

KIRTLAND'S WARBLERS IN ANTHROPOGENICALLY DISTURBED EARLY-SUCCESSIONAL HABITATS ON ELEUTHERA, THE BAHAMAS

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Abstract. To characterize the nonbreeding habitat of Kirtland's Warbler (*Dendroica kirtlandii*) on Eleuthera, The Bahamas, we quantified the habitat at sites where we captured the warblers and compared these traits with those of random sites and sites of tall coppice. On the basis of a chronosequence of satellite imagery, 153 capture sites ranged in age from 3 to 28 years after human disturbance, mean 14.6 years $\pm$ 6.3 (SD). Capture sites had been abandoned after clearing (65%), converted to goat pasture (26%), burned (2%), or were young second growth following unknown disturbance (7%). Canopies in 104 capture plots were lower (mean 1.8 m) than canopies in random plots (mean 2.7 m) and plots of late-successional tall coppice (mean 6.3 m). At seven sites mean foliage density in capture plots was consistently greatest at 0.5 to 1.0 m height, but the sites were heterogeneous for other foliage-height classes <3 m and for time since disturbance, canopy height, stem density, and five ground-cover traits. Plots did not differ by the sex of the captured bird except for a difference ($P = 0.05$) in foliage density at heights <3 m. Kirtland's Warblers frequently consumed fruit (69% of 499 observations), especially from *Lantana involucrata*, *Erithalis fruticosa*, and *Chiococca alba*. Foliage of these plants was more abundant in capture plots than random plots. Because the warblers consume fruit extensively and fruit is more abundant in early successional habitat, this species, like other nearctic–neotropical migrants that breed in early successional habitats, is absent from mature forests on the wintering grounds.

Key words: *Dendroica kirtlandii*, early succession, frugivory, Kirtland's Warbler, nonbreeding habitat.

Dendroica kirtlandii en Hábitats de Sucesión Temprana Disturbados por el Hombre en Eleuthera, Bahamas

Resumen. Para caracterizar el hábitat que utiliza *Dendroica kirtlandii* fuera de la estación de cría en Eleuthera, Bahamas, cuantificamos el ambiente en sitios donde capturamos las aves y comparamos estas características con aquellas de sitios seleccionados al azar y de rebrote alto. Con base en una cronosecuencia de imágenes satelitales, 153 sitios de captura presentaron edades de entre 3 y 28 años luego de un disturbio humano, con una media de 14.6 años $\pm$ 6.3 (DE). Los sitios de captura habían sido abandonados luego de ser deforestados (65%), convertidos en pasturas para cabras (26%), quemados (2%) o fueron sitios de crecimiento secundario temprano luego de disturbios desconocidos (7%). Los doseles de 104 parcelas de captura fueron más bajos (media 1.8 m) que los doseles en parcelas al azar (media 2.7 m) y que los sitios de sucesión tardía de rebrote alto (media 6.3 m). En siete sitios, la densidad media del follaje en las parcelas de captura fue consistentemente mayor a una altura entre 0.5 y 1.0 m, pero los sitios fueron heterogéneos para otras clases de altura del follaje <3 m y para el tiempo desde el disturbio, la altura del dosel, la densidad de troncos y cinco medidas de cobertura del suelo. Las parcelas no difirieron en términos del sexo del ave capturada excepto para una diferencia ($P = 0.05$) en la densidad del follaje a alturas <3 m. *D. kirtlandii* consumió frecuentemente frutas (69% de 499 observaciones), especialmente de *Lantana involucrata*, *Erithalis fruticosa* y *Chiococca alba*. El follaje de estas plantas fue más abundante en las parcelas de captura que en las parcelas al azar. Debido a que *D. kirtlandii* consume frutas en grandes cantidades y a que las frutas son más abundantes en los hábitats de sucesión temprana, esta especie, como otras aves migratorias neárticas-neotropicales que crían en hábitats de sucesión temprana, no se encuentra en los bosques maduros en los sitios de invernada.

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INTRODUCTION

Birds migrating between the Nearctic and Neotropical regions vary in their degree of behavioral plasticity in seasonal use of habitats and food resources (Mettke-Hofmann and Greenberg 2005). Migrants that breed in mature terrestrial habitats illustrate these differences well. Most of these species overwinter in a variety of habitats or in completely different habitats (Lynch 1989, Greenberg 1992, Wunderle and Waide 1993), including those that are early in succession. Dietary shifts may drive these patterns; indeed, many migrants switch from an arthropod-rich diet on the breeding grounds to a fruit-rich diet on the wintering grounds (Morton 1971, Greenberg 1981, Martin 1985, Loiselle and Blake 1990). It is not surprising that in the tropics migrants can be especially abundant in early-successional habitats (Karr 1976, Chipley 1977, Hutto 1980, Martin 1985), particularly as these habitats offer higher densities of fruit than do mature forests (Martin 1985, Levey 1988, Blake and Loiselle 1991). Alternatively, these patterns may be due to the sexes varying in the degree to which they shift between breeding and wintering habitats (Lynch et al. 1985, Lopez Ornat and Greenberg 1990, Stutchbury et al. 2005) and diets (Wunderle 1995).

Migratory species that breed in early-successional habitats avoid mature forests on the wintering grounds and are largely restricted to early seres (Lynch 1989, Wunderle and Waide 1993). On tropical wintering grounds, many species of migrants specialize on different seres (Greenberg 1992), although some may shift seasonally among seres or expand the range of seres occupied. The winter distribution among various early-successional habitats of migrants that use such habitats year round is not well known. For these species, it may be critical to determine whether factors such as sexual segregation or structure and resource levels explain their winter distribution.

The Kirtland's Warbler (*Dendroica kirtlandii*) is a classic example of an early-successional species. It is confined to fire-dependent jack pine (*Pinus banksiana*) barrens 1.4 to 5.0 m in height (Mayfield 1960, Walkinshaw 1983) on its breeding grounds in Michigan, Wisconsin, and Ontario. The warblers first breed at a site approximately 6 years after fire, when new growth is most dense, and continue to occupy it for about 15 years before abandoning it. Given the breeding warbler's reliance on early-successional sites, its consumption of fruit and arthropods both in Michigan (Deloria-Sheffield et al. 2001) and on the wintering grounds in the Bahamian archipelago (including the Turks and Caicos islands) (Chapman 1908, Sykes 1989, Sykes and Clench 1998), and the evidence of other migrants that winter exclusively in early-successional habitats, it is reasonable to expect wintering Kirtland's Warblers to occupy early-successional sites and avoid mature broadleaf forests in the Bahamian Archipelago. Earlier studies indicate that in The Bahamas, wintering Kirtland's Warblers occur in broadleaf scrub or shrubby habitats (Challinor 1962, Mayfield 1972, 1992, 1996, Radabaugh 1974, Sykes and Clench 1998) and rarely under pines (*Pinus caribaea*; Lee et al. 1997, Haney et al. 1998).

In addition, previous studies suggest that Kirtland's Warblers use successional habitats resulting from natural (e.g., fire or hurricanes) or anthropogenic disturbances (Lee et al. 1997, Sykes and Clench 1998, Haney et al. 1998, Wunderle et al. 2007) and avoid mature broadleaf forest (i.e., tall coppice). These conclusions, however, lack quantitative support. Detailed knowledge of this threatened species' requirements for nonbreeding habitat is a research priority (USFWS 1985) because of its importance for conservation on the wintering grounds.

To test the hypothesis that wintering Kirtland's Warblers are associated with early-successional habitats, we quantified habitat traits and age of plots where birds were captured and compared them to traits of randomly selected plots and plots of tall coppice on the island of Eleuthera, The Bahamas. For plots where birds were captured, we also determined if habitat varied by individual and by sex. In addition, we identified the fruit species most frequently consumed by Kirtland's Warblers and compared the abundance of the preferred plant species in capture plots to their abundance in random and tall-coppice plots.

METHODS

STUDY AREA

The Bahamas consist of about 29 low-lying (maximum elevation 63 m) subtropical islands of marine limestone, covered by either swampy or dense broadleaf vegetation (locally known as coppice), mostly low coppice and arid scrub. Extensive Caribbean pine (*Pinus caribaea*) forest occurs on the wetter northern islands, but coppice covers the drier central and southern islands. Our study was conducted in the central Bahamas on the 457-km² island of Eleuthera (25° N, 76° W), which is dominated by broadleaf trees and shrubs that form dense areas of dry forest and scrub (Sykes and Clench 1998). Historically, Eleuthera was farmed extensively (Mooney 1905, Young 1966), but more recently, most cultivation has ceased, resulting in a mosaic of abandoned agricultural plots with broadleaf habitats of different ages.

We concentrated our efforts to capture Kirtland's Warblers on seven sites (Table 1) on southern Eleuthera located between Tarpum Bay and 3 km south of Wemyss Bight and Green Castle. All study sites had black soils (soils described in Mooney 1905) and secondary black-land plant communities, but approximately half of the DD Road site also included white sand covered with remnant coastal coppice (plant communities described in Correll 1979 and Correll and Correll 1982). The vegetation of all study sites has been disturbed by human activities at various times (Table 1).

