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A QUANTITATIVE ANALYSIS OF MINTER DISTRIBUTION AND HABITATS OF KIRTLAND'S WARBLERS IN TAB BAHAMAS¹

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Abstract. We compiled and analyzed 101 accessible reports of 194 individual Kirtland's Warblers (*Dendroica kirtlandii*) from the Bahama Archipelago, 1841–1997. Most individuals were reported from northern islands (88%), and most sight reports (84%) and specimen/banding records (76%) were on island groups that support or formerly supported open woodlands of Caribbean pine (*Pinus caribaea*). Where habitat descriptions were provided, 60% mentioned specifically pines or pine understory. After analyses for potential biases from misidentification in sight reports and unequal effort across islands, we found no evidence to support previous claims that Kirtland's Warblers prefer scrub or avoid pine habitats. Rather, based upon 1995–1997 winter surveys using acoustic broadcasts, Kirtland's Warblers were detected in pine woodlands of Abaco and Grand Bahama more frequently than expected compared to encounter rates generated by a null model of random habitat use. Two periods of apparent decline of the Kirtland's Warbler this century, and a modest population increase on the breeding grounds since 1990, occurred contemporaneously with degradation and recovery, respectively, of the fire-dependent pine ecosystem in the northern Bahamas. We recommend a rigorous re-evaluation of conservation priorities now premised largely upon breeding-season limitation.

Key words: Bahama Islands, Caribbean pine, Dendroica kirtlandii, Kirtland's Warbler, Pinus caribaea, winter habitats.

INTRODUCTION

The striking feature of the endangered Kirtland's Warbler (*Dendroica kirtlandii*) is a restricted distribution on both its breeding and wintering grounds. Regarded as one of North America's scarcest songbirds, its rarity is usually attributed to scarce breeding habitat (fire-dependent jack pine *Pinus banksiana*) and excessive brood parasitism by the Brown-headed Cowbird *Molothrus ater* (Mayfield 1961, Walkinshaw 1972, Kelly and DeCapita 1982).

Although it winters across widely-dispersed islands of the Bahama Archipelago (Mayfield 1992), the Kirtland's Warbler has been extraordinarily difficult to find and study there (Radabaugh 1974, Sykes 1989). Winter habitat was believed to consist of low, sparse, regenerating vegetation (Mayfield 1992). The warbler was thought to avoid woodlands of Caribbean pine (*Pinus caribaea*) (Mayfield 1996), a vegetation type which possesses some of the structural characteristics of breeding habitat in Michigan (Radabaugh 1974).

Despite few successful searches (Mayfield 1972, Radabaugh 1974, Sykes 1989), the warbler's status outside the breeding season has

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been a topic of ample speculation. It was asserted that the winter habitats of the warbler have "... changed little over the last century" (Mayfield 1992), do "... not appear to be threatened by human activities" (Mayfield 1996), and "... do not appear to be a problem" (Sykes 1997). Management for this endangered species has been based largely on the belief that winter habitats were stable: "since ... the climate and vegetation there [Bahamas] have changed little in centuries, we see no cause for alarm there at present" (Mayfield 1988). Consequently, active management of Kirtland's Warbler has been directed solely towards the breeding grounds (Probst 1986, Kepler et al. 1996).

In this study we synthesize winter reports of the Kirtland's Warbler accumulated since 1841, and conduct the first quantitative evaluation of the species' habitat use and distribution during this season. We include recent unpublished reports, and analyze irregularly-collected data for biases that might influence apparent patterns of distribution and habitat use. We present results from recent surveys of Kirtland's Warblers that used acoustic broadcasts to elicit detection on its wintering grounds. Finally, we present evidence that variability in this species' population on the breeding grounds corresponded to periods of habitat alteration in the Bahamas. Our main objective was to test previous hypotheses that wintering Kirtland's Warblers depend upon transitional scrub habitats and avoid pine woodlands. Because winter and breeding season factors act to limit migratory bird populations (Böhning-Gaese et al. 1993, Rappole and McDonald 1994, Sherry and Holmes 1995), we discuss conservation of this warbler within the context of changes in land-use that occurred in the Bahama Islands since the beginning of this century.

METHODS

DATA SOURCES

We compiled all accessible reports (sightings, banding records, specimen records; n = 107) of Kirtland's Warblers available to us from outside the continental United States during the postbreeding season (5 August to 5 May; Appendix 1). A single report consisted of one or more individual warblers. In addition to winter surveys for this species (Challinor 1962, Mayfield 1972, Radabaugh 1974, Clench 1978, Sykes 1989), we consulted bibliographies (Huber 1982, D. Pash-

TABLE 1. Distribution of wintering Kirtland's Warblers from the Bahamas (islands and island groups possessing or formerly possessing pine woodland indicated by *). Records which give only a general location, such as "Bahama Islands," not included (four reports of six individuals).

Island	No. reports	(% of total)	No. indivi- duals	(% of total)
Northern island groups				
Bimini	3	(3%)	3	(2%)
Grand Bahama*	30	(30%)	59	(30%)
Abaco*	10	(10%)	11	(6%)
Berry Islands*	2	(2%)	4	(2%)
Andros*	6	(6%)	8	(4%)
New Providence*a	20	(20%)	64	(33%)
Eleuthera	10	(10%)	18	(9%)
Cat	3	(3%)	3	(2%)
Subtotal	84	(83%)	170	(88%)
Southern island groups				
Exuma	0	(0%)	0	(0%)
Long	0	(0%)	0	(0%)
Rum Cay	≥1	(1%)	≥1	(<1%)
San Salvador	3	(3%)	6	(3%)
Crooked	1	(1%)	1	(<1%)
Acklins	0	(0%)	0	(0%)
Mayaguana	0	(0%)	0	(0%)
Great Inagua	5	(5%)	6	(3%)
Little Inagua	0	(0%)	0	(0%)
Caicos Bank*b	7	(7%)	10	(5%)
Subtotal	≥17	(17%)	≥24	(12%)
Total	101	(194°	(== ///)

 ^a Including Paradise Island and Green Cay.
^b Pine woodland only on North Caicos, Middle Caicos, and Pine Cay.
^c Minimum figure reflecting known islands-of-occurrence only (one recomplete the second seco ord attributable to the "Bahamas" and another collected at sea not included; Appendix 1).

ley, pers. comm.), museum specimen records (Cory 1891, Ridgway 1891, Bangs 1900, Bonhote 1903), reports in Aububon Field-Notes and American Birds, and regional avifaunal surveys (Cory 1886, Grantz 1963, Hundley 1967, Buden 1987, 1990, 1992, Howe et al. 1989, Buden and Sprunt 1993, Norton 1993, Wunderle and Waide 1993). We also contacted ornithologists and other field researchers who frequented the Bahama wintering grounds for unpublished information.

Reports were then sorted by island or island group into two categories based upon the presence or absence of pine woodland (Table 1). In the Bahama Archipelago, woodland of Caribbean pine is currently confined to, or was formerly found on, Grand Bahama, Great and Little Abaco, Andros, New Providence, the Berry Islands, and North Caicos, Middle Caicos, and Pine Cay on the Turks and Caicos Bank (Coker 1905, Britton and Millspaugh 1962). Total island

Island	Human population size ^a	Human population density ^a	Reporting effort ^b	Distance to mainland (km)	Island area (km ²)
Bimini	1,638	70.3	14	161	23
Grand Bahama*	41,035	29.7	127	845	1,373
Abaco*	10,061	6.2	105	1,151	1,681
Berry Islands*	634	20.5	13	1,055	36
Andros*	8,755	1.6	85	918	5,957
New Providence*c	171,542	827.8	47	1,336	207
Eleuthera	10,524	20.5	21	1,650	518
Cat	1,678	4.2	2	2,004	389
Exuma	3,539	12.4	2	1,932	290
Long	3,107	5.4	3	2,318	596
Rum Cay	53	0.8	2	2,318	78
San Salvador	486	3.1	21	2,648	163
Crooked	423	1.9	8	2,673	181
Acklins	428	0.8	2	3,011	285
Mayaguana	308	1.2	1	2,882	285
Great Inagua	985	0.8	29	3,059	1,551
Little Inagua	0	0	0	3,180	127
Caicos Bank*d	12,400	24.7	274	3,341	500

TABLE 2. Independent variables used in regression models that evaluated which and how many factors might explain variability of total numbers of Kirtland's Warblers recorded across the Bahama Islands. Islands with pines indicated with asterisk.

