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Winter Avian Distribution and Relative Abundance in Six Terrestrial Habitats on Southern Eleuthera, The Bahamas

DAVE CURRIE[1], JOSEPH M. WUNDERLE JR.[2,5], DAVID N. EWERT[3], ANCILLENO DAVIS[4], AND ZEKO MCKENZIE[4]

[1]*Puerto Rico Conservation Foundation c/o International Institute of Tropical Forestry, USDA Forest Service, Sabana Field Research Station, HC 02 Box 6205, Luquillo, Puerto Rico 00773, USA.*
[2]*International Institute of Tropical Forestry, USDA Forest Service, Sabana Field Research Station, HC 02 Box 6205, Luquillo, Puerto Rico 00773, USA.*
[3]*The Nature Conservancy, 101 East Grand River, Lansing, MI 48906, USA.*
[4]*The Bahamas National Trust, P.O. Box N-4105, Nassau, The Bahamas.*
[5]*Corresponding Author (Wunderle@coqui.net)*

ABSTRACT.—We studied winter avian distribution and relative abundance in six common terrestrial broadleaf habitats, selected on a continuum of disturbance from recently disturbed (abandoned plantation) to mature vegetation (tall coppice), on the island of Eleuthera, The Bahamas. During 158-point counts conducted 22 January—10 March 2003, 1357 individuals were detected, comprising 33 species. Winter residents comprised 47% of species detected and 20% (248/1357) of individuals. The abundance of both permanent and winter residents was highest in taller, more mature vegetation (short and tall coppice) and lowest in more recently disturbed shorter vegetation (abandoned plantations). Four permanent residents: *Vireo crassirostris*, *Loxigilla violacea*, *Tiaris bicolor*, and *Aramus guarauna*; and three winter residents *Geothlypis trichas*, *Dendroica palmarum*, and *Dumetella carolinensis* were unevenly distributed among habitats; three (*V. crassirostris, L. violacea, D. carolinensis*) were more commonly detected in mature habitats and four (*T. bicolor, A. guarauna, G. trichas, D. palmarum*) in more recently disturbed environments. There were marked similarities in the composition of bird communities among all habitats; the largest differences were between the least and most disturbed habitats. There was little evidence of habitat specialization by either permanent or winter residents. Intra-specific variation in abundance of permanent and winter residents is discussed in relation to habitat structure and disturbance regimes.

Keywords.—Avian habitat use, *Dendroica kirtlandii*, disturbance ecology, *Geothlypis rostrata*, Nearctic-Neotropical migrant birds, *Saurothera merlini*

INTRODUCTION

Natural disturbances such as drought and hurricanes can have severe effects on some Caribbean bird populations and their habitats, which can be exacerbated by anthropogenic factors (e.g., Faaborg et al. 1984; Wiley and Wunderle 1994). Habitat loss or conversion resulting from human activities has been the most important form of anthropogenic disturbance of Caribbean habitats (Lanly 1982); it has been estimated that only ca. 21% of total land area is forested in the Caribbean (Wunderle and Waide 1993). However, despite the importance of various types of habitat disturbance in determining the distribution and abundance of Caribbean birds, relatively few studies have quantified avian habitat distribution among different terrestrial habitats (e.g., Askins and Ewert 1991; Wunderle et al. 1992; Wauer and Wunderle 1992). In particular, these disturbances can threaten species with small populations and specialized habitat requirements.

The importance of The Bahamas archipelago for birds is well documented and it is listed as both an Important Bird Area (IBA) and an Endemic Bird Area (EBA; Stattersfield et al. 1998). Over 300 species

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have been recorded in the archipelago, more than 200 birds regularly occur, and there are 109 breeding species including three extant endemics and 34 endemic subspecies (White 1998). Nearctic-Neotropical migrants are documented as comprising up to 50% of terrestrial birds species during the winter (e.g., Wunderle and Waide 1993; Lee 1996a, b), one of which, the Kirtland's Warbler *Dendroica kirtlandii*, winters exclusively in the archipelago (e.g., Mayfield 1972; Sykes and Clench 1998).

Although comprehensive bird lists have been compiled for many of the islands in the archipelago (see White 1998), few quantitative data compare bird distribution and densities among habitats (e.g., Grand Bahama, Emlen 1977; Andros Baltz 1993; New Providence, Great Inagua, Wunderle and Waide 1993; Abaco, Lee 1996a, b). Given the high rate of deforestation and development in the Caribbean, including The Bahamas (Lanly 1982; Wunderle and Waide 1993), quantifying baseline bird distributions and identifying important habitats for both migrants and residents, especially threatened migrant species and regional endemics, is crucial for developing effective conservation programs and policies. In this paper we describe avian abundance and characterize winter bird assemblages in six habitats, at various stages of succession on Eleuthera. We describe the effect of disturbance and vegetation structure on bird assemblages, habitat distribution of individual species, and identify habitats used by both permanent and winter resident species.

Methods and Materials

Study site

The Bahamas are low-lying sub-tropical islands (maximum height is 64 m asl). Northern islands experience more rainfall than the southern islands: the wettest months are May-November. The study was conducted on Eleuthera (c. 25°N, 76°W) from 22 January to 10 March 2003 (Fig. 1). Eleuthera is dominated by broadleaved trees and shrubs e.g., *Acacia choriophylla*, *Bursera simaruba* and *Coccoloba* sp, *Lysiloma latisiliquum*, *Metopium toxiferum*, *Reynosia septentionalis*, *Erithalis fruticosa*, *Eugenia* sp., *Chiococca* sp., *Smilax auriculata,* and *Lantana involucrata*, which form dense areas of dry forest and scrub. Historically, Eleuthera was extensively farmed, however more recently farming has declined resulting in a mosaic of broadleaf habitats of different ages.

Point counts

Fixed-radius point counts were conducted in six common terrestrial habitats following methods of Hutto et al. (1986). At each point we recorded the following data: (i) the number of individuals of each species detected within a 25-m radius surrounding the observer; (ii) the number of individuals of each species detected beyond the 25-m radius but still within the habitat of interest; and (iii) species detected during 5 min of playback of mixed warbler chips (conducted after the five minutes of silence) within a 25 m radius surrounding the observer. Tape playback included chip notes of six winter residents: Ovenbird, American Redstart, Northern Paula, Black-and-white Warbler, Black-throated Blue Warbler (scientific names in Table 2), and Hooded Warbler (*Wilsonia citrina*). An additional two minutes were used to identify any species that responded to tape. Total sampling time per point was 12 minutes. While walking between points, we recorded additional species not found at point count stations to better assess the avifauna in each habitat. All bird names follow Raffaele et al. (1998).

Points were at least 150 m apart, and a minimum of 50 m from a habitat edge. Counts were conducted between sunrise and 1030 h EST. Because of the dense nature of vegetation all point counts were non-randomly conducted along existing narrow paths and unpaved tracks where habitat was similar on both sides of the track. Playback of Kirtland's Warbler chips, calls, and song were played while walking between the fixed points, but was stopped 30 m from the subsequent fixed point. Point counts were not conducted during rain or wind.

Counts were conducted in the following six terrestrial habitats listed in order from

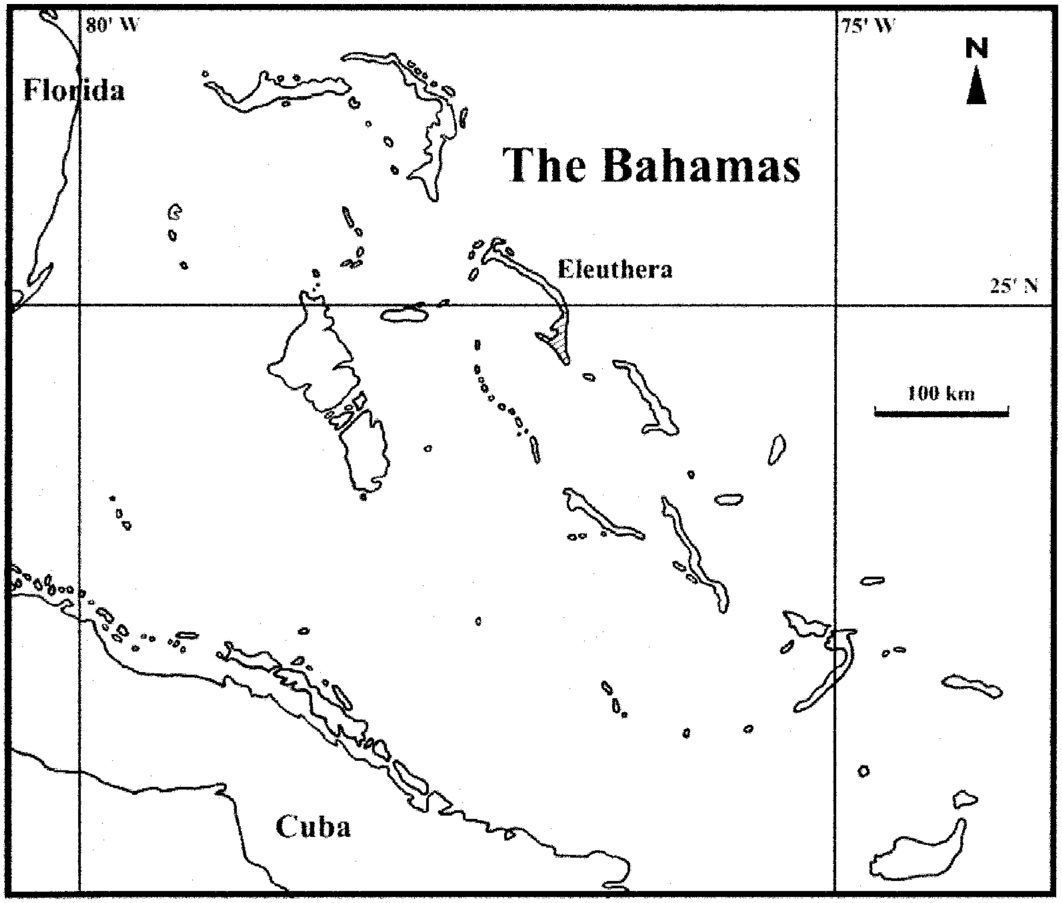

FIG. 1. The Bahamas archipelago showing our study area (hatched area) on southern Eleuthera.

least to most mature: (i) recently abandoned plantation; (ii) early secondary shrub; (iii) mature secondary shrub; (iv) coastal coppice; (v) short coppice less than 4.6 m; and (vi) tall coppice.—greater than 4.6 m in height. Habitats (iii)-(vi) are based on definitions in Sykes and Clench (1998). Recently abandoned plantations were areas originally cleared for agriculture (by slash and burn) and subsequently left fallow for several years, and were characterized by short shrubs and relic agricultural plant species, interspersed with patches of grasses. Early secondary shrub is intermediate between recently abandoned plantation and mature secondary shrub. Habitats (i) through (v) can be considered to occur along a chronosequence relative to disturbance starting with abandoned plantation (the most recently disturbed) to tall coppice (climax or mature vegetation). Native shrub (coastal coppice) does not fit into this continuum and is presumably an edaphic climax type. Nonetheless, canopy height can also be used to ordinate the habitats and as a result coastal coppice falls between mature secondary and short coppice habitats. Sites of secondary vegetation dominated by the invasive exotic, *Leucaena leucocephala,* were not censused.