LOCATING AND CAPTURING BIRDS

We frequently located Kirtland's Warblers for capture by broadcasting recordings played on a Sony TCM 5000 tape recorder. We estimate that broadcasts could be heard from ~100 to 150 m from the speaker. Tapes consisted of a mix of

TABLE 1. Characteristics of sites at which Kirtland's Warblers were captured, on Eleuthera, The Bahamas, 2003–2007. Size of the site is the area of the study site in which searching and mist netting were conducted. Capture periods refer only to the winter period from 1 October through 30 April, unless otherwise indicated. For each study site the mean calendar year, range of calendar years, and mean age of capture sites are based on the age (i.e., number of years after disturbance) of the individual capture sites as determined from a chronosequence of satellite imagery. Sample sizes are given for the number of capture sites in each study site and the number of 0.03-ha plots in which vegetation structure and ground cover were measured as well as the number of plots in which vegetation structure, ground cover, and plant composition were measured. Also shown are traits of capture sites at 12 other locations on Eleuthera. See text for definitions and methods.

Study site	Size (ha)	Capture period	Year of disturbance at capture site (mean)	Years after disturbance at capture sites (range)	Age of capture sites (mean $\pm$ SE)	Capture sites (<i>n</i>)	Capture plots with structure measured (<i>n</i>)	Capture plots with structure and plants measured (<i>n</i>)
Ocean Hole	1.7	Mar 2004–Apr 2005	1998	1998	6.0 $\pm$ 0.1	18	17	0
Goat Farm	10.0	Feb 2006–Apr 2007	1994	1990–1998	11.3 $\pm$ 0.9	34	17	17
Wemyss Bight	11.7	Apr 2003, Oct 2003–Apr 2005	1985	1981–1990	17.7 $\pm$ 0.6	9	9	0
Rock Sound	18.7	Apr 2003, Oct 2003–Apr 2007	1984	1977–1998	18.7 $\pm$ 1.2	23	13	2
Gibson Estate	20.0	Mar 2003–Apr 2006	1985	1977–2000	18.1 $\pm$ 3.1	8	6	2
DD Road	31.1	Oct 2003–Apr 2007	1983	1977–1990	20.6 $\pm$ 2.0	9	6	1
Madera Road	50.5	Mar, Oct, Nov 2002, Oct 2004–Apr 2007	1986	1986	16.0 $\pm$ 0.4	35	22	14
Other capture sites at 12 locations		Apr 2003–Apr 2007	1993	1977–2000	13.3 $\pm$ 2.9	17	14	8

primary songs recorded on the breeding grounds and “chip” notes recorded from Kirtland's Warblers on Eleuthera. We located individuals by broadcasting taped playback throughout a habitat while two or more observers walked slowly along trails and roads from after sunrise until about 09:30 EST and from 15:30 EST to sunset. Initial searches, during two weeks in March and April 2002 and from 20 October through November 2002 concentrated on Madera Road. However, from 1 December 2002 through April 2003 we conducted extensive searches, some of which included point counts (Currie et al. 2005), from Governor's Harbour airport to the southern end of Eleuthera. We revisited all sites where Kirtland's Warblers were detected in an effort to capture birds at these sites.

After widespread searches in the winter of 2002–2003, we concentrated search and capture efforts at sites where at least four Kirtland's Warblers were found within 200 m of each other. On all study sites but one, we established access trails or a grid of trails to find and capture warblers. The number of study sites used varied each winter depending on access or site disturbance (Table 1). In addition to the main study sites, we found and captured birds at new locations outside the study sites and revisited other sites where Kirtland's Warblers had been found previously to ensure that the full range of variation in winter habitats on southern Eleuthera was sampled.

We captured birds from 1 October through 30 April, beginning in March 2002 and ending in April 2007. Birds were captured in 30-mm-mesh mist nets, 12 or 6 m long, set to a maximum height of 2.6 m. Three netting methods were used: target netting with playback, long net lines with playback, and long net lines without playback. Target netting with playback

was used in all areas to locate and attract an individual to the net. Once a responsive bird was located, a net was set up, a speaker was placed below the center of the net and operated remotely by an observer 2 to 6 m from the net. Long lines of mist nets operated with or without playback were placed only in the seven study sites and were set in various configurations along trails or abandoned roads and included up to 42 12-m nets. For analysis, net captures (target or long line) involving playback are designated as “playback” captures in contrast to captures without playback, which are designated as “passive” captures. As no significant differences ($P > 0.20$) were found between playback and passive captures for any of the measured habitat variables, data from the two methods were pooled for all analyses.

Coordinates of all capture sites were obtained with a GPS unit accurate to within 5 m. Standard measurements and mass were taken for all captured birds, and sex was determined by wing length (chord) and plumage (Goodman 1982, Pyle et al. 1987). Birds were banded with a unique combination of three plastic color bands and an aluminum U.S. Geological Survey band and released.

FORAGING OBSERVATIONS

Most foraging observations were made from sunrise to 10:30 EST; some were made from 16:00 EST until sunset. Observers walked slowly through study sites until they located a foraging bird. They recorded the foraging behavior 5 sec after encountering an individual to avoid a bias toward more conspicuous feeding behaviors. Each observer recorded only one instance of foraging per individual in a morning. Occasionally,

however, different observers independently encountered the same color-banded individual during the same day (12% of 499 observations were of individuals seen twice on the same day), but only observations separated by at least a half hour were included in the analysis.

HABITAT MEASUREMENTS

In the winter of 2003–2004 we randomly selected capture sites for habitat measurements within each study site by using a stratified random design. To correct for a male bias in captures, however, in the winters of 2004–2005 through 2006–2007 we measured habitat at all sites where female warblers were captured in the study sites and at randomly selected sites where males had been captured. In addition, we obtained habitat measurements at all capture sites (for both males and females) outside of the seven study sites (Table 1).

We measured habitat characteristics in 0.03-ha circular plots at 103 sites where Kirtland's Warblers were initially captured and one site where a Kirtland's Warbler escaped (i.e., capture plots). Each plot was centered 15 m from the capture site in the direction from which each bird initially approached the net. Of the 104 capture plots, 90 were sampled in the same winter as the initial capture, 12 were sampled in the following winter, and two were sampled in the third winter after initial capture. The habitat was measured in October (2%), February (33%), March (3%), and April (62%). In addition to measuring vegetation structure and ground cover, we identified species of trees and shrubs with foliage present in the foliage height profiles (described below) of the last 44 of the 104 capture plots measured (n values in Table 1). We measured and recorded diameter at breast height (1.3 m, DBH) for all trees ≥ 3 cm and categorized them by size as per Wunderle and Waide (1993). To measure the abundance of small woody stems, an observer walked along each of the four 10-m transects radiating in the cardinal directions from the plot center and counted all live vertical woody stems < 3 cm DBH that touched his or her body and outstretched arms.

We determined foliage height profiles (percent cover and species) at 20 points at 2-m intervals along the north, south, east, and west radii of the circular plot by using the method of Schemeske and Brokaw (1981) as modified by Wunderle and Waide (1993). Percent cover was determined at height intervals and 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. Species of trees and shrubs whose leaves were present within a height interval were identified, and the number of height intervals in which each species was present was tallied for each capture plot sampled during the winters of 2005–2006 and 2006–2007. Because foliage profiles were often measured in the March to May dry season when the tree *Bursera simaruba* had lost some leaves, we determined the potential effect of this leaf loss on our foliage profiles (Appendix).

We calculated the mean canopy height of each plot by determining the median value of the highest height class of each of the 20 points measured along the plot's four radii and calculating the mean. In addition, ground cover at each of the 20 points along the radii was evaluated by an observer standing and looking at the ground through a 5-cm-diameter tube and recording the presence of live leaves (i.e., shrub cover), leaf litter, grass, wood, rock, and bare ground. The percentage of 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 ($n = 20$) and multiplying by 100.

DETERMINATION OF TIME SINCE DISTURBANCE (AGE) AND DISTURBANCE TYPE

Age and disturbance type of capture sites and reference sites (see below) was determined from a map of forest age and disturbance type (E. H. Helmer et al., unpubl. data). The map was developed from a chronosequence of satellite image mosaics in which cloud cover was minimized by mosaicking the clear parts of two or more scenes for each time step, normalized by a regression tree (Helmer and Ruefenacht 2005). The image sequence included Landsat Thematic Mapper images for 1984, 1988, 1993, 1996, and 2000, Landsat Enhanced Thematic Mapper images for 2001 and 2003, and an Advanced Land Imager image from 2005. All spectral bands from each image mosaic were used in the classification, and the imagery had a pixel size of 28.5 m. Age of a site was calculated by taking the midpoint of the images available the year before and after the woody vegetation regrowth at a site became apparent visually (see Helmer et al. 2009). In most cases woody regrowth began soon after disturbance. The map included two classes of forest age in the earliest image (1984). The younger class was estimated to have been disturbed between 1974 and 1979, while the oldest class was estimated to have been disturbed before 1970 and was ≥ 37 years old in 2007.