Persons km-2; Sealey and Burrows 1982.

^b Numbers of rare or notworthy bird records reported by field workers by island, 1947–1990; see text.
^c Including Paradise Island and Green Cay.
^d Turks and Caicos Islands; pine woodland only on North Caicos, Middle Caicos, and Pine Cay.

area with and without pine (Sealey and Burrows 1982) was used to construct a model that compared observed to expected numbers of warblers in tests of frequencies. All individual warblers with specific winter localities (island) were used in these analyses.

DATA EVALUATION

To check for bias from potential misidentification and uncertain quality of sight reports, we conducted three exploratory analyses. Because an endemic, highly-distinctive race of Yellowthroated Warbler (Dendroica dominica flavescens) is thought to be often confused with Kirtland's Warbler (Mayfield 1996, White 1996), we deleted all sight reports (n = 65) from the two islands where these two species co-occur (Grand Bahama and Abaco). We then ran a separate analysis of warbler frequencies in remaining islands/island groups based upon presence or absence of pine. We used a contingency chi-square test to examine whether sight reports were biased relative to specimen and banding records in ascribing birds to pine and nonpine islands. Finally, we conducted a test for frequency of Kirtland's Warblers on pine versus nonpine islands using only specimen and banding records.

As no systematic, archipelago-wide searches

for the Kirtland's Warbler have been attempted during winter, unequal effort could skew patterns of island and habitat use. We used regression models to explore whether total numbers of wintering warblers might be linked to effort. Because visitors are likely to depend upon infrastructure such as roads, lodging facilities, and transportation centers, we used island-specific total human population and population density (Table 2) as two proxies for effort. We also used a third proxy, reporting effort, based upon the number of entries that highlighted bird species that were rare, unusual, or otherwise of special interest from individual islands in the Bahamas (boldfaced entries in Audubon Field-Notes and American Birds, 1947-1990).

Prior to constructing regression models, we checked whether the variance of the enumerated dependent variable (y; total warbler numbers) could be stabilized (Snedecor and Cochran 1980). Of transformations attempted $(\ln[y],$ $\log_{10}[y], \ln[y + 1], \log_{10}[y + 1], y^{0.5}, [y + 1]^{0.5}),$ the best was $(y + 1)^{0.5}$, with the CV on y reduced from 177.2 to 77.7. Using the least-squares MGLH program in SYSTAT (Wilkinson 1989), the dependent variable was then regressed individually on the three independent variables (x)described above plus two geographic variables:

island area and distance of each island from the mainland of the southeastern United States. Distance from the U.S. mainland was measured along a standardized vector of 138° from eastern Florida.

To check whether all variables were needed in a model to predict total warbler numbers, we used the forward selection, stepwise regression option in the MGLH routine of SYSTAT (Wilkinson 1989) to identify a potential subset of predictors (Dowdy and Wearden 1991). Alphato-enter and alpha-to-remove a variable were set at 0.15. Three predictors were chosen: human population ($r^2 = 0.61$), human population density ($r^2 = 0.85$), and island distance ($r^2 = 0.89$). A two-variable regression model was ultimately built with these predictors because the variable human population density was redundant with the variable human population.

Discrepancies between estimated and observed values in regression models were used to identify potential biases in effort for individual islands. Because Freeport, Grand Bahama, and Nassau, New Providence, serve as major transportation centers or final destinations for many visitors, we hypothesized that more warbler reports than expected might occur on these two islands. Diagnostics from individual islands were examined for both the multivariate model and those univariate regression models based upon effort (human population size, human population density, reporting effort).

Diagnostics included leverage statistics for detection of outliers and normal distributions in the independent variables, and Studentized residuals for detection of outliers in the dependent variables (warbler numbers). Because tests of inference using Studentized residuals were directional, we used one-tailed t-tests with n-m degrees of freedom (n = total sample size; m =number of predictors in regression model, including the constant). We also used Cook's F to examine regression coefficients (Velleman and Welsch 1981, Wilkinson 1989). The Cook test statistic has m, n-m degrees of freedom and combines leverage and Studentized residuals to examine any influence of separate observations on estimates of the regression coefficients.

TRANSECT SURVEYS

Because acoustic broadcasts increase search efficiency compared to visual survey techniques (Wunderle 1992, Graves 1996), we used recorded songs and calls of Kirtland's Warblers in attempts to elicit observations during winter in pine habitats on Grand Bahama and Abaco. Visual surveys were conducted 25 and 27 November 1995 on Grand Bahama, and 1–5 December 1995 on Abaco; acoustic and visual surveys were conducted on 14–18 December 1996 on Abaco, and 9–13 February 1997 on Grand Bahama for a total of 18 survey-days. Surveyors generally worked in parties of two; two parties were deployed on some days.

While broadcasting calls and songs intermittently from amplified recordings in all directions, we walked slowly along roads or trails, stopping frequently about every 25–50 m, and waiting up to 10–20 min to see whether any warblers responded. The open character of Bahamian pine woodland (Emlen 1977) allowed broadcasts to penetrate far laterally along the survey route; acoustic broadcasts were audible to us at least 100 m away. No surveys were attempted during strong winds or rain. Surveys were conducted in the morning and generally completed within 4 hr.

After a warbler responded, the location was marked with flagging. Total distance surveyed was then measured directly with an automobile odometer, or pacing calibrated by an odometer. After a warbler was detected, surveys were moved to locations several km away to insure independence. The product of transect length and width gave the continuous area surveyed for a single warbler encounter. We used 150 m as the effective transect width, the corridor within which wintering warblers respond to acoustic broadcasting (Graves 1996).

To examine whether Kirtland's Warblers occurred in pine habitats more than expected by chance, we constructed a binomial model to test the null hypothesis of nonpreferential or random use of this habitat. The probability of finding a warbler (\hat{p}) can be expressed as the product of the area censused (A) and expected density of wintering warblers (B). Because this is one of very few bird species for which essentially complete censuses exist for the entire breeding population, we estimated expected densities (B) for each of the two winter seasons by dividing the postbreeding size of the population by the area of the entire Bahama archipelago (14,600 km²; Sealey and Burrows 1982).

Total postbreeding population sizes were estimated as 3,185 and 2,904 individuals for the 1995–1996 and 1996–1997 winters, respectively. These figures were obtained by adding the number of females (based on 85% pairing success; Probst and Hayes 1987) and young of the year (2.76 fledged young pair⁻¹; Kelly and DeCapita 1982) to the annual census of singing males (759 and 692 for 1995 and 1996, respectively).

We assumed that all warblers in the breeding population arrived and wintered only in the Bahamas (without mortality). This procedure inflates the true number of warblers that reach and survive on the islands, leading to increased risk of Type II error in subsequent analyses. We were most concerned, however, with making a false conclusion that Kirtland's Warblers used pine habitat more than expected (Type I error). Thus, estimated probabilities (\hat{p}) are best viewed as upper bounds on the likelihood of encountering a warbler during a winter survey. Under these assumptions, maximum expected density (*B*) of warblers for the two winter seasons was 0.20 and 0.22 warblers km⁻², respectively.

Each individual survey was then used to estimate the likelihood of encountering a single warbler. Each survey was considered as a binomial trial with the cumulative probability of the outcome of multiple surveys (P) equal to the product of individual surveys that were either successful (\hat{p}) or unsuccessful (\hat{q}) in detecting a warbler. Statistical tests were considered significant at P < 0.05 unless otherwise indicated; values listed are means \pm standard error.

RESULTS

DISTRIBUTION AND HABITATS

Only 3 of 107 winter reports originated from outside the Bahama Archipelago (2 sightings from the northern Dominican Republic, 1 sighting from coastal Mexico). Of 104 Bahama reports, 3 could not be linked to a specific island or island group. Most Bahama winter reports were from northern (88%), pine-dominated islands (74%; Table 1). Kirtland's Warblers occurred on each of the pine island groups in the northern archipelago: Grand Bahama, Abaco, Berry Islands, Andros, and New Providence. Reports from each of these five island/island groups included specimen or banding records. Kirtland's Warblers were recorded from the only other part of the archipelago with pine, the Turks and Caicos, including those islands that are pinedominated (specimen records from Middle Caicos; sight reports from Middle Caicos and Pine Cay: Sanderson 1982).

