The Wilson Journal of Ornithology 121(1):41–53, 2009

RELATIVE ABUNDANCE, HABITAT USE, AND LONG-TERM POPULATION CHANGES OF WINTERING AND RESIDENT LANDBIRDS ON ST. JOHN, U.S. VIRGIN ISLANDS

DAVID W. STEADMAN,[1,4] JENSEN R. MONTAMBAULT,[1] SCOTT K. ROBINSON,[1] SONJA N. OSWALT,[2] THOMAS J. BRANDEIS,[2] A. GUSTAVO LONDOÑO,[1] MATTHEW J. REETZ,[1] WENDY M. SCHELSKY,[1] NATALIE A. WRIGHT,[1] JEFFREY P. HOOVER,[1,3] JILL JANKOWSKI,[1] ANDREW W. KRATTER,[1] ARI E. MARTÍNEZ,[1] AND JORDAN SMITH[1]

ABSTRACT.—St. John, U.S. Virgin Islands, is one of the most forested islands in the West Indies and provides an opportunity to conserve both resident birds and wintering neotropical migrants. We conducted double-observer point counts of landbirds in December 2005 and 2006 in Forest Inventory and Analysis (FIA) plots and National Park Service (NPS) trails in Virgin Islands National Park (VINP) to assess population trends of birds in subtropical dry and moist forests. We recorded 2,270 individual birds representing 35 species at 150 point count stations in 2005, and 3,092 individuals of 32 species at 143 of these stations in 2006. The increase in birds per point from 2005 (15.1) to 2006 (21.6) was due to resident species, 17 of which were recorded more frequently in 2006. The 17 species of neotropical migrants composed 11.8% of all registrations in 2005 and 2006. Subtropical moist and dry forest habitats differed strongly in vegetation characteristics and plant species, but no species of birds exhibited a strong affiliation with either habitat type on FIA plots. Data from NPS trails showed that most migrant species were detected more often in moist, mature forest. The resident Bridled Quail-Dove (*Geotrygon mystacea*) also was correlated with mature forest. Plant and bird species co-occurrence with positive correlations that may carry a signal of preferred frugivory included *Guettarda odorata* (Rubiaceae) with Bridled Quail-Dove, and *Myrciaria floribunda* (Myrtaceae) with Pearly-eyed Thrasher (*Margarops fuscatus*). Migrant species did not exhibit strong long-term changes in relative abundance since founding of VINP in 1957, but four open-country resident species declined significantly between 1957 and 2006 as the forest matured. Forest maturation should continue on St. John, yielding a bright future for most of its landbirds barring catastrophic hurricanes, pathogens, or invasive plants. *Received 24 November 2007. Accepted 29 May 2008.*

Populations of both migratory and resident species of West Indian birds have been affected by humans through land-use changes, introduced mammals, and direct hunting since the islands were first settled several thousand years ago (Pregill et al. 1994). Habitat loss may be the most important threat to persistence of endemic and resident birds in the West Indies (Arendt 1992, Raffaele et al. 1998). The extent to which this habitat loss influences populations of neotropical migrants is potentially substantial. Understanding the causes of current population trends in migratory species requires monitoring in both breeding and wintering areas (Rappole 1995).

The resident bird life in the U.S. Virgin Islands (USVI; Fig. 1) comprises a unique faunal mixture originating in both the Greater and Lesser Antilles. Neotropical migrants in the USVI tend to be species that are widespread on their Antillean wintering areas (Leck and Norton 1991, Arendt 1992, Raffaele et al. 1998). Previous bird censuses on St. John (Robertson 1962, Askins and Ewert 1991) reported a large decrease in the proportion of resident species associated with open and early successional habitats (49.8% in 1957 vs. 10.7% in 1987) and a concomitant increase in habitat generalists (36.2 vs. 68.2%); the proportion of neotropical migrants increased slightly from 15% in 1957 to 20.8% in 1987. These changes presumably reflect reforestation following acquisition of 54% of St. John as Virgin Islands National Park (VINP) in 1956 (MacDonald et al. 1997). The detection rate of migrants was nearly six times higher on St. John (50 km², elevation 389 m) than in

[1] Florida Museum of Natural History, P. O. Box 117800, University of Florida, Gainesville, FL 32611, USA.

[2] U.S. Department of Agriculture, Forest Service, Southern Research Station, Forest Inventory and Analysis, 4700 Old Kingston Pike, Knoxville, TN 37919, USA.

[3] Illinois Natural History Survey, 1816 South Oak Street, Champaign, IL 61820, USA.