In addition to age since disturbance, the map distinguished between three disturbance types for regrowth that began after 1984: burned but not followed by clearing (typically from escaped fire), cleared for agriculture or construction and then abandoned, and cleared and grazed by goats. Disturbance type and time since disturbance of each capture and reference site was determined by using the majority category in a 3 pixel by 3 pixel, 85.5-m square. Classification was verified by inspection of the sites in the field. We verified the time since disturbance and the type of disturbance determined from the satellite imagery by talking with those familiar with the site.

REFERENCE PLOTS

We compared habitat characteristics of capture plots with those of reference plots located by a stratified random sampling design, stratified by disturbance age and type as indicated in the satellite image-based map. When a randomly selected plot was inaccessible from a road, the next plot in the randomized

sequence of potential plots for each category was selected. The reference plots include those of tall coppice, but for some analyses we also compared traits of capture plots with those of only the tall coppice.

Habitat variables were measured in the 12 plots with tall coppice on 25 April 2006 and from 10 February to 21 March 2007, as for the capture plots. Foliage profiles, as obtained in capture plots, were the only measurements made in the remaining 40 reference plots from 7 March to 1 May 2007. In these plots we tallied the number of height categories containing foliage of fruit plants (i.e., *Chiococca alba*, *Erithalis fruticosa*, *Lantana involucrata*) important to Kirtland's Warbler and one species, *L. bahamensis*, whose fruit is rarely consumed (Wunderle et al. unpubl. data). We include *L. bahamensis* in our analyses to describe the spatial relationship between Kirtland's Warbler and the species whose fruit it frequently and infrequently consumes.

STATISTICAL ANALYSES

Statistical analyses, using SPSS (SPSS 1990), followed Sokal and Rohlf (1995). We determined normality of data by inspecting a normal probability plot in SPSS and checking homogeneity of variances with the Levene *F*-test. Percentage foliage cover above 3 m was converted to a normal distribution with $\ln + 1$.

When assumptions of normality and homogeneity of variances were met, we conducted several parametric analyses. We used one-way analysis of variance (ANOVA) to test for significant heterogeneity among winter periods (early, October–December; mid, January–February; late, March–April) in mean counts of foliage height categories per plot for each of four fruit plant species and to test for differences between capture plots and reference plots in mean principal component (see below) scores, among winters in mean plot age, and among winters in plots' mean canopy height. Two-factor ANOVAs were performed to determine if mean canopy height of capture plots and mean woody stems <3 cm DBH per transect differed by study site and sex. In addition, a two-factor ANOVA was performed to determine if mean counts of foliage categories per plot varied by winter and plant species. A multivariate analysis of variance (MANOVA), with Wilks' λ and Rao's *F* statistic was performed to determine if mean count of foliage height categories per plot in the six foliage-height classes between 0 to 3 m differed by study site and sex. When data were normal we compared means by *t*-tests, considering variances equal or unequal on the basis of the outcome of the Levene test. In cases where data were not normal and variances were not equivalent, we used nonparametric tests to compare median values of two groups (Mann–Whitney *U*-test) or median values of more than two groups (Kruskal–Wallis test).

For categorical analyses, we compared sex ratios in net captures with a χ^2 goodness-of-fit test and used a row-by-column test of independence with a *G*-statistic to compare sex

ratios among four study sites and to compare presence versus absence of species of fruiting plants in foliage profiles of goat-grazed and abandoned plots. Because of small sample sizes (<5) in the cells of 2×2 tables, we used Fisher's exact tests to compare foliage profiles of capture and tall-coppice plots for presence versus absence of specified fruiting plants.

Standard error (SE) was used to compare means, and standard deviation (SD) was used to gauge variation around means. Coefficient of variation (CV) was used to compare the variance in canopy height with the mean canopy height of plots. In all analyses, a probability of type I error <0.05 was considered significant, but greater values are also shown. Bonferroni-adjusted *P* values (Miller 1981), designated here as P_B , were used to determine the significance levels for Pearson correlations (*r*) of plot age with various structural traits as well as in *t*-tests comparing percent foliage cover in various height categories in capture plots versus those in reference or tall-coppice plots.

Principal component analysis, based on a correlation matrix, was used to assess variation of eight habitat variables among 44 capture plots in five of the seven study sites and outlying sites and 51 reference plots.

RESULTS

CAPTURE DATA

A total of 153 Kirtland's Warblers (92 males, 53 females, 8 sex undetermined) were captured on Eleuthera. Among birds sexed definitively, those captured with playback were significantly biased toward males (69.4% of 85; $\chi^2 = 11.91$, *df* = 1, *P* = 0.001), but those captured passively were not (56.6% of 60; $\chi^2 = 1.60$, *df* = 1, *P* = 0.21). Males were captured more frequently with playback than without it (63.4% of 92 males; $\chi^2 = 6.72$, *df* = 1, *P* = 0.010), in contrast to females, for which the number of captures by the two methods was equivalent (50.9% of 53 females by playback; $\chi^2 = 0.019$, *df* = 2, *P* = 0.891). Combining all passive captures (initial passive captures plus passive recaptures of birds previously captured with playback) resulted in a suggestive, but not significant, male-biased sex ratio (59.1% of 88 birds; $\chi^2 = 2.90$, *df* = 1, *P* = 0.088). Sex ratios of birds captured passively did not vary significantly (row-by-column test of independence, *G* = 1.90, *df* = 3, *P* = 0.594) among the four study sites with adequate sample sizes (male:female ratio for Madera, 13:8; Ocean Hole, 12:5; Rock Sound, 9:7; goat farm, 12:12).

AGE AND DISTURBANCE OF CAPTURE SITES

The age (time since disturbance) of the 153 capture sites ranged from 3 to 28 years (Fig. 1) with an average age of 14.6 years $\pm$ 6.4 SD, which did not differ significantly (*t* = 1.07, *df* = 57.6, *P* = 0.30) from the age of the reference plots ($\bar{x}$ = 15.4 years $\pm$ 1.83 SE, range 3 to >37 years since disturbance) but was significantly (*t* = 48.86, *df* = 151, *P* < 0.001) younger than the age of the 12 plots with tall coppice (>37 years since disturbance).

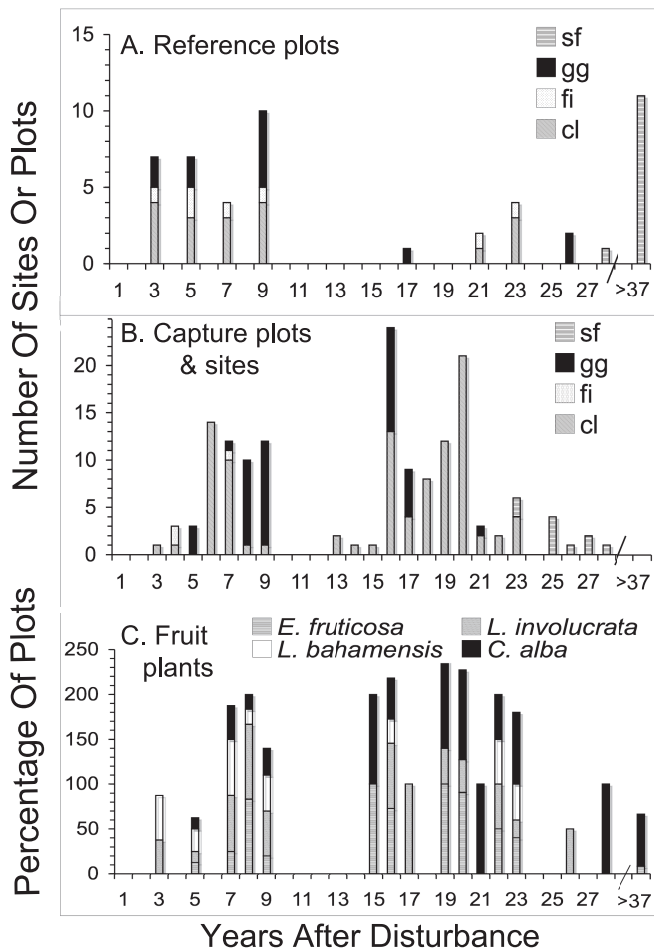


FIGURE 1. Distribution of disturbance ages of reference plots (A) and Kirtland's Warbler capture sites (B) and percentage of plots sampled with four species of fruit plants (C) on Eleuthera, The Bahamas. Disturbance age was estimated from a chronosequence of satellite imagery, which was also used to classify disturbance type into second-growth forest (sf), cleared and goat grazed (gg), fire (fi), and cleared and abandoned (cl). Fruit plants include *Chiococca alba* (snowberry), *Lantana bahamensis* (Bahama sage), *Lantana involucrata* (wild sage), and *Erithalis fruticosa* (black torch).

Capture and reference sites differed in the proportion of disturbance types (Fig. 1). The 153 capture sites were most frequently disturbed by (1) clearing followed by abandonment (65%, either bulldozed, or cut and then burned; henceforth designated as abandoned), (2) clearing followed by goat grazing (26%; henceforth grazed), (3) fire (2%, burned without cutting of trees; henceforth burned) or in 1984 were young second growth for which the type of disturbance was unknown (7%; henceforth second-growth forest). In contrast, the 51 reference sites were abandoned (36%), grazed (26%), burned (14%), or were second-growth forest (24%) of either short stature (1 site) or of tall stature (12 tall-coppice sites).

