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# Bird Community Dynamics and Habitat Associations in Karst, Mangrove and *Pterocarpus* Forest Fragments in an Urban Zone in Puerto Rico

MIGUEL A. ACEVEDO[1,2] AND T. MITCHELL AIDE[2]

[2]*Department of Biology, University of Puerto Rico PO Box 23360 San Juan PR 00931*
[1]*miguel_a_acevedo@yahoo.com*

**ABSTRACT.—Puerto Rico's forest cover decreased to less than 10% in the early 1900's leaving few forest patches available for migrant and resident birds. In this process of deforestation karst hills and coastal wetlands have been some of the most severely modified forest types; however, we know little about their bird community dynamics and their relation with habitat variables. To address this issue we studied bird species composition and habitat characteristics in karst forest and two coastal forested wetlands (mangrove and *Pterocarpus* forest) in the Caribbean island of Puerto Rico. In each forest type, we conducted 10 point counts monthly for two years and characterized habitat variables. We performed a non-metric multidimensional scaling (NMS) ordination and a multi-response permutation procedure (MRPP) for each year to determine the similarity of bird species composition among monthly censuses and the relation between species composition and habitat variables. This ordination technique grouped censuses into three groups: karst forest, *Pterocarpus* and mangrove in the migratory period, and *Pterocarpus* and mangrove in the non-migratory period. The high tree species richness in the karst forest, and the presence of standing water in coastal wetlands were the most important habitat variables associated with the different bird communities. Our results demonstrate that the karst and coastal wetlands forests, even if they are small patches surrounded by a mixed matrix of pasture and urban settlements may be important habitat for both residents and migrants, and suggest that the protection and restoration of these habitats should be high management and conservation priorities.**

**KEYWORDS.—bird community dynamics, Caribbean, coastal wetlands, karst, neotropical migrants, Puerto Rico and resident birds**

## INTRODUCTION

During the 19$^{th}$ and 20$^{th}$ century most Caribbean islands were severely deforested for agriculture and other uses (Lugo et al. 1981, Grau et al. 2003, Aide and Grau 2004). Dry, moist, wet and karst forests were all severely deforested, but the conversion of lowland forest, particularly wetlands, to sugarcane plantations lead to the greatest reduction in forest cover. By the 1940's in Puerto Rico only 7% of the original forest cover remained (Dietz 1986), but socioeconomic changes in the 1950's initiated a shift from agriculture to small-scale industry. This socioeconomic shift resulted in the abandonment of most agricultural fields and by 2000 forest cover had increased to approximately 40% (Martinuzzi et al. 2003). Today these new secondary forests and the few remaining patches of old-growth forests are the forest habitats available for resident and migrant birds.

Although forest cover has increased, resident and migrant birds differ in the habitat use of these new secondary forests and forest remnants. For example, resident species, especially forest interior and endemic species occur throughout the island, but are more abundant in the central mountains and karst hills (Acevedo and Restrepo 2008). These regions contain areas of old forest and old secondary forest and thus have a complex forest structure and abundant fruit and seed resources for frugivores and granivores (Carlo et al. 2003, Lugo et al. 2001). In contrast, nearctic/neotropical migrants use both disturbed and undisturbed forests (Blake and Loiselle 1992, Kricher and Davis 1992, Robbins et al. 1992, Conway et al. 1995, Currie et al. 2005); however, coastal brackish and freshwater forested wetlands are one of the habitats with the highest abundance of migratory birds (Lynch 1989), especially on Caribbean islands (Wunderle and Waide 1993). This preference for coastal wetlands is related to the high insect biomass associated with standing water (Johnson and Sherry 2001). In addition to coastal wetlands, the Caribbean karst hills are also habitat for >100 species of migrant birds (Lugo et al. 2001).

Even though coastal wetlands and karst hills are important habitats for both resident and migrant birds (Carlo et al. 2003), most studies in the Caribbean have focused on sub-tropical rain forest (Waide and Narins 1988, Pardieck and Waide 1992, Wunderle 1995b, Latta and Wunderle 1996) and sub-tropical dry forest (e.g. Faaborg and Winters 1979, Faaborg 1982, Faaborg et al. 1984, Arendt and Faaborg 1989, Faaborg and Arendt 1995). However there is little information on bird community composition and dynamics on these new secondary forests and forest remnants, which are often surrounded by an urban matrix. To address this issue we studied bird species composition and habitat characteristics in karst forest and two coastal forested wetlands (mangrove and *Pterocarpus* forest) on the Caribbean island of Puerto Rico. Specifically, we ask the following questions, (1) How does bird species composition vary among these three forest types? (2) How does species composition change throughout the year? (3) What are some of the important habitat variables associated with different bird species composition in these forest types?

## METHODS

### *Study Site*

The study was conducted in the municipality of Toa Baja, in northern Puerto Rico (18° 28′ N, 66° 13′ W) where we censused three lowland forest types: karst (15 ha), mangrove (41 ha), and *Pterocarpus* (12 ha). The karst forest is associated with the karst geology that extends along the northern coast of Puerto Rico. It is characterized by a high diversity of plant species and complex forest structure (Chinea and Helmer 2003, Brandeis 2006). The mangrove forest, dominated by *Laguncularia racemosa*, is one of the largest mangrove patches in the north coast of the island. The *Pterocarpus* forest is a brackish-water forested wetland dominated by *Pterocarpus officinalis*. This site is the third largest *Pterocarpus* forest on the island (Cintrón 1983, Alvarez-López 1990, Rivera-Ocasio et al. 2007). These forest fragments are contiguous to each other and are surrounded by a complex matrix of seasonally flooded wetlands dominated by *Typha dominguensis*, cattle pastures and urban settlements.

### *Bird Censuses*

We censused bird species for two years in the three forest types: karst, mangrove and *Pterocarpus* forest. Monthly censuses were conducted between August 2002 and July 2004. Ten census points were established in each forest type. The distance between points was 100-300 m with the exception of two points in the karst forest, which were separated by 75 m due to the topography of the hills. Each point was visited once a month. Birds were surveyed using 20 m fixed-radius point counts (Hutto et al. 1986, Wunderle 1994). The same observer recorded all birds seen or heard during a 10-minute period at each point for the duration of the study. The position of each bird was determined to be inside the 20 m radius or outside. Censuses started at sunrise and ended no later than 10:00 hrs. Each census included the 10 points in each forest type. Censuses were cancelled if there was rain in the morning or the night before the census. After nine months we analyzed species area curves. These species area curves included the cumulative number of species detected by increasing number of points for each forest type and for each of the nine months, to determine if 10 points were sufficient for documenting species richness. All curves approached an asymptote.