Vegetation profiles

Two 20 m diameter circular plots (0.03 ha) were used to quantify vegetation in each habitat sampled with point counts. Two point count centers were randomly selected in each habitat and sample plots centered on the selected point count locations.

Within each plot, we measured diameter at breast height (DBH) for trees greater than 3 cm. These data were recorded in the following diameter classes: 3-8 cm, >8-15 cm, >15-23 cm, >23-38 cm, and >38 cm.

Shrub density at 1.3 m height was estimated along four 8-m transects running in the cardinal directions centered within the 0.03 ha circle. Density was determined by an observer walking along the transects and counting all live woody stems (<3 cm) touching the observer's body and outstretched arms at breast height. These were categorized as broadleaf and other (which included non-broadleaf and grass).

We determined foliage height profiles at 20 points at 2 m intervals along the north, south, east, and west radii of the circular plot (after Schemske and Brokaw 1991). A 3-m and 2.0 cm pole marked at 0.5 m intervals was placed vertically at each sample point. The presence or absence of foliage touching the pole within each height class was recorded for each height class. For height intervals above 3 m we sighted along the upright pole and recorded the presence or absence of foliage in each of the following estimated height intervals: >3-4, >4-6, >6-8, >8-10, >10-12, >12-15, >15-20, and >20-25 m. Percent cover, for each height interval, was calculated by dividing the number of points in which foliage was present in that height interval by the total number of sample points (n = 20) and multiplying by 100. Heights of the five tallest canopy trees were estimated by reference to the 3 m upright pole.

Canopy cover was evaluated by sighting vertically upwards through a 4.5-cm diameter tube at each of the 20 points along the four radii. Presence or absence of broadleaf canopy cover was noted at each point and mean percent canopy cover determined by dividing the number of points with the specified cover type by the total number of sample points (n = 20). Also, ground cover at each point was evaluated by sighting vertically down at the ground and recording the presence of broadleaf cover, ferns, herbs, grass, and bare ground. The percentage ground cover for each of these categories was calculated by dividing the number of points with the specified cover category by the total number of sample points (n = 20).

Analyses

All birds were identified to species, when known, with two exceptions. Doves in the genus *Zenaida* were not identified to species (Mourning Dove *Z. macroura* and Zenaida Dove *Z. aurita*), because their calls are frequently difficult to distinguish (Raffaele et al. 1998). In addition, a winter resident warbler was identified only to the genus *Oporornis*. Eight birds were not identified (including two observed *Dendroica* sp.), and were not included in the analyses.

For each habitat, we calculated the mean number of individuals detected (by sight and sound) per fixed radius point, as well as the frequency of points in which a species occurred within the 25-m radius. In addition, we also calculated the mean number of detections per point with unlimited radius. We used the methods of Hutto et al. (1986) to calculate detectability ratios for each species in each habitat. The ratio is equivalent to the number of point counts at which a given species was recorded only beyond the 25-m radius, divided by the total number of counts at which the species was recorded in a given habitat. The maximum number of individuals (MNI), detected in either the five minutes of silence or five minutes of playback within the fixed radius, was calculated for each species during each point count and used as an additional measure of species abundance at each point. We refer to winter residents as species present through the winter months (October-April) and permanent residents, as those species present throughout the year.

We calculated a Similarity Coefficient (SC) to compare winter bird assemblages between habitat pairs using the equation: $SC = 2W/(a+b)$ from Cox and Ricklefs (1977), where W = the sum of the lesser abundance values for each species common to the two habitats (the abundance value is the percentage of points with the particular species within the 25-m fixed radius). The values a and b are the sum of the abundance values (i.e., percentage of points) for all species in the two habitats. The coefficient varies from 0 to 1, with 1 representing complete overlap of bird assemblages in the two habitats. In addition, the degree of habitat specialization for each species was measured as the exponential of the Shannon-Weiner diversity statistic (H′) calculated from the relative rates of occurrence in the different habitats (Lynch 1989). These values can vary from a minimum of 1.0 (complete specialization on a habitat type) to a maximum of 6.0 (equal use of all six habitats). Statistical tests follow Sokal and Rohlf (1981) and Siegel and Castellan (1988). Data were analyzed using SYSTAT (Wilkinson 1989). Statistical tests are two-tailed and corrected for ties when appropriate. For all statistical tests, a probability of type I error of 0.05 or less was accepted as significant, but greater values are shown for descriptive purposes.

RESULTS

Habitat structure

There were marked differences between habitats in vegetation height, the density of shrub layer, and the extent of ground cover (Fig. 2, Table 1). Some of these differences reflect the time since the last disturbance, with more recently disturbed vegetation (e.g., abandoned plantation, early and mature secondary shrub) being typically shorter, having less canopy cover, a denser shrub layer, and increased ground cover than less recently disturbed habitats (e.g., short and tall coppice).

Other differences in vegetation structure reflect variation in soil type, and although the structure of coastal coppice closely resembles mature secondary shrub, this is at-

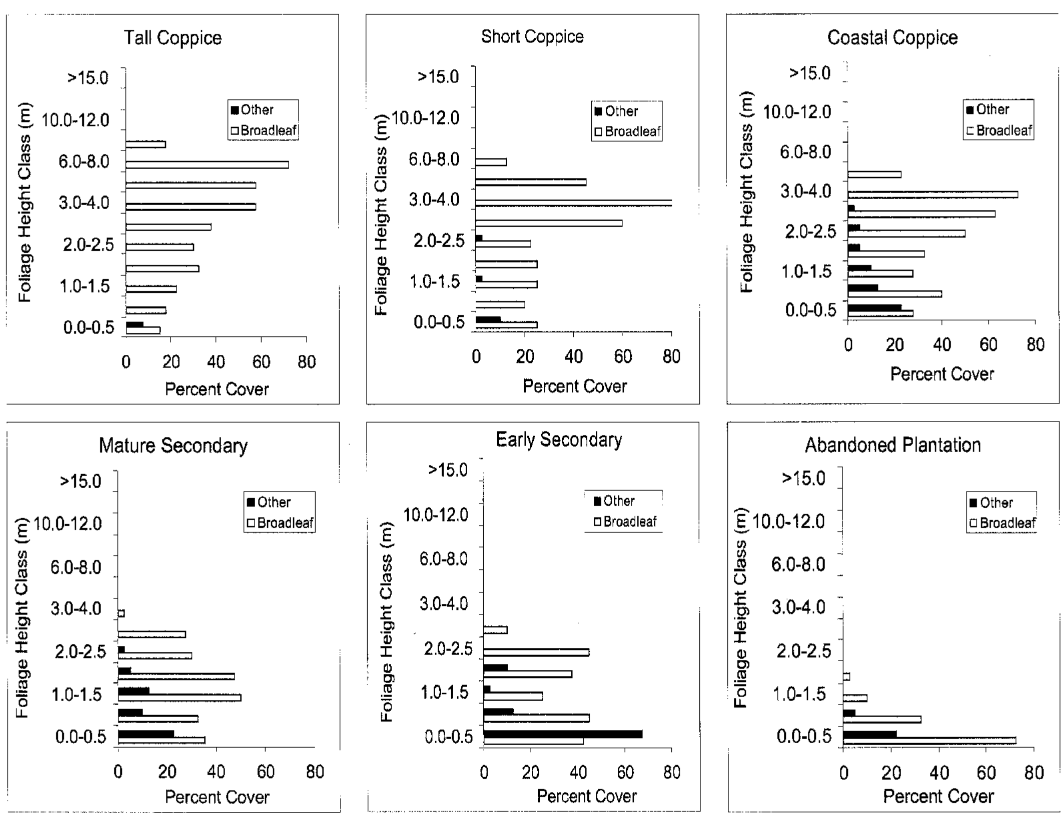

FIG. 2. Foliage height profiles for six habitats in which birds were sampled 22 January-10 March 2003 in southern Eleuthera, The Bahamas. Each foliage height class includes all foliage present in categories greater than the first height value of each respective height class. Values are shown separately for broadleaf and 'other' foliage types.

TABLE 1. Means of five vegetation traits in six habitats sampled for birds on southern Eleuthera, The Bahamas. Habitat variables and vegetation variables are described and defined in the text.

	Habitat					
Habitat trait	Tall coppice	Short coppice	Coastal coppice	Mature secondary	Early secondary	Abandoned plantation
Canopy height (m)	11.9	5.9	4.3	3.7	3.3	1.8
DBH (cm)	8.2	5.9	6.6	5.5	5.5	—
Shrub density*						
Broadleaf	23.9	67.5	79.4	153.3	103.1	11.5
Other	0.9	3.5	1.5	1.8	0.8	0.0
Canopy cover (%)						
Broadleaf	97.5	97.5	92.3	50.0	30.0	0
Other	0	0	0	3	0	0
Ground cover (%)						
Broadleaf	42.3	55.0	69.3	90.0	85.0	95.0
Other	17.5	15.0	15.4	37.5	60.0	23.0

*Mean stems per 15 m^2.

tributed to exposure to saline conditions or a less fertile 'whiteland' soil type, and not due to anthropogenic factors, as coastal coppice is considered to be a late successional vegetation type. In contrast, the five other habitat types surveyed were typically associated with the more fertile 'blackland' soil type.

Despite differences in the disturbance regime and soil type, there were similarities in the composition of tree and shrub species between the respective areas (e.g., *Acacia choriophylla*, *Bursera simaruba*, *Coccoloba* sp., *Lysiloma latisiliquum*, *Metopium toxiferum, Eugenia* sp., *Chiococca* sp., and *Smilax auriculata)*. The exception to this was abandoned plantation, which contained agricultural species (e.g., bananas *Musa sapienium*) and open grassy areas.

Point counts

One hundred and fifty-six point counts were conducted in six habitats, with 30 points in each habitat except for abandoned plantation (17 points) and early secondary shrub (19 points), because of the relative rarity of these two habitats. One thousand three hundred fifty-seven individuals representing 33 bird species (18 permanent residents and 15 winter residents) were recorded during the 5 min of silence: winter residents comprised 47% (14/30) of all species detected and 20% of individuals. In addition, three winter resident species were detected during playback of warbler chips (Northern Waterthrush, Red-winged Blackbird and White-eyed Vireo; scientific names in Table 2), and an additional two species, one resident (Green Heron *Butorides virescens*) and one migrant (Merlin *Falco columbarius*), were recorded either moving between points or flying over during the counts, but not during counts themselves.

Median detectability indices for permanent residents in all habitats (median = 0.64) were significantly higher than median values for winter residents (median = 0) in all habitats (Mann Whitney U = 59.5, P = 0.005; Table 2). Because detectability indices varied considerably among species and habitats, we restricted our quantitative analyses to the 25-m fixed radius point counts. These counts included 627 individuals comprising 30 species, with winter residents comprising 47% (14/30) of species detected and 25% of individuals (155/627). Resident species were more frequently detected than winter residents in all habitats (mean proportion of migrant species = 43% of species; range 38-50%).

Mean total birds per fixed radius point as well as mean number of species per point varied significantly among habitats. Both measures were lowest in recently abandoned plantation and highest in tall coppice (Table 2), based on the five-minute silent sampling protocol. Habitat variation in

TABLE 2. Occurrence of birds in six different habitats sampled from 22 January to 10 March 2003 in southern Eleuthera, Bahamas. Occurrence is based on the average number of detections per point (×100) in point counts of 5-min duration within a 25 m radius. Values in parentheses show MNI (maximum number detected within 25 m in either 5-min period of silence and a following 5-min period with a broadcast of warbler chip notes (×100). Letters following scientific name indicate status (P = permanent resident, W = winter resident) and diet (FF = fruit/seeds, N = nectar, I = insects). P-value indicates significance level for comparison of point counts (5-min silent duration with a 25 m radius) among six habitats based on Kruskal-Wallace Test. Detection ratio is the number of points at which a given species was recorded only beyond the 25-m radius, divided by the total number of counts at which the species was recorded (Hutto et al. 1986).

	Occurrence (MNI) per habitat							
Species	Tall coppice	Short coppice	Coastal coppice	Mature secondary	Early secondary	Abandoned plantation	*P*	Detection ratio
Limpkin	0	0	0	0	0	10.5	0.013	0.78
Aramus guarauna P, S	(0)	(0)	(0)	(0)	(0)	(10.5)	(0.013)	
Common Ground-dove	0	0	0	6.7	0	42.1	0.078	0.75
Columbina passerina P, F	(0)	(0)	(0)	(6.7)	(0)	(42.1)	(0.078)	
Zenaida spp. P, F	0	3.3	0	0	0	0	0.52	0.95
	(0)	(3.3)	(3.3)	(0)	(0)	(0)	(0.66)	
Key West Quail-Dove	6.7	3.3	0	0	0	0	0.33	0.89
Geotrygon chrysia P, F	(6.7)	(3.3)	(0)	(0)	(0)	(0)	(0.33)	
White-crowned Pigeon	6.7	6.7	3.3	0	5.9	0	0.63	0.63
Columba leucocephala P, F	(6.7)	(6.7)	(3.3)	(0)	(5.9)	(0)	(0.63)	
Mangrove Cuckoo	0	0	0	0	5.9	0	0.15	0
Coccyzus minor P, I	(0)	(0)	(0)	(0)	(5.9)	(0)	(0.15)	
Great Lizard-Cuckoo	0	3.3	3.3	3.3	11.8	0	0.81	0.91
Saurothera merlini P, I, V	(3.3)	(10.0)	(6.7)	(6.7)	(11.8)	(0)	(0.8)	
Smooth-billed Ani	0	0	0	0	0	0	1.0	1.0
Crotophaga ani P, I	(0)	(0)	(0)	(6.7)	(23.5)	(31.6)	(0.01)	
Bahamas Woodstar	0	3.3	16.7	3.3	5.9	5.3	0.56	0
Calliphlox evelynae P, I	(10)	(10)	(23.3)	(6.7)	(35.3)	(5.3)	(0.14)	
La Sagra's Flycatcher	0	0	0	0	0	0	1.0	1.0
Myiarchus sagrae P, I	(3.3)	(10)	(0)	(3.3)	(0)	(5.3)	(2.9)	
Red-legged Thrush	0	3.3	0	3.3	0	0	1.0	0
Turdus plumbeus P, F	(0)	(6.7)	(6.7)	(3.3)	(0)	(0)	(0.52)	
Gray Catbird	60	30	13.3	16.7	5.9	5.3	0.004	0.53
Dumetella carolinensis W, F	(70.0)	(80.0)	(20.0)	(53.3)	(17.7)	(10.5)	(0.001)	
Northern Mockingbird	0	6.7	0	0	0	0	0.13	0
Mimus polyglottos P, F	(0)	(6.7)	(0)	(0)	(0)	(0)	(0.13)	
Bahama Mockingbird	60	56.7	33.3	46.7	29.4	15.8	0.13	0.69
Mimus gundlachii P, F	(86.7)	(70.0)	(50.0)	(63.3)	(47.1)	(21.1)	(0.06)	
Thick-billed Vireo	100.0	116.7	53.3	86.7	135.3	36.8	0.02	0.52
Vireo crassirostris P, I	(186.7)	(213.3)	(133.3)	(140.0)	(200.0)	(73.7)	(0.001)	
White-eyed Vireo	0	0	0	0	0	0	1.0	—
Vireo griseus W, I	(3.3)	(0)	(0)	(0)	(0)	(0)	(0.52)	
Northern Parula	0	0	3.3	0	0	0	0.19	0
Parula americana W, I	(6.7)	(3.3)	(3.3)	(0)	(0)	(0)	(0.19)	
Cape May Warbler	6.7	0	0	0	0	0	0.13	0
Dendroica tigrina W, N	(10.0)	(3.3)	(0)	(0)	(11.8)	(0)	(0.19)	
Black-throated Blue Warbler	0	0	0	0	0	5.3	0.21	0
Dendroica caerulescens W, I	(0)	(0)	(0)	(3.3)	(5.9)	(5.3)	(0.47)	
Black-thr. Green Warbler	0	0	0	3.3	0	0	0.52	0
Dendroica virens W, I	(0)	(0)	(0)	(3.3)	(5.8)	(0)	(0.52)	
Yellow-rumped Warbler	23.3	26.7	30.0	20.0	23.5	31.6	0.99	0.38
Dendroica coronta W, I	(63.3)	(46.7)	(43.3)	(20.0)	23.5	(36.8)	(0.32)	
Kirtland's Warbler	0	0	0	0	0	0	1.0	—
Dendroica kirtlandii W, I	(0)	(0)	(0)	(3.3)	(0)	(0)	(0.52)	

TABLE 2. Continued.

Species	Occurrence (MNI) per habitat						P	Detection ratio
	Tall coppice	Short coppice	Coastal coppice	Mature secondary	Early secondary	Abandoned plantation		
Prairie Warbler	16.7	3.3	13.3	6.7	5.9	5.3	0.63	0.14
Dendroica discolor W, I	(43.3)	(50.0)	(43.3)	(40.0)	(94.1)	(52.6)	(0.28)	
Palm Warbler	10.0	6.7	0	13.3	35.3	47.4	0.007	0.37
Dendroica palmarum W, I	(10.0)	(6.7)	(13.3)	(20.0)	(52.9)	(105.3)	(0.001)	
Black-and-white Warbler	0	0	3.3	3.3	0	0	0.66	0
Mniotilta varia W, I	(6.7)	(3.3)	(3.3)	(10.0)	(11.7)	(21.1)	(0.76)	
American Redstart	26.7	16.7	6.7	6.7	0	10.5	0.08	0.11
Setophaga ruticilla W, I	(56.7)	(43.3)	(13.3)	(10.0)	(11.8)	(10.5)	(0.001)	
Worm-eating Warbler	0	3.3	0	0	0	0	0.52	0
Helmitheros vermivora W, I	(10)	(3.3)	(0)	(0)	(0)	(0)	(0.10)	
Ovenbird	13.3	3.3	0	3.3	5.9	0	0.16	0.36
Seiurus aurocapillus W, I	(56.7)	(26.7)	(16.7)	(20.0)	(41.2)	(0)	(0.002)	
Northern Waterthrush	0	0	0	0	0	0	1.0	—
Seiurus noveboracensis W, I	(0)	(0)	(0)	(0)	(0)	(10.5)	(0.21)	
Common Yellowthroat	0	0	0	0	5.9	15.8	0.048	0.25
Geothlypis trichas W, I	(0)	(3.3)	(6.7)	(3.3)	(0)	(31.58)	(0.008)	
Bahama Yellowthroat	3.3	10	3.3	6.7	11.8	5.3	0.79	0.58
Geothlypis rostrata P, I	(23.3)	(23.3)	(13.3)	(16.7)	(41.2)	(15.8)	(0.55)	
Bananaquit	80	83.3	33.3	53.3	23.5	0	0.0001	0.32
Coereba flaveola P, N	(120)	(113.3)	(56.7)	(83.3)	(41.2)	(5.3)	(0.001)	
Black-faced Grassquit	0	13.3	53.3	33.3	76.5	65.2	0.0001	0.36
Tiaris bicolor P, F	(6.7)	(13.3)	(56.7)	(36.7)	(82.3)	(94.7)	(0.001)	
Greater Antillean Bullfinch	90	76.7	60	30	29.4	5.3	0.0001	0.07
Loxigilla violacea P, F	(106.7)	(103.3)	(83.3)	(53.3)	(52.9)	(5.3)	(0.001)	
Red-winged Blackbird	0	0	0	0	0	0	1.0	—
Agelaius phoeniceus W, I	(0)	(0)	(3.3)	(0)	(0)	(0)	(0.52)	
Oporornis sp. W, I	0	0	0	0	0	5.3	0.21	0
	(0)	(0)	(0)	(0)	(0)	(5.3)	(0.21)	
Mean number of individuals	5.0	4.8	3.3	3.5	4.2	3.1	0.015	—
per point (all species)	(8.9)	(8.6)	(6.0)	(6.1)	(8.0)	(5.7)	(0.001)	
Mean number of species per	3.7	3.5	2.6	2.6	2.9	2.2	0.008	—
point (all species)	(6.0)	(6.0)	(4.5)	(4.4)	(5.5)	(3.8)	(0.001)	
Mean number of winter	1.2	0.8	0.6	0.5	0.7	0.9	0.076	—
resident species per point	(2.5)	(2.2)	(1.4)	(1.4)	(1.9)	(2.0)	(0.006)	
Mean number of winter	1.6	0.9	0.7	0.7	0.8	1.3	0.091	—
resident individuals per point	(3.4)	(2.7)	(1.7)	(1.9)	(2.8)	(2.9)	(0.01)	
Mean number of permanent	2.5	2.7	2.0	2.1	2.3	1.3	0.003	
resident species per point	(3.5)	(3.8)	(3.1)	(3.0)	(3.5)	(1.8)	(0.0001)	
Mean number of permanent	3.5	3.9	2.6	2.7	3.4	1.8	0.004	—
resident individuals per point	(5.6)	(5.9)	(4.4)	(4.2)	(5.2)	(2.8)	(0.0001)	
Mean number of	1.3	1.6	0.9	1.3	2.2	1.3	0.087	—
insectivorous individuals per point (all species)	(2.7)	(3.8)	(2.7)	(2.7)	(4.8)	(3.3)	(0.003)	
Mean number of	2.5	2.3	1.9	1.6	1.7	1.6	0.056	—
frugivorous individuals per point (all species)	(3.8)	(3.8)	(2.7)	(2.6)	(2.2)	(1.9)	(0.001)	
Mean number of	0.9	0.9	0.5	0.6	0.3	0.1	0.001	—
nectarivorous individuals per point (all species)	(1.3)	(1.0)	(0.6)	(0.7)	(0.5)	(0.1)	(0.001)	

Additional species detected during the survey: Green Heron *Butorides virescens* R, I, V; Merlin *Falco columbarius* W, I, V.

TABLE 3. Similarity coefficients calculated for bird assemblages counted in fixed-radius point counts in six terrestrial habitats in southern Eleuthera, The Bahamas, January through March 2003. Similarity Coefficients follow Cox and Ricklefs (1977). Habitats are described in the text.

	Habitat					
Habitat	Tall coppice	Short coppice	Coastal coppice	Mature secondary	Early secondary	Abandoned plantation
Tall coppice	x					
Short coppice	0.83	x				
Coastal coppice	0.54	0.61	x			
Mature secondary	0.69	0.77	0.76	x		
Early secondary	0.57	0.66	0.71	0.76	x	
Abandoned plantation	0.34	0.41	0.57	0.5	0.63	x

avian abundance was largely attributed to permanent residents (both mean number of individuals and mean number of species per point). Winter residents were evenly distributed among habitats, although there was a non-significant tendency for fewer winter residents in coastal coppice and more in tall coppice (Table 2). Patterns and differences in detections using MNIs mirrored that for 5 min of silence; results for permanent resident species remained unchanged using MNIs, with higher detections in mature habitat and less in recently disturbed habitats. However, the use of playback increased the detection of winter residents (see below), and MNI detections for these species (both number of species and number of individuals) showed significant heterogeneity in detections among habitats. Both the mean number of migrant individuals and species in MNI detections were highest in tall vegetation and lowest in coastal coppice (number of individuals) and mature secondary shrub (number of species).

In general, winter bird assemblages (permanent and winter residents combined) in the six broadleaf habitats (Table 3) were similar: Mean Similarity Coefficient (SC) = 0.62 ± 0.04 (SE). Avian assemblages differed most between recently abandoned plantation and tall coppice (0.34), and least between mature secondary shrub and short coppice (0.88).

There was no significant (Mann-Whitney U = 82.5, P = 0.21) difference in degree of habitat specialization (measured as the exponential of the Shannon-Weiner diversity statistic; H′) between winter residents (median = 1.38) and permanent residents (median = 1.78).

Playback of mixed warbler chip notes increased the detection of all bird species within the fixed radius: number of individuals per species detected prior to playback vs. number of individuals detected using playback, all habitats combined (Wilcoxon sign-ranks, z = 1.99, P = 0.047). This difference was significant for winter residents (Wilcoxon signed-ranks, z = 2.97, P = 0.003), but not for permanent species (Wilcoxon signed-ranks, z = −0.05, P = 0.96).

Species differences

The five most common resident species, ranked in mean order of abundance across the six habitats were Thick-billed Vireo, Greater Antillean Bullfinch, Bahama Mockingbird, Black-faced Grassquit, and Bananaquit, whereas the five most common migrants, also ranked in mean order of abundance across all habitats, were Yellow-rumped Warbler, Gray Catbird, Prairie Warbler, Palm Warbler, and American Redstart.

Five (31%) permanent residents were unevenly distributed in the six habitats: Thick-billed Vireo, Greater Antillean Bullfinch, and Bananaquit were more frequently detected in taller vegetation and less often in more recently disturbed habitats, whereas Black-faced Grassquits and Limpkins were more commonly detected in shorter, more recently disturbed habitats (Table 2). In addition, although not significant, Common Ground-Doves tended to be most abundant in recently abandoned plantations ($P = 0.07$). Resident species habitat differences remained unchanged when MNIs were analyzed, with the exception of the Bahama Mockingbird, which tended ($P = 0.06$) to be more common in tall coppice and least common in early successional habitats such as abandoned plantations.

Of the winter residents, only three (21%) occurred disproportionately in different habitats. Both Common Yellowthroats and Palm Warblers were more frequent in early successional (short) vegetation, specifically abandoned plantation and early secondary shrub, whereas Gray Catbirds were more commonly encountered in tall coppice (Table 2). Although not statistically significant, American Redstarts were also more frequently encountered in taller vegetation (short and tall coppice; $P = 0.08$). Playback increased detection of migrants and, in addition to the significant habitat differences in abundances for migrant species, variations in detections among habitats using MNIs were also significant for American Redstarts and Ovenbirds, both of which were more frequently detected in less recently disturbed habitats, typically tall and short coppice (Table 2).

Diet

The majority of winter residents were insectivorous (93%; 14/15), but the majority of permanent residents detected were frugivorous (57%; 9/16). Detections of the three diet guilds—insectivores, frugivores, and nectarivores, winter and permanent residents combined—showed significant heterogeneity among habitats in both fixed radius counts and MNI. Insectivore detections (number of individuals per point) were typically lower in coastal coppice; frugivores more frequent in mature and taller habitats (tall and short coppice) and lower in more recently disturbed habitats; nectarivores were more common in mature habitats and less abundant in recently disturbed habitats, i.e., abandoned plantation and early secondary (Table 2).

Discussion

During our surveys we detected 64% (18/28; 16 within fixed radius) of the permanent resident land birds (excluding raptor, owl, and swallow species), and 39% (15/38; 14 within fixed radius) of the winter residents, recorded on Eleuthera (see White 1998 for avifaunal list).

Historically, The Bahamas, as with most islands in The Caribbean, have been drastically disturbed by humans for agriculture and development of infrastructure (Mooney 1905; Byrne 1980). However, long-term detrimental effects on the flora appear to have been less acute in The Bahamas than on other islands in the Caribbean (Byrne 1980). This has been attributed to several factors specific to The Bahamas, especially the relatively high frequency of natural disturbance (hurricanes, drought, and fire), and thus the flora is relatively tolerant of disturbances (Byrne 1980), including anthropogenic disturbances. The composition of the extant Bahamian permanent resident land bird avifauna tends to be comprised of generalist species that are widely distributed across the northern Caribbean and Greater Antilles (Emlen 1977; Raffaele et al. 1998). For example, there are 34 endemic subspecies, but only three extant endemics, none of which are single island species (White 1998).

Despite an apparent tolerance to disturbance, there were still significant differences in the distributions of permanent residents among habitats on a continuum of disturbance, and their overall detection was typically higher in mature less recently disturbed habitats and lower in more recently disturbed areas. A similar pattern in detections also applied to winter residents. Despite higher detection of birds in mature coppice habitats, there was no significant difference in the degree of habitat specialization between winter and permanent residents, and both were able to exploit a range of broadleaf habitats, which is reflected in the relatively high similarity in the bird communities across the six habitats surveyed. The ability to exploit a diversity of habitats, including disturbed sites, likely facilitates survival on islands in hurricane-prone regions (e.g., Wauer and Wunderle 1992).

The diversity and density of birds can correlate with foliage biomass and structural complexity (Emlen 1977; Wunderle and Waide 1993), both are characteristics of mature vegetation (e.g., Table 1), which is consistent with general pattern of detections being higher in mature coppice habitats in this study. However, coastal coppice (climax vegetation) had a relatively low abundance of winter residents, which suggests that vegetation structure and time to last disturbance were not always the determining factor in structuring bird communities. The majority (93%) of winter residents detected were primarily insectivorous (though many supplement their winter diet with fruit; e.g., Morton 1980; Blake and Loiselle 1992), and the lower density of migrants in coastal coppice may reflect reduced invertebrate availability due to the more impoverished 'whiteland' soils or a greater marine influence. This contrasts with permanent residents in which the majority is documented as being primarily frugivorous (57%), although many are able to supplement their diet with invertebrate and even small vertebrate prey (e.g., Emlen 1977; Lack 1978). The subtle differences in the distributions between winter and permanent residents detected therefore may also reflect differences in diet and overall seasonal variation in resource availability.

The detectability of permanent residents during point counts was higher than winter resident species. This was expected, as all migrant species recorded during counts were passerines, whose vocalizations on the wintering grounds are usually limited to infrequent chips. Permanent residents in contrast produced various vocalizations, including song. In addition, the surveys were conducted in late winter (January-March), before the breeding season of many resident species (April-August; Raffaele et al. 1998) when song and vocalizations were increasing. The detection of winter residents was facilitated by the use of playback (see also Sliwa and Sherry 1992), however, even then their detection was low. This limited conclusions on species-specific patterns of winter resident habitat use: only five species exhibited heterogeneity between habitats ($P < 0.1$)—two preferred open areas (Palm Warbler and Common Yellowthroat), and three occurred in mid-tall coppice habitats (Ovenbird, American Redstart and Gray Catbird). These patterns of habitat distribution were consistent with those found in a broader survey of migrant winter habitat distribution in the Bahamas and the Greater Antilles (Wunderle and Waide 1993), indicating that wintering migrants are consistent in their habitat use among different islands.

Winter residents on Eleuthera were not observed to form mixed-species flocks, as found elsewhere in the Caribbean (Ewert and Askins 1991; Latta and Wunderle 1996). However, three species, all of which were winter residents, were observed to associate with conspecifics. For instance, both Yellow-rumped and Palm Warblers were observed in small conspecific flocks. Yellow-rumped Warblers have been found to wander in groups as they track winter fruit distribution (e.g., Borgmann et al. 2004). Gray Catbirds also congregated in fruit-rich sites, but did not appear to move around in flocks.

Species of interest

Two of the three Bahamian endemics were detected during the study: Bahama Woodstar and Bahama Yellowthroat. These species are widely distributed across the northern Bahamas (White 1998) and were found across all habitats sampled on southern Eleuthera, although there was no significant preference exhibited by either species. The distribution of the endemic yellowthroat contrasted markedly with that of the migrant Common Yellowthroat, which was more frequently found in open, more recently disturbed areas (abandoned plantation).

Seven of the 10 endemic subspecies of land bird recorded on southern Eleuthera (White 1998) were also detected during the survey. Of these, the Bananaquit, Greater Antillean Bullfinch, and Thick-billed Vireo were all common, being in the top five most frequently detected resident species; all showed significant variation in their respective detections among habitats and were more frequently found in mature vegetation. Another endemic subspecies observed in this survey was the Great Lizard-Cuckoo, which is also found in Cuba, but within the Bahamas is restricted to the islands of Andros, Eleuthera, and New Providence. However, there have been few recent sightings of the cuckoo on the latter island (no records since 1997, T. White pers. comm.). We detected lizard cuckoos in all six habitats and Eleuthera is clearly an important site for this species within The Bahamas (see also White 1998). Two other endemic subspecies, detected outside the survey, were the Cresent-eyed Pewee *Contopus caribaeus* and Stripe-headed Tanager *Spindalis zena*, both of which appear to be localized in their distribution on Eleuthera.

The Kirtland's Warbler, which winters exclusively in the Bahamas archipelago (e.g., Mayfield 1972; Sykes and Clench 1998), is of particular conservation importance. Few have been detected since it was first described in the 1850s. Only one individual was recorded during point counts, but at least five birds (at two different sites) were detected while walking between points using playback. All individuals occurred in secondary vegetation, as were most of the 24 other Kirtland's Warblers located at nine other sites on southern Eleuthera during December 2002-April 2003.

On Eleuthera, currently, there are extensive tracts of mature second-growth habitat, some farms, and localized urban development. Although development is expected to increase, it is unclear how projected land use may affect habitat availability and distribution, and thus avian communities on Eleuthera. There is, therefore, a need to both identify important habitats and prioritize areas for bird conservation, especially for species of concern or special interest (particularly endemics and those with a restricted distribution on their breeding or wintering range), such as the Great Lizard-Cuckoo and Kirtland's Warbler.

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