[4] Corresponding author; e-mail: dws@flmnh.ufl.edu

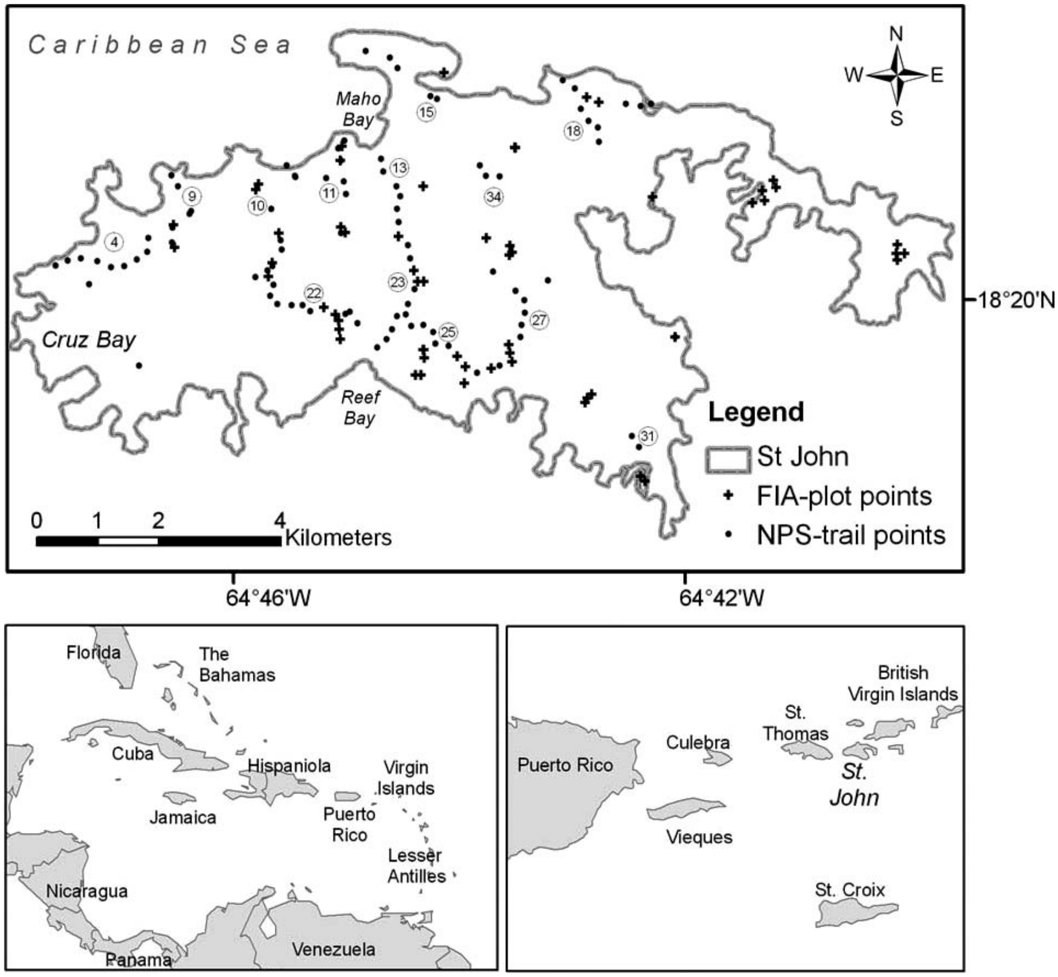

FIG. 1. Localities of all point counts for birds, St. John, U.S. Virgin Islands, December 2005 and 2006. FIA-plot points are sampling stations affiliated with FIA plots. NPS trail points are sampling stations not affiliated with FIA plots and National Park Service maintained trails. Circled numbers designate NPS trails.

Luquillo Experimental Forest on nearby Puerto Rico (8,865 km^2, elevation 1,338 m) in both 1957 and 1987 (Askins et al. 1992, Wunderle and Waide 1993).

Migrant birds wintering in the Caribbean have demonstrated affiliation with certain habitats and may also be associated with particular plant species (Faaborg 1984, Arendt 1992). The presence of frugivores and nectarivores, in particular, may be influenced by drought and other factors that affect flowering and fruiting of plants (Ewert and Askins 1991). Migrants, such as Black-and-white Warbler, Northern Parula, Cape May Warbler, Black-throated Blue Warbler, and American Redstart (scientific names of all birds are in Table 1), accounted for most of wintering bird visits to fruiting *Cecropia* trees in Puerto Rico to consume fruit or insects (Leck 1972).

The USDA Forest Service Forest Inventory and Analysis program (FIA) collects data on variables related to forest health across the United States, including the USVI and Puerto Rico (USDA 2002, Bechtold and Patterson 2005). Data gathered at FIA plots include characteristics important for evaluating avian habitat, such as tree and vascular herbaceous plant composition, vegetation cover, standing dead trees (snags), and downed woody materials, among others (Bechtold and Scott 2005).

TABLE 1. Birds detected at point count stations, December 2005 and 2006, St. John, U.S. Virgin Islands. Mean (± SE) birds/point was calculated for species with > 5 registrations in any survey year. Based on 150 point counts in 2005 and 143 in 2006.

	Registrations		Mean birds/point	
Species	2005	2006	2005	2006
Migrant Landbirds				
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0	2		
Barn Swallow (*Hirundo rustica*)	4	0		
White-eyed Vireo (*Vireo griseus*)	0	1		
Blue-winged Warbler (*Vermivora pinus*)	3	2		
Northern Parula (*Parula americana*)	51	48	0.34 ± 0.05	0.34 ± 0.05
Magnolia Warbler (*Dendroica magnolia*)	2	3		
Cape May Warbler (*D. tigrina*)	1	0		
Black-throated Blue Warbler (*D. caerulescens*)	1	1		
Yellow-rumped Warbler (*D. coronata*)	4	0		
Black-throated Green Warbler (*D. virens*)	1	0		
Blackburnian Warbler (*D. fusca*)	3	2		
Prairie Warbler (*D. discolor*)	44	32	0.29 ± 0.06	0.22 ± 0.09
Black-and-white Warbler (*Mniotilta varia*)	48	36	0.32 ± 0.04	0.25 ± 0.03
American Redstart (*Setophaga ruticilla*)	98	66	0.65 ± 1.00	0.46 ± 0.82
Worm-eating Warbler (*Helmitheros vermivorus*)	10	8	0.07 ± 0.00	0.06 ± 0.03
Ovenbird (*Seiurus aurocapilla*)	47	50	0.31 ± 0.05	0.35 ± 0.04
Northern Waterthrush (*S. noveboracensis*)	35	15	0.23 ± 0.09	0.10 ± 0.05
Hooded Warbler (*Wilsonia citrina*)	10	6	0.07 ± 0.03	0.04 ± 0.04
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	1	0		
Resident Landbirds				
Scaly-naped Pigeon (*Patagioenas squamosa*)	5	16		0.11 ± 0.04
Zenaida Dove (*Zenaida aurita*)	27	54	0.18 ± 0.04	0.38 ± 0.06
Common Ground-Dove (*Columbina passerina*)	7	13	0.05 ± 0.08	0.09 ± 0.16
Bridled Quail-Dove (*Geotrygon mystacea*)	47	50	0.31 ± 0.07	0.35 ± 0.10
Mangrove Cuckoo (*Coccyzus minor*)	17	19	0.11 ± 0.02	0.13 ± 0.05
Smooth-billed Ani (*Crotophaga ani*)	8	21	0.05 ± 0.03	0.15 ± 0.10
Green-throated Carib (*Eulampis holosericeus*)	31	57	0.21 ± 0.03	0.40 ± 0.05
Antillean Crested Hummingbird (*Orthorhyncus cristatus*)	74	112	0.49 ± 0.05	0.78 ± 0.07
Caribbean Elaenia (*Elaenia martinica*)	519	634	3.46 ± 0.20	4.43 ± 0.31
Puerto Rican Flycatcher (*Myiarchus antillarum*)	1	3		
Grey Kingbird (*Tyrannus dominicensis*)	135	448	0.90 ± 0.12	3.13 ± 0.26
Northern Mockingbird (*Mimus polyglottos*)	2	5		
Pearly-eyed Thrasher (*Margarops fuscatus*)	403	517	2.69 ± 0.14	3.62 ± 0.18
Black-whiskered Vireo (*Vireo altiloquus*)	2	4		
Yellow Warbler (*Dendroica petechia*)	61	60	0.41 ± 0.10	0.42 ± 0.13
Bananaquit (*Coereba flaveola*)	368	565	2.45 ± 0.13	3.95 ± 0.24
Black-faced Grassquit (*Tiaris bicolor*)	49	18	0.33 ± 0.58	0.13 ± 0.08
Lesser Antillean Bullfinch (*Loxigilla noctis*)	151	224	1.01 ± 0.09	1.57 ± 0.14

The USDA Forest Service also has developed a Multiple Species Inventory and Monitoring protocol for collecting terrestrial faunal data on FIA plots, including those in the Caribbean (Brandeis 2003, Manley et al. 2004).