HABITAT STRUCTURE

Canopy height. Canopy height (ln conversion) was strongly and positively correlated with the ages of both the 51 reference plots ($r = 0.76$, $P_B < 0.01$) and the 104 capture plots ($r = 0.65$, $P_B < 0.01$). Canopies of capture plots were mostly short ($\bar{x} = 1.8 \text{ m} \pm 0.89 \text{ SE}$, $n = 104$), significantly ($t = -15.23$, $df = 113$, $P < 0.001$) shorter than canopies in the reference plots ($\bar{x} = 2.7 \text{ m} \pm 0.33 \text{ SE}$) as well as canopies in tall coppice ($\bar{x} = 6.3 \text{ m} \pm 0.35 \text{ SE}$, $n = 12$; $t = -2.70$, $df = 57.45$, $P = 0.009$). Moreover, the heights of canopies were significantly ($t = 6.08$, $df = 113$, $P < 0.001$) more variable in capture plots than in tall coppice, when corrected for mean height (CV: $\bar{x} = 63.5 \pm 2.6 \text{ SE}$ and $38.5 \pm 3.2 \text{ SE}$, respectively) but not more variable than the heights of canopies in reference plots (CV: $\bar{x} = 61.3 \pm 3.9 \text{ SE}$; $t = 4.75$, $df = 153$, $P = 0.64$).

Foliage distribution. Percent foliage cover (ln + 1 conversion) in the 3–4-m height category showed the strongest positive correlation with plot age for both the reference ($r = 0.61$, $n = 51$, $P_B < 0.01$) and capture plots ($r = 0.63$, $n = 104$, $P_B < 0.01$). In all capture plots foliage was concentrated in the lower height categories and densest at 0.5–1.0 m (Fig. 2a). Capture plots had significantly (t -tests, $P_B < 0.05$) less foliage at the upper heights than both the reference and tall-coppice plots (Fig. 2a). The variation in foliage distributions among the capture plots is illustrated in the foliage profiles for Ocean Hole and Wemyss Bight (Fig. 2).

Stem density. The mean number of small woody stems (<3 cm DBH) in capture plots was weakly correlated with plot age ($r = 0.39$, $n = 104$, $P_B < 0.01$), indicating that the density of small stems increased with age across the 3- to 28-year age range of the capture sites. But in older plots the density of small stems declined, as evident in the finding ($t = 6.12$, $df = 113$, $P < 0.001$; Fig. 3) that small stems were nearly twice as abundant in capture plots ($\bar{x} = 60 \text{ 171 stems ha}^{-1} \pm 3086 \text{ SE}$) as in tall-coppice plots ($\bar{x} = 35 \text{ 885 stems ha}^{-1} \pm 2514 \text{ SE}$).

For large woody stems ($\geq 3 \text{ cm DBH}$), the correlation of mean number of stems with plot age was strongest in the 3–8-cm DBH class ($r = 0.59$, $n = 104$, $P_B < 0.01$). Consistent with this relation was the finding that large stems were more dense ($t = 7.407$, $df = 10.67$, $P < 0.001$) in tall-coppice plots ($\bar{x} = 9297 \text{ stems ha}^{-1} \pm 968.9 \text{ SE}$) than in capture plots ($\bar{x} = 2004 \text{ stems ha}^{-1} \pm 174.4 \text{ SE}$). Tall-coppice plots also had significantly (Mann–Whitney $U = 31.00$, $P < 0.001$) larger stems than did capture plots (median = 7.7 cm vs. 5.6 cm, respectively; Fig. 3).

Ground cover. On capture plots, ground cover varied with plot age, as evidenced by negative correlations of plot age with percentage rock cover ($r = -0.55$, $n = 104$, $P_B < 0.01$) and percentage exposed soil ($r = -0.51$, $n = 104$, $P_B < 0.01$) and a positive correlation with percentage woody debris ($r = 0.61$, $n = 104$, $P_B < 0.01$). Ground cover in capture plots differed significantly from that of tall-coppice plots in having higher percent cover of rock, exposed soil, and grass and lower percent cover of leaf litter and woody debris (Fig. 4). In shrub cover, however, capture and tall-coppice plots did not differ significantly.

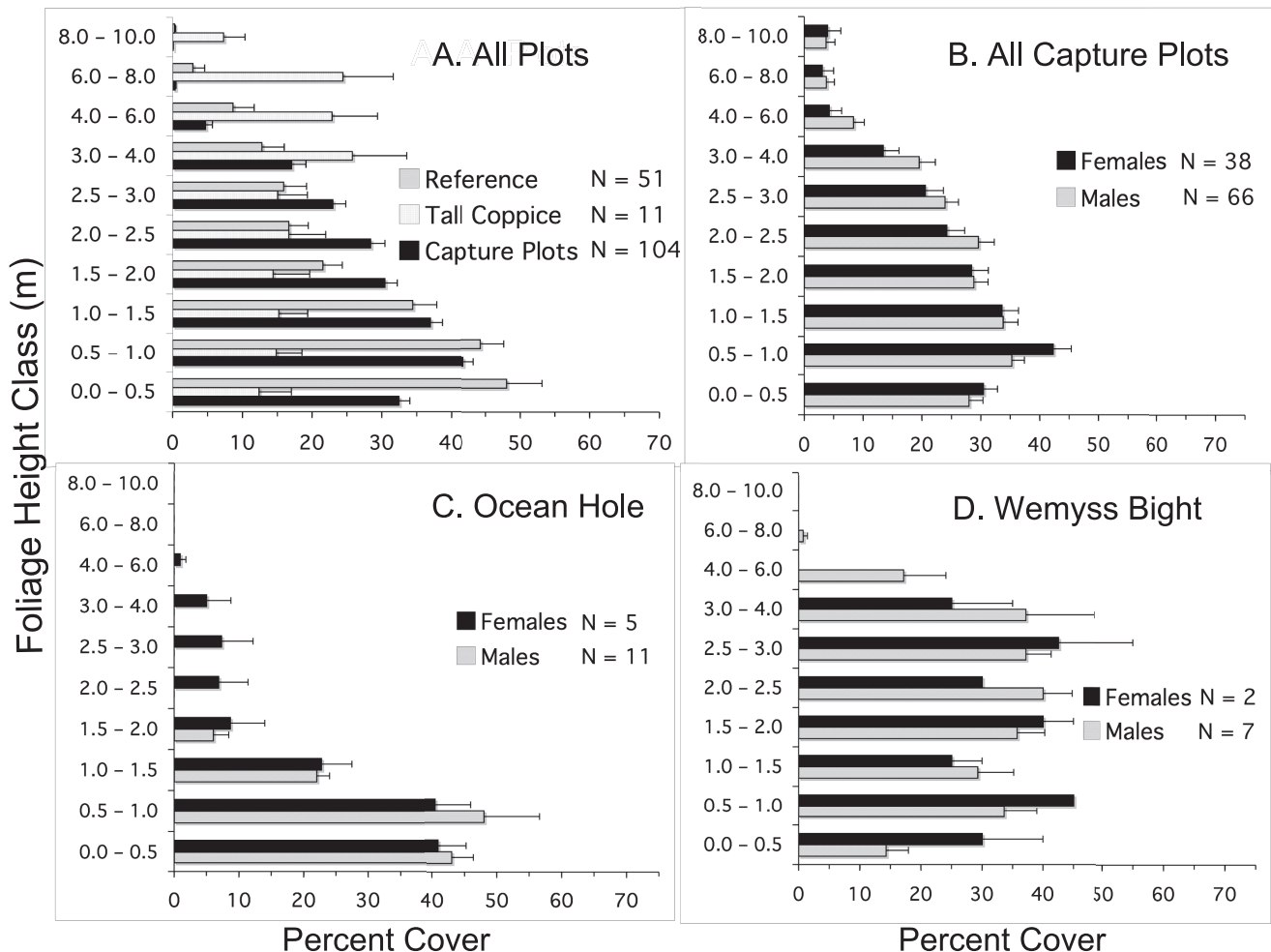


FIGURE 2. Foliage-height profiles showing percent foliage cover at various height categories sampled in vegetation plots in southern Eleuthera, The Bahamas. Foliage-height profiles are shown by category of plot (reference, tall coppice, and Kirtland's Warbler capture plots) for all plots (A) and by sex for all capture plots (B), capture plots at Ocean Hole (C), and capture plots at Wemyss Bight (D). *N*, number of plots sampled for each category.

Relationship of habitat traits to the sex of birds captured on study sites. The sexes did not differ ($t = -1.05$, $df = 58$, $P = 0.30$) in the average age of sites at which they were captured (male $\bar{x} = 14.7$ years ± 0.51 SE; female $\bar{x} = 16.7$ years ± 1.87 SE). Corresponding with a lack of sex difference in the ages of capture sites was an absence of significant differences in structural and ground-cover traits of capture plots at the seven study sites (t -test and P values in Table 2). However, a sex difference in density of foliage in height classes <3.0 m in capture plots (Fig. 2b) was strongly suggested but not quite significant ($P = 0.05$). Moreover, there were no significant interactions between sex of birds captured and study site for foliage density in height classes <3.0 m, canopy height, or mean density of small stems (<3 cm DBH) in capture plots.

