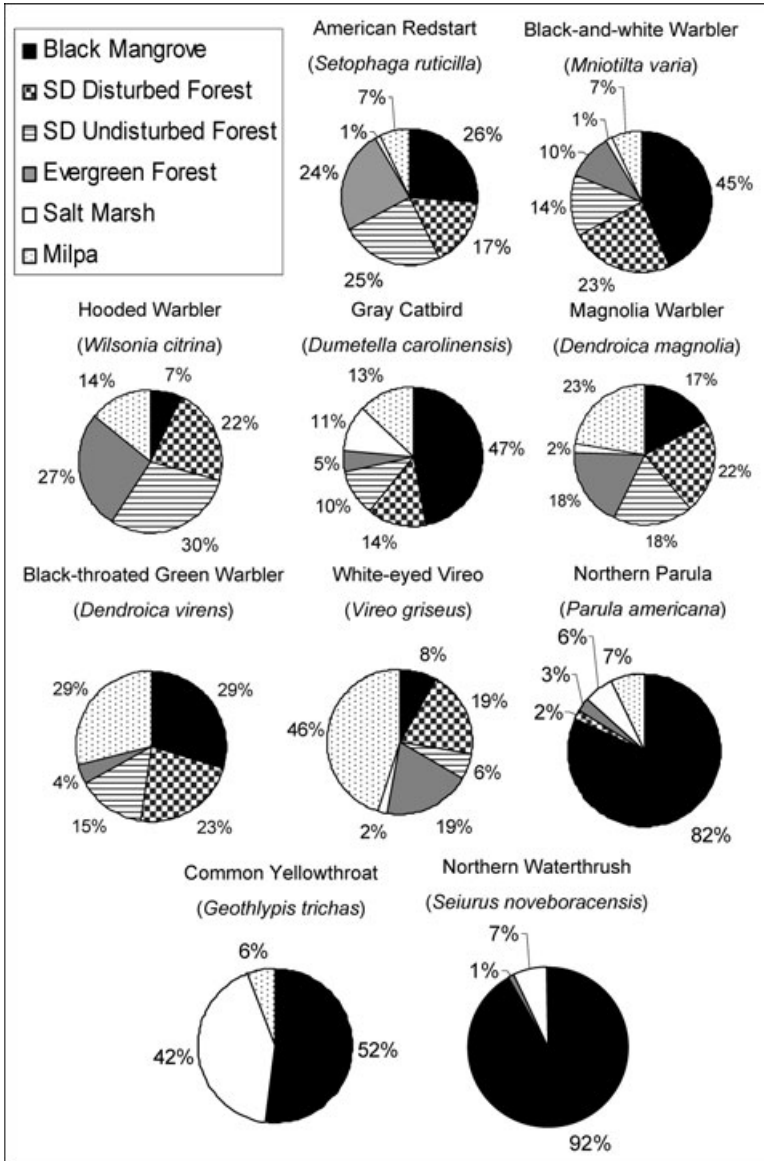
Fig. 3.   Relative abundance by habitat of the 10 most common species of Neotropical migratory birds wintering in northeast Belize. Corrections have not been made for varying detectability between habitats. Percentages were generated by converting unadjusted density estimates into the percentage of individuals in a hypothetical population occupying each of the six habitats.

detect small changes (only changes >60% were significant). In black mangrove habitat, densities of Gray Catbirds (*Dumetella carolinensis*) and Northern Parulas (*Parula americana*) decreased from early to late winter, whereas densities of Northern Waterthrushes (*Seiurus noveboracensis*) and Common Yellowthroats (*Geothlypis trichas*)

increased (Table 4). In semideciduous disturbed forest, densities of Black-throated Green Warblers increased significantly from early winter to late winter (Table 4).

Habitat prioritization.   Habitats with the highest migrant species richness also had the highest PDI scores (Table 5). Evergreen forest

Table 3. Adjusted density estimates (individuals/km² ± SE), corrected for detectability, of four species of Neotropical migrants in five habitat types in northeast Belize during late winter (28 January–29 February). Number of individuals detected is given in parentheses.

Species[a]	Black mangrove	Semideciduous disturbed forest	Milpa	Semideciduous undisturbed forest	Evergreen forest
Magnolia Warbler	210.8 ± 57.4 (52)	198.7 ± 33.1 (104)	206.7 ± 59.8 (75)	206.6 ± 59.8 (36)	129.2 ± 25.0 (43)
American Redstart	154.8 ± 45.3 (42)	119.7 ± 28.9 (47)	–	136.5 ± 27.0 (34)	–
Hooded Warbler	–	52.3 ± 11.5 (32)	–	114.2 ± 32.0 (20)	111.8 ± 20.3 (24)
Black-throated Green Warbler	176.1 ± 24.3 (35)	118.6 ± 33.4 (56)	116.8 ± 26.9 (44)	–	–

[a]See Table 1 for scientific names.

and semideciduous disturbed forest had the highest PDI ranking, followed by black mangrove. Density estimates alone (see above), if considered as an indication of habitat quality, would give black mangrove a higher ranking than either species richness or PDI scores.

DISCUSSION

The composition of the Neotropical migrant community wintering in our study area was similar to that reported in other areas of Belize and the wider Yucatan (Greenberg 1992, Petit et al. 1992). However, the relative abundance of individual species differed from other studies, likely reflecting the unique habitat matrix in northeast Belize. Because our data were collected over just one winter and much of our study area had recently been affected by a hurricane, our results may not represent typical or average conditions. Additional study in the region is needed to fully understand the migrant communities and the impact hurricanes may have on them. Nevertheless, the broad-scale patterns that we found for previously unstudied habitats, for example, salt marsh, improve our understanding of the use of the diverse habitats present in the Neotropics by migrants. Also, both our unadjusted and adjusted density estimates for migrants in the Yucatan region should provide a point of comparison for future studies.

Among individual species, Wood Thrushes (*Hylocichla mustelina*), Ovenbirds (*Seiurus auricapillus*), and Kentucky Warblers (*Oporornis formosus*) have been found to be more abundant in central Belize (Piaskowski et al. 2005) and in the Maya Mountains than at our study sites (pers. obs., see also Conway et al. 1995). Other species, such as Magnolia Warblers and Gray Catbirds, were among the most abundant species both in our study in northeast Belize and in studies conducted elsewhere (Kricher and Davis 1992 Piaskowski et al. 2005). The composition of species and abundances in northeast Belize most closely reflected that recorded further north on the Yucatan Peninsula of Mexico (Lynch 1989, 1992, Greenberg 1992), likely because of the intermediate position of our study area and the presence of forest types that represent the transition from Yucatan dry forests to the humid evergreen forests of southern Belize.

Table 4. Unadjusted density estimates[a] of common Neotropical migrants in "early" and "late" winter in three habitat types in northeast Belize and the significance of changes between periods. Species inclusion was dependent on at least one individual being recorded per 500 m transect in one period. No correction has been made for differences in detectability. Thus, comparisons should only be made within and not between habitats. SD = semideciduous.

	Species[b]	Unadjusted density estimates (Individuals/km^2)		
		Early winter[c]	Late winter[d]	P[e]
Black Mangrove	Gray Catbird	117.5	71.8	**0.035**
	Northern Parula	226.0	65.4	**<0.001**
	Black-throated Green Warbler	58.8	71.8	0.55
	Magnolia Warbler	76.8	99.2	0.21
	Black-and-White Warbler	67.8	54.9	0.58
	American Redstart	94.9	86.5	0.82
	Northern Waterthrush	131.1	251.2	**0.003**
	Common Yellowthroat	36.2	90.8	**0.012**
SD Disturbed Forest	White-eyed Vireo	28.2	41.4	0.17
	Black-throated Green Warbler	18.8	65.7	**0.001**
	Magnolia Warbler	105.9	127.1	0.22
	American Redstart	51.8	58.6	0.87
	Hooded Warbler	56.5	37.1	0.16
Milpa	White-eyed Vireo	108.0	85.5	0.84
	Black-throated Green Warbler	40.0	74.5	0.13
	Magnolia Warbler	100.0	120.0	0.42
	Hooded Warbler	48.0	21.8	0.16

[a]Unadjusted density estimates were calculated by summing all individuals recorded within a 25-m strip on either side of transects and multiplying by an appropriate factor to give a value per km^2.
[b]See Table 1 for scientific names.
[c]Early winter = 21 November–21 December.
[d]Late winter = 28 January–29 February.
[e]Significance tests were conducted using a repeated measures General Linear Model with Poisson distributed errors.

The mean proportion of migrants to resident birds detected in our study (43 ± 13.2%) was comparable to that reported in other areas of natural habitat in Belize and the Yucatan (30–58%, Lynch 1992; 31.7–50.8%, Piaskowski et al. 2005). As in previous studies, we found that the proportion of migrants was lower in undisturbed forest habitats than in modified habitats. For example, Petit et al. (1992) found that 25% of birds captured in mist nets were

Table 5. Comparison of species richness, endangered and endemic species richness, and Priority Diversity Indices (PDI) for six habitat types in northeast Belize.

Habitat	Total number of species	Migrant species richness	Resident species richness	Endangered and endemic species	PDI—all species
Black mangrove	71	17	54	6	13,845
Milpa	79	16	63	6	13,430
Semideciduous undisturbed forest	60	11	49	6	8214
Evergreen forest	80	17	63	5	23,720
Semideciduous disturbed forest	92	17	75	6	21,583
Salt marsh	50	10	40	5	8285

migrants in evergreen forests in central Belize, comparable to the 28.6% observed in evergreen forest in our study. In contrast, Mills and Rogers (1992) found that 50–80.6% of birds in Belizean citrus plantations were migrants, and we found that disturbed forest and milpa both supported higher percentages of migrants than their unmodified counterparts. A possible explanation for the higher percentages of migrants in modified habitats could be that certain species are better able to adapt to changes in their environment or to take advantage of new conditions. Alternatively, intermediate levels of disturbance may increase species richness because disturbed areas may provide a more diverse selection of microhabitats and resources (Huston 1979).

Density and relative abundance by habitat. Many of the species we observed were found in all habitats, especially if salt marsh is excluded. However, some species occurred primarily (>50%) in one habitat, such as Northern Waterthrushes, Northern Parulas, and Common Yellowthroats in black mangrove (Fig. 3). Even for species recorded more uniformly across habitats, our density measures suggest there are habitat preferences, for example, American Redstarts and Black-and-White Warblers (*Mniotilta varia*) were found at lower densities in open habitats (i.e., salt marsh and milpa) and at higher densities in closed forest habitats. For species exhibiting a strong affiliation to one or a few habitats, for example, Northern Parulas, the implications for habitat use and quality are clear. For species found in a range of habitats, preferences are not immediately clear and careful consideration of our various density estimates and seasonal changes in abundance is required to assess habitat preference and quality for these species. Although higher densities may result if a habitat provides more or higher quality resources than surrounding habitats, higher densities could also be the result of competitive exclusion from favored habitats (Rappole 1995, Wunderle 1995, Latta and Faaborg 2001, 2002). Alternatively, high densities could be a product of scale-dependent factors acting at the landscape level, such as total habitat area and its distribution within the habitat matrix (Wunderle and Latta 2000). Ideally, initial density estimates, such as those we present, should be used to generate hypotheses about relative habitat quality that can be tested through detailed studies comparing relative survival among habitats (Conway et al. 1995, Marra and Holmes 2001, Johnson et al. 2006, Faaborg et al. 2007).

We found differences in densities among habitats at the community and species level. Indeed, the average density of migrants of all species in black mangrove, a habitat not previously studied in either Belize or the wider Yucatan, was two times higher than in any of the other five habitats. High densities of birds in black mangrove suggest that, in the landscape context of our study where small patches of black mangrove were surrounded by a matrix of salt marsh and semideciduous forest, this habitat might provide crucial resources for migrants. Indeed, individuals wintering in black mangrove in the Caribbean have higher-survival rates than those wintering in dry scrub (Marra and Holmes 2001). The high quality of black mangrove habitat has been attributed to higher drought resistance. Such resistance means that prey availability remains high and the microhabitat climate remains suitable well into the dry season, unlike habitats such as dry scrub (Marra and Holmes 2001).

Although the density of many migrant species was highest in black mangrove, the implications this has for habitat quality must be carefully considered (Marra and Holmes 2001). Other investigators have found that habitats with lower densities can be of higher quality if dominant individuals defend larger territories (Wunderle 1995, Latta and Faaborg 2002). In our study, all habitats except milpa occurred in relatively large continuous patches, whereas the areas of black mangrove we sampled were small (<1 km^2) and isolated. One hypothesis is that limited availability of black mangrove may have increased competition within patches, making it energetically impossible for dominant individuals to maintain large territories, thereby giving rise to smaller territories and higher densities. On the other hand, density may not depend on territory size, but on the number of nonterritorial wanderers using a habitat, that is, a small patch of "good quality" black mangrove could support many nonterritorial wanderers from adjacent lower-quality salt marsh and semideciduous forest when resource levels are high (Latta and Faaborg 2001, Marra and Holmes 2001). Relating landscape-scale factors to densities and survival rates by habitat is an important future direction for the study of habitat use during the nonbreeding season.

The importance of any habitat to migrant populations is also dependent on its area. Although black mangrove may be of high quality in northeast Belize, preservation of black mangrove alone would conserve only an estimated 10% of the birds wintering in our study area (Table 2). Conversely, evergreen forest covers a large area and is expected to support around 70% of wintering individuals. In addition, a number of species of concern were found almost exclusively in evergreen forest, including Wood Thrushes, Worm-eating Warblers (*Helmitheros vermivorus*), and Kentucky Warblers (Butcher et al. 2007). Salt marsh also covered a large area and, although it supported the lowest densities of any habitat, its widespread availability makes it a potentially important habitat for species such as Northern Waterthrushes and Common Yellowthroats.

Finally, the densities presented here and the significance they have for habitat quality must be considered with respect to the impact of Hurricane Dean. The canopy damage caused by this hurricane may have influenced the carrying capacity of the forested habitats and relative densities and species occupancy may change as the forest recovers (Faaborg et al. 2007). For example, semideciduous forests may have been subject to greater drying because of canopy gaps, thereby reducing their suitability to species that appear to prefer moister evergreen forest, such as Kentucky Warblers.

Seasonal persistence by habitat. Just as the abundance of migrants varied among habitats, so did the persistence of species within habitats from early to late winter. Of the significant changes in our study, most occurred in black mangrove. These changes could have been a response to the effects of the dry season, with food abundance decreasing along with the area of standing water (>90% in December and decreasing to <10% in February) and opportunistic birds moving to other locations (Lefebvre et al. 1994, Lefebvre and Poulin 1996). However, hurricane damage (e.g., reduced canopy cover) may have caused the black mangrove to dry faster than usual, giving rise to a greater reduction in food abundance and an increased emigration rate than in other years (Lynch 1991, Wallace et al. 1996). Regardless of the cause of these movements into and out of black mangrove, our results reinforce the idea that interconnected habitats are important

for overwinter survival (Murphy et al. 2001). Such connectivity still exists in northeast Belize and further study is required to determine how movements between habitats may enhance survival.

At the species level, Black-throated Green Warblers showed an interesting pattern with an increase in the number of individuals in the three habitats examined. This may reflect not just movements between habitats, but immigration from other areas. The importance of this result is that individuals may not only use more than one habitat during the nonbreeding season, but more than one region (Latta and Faaborg 2001, Marra and Holmes 2001). Although more study is needed, such movements must be considered when determining the importance of habitats and regions for migratory birds to ensure that all areas important for survival are identified.

Habitat prioritization. Based on species richness and migrant densities, black mangrove would be the first priority in terms of habitat protection, followed by milpa, the forested habitats and, finally, salt marsh. However, when considering habitat availability within the landscape context of our study area and our findings on seasonal persistence, black mangrove occupied the smallest area and appeared to decline in quality for some species during the winter. In contrast, evergreen forest is expected to hold the largest population of migrants in northeast Belize and supported the same species richness as black mangrove. If we also consider resident species by giving weight to range restricted species and site endemics (through the PDI), evergreen forest was ranked highest followed by semideciduous disturbed forest and black mangrove. Given that priorities set by differing criteria do not coincide and also that migrant communities varied by habitat, our results support the conclusions of other investigators (Petit et al. 1992, Latta and Faaborg 2001) that protection of a variety of habitats is required to conserve adequate nonbreeding habitat for Neotropical migratory landbirds.

The apparent movements between both habitats and regions in northeast Belize also suggest that interconnected habitats may enable individuals to maximize survival. This is an important topic for future research and for defining habitat prioritization criteria. Further, a deeper understanding of how landscape scale processes affect densities is necessary to fully understand

the relationship between density and habitat quality. In particular, examining how densities and survival vary by patch size in black mangrove would permit a more effective assessment of the value of this habitat for migrants in Central America.

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