The objectives of our research were to: (1) provide current information on migratory and resident landbirds in St. John's subtropical forests, (2) inform and improve management of these public lands, and (3) contribute data on overall trends in bird communities. We combined habitat data from FIA plots with census data on resident and migrant landbirds at point counts associated with both FIA plots and National Park Service (NPS) trails. We assessed the relationship among bird species and habitat type, vegetation characteristics, and plant occurrence with FIA-plot affiliated point counts. We also investigated landscape-level trends in birds throughout the VINP with

NPS-trail affiliated point counts. We reviewed historical data on relative abundance of birds from 1957 to 2006 to evaluate the effects of habitat changes on the bird community of St. John.

METHODS

Vegetation.—Habitat data were collected on St. John by a team led by SNO and TJB in June-July 2004 using the USDA Forest Service FIA sample design (USDA 2002). Twenty plots, each consisting of four abutting circular subplots of 17.9-m radius, were arranged on an unbiased, systematic hexagonal sample grid across the island. Hexagons covered ~200 ha each with one sample plot randomly located in each hexagon. FIA field crews collected forest inventory, understory structure and composition, and physiographic data on each subplot. Diameter at breast height (dbh, taken at 1.37 m), total height, and other parameters were measured on all trees of dbh ≥12.5 cm in each subplot; dbh and total height were measured on saplings of dbh ≥2.5 cm within a 2.1-m radius microplot in each subplot (USDA 2002, Bechtold and Scott 2005). The vegetation analyses divided the forests of St. John into two major categories, subtropical dry forest and subtropical moist forest (Oswalt et al. 2006) following Holdridge (1967) and Ewel and Whitmore (1973). Each of these life zone types has different indicator plants, as well as species composition and habitat structure distinct from areas dominated by anthropogenic disturbance (Oswalt et al. 2006).

Bird Censuses.—Teams of qualified observers (JPH, JJ, AWK, GAL, AEM, JRM, MJR, SKR, WMS, DWS, JVS, and NAW) conducted double-observer, unlimited-radius, circular-plot point counts (Emlen 1971, Ralph et al. 1993) from 5 to 24 December 2005 and 4 to 18 December 2006. Controlled experiments have shown that unlimited-radius point counts provide better estimates of actual population sizes than fixed radius (Simons et al. 2007), and that double-observer point counts record avian abundance with high levels of precision (Nichols et al. 2000). Effort in double-observer days was 68 for 2005 and 48 for 2006; the difference was related to the much greater time spent clearing trails and locating plots during the first year.

Two to five stations were arrayed around a central location slightly offset from the 18 accessible FIA plot centers on St. John, as recommended by USFS-MSIM protocols (Manley et al. 2004), for a total of 45 FIA-affiliated stations, yielding a mean of 2.5 point counts/FIA plot. Adjacent point-count stations were at least 200 m apart, and all stations on any given FIA plot were sampled on the same day. Our point counts were made during times of little or no rain, wind <10 km/hr, and within 4 hrs of daybreak. We augmented the FIA sample with 105 additional census points at intervals ≥200 m along maintained NPS trails, for a total of 150 point count stations in 2005 (Fig. 1). The 45 points affiliated with FIA plots and 95 of the 105 points affiliated with NPS trails were resampled in 2006. Three additional point counts on NPS trails were also sampled in 2006, for a total of 143 points. Our analyses focus on the 140 point count stations that were sampled in both 2005 and 2006 (45 at FIA plots, 95 on NPS trails).

All species of birds detected by sight or sound during point counts were recorded by time interval of first detection (0–5 min vs. 5–10 min, followed by a 3 min "pish" call to confirm identity of certain birds and to lure in nearby silent birds not detected during the point count), distance (rounded to 5 m for 0–50 m, to 10 m for >50 m), and direction (to nearest 45°). Each observer in the pair registered individual birds separately, and then combined and confirmed detections immediately following the point count. The mean number of each species per point was calculated with an understanding that sound attenuation leads to underestimates in some species (Waide and Narins 1988). Seabirds, shorebirds, raptors, and landbirds observed flying over the point-count stations were recorded but not analyzed.

Each pair of observers carried a GPS (Global Positioning System) receiver and recorded the exact location of observation points affiliated with FIA plots and NPS trails in 2005 when the points were given non-permanent markers. The GPS data and markers were used to relocate points in 2006. Coordinate data were added to the spatial analysis program ArcGIS 9.1 and projected onto orthorectified aerial photographs provided by the USDA Forest Service (Fig. 1).

Analyses.—We tabulated the number of individual birds observed (registrations) at each FIA plot- and NPS trail-affiliated point separately for 2005 and 2006. Of these points, 140 were sampled during both years and the abundance (number of registrations) of each species was averaged for these points over the 2 years. The results of the points affiliated with each FIA vegetation plot were averaged to give a single average abundance for each species by FIA plot. The 15 species of birds detected at six or more of the 18 FIA plots were included in further analysis. Each FIA plot and its associated avian sampling points were classified as subtropical dry (10 FIA plots, 26 points) or moist forest (8 FIA plots, 19 points) (Oswalt et al. 2006).

We used a Welch two-sample *t*-test to evaluate if individual species occurred more often in points classified as moist versus dry habitat. We used the same test to examine whether habitat structure characteristics (trees/ha, height of tallest tree, average height of all trees, canopy height, basal area/ha, above ground biomass/ha, crown area/ha, crown volume/ha) differed between the two habitats. Linear regression was used to test the relationship between average abundance of each species of bird and structural characteristics of habitat. We also tested the relationship between occurrence of landbirds and vascular plant species within each habitat type using a Pearson's product moment correlation coefficient.

Abundance (number of registrations) for the 95 points on NPS trails was averaged for each point over the 2 years. We assigned 84 of these points to 13 distinct trails each with at least three sampling stations (mean = 6.5 points/trail, range 3–16). Each trail covered relatively homogenous habitat and all points on a trail were sampled on the same day. We used a one-way ANOVA to test for the effect of trail affiliation on abundance of the eight most common migrants (Northern Parula, Prairie Warbler, Black-and-white Warbler, American Redstart, Worm-eating Warbler, Ovenbird, Northern Waterthrush, and Hooded Warbler).

We used data from surveys in 1957, 1987, and 1990, in addition to our own from 2005 and 2006, to examine historical trends in bird abundance. Robertson (1962) counted every bird he observed in February and March 1957 over 152 hrs of traversing trails and dry stream beds throughout VINP. Robertson's study included moist and dry forest, as well as mangroves (primarily *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*), which we did not sample. Askins and Ewert (1991) assessed the birds in VINP with 25-m fixed-radius point counts. They had 55 point counts in moist forest and 35 in dry forest from 31 October to 3 December 1987, and 40 in moist forest and 22 in dry forest from 10 to 16 January 1990.

The 1957 survey used observations/hr; the radius of the 1987 and 1990 points was different than ours in 2005 and 2006, and we used relative abundance for the comparisons (Bibby et al. 2000). Species that occurred rarely were removed from the analysis. The significance of the trends was calculated in terms of *P*-value using linear regression of the relative abundance of each analyzed species (dependent variable) for each of the 5 calendar years (independent variable).

We report statistical significance at $P < 0.05$, although we apply a Bonferroni adjustment for comparisons involving all 73 plant species ($P < 0.0007$) and 15 non-rare bird species ($P < 0.0033$). These analyses were completed in program R, Version 2.3.1 (R Core Development Team 2007).

RESULTS

We recorded 2,270 individuals of 35 species of landbirds in December 2005 and 3,092 individuals of 32 species of landbirds in December 2006. The mean ($\pm$ SE) number of individual landbirds per point was 15.13 $\pm$ 0.59 in 2005, and 21.62 $\pm$ 0.90 in 2006. The resident Caribbean Elaenia was the most frequently detected species in 2005 and 2006 with 3.46 and 4.43 birds/point, respectively (Table 1). Next most abundant were Pearly-eyed Thrasher (2.69 and 3.62 birds/point in 2005 and 2006), Bananaquit (2.45, 3.95), and Grey Kingbird (0.90, 3.13).

FIA Plot Affiliated Points.—The Hooded Warbler was found more often in wet forest ($P < 0.01$) and Grey Kingbird and Yellow Warbler were observed more often in dry forest ($P = 0.01$ for both species), but none of the bird associations with moist versus dry forest in FIA-affiliated points (Fig. 2) was sta-

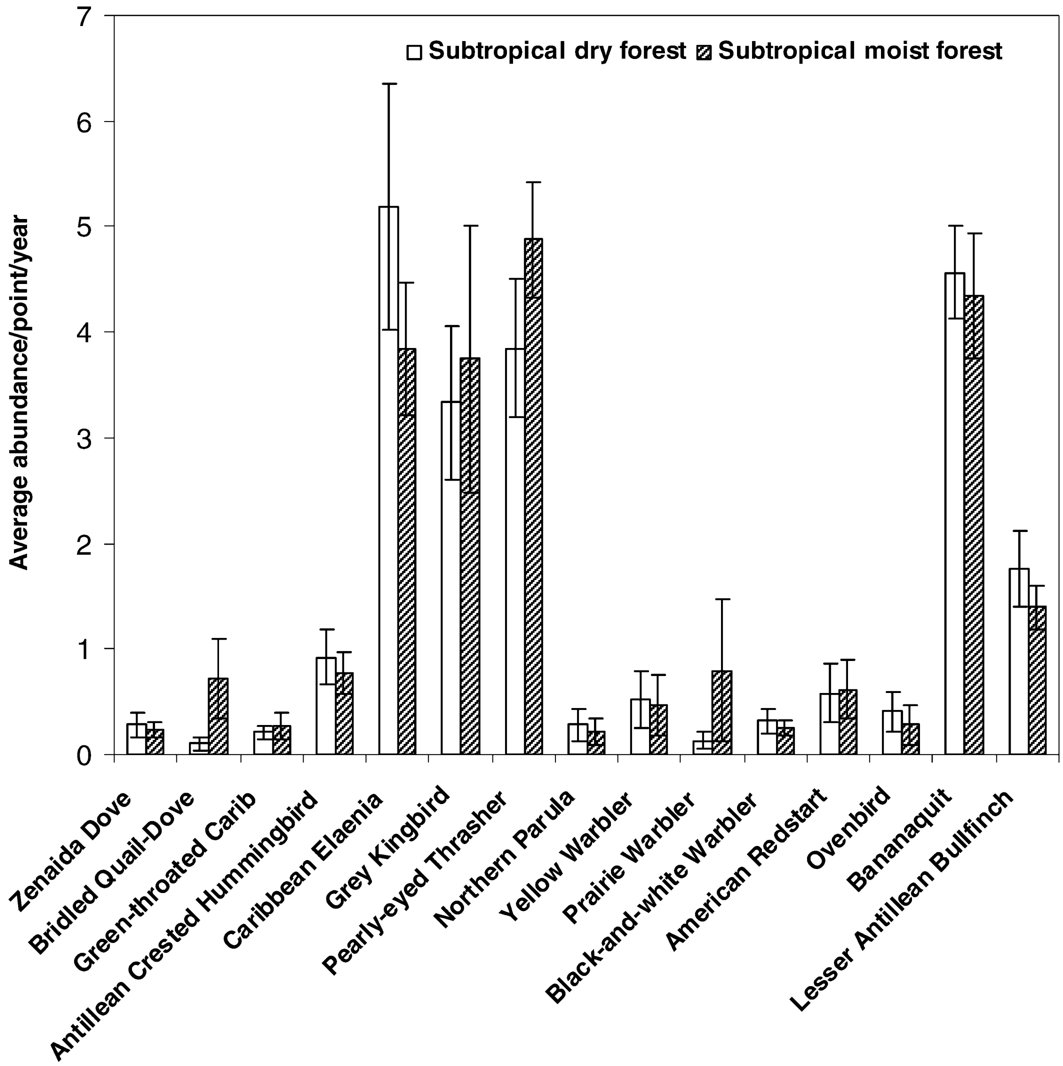

FIG. 2. Association of common migrant and resident landbirds with habitat types (10 FIA plots in subtropical dry forest and 8 in subtropical moist forest). Abundance averaged over 2005 and 2006 for 26 avian point counts affiliated with FIA plots in dry habitat and 19 associated with FIA plots in moist habitat. Bars represent SE.

tistically significant using the Bonferroni correction. Vegetation characteristics were distinct between the two habitat types (Table 2). The tallest tree, average canopy height, crown area/ha, and crown volume/ha were all higher ($P < 0.05$; $t = -2.57, -2.37, -2.71, -2.67$) in subtropical moist forest than in subtropical dry forest plots. Basal area/ha and aboveground biomass/ha were higher ($P < 0.01$; $t = -3.72$ and -3.20) in moist than in dry forest.

Three resident species of birds were significantly associated with particular vegetation characteristics. The Bridled Quail-Dove had a positive relationship with crown volume/ha ($P = 0.003$) and with height of the tallest tree ($P = 0.06$). The Caribbean Elaenia had a negative relationship with basal area ($P = 0.004$) and a positive ($P = 0.002$) relationship with above-ground biomass. The Scaly-naped Pigeon had a positive ($P = 0.047$) relationship with canopy cover.

Ten individual species of plants in the 18 FIA plots were correlated with moist forest

TABLE 2. Vegetation characteristics at FIA plots in 10 subtropical dry forest and 8 subtropical moist forest locations. Means (± SD) are reported. *P*-value from Welch two-sided *t*-test.

	Dry forest	Moist forest	*P*-value
Trees >12.5 cm dbh/ha	4630.2 ± 2022.7	6446.7 ± 2272.5	0.098
Height of tallest tree, m	8.5 ± 1.9	11.0 ± 2.0	0.021*
Average height of all trees, m	5.3 ± 0.8	6.3 ± 1.2	0.073
Canopy height, m	6.3 ± 1.4	7.9 ± 1.5	0.032*
Basal area, m^2/ha	13.4 ± 5.0	25.3 ± 7.8	0.003**
Above ground biomass, m^3/ha	52.4 ± 19.6	89.2 ± 27.3	0.007**
Crown area, m^2/ha	249.6 ± 147.2	757.4 ± 513.6	0.027*
Crown volume, m^3/ha	706.0 ± 472.5	2465.2 ± 1814.5	0.029*

* $P < 0.05$; ** $P < 0.01$.

and 11 with dry forests (Table 3). Only *Commelina erecta* exhibited a significant relationship with dry forest when a Bonferroni correction was applied to multiple comparisons among the 73 plant species. A greater proportion of the species had bird-dispersed fruits in moist (7 of 10) than dry forest (4 of 11), but this difference was not statistically significant when subjected to a Welch *t*-test.

We also tested the relationship of bird and plant species within habitat type (Table 4). The two largest birds, Scaly-naped Pigeon and Bridled Quail-Dove, had a positive association with at least one plant species in moist forest. Migrant Prairie Warbler, American Redstart, and Ovenbird, and resident Pearly-eyed Thrasher, Yellow Warbler, Bananaquit, and Black-faced Grassquit were positively affiliated with at least one plant species in dry forest.

NPS-trail Affiliated Points.—Most migrants (5 of the 8 most common and several rare spe-

TABLE 3. Plant species affiliation with forest types (8 and 10 FIA plots, respectively) using a *t*-test for unequal variance. Significant results are for $P < 0.05$. [F]indicates bird-dispersed fruits.

	Common names (ITIS 2008)	Life form
Subtropical Moist Forest		
Ardisia obovata (Myrsinaceae)	Guadeloupe marlberry	Tree
Cestrum laurifolium (Solanaceae)	Galen del monte	Shrub
Chiococca alba (Rubiaceae)	West Indian milkberry	Liana/shrub[F]
Chionanthus compactus (Oleaceae)	Bridgotree	Shrub/tree[F]
Coccothrinax barbadensis (Arecaceae)	Puerto Rico silver palm	Shrub/tree
Eugenia monticola (Myrtaceae)	Birdcherry	Tree[F]
E. rhombea (Myrtaceae)	Red stopper	Shrub/tree[F]
Faramea occidentalis (Rubiaceae)	False coffee	Shrub[F]
Guettarda scabra (Rubiaceae)	Wild guava	Shrub/tree[F]
Nectandra coriacea (Lauraceae)	Lancewood	Shrub/tree[F]
Subtropical Dry Forest		
**Commelina erecta* (Commelinaceae)	Whitemouth dayflower	Herb
Erythroxylum brevipes (Erythroxylaceae)	Brisselet	Shrub/tree[F]
Gouania lupuloides (Rhamnaceae)	Whiteroot	Liana
Guettarda odorata (Rubiaceae)	Cucubano de Vieques	Shrub/tree[F]
Pilosocereus royenii (Cactaceae)	Royen's tree cactus	Shrub/tree[F]
Piscidia carthagenensis (Fabaceae)	Stinkwood	Tree
Plumeria alba (Apocynaceae)	Nosegaytree	Tree
Solanum polygamum (Solanaceae)	Cakalaka berry	Shrub[F]
Tillandsia recurvata (Bromeliaceae)	Small ballmoss	Epiphyte
T. utriculata (Bromeliaceae)	Spreading airplant	Epiphyte
Tragia volubilis (Euphorbiaceae)	Fireman	Vine

* Bonferroni adjustment, $P < 0.0007$.

TABLE 4. Bird species positively (+) or negatively (−) associated with plant species using Pearson's correlation ($P < 0.0007$, significant using the Bonferroni correction for 73 plant species). [F]indicates bird-dispersed fruit. M indicates moist and D dry forest habitat.

Plant species	Common name	Life form	Scaly-naped Pigeon	Bridled Quail-Dove	Pearly-eyed Thrasher	Northern Water-thrush	Prairie Warbler	American Redstart	Oven-bird	Yellow Warbler	Banana quit	Black-faced Grassquit	Lesser Antillean Bullfinch
Bromelia pinguin													
Bromeliaceae	Pinguin	Herb	M(+)				D(+)	D(−)	D(+)				
Capparis hastate													
Capparaceae	Broadleaf caper	Tree									D(+)	D(+)	
C. indica													
Capparaceae	Linguam	Shrub/tree		M(−)		M(−)							
Eugenia rhombea													
Myrtaceae	Red stopper	Shrub/tree[F]								D(+)			
Guettarda odorata													
Rubiaceae	Cucubano de Vieiques	Shrub/tree[F]		M(+)									
Heteropterys purpupea													
Malpighiaceae	Bull withe	Vine										D(−)	
Jacquemontia pentanthos													
Convolvulaceae	Skyblue clustervine	Vine			M(−)				D(+)				
Lasiacis divaricata													
Poaceae	Smallcane	Grass		M(−)									
Myrciaria floribunda													
Myrtaceae	Guavaberry	Tree			D(+)								
Randia aculeate													
Rubiaceae	White indigoberry	Shrub[F]		M(−)									
Rondeletia pilosa													
Rubiaceae	Cordobancillo peludo	Shrub[F]						D(+)					
Solanum polygamum													
Solanaceae	Cakalaka berry	Shrub			D(−)								D(−)

TABLE 5. Relative abundance (registrations/number of individual birds) of resident and migrant landbirds on St. John, U.S. Virgin Islands between 1957 and 2006. *P*-value represents the linear regression trend of relative abundance by survey year.

	1957[a]	1987[b]	1990[b]	2005[c]	2006[c]	*P*-value
Migrant Landbirds						
Northern Parula	0.031	0.102	0.054	0.023	0.016	0.76
Magnolia Warbler	0.001	0.008	0.012	0.001	0.001	0.99
Cape May Warbler	0.001	0.004	0.000	0.000	0.000	0.70
Black-throated Blue Warbler	0.003	0.000	0.000	0.000	0.000	0.09*
Prairie Warbler	0.013	0.008	0.008	0.020	0.010	0.74
Black-and-white Warbler	0.020	0.037	0.021	0.021	0.012	0.72
American Redstart	0.024	0.026	0.033	0.044	0.022	0.54
Worm-eating Warbler	0.004	0.006	0.008	0.004	0.003	0.81
Ovenbird	0.005	0.018	0.042	0.021	0.016	0.46
Northern Waterthrush	0.011	0.000	0.021	0.016	0.005	0.98
Hooded Warbler	0.001	0.016	0.021	0.004	0.002	0.90
Resident Landbirds						
Scaly-naped Pigeon	0.020	0.055	0.046	0.002	0.005	0.62
Zenaida Dove	0.105	0.014	0.047	0.012	0.018	0.03**
Common Ground-Dove	0.091	0.008	0.004	0.003	0.004	0.03**
Bridled Quail-Dove	0.012	0.008	0.004	0.021	0.016	0.45
Mangrove Cuckoo	0.004	0.008	0.004	0.008	0.006	0.29
Smooth-billed Ani	0.020	0.014	0.012	0.004	0.007	0.01**
Green-throated Carib	0.016	0.014	0.008	0.014	0.019	0.95
Antillean Crested Hummingbird	0.019	0.067	0.033	0.033	0.036	0.61
Caribbean Elaenia	0.017	0.049	0.041	0.231	0.206	0.09
Grey Kingbird	0.060	0.035	0.033	0.060	0.146	0.49
Pearly-eyed Thrasher	0.214	0.229	0.269	0.179	0.168	0.50
Yellow Warbler	0.024	0.012	0.021	0.027	0.020	0.98
Bananaquit	0.079	0.229	0.178	0.164	0.184	0.21
Black-faced Grassquit	0.207	0.010	0.029	0.022	0.006	0.03**
Lesser Antillean Bullfinch	0.000	0.027	0.050	0.067	0.073	0.007**

* $P < 0.1$, ** $P < 0.05$.
[a] Robertson (1962).
[b] Askins and Ewert (1991).
[c] Present study.

cies) were observed most frequently on the three NPS trails through moist, mature forest. Three common migrants (Black-and-white Warbler, Worm-eating Warbler, and Hooded Warbler) were associated with Trail 23, NNE from Reef Bay across the island in a south-flowing stream basin with some of the most mature forest on St. John (Fig. 1). Uncommon migrant species, such as Blue-winged, Black-throated Blue, and Black-throated Green warblers, also were recorded on this trail. American Redstart, Northern Parula, and Black-throated Blue Warbler were observed on Trail 13, a continuation of Trail 23 that follows a north-flowing stream basin through similar habitat (Fig. 1) ending at Maho Bay. American Redstart and Northern Parula also were recorded on Trail 22, which traverses ravine habitat NW from Reef Bay (Fig. 1). Prairie Warbler was recorded on Trails 4 and 27, both dry ridge trails with scrubby forest. The only other migrant observed on these two trails was the rare Cape May Warbler.

Long-term Trends.—The relative abundance of Zenaida Dove, Common Ground-Dove, Smooth-billed Ani, and Black-faced Grassquit was significantly less ($P < 0.05$) in 2006 than in 1957 (Table 5). These four species prefer open, edge, or successional habitats (Askins and Ewert 1991). The relative abundance of Lesser Antillean Bullfinch increased ($P = 0.007$).

DISCUSSION

Habitat Associations.—Resident species dominated the bird community of St. John.

Only two of the 17 species of neotropical migrants ranked among the 10 most frequently detected species. The migrant bird community was similar to that of dry forest in Puerto Rico where individuals exhibit high site fidelity (Faaborg et al. 2007). None of the species we observed had a significant affiliation with habitat type on FIA plots even though evidence from previous studies, and from our point counts on NPS trails, suggests that migrants tend to be more frequent in moist forest. Askins and Ewert (1991) reported flocks of wintering songbirds were most frequent in moist forest on St. John, whereas residents tended not to prefer any forest type. The relative abundance of migrants in the Bahamas increased with increasing annual rainfall and was higher in moist rather than dry lowland forests on Greater Antillean islands (Wunderle and Waide 1993). Arendt (1992) found most migrants on St. John to be generalists with only Black-throated Green Warbler, Magnolia Warbler, and Ovenbird failing to occur in dry forests. The lack of significant affiliations in our bird data from FIA plots suggests that, given the extensive anthropogenic and natural changes in habitat on St. John, all resident species are generalists to some extent. Alternatively, our results could be due to small sample size, since habitat was not formally evaluated other than at FIA plots. The FIA sampling structure on St. John is too coarse to trace the effects of environmental gradients on plant communities (Oswalt et al. 2006), and we suspect the same is true for bird communities.

The two types of habitat differed greatly in vegetation characteristics, some of which correlate with a particular species of bird. The Bridled Quail-Dove, for example, occurred much more frequently in moist forest and was associated with high crown volume/ha and tall trees, i.e., mature forest (Table 2). This supports earlier findings that intact moist forests of St. John, particularly in VINP, may sustain one of the most important populations of Bridled Quail-Dove. This formerly common and widespread resident in the USVI and Lesser Antilles now persists in only scattered remnant populations (Seaman 1966, Wauer and Wunderle 1992, Pregill et al. 1994, Reis and Steadman 1999). Tree height was reported to have a positive effect also on the abundance of winter-resident birds on St. John as well as on St. Thomas (Askins et al. 1992).

The strong preference of many migrants for a few trails likely reflects an affinity for mature, moist forest. Eight migrant species (Northern Parula, Blue-winged Warbler, Black-throated Blue Warbler, Black-throated Green Warbler, Black-and-white Warbler, American Redstart, Worm-eating Warbler, and Hooded Warbler) were associated with the three trails (13, 22, 23) in VINP that host the most mature moist forest. Prairie Warbler and Cape May Warbler were affiliated with dry ridge trails in scrubby forest. Management of VINP to conserve mature forest and to maintain a mosaic of both dry and moist forest habitat should benefit a broad range of migrant species.

Vegetation Structure and Composition.—Vegetation structure is an important factor affecting distribution and abundance of birds on West Indian islands (e.g., Tossas and Thomlinson 2007). The Scaly-naped Pigeon's significant positive association with canopy cover is not surprising for a primarily arboreal species (Raffaele et al. 1998). The Caribbean Elaenia's negative correlation with basal area and strong positive relationship with above-ground biomass support our field observations that this vocal, widespread species favors habitat with a dense shrub layer more than mature forest. Above-ground biomass is closely related to stem density, a significant factor in how forests on St. John respond to natural disturbances, and also influences avian distributions elsewhere in the Caribbean (Reilly 1991, Currie et al. 2005).

Negative correlations between plants and birds (Table 4) are difficult to interpret without relating them to structure of the associated plant community. Positive correlations also can lack obvious explanation, such as that of the bromeliad *Bromelia pinguin* (Bromeliaceae) with Scaly-naped Pigeon, Prairie Warbler, and Ovenbird. Bromeliad fruit has little palatability to birds, but may attract insects sought by the two parulids. The positive correlation between the vine *Jacquemontia pentanthos* (Convolvulaceae) and Ovenbird may reflect only that *J. pentanthos* is an indicator of good Ovenbird habitat, but does not supply any direct resources to the bird.