Most individuals (75%; n = 194) also were from northern islands that support(ed) Caribbean pine (Table 1). Between 1841 and 1915, 78% of all specimen records (n = 81 individuals linked to specific islands) were obtained from pinedominated islands. More individual Kirtland's Warblers occurred on pine-dominated islands than expected ($\chi^{2}_{1} = 14.6$, P < 0.001). Conversely, several of the larger islands where pines are absent accounted for very few reports (Table 1 and 2).

Although association with pine-dominated islands by itself does not indicate that warblers use this vegetation, Hundley (1967) remarked of the Grand Bahama reports in the late 1950s and 1960s: "almost all birds were seen in areas of Caribbean pine (*Pinus caribaea*) with an understory of poison wood (*Metopium toxiferum*) and palmetto (*Serenoa repens*)." Only 2 of 52 reports came from the western end of this island where pine was absent. Although a few warblers have been observed in xeric scrub habitats in the southern part of the Bahama Archipelago, where habitat descriptions for birds were provided (67 reports throughout the archipelago), 60% were in pines or pine understory (Appendix 1).

ANALYSES FOR IDENTIFICATION BIAS

Despite reduced sample size from deleting all sight reports from Grand Bahama and Abaco, the remaining reports of individual Kirtland's Warblers exhibited a significant association with the remaining pine-dominated islands ($\chi^{2}_{1} = 7.3$, P < 0.01). Therefore, this analysis provided no evidence that misidentified *D. d. flavescens* accounted for the association with pine-dominated islands.

Similarly, we found no evidence that sight reports (n = 88 and 17 on pine and nonpine islands, respectively) were biased relative to the proportions of specimen/banding records across pine (n = 68) and nonpine islands (n = 21; contingency χ^{2}_{1} with continuity correction = 1.2, P = 0.27). Moreover, the warbler's affinity for pine-dominated islands was marginally significant when we analyzed the smaller sample consisting solely of specimen and banding records ($\chi^{2}_{1} = 3.2, P = 0.07$).

Independent variable (x)	y intercept (a) \pm SE	Slope (b)	r ²	Pb
Human population	2.13 ± 0.35	0.00004	0.61	< 0.001
Human pop. density	2.33 ± 0.41	0.0027	0.42	< 0.01
Reporting effort	2.16 ± 0.54	0.014	0.20	0.06
Distance from mainland	4.79 ± 1.12	-0.0016	0.20	0.06
Island area	$2.54~\pm~0.59$	0.00066	0.03	0.51

TABLE 3. Univariate regression models (y = a + bx) used to evaluate variability in total numbers of Kirtland's Warblers^a reported among 18 individual islands or island groups in the Bahama Archipelago, 1841–1997.

^a Dependent variable $(y + 1)^{0.5}$, where y = total warbler numbers. ^b Observed significance levels for H_o that b = 0.

WARBLER NUMBERS AND EFFORT

Transformed total warbler numbers were significantly correlated with two proxies for effort: human population and human population density (Table 3). Transformed warbler numbers were correlated marginally with reporting effort and distance of island from the U.S. mainland (both P = 0.06; Table 3).

A two-variable regression model explained 67% of the variability in transformed warbler numbers across islands (Table 4). Large tolerances (> 0.92) indicated that the two predictor variables were not intercorrelated (Wilkinson 1989). Human population size explained 61% of the variability in transformed total warbler numbers among islands (adjusted multiple $r^2 = 0.58$, $F_{1.16} = 24.8, P < 0.001$). Transformed warbler numbers declined with increasing distance southeastward through the Bahama Archipelago, although the amount of variability explained by this predictor was low (20%; adjusted multiple $r^2 = 0.15$, $F_{1.16} = 4.0$, P = 0.06). New Providence had an especially large influence on the calculation of the regression coefficients in this model (Cook's distance, $F_{3,15} = 70.7$, P < 0.01).

Univariate models based on human population and human population density identified Grand Bahama as having a disproportionately large number of the total warbler reports (Studentized residuals, one-tailed $t_{16} = 4.33$ and 5.15, respectively; both P < 0.001). The model for reporting effort also implicated this island $(t_{15} = 2.42, P < 0.03)$. Grand Bahama had more warblers than expected in the two-variable regression model as well ($t_{15} = 3.88, P < 0.005$).

Results for New Providence were inconsistent. Contrary to expectations, the two-variable regression model gave fewer warblers than expected $(t_{15} = -6.12, P < 0.001)$, similar to the univariate model for human population $(t_{16} =$ -6.87, P < 0.001). The model for human population density did not implicate New Providence as having either more or fewer warblers than expected ($t_{16} = -1.06$, P > 0.10), and the reporting effort model actually flagged this island as having more warblers than predicted (t_{16}) = 3.69, P < 0.005). The only other island/island group identified as having disproportionate numbers of warblers was the Caicos Bank, with the model for reporting effort implicating this island group as having fewer reports than expected (t_{16}) = -3.05, P < 0.005).

TRANSECT SURVEYS

We detected four Kirtland's Warblers with, and two without, using tape broadcasts. In contrast to some other studies of wintering parulids (Graves 1996), none of the birds that were visually confirmed responded to acoustic broadcasts with vocalizations of their own. Broadcasts did elicit vocal responses from three birds having chip notes identical to Kirtland's Warblers;

TABLE 4. Parameters for two-variable multiple regression model used to evaluate variability in total numbers of Kirtland's Warblers^a reported among 18 individual islands or island groups in the Bahama Archipelago, 1841-1997.

Independent variable (x)	Parameter coefficient ± SE	
Constant Human population (x_1) Distance from mainland (x_2)	$\begin{array}{r} 3.37 \pm 0.80 \\ 0.00004 \pm 0.00001 \\ -0.00094 \pm 0.00056 \end{array}$	4.19** ^b 4.61* -1.69

^a Dependent variable $(y + 1)^{0.5}$, where y = total warbler numbers. ^b Observed significance levels; * P < 0.001, ** P < 0.001.

TABLE 5. Test for nonpreferential use of winter habitat by Kirtland's Warblers in the Bahamas. Outcomes reflect statistical likelihood of finding the numbers actually observed in pine habitat on Grand Bahama and Abaco under an assumption of random habitat use.

Island/Year ^a	No. birds	Transect length (km)	Area censused (km ²) ^b	Probability of outcome, \hat{p} or \hat{q}^{c}	Cumulative probability, <i>P</i> ^d
GB-95	1	3.00	0.45	0.10	0.10
AB-95	1	5.00	0.75	0.16	0.02
AB-96-1	1	3.80	0.57	0.11	0.002
AB-96-2	1	10.00	1.50	0.30	< 0.001
GB-97-1	1	7.65	1.15	0.23	< 0.001
GB-97-2	1	8.74	1.31	0.26	< 0.001
GB-97-3	0	6.89	1.03	0.79	< 0.001

^a GB = Grand Bahama; AB = Abaco. Dates, locations, and other details

traction by wintering warblers to acoustic playback: Graves 1996). ^c Under null hypothesis of nonpreferential or random habitat use, proba-

bility of each outcome (\hat{p}) equals the product of area censused and expected density of wintering warblers (see text). In one case where censusing effort failed to detect a Kirtland's Warbler (GB-97-3), probability of outcome (\hat{q})

is equal to $1 - \beta$. ^d Cumulative probability (P) of binomial outcomes in this sequential series of independent trials

these birds were not seen, however, and are not included in any of the analyses or compilations reported here. Most visual detections were brief and easily overlooked as birds returned quickly to dense cover. Some responses appeared to be delayed as one bird was observed after retracing our survey route. All six warblers were observed in pine woodland, but understories at each site differed somewhat in fire history and height of vegetation (Lee et al. 1997).

Given the level of our survey effort and expected densities, the probability of encountering even one Kirtland's Warbler was less than 30% (Table 5). All warblers were encountered on surveys that ranged from 3 to 10 km in length. We failed to find a warbler during one 6.9-km survey on Grand Bahama. Under the assumption that warblers are randomly distributed on islands and exhibit no habitat preferences, and based upon both successful and unsuccessful surveys, the cumulative probability of finding all six warblers was < 3 in 100,000 (binomial test for independent trials; Table 5).

DISCUSSION

HABITAT USE

Contrary to previous claims (Mayfield 1983, Sykes 1997), we found no evidence that Kirtland's Warblers prefer scrub habitats or avoid pine woodlands on their Bahamian wintering grounds. All analyses implicated pine habitat or

pine-dominated islands as having the majority of winter reports. Although individual or collective quality of sightings can be questioned, it is not obvious why visual misidentification of Kirtland's Warblers should be limited to, or more likely in, any one habitat. In any case, the majority of specimen records were certainly obtained from pine-dominated islands.

Previous attempts to describe winter habitat use of Kirtland's Warblers either lacked quantitative analyses entirely (e.g., Mayfield 1972, 1996), or they relied upon extremely small sample sizes (Radabaugh 1974, Sykes 1989). Despite lack of quantitative evidence, subjective assessment of distribution and habitat greatly influenced the direction of winter research on this endangered species. For example, additional searches for appropriate winter habitat were based upon an unfounded assumption that Kirtland's Warblers depend upon transient, early successional habitats (Miller and Conroy 1990). During the winter surveys conducted by the U.S. Fish and Wildlife Service in 1985 and 1986, northern islands were largely by-passed because it was mistakenly assumed that pine habitat was not used (M. DeCapita and C. Faanes, pers. comm.).

Variable observer effort seems to have influenced the relative allocation of records and reports across islands (Table 3 and 4). In particular, Grand Bahama had a large number of warbler reports. On the other hand, other pine-dominated islands did not have more warbler reports than expected based upon the regression models. Furthermore, some relatively well-traveled (but pine-free) islands have conspicuously few reports of Kirtland's Warbler. San Salvador is frequently visited by naturalists due to its marine research station, yet this island accounted for only three reports. As Miller (1978) noted, "... in our hundreds of man-hours in the field we have never seen the bird though always watchful for it." Similarly, Inagua has been visited often by workers involved with the endangered Bahama Parrot (Amazona leucocephala bahamensis) but has only four reports. Mayr (1953) reported no Kirtland's Warblers from Bimini despite a diligent search there.

Systematic transects using acoustic broadcasts gave the strongest evidence that Kirtland's Warblers use pine habitats more than expected. We could not reconcile numbers actually observed with the numbers expected if estimates of breeding population sizes were accurate and wintering birds are truly distributed randomly (Table 5). Several factors made this analysis conservative: (1) high expected densities due to an assumption of no postbreeding mortality, (2) use of an effective survey width of 150 m, even though 120 m is the probable limit for visual detection in this habitat (Emlen 1971), (3) an assumption that all birds within auditory range respond, and (4) an assumption that human observers detected all responding birds. Nevertheless, habitat selection and geographic distribution are hard to distinguish because the warbler's apparent preference for pine woodland could be incidental to aggregation in the northern archipelago. After their autumnal flights over water, migrants may stop on the first islands encountered, islands which happen to be pine dominated (see analysis of "Distance from mainland;" Table 3). Whatever the proximate cause for occurrence in this habitat, however, management considerations are the same (see below).

Kirtland's Warblers thus use at least two major Bahamian habitat types (Appendix 1). Because low broad-leaved scrub is widespread throughout the Bahama Archipelago (Mayfield 1972), Kirtland's Warblers might be expected to use it occasionally. The warbler may occupy regenerating scrub merely because other habitats were (and to some extent still are) degraded. A concentrating effect could explain why large numbers of Kirtland's Warblers were reported from the 1950s and 1960s in remnant pine woodlands (Appendix 1). Habitat limitation is significant to wintering Neotropical migrants because sex- and age-related segregation (Greenberg 1986) may result from defending optimal sites from conspecifics (Holmes et al. 1989, Sliwa and Sherry 1992), and subordinate "floaters" may fill optimal winter territories only when vacated (Rappole and Warner 1980, Marra et al. 1993).

The hypothesis that this warbler prefers scrub habitat is weakened further by that vegetation's recent expansion, transitory nature, and anthropogenic origin. Bahamian scrub displays inherently "weedy" habits, including rapid succession and consolidation between plants (Byrne 1980). Byrne considered scrub to be a direct result of agricultural failures such as small-scale cotton farming in the 1700s, large-scale cotton growing from the late 1700s through 1860s, a short-lived, extensive sisal industry (1887– 1896), and unsuccessful growing of bowstring hemp (1887–1940).

Given Byrne's assessment, it is difficult to conceive how the Kirtland's Warbler could have evolved specific preferences for a vegetation type that became more extensive and persistent only in historical times. Anthropogenic disturbance did not play a role during the warbler's speciation because humans did not occupy the Bahamas until about 1,000 years BP (when the Arawak or Lucaya arrived; Byrne 1980, Kjellmark 1996). By 500 years BP, the indigenous population had been relocated and settlement on the Bahamas languished for the next 200 years. Other mechanisms would have had to produce and maintain habitats at geological time scales if the warbler evolved specific preferences for vegetation types.

COEVOLUTION WITH PINE WOODLAND?

As Radabaugh (1974) remarked, "... [winter] habitat had somewhat the same configuration as do the jack pine (*P. banksiana*) areas on a typical, optimum breeding territory." Several structural and functional characteristics are shared between the Kirtland's Warbler's winter and breeding habitats: highly-porous geology, some bare or open ground, several vertical layers of vegetation, a forest type dominated by pine, and an ecosystem type maintained by recurring fire.

All responses to our acoustic broadcasts were in open pine forest that had recently experienced low-intensity fire (Lee et al. 1997). Spacing in this vegetation type persists (Hawkes and Menges 1996) between burn intervals that average 2-5 years (J. Segar, pers. comm.). Whereas optimum breeding habitat is created by intense, catastrophic fire, physiognomy of Bahamian pine woodland would have been maintained historically primarily by summer, lightning-induced fires (Byrne 1980, Perry 1991). New growth and a flush of insect and/or fruit would follow summer precipitation after these fires and prior to the warblers' autumn arrival. Pine overstory and a herb-shrub understory also may provide visual clues similar to those on breeding grounds. Throughout the year, structural clues are known to influence precise choice of microhabitats exploited by wood warblers (Emlen and DeJong 1981, Parrish 1995a, 1995b).

That the Bahamas have always been the wintering ground of the Kirtland's Warbler is suggested by two lines of evidence. First, in the

West Indies open pine woodlands are found at sea level primarily in the Bahamas (Mirov 1967, Perry 1991); pine forest elsewhere occurs at high elevations where fire would have been less frequent due to moister conditions. Second, paleogeography suggests that during the Pleistocene Kirtland's Warblers were short-distance migrants that bred closer to the Bahamas in the nearby coastal plain of the southeastern United States (Mayfield 1988, Williams and Webb 1996). Extensive jack pine forest gradually migrated north and west within the 10,000 years following Wisconsin glaciation (Mengel 1964). Pine forests have been present on the northern Bahamas since at least the late Pleistocene because the fossil record contains several extant bird taxa that essentially are confined to pines (Brodkorb 1959, Olson and Hilgartner 1982, Lee et al. 1997). Over time the warbler came to exploit two fire-dependent pine ecosystems that became increasingly disjunct as changes in continental climate altered landscapes between the Bahamas and their current breeding grounds.

DISTURBANCE OF THE BAHAMIAN PINE ECOSYSTEM

Despite repeated claims that interior habitats on these islands were never altered appreciably (Mayfield 1983, 1988, 1992, 1996), major changes in Bahamian land use have taken place. Moreover, these changes occurred while Kirtland's Warblers became scarce on both their breeding and wintering grounds. For the archipelago at large, Byrne (1980:157) concluded that:

... the evidence recovered clearly shows that the Bahamas have not escaped the processes of change that have affected nearly all tropical islands during the period of human settlement. In the comparatively short period of a thousand years [indigenous Arawak occupation extended only from 1,000–500 years BP], the Cat Island woodland has been drastically disturbed. ..As a result of clearing, burning, selective cutting, grazing, and browsing, sensitive [plant] species have become rare, and have survived as important members of the woodland only in remote, relatively undisturbed areas.

The original, native pine forest did not escape alteration (Nickrent et al. 1988). Primary forest of Caribbean pine once achieved a maximum height of 30 m with some trees as large as 0.75-1.5 m in diameter (Britton and Millspaugh 1962, Campbell 1978). Large-scale anthropogenic disturbance of the pine ecosystem began in the Bahamas in the 1890s when the Kirtland's Warbler was still readily found on its wintering grounds (Appendix 1). At this time, Coker (1905) described the wood of the Caribbean pine as having little commercial value due to its "rapid decay." Prior to this period, turpentine and resin were extracted, but this localized industry (which required living trees) was no longer active in the Bahamas by the turn of the century (Coker 1905). Pines were present on the Berry Islands until at least 1891 when Kirtland's Warblers were originally reported from this island group (Cory 1891, Gardiner and Brace 1889), but pine woodland was logged completely by the early 20th century (Campbell 1978).

Large-scale commercial exploitation of the pine ecosystem started in 1905 with logging of primary forest near Wilson City on Abaco (Campbell 1978). This operation ran for 20 years. Little is known about impacts from lumbering during this period, but by 1943 nearly all original forest had been cut, forcing the industry to then turn to immature trees and short rotations for pulp (Campbell 1978). This initial period of ecosystem manipulation (ca. 1900–1920) occurred during the same time that Kirtland's Warblers apparently declined on their breeding grounds (Mayfield 1960).

A second era of exploitation ran from the 1950s through the early 1970s (Radabaugh 1974). Small pulpwood operations were carried out on Grand Bahama from about 1948 to 1955. From 1956–1959, larger operations were established on Grand Bahama (Henry 1974). Lumbering removed 53,000 ha of pineland from this 111,000-ha island. This was most of the pine ecosystem as part of this island is covered in mangrove or other vegetation, and pine woodland was always absent from the island's western end. Lumbering also occurred on Abaco where it continued there until 1970. On Andros, lumbering started in 1968 and apparently ceased by 1973 (Radabaugh 1974).

These operations severely degraded the original ecosystem. Radabaugh (1974) commented that the "...most significant environmental alteration I observed—and probably the most significant single change ever to occur in the Bahamas—was the lumbering of the Caribbean pines." C. R. Mason reported that where once there was unbroken pine woodland "most of the land is cut over, burned over, much of it being planted in cane" (*Audubon Field-Notes* 22:30). King et al. (1979) described how except for a small 1,620-ha tract on Little Abaco and a smaller area at the southern end of Great Abaco, all pines had been removed by 1976–1977. Radabaugh (1974) estimated that 200 km² of Abaco was completely treeless. One 17,820-ha tract of logged-over land was planted in sugar cane (Snyder et al. 1982), an area equivalent to 11% of Great and Little Abaco combined.

Subsequent regeneration of pine was uneven at best, poor to nonexistent at worst. Snyder et al. (1982) noted that hurricanes on Abaco leveled most residual seed trees and damaged others sufficiently that they were later lost to insect outbreaks. Moreover, the large amounts of slash produced intense and extensive fires. Radabaugh (1974:380) observed unattended fires burning for days on Grand Bahama and Andros, noting that:

pulpwood operations at least temporarily remove, and sometimes completely destroy, the Caribbean pine ecosystem over vast areas ... to the extent that the Kirtland's Warbler, as a species, relies on pinelands in winter, lumbering could well have been detrimental to the point of having contributed to the recent decline in numbers.

This later period of ecosystem manipulation (1956–1973) encompasses the precipitous 60% decline in warblers observed between the 1961 and 1971 breeding censuses.

CONSERVATION IMPLICATIONS

Because breeding or wintering season conditions can simultaneously influence bird populations (Sherry and Holmes 1995), factors during either or each period could conceivably limit recovery. Rappole and McDonald (1994) list predictions that might identify whether winter factors are important for Neotropical migrants. One such prediction is that breeding habitat of Kirtland's Warbler should appear filled if it is breeding] tracts that appear promising are not occupied" (Mayfield 1992). Failure to occupy even all optimal habitat (Nelson and Buech 1996) weakens support for strict breeding season limitation. Furthermore, at some 21,760 km² (Mayfield 1960), the breeding range is roughly 35% larger than the area of the entire Bahama archipelago, and 10 times larger than the area of pine wood-land (1,920–2,042 km²; Allan 1986, N. Sealey, pers. comm.). Thus, a more geographically-contracted winter range could be even less able than the breeding grounds to absorb extensive habitat modification.

Cowbird control on the breeding grounds, although arresting the warbler's decline and raising productivity (Robinson et al. 1995), failed to initiate an immediate increase in the population (James and McCulloch 1995). In general, strong inferences about population trends of Neotropical migrants are made difficult from confounding events on both breeding and wintering grounds (Latta and Baltz 1997). We extend this caution specifically to the Kirtland's Warbler, and emphasize that potential causes impacting populations on the wintering grounds also were coincident in time with the warbler's general decline. The initial decline is attributed usually to reduction in breeding range after a particularly large fire had earlier created extensive habitat (ca. 500,000 ha) in 1871 (Mayfield 1993). But this decline also corresponds to land-use changes in the Bahamas, including commercialscale logging. Notably, Maynard seemed to have had little difficulty in collecting the warbler in the Bahamas as late as 1915 (Appendix 1), long after (44 years) the extensive breeding habitat noted above would have lost its suitability (6-25 years postfire: DeGraaf and Rappole 1995).

An upswing in numbers of warblers since about 1990 occurred after a period in which Bahamian pine woodland recovered from the compressed period of short-rotation logging in the 1970s. Pines regenerated on some sites where cutting was severe (Abaco) and matured on thinned sites (Emlen's [1977] study sites on Grand Bahama). Normal fire regimes also may be returning now, as we saw evidence of lowintensity fire in virtually all areas of Abaco and Grand Bahama that we surveyed.

Habitat loss, incompatible silviculture, and altered fire regimes pose both direct and indirect threats to birds that rely on pine ecosystems (Jackson 1986, Rudolph and Conner 1996, James et al. 1997). Declines of endemic taxa confined to pines in this archipelago (Allen 1996) occurred during the periods of habitat modification. A subspecies of Brown-headed Nuthatch (*Sitta pusilla insularis*) is now much reduced (Smith and Smith 1994). The Brace's Emerald (*Chlorostilbon bracei*) is gone from New Providence (Olson and Hilgartner 1982), and an endemic race of the West Indian Woodpecker (*Centurus superciliaris*) has disappeared from Grand Bahama (Emlen 1977, Smith and Smith 1994). Bahamian pine forest is lost at high rates and is the least protected category of habitat types in Latin America and the Caribbean (Dinerstein et al. 1995).

The winter stage of the warbler's annual cycle has been mostly ignored compared to protection efforts on the breeding grounds. At a minimum, we believe that maintaining the current view of a population that is strictly breeding season-limited (Sykes 1997) carries great risk. Our analyses show that open canopy pine forest on the large islands of the northern Bahamas provides extensive natural habitat for wintering Kirtland's Warblers. Winter habitat should be included in planning for the long-term conservation of this endangered Neotropical migrant, otherwise, current management efforts could be compromised.

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LITERATURE CITED

- ALLAN, T. G. 1986. Management plan for the pine forests of the Bahamas. UTF/BHA BHA Consultancy Rep. No. 2. Food and Agriculture Organization of the United Nations, Rome.
- ALLEN, P. E. 1996. Breeding biology and natural history of the Bahama Swallow. Wilson Bull. 108: 480–495.
- BAIRD, S. F. 1865. Review of American birds in the museum of the Smithsonian Institution, Pt. 1, North and Middle America. Smithson. Misc. Coll. Vol. 12, Part 1.

- BANGS, O. 1900. Notes on a collection of Bahama birds. Auk 17:283–293.
- BLANCHARD, D. 1965. Kirtland's Warbler in winter on Grand Bahama Island. Jack-Pine Warbler 43:39– 42.
- BÖHNING-GAESE, K., M. L. TAPER, AND J. H. BROWN. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conserv. Biol. 7:76–86.
- BOND, J. 1951. First supplement to the checklist of birds of the West Indies (1950). Acad. Nat. Sci. Philadelphia, Philadelphia, PA.
- BOND, J. 1957. Second supplement to the checklist of birds of the West Indies (1956). Acad. Nat. Sci. Philadelphia, Philadelphia, PA.
- BOND, J. 1968. Thirteenth supplement to the checklist of birds of the West Indies (1956). Acad. Nat. Sci. Philadelphia, Philadelphia, PA.
- BONHOTE, J. L. 1903. On a collection of birds from the northern islands of the Bahama groups. Ibis 3: 273–315.
- BRITTON, N. L., AND C. F. MILLSPAUGH. 1962. The Bahama flora. Hafner, New York.
- BRODKORB, P. 1959. Pleistocene birds from New Providence Island, Bahamas. Bull. Florida State Mus. 4:349-371.
- BUDEN, D. W. 1987. The birds of Cat Island, Bahamas. Wilson Bull. 99:579-600.
- BUDEN, D. W. 1990. The birds of Rum Cay, Bahama Islands. Wilson Bull. 102:451-468.
- BUDEN, D. W. 1992. The birds of the Exumas, Bahama Islands. Wilson Bull. 104:674-698.
- BUDEN, D. W., AND A. SPRUNT IV. 1993. Additional observations on the birds of the Exumas, Bahama Islands. Wilson Bull. 105:514-518.
- BYRNE, R. 1980. Man and the variable vulnerability of island life: a study of recent vegetation change in the Bahamas. Atoll Res. Bull. No. 240, Smithson. Inst., Washington, DC.
- CAMPBELL, D. G. 1978. The ephemeral islands: a natural history of the Bahamas. Macmillan, London.
- CHALLINOR, D., JR. 1962. Recent sight records of Kirtland's Warbler in the Bahama Islands. Wilson Bull. 74:290.
- CHAPMAN, F. M. 1898. Kirtland's Warbler (Dendroica kirtlandii). Auk 15:289–293.
- CHAPMAN, F. M. 1899. Further notes on Dendroica kirtlandii. Auk 16:81.
- CHAPMAN, F. M. 1908. Camps and cruises of an ornithologist. D. Appleton, New York.
- CLENCH, M. H. 1978. Search ends: a Kirtland's at last. Bull. Audubon Soc. West. Pennsylvania 42:8.
- COKER, W. C. 1905. Vegetation of the Bahama Islands. MacMillan, London.
- CORY, C. B. 1879. Capture of Kirtland's Warbler (*Dendroica kirtlandii*) in the Bahama Islands. Bull. Nuttall Ornithol. Club 4:118.
- CORY, C. B. 1886. The birds of the West Indies, including the Bahamas Islands, the Greater and Lesser Antilles, excepting the islands of Tobago and Trinidad. Auk 3:1–59.
- CORY, C. B. 1891. List of birds collected by C. L. Winch in the Caicos Islands and Inagua, Bahamas

during January and February and in Abaco, in March, 1891. Auk 8:295-298.

- DEGRAAF, R. M., AND J. H. RAPPOLE. 1995. Neotropical migratory birds. Cornell Univ. Press, Ithaca, NY.
- DINERSTEIN, E., D. M. OLSON, D. J. GRAHAM, A. L. WEBSTER, S. A. PRIMM, M. P. BOOKBINDER, AND G. LEDEC. 1995. A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. The World Bank, Washington, DC.
- DOWDY, S., AND S. WEARDEN. 1991. Statistics for research. John Wiley and Sons, New York.
- DUNNELL, A., AND K. DUNNELL. 1985. Kirtland's Warbler at Great Stirrup Cay. Jack-Pine Warbler 63: 61.
- EMLEN, J. T. 1971. Population densities of birds derived from transect counts. Auk 88:323-342.
- EMLEN, J. T. 1977. Land bird communities of Grand Bahama Island: the structure and dynamics of an avifauna. Ornithol. Monogr. 24.
- EMLEN, J. T., AND M. J. DEJONG. 1981. Intrinsic factors in the selection of foraging substrates by pine warblers: a test of an hypothesis. Auk 98:294– 298.
- FAANES, C. A., AND J. C. HANEY. 1989. First record of Kirtland's Warbler from the Dominican Republic and additional bird observations. Caribbean J. Sci. 25:30–35.
- GARDINER, J., AND L. J. K. BRACE. 1889. Provisional list of the plants of the Bahama Islands. Proc. Acad. Nat. Sci. Philadelphia, Philadelphia, PA.
- GRANTZ, C. C. 1963. More listed birds for Grand Bahama. Florida Nat. 36:78.
- GRAVES, G. R. 1996. Censusing winter populations of Swainson's Warblers: surveys in the Blue Mountains of Jamaica. Wilson Bull. 108:94–103.
- GREENBERG, R. 1986. Competition in migrant birds in the nonbreeding season. Current Ornithol. 3:281– 307.
- HAWKES, C. V., AND E. S. MENGES. 1996. The relationship between open space and fire for species in a xeric Florida scrubland. Bull. Torrey Bot. Club 123:81–92.
- HENRY, P. W. T. 1974. The pine forests of the Bahamas. British Foreign and Commonwealth Office Land Resource Study 16. Nassau, New Providence.
- HOLMES, R. T., T. W. SHERRY, AND F. W. STURGES. 1989. Population structure, territoriality, and overwinter survival of two migrant warbler species in Jamaica. Condor 91:545–561.
- HOWE, W. H., D. M. TAYLOR, AND D. A. JETT. 1989. Additional records of birds from Cat Island, Bahamas. Wilson Bull. 101:115–117.
- HUBER, K. R. 1982. The Kirtland's Warbler (Dendroica kirtlandii): an annotated bibliography 1852–1980. Mus. Zool., Univ. Michigan, Ann Arbor, MI.
- HUNDLEY, M. 1967. Recent wintering records of the Kirtland's Warbler. Auk 84:425–426.
- JACKSON, J. A. 1986. Biopolitics, management of federal lands, and the conservation of the Red-cockaded Woodpecker. Am. Birds 40:1162–1168.
- JAMES, F. C., C. A. HESS, AND D. KUFRIN. 1997. Spe-

cies-centered environmental analysis: indirect effects of fire history on Red-cockaded Woodpeckers. Ecol. Appl. 7:118–129.

- JAMES, F. C., AND C. E. MCCULLOCH. 1995. The strength of inferences about causes of trends in populations, p. 40–51. *In* T. E. Martin and D. M. Finch [eds.], Ecology and management of Neotropical migratory birds. Oxford Univ. Press, New York.
- KELLY, S. T., AND M. E. DECAPITA. 1982. Cowbird control and its effect on Kirtland's Warbler reproductive success. Wilson Bull. 94:363–365.
- KEPLER, C. B., G. W. IRVINE, M. E. DECAPITA, AND J. WEINRICH. 1996. The conservation management of Kirtland's Warbler *Dendroica kirtlandii*. Bird Conserv. Int. 6:11–22.
- KING, W. B., N. F. R. SNYDER, M. S. SEGNESTAM, AND J. GRANTHAM. 1979. Noteworthy ornithological records from Abaco, Bahamas. Am. Birds 33: 746–748.
- KJELLMARK, E. 1996. Late Holocene climate change and human disturbance on Andros Island, Bahamas. J. Paleolimnol. 15:133–145.
- LANE, J. 1975. Kirtland's Warbler in Mexico. Am. Birds 29:144.
- LATTA, S. C., AND M. E. BALTZ. 1997. Population limitation in Neotropical migratory birds: comments on Rappole and McDonald (1994). Auk 114:754– 762.
- LEE, D. S., M. WALSH-MCGHEE, AND J. C. HANEY. 1997. A history, biology and re-evaluation of Kirtland's Warbler habitat in the Bahamas. Bahama J. Sci. 4:19–29.
- MARRA, P. P., T. W. SHERRY, AND R. T. HOLMES. 1993. Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American Redstarts (*Setophaga ruticilla*). Auk 110:565–572.
- MAYFIELD, H. F. 1960. The Kirtland's Warbler. Cranbrook Inst. Sci. Bull. No. 40. Bloomfield Hills, MI.
- MAYFIELD, H. F. 1961. Cowbird parasitism and the population of the Kirtland's Warbler. Evolution 15:174–179.
- MAYFIELD, H. F. 1972. Winter habitat of Kirtland's Warbler. Wilson Bull. 84:347–349.
- MAYFIELD, H. F. 1983. Kirtland's Warbler: victim of its own rarity? Auk 100:974–976.
- MAYFIELD, H. F. 1988. Where were Kirtland's Warblers during the last ice age? Wilson Bull. 100: 659-660.
- MAYFIELD, H. F. 1992. Kirtland's Warbler (Dendroica kirtlandii). In A. Poole, P. Stettenheim, and F. Gill [eds.], The birds of North America, No. 19. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.
- MAYFIELD, H. F. 1993. Kirtland's Warblers benefit from large forest tracts. Wilson Bull. 105:351– 353.
- MAYFIELD, H. F. 1996. Kirtland's Warblers in winter. Birding 28:34–39.
- MAYNARD, C. J. 1896. The birds of eastern North America. Maynard, Newtonville, MA.

- MAYR, E. 1953. Additional notes on the birds of Bimini, Bahamas. Auk 70:499–501.
- MENGEL, R. M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). Living Bird 3:9–43.
- MILLER, J. R. 1978. Notes on birds of San Salvador Island (Watlings), the Bahamas. Auk 95:281–287.
- MILLER, K. V., AND M. J. CONROY. 1990. Spot satellite imagery for mapping Kirtland's Warbler wintering habitat in the Bahamas. Wildl. Soc. Bull. 18:252– 257.
- MIROV, N. T. 1967. The genus *Pinus*. Ronald Press, New York.
- NELSON, M. D., AND R. R. BUECH. 1996. A test of three models of Kirtland's Warbler habitat suitability. Wildl. Soc. Bull. 24:89–97.
- NICKRENT, D. L., W. H. ESHBAUGH, AND T. K. WILSON. 1988. The vascular flora of Andros Island, Bahamas. Kendall Hunt, Dubuque, IA.
- NORTON, R. L. 1993. First autumnal report of birds from Rum Cay, Bahamas. Wilson Bull. 105:361– 364.
- OLSON, S. L., AND W. B. HILGARTNER. 1982. Fossil and subfossil birds from the Bahamas. Smithson. Contrib. Paleobiol. 48:22–60.
- PARRISH, J. D. 1995a. Effects of needle architecture on warbler habitat selection in a coastal spruce forest. Ecology 76:1813–1820.
- PARRISH, J. D. 1995b. Experimental evidence for intrinsic microhabitat preferences in the Blackthroated Green Warbler. Condor 97:935–943.
- PERRY, J. P. 1991. The pines of Mexico and Central America. Timber Press, Portland, OR.
- PROBST, J. R. 1986. A review of factors limiting the Kirtland's Warbler on its breeding grounds. Am. Midl. Nat. 116:87-100.
- PROBST, J. R., AND J. P. HAYES. 1987. Pairing success of Kirtland's Warblers in marginal vs. suitable habitat. Auk 104:234-241.
- RADABAUGH, B. E. 1974. Kirtland's Warbler and its Bahama wintering grounds. Wilson Bull. 86:374– 383.
- RAPPOLE, J. H., AND M. V. MCDONALD. 1994. Cause and effect in population declines of migratory birds. Auk 111:652–660.
- RAPPOLE, J. H., AND D. W. WARNER. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico, p. 353–393. In A. Keast and E. S. Morton [eds.], Migrants in the Neotropics: ecology, behavior, distribution, and conservation. Smithson. Inst. Press, Washington, DC.
- RIDGWAY, R. 1891. List of birds collected on the Bahama Islands by the naturalists of the Fish Commission steamer *Albatross*. Auk 8:333–334.
- ROBINSON, S. K., S. I. ROTHSTEIN, M. C. BRITTINGHAM, L. J. PETIT, AND J. A. GRZYBOWSKI. 1995. Ecology and behavior of cowbirds and their impact on host populations, p. 428–460. *In* T. E. Martin and D. M. Finch [eds.], Ecology and management of Neotropical migratory birds. Oxford Univ. Press, New York.
- RUDOLPH, D. C., AND R. N. CONNER. 1996. Red-cockaded Woodpeckers and silvicultural practice: is

uneven-aged silviculture preferable to even-aged? Wildl. Soc. Bull. 24:330–333.

- SANDERSON, D. J. 1982. Birds of the Turks and Caicos Islands. Turks and Caicos Current Nov/Dec:35– 42.
- SEALEY, N., AND E. J. BURROWS. 1982. School atlas for the Commonwealth of the Bahamas. Longman House, Essex, UK.
- SHERRY, T. W., AND R. T. HOLMES. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence?, p. 85–120. *In* T. E. Martin and D. M. Finch [eds.], Ecology and management of Neotropical migratory birds. Oxford Univ. Press, New York.
- SLIWA, A., AND T. W. SHERRY. 1992. Surveying wintering warbler populations in Jamaica: point counts with and without broadcast vocalizations. Condor 94:924–936.
- SMITH, P. W., AND S. A. SMITH. 1994. Preliminary assessment of the Brown-headed Nuthatch in the Bahamas. Bahamas J. Sci. 2:22–26.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods, 7th ed. Iowa State Univ. Press, Ames, IA.
- SNYDER, N. F. R., W. B. KING, AND C. B. KEPLER. 1982. Biology and conservation of the Bahama Parrot. Living Bird 19:91–114.
- SYKES, P. W., JR. 1989. Kirtland's Warblers on their wintering grounds in the Bahamas Archipelago preliminary report. Proc. Kirtland's Warbler Symposium, USDA Forest Service, Lansing, MI.
- SYKES, P. W., JR. 1997. Kirtland's Warbler: a closer look. Birding 29:220–227.
- TOWNSEND, C. H. 1927. Old times with the birds: autobiographical. Condor 29:224-232.
- VAN TYNE, J. 1951. The distribution of the Kirtland's Warbler (*Dendroica kirtlandii*). Proc. Int. Ornithol. Congr. 10:537–544.
- VELLEMAN, P. F., AND R. E. WELSCH. 1981. Efficient computing of regression diagnostics. Am. Statistician 35:234-242.
- WALKINSHAW, L. H. 1972. Kirtland's Warbler—endangered. Am. Birds 26:3–9.
- WALLACE, G. J. 1968. Another August record of Kirtland's Warbler on its wintering grounds. Jack-Pine Warbler 46:7.
- WHITE, T. 1996. Kirtland's versus Yellow-throated Warblers. Birding 28:269–270.
- WILKINSON, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL.WILLIAMS, T. C., AND T. WEBB III. 1996. Neotropical
- WILLIAMS, T. C., AND T. WEBB III. 1996. Neotropical bird migration during the ice ages: orientation and ecology. Auk 113:105–118.
- WUNDERLE, J. M., JR. 1992. Sexual habitat segregation in wintering Black-throated Blue Warblers in Puerto Rico, p. 299–307. *In J. M. Hagan III and D. W. Johnston [eds.]*, Ecology and conservation of Neotropical migrant landbirds. Smithson. Inst. Press, Washington, DC.
- WUNDERLE, J. M., JR., AND R. B. WAIDE. 1993. Distribution of overwintering Nearctic migrants in the Bahamas and Greater Antilles. Condor 95:904– 933.

Island	Location	Number/sex	Date	Observer	Habitat	Source ^b
near Abaco	ľ	-*	2nd wk Oct. 1841	S. Cabot Jr.	at sea	Baird 1865
Great Abaco	-	*1	21 Mar. 1891	C. I. Winch		Corv 1801
Great Abaco	near Marsh Harbor	2	9–11 Nov. 1967	Fla. Aud. Soc.		And Field Notes 27.
						30
Great Abaco		1	carly 1969	banded		Bond 1969
Great Abaco	Abaco National Park	1	13 Nov. 1987	R. Gnam	pine	Am. Birds 42:144.
Great Abaco	n. Abaco National Dort	1ð	17 Aug. 1990	M. Walsh-McGehee	pine	this study
Great Abaco	Abaco National Park	1	25 Aug. 1990	R. Gnam	pine	R. Gnam. pers.
i			1		4	comm.
Great Abaco	Abaco National Park	1 (imm.)	1–3 Dec. 1995	D. Lee	pine	this study
Great Abaco	Abaco National Park	-1	15 Dec. 1996	D. Lee, M. Walsh- McGehee	pine	this study
Great Abaco	near Crossing Rocks	1	17 Dec. 1996	D. Lee, M. Walsh- McGehee	pine	this study
Little Abaco		1♂*	20 Mar. 1902	J. L. Bonhote	ļ	Ronhote 1903
Andros	Hawk's Nest	19*	9 Jan. 1879	C. B. Corv	thick brush	Corv 1879
Andros	Southern Bight	1*	1884?	C. J. Maynard		Mavnard 1896
Andros	Fresh Creek	1	16 Nov. 1967	A. Paterson	pine?	Aud. Field Notes 22:
Andros	Fresh Creek	1	30 Mar.–6 Apr. 1968	A. Paterson	pine?	ou. Aud. Field Notes 22: \$10
Andros	1	1	1970	J. T. Emlen		219. Radahanoh 1074
Andros	I	1–3	1968-1971	A. Paterson	pine?	Radabaugh 1974
"Bahamas"		1*	1886			Townsend 1927
Berry Islands	I	3*	3 and 20 Apr. 1891	C. S. Winch	1	Cory 1891
Berry Islands	Great Stirrup Cay	1	31 Mar. 1984	A. and P. Dunnell	1	Dunnell and Dunnell
Cat Cay (Bimini)		1	27 or 28 Apr. 1907	F. Chapman	-	Chapman 1908
Cat Cay		1*	1913	C. J. Maynard		Van Tyne 1951
Cat Cay	1	1*	1915	C. J. Maynard	ł	Van Tyne 1951
Cat Island		1*	20 Nov. 1890	J. P. Moore		ANSP 48134
Cat Island		1*	1891	J. P. Moore	1	Mayfield 1960
Cat Island	Port Howe	1*	20 Nov. (1950?)	J. P. Moore	[Bond 1951
Crooked	900 m n. of sea	1ð	11-22 Mar. 1973	B. Radabaugh	shrub	Radabaugh 1974
Dominican Rep.	1 km. n. Laguna Sa- ladilla	19	14–15 Mar. 1985	C. Haney, C. Faanes	dry forest	Faanes and Haney
Dominican Ren		-		117 A 44		1969
	1	1		w. Arenat		Wunderle and Walde 1993

	Number/s
	Location
Continued.	
ENDIX 1.	Island

APPENDIX 1. Continued.						
Island	Location	Number/sex	Date	Observer	Habitat	Source ^b
Eleuthera		2*	22 Apr. 1884	C. J. Maynard	low scrub	Chapman 1898
Eleuthera	1	5*	13 Nov2 Dec. 1891	C. S. Winch	I	Mayfield 1960
Eleuthera		3* (13.19)	20–22 Apr. 1897	C. J. Maynard		Chapman 1898
Eleuthera	Harbour Island	1	9 Mar. 1956	A. M. Bagg		Bond 1957
Eleuthera	ļ	1	11 Nov. 1961	1	scrub	Hundley 1967
Eleuthera		1	30 Nov. 1963	C. R. Mason	scrub	Hundley 1967
Eleuthera	-	1	9 Nov. 1975			Anon.
Flenthera	Governor's Harbor	fc	20 Feb. 1985	C. Faanes	shrub	Am. Birds 43:372.
Elenthera		16.19	Dec. 1985–28 Mar.	P. Sykes; banded	shrub	Am. Birds 40:339,
		 	1986	•		529.
Eleuthera	Governor's Harbor	1	14 Feb. 1989	J. Siphron	shrub	Am. Birds 43:372.
Grand Bahama	Lucayan National	1	24 Nov. 1955		pine	R. Oliver, pers.
	Park				1	comm.
Grand Bahama	West End airport	1	14 Nov. 1959	Bonney, Brigham	scrub ^c	Blanchard 1965
Grand Rahama	e. of Freenort		19 Nov. 1960	C. R. Mason	pine-land scrub	Hundley 1967
Grand Bahama	e of Freenort		late Dec 1961		pine	Hundley 1967
Croud Dehome	e of Freenort		Dec 1961	C R Mason	nine	Hundley 1967
		1-	24 Nov. 1047			Hundley 1067
Grand Bahama	e. of Freeport		24 NOV. 1902	C. R. Masoli	puic	
Grand Bahama	8 km w. of Freeport	-	Dec. 1962	· · ·	.	Uraniz 1903
Grand Bahama	Pineland Wildl.	1	16 Nov. 1963	D. Blanchard	pine	Blanchard 1965
	Sanct.					
Grand Bahama	e. of Freeport	S	12 Feb. 1964	C. R. Mason	pine	Hundley 1967
Grand Bahama	e. of Freeport	2	24 Mar. 1964	C. R. Mason	pine	Hundley 1967
Grand Bahama	e. of Freeport	1	27 Mar. 1964	C. R. Mason	pine	Hundley 1967
Grand Bahama	e of Freenort	13.12	27 Apr. 1964	C. R. Mason	pine	Hundley 1967
Grand Bahama	Pineland Wildl		5 Aug 1964	C. R. Mason	pine	Blanchard 1965
Otalia Dalianta	Sanct	4			ч	
Carriel Dickson	o of Econom	10 20	70 Aug 1064	C B Mason	nine	Hundley 1967
		20,1+	2) Aug. 1904			Hundley 1067
Grand Bahama	e. or Freeport	n (2 Oct. 1904		puic.	
Grand Bahama	Pineland Wildl.	7	13 Nov. 1964	C. R. Mason	pine	Blanchard 1900
	Sanct.					
Grand Bahama	e. of Freeport	13.19	27 Nov. 1964	C. R. Mason	pine	Hundley 1967
Grand Rahama	e of Freenort	1.	9 Feb. 1965	C. R. Mason	pine	Hundley 1967
Grand Bahama	e of Freenort		15 Feb. 1965	C. R. Mason	pine	Hundley 1967
Crund Bahama	e of Freenort) 	17 Eeh 1965	C R Mason	, Dine	Hundley 1967
Grand Debomo	e of Freenort		16 Oct 165		nine	Hundley 1967
	c. of Freepoil	۱ ر	21 Oct 1066	C D Mason	nine	Hundley 1967
Grand Bahama	e. or Freeport	4	21 Oct. 1900	C. N. MASUI	purc	Unudlay 1067
Grand Bahama	e. of Freeport	7	22 UCI. 1900		plife	nuluicy 1907
Grand Bahama	e. of Freeport	I	5 Aug. 1967].	Bond 1908
Grand Bahama]	1	Apr. 1969	P. Fluck; banded	pine	Mayheld 19/2
Grand Bahama	West End	1	28 Dec. 1969	C. F. Walker	broad-leaved shrubs	Mayfield 1972

Island	Location	Number/sex	Date	Observer	Habitat	Source ^b
Grand Bahama		≥5	1959-1974	P. Fluck; 1 banded		Radabaueh. unnubl. ren.
Grand Bahama	1	45	1969–1974	P. Fluck	young pine	Radabaugh 1974
Grand Bahama	Lucayan National	1ð	25-27 Nov. 1995	C. Haney, D. Lee, C.	pine 1	this study
Grand Bahama	Park e of Freenort		0 Eab 1007	Faanes		والمارد مشتطين
Grand Bahama	e. of Freeport	1 1 2	10 Feb. 1997	C Haney M DeCanita	pinc	this study
Grant Turk	-	23,19	11 Feb. 1985	C. Faanes, P. Sievert	xeric scrub	C. Faanes, pers.
Level Barry		*		((comm.
Urand Jurk	I	16	7 Mar. 1985	C. Faanes	shrub	C. Faanes, pers.
Grand Turk		1ð	27 Dec. 1985	C. Faanes, P. Sievert	xeric scrub	comm. C. Faanes, pers.
		·				comm.
Great Inagua	w. side	12	6 Mar (1923-1940?) 29 Mar 1979	J. Bond S. Snrint N and H	scrub near sea	Van Tyne 1951 S Sprint pare
ſ				Snyder	numpron undo	o. optunt, poto. comm.
Great Inagua	1	23	20, 22 Mar. 1985	C. Faanes, P. Sