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Habitat Distribution of Birds Wintering in Central Andros, The Bahamas: Implications for Management

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ABSTRACT.—We studied winter avian distribution in three representative pine-dominated habitats and three broadleaf habitats in an area recently designated as a National Park on Andros Island, The Bahamas, 1-23 February 2002. During 180 five-minute point counts, 1731 individuals were detected (1427 permanent residents and 304 winter residents) representing 51 species (29 permanent and 22 winter residents). Wood warblers (Family Parulidae) comprised the majority (81%) of winter residents. Total number of species and individuals (both winter and permanent residents) were generally highest in moderately disturbed pine-dominated habitats. The composition of winter bird communities differed between pine and broadleaf habitats; the extent of these differences was dependent broadleaf on composition and age in the pine understory. Fifteen bird species (nine permanent residents and six winter residents) exhibited significant habitat preferences. There was no significant difference in the degree of habitat specialization between permanent and winter residents. Most species occurred across a range of habitats; only three species were found in one habitat type. Intra-specific variation in detection of permanent and winter residents is discussed in relation to diet, habitat structure, and disturbance regime. Avian distribution in pine forest is also discussed in relation to fire frequency.

KEYWORDS.—Avian habitat use, *Dendroica kirtlandii*, fire ecology, fire management, *Geothlypis rostrata*, Nearctic, Neotropical migrant birds, pine forest, *Saurothera merlini*.

INTRODUCTION

The importance of the Bahamas archipelago, which comprises more than 700 islands, cays and rocks from just off Florida south to Cape Haiten (Saunders 1988), for birds is well documented. The Bahamas archipelago is listed as both an Important Bird Area (IBA) and an Endemic Bird Area (EBA; Stattersfield et al. 1998): more than 300 species have been recorded in the archipelago, more than 200 birds regularly occur, and the 109 breeding species include three endemics and 34 endemic subspecies (White 1998). Neotropical and nearctic migrants are documented as comprising up to 50% of terrestrial birds species during the winter (Wunderle and Waide 1993; Lee 1996a, b), one of which, the Kirtland's warbler *Dendroica kirtlandii*, overwinters exclusively in the archipelago (Mayfield 1972; Sykes and Clench 1998; Haney et al. 1998).

Although comprehensive bird lists have been compiled for many of the islands in the archipelago (White 1998 and references therein), quantitative data on bird distributions and densities within and between habitats is scarce (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/development

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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 conservation policy.

In this paper we characterize winter bird communities and habitat distribution of individual species in six habitats on Andros Island within the boundaries of a recently designated national park. We discuss findings from this study relevant to park management, in particular the use of fire in pine habitats.

Methods and Materials

Study site

The Bahamas are low-lying sub-tropical islands (maximum elevation 64 m asl). The wettest months are May to November and northern islands have higher rainfall than the southern islands. The study was conducted on central Andros Island (Fig. 1), the largest island in The Bahamas archipelago, from 1 to 23 February 2002. As with most of the northern islands in the archipelago, the dominant vegetation type is Caribbean Pine, *Pinus caribaea*.

Point counts

A fixed-radius point count method (Hutto et al. 1986) was used to sample birds in six common terrestrial habitats. Playback of mixed warbler chips was conducted for five minutes after the five minutes of silence. An additional two min were used to identify any species that responded to the tape. Total sampling time per point was 12 min. At each point an observer recorded: (1) the number of individuals of each species detected (seen or heard) within a 25 m radius, (2) the number of individuals of each species detected beyond the 25 m radius but still within the designated habitat, and (3) any species detected by the observer walking between points not detected during the point counts themselves. The latter contributed to the completeness of the species list for a given habitat, but were not used in any of the analyses. All bird names follow Raffaele et al. (1998).

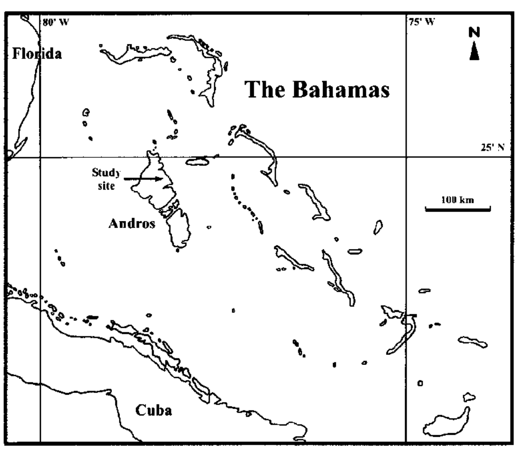

FIG. 1. The Bahamas archipelago showing our study area on central Andros Island (arrow).

Points were at least 150 m apart, and a minimum of 50 m from a habitat edge. Counts were conducted between 0700 and 1000 EST. Playback of Kirtland's Warbler chips, calls and song was played while walking between points, but was stopped 30 m from the subsequent point. In dense habitats (e.g., short coppice) point counts were conducted along trails and narrow unpaved roads. Point counts were not conducted during winds or rain.

Thirty point counts were conducted in each of the following six habitats: (i) Shrubby field—Abandoned or fallow agricultural fields with grasses, herbs, shrubs, and saplings; (ii) Pine with poisonwood/palmetto understory (PMP)—An even-aged stand of approximately 20-30 year old Caribbean pine with a mixed understory of poisonwood (*Metopium toxiferum*), cabbage palm (*Sabal palmetto*), and various small shrubs. The sabal palm is an indicator of wet pine woodlands, as this species grows where the water table (fresh water) is near the ground surface; (iii) Pine with fern understory (PF)—An even-aged stand of approximately 20-30 year old Caribbean pine with a bracken fern (*Pteridium* sp.) understory often less than 1 m tall; (iv) Pine with shrub understory (PC)—An even-aged stand of approximately 20-30 year old Caribbean pine with a 2-3 m shrubby understory; (v) Short Coppice—Broadleaf woodland <4.6 m in height; and (vi) Tall Coppice—Broadleaf woodland >4.6 m in height.

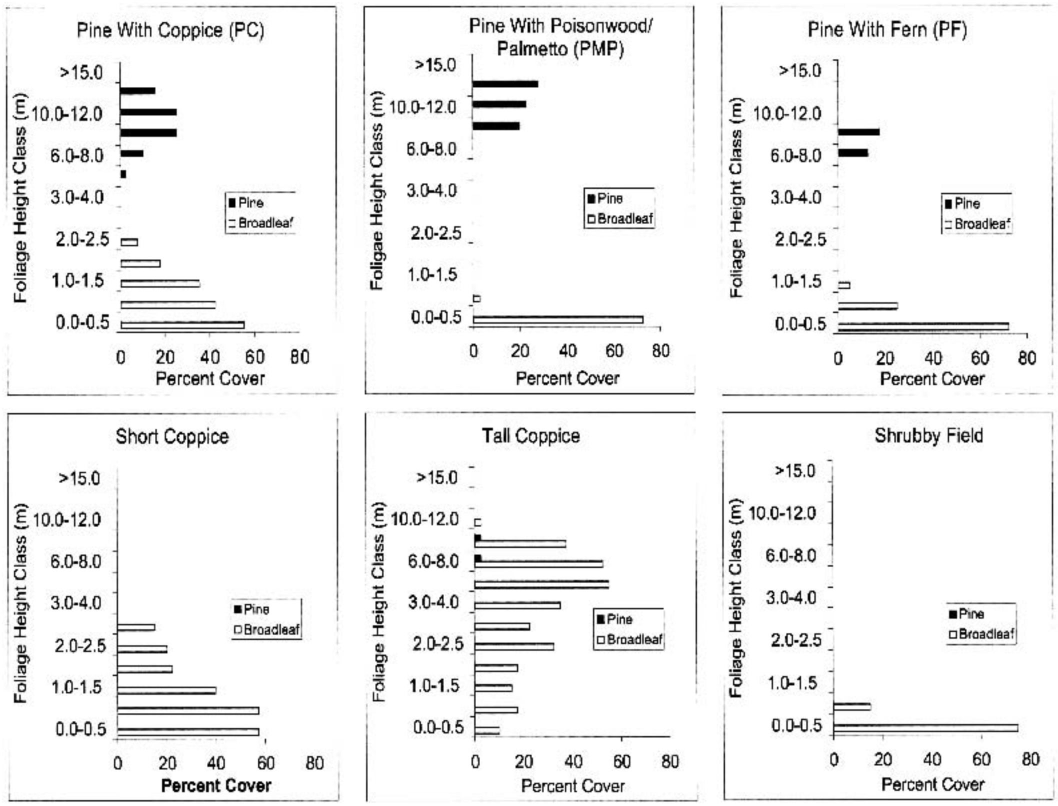

FIG. 2. Foliage height profiles for six habitats in which birds were sampled during 1-23 February 2002 in central Andros, The Bahamas. Each foliage height class includes all foliage present in categories greater than the first height value of each respective height class. Mean values are shown separately for pine and broadleaf foliage.

Vegetation measurements

We used two 20-m diameter circular plots (0.03 ha) to quantify vegetation (modified after Wunderle and Waide 1993) in each of the six habitats. Placement of plots was determined by randomly selecting a point count site in the first 15 sites and another in the last 15 sites. Plots were centered on the randomly selected points. Within each plot, we measured the diameter of all trees at 1.3 m above the ground with diameter greater than 3 cm at breast height (DBH) and recorded each within the following diameter classes: >3-8 cm, >8-15 cm, >15-23 cm, >23-38 cm, and >38 cm DBH. Trees were classified as broadleaf or pine.

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 woody stems (<3 cm) touching the observer's body and outstretched arms at breast height; broadleaf shrubs and young pines were recorded separately.

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 pole of 3-m length and 2.0 cm diameter 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 height intervals above 3 m we sighted along the upright pole and recorded the presence/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 was calculated by dividing the number of points in which foliage was present in that 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 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 pine or broadleaf canopy cover was noted at each point and percent canopy cover determined for pine and broadleaf separately 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 or absence of woody broadleaf cover, ferns, herbs, and bare ground. The percentage ground cover for each category was calculated by dividing the number of points with the specified cover category by the total number of sample points (n = 20). The sum of the percentage ground cover for all the cover categories does not add up to 100.

Analyses

For each habitat we calculated the mean number of birds detected 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. We refer to winter residents as species present through the winter months (October-April) and permanent residents as those present throughout the year. Three species (Mourning Dove, Blue-gray Gnatcatcher, Pine Warbler; see Table 2 for scientific names) are represented by both winter and permanent residents that can not be distinguished in the field. Therefore, these species were treated as permanent residents in our analyses, but we recognize that some individuals may represent wintering birds. Birds were classified into diet guilds based on Emlen (1977).

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 1.0 (complete specialization on a habitat type) to 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

The six habitats can be divided into two general types: (1) pine-dominated habitats (Pine with poisonwood/palmetto understory, PMP; Pine with fern understory, PF; and Pine with shrubby understory, PC) and (2) broadleaf-dominated (shrubby field; short coppice; and tall coppice). Some overlap occurred between pine and broadleaf dominated habitats as the pine understory included a range of broadleaf vegetation types, the composition of which was dependent on the history of disturbance by fire; PMP and PF had been more recently disturbed by fire than PC (Fig. 2). Although recently disturbed shrubby field is currently dominated by broadleaf vegetation, it may revert to either pine or broadleaf dominated vegetation later in the successional process.

All pine habitats and tall coppice were similar in canopy height, and all had extensive canopy cover, whereas canopy cover was less extensive in short coppice and completely absent in shrubby field. A dense shrub layer characterized mature broadleaf habitats, in particular short coppice, whereas the understory was more open in recently disturbed broadleaf and pine habitats. PC was associated with a denser understory than PMP or PF.

The similarities between the three pine habitats in DBH and canopy height (Table 1) indicates the uniform age of the pine trees throughout the study area, which was uniformly harvested for timber in 1970s. Despite the uniform age of the pine, there was considerable variation in the age of the understory, which indicated different histories: more recently disturbed pine habitats were characterized by an open understory (PF and PMP), whereas more mature understory habitats had a higher density of shrubs (PC). Similarly, the variation in broadleaf habitat structure also reflected a continuum of disturbance—recently disturbed (shrubby field) to tall coppice (late succession vegetation).

Point counts

One hundred and eighty point counts were conducted in six habitats (30 points in each habitat) where we detected 1427 permanent residents and 306 winter residents representing 51 species including 29 permanent residents and 22 winter residents (Table 2).

Detectability indices varied considerably among species and habitats. Permanent residents had higher detectability indices than winter residents (median detectability indices for all habitats, winter vs. permanent residents; 0.10 vs. 0.83; Mann-Whitney, $U = 150$, $P = 0.002$). Therefore, we restricted our quantitative analyses to the 25 m fixed-radius point counts. We detected 585 permanent residents and 164 winter residents in the fixed radius counts, representing 39 species (18 winter and 21 permanent residents). Of the 18 winter resident species detected within a 25 m radius, 16 (88.9%) were wood warblers (Subfamily Parulinae). In general, resident species were more frequently detected than

TABLE 1. Mean vegetation traits of six habitats sampled on Andros, Bahamas. Habitats include shrubby field, short coppice, tall coppice, pine with poisonwood/palmetto understory (PMP), pine with fern understory (PF), and pine with short coppice understory (PC). Habitat variables are described in the methods section.

	Broadleaf habitats			Pine habitats		
Vegetation trait	Shrubby field	Short coppice	Tall coppice	PMP	PF	PC
Canopy height (m)	0	3.62	11.43	12.1	13.73	12.8
Canopy cover (%)						
Broadleaf	0	30	100	0	0	5
Pine	0	0	2.5	77.5	50	80
DBH (cm)						
Broadleaf		5.7	7.3	—	—	10.0
Pine		—	—	13.2	16.3	11.3
Palm		—	—	15.9	—	—
Shrub density*						
Broadleaf	0	290.9	45.6	0.6	3.4	27.6
Other	0	0	0	0	0	0
Ground cover (%)						
Broadleaf	27.5	100	45	57.5	52.5	87.5
Fern	0	2.5	0	62.5	67.5	22.5
Herb	92.5	47.5	20	42.5	45	22.5
Ground	5	0	37.5	5	5	7.5

*Mean stems per 15 m^2.

TABLE 2. Occurrence of birds in six different habitats sampled 1 to 23 February 2002 on Andros Island, The Bahamas. Occurrence is based on the average number of detections per point (×100) in point counts of 5-min duration with a 25 m radius. Values in italics show average number of detections per point (×100) in point counts of 5-min duration with an unlimited radius. Letters following scientific name indicate status (P = permanent resident, W = winter resident) and diet (F = fruit/seeds, N = nectar, I = insects, S = snails, V = vertebrates). *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 point counts at which a given species was recorded only beyond the 25 m radius divided by the total number of counts at which a species was recorded (Hutto et al. 1986).

	Habitat							
Species	Pine with fern	Pine with poisonwood/ palmetto	Pine with coppice	Short coppice	Tall coppice	Shrubby field	*P*	Detection ratio
Limpkin	0	0	0	0	0	0	1.00	1.00
Aramus guarauna P, S	*0*	*0*	*0*	*0*	*0*	*96.7*		
Common Ground-Dove	0	0	0	0	0	3.3	0.42	0
Columbina passerina P, F	*0*	*0*	*0*	*0*	*0*	*3.3*		
Eurasian Collared-Dove	0	0	0	0	0	0	1.00	1.00
Streptopelia decaocto P, F	*0*	*0*	*0*	*13.3*	*0*	*36.7*		
Mourning Dove	0	0	0	3.3	0	0	0.42	0
Zenaida macroura P & W, F	*0*	*0*	*0*	*3.3*	*0*	*0*		
Great Lizard-Cuckoo	0	3.3	0	0	0	3.3	0.55	0.92
Saurothera merlini P, I, V	*0*	*20.0*	*13.3*	*6.7*	*10.0*	*40.0*		
Smooth-billed Ani	0	0	0	0	0	16.7	0.07	0.87
Crotophaga ani P, I	*0*	*0*	*0*	*10.0*	*0*	*153.3*		
Cuban Emerald	53.3	43.3	26.7	6.7	0	53.3	0.001	0.14
Chlorostilbon ricordii P, N	*56.7*	*53.3*	*33.3*	*6.7*	*0*	*73.3*		
Bahama Woodstar P, N	0	3.3	0	10.0	0	6.7	0.06	0.14
Calliphlox evelynae P, N	*0*	*3.3*	*0*	*13.3*	*0*	*6.7*		
Hairy Woodpecker	6.7	3.3	0	0	0	0	0.22	0.87
Picoides villosus P, I	*23.3*	*23.3*	*23.3*	*3.3*	*10.0*	*0*		
Crescent-eyed Pewee	20.0	6.7	3.3	0	0	6.7	0.05	0.81
Contopus caribaeus P, I	*80.0*	*36.7*	*53.3*	*0*	*13.3*	*30.0*		
La Sagra's Flycatcher	0	0	6.7	3.3	20.0	3.3	0.007	0.71
Myiarchus sagrae P, I	*10.0*	*0*	*23.3*	*26.7*	*53.3*	*13.3*		
Loggerhead Kingbird	6.7	3.3	0	0	0	0	0.55	0.90
Tyrannus caudifasciatus P, I	*16.7*	*56.7*	*6.7*	*0*	*0*	*26.7*		
Bahama Swallow	0	0	0	0	0	0	1.00	1.00
Tachycineta cyaneoviridis P, I	*3.3*	*0*	*0*	*3.33*	*0*	*0*		
Blue-gray Gnatcatcher	86.7	70.0	90.0	0	3.3	10.0	0.0001	0.55
Polioptila caerulea P & W, I	*196.7*	*170.0*	*206.7*	*0*	*3.3*	*86.7*		
Red-legged Thrush	6.7	0	3.3	0	6.7	0	0.31	0.44
Turdus plumbeus P, I, F	*6.7*	*0*	*13.3*	*0*	*10.0*	*0*		
Gray Catbird	0	0	0	3.3	0	10.0	0.048	0.82
Dumetella carolinensis W, F	0	0	*0*	*23.3*	*3.33*	*80.0*		
Northern Mockingbird	0	0	0	0	0	3.3	0.42	0.95
Mimus polyglottos P, F	*0*	*0*	*0*	*20.0*	*0*	*83.3*		
Bahama Mockingbird	0	0	0	0	0	0	1.00	1.00
Mimus gundlachii P, F	*0*	*0*	*0*	*3.3*	*0*	*0*		
Thick-billed Vireo	0	3.3	13.3	50.0	53.3	10.0	0.0001	0.74
Vireo crassirostris P, I	*73.3*	*56.7*	*190.0*	*190.0*	*140.0*	*200.0*		
Northern Parula	0	0	0	0	3.3	0	0.42	0
Parula americana W, I	*0*	*0*	*0*	*0*	*3.3*	*0*		
Magnolia Warbler	0	0	0	0	3.3	0	0.42	0
Dendroica magnolia W, I	*0*	*0*	*0*	*0*	*3.3*	*0*		
Cape May Warbler	0	0	0	0	3.3	0	0.42	0
Dendroica tigrina W, N	*0*	*0*	*0*	*0*	*3.3*	*0*		

TABLE 2. Continued.

Species	Habitat: Pine with fern	Pine with poisonwood/ palmetto	Pine with coppice	Short coppice	Tall coppice	Shrubby field	*P*	Detection ratio
Black-throated Blue Warbler	0	0	0	3.3	3.3	0	0.55	0.00
Dendroica caerulescens W, I	*0*	*0*	*0*	*3.3*	*3.3*	*0*		
Yellow-rumped Warbler	0	10.0	3.3	3.3	3.3	0	0.29	0.25
Dendroica coronata W, F	*0*	*13.3*	*10.0*	*3.3*	*3.3*	*0*		
Yellow-throated Warbler	0	20.0	0.0	0	0	0	0.000	0.29
Dendroica dominica W, I	*0*	*20.0*	*6.7*	*0*	*0*	*0*	1	
Pine Warbler	136.7	96.7	33.3	0	0	6.7	0.000	0.51
Dendroica pinus P & W, I	*270.0*	*313.3*	*186.7*	*0*	*0*	*3.3*	1	
Kirtland's Warbler	0	0	0	0	3.3	0	0.42	0
Dendroica kirtlandii W, I	*0*	*0*	*0*	*0*	*3.3*	*0*		
Prairie Warbler	6.7	26.7	10.0	30.0	30.0	20.0	0.14	0.20
Dendroica discolor W, I	*6.7*	*26.7*	*13.3*	*30.0*	*30.0*	*56.7*		
Palm Warbler	30.0	100.0	10.0	0.0	0	30.0	0.000	0.39
Dendroica palmarum W, I	*53.3*	*170.0*	*26.7*	*3.3*	*0*	*100.0*	1	
Back-and-white Warbler	0	0	3.3	0	6.7	0	0.70	0
Mniotilta varia W, I	*0*	*0*	*3.3*	*0*	*6.7*	*0*		
American Redstart	3.3	10.0	13.3	3.3	33.3	6.7	0.002	0.09
Setophaga ruticilla W, I	*3.3*	*10.0*	*16.7*	*3.3*	*33.3*	*10.0*		
Worm-eating Warbler	0	0	0	0	3.3	0	0.42	0
Helmitheros vermivorus W, I	*0*	*0*	*0*	*0*	*3.3*	*0*		
Ovenbird	0	0	0	10.0	23.3	0	0.001	0.10
Seiurus aurocapillus W, I	*3.3*	*0*	*0*	*10.0*	*23.3*	*0*		
Northern Waterthrush	0	0	0	3.3	0	0	0.42	0
Seiurus noveboracensis W, I	*0*	*0*	*0*	*3.3*	*0*	*0*		
Common Yellowthroat	6.7	3.3	0	0	0	33.3	0.000	0.37
Geothlypis trichas W, I	*6.7*	*10.0*	*0*	*0*	*0*	*90.0*	1	
Bahama Yellowthroat	13.3	20.0	40.0	16.7	26.7	0	0.003	0.44
Geothlypis rostrata P, I	*16.7*	*53.3*	*90.0*	*33.3*	*26.7*	*13.3*		
Hooded Warbler	0	0	0	0	6.7	0	0.07	0
Wilsonia pusilla W, I	*0*	*0*	*0*	*0*	*6.7*	*0*		
Bananaquit	0	6.8	10.0	23.3	3.3	3.3	0.007	0.28
Coereba flaveola P, N	*0*	*10.0*	*23.3*	*23.3*	*3.3*	*6.7*		
Stripe-headed Tanager	3.3	0	0	0	6.7	6.7	0.31	0.92
Spindalis zena P, F	*30.0*	*0*	*46.7*	*23.3*	*66.7*	*136.7*		
Indigo Bunting	0	0	0	0	0	0	0.07	1.00
Passerina cyanea W, F	*0*	*0*	*0*	*6.7*	*0*	*0*		
Black-faced Grassquit	10.0	36.7	3.3	6.7	0	30.0	0.031	0.40
Tiaris bicolor P, F	*26.7*	*43.3*	*10.0*	*6.7*	*3.3*	*56.7*		
Greater Antillean Bullfinch	0	0	0	13.3	13.3	6.7	0.06	0.73
Loxigilla violacea P, F	*16.7*	*6.7*	*10.0*	*33.3*	*46.7*	*26.7*		
Savannah Sparrow	0	0	0	0	0	0	1.00	1.00
Passerculus sandwichensis W, F	*0*	*0*	*0*	*0*	*0*	*3.3*		
Red-winged Blackbird	0	0	0	0	0	0	1.00	1.00
Agelaius phoeniceus W, I	*0*	*0*	*0*	*0*	*0*	*36.7*		
Black-cowled Oriole	0	0	0	3.3	0	6.7	0.55	0.83
Icterus dominicensis P, F	*0*	*0*	*26.7*	*10.0*	*3.3*	*20.0*		
Mean number of species per point (all species detected)	2.46	3.27	2.23	1.77	2.43	2.40	0.03	
Mean number of individuals per point (all species detected)	3.90	4.67	2.70	1.93	2.63	2.77	0.001	

TABLE 2. Continued.

Species	Habitat							
	Pine with fern	Pine with poisonwood/ palmetto	Pine with coppice	Short coppice	Tall coppice	Shrubby field	*P*	Detection ratio
Mean number of winter resident species per point	0.37	1.33	0.4	0.53	1.23	0.93	0.0001	
Mean number of winter resident individuals per point	0.47	1.73	0.4	0.57	1.30	1.0	0.0001	
Mean number of permanent resident species per point	2.10	1.93	1.83	1.23	1.20	1.47	0.0001	
Mean number of permanent resident individuals per point	3.43	2.93	2.3	1.37	1.33	1.77	0.0001	
Mean number of insectivorous individuals per point (all species)	3.16	3.7	2.23	1.2	2.2	1.47	0.0001	
Mean number of frugivorous individuals per point (all species)	0.20	0.47	0.10	0.3	0.37	0.67	0.08	
Mean number of nectarivorous individuals per point (all species)	0.53	0.50	0.37	0.4	0.07	0.63	0.004	

Additional species detected during the survey: Great Egret *Ardea alba*; Turkey Vulture *Cathartes aura*; Red-tailed Hawk *Buteo jamaicensis*; Merlin *Falco columbarius*; Greater Yellowlegs *Tringa melanoleuca*; Killdeer *Charadrius vociferous*.

winter residents (mean proportion of migrant species = 37% of species; range 24-60%). Winter residents comprised more species in only one habitat; tall coppice (60%; 12/20).

Mean total birds detected per fixed radius point, as well as mean number of species detected per point, varied significantly among habitats and both were lowest in short coppice and highest in PMP (Table 2). These results differed when winter and permanent residents were considered separately. For permanent residents, the number of individuals and species per point was highest in PC and lowest in tall coppice, while the number of migrant species per point and total number of migrants per point was highest in PMP; the number of winter resident species per point was lowest in PF, and the number of winter residents (individuals) was lowest in PC.

There was a wide range in the degree of similarity of winter bird communities between the six habitats (range in similarity coefficients = 0.15-0.66; Table 3). The composition of bird communities in pine habitats typically differed markedly from that of mature coppice habitats. This was most pronounced between PF and short and tall coppice (0.1.-0.15), and PMP and short and tall coppice (0.21-0.27). Bird communities were more similar between PC and the two exclusively broadleaf habitats (0.31-0.58). The similarity between shrubby field and pine habitats (0.39-0.52), in particular PF or PMP, indicates that bird species that occupied early secondary broadleaf vegetation also inhabited the understory of these pine habitats

There was no significant difference (Mann-Whitney U = 82.5, P = 0.21) in degree of habitat specialization (measured as the exponential of the Shannon-Weiner diversity statistic; H') between winter residents (median = 1.25) and permanent resident species (median = 1.69) detected within the fixed radius.

TABLE 3. Similarity Coefficient calculated for assemblages of birds in fixed-radius point counts conducted in six habitats on central Andros, The Bahamas, 1 to 23 February 2002. Coefficients were calculated following Cox and Ricklefs (1977). Habitats are described in the text.

	Habitats					
	Pine with fern	Pine poisonwood/ palmetto	Pine with coppice	Short coppice	Tall coppice	Shrubby field
Pine with fern	x	0.66	0.55	0.17	0.15	0.49
Pine poisonwood/palmetto		x	0.55	0.27	0.21	0.52
Pine with coppice			x	0.31	0.35	0.39
Short coppice				x	0.58	0.43
Tall coppice					x	0.25
Shrubby field						x

Species differences

The five most common resident species (ranked in order of abundance across the six habitats) were Pine Warbler, Blue-gray Gnatcatcher, Cuban Emerald, Thick-billed Vireo, and Bahama Yellowthroat, whereas the five most common migrants, also ranked in mean order of detections across all habitats, were Palm Warbler, Prairie Warbler, American Redstart, Common Yellowthroat, and Ovenbird (scientific names in Table 2).

Of the 39 species detected within the fixed-radius point counts, 15 (nine permanent and six winter residents) showed significant differences in abundance among habitats (Table 2). The nine permanent residents were Pine Warbler, Blue-gray Gnatcatcher, Cuban Emerald, Thick-billed Vireo, Bahama Yellowthroat, Black-faced Grassquit, Bananaquit, Crescent-eyed Pewee, and La Sagra's Flycatcher. Pine Warblers were most common in pine-dominated habitats and were absent from habitats that were exclusively broadleaf. Blue-gray Gnatcatchers were also nearly restricted to pine-dominated habitats and only very rarely found in broadleaf or scrub habitats. The Cuban Emerald was detected in pine habitats and open areas, but was mostly absent from denser broadleaf habitats. Thick-billed Vireos were most common in exclusively broadleaf dominated habitats. The Bahama Yellowthroat was absent from exclusively open areas and most common in vegetation that had broadleaf understory, under either a broadleaf or pine canopy. Black-faced Grassquits were absent from mature broadleaf habitats and more frequently detected in pine without an exclusive broadleaf understory. Bananaquits were absent in habitats lacking broadleaf vegetation and were most common in short coppice. Crescent-eyed Pewees were found in open areas and pine dominated habitats and absent from tall coppice. La Sagra's Flycatchers were most common in tall coppice, but absent from areas without broadleaf vegetation (either as canopy or understory). Three species exhibited marked, but non-significant trends in their distribution; Smooth-billed Anis were found only in shrubby field ($P = 0.07$); Bahama Woodstars were more frequently detected in recently disturbed broadleaf habitats (shrubby field and short coppice; $P = 0.06$); and the Greater Antillean Bullfinch was detected mostly in broadleaf habitats, mainly short and tall coppice ($P = 0.06$).

The six winter resident species that exhibited significant variation in abundances among habitats included Palm Warbler, American Redstart, Common Yellowthroat, Ovenbird, Yellow-throated Warbler, and Gray Catbird (Table 2). American Redstarts were most commonly detected in tall coppice and less frequently in shorter broadleaf and pine-dominated vegetation. Palm Warblers were most frequently detected in pine-dominated and open habitats (specifically PMP) and were absent from exclusively broadleaf habits (short and tall coppice). Common Yellowthroats were detected in open habitats or pine habitats with an open broadleaf understory (PF, PMP), and were absent from habitats with a dense shrub layer (PC, short coppice). Catbirds were only detected in scrub and short coppice and were absent from pine-dominated habitats and tall coppice. Ovenbirds were only detected in broadleaf-dominated habitats and Yellow-throated Warblers were only found in PMP. In addition, two species exhibited marked but non-significant trends in their distributions—Hooded Warblers, were only found in tall coppice and Indigo Buntings were only detected in short coppice.

Diet guilds

The majority of winter and permanent residents were insectivorous (14/18 = 77.8% and 11/21 = 52%, respectively), and a significant number in both groups were frugivorous (3/18 = 16.7% and 8/21 = 38.1%, respectively). Insectivores, frugivores and nectarivores (winter and permanent residents combined) showed significant heterogeneity among habitats. Insectivore detections (number of individuals per point) were typically higher in PMP and lowest in short coppice; frugivores were more frequently detected (albeit not significantly so; $P = 0.08$) in shrubby field and less often in pine with a coppice understory, and nectarivores were more frequently detected in secondary broadleaf vegetation (shrubby field), and less so in tall coppice.

Discussion

During our surveys we detected 81% (26/32; 18 within the fixed radius) of the permanent resident land birds (excluding water-birds, raptors, owls, and swallows), and 62% (22/35; 18 within the fixed radius) of the winter residents, recorded from Andros (White 1998); wood warblers comprised the majority of winter residents detected (see Table 2).

Patterns of distribution of both permanent and winter residents within pine habitats recorded in this study were comparable to those observed on pine islands in The Bahamas (Grand Bahama, Emlen 1977; Abaco, Lee 1996a, b; Baltz 1993). The density and diversity of birds was generally highest in pine-dominated habitats with a 2-3 m tall deciduous understory; PMP for total bird species and winter residents, and PF for resident species. This is consistent with previous findings that indicated that increased habitat structural complexity (at least in a pine-dominated ecosystem) was usually associated with both a higher density and diversity of birds (Emlen 1977); both PMP and PF typically had higher detections of birds than uniform stands of broadleaf vegetation (tall and short coppice). Both permanent resident and winter resident species utilized a range of habitats; most species used both broadleaf and pine habitats; there was no difference in their degree of habitat specialization (exp H′). Only three bird species were found exclusively in pine forest (Yellow-throated and Pine Warblers) or broadleaf coppice (Ovenbird).

Fire and the composition of the pine understory

Fire is an important factor in maintaining open Caribbean pine forest; fire frequency and intensity play a large role in dictating the diversity, growth and relative dominance of understory plants. Fire often affects the understory and leaf litter and less commonly the mature pine (Lee 1996a, Lee et al. 1997). Lee et al. (1997) suggest that sufficient fuel accumulates in Bahamian pine forests after approximately three years to sustain a surface fire. The period following a burn is characterized by a rapid regrowth by herb species and resprouting by hardwood shrubs from surviving stems and from below ground (Lee et al. 1997); in 10-15 years the herbaceous plants (e.g., PF & PMP) become shaded out by the development of closed hardwood layer (PC). Without fire, pine forest is gradually replaced (although not necessarily completely) by broadleaf species, which can take ~10-50 years depending on local conditions (Campbell 1978).

In the current study the uniform age of pine forest (an artifact of previous timber operations) contrasted with the difference in the composition of bird communities within the various pine habitats (PC, PMP, PF). These differences are attributed to variation in the composition and structure of the understory induced by fires (Emlen 1977; Lee 1996a). Lightning is the only non-anthropogenic source of fire, and its occurrence mainly in the late dry-wet season (May-September) probably limits the fires to localized areas. We therefore attribute most of the many and extensive recent (1-3 year old) burns observed during our survey to anthropogenic factors. Recently burned areas were omitted from the study due to the depauperate bird fauna (J. Wunderle pers. obs.).

In contrast, disturbance regimes in broadleaf habitats are not usually so fire dependent, and are often a result of other natural (e.g., hurricanes) or anthropogenic factors (e.g. agricultural practices). The effect of disturbance on the availability of food resources appeared to be important in the distribution of nectar and fruit feeding species. These species were typically found in most recently disturbed habitats. Early successional plant species characteristic of disturbed habitats frequently produce an abundance of fruits and flowers resulting in localized patches of high resource availability. This contrasted with insectivorous species (many of them winter residents), which were more frequently detected in more structurally complex habitats, specifically PMP.

Despite differences in the winter bird communities between pine and broadleaf habitats, there was considerable overlap in bird species composition, perhaps because of the broadleaf understory common to both pine and broadleaf forests. This was most marked between PMP/PF and shrubby field, despite the differences in canopy structure (0-13 m). A low-density shrub layer, resulting in an overlap in bird species, including Palm Warbler and Common Yellowthroat, characterized all three habitats.

Species of conservation interest

All three Bahamian endemic species were recorded during the survey: Bahama Woodstar, Bahama Swallow, and Bahama Yellowthroat. The woodstar and yellowthroat are widely distributed across the northern Bahamas, on both broadleaf and pine-dominated islands, and the swallow is restricted to the northern pine-dominated islands (Stattersfield et al. 1998; White 1998). The Bahama Yellowthroat was common on Andros in most mature habitats (PMP and tall coppice), but was absent from recently disturbed areas (shrubby fields), unlike the migrant Common Yellowthroat, which was more frequently found in open more recently disturbed areas (see also Emlen 1977; Currie et al. 2005).

Thirteen of the 14 endemic Bahamian subspecies of land birds recorded on Andros (White 1998) were detected during the survey. Of these, the Pine Warbler, Thick-billed Vireo, Bananaquit, Crescent-eyed Pewee and La Sagra's Flycatcher were unevenly distributed across the sampled habitats (Table 2). Only the Pine Warbler was restricted to pine-dominated habitats—the others were found in a range of broadleaf and pine habitats.

Several of these endemic subspecies are of conservation concern in The Bahamas, because of their small population and limited distribution. Two were detected during the current survey: The Great Lizard-Cuckoo and the Black-cowled Oriole. Outside Cuba, the Great Lizard-Cuckoo is only recorded from The Bahamas (Andros, Eleuthera, and New Providence). However, there have been no records on New Providence since 1997 (T. White pers. comm.), thus highlighting the importance of the Andros and Eleuthera populations. The Black-cowled Oriole is also of concern, especially since the recent arrival of lethal yellow, a mycoplasma, which kills coconut palms *Cocos nucifera*, an important nesting tree for this species. The oriole was detected across all broadleaf habitats surveyed and in pine with a mature broadleaf understory (PC). It appears to be extirpated from other islands in the archipelago (White 1998). Not only is palm tree loss a likely factor in the oriole's decline, but parasitism by the Shiny Cowbird *Molothrus bonariensis* may further contribute to the relic population's decline (Baltz 1995, 1997).

The survey highlighted the continued importance of The Bahamas for over wintering wood warblers, which comprised the majority of winter resident species detected (see also Emlen 1977; Lee 1996a, b). A winter resident in The Bahamas of significant conservation importance is the Kirtland's Warbler. Only one Kirtland's Warbler, which winters exclusively in The Bahamas archipelago (Mayfield 1972), was found during the current study. Its detection was probably facilitated by the use of playback. It was detected only during the post count playback of migrant chips. The individual was detected in tall coppice, which appears inconsistent with many records indicating that the species over-winters in short coppice and secondary vegetation either exclusively broadleaf or as understory under a pine canopy (Sykes and Clench 1998; Lee et al. 1997). However, the detection site was within approximately 40 m of short coppice and use of Kirtland's Warbler vocalization playback between points and/or post-count broadcast of mixed migrant chips may have attracted the individual into the tall coppice site from the nearby low coppice.

Implications for conservation

Five of the habitats surveyed in this study (three pine dominated and two broadleaf dominated) are found in the recently created Andros National Park. The survey documented the subtle differences in winter bird communities among pine-dominated habitats, which were attributed to differences in the composition and age of the understory. Pine habitats typically contained the highest density of birds and more diverse winter communities, which further highlights the importance of the pine ecosystem in The Bahamas for migrant birds (Emlen 1977; Lee 1996 a, b). Consequently, fire management will need careful attention. Table 4 highlights those species, which would benefit from a specific burn regime. Pine community restricted species typically use the canopy, and the understory composition may have little direct effect on these species. Objectives for prescribed burns need to be clear and care taken to avoid an over abundance of very recently burned pine habitats, which are associated with more depauperate bird communities. In a given pine forest patch, fire frequency will be 'optimal' when it (i) allows pine seedlings to reach canopy stage and (ii) prevents overtopping of pine seedlings and saplings by broadleaf shrubs, but is not so frequent that it eliminates the recruitment classes during every burn. The survey also highlighted the marked differences in winter bird communities between broadleaf and pine habitats on Andros (Table 3): 11 bird species were only recorded from coppice (SC, TC). In northern and central Andros, coppice habitat is less common than pine-dominated habitats (M. Baltz pers. comm.), and conservation efforts within the national park should also include preservation and management of broadleaf habitats.

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TABLE 4. Three classes of fire frequency in pine forest on Andros Island, The Bahamas, and the bird species likely to benefit from each. Only species exhibiting marked differences ($P < 0.1$) in detections within fixed radius point counts across the six habitats surveyed are shown (see Table 2).

Fire frequency		
High frequency (1-5 years)	Moderate frequency (5-10 years)	Low frequency (>15 years)
Palm Warbler	Cuban Emerald	Ovenbird
Black-faced Grassquit	Bananaquit	American Redstart
Common Yellowthroat	Prairie Warbler	La Sagra's Flycatcher
	Thick-billed Vireo	Hooded Warbler
	Crescent-eyed Pewee	Bahama Yellowthroat
	Bahama Woodstar	Greater Antillean Bullfinch
Pine Warbler	Pine Warbler	
Blue-gray Gnatcatcher	Blue-gray Gnatcatcher	Blue-gray Gnatcatcher

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LITERATURE CITED

Baltz, M. E. 1993. Abundance of neotropical migrant songbirds on North Andros Islands, Bahamas. **Florida Field Naturalist** 21:115-117.

Baltz, M. E. 1995. First records of the Shiny Cowbird (*Molothrus bonariensis*) in The Bahama Archipelago. *Auk* 112:1039-1041.

Baltz, M. E. 1997**.** Shiny Cowbird in the Bahamas: a threat to the Archipelago's avifauna? *Pitirre* 10:21.

Campbell, D. G. 1978. *The Ephemeral Islands: A Natural History of The Bahamas*. London: McMillan Education Limited.

Cox, G. W., and R. E. Ricklefs. 1977**.** Species diversity and ecological release in Caribbean bird faunas. *Oikos* 28:113-122.

Currie, D., J. M. Wunderle Jr., D. N. Ewert, A. Davis, and Z. McKenzie. 2005. Winter avian distribution and relative abundance in six terrestrial habitats on southern Eleuthera, The Bahamas. Carribean Journal of Science 41:xx-xx.

Emlen, J. T. 1977. Land bird communities of Grand Bahama Island: the structure and dynamics of an avifauna. *Ornithological Monographs* No 24:1-129.

Haney, J. C., D. S. Lee, and M. Walsh-McGehee. 1998. A quantitative analysis of winter distribution and habitats of Kirtland's Warbler in The Bahamas. *Condor* 100:201-217.

Hutto, R. L, S. M. Pletschet, and P. Hendricks.1986. A fixed-radius point count method for non-breeding and breeding season use. *Auk* 103:593-602.

Lanly, J. P. 1982. Tropical forest resources. Food and Agriculture Organization of the United Nations, Rome.

Lee, D. S. 1996a. Winter avifauna of the Abaco national park (part 1). *Bahamas Journal of Science* 6:8-15.

Lee, D. S. 1996b. Winter avifauna of the Abaco national park (part 2). *Bahamas Journal of Science* 6:29-34.

Lee, D. S., M. Walsh-McGehee, and C. J. Haney. 1997. A history, biology and re-evaluation of the Kirtland's Warbler habitat in The Bahamas. *Bahamas Journal of Science* 2:19-29.

Lynch, J. F. 1989. Distribution of over wintering nearctic migrants in the Yucatan Peninsula I: general patterns of occurrence. *Condor* 91:515-544.

Mayfield, H. 1972**.** Winter habitat of the Kirtland's Warbler. *Wilson Bulletin* 84:347-349.

Raffaele, J. Wiley, O. Garrido, A. Keith, and J. Raffaele. 1998. A guide to the birds of the West Indies. Princeton, New Jersey: Princeton University Press.

Saunders, G. 1988. The Bahamas, a family of islands. Macmillan Publishers, Hong Kong.

Schemske, D. W. and N. Brokaw. 1991**.** Tree fall and the distribution of understory birds in a tropical forest. *Ecology* 62:938-945.

Siegel, S., and N. J. Castellan. 1988. *Non-Parametric Statistics for the Behavioral Science*s. Singapore: McGraw-Hill Co.

Sliwa, A., and T. W. Sherry. 1992. Surveying wintering warbler populations in Jamaica: point counts with and without broadcast vocalizations. *Condor* 94: 924-936.

Sokal, R. R., and F. J. Rohlf. 1981. *Biometr*y, San Francisco, California: W. H. Freeman.

Stattersfield, A. J., M. J. Crosby, A. J. Long, and D. C. Wege. 1998**.** *Endemic Bird Areas of the World.* Cambridge, UK: Birdlife International.

Sykes P. W., Jr., and M. H. Clench. 1998. Winter habitat of Kirtland's warbler: an endangered nearctic/ neotropical migrant. *Wilson Bulletin* 110:244-261.

White, A. W. 1998**.** *A Birder's Guide to The Bahama Islands (including Turks and Caicos).* Colorado Springs, Colorado: American Birding Association.

Wilkinson, L. 1989. SYSTAT: The system for statistics. SYSTAT Inc., Evanston, Illinois.

Wunderle, J. M., Jr., and R. B. Waide. 1993. The distribution of over-wintering nearctic migrants in The Bahamas and Greater Antilles. *Condor* 95:904-933.