Differences among the study sites in habitat traits of capture plots. Among the seven study sites, heterogeneity in the ages of capture plots was significant (Kruskal-Wallis $\chi^2 = 57.09$,

$df = 6$, $P < 0.001$; Table 1). Corresponding with variation among study sites in capture-plot ages was significant heterogeneity among study sites for almost all of the structural habitat traits measured in the capture plots (t -test and P values in Table 2). For example, significant heterogeneity among study sites was found in mean canopy heights, densities of small stems (<3 cm DBH), densities of large stems (≥ 3 cm DBH), stem diameters (≥ 3 cm DBH), and ground-cover traits including percent rock cover, leaf litter, grass, and woody debris but not in percent shrub cover or exposed soil. Also, significant heterogeneity among study sites was found for foliage density in all height classes <3 m except for 0.5–1.0 m.

FRUGIVORY AND PRINCIPAL FRUITING PLANT SPECIES

Foraging observations. Of the 499 observations of foraging Kirtland's Warblers, fruit was consumed in 68.6%,

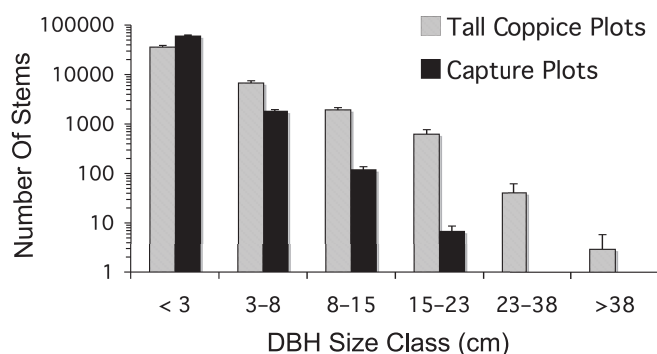


FIGURE 3. Mean ($\pm$ SE) number of woody stems per hectare for various classes of stem diameter measured at a height of 1.3 m (DBH) in Kirtland's Warbler capture plots ($n = 104$) and randomly selected tall-coppice plots ($n = 12$) in southern Eleuthera, The Bahamas. Note that number of stems is shown on a log scale. Stems < 3 cm in diameter were measured by an observer walking along each of four 10-m transects radiating in the cardinal directions from the center of a 0.03-ha plot and counting all live vertical woody stems < 3 cm diameter touching the observer's body and outstretched arms. All stems ≥ 3 cm in the 0.03-ha plots were measured.

arthropods were presumably consumed in 31.4%, and flowers were probed in 0.4%. Of the 250 observations in which fruit was consumed, 73.3% involved unidentified species of *Lantana*. The warblers consumed fruit from a variety of species, however, as evident in 89 foraging observations for which all fruits were identified to species and included *Lantana involucrata* (36.0%), *Erithalis fruticosa* (23.6%), *Chiococca alba* (16.9%), *Bursera simaruba* (5.6%), *Bourreria ovata* (4.5%), *Guapira obtusata* (2.3%), *Tournefortia volubilis* (2.3%), *Cassytha filiformis* (2.2%), *Coccoloba diversifolia* (1.1%),

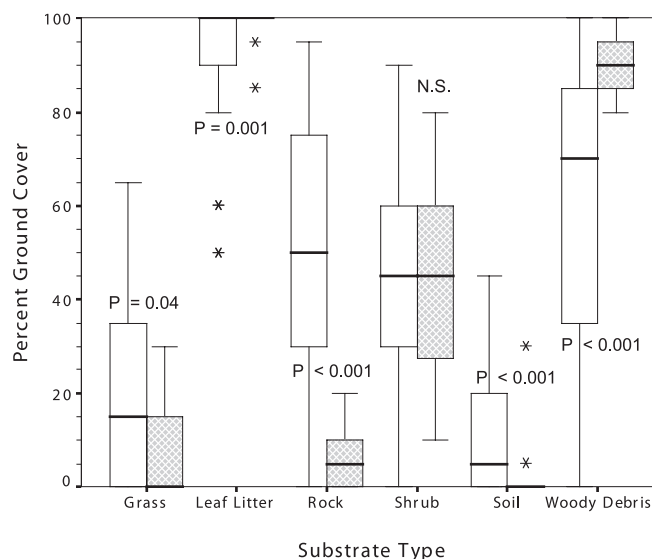


FIGURE 4. Box plots of percentage of ground covered in grass, leaf litter, rock, shrubs, exposed soil, and woody debris, measured in 0.03-ha plots at 104 points at which Kirtland's Warblers were captured (open box) and 11 tall-coppice (box with pattern) plots in southern Eleuthera, The Bahamas. Box plots show the median (dark horizontal bar), interquartile range, and outliers. P values represent levels of significance for differences between capture and tall-coppice plots as determined by a Mann-Whitney U -test.

Psychotria ligustrifolia (1.1%), *Psychotria nervosa* (1.1%), *Guettarda scabra* (1.1%), *Trema lamarckianum* (1.1%), and *Zanthoxylum fragra* (1.1%).

Presence of important fruiting plants. In the foliage height profiles, plants that bear fruits important to Kirtland's Warbler (principal fruit species) were more frequent in

TABLE 2. Summary of statistical tests and significance levels for comparisons of traits of Kirtland's Warbler capture plots (0.03 ha) among seven study sites on Eleuthera, The Bahamas. See text for methods for measurement of vegetation and ground cover traits; Table 1 for study sites and sample sizes of capture plots.

Trait	Among study sites		Between sexes		Interaction (study site $\times$ sex)	
	Test	P	Test	P	Test	P
Canopy height	$F_{6,76} = 3.33$	0.006	$F_{1,76} = 0.53$	0.468	$F_{6,76} = 1.61$	1.61
Foliage density at 0–3 m ^a	Rao's $F_{36,315} = 4.91^*$	< 0.0001	Rao's $F_{6,71} = 2.27^{**}$	0.05	Rao's $F_{36,315} = 0.74^{***}$	0.74
Density of stems < 3 cm DBH	$F_{6,76} = 7.71$	< 0.001	$F_{1,76} = 0.51$	0.48	$F_{6,76} = 0.43$	0.43
Density of stems > 3 cm DBH	K-W $\chi^2_6 = 51.06$	< 0.001	K-W $\chi^2_8 = 0.55$	0.58		
Mean DBH of stems > 3 cm DBH	K-W $\chi^2_6 = 38.81$	< 0.001	K-W $\chi^2_{102} = 0.14$	0.89		
Percentage of ground cover						
Rock	K-W $\chi^2_6 = 51.04$	< 0.001	K-W $\chi^2_6 = 0.83$	0.931		
Leaf	K-W $\chi^2_6 = 23.98$	0.001	K-W $\chi^2_6 = 0.21$	0.833		
Grass	K-W $\chi^2_6 = 33.46$	< 0.001	K-W $\chi^2_6 = 0.54$	0.588		
Woody debris	K-W $\chi^2_6 = 30.25$	< 0.001	K-W $\chi^2_6 = 1.46$	0.147		
Shrub	K-W $\chi^2_6 = 4.59$	0.597	K-W $\chi^2_6 = 0.16$	0.987		
Soil	K-W $\chi^2_6 = 11.58$	0.072	K-W $\chi^2_6 = 1.03$	0.306		

^a Test results: *MANOVA, Wilks' $\lambda = 0.141$; **MANOVA, Wilks' $\lambda = 0.842$; ***MANOVA, Wilks' $\lambda = 0.699$.

the 44 capture plots than in the 51 reference plots. For *Chiococca alba* (snowberry) the difference was 66% vs. 35% ($G = 9.00$, $df = 1$, $P = 0.003$), for *Erithalis fruticosa* (black torch) 70% vs. 14% ($G = 33.665$, $df = 1$, $P < 0.001$), and for *Lantana involucrata* (wild sage) 55% vs. 25% ($G = 8.483$, $df = 1$, $P = 0.004$). In contrast to those of its congener, foliage height profiles of the endemic *L. bahamensis* in capture and reference plots did not differ (23% vs. 24%; $G = 0.009$, $df = 1$, $P = 0.926$). At least one of the three principal fruit species was more frequent in the foliage height profiles of capture plots than in those of reference plots (98% vs. 61%; $G = 22.510$, $df = 1$, $P < 0.001$). The plots did not differ significantly ($P > 0.05$) by sex of the captured bird in presence of any of the principal fruit species or of *L. bahamensis* in the foliage profiles.

Even after restricting the analysis to the reference plots by eliminating the 12 older tall-coppice plots (i.e., to the remaining 39 reference plots with $\bar{x}$ age = 10.4 years $\pm$ 1.27 SE), we still found a greater percentage of the principal fruit plants in the foliage height profiles of the 44 capture plots ($\bar{x}$ age = 14.6 years $\pm$ 0.52 SE) than in the remaining 39 reference plots for *C. alba* (66% vs. 28%; $G = 12.09$, $df = 1$, $P = 0.001$) and *E. fruticosa* (70% vs. 15%; $G = 27.19$, $df = 1$, $P < 0.001$). A similar but only suggestive pattern was observed for *L. involucrata* (55% vs. 33%; $G = 3.80$, $df = 1$, $P = 0.051$). Even without the tall-coppice plots in the analysis, principal fruit species were still found in more of the capture plots than in the 39 reference plots (98% vs. 56%; $G = 23.84$, $df = 1$, $P < 0.001$).

The 44 capture plots differed from the 12 tall-coppice plots in having higher percentages of plots with *E. fruticosa* (70% vs. 9%; Fisher's exact test, $P < 0.001$) and *L. involucrata* (55% vs. 0%; Fisher's exact test, $P = 0.001$), but for *C. alba* (66% vs. 64%; Fisher's exact test, $P = 1.00$) and *L. bahamensis* (23% vs. 0%; Fisher's exact test, $P = 0.184$) the percentages were similar. Furthermore, a significantly higher percentage of capture plots had foliage of at least one of the three principal fruit species than did the tall-coppice plots (98% vs. 64%; Fisher's exact test, $P = 0.004$).

Age and disturbance history of plots with Kirtland's Warbler's principal fruit plants. Capture and reference plots did not differ significantly in median time since disturbance if they contained *E. fruticosa* ($P = 0.16$), *L. involucrata* ($P = 0.21$) or *L. bahamensis* ($P = 0.53$). Where *C. alba* was present, however, time since disturbance differed significantly (Mann-Whitney $U = 147.000$, $P = 0.012$), the median being 20.0 years for capture plots and 23.0 years for reference plots), reflecting this plant's higher frequency in the older tall-coppice plots. The median age of capture plots with *L. involucrata* was 15.5 years (range 3–22 years), of those with *E. fruticosa* 19.0 years (range 8–23 years), and of those with *C. alba* 20.0 years (range 6.5–28 years). The heterogeneity of these ages is significant (Kruskal-Wallis $\chi^2 = 8.801$, $df = 2$, $P = 0.012$). Taken together, capture plots with at least one of the principal fruit species in the foliage profiles spanned the full range of ages since disturbance represented in the 153 capture sites (3–28 years, Fig. 1c).

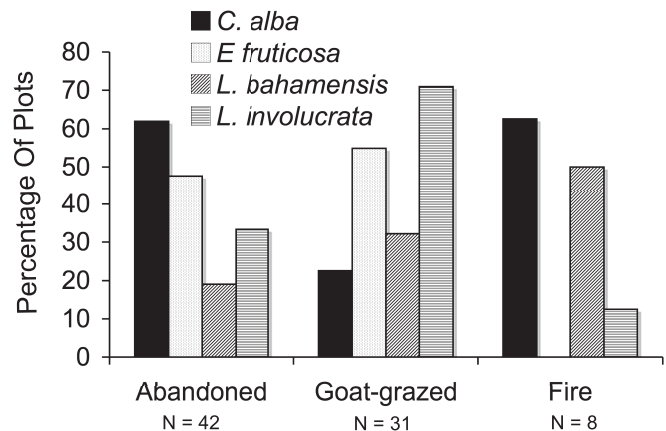


FIGURE 5. Percentage of plots (capture and reference plots) with foliage of specified plant species present in foliage-height profiles at sites that had been cleared and abandoned (abandoned), cleared and grazed by goats (goat-grazed), or had been burned (fire). Plants included *Chiococca alba*, *Erithalis fruticosa*, *Lantana bahamensis* and *L. involucrata*. N , number of plots sampled for each disturbance type.

Three of the fruiting plants (*C. alba* and the two *Lantana* species) were represented in the foliage profiles of the abandoned, goat-grazed, and burned reference and capture plots (Fig. 5). *Erithalis fruticosa* was also present in the abandoned and goat-grazed plots but absent from the burned reference and capture plots. In the abandoned and goat-grazed plots the distribution of two of the plant species differed significantly, with highest counts of foliage height categories with *C. alba* in abandoned plots ($G = 11.589$, $df = 1$, $P = 0.001$) and highest counts of foliage height categories with *L. involucrata* in goat-grazed plots ($G = 10.367$, $df = 1$, $P = 0.001$). These differences between *C. alba* and *L. involucrata* in the two plot types may have resulted partly from the significant ($t = 2.188$, $df = 70.81$, $P = 0.032$) difference in time since disturbance between abandoned ($\bar{x} = 15.0$ years $\pm$ 1.16 SE) and goat-grazed ($\bar{x} = 11.6$ years $\pm$ 1.5 SE) plots. Burned plots were the youngest in age ($\bar{x} = 9.0$ years $\pm$ 2.54 SE).

Date of capture and fruit plants. Given the importance of the three principal fruit plants to Kirtland's Warbler and the differences among them in timing of fruiting, we expected that their abundance in capture plots, as represented by a mean count of height categories with the species' foliage (foliage abundance), would vary with captures in early, mid, and late winter. Indeed, we found a significant ($F_{4,123} = 4.678$, $P = 0.002$) interaction between foliage abundance of fruit plants and winter period; the abundance of foliage of the three principal fruit species in the capture plots varied seasonally. For example, the mean foliage abundance ($\bar{x} \pm$ SE) in capture plots varied significantly among the three periods for *C. alba* (early = 3.4 ± 0.6 ; mid = 3.6 ± 0.7 ; late = 1.3 ± 0.4 ; $F_{2,41} = 9.422$, $P < 0.001$) and *E. fruticosa* (early = 2.7 ± 0.6 ; mid = 3.1 ± 0.7 ; late = 1.4 ± 0.3 ; $F_{2,41} = 3.921$, $P = 0.028$) but not for *L. involucrata* (early = 0.43 ± 0.5 ; mid = 0.82 ± 0.5 ; late = 1.3 ± 0.2 ; $F_{2,41} = 1.638$,

TABLE 3. Component scores or factor loadings for the first two principal components from a principal component analysis of eight habitat variables and plot age measured in 0.03-ha circular plots at 44 Kirtland's Warbler capture plots and 51 reference plots in southern Eleuthera, The Bahamas. Capture plots were located at five of the seven study sites and outlying sites (Table 1). Variables are described in the text.

Variable	PC1	PC2
Canopy height	-0.857	-0.029
Age since disturbance	-0.794	0.116
Foliage at 0–0.5 m	0.618	0.188
Foliage at 0.5–1.0 m	0.410	0.628
<i>Lantana involucrata</i>	0.598	0.278
<i>Erithalis fruticosa</i>	-0.046	0.772
<i>Chiococca alba</i>	-0.392	0.669
<i>Lantana bahamensis</i>	0.557	-0.242
Eigenvalue	2.74	1.64

$P = 0.21$). Corresponding with the decrease in foliage of *C. alba* and *E. fruticosa* in capture plots in late winter was a change in mean age of capture plot with period (early $\bar{x} = 17.3$ years ± 0.8 ; mid $\bar{x} = 13.6$ years ± 1.2 ; late $\bar{x} = 13.2$ years ± 0.7 ; $F_{2,151} = 7.178$, $P = 0.001$) and mean canopy height per plot (early $\bar{x} = 2.2$ m ± 0.1 ; mid $\bar{x} = 1.8$ m ± 0.2 ; late $\bar{x} = 1.6$ m ± 0.1 ; $F_{2,103} = 4.503$, $P = 0.013$).

Habitat structure and composition of reference vs. capture plots. We used principal components analysis to evaluate differences between the 51 reference plots and the 44 capture plots in eight vegetation traits and time since disturbance (Table 3). The first three principal components explained 67.6% of the variation in the habitat characteristics, with 34.2% contributed by PC-1, 20.5% by PC-2, and 12.9% by PC-3. The highest positive loadings for PC-1 were foliage at 0–0.5 m and the two *Lantana* species. In contrast, the highest negative loadings were canopy height, plot age, and *C. alba*. Corresponding with the separation of plots by age and vegetation traits by PC-1 was the separation by disturbance type: second-growth forest plots at the negative extreme were separated from abandoned plots, which in turn were separated from goat-grazed plots at the positive extreme (Fig. 6). The burned plots had intermediate PC-1 values. Therefore, PC-1 indicates that younger plots with lower canopies had more foliage within 0.5 m of the ground and more *Lantana* foliage (e.g., goat-grazed) than older plots with higher canopies, which had more foliage of *C. alba* (e.g., second-growth forest and abandoned). For PC-2, *E. fruticosa* foliage, *C. alba* foliage, and foliage at 0.5–1.0 m had the highest positive loadings, while *L. bahamensis* foliage and canopy height had the highest negative loadings. The separation of disturbance types by PC-2 was weak, with abandoned plots spanning the full range of PC-2 values and overlapping goat-grazed plots, which had intermediate values,

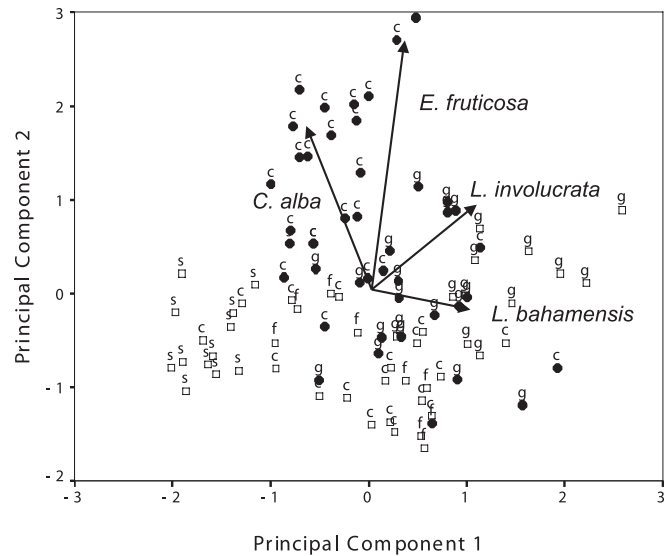


FIGURE 6. Graph of principal component 1 against principal component 2 based on habitat characteristics of 51 reference plots (open squares) and 44 Kirtland's Warbler capture plots (black dots) from southern Eleuthera, The Bahamas. Habitat characteristics of the 0.03-ha plots included mean canopy height, age since disturbance, percent foliage cover in the 0–0.5 m and 0.5–1.0 m height classes and counts of height categories with foliage of the fruit plants (*Chiococca alba*, *Erithalis fruticosa*, *Lantana bahamensis*, and *L. involucrata*). Arrows indicate the relative contribution of each plant in the ordination. Disturbance types are indicated by letters for secondary forest (s), cleared and abandoned (c), cleared and goat grazed (g), and burned (f).

and second-growth forest and burned plots, which loosely clustered toward the negative values (Fig. 6). Therefore, PC-2 separated those plots with an abundance of foliage at 0.5–1.0 m, especially of *E. fruticosa* and *C. alba*, from plots with an abundance of *L. bahamensis* foliage.

PC-2 was the only axis on which mean PC scores of capture and reference plots differed significantly ($t = -6.310$, $df = 64.9$, $P < 0.001$). The mean PC-2 scores being higher for capture plots ($\bar{x} = 0.603 \pm 0.158$ SE) than for reference plots ($\bar{x} = -0.519 \pm 0.081$ SE) indicates higher abundance of foliage of *E. fruticosa*, *C. alba*, *L. involucrata*, and more foliage at 0.5–1.0 m in capture plots than reference plots.

DISCUSSION

WINTER DISTRIBUTION OF A WARBLER BREEDING IN EARLY-SUCCESSIONAL HABITAT

This study confirms that on Eleuthera Kirtland's Warblers use early-successional habitat, as expected for a species dependent on early-successional habitats on the breeding grounds. Habitat at these successional sites where we captured Kirtland's Warblers ranged from the youngest and shortest at Ocean Hole ($\bar{x}$ age = 6.0 years; $\bar{x}$ canopy = 1.2 m) across a continuum to the oldest and tallest at Wemyss Bight ($\bar{x}$ age = 18 years; $\bar{x}$ canopy

= 2.5 m) and DD Road ($\bar{x}$ age = 21 years; $\bar{x}$ canopy = 1.8 m). This variation encompasses the range of structural variation in Kirtland's Warblers' wintering sites previously described from the archipelago, at least for broadleaf vegetation. For example, Maynard (1896) described the habitat on New Providence as "old fields grown up in low shrubbery" reaching "3 to 4 feet in height." Similarly, Mayfield (1972) described the winter habitat as broad-leaved scrub, especially on cleared sites where it was allowed to grow back before reaching maximum height and density. He emphasized that no one had reported Kirtland's Warblers from tall coppice or scrub with trees ≥ 4.6 m. Others concurred with these descriptions and added that wintering Kirtland's Warblers use upland habitats with a low scrub/shrub component but not tall coppice (Rada-baugh 1974, Sykes and Clench 1998). Even where Kirtland's Warblers were found in pines (Lee et al. 1997), the understories of broadleaf shrubs were characterized as open and short (0.5–2.0 m). Our findings further refine these descriptions: the average density of foliage in our capture plots was not only greatest at 0.5 to 1.0 m, but foliage density at this height was also statistically invariant among capture plots in our seven study sites despite significant heterogeneity among the sites for all other foliage-height classes below 3 m.

All plots on which Kirtland's Warblers were captured were at sites disturbed 3 to 28 years earlier. Of the few winter sites whose ages have been reported, descriptions indicate that the sites had been recently disturbed (e.g., Maynard 1896, Mayfield 1972). Similarly, Lee et al. (1997) and Haney et al. (1998) concluded that wintering Kirtland's Warblers use early-stage disturbed landscapes, but they argued that the fire-dependent subclimax pine forest provides the only consistent open broadleaf habitat of low stature used by the warbler. Although the six sites where Lee et al. (1997) found Kirtland's Warblers were in open-canopy pine forests with different and unspecified fire histories, their descriptions of low open shrubby understories suggest recent burning. While some winter habitat of Kirtland's Warbler described as shrub/scrub or low coppice could be mature (Byrne 1980, Correll 1979), we suspect that most were in the early to middle successional stages. Thus, there is a need for future observers to estimate the ages of sites where they encounter wintering Kirtland's Warblers.

In some respects the early-successional habitats used by the warbler on the breeding and wintering grounds are similar. For example, in both locations the habitats are situated on highly porous, well-drained, nutrient-poor soils where drought is frequent and consequently many plants show xerophytic adaptations. In both places, the flat to gently rolling topography with associated edaphic and microclimatic differences contributes to variation in rates of plant growth and succession after disturbance (Byrne 1980, Kashian et al. 2003). Differences in succession rates, varying across the Michigan landscape, contribute to variation in the age of colonization and the number of years Kirtland's Warblers occupy a site (Probst

1988, Probst and Weinrich 1993, Kashian et al. 2003). We believe that age at colonization and number of years a winter site is occupied will also vary with factors affecting succession rates in the archipelago, as shown by marked differences in succession rates on whitelands, blacklands, or flatlands (Byrne 1980). Also similar are the span of post-disturbance ages of sites the warbler occupies, which range from 5 to 23 years in Michigan (Walkinshaw 1983, Probst 1988, Probst and Weinrich 1993) and 3 to 28 years on Eleuthera.

Ground cover varies with succession (this study; Guariguata and Ostertag 2001) and among Kirtland's Warbler sites on both the wintering and breeding grounds where, on the latter, fire, shade history, and microclimate contribute to the variation (Probst and Donnerwright 2003). Probst and Donnerwright (2003) attributed the warbler's use of a range of variation in ground cover on breeding territories to its opportunistic ground-foraging behavior, which Fussman (1987) showed includes gleaning arthropods from a diversity of ground covers while perched on various substrates. Similarly on Eleuthera, Kirtland's Warblers foraging on the ground picked arthropods from leaf litter, bare soil, rocks, woody debris, stems, trunks, and leaves of shrubs and grasses (Wunderle et al., unpubl.data). This opportunistic gleaning from various substrates on the ground is likely important given that a high proportion of the warbler's winter gleaning maneuvers are made on the ground (69% of 155 maneuvers foraging for arthropods; Wunderle et al., unpubl. data).

DISTURBANCE AND EARLY-SUCCESSIONAL HABITATS

The abundance of early-successional scrub on Eleuthera is attributable, in part, to anthropogenic disturbance. Byrne (1980) suggested that the islands of The Bahamas not covered in pine were covered in hardwood forests prior to colonization, but that by the late 1800s much of the timber had been removed. Deforestation throughout the archipelago was followed by a series of agricultural failures, resulting in a mosaic of abandoned fields grown to scrub (Byrne 1980). This is the pattern on Eleuthera, which by Bahamian standards has relatively good soils, and consequently this island became one of the most disturbed in The Bahamas (Mooney 1905, Young 1966). Thus it is not surprising that all capture sites showed evidence of anthropogenic disturbance, as did our reference sites, even the older tall-coppice sites where remains of rock walls persist.

Anthropogenic disturbance in the archipelago may also be complemented by hurricanes. In pre-settlement times (i.e., >1000 ago; Kjellmark 1996) hurricanes likely were a dominant factor in producing Kirtland's Warbler habitat on non-pine islands and complemented disturbance by natural fires on the pine islands (Lee et al. 1987, Haney et al. 1998, Wunderle et al. 2007). The archipelago is especially prone to hurricanes (Shaklee 1996): from 1886 to 1992, 55 hurricanes passed within 139 km of Eleuthera, indicating hurricane

influences approximately every 2 years (Rappaport and Sheets 1993). Hurricanes this frequent are sufficient to determine the structure and composition of biotic communities (Wadsworth and Englerth 1959, Odum 1970, Walker et al. 1991). Given the importance of hurricanes in the region's disturbance regime, it is likely that such storms contribute to the availability of Kirtland's Warbler habitat in several ways (Wunderle et al. 2007). For instance, storm damage to the canopy of tall coppice can stimulate the fruiting of understory shrubs provided with more light in the storm's aftermath (Levey 1988); accumulated debris can increase the likelihood of fires after a hurricane (Furley and Newey 1979, Whigham et al. 1991). Storm surges in low-lying areas can inundate extensive areas (Sealey 2006), which may be colonized by early-successional plants, some used by Kirtland's Warblers.