To examine changes in detectability of resident species due to increased activity during the breeding season we used the detectability index described by Hutto et. al.

(1986). We compared detectability during and outside the breeding season. For examples on the use of this index see Wunderle (1995a). We did not find any significant difference in detectability for any of the species in any of the forest types, with the exception of the Black-whiskered Vireo in mangrove ($U = 28.0$, $P = 0.03$) and karst ($U = 33.0$, $P = 0.01$). This species is a summer resident that migrates the rest of the year, but some individuals stay year-round (Cruz 1980). Thus it was more detectable in the summer. Since we only found differences in detectability in one species we assume that our observations and results are not biased.

*Habitat Characterization*

We characterized the habitat within each of the 30 census points. We identified and measured the diameter at breast height (DBH) of all trees greater than 10 cm inside the 20 m radius census point (1,256 $m^2$). Two perpendicular 40 x 2 m transects were established in each census area in which we identified and measured trees smaller than 10 cm. These transects were also used to calculate the number of foliage layers, percent canopy cover and percent ground cover (herbs, leaf litter, woody litter, rock, and standing water). For all variables we took 10 measures (one measure every 4 m) in each transect for a total of twenty measures for each census plot ($N = 20$). We used a 4.5 cm diameter sighting tube to estimate percent canopy cover and percent ground cover of rock, bare soil, water, herbs, woody litter, and leaf litter.

*Statistical Analyses*

Non-metric Multidimensional Scaling (NMS) was used to analyze monthly censuses based on bird species composition and abundances and their relation to habitat variables. NMS makes an iterative search for the least stress position of data on *k*-dimensions and uses ranked distances measured in community data sets to present relationships between sites or species, and between species and habitat measures, in our case bird species abundances and habitat variables (Clarke 1993, McCune & Grace 2002). NMS is an ordination technique that has several advantages over others traditionally used for the same purposes (e.g., DCA and CCA) because it does not assume linearity of the data nor does it require data transformation (Clarke 1993, McCune & Grace 2002). All ordination analyses were done using PC ORD 4.

The NMS ordination grouped monthly censuses based on bird species abundances. To perform these analyses we used the Sørensen index to create the distance matrix, a random starting configuration with a maximum of 6 axes, a stability criterion = 5 $x10^{-5}$, 50 permutations with real data, and a Monte Carlo test based on 50 permutations. The final solution was determined by a combination of results from the Monte Carlo test, and the minimum number of dimensions that provided the lowest stress and instability (McCune & Grace 2002). In addition, we performed a cluster analysis and a multi-response permutation procedure (MRPP). A Sørensen distance measure was used to perform the MRPP analysis. These analyses are used to group ordination points (i.e. monthly censuses) and identify the number of groups that best describes the ordination.

Given the high sensitivity of NMS ordinations for outliers, we performed an outlier analysis. This outlier analysis suggested that the Bananaquit, which is the most common species in all three forest types, should be removed from the analysis because its average distance in ordination space (206.59) was much higher than Adelaide's Warbler (59.75) and Northern Waterthrush (47.50) which were the species with the highest average distances following the Bananaquit.

Habitat characteristics were included as a secondary matrix in the NMS analysis to show correlations between habitat variables and monthly censuses. In addition these habitat variables were compared among sites using a Kruskall-Wallis nonparametric test. Each census point was considered as an independent observation. Since the Kruskall-Wallis analysis is sensitive to a difference of a single treatment (i.e.

forest type), we used a Mann-Whitney test for post-hoc pair-wise comparison.

## RESULTS

Comparison of Habitat Characteristics—Forest structure varied greatly among the three forest types (Table 1). The karst forest was characterized by a high abundance of small trees (1-10 cm DBH), and a high richness of woody species. The *Pterocarpus* forest was characterized by the highest average percent canopy cover, the lowest abundance of smaller trees, but the highest abundance of larger trees (10-30 cm DBH). The mangrove forest had the highest average canopy height and the highest number of foliage layers. It also had intermediate values in all categories of tree abundance. Ground cover variables also varied among sites. The karst forest was characterized by a high percent cover of leaf litter, woody litter, herbs, and rock (Table 1). The *Pterocarpus* forest was characterized by the highest percent cover of standing water, while the mangrove forest had the highest percent cover of bare soil.

The karst habitat was very different in comparison to the two wetland habitats. For instance, the *Pterocarpus* forest had a significantly higher mean abundance of trees 15-20 cm DBH and 20-25 cm DBH size classes ($U = 67.0$, $P = 0.0046$; $U = 66.5$, $P = 0.0041$). In addition it had a higher percent of standing water ($U = 71.0$, $P = 0.0113$) and greater canopy cover ($U = 72.5$, $P = 0.0156$). In contrast, the mangrove forest had a higher abundance of trees in the 5-10 cm DBH size class ($U = 139.0$, $P = 0.0113$). In addition, the mangrove forest had a higher number of foliage layers ($U = 152.0$, $P = 0.0004$) and a greater cover of bare soil ($U = 151.0$, $P = 0.0006$).

Bird Community and Composition Dynamics—A total of 7200 min of observations were conducted in the three forest types over a two-year period and a total of 39 species were observed (see Appendix for common and scientific names of species and mean detections per habitat). A species-time curve (Fig. 1) for these forest

TABLE 1. Comparison of habitat variables measured at a total of 30 point-count sites (10 in each forest type) in karst, mangrove, and *Pterocarpus* forest fragments on the north coast of Puerto Rico. See text for description of variables and their measurement. *P* values shown for the Kruskall-Wallis test.

| Habitat variables | Forest types (mean ± SD) | | | KW test results |
|---|---|---|---|---|
| | Karst | Mangrove | Pterocarpus | |
| Floristics | | | | |
| Tree species richness | 14.7 ± 3.47 | 2.8 ± 1.14 | 2.2 ± 0.63 | $H = 20.06$, $P < 0.001$ |
| Forest structure | | | | |
| Canopy Height (m) | 7 ± 1.83 | 10 ± 1.23 | 9 ± 1.17 | $H = 9.39$, $P = 0.009$ |
| Canopy Cover (%) | 60 ± 9.91 | 60 ± 6.23 | 69 ± 5.57 | $H = 6.86$, $P = 0.032$ |
| Foliage Layers | 3.5 ± 1.09 | 3.9 ± 0.69 | 2.1 ± 0.71 | $H = 15.45$, $P < 0.001$ |
| Trees abundance size classes (# trees/0.13 ha) | | | | |
| 1-3 cm DBH | 43.1 ± 11.69 | 16.9 ± 5.76 | 13.7 ± 10.20 | $H = 15.99$, $P < 0.001$ |
| 3-5 cm DBH | 20.8 ± 11.39 | 10.6 ± 3.84 | 7 ± 5.06 | $H = 11.14$, $P = 0.004$ |
| 5-10 cm DBH | 14.2 ± 6.78 | 7.7 ± 5.14 | 2.8 ± 3.19 | $H = 15.37$, $P < 0.001$ |
| 10-15 cm DBH | 28.8 ± 11.37 | 26.9 ± 15.16 | 39 ± 32.05 | $H = 0.95$, $P = 0.622$ |
| 15-20 cm DBH | 14.6 ± 7.28 | 14.9 ± 4.53 | 35 ± 18.86 | $H = 10.61$, $P = 0.005$ |
| 20-25 cm DBH | 6.9 ± 4.04 | 10.1 ± 4.68 | 28.4 ± 13.57 | $H = 12.97$, $P = 0.002$ |
| 25-30 cm DBH | 3.5 ± 2.46 | 9.8 ± 5.63 | 14 ± 7.80 | $H = 11.06$, $P = 0.004$ |
| Ground cover (%) | | | | |
| Leaf Litter | 52 ± 17.48 | 11 ± 9.17 | 17 ± 13.22 | $H = 17.25$, $P < 0.001$ |
| Woody Litter | 23 ± 9.56 | 20 ± 10.15 | 14 ± 7.44 | $H = 5.09$, $P = 0.078$ |
| Standing water | 0 | 42 ± 14.44 | 64 ± 18.40 | $H = 22.34$, $P = 0.001$ |
| Bare soil Ground | 4 ± 8.29 | 15 ± 13.29 | 2 ± 2.72 | $H = 13.30$, $P = 0.001$ |
| Herbs Ground | 14 ± 8.68 | 11 ± 9.66 | 4 ± 2.52 | $H = 9.07$, $P = 0.011$ |
| Rock Ground | 6 ± 4.43 | 0 | 0 | $H = 15.68$, $P < 0.001$ |

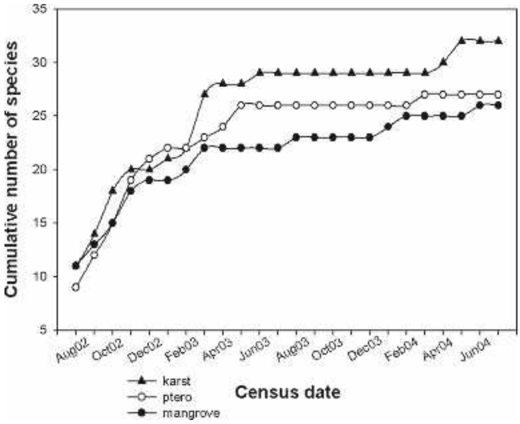


FIG. 1. Species time curves for two years (August 2002-July 2004) of bird censuses in karst, mangrove, and *Pterocarpus* forest fragments on the north coast of Puerto Rico.

types shows that after eight months of censuses we had detected 84% of the total bird species detected in two years.

The karst forest had the highest number of bird species (32 species) followed by the *Pterocarpus* forest (27 species) and the mangrove forest (26 species) (Fig. 1). In March 2003 there was a marked increase in number of species detected corresponding to the time in spring when migrants depart for North America. Migrants are highly detectable on arrival in October-November when they are searching for a place to settle and in spring because they are departing. The other additions to the cumulative number of species were single individuals of rare species.

Migrant and resident bird species richness varied largely depending on month and forest type. There were two main peaks in species richness shared by the three forest types. One corresponds to March, April, and May, which is the breeding season for most of the resident bird species. The second corresponds to November through February the period when migrants arrive or pass through Puerto Rico (Fig. 2).

The NMS ordination based on bird abundance for year 1 (August 2002-July 2003) extracted two axes that explained most of the variance. Axis 1 explained 18.3% of the variance and axis two explained 62.6% (not rotated; orthogonality = 99.0%; Fig. 3a). A cluster analysis followed by a MRPP grouped census points in four groups ($A$ = 0.3113, $P$ < 0.001). Axis 2 separated wetland censuses (*Pterocarpus* and mangrove) from the karst censuses. All censuses corresponding to the karst were classified as a single group because the Scaly-naped Pigeon, Puerto Rican Lizard Cuckoo, Nutmeg Mannikin, Adelaide's Warbler, Puerto Rican Bullfinch and the Puerto Rican Tody were unique to this forest type. Axis 1 further divides the wetland habitats into three groups: *Pterocarpus* and mangrove during spring and autumn migration period (~November-March), *Pterocarpus* and mangrove in the non-migratory period (~April-October), and one group with two *Pterocarpus* censuses (April and June; *Pterocarpus* I). In these two censuses only nine and three species were detected, respectively. The *Pterocarpus* census in September was classified in the group corresponding to the migratory period. Even though this census had no migratory species, the resident species composition was similar to the resident composition in the migratory period.

The NMS ordination based on bird abundance for year 2 (August 2003-July 2004) extracted two axes. Axis 1 explained 18.5% of the variance and axis two explained 64.0% (not rotated; orthogonality = 96.5%; Fig. 3b). A cluster analysis followed by a MRPP grouped the census points into four groups ($A$ = 0.3563, $P$ < 0.001). The pattern in year 2 resembles that of year 1. Axis 1 divided the wetland censuses from karst censuses, which again appeared as a single group. Axis 2 further divided the mangrove and *Pterocarpus* forests into three groups: mangrove and *Pterocarpus* forests in the migratory period, mangrove and *Pterocarpus* forests in the non-migratory period and a single *Pterocarpus* forest census in April that was separated from the rest due to its low bird diversity. Mangrove forest censuses in February and March were grouped within the cluster corresponding to the non-migratory period due to an increased abundance of Zenaida Dove, Loggerhead Kingbird, Mangrove Cuckoo, Black-whiskered Vireo, Puerto Rican Flycatcher, and Red-legged Thrush. This in-