Positive correlations that may suggest preferred frugivory would be the shrubs/trees *Guettarda odorata* (Rubiaceae) with Bridled Quail-Dove, and *Myrciaria floribunda* (Myrtaceae) with Pearly-eyed Thrasher. The significant associations between the shrubs/trees *Eugenia rhombea* (Rubiaceae) and Yellow Warbler, and *Rondeletia pilosa* (Rubiaceae) with American Redstart, may be related to both frugivory and insectivory. The positive correlation with the Bananaquit and the shrub/tree *Capparis hastate* (Capparaceae) might reflect nectarivory, whereas that with the Black-faced Grassquit is unlikely to be related to feeding, as seeds of *C. hastate* are too large for the granivorous grassquit to consume. The grassquit eats mainly grass seeds at forest edges, and its correlation with *C. hastate* probably is because this shrub/tree tends to grow at edges.

Short-term Changes.—The difference in number of registrations between 2005 and 2006 is a result of more records of resident birds, particularly Grey Kingbird, which increased from 0.90 to 3.13 birds/point. One advantage of using of multi-year studies, such as ours, over single-year surveys is to highlight such fluctuations. The Grey Kingbird is an ''interisland-migrant'' as some individuals migrate to islands such as St. John after breeding on other islands, whereas others probably are permanent residents in USVI (Arendt 1992). The number of wintering resident insectivores and omnivores, such as Grey Kingbirds, tends to fluctuate in the Virgin Islands and may be linked to rainfall (Faaborg et al. 1984). It is also possible that delayed migration in 2006 may have led to counts of Grey Kingbirds that were inflated by the presence of both migrants and winter residents.

Long-term Community Changes.—Changes in land-use on St. John since most plantation farming ended in the 1850s (Dookhan 1994, MacDonald et al. 1997) undoubtedly have contributed to trends in resident and migrant landbirds. In particular, the large area of maturing forest on St. John controlled by the NPS makes this area important for migrant landbird conservation (Arendt 1992). Askins and Ewert (1991) attributed the decreased abundances of Scaly-naped Pigeon, Antillean Crested Hummingbird, and Northern Parula between 1987 and 1990 to the impact of Hurricane Hugo in 1989. This suggests that habitat associations and changes, caused by both anthropogenic and natural events, may provide effective explanations for migratory and resident bird abundance on St. John.

We examined differences between bird species occurrence, vegetation structure, and plant species occurrence in the two different habitat types to assess the importance of generalized habitat associations. None of the long-term changes was statistically significant with the Bonferroni adjustment for 26 species, but the trends we found help clarify the effects of conservation activities that have occurred on St. John since the creation of VINP in 1956. The only near-significant historical trend (1957–2006) for migrants was a decline of Black-throated Blue Warblers (Table 5). This decline could be important for the migrant community as this species has been shown to be a core species for organization of mixed winter flocks on other Caribbean islands (Eaton 1953). Low overall abundance of Black-throated Blue Warblers on St. John is typical of numbers recorded in the British Virgin Islands from 1994 to 2004 (Boal et al. 2006). The Cape May Warbler was regarded as a fairly common winter resident in the Virgin Islands in the late 1970s (Norton 1979), but now is rare (Boal et al. 2006). However, sample sizes for both species are too low to draw strong conclusions.

Among residents, Zenaida Dove, Common Ground-Dove, Smooth-billed Ani, and Black-faced Grassquit have declined in relative abundance since establishment of VINP. This is probably due to the increasing maturity of forest in and near the Park, which limits the habitat for these open country species. Caribbean Elaenia and Lesser Antillean Bullfinch have increased in relative abundance during the same period. The Lesser Antillean Bullfinch, not present in 1957, now is among the most common resident species on St. John. The bullfinch was first observed in the USVI in the 1960s, and the first report of nesting on St. John was in 1971–1972 and on St. Croix in 1983 (Jaden 1985, Leck and Norton 1991). Possible mechanisms for this range expansion include transportation as pets, natural dispersal from islands in the northern Lesser Antilles, and hurricanes Donna (1960) and Faith (1966) (Raffaele and Roby 1977). Both Caribbean Elaenia and Lesser Antillean Bullfinch tend to inhabit woodlands and shrubby or scrubby areas (Raffaele et al. 1998). Their increased relative abundance may reflect increased secondary growth as areas in VINP that were once residential or agricultural revert to forest.

CONSERVATION IMPLICATIONS

The establishment of Virgin Islands National Park appears to leave most of the resident and migratory bird species of St. John in a secure position. The forests of protected ravines in the center of the island should continue to provide habitat for most neotropical migrants and for the Bridled Quail-Dove, which occur more abundantly in mature, moist forest. The drier ridges that are more exposed to hurricanes will continue to provide habitat for species that prefer drier, more stunted forests. Most species of open habitats remain in large numbers on parts of the island where humans live (DWS and SKR, pers. obs.). The avian conservation outlook for St. John is bright.

ACKNOWLEDGMENTS

We thank the USDI Fish and Wildlife Service, USDA Forest Service Southern Research Station, USDA Forest Service International Institute for Tropical Forestry, University of Florida, and Florida Museum of Natural History for funding this project. We also thank personnel of Virgin Islands National Park for assistance. Special appreciation is due to Humfredo Marcano, Luis Ortíz-Vega, Iván Vicéns, and Britta Dimick for botanical and navigational expertise in the field. We also thank Eileen Helmer and Ariel Lugo for assistance throughout the project, Amelia Savage for data entry and library work, and the staff at Virgin Islands Environmental Research Station for housing and all manner of logistical support.

LITERATURE CITED

ARENDT, W. J. 1992. Status of North American migrant landbirds in the Caribbean region: a summary. Pages 143–171 *in* Ecology and conservation of neotropical migrant landbirds (J. M. Hagan and D. W. Johnston, Editors). Smithsonian Institution, Washington, D.C., USA.

ASKINS, R. A. AND D. N. EWERT. 1991. Impact of Hurricane Hugo on bird populations on St. John, U.S. Virgin Islands. Biotropica 23:481–487.

ASKINS, R. A., D. N. EWERT, AND R. L. NORTON. 1992. Abundance of wintering migrants in fragmented and continuous forests in the U.S. Virgin Islands. Pages 197–206 *in* Ecology and conservation of neotropical migrant landbirds (J. M. Hagan and D. W. Johnston, Editors). Smithsonian Institution, Washington, D.C., USA.

BECHTOLD, W. A. AND P. L. PATTERSON (Editors). 2005. The enhanced forest inventory and analysis program - national sampling design and estimation procedures. USDA, Forest Service, General Technical Report SRS-80. Southern Research Station, Asheville, North Carolina, USA.

BECHTOLD, W. A. AND C. T. SCOTT. 2005. The forest inventory and analysis plot design. Pages 27–42 *in* The enhanced forest inventory and analysis program-national sampling design and estimation procedures (W. A. Bechtold and P. L. Patterson, Editors). USDA, Forest Service, General Technical Report SRS-80. Southern Research Station, Asheville, North Carolina, USA.

BIBBY, C. J., N. D. BURGESS, AND D. A. HILL. 2000. Bird census techniques. Harcourt Brace, London, United Kingdom.

BOAL, C. W., F. C. SIBLEY, T. S. ESTABROOK, AND J. LAZELL. 2006. Insular and migrant species, longevity records, and new species records on Guana Island, British Virgin Islands. Wilson Journal of Ornithology 118:218–224.

BRANDEIS, T. J. 2003. Puerto Rico's forest inventory: adapting the forest inventory and analysis program to a Caribbean island. Journal of Forestry 101:8–13.

CURRIE, D., J. M. WUNDERLE, D. N. EWERT, M. R. ANDERSON, A. DAVIS, AND Z. MCKENZIE. 2005. Winter avian distribution and relative abundance in six terrestrial habitats on southern Eleuthera, The Bahamas. Caribbean Journal of Science 41: 88–100.

DOOKHAN, I. 1994. A history of the Virgin Islands of the United States. Canoe Press, Kingston, Jamaica.

EATON, S. W. 1953. Wood warblers wintering in Cuba. Wilson Bulletin 65:169–174.

EMLEN, J. T. 1971. Population densities of birds derived from point counts. Auk 88:332–342.

EWEL, J. J. AND J. L. WHITMORE. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA, Forest Service, Research Paper ITF-018. Institute of Tropical Forestry, Río Piedras, Puerto Rico.

EWERT, D. N. AND R. A. ASKINS. 1991. Flocking behavior of migratory warblers in winter in the Virgin Islands. Condor 93:864–868.

FAABORG, J. 1984. Population sizes and philopatry of winter resident warblers in Puerto Rico. Journal of Field Ornithology 55:376–378.

FAABORG, J., W. J. ARENDT, AND M. S. KAISER. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: a nine year study. Wilson Bulletin 96:575–593.

FAABORG, J., K. M. DUGGER, AND W. J. ARENDT. 2007. Long-term variation in the winter resident bird community of Guánica Forest, Puerto Rico: lessons for measuring and monitoring species richness. Journal of Field Ornithology 78:270–278.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

INTEGRATED TAXONOMIC INFORMATION SYSTEM (ITIS). 2008. Integrated Taxonomic Information System on-line database. http://www.itis.gov. (accessed 21 April 2008).

JADEN, D. 1985. A guide to the natural history of St. John: bird checklist. Environmental Studies Program, St. John, Virgin Islands.

LECK, C. F. 1972. Observations of birds at *Cecropia* trees in Puerto Rico. Wilson Bulletin 84:498–500.

LECK, C. F. AND R. L. NORTON. 1991. An annotated checklist of the birds of the U.S. Virgin Islands. Antilles Press, Christiansted, St. Croix, Virgin Islands.

MACDONALD, L. H., D. M. ANDERSON, AND W. E. DIETRICH. 1997. Paradise threatened: land use and erosion on St. John, U.S. Virgin Islands. Environmental Management 21:851–863.

MANLEY, P. N., W. J. ZIELINSKI, M. D. SCHLESINGER, AND S. R. MORI. 2004. Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. Ecological Applications 14: 296–310.

NICHOLS, J. D., J. E. HINES, J. R. SAUER, F. W. FALLON, J. E. FALLON, AND P. J. HEGLUND. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117:393–408.

NORTON, R. L. 1979. New records of birds for the Virgin Islands. American Birds 33:145–146.

OSWALT, S. N., T. J. BRANDEIS, AND B. P. DIMICK. 2006. Phytosociology of vascular plants on an International Biosphere Reserve: Virgin Islands National Park, St. John, U.S. Virgin Islands. Caribbean Journal of Science 42:53–66.

PREGILL, G. K., D. W. STEADMAN, AND D. R. WATTERS. 1994. Late Quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. Bulletin of the Carnegie Museum of Natural History 30:1–51.

R CORE DEVELOPMENT TEAM. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RAFFAELE, H. A. AND D. ROBY. 1977. The Lesser Antillean Bullfinch in the Virgin Islands. Wilson Bulletin 89:338–342.

RAFFAELE, H., J. WILEY, O. GARRIDO, A. KEITH, AND J. RAFFAELE. 1998. A guide to the birds of the West Indies. Princeton University Press, Princeton, New Jersey, USA.

RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Handbook for field methods for monitoring landbirds. USDA, Forest Service, General Technical Report PSW-GTR-144. Southwest Research Station, Albany, California, USA.

RAPPOLE, J. H. 1995. The ecology of migrant birds: a neotropical perspective. Smithsonian Institution Press, Washington, D.C., USA.

REILLY, A. 1991. The effects of hurricane Hugo in three tropical forests in the U.S. Virgin Islands. Biotropica 23:414–419.

REIS, K. R. AND D. W. STEADMAN. 1999. Archaeology of Trants, Montserrat. Part 5. Prehistoric avifauna. Annals of Carnegie Museum 68:275–287.

ROBERTSON, W. B. 1962. Observations on the birds of St. John, Virgin Islands. Auk 79:44–76.

SEAMAN, G. A. 1966. Foods of the Quail Dove (*Geotrygon mystacea*). Caribbean Journal of Science 6: 177–179.

SIMONS, T. R., M. W. ALLDREDGE, K. H. POLLOCK, AND J. M. WETTROTH. 2007. Experimental analysis of the auditory detection process on avian point counts. Auk 124:986–999.

TOSSAS, A. G. AND J. R. THOMLINSON. 2007. Landscape characteristics of Puerto Rican Vireo (*Vireo latimeri*) nesting habitat, with source-sink implications. Ornitología Neotropical 18:233–242.

U.S. DEPARTMENT OF AGRICULTURE (USDA). 2002. Field procedures for Puerto Rico and the Virgin Islands. Supplement C to SRS Regional Manual 1.56. USDA, Forest Service, Southern Research Station, Forest Inventory and Analysis Research Work Unit, Knoxville, Tennessee, USA. Online manual http://srsfia2.fs.fed.us/data_acquisition/manual.shtml. Accessed 21 April 2008.

WAIDE, R. B. AND P. M. NARINS. 1988. Tropical forest bird counts and the effect of sound attenuation. Auk 105:296–302.

WAUER, R. H. AND J. M. WUNDERLE. 1992. The effect of hurricane Hugo on bird populations on St. Croix, U.S. Virgin Islands. Wilson Bulletin 104: 656–673.

WUNDERLE, J. M. AND R. B. WAIDE. 1993. Distribution of overwintering nearctic migrants in the Bahamas and Greater Antilles. Condor 95:904–933.