FRUIT AND FRUITING PLANTS AS A FUNCTION OF DISTURBANCE

We attribute much of Kirtland's Warbler's use of early-successional habitats to its consumption of fruit, which is often abundant in these habitats and has been previously noted in the warbler's diet at various sites (Chapman 1908, Sykes 1989, Lee et al. 1997, Sykes and Clench 1998). Consistent with these observations was our finding that 69% of all food items were fruit. Given the importance of wild sage fruit in the Kirtland's Warbler's diet (36% of fruit identified to species) it was not surprising that 55% of the capture plots but only 25% of reference plots had wild sage foliage. In contrast to wild sage, we only rarely observed Kirtland's Warblers consuming fruit of the congeneric *Lantana bahamensis* (Wunderle et al., unpubl. data), despite its availability (foliage in 24% of reference plots). Consistent with the rarity of this fruit in the diet of the Kirtland's Warbler, we found no difference between capture and reference plots in the percentage of plots with *L. bahamensis* foliage, suggesting that the fruits of the two sages differ in suitability. In addition to wild sage, fruits of black torch and snowberry constituted an appreciable portion of the fruit consumed, and foliage of each species was found in a higher percentage of capture plots than of reference plots. Finally, the importance of these three plant species was demonstrated by the finding that 98% of the capture plots had foliage of at least one of the three principal fruit plants (vs. 61% of reference plots).

The post-disturbance ages of plots with at least one of the three principal fruit species consumed by Kirtland's Warbler spanned the 3-to-28-year range of the 153 capture sites, although the species differed in the periods during which they occurred in the successional gradient. For example, wild sage occurred in the youngest capture plots (3–22 years), as expected for an early pioneer species that requires disturbance for establishment on exposed soil and full sunlight to grow and reproduce (Francis 2004). Wild sage's ability to quickly colonize disturbed sites and set fruit undoubtedly explains the appearance of Kirtland's Warblers on sites such as Ocean Hole shortly after disturbance.

Although black torch also colonizes bare soils (Francis 2004), it may take several years to set fruit (Wunderle et al., unpubl. obs.). In contrast to these two species, snowberry persisted on older sites and consequently spanned the greatest period in the capture plots (6.5 to 28 years); it also occurred in tall-coppice plots. Despite snowberry's presence under the closed canopy of tall coppice we never observed it fruiting there, which is consistent with findings that, with succession, shrubs' fruit production declines in the shade of mature forest (Martin 1985, Levey 1988, Blake and Loiselle 1991).

Birds that rely on fruit often move widely as they track changes in fruit abundance, which varies in space and time (Martin and Karr 1986, Loiselle 1988, Levey 1988, Blake and Loiselle 1991). Kirtland's Warbler fits this pattern by declining in abundance at sites where fruit declines and increasing in abundance elsewhere when fruit increases (Wunderle et al., unpubl. data). Given that Kirtland's Warblers track winter fruit abundance by moving from site to site, it was not surprising that we found in mean foliage abundance per capture plot a statistical interaction between the principal fruit plant species and subset of the winter. These results are consistent with the warbler's responses to variation in fruit abundance of the three principal plants. For instance, snowberry produced fruit in early and mid winter but rarely in late winter, as also found by Acevedo-Rodriguez and Woodbury (1985). As expected for a lack of fruit in late winter, snowberry foliage was less abundant in plots in which birds were captured in late winter than in those in which they were captured earlier in the winter. Similarly, black torch foliage was lowest in plots where birds were captured in late winter, which also corresponded to a decrease in black torch fruiting (Wunderle et al., unpubl. data). In contrast, wild sage sets fruit throughout the year (Francis 2004), and we have seen it fruiting on at least one study site during every month of the winter, although not continuously at a site and rarely synchronously with other study sites. As a result, wild sage fruit is usually available somewhere on Eleuthera during the winter, likely contributing to our finding that abundance of wild sage foliage in capture plots did not vary through the winter. Therefore we interpret the statistical interaction of winter period and the abundance of foliage of Kirtland's Warbler's principal fruit plants in capture plots as an outcome of the warbler's movements in response to changes in fruit abundance due to differences among species in their phenology of fruiting.

EVIDENCE FOR SEXUAL SEGREGATION

We found no significant difference among study sites in sex ratios of warblers captured passively, although Ocean Hole had a suggestive ($P = 0.09$) male bias (71%). Thus, if there is sexual habitat segregation in wintering Kirtland's Warblers, it is more subtle than previously reported for other wintering warblers (e.g., Lynch et al. 1985, Lopez Ornat and Greenberg 1990, Wunderle 1992). Results of our passive netting suggest a slight but nonsignificant ($P = 0.09$), bias (59%) in captures.

While the tertiary sex ratio of the Kirtland's Warbler is unknown, our bias in captures is consistent with a bias toward males in post-breeding netting data (57% of 96 captures; $P = 0.11$), which suggests a male bias on the breeding grounds (Probst and Hayes 1987). Our sex-ratio findings provide no evidence for geographic segregation of the sexes. If there is sexual habitat segregation on the wintering grounds, it is likely subtle and requires future study.

CONSERVATION OF MIGRANTS RELIANT ON EARLY-SUCCESSIONAL HABITAT

Neotropical–nearctic migrants reliant on early-successional habitats on their tropical wintering grounds have not been a focus of conservation concern, partly because many of their populations have increased in recent years while species overwintering in mature forests have declined (Robbins et al. 1989). Although anthropogenic disturbances to the wintering grounds are presumed to have contributed to declines of some forest-dwelling migrants (e.g., Robbins et al. 1989), some disturbances, as we have found, benefit early-successional species such as the Kirtland's Warbler. Despite the benefits of some anthropogenic disturbances for wintering Kirtland's Warblers, we believe that concern for the conservation of the Kirtland's Warbler's winter habitat is warranted given the warbler's limited geographic distribution. Although Kirtland's Warbler has been found throughout the Bahamian archipelago, habitat continues to be lost to residential and commercial development, and much of the extensive pine habitat it formerly occupied has become unsuitable because of altered fire regimes (Haney et al. 1998). Moreover, if global warming continues, predicted rises in sea level (IPCC 2007) could exacerbate habitat loss on these low-lying islands, and expected increases in frequency of droughts (Neelin et al. 2006) could periodically diminish winter food resources, reducing habitat suitability on the drought-prone soils.

The reliance of wintering Kirtland's Warblers on early-successional habitats poses a challenge for conservation of the warbler's habitat, given the need for periodic disturbance to produce such habitat. In prehistoric times, when the islands were extensively forested, the frequency of natural disturbances such as hurricanes and fires was likely sufficient to produce quantities of disturbed habitat adequate for Kirtland's Warbler. More recently, agriculture has also contributed to the production of habitat. However, as agriculture continues to decline, and habitats are lost, less area is available to disturbances that produce Kirtland's Warbler habitat. Simply protecting parcels of land in which succession is allowed to run its course in the absence of disturbance will likely be insufficient to provide adequate winter habitat for the warbler in the future. Therefore, in the Bahamian archipelago as on the breeding grounds, management at a landscape scale will likely be required to sustain sufficient patches of early-successional habitat with the fruits appropriate for Kirtland's Warbler.

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APPENDIX

Because reference plots were measured during the dry season (7 March–1 May 2007), there was some leaf loss in the overstory tree *Bursera simaruba*. To determine the effect of this loss, we estimated the amount of foliage cover by assuming the presence of *B. simaruba* leaves in the foliage profiles of those reference plots in which *B. simaruba* was found (22% of 51 reference plots; none in tall-coppice plots). We assumed *B. simaruba* foliage to be present in a foliage-height category in the wet season if a branch occurred in a height category of the vertical profile. In 11 reference plots in which the species occurred, estimates of *B. simaruba* foliage increased foliage cover by a maximum of 10% in the 4–6-m height class, followed by 5.5% in the 3–4-m class, 4% in the 2.5–3-m class, and 2% or less in height classes below 2.5 m. No *B. simaruba* was found or estimated to occur above 6 m. A comparison of our estimates for missing *B. simaruba* foliage with the actual measures of foliage cover indicated no significant differences

in foliage density for any height classes (*t*-tests, $P > 0.48$). Mean canopy height, however, did increase (10% from 3.0 m to 3.3 m) significantly in the 11 reference plots in which foliage estimates were compared with the actual *B. simaruba* foliage present (paired *t*-test, $t = 3.705$, $df = 10$, $P = 0.005$). Therefore, because all reference plots and most capture plots were measured in March and April when *B. simaruba* had lost leaves, our reported values may underrepresent wet-season canopy heights and foliage cover in the higher height classes. Nonetheless, we believe the effect of leaf loss is minor given that *B. simaruba* was present in 22% of the reference plots and 30% of the 44 capture plots in which plants were identified. In addition, our depiction of the range in foliage cover from Ocean Hole (Fig. 2c) to Wemyss Bight (Fig. 2d) was unaffected by *B. simaruba* leaf loss, as this tree was absent from the former site and measured before leaf loss at the latter site.