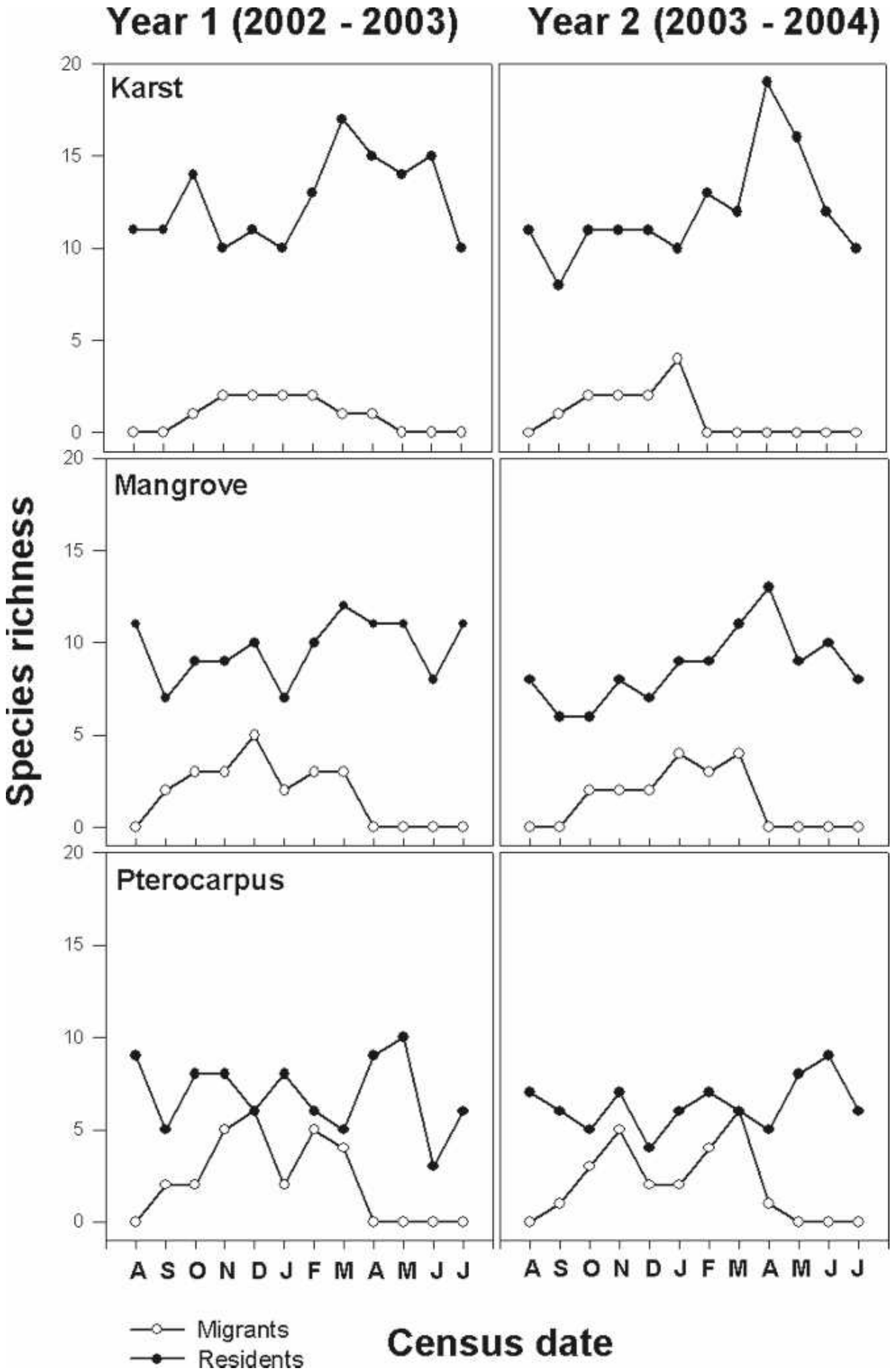


FIG. 2. Monthly dynamics of point counts of nearctic/neotropical migratory and resident bird species richness in karst, mangrove, and *Pterocarpus* forest fragments on the north coast of Puerto Rico. Note the peaks in November-February for nearctic/neotropical migrants, and in March-May for resident species.

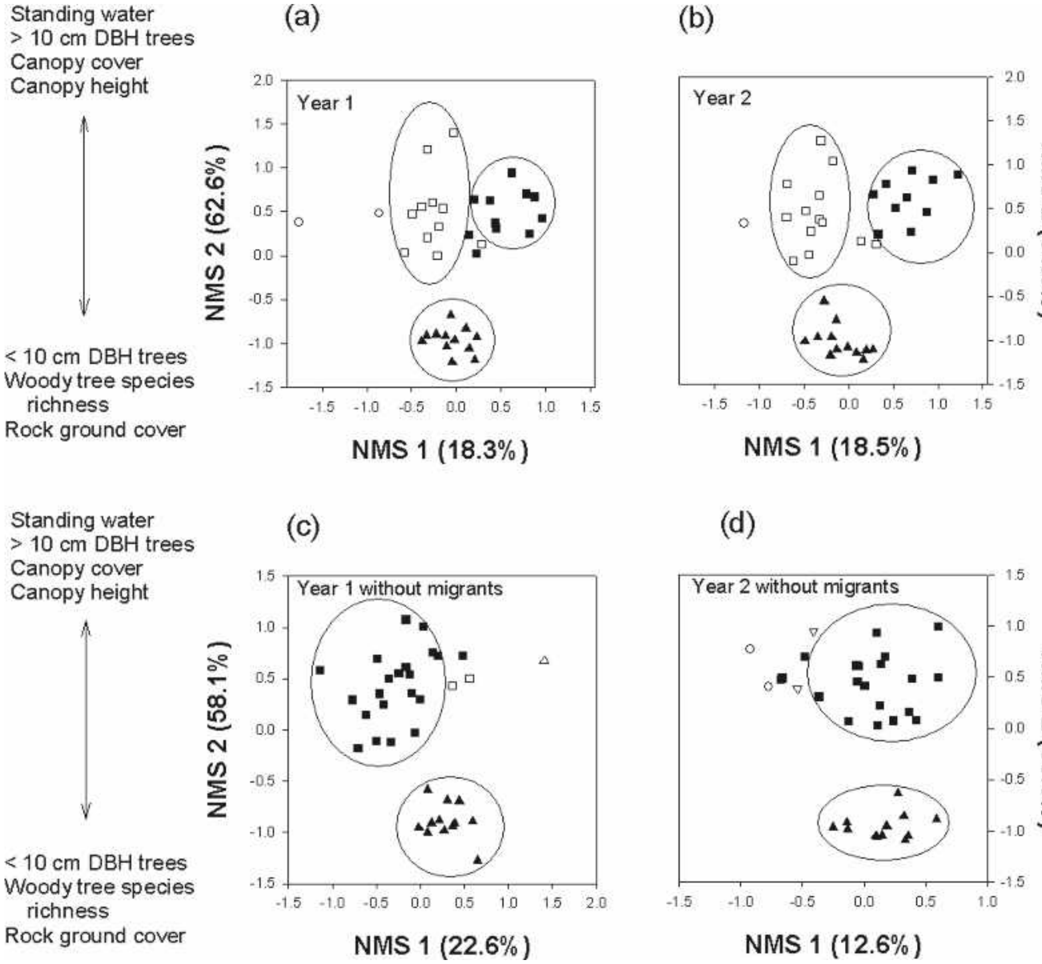


FIG. 3. NMS ordination of monthly census based on bird species abundances based on fixed radius point counts in karst, mangrove, and *Pterocarpus* forest fragments on the north coast of Puerto Rico for (a) year 1 (2002-2003) and (b) year 2 (2003-2004). In year 1 shaded triangles represent all monthly census in the karst. Open squares represent mangrove censuses in August, September, March, April, May, June and July and *Pterocarpus* censuses in August, March, May, and July. These censuses represent the non-migratory period. Shaded squares represent mangrove censuses in October, November, December, January, and February and *Pterocarpus* censuses in September, October, November, December, January and February. These censuses represent the migratory period. Open circles represent two censuses of *Pterocarpus* in June and April. In the second year (b) again shaded triangles represent all monthly censuses in karst. Open squares represent mangrove censuses in August, September, February, March, April, May, June, and July, and *Pterocarpus* censuses in August, September, May, June and July. Shaded squares represent mangrove censuses in October, November, December and January, and Ptero*carpus* censuses in October, November, December, January, February and March. Open circles represent a single census in *Pterocarpus* in the month of April. In the analysis of the first year without migrants (c) shaded triangles represent all monthly censuses in the karst. Shaded squares represent most of the *Pterocarpus* and mangrove censuses which includes all mangrove censuses (August-July), and *Pterocarpus* censuses in August, September, October, January, February, March, April, May, and July. Open squares include *Pterocarpus* censuses in November and December. An open triangle includes a *Pterocarpus* census in June. In the analysis of the second year without migrants (d) shaded triangles again represent all monthly censuses in the karst. Shaded squares represent most *Pterocarpus* and mangrove censuses which includes all mangrove censuses (August-July), and *Pterocarpus* censuses in August, September, October, November, January, May, June, July. Open circles represent *Pterocarpus* censuses in December and February. Open triangles represent *Pterocarpus* censuses in April and March. The circles represent the groups defined by the MRPP and cluster analysis, which include the most number of censuses. Habitat characteristics with correlation >0.70 (above: positive correlation, below: negative correlation) are listed along axis 2. There were no highly correlated variables with NMS axis 1.

crease corresponds to the beginning of the breeding season.

To study the monthly community dynamics of only the resident bird species, we performed the same NMS removing migrants from analysis. The NMS ordination without migrants for year 1 (August 2002-July 2003) extracted two axes. Axis 1 explained 22.6% of the variance and axis 2 explained 58.1% of the variance (not rotated; orthogonality = 92.2%; Fig. 3c). A cluster analysis followed by a MRPP grouped census points into four groups ($A$ = 0.2888, $P$ < 0.001). Axis 2 separated wetland censuses from karst censuses. Axis 1 divided a large cluster which included all mangrove and most *Pterocarpus* censuses from two groups, one which includes two *Pterocarpus* censuses in the migratory period (November and December) and one characterized by censuses with low species richness (June; Fig. 3c).

The NMS ordination without migrants for year 2 (August 2003-2004 July) extracted two axes. Axis 1 explained 12.6% of the variance and axis 2 explained 68.5% of the variance (not rotated; orthogonality = 90.8%; Fig. 3c). A cluster analysis followed by a MRPP grouped census points into four groups ($A$ = 0.3094, $P$ < 0.001). Axis 2 separated wetland censuses from karst. Axis 1 divided a large cluster, which included all mangrove and most *Pterocarpus* censuses from two grouped *Pterocarpus* censuses characterized by low species diversity which were classified in two additional groups (Fig. 3c).

The most significant habitat variables associated with the wetland habitats were large trees (>10 cm DBH), the presence of standing water, a higher percentage of canopy cover and a higher canopy height. In contrast, the most significant habitat variables associated with the karst were smaller trees (<10 cm DBH), a greater diversity of woody tree species and the presence of rock. There were no significant habitat variables separating the *Pterocarpus* forest and mangrove in ordination space (Fig. 3).

From the ordination analysis above we see the dramatic effect of migratory species on bird species composition in the wetland habitats (*Pterocarpus* and mangrove). This effect is not as marked in karst (Fig. 4). The Northern Waterthrush was the second most abundant species in both wetland habitats (0.265 mean detections per point in *Pterocaprus* and 0.785 in mangrove) during the migratory period. In contrast, the most abundant migrant in karst was the Black-and-white Warbler (0.19 mean detections per point). The other migratory species had higher abundance in wetland habitats than in the karst (Appendix).

## Discussion

We addressed three research questions regarding bird community dynamics of three Caribbean forest types (karst, *Pterocarpus* and mangrove forests). First, we asked, how does bird species composition vary among these forest types and second how does species composition changed throughout the year. Our results showed three distinct bird communities (i.e. three groups with different bird species composition), but they did not correspond to the three forest types. Instead they corresponded to (1) the karst forest, (2) *Pterocarpus* and mangrove forests together in the same group during the migratory period (October to March), and (3) *Pteorcarpus* and mangrove forests in the non-migratory period. In the third question we asked what are the most important habitat characteristics associated with different bird species composition in these forest types. We found that the presence of standing water was the most important habitat characteristic associated with the wetland sites (both *Pterocarpus* and mangrove forests) while the high diversity of woody tree species was the most important habitat characteristic in the karst forest.

One important aspect of our work is the observation of monthly changes in bird species composition. Are these real bird species composition differences or just differences in observed activity patterns due to seasonal changes in detectability? With only one exception, we did not find any seasonal difference in detectability in resident species. However, the detectability in-

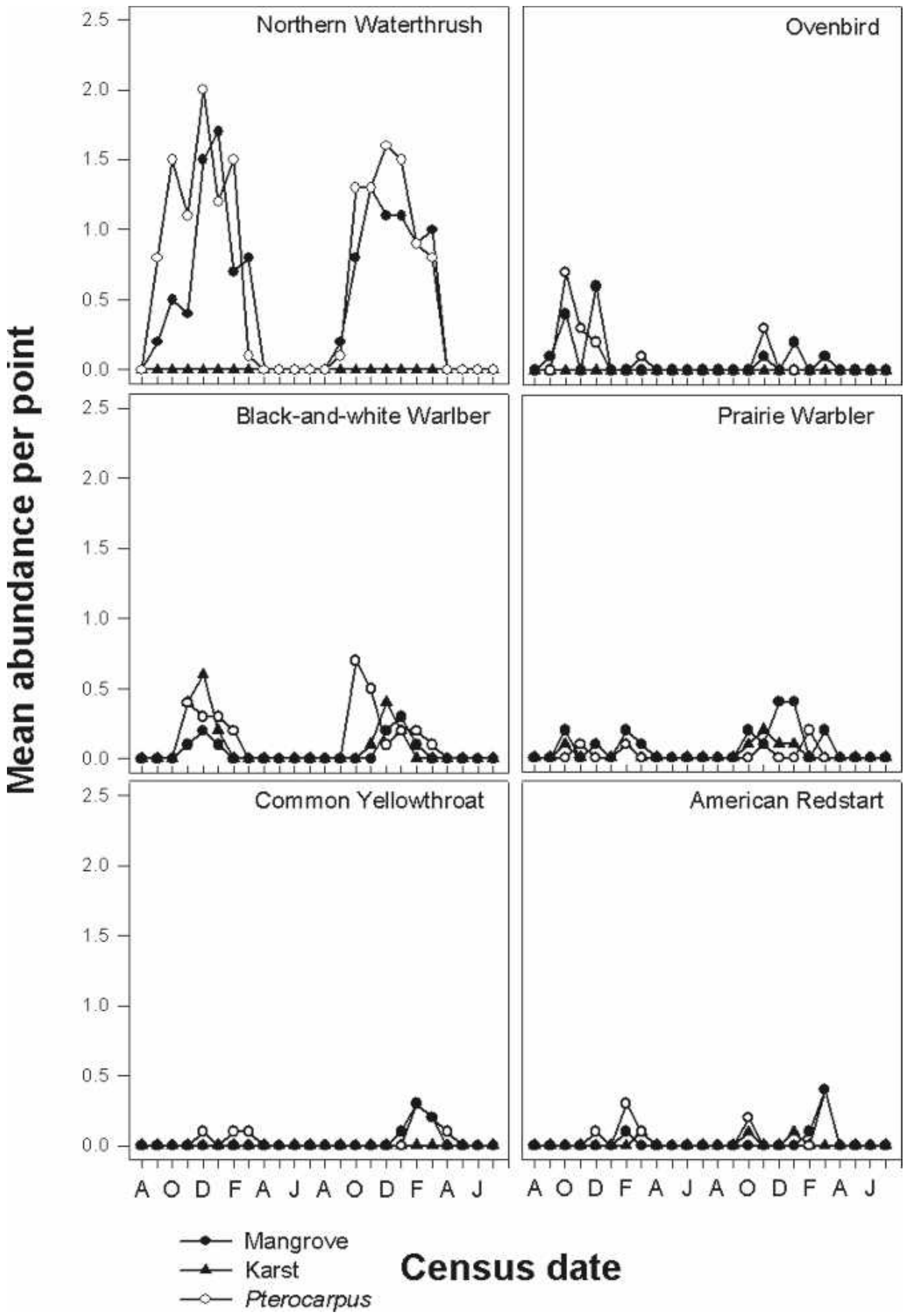


FIG. 4. Mean monthly abundance based on fixed-radius point counts of the six most abundant nearctic/neotropical migrant species for karst, mangrove, and Pterocarpus forest fragments in northern Puerto Rico.

dex we used (Hutto et al. 1986) only considers differences in species detected inside and outside the 20-m radius. Given that we compared species detectability during and outside the breeding season changes in migratory species detectability could not be analyzed. Recently published work about long-term migratory bird species dynamics in the neotropics shows that mist nets performed better than point-counts detecting the most diversity of neotropical migrants (Faaborg et al. 2007). Thus, our censuses may be under detecting migrant species because of the use of point-counts. However, given that we used the same methods in all three habitats, we assume that the levels of detectability are equivalent among habitats and not likely to affect the results of the ordination analysis. In addition, the detectability index used does not indicate that species detected in some censuses were not detected in others due to detectibilty changes. Species detected only in some censuses are responsible for the monthly variation in bird species richness. The increases in species richness in the migratory period and in the breeding season are examples of this variation. The increase in species richness in the migratory period is expected because of the arrival of neotropical migrants. The increase in species richness in the breeding season is caused by the detection of species not detected in other censuses. For example, the White-winged Dove and the White-crowned Pigeon were only detected during the breeding season (April-May) suggesting that they were present but were not detected or that they were using other habitats during the rest of the year (Rivera-Milán 1992).

*Habitat Use.*—Resident bird species composition in our sites was similar in wetlands habitats (*Pterocarpus* and mangroves), but varied greatly between karst and wetlands. Habitat characteristics such as floristic composition, density of trees of different DBH size classes and the presence/absence of standing water were important variables distinguishing the different bird communities in the karst and wetland habitats (*Pterocarpus* and mangrove). Wetland habitats were characterized by the presence of standing water, low woody tree species diversity (*Pterocarpus* had 7 while mangrove 6) and bigger trees (>10 cm DBH), while the karst forest was characterized by absence of standing water, the highest number of woody tree species (47) and a greater abundance of smaller trees (<10 cm DBH). Most tree species in the karst forest provide fleshy fruits, which are an important food resource for frugivores. In contrast, *Pterocarpus officinalis* and *Laguncularia racemosa*, the two most common tree species in the *Pterocarpus* forest and mangrove respectively, do not provide an edible fruit for birds. This difference in woody tree species richness may explain the occurrence of the Puerto Rican Bullfinch, which is almost exclusively frugivorous, only in the karst hills. The presence of standing water in wetlands may explain the exclusive occurrence of the Green Heron, and Northern Waterthrush in wetlands. These species feed on invertebrates and small fish associated with the standing water.

*Migratory Species: Local Habitat Use and their Effect on Resident Communities*

The presence of migratory species in most tropical forested ecosystems suggests a generalist behavior in their habitat use (e.g., Blake and Loiselle 1992, Kricher and Davis 1992, Robbins et al. 1992, Conway et al. 1995, Confer and Holmes 1995, Currie et al. 2005), but at the same time migrants may have preferred habitats. Our results showed that migratory species were more abundant and had a larger effect on total bird species composition in wetland habitats (*Pterocarpus* and mangrove forests), than in the karst forest. This high diversity of migratory species in wetland habitats has been related to food availability (Hutto 1980, Lynch 1989, Lefebvre et al. 1994, Lefebvre and Poulin 1996). Wetland habitats are characterized by a high diversity and abundance of insects (Meades et al. 2002), and most migratory species visiting wetland habitats are insectivores (Russell 1980, Wunderle and Waide 1993, Lefebvre et al. 1994). In this sense, migrant species may be taking advantage of superabundant insect resources (Moreau 1952) in wetland habitats to decrease competition with resident birds and insectivores from other taxa (e.g. lizards and frogs) in other habitats (such as karst) in which arthropod abundance is not as high. This supports the idea that migrants are using resources not used or scarcely used by residents, which minimizes competition (Leck 1972, Post 1978, Hutto 1980, Keast 1980, Fitzpatrick 1982, Rappole et al. 1983, Morton 1992).

*Conservation implications.*—Our study site is composed of relatively small patches of each forest type (karst, *Pterocarpus* forest and mangrove) surrounded by a complex matrix of urban settlements and pastures, thus our results may not apply to bigger forest patches in other parts of the island or the Caribbean. However, they represent a good example of the common condition of coastal forest fragments. The high diversity and complex bird community dynamics in these sites, stress the importance of these three forest types (karst, *Pterocarpus* and mangrove forests) for the conservation of both resident and neotropical migrant birds. Most of the land transformation that took place in the karst included agriculture and timber extraction. Karst valleys were heavily deforested for agriculture and homesteads (Rivera et al. 2000). On the other hand, karst hill sides and tops were not used for intensive agriculture; instead, they were deforested for timber and firewood (Picó 1950, Rivera et al. 2000, Lugo 2001). The vegetation on hill top and side that survived was the seed source responsible for the high rate of karst forest recovery. These rapidly recovering Puerto Rican karst hills are known to provide habitat for a high diversity of resident and migrant bird species, which include 16 of the 17 endemic bird species of the island (Lugo et al. 2001). Some of these bird species (some of the residents) may be important seed dispersers that are aiding in the process of forest recovery (Carlo et al. 2003). This relatively high bird species richness may be due to the complex forest structure, which includes high diversity and density of woody species, and a complex understory with high percent cover of herbs and litter. The high rate of recovery of the karst forest in conjunction with the rugged topography of the hills makes them less suitable for urban use. This combined with recent private and public efforts to conserve these forests (Aukema et al. 2007), present a positive scenario for the preservation of the karst.

On the other hand, coastal wetlands have been the most severely deforested habitat in the island of Puerto Rico. Today less than half of the original area of mangrove forest remains on the island (~32,000 ha; Lopez-Marrero and Villanueva-Colón 2006) and there are only 15 forest patches of *Pterocarpus* forest with a total area of only 240 ha (Cintrón 1983). These coastal wetlands were deforested mainly for the establishment of sugar cane plantations (Lugo 1988). These sugar cane plantations have been abandoned (Aide et al. 2000) and today these areas are dominated by urban areas, pastures or wetland grasses (e.g. *Typha*), which are not suitable habitat for most bird species due to the lack of vertical structure (Acevedo 2007).

Land-use change is not the only threat to these coastal habitats. An increase in salinity associated with sea-level rise and global climate change has been projected to reduce wetland areas throughout the world (Howard & Mendelssohn 1999, Williams *et al.* 1999, Nicholls 2004). Moreover, *Pterocarpus* forests, which already have a limited distribution in the island, are sensitive to small changes in salinity (Rivera-Ocasio et al. 2007). Even though, these forests may be able to respond to an increase in salinity by migrating inland, most of these inland sites are already occupied by other kinds of land use (Alongi 2002). These results strengthen the importance of restoring and appropriately managing karst and coastal forested wetlands to ensure habitat for resident and migrant birds.

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APPENDIX. Families, common name, scientific name, and mean number of individuals per 20-m fixed-radius point count per habitat in year 1 (Aug 2002-Jul 2003) and year 2 (Aug 2003-July 2004; line below) in mangrove, *Pterocarpus* and karst forest fragments at Sabana Seca, Puerto Rico. Mean values based on monthly censuses at 10 point count sites in each habitat type. Status refers to residents (R) and nearctic/neotropical migrants (M), with the exception of the Black-whiskered Vireo which is a neotropical migrant that breeds in Puerto Rico. Mean number of individual resident species is based on the mean for 12 months, and mean value for nearctic/neotropical migrants is based on the mean for six months (October-March). Mean values for the Black-whiskered Vireo are based on six months (March-August).

| Family | Common name | Scientific name | Status | Karst | Pterocarpus | Mangrove |
|---|---|---|---|---|---|---|
| Ardeidae | Green Heron | *Butorides virescens* | R | 0 | 0.42 | 0.43 |
| | | | | 0 | 0.57 | 0.32 |
| Falconidae | American Kestrel | *Falco sparverius* | R | 0 | 0.01 | 0.02 |
| | | | | 0 | 0.01 | 0 |
| Columbidae | Zenaida Dove | *Zenaida aurita* | R | 0.24 | 0.26 | 0.33 |
| | | | | 0.23 | 0.37 | 0.23 |
| Columbidae | White-winged Dove | *Zenaida asiatica* | R | 0.01 | 0 | 0 |
| | | | | 0 | 0 | 0 |
| Columbidae | Scaly-naped Pigeon | *Patagioenas squamosa* | R | 0 | 0 | 0 |
| | | | | 0.01 | 0 | 0 |
| Columbidae | White-crowned Pigeon | *Patagioenas leucocephala* | R | 0 | 0 | 0 |
| | | | | 0.02 | 0 | 0.01 |
| Columbidae | Common Ground-Dove | *Columbina passerina* | R | 0 | 0 | 0 |
| | | | | 0 | 0.02 | 0.02 |
| Cuculidae | Puerto Rican Lizard-Cuckoo | *Saurothera vieilloti* | R | 0.42 | 0 | 0 |
| | | | | 0.26 | 0 | 0 |
| Cuculidae | Mangrove Cuckoo | *Coccyzus minor* | R | 0.02 | 0.21 | 0.55 |
| | | | | 0.08 | 0.69 | 0.22 |
| Cuculidae | Smooth-billed Ani | *Crotophaga ani* | R | 0.03 | 0.07 | 0.1 |
| | | | | 0.03 | 0.02 | 0.01 |
| Trochilidae | Green Mango | *Anthracothorax viridis* | R | 0.02 | 0 | 0.01 |
| | | | | 0.01 | 0 | 0 |
| Todidae | Puerto Rican Tody | *Todus mexicanus* | R | 0.14 | 0 | 0 |
| | | | | 0.12 | 0 | 0 |
| Picidae | Puerto Rican Woodpecker | *Melanerpes portoricensis* | R | 0.67 | 0.2 | 0.83 |
| | | | | 0.76 | 0.49 | 0.21 |
| Tyrannidae | Gray Kingbird | *Tyrannus dominicensis* | R | 0.91 | 0.36 | 0.31 |
| | | | | 0.72 | 0.17 | 0.24 |
| Tyrannidae | Loggerhead Kingbird | *Tyrannus caudifasciatus* | R | 0.06 | 0 | 0.07 |
| | | | | 0.03 | 0.02 | 0 |
| Tyrannidae | Puerto Rican Flycatcher | *Myiarchus antillarum* | R | 0.13 | 0.05 | 0.14 |
| | | | | 0.08 | 0.2 | 0.14 |
| Vireonidae | Black-whiskered Vireo | *Vireo altiloquus* | M | 0.85 | 0 | 0.24 |
| | | | | 0.6 | 0.23 | 0 |
| Vireonidae | Puerto Rican Vireo | *Vireo latimeri* | R | 0.04 | 0 | 0 |
| | | | | 0.05 | 0 | 0 |
| Turdidae | Red-legged Thrush | *Turdus plumbeus* | R | 0.36 | 0.05 | 0.12 |
| | | | | 0.41 | 0.14 | 0.04 |

APPENDIX. Continued.

| Family | Common name | Scientific name | Status | Karst | Pterocarpus | Mangrove |
|---|---|---|---|---|---|---|
| Mimidae | Northern Mockingbird | *Mimus polyglottos* | R | 0.1 | 0 | 0 |
| | | | | 0.04 | 0 | 0 |
| Mimidae | Pearly-eyed Thrasher | *Margarops fuscatus* | R | 0.03 | 0.02 | 0 |
| | | | | 0.06 | 0.01 | 0 |
| Parulidae | Adelaide's Warbler | *Dendroica adelaidae* | R | 1.88 | 0 | 0 |
| | | | | 1.76 | 0 | 0 |
| Parulidae | Northern Waterthrush | *Seiurus noveboracensis* | M | 0 | 0.82 | 0.58 |
| | | | | 0 | 0.79 | 0.75 |
| Parulidae | Ovenbird | *Seiurus aurocapilla* | M | 0 | 0.13 | 0.11 |
| | | | | 0 | 0.04 | 0.04 |
| Parulidae | Black-and-white warbler | *Mniotilta varia* | M | 0.12 | 0.12 | 0.04 |
| | | | | 0.07 | 0.06 | 0.18 |
| Parulidae | Prarie Warbler | *Dendroica discolor* | M | 0.03 | 0.02 | 0.06 |
| | | | | 0.05 | 0.13 | 0.03 |
| Parulidae | Common Yellowthroat | *Geothlypis trichas* | M | 0 | 0.03 | 0 |
| | | | | 0 | 0.06 | 0.06 |
| Parulidae | American Redstart | *Setophaga ruticilla* | M | 0.01 | 0.05 | 0.01 |
| | | | | 0.02 | 0.05 | 0.06 |
| Parulidae | Prothonotary Warbler | *Protonotaria citrea* | M | 0.02 | 0.04 | 0.03 |
| | | | | 0 | 0 | 0.01 |
| Parulidae | Northern Parula | *Parula americana* | M | 0.01 | 0 | 0.01 |
| | | | | 0.01 | 0.01 | 0.02 |
| Parulidae | Yellow Warbler | *Dendroica petechia* | R | 0 | 0.01 | 0 |
| | | | | 0 | 0 | 0 |
| Coerebidae | Bananaquit | *Coereba flaveola* | R | 3.85 | 4.97 | 3.56 |
| | | | | 3.3 | 3.24 | 3.55 |
| Thraupidae | Puerto Rican Spindalis | *Spindalis portoricensis* | R | 0.35 | 0.03 | 0 |
| | | | | 0.31 | 0.01 | 0 |
| Emberizidae | Puerto Rican Bullfinch | *Loxigilla portoricensis* | R | 0.12 | 0 | 0 |
| | | | | 0.12 | 0 | 0 |
| Emberizidae | Black-faced Grassquit | *Tiaris bicolor* | R | 0.03 | 0.02 | 0 |
| | | | | 0 | 0 | 0 |
| Icteridae | Greater Antillean Grackle | *Quiscalus niger* | R | 0.04 | 0.11 | 0.84 |
| | | | | 0.1 | 0.62 | 0.3 |
| Icteridae | Shiny Cowbird | *Molothrus bonariensis* | R | 0 | 0.01 | 0.07 |
| | | | | 0.01 | 0.07 | 0.01 |
| Estrildidae | Nutmeg Mannikin | *Lonchura punctulata* | R | 0.01 | 0 | 0 |
| | | | | 0 | 0 | 0 |
| Estrildidae | Oranged-cheeked Waxbil | *Estrilda melpoda* | R | 0.01 | 0.01 | 0 |
| | | | | 0.01 | 0 | 0 |
| Total | 39 | | | 32 | 27 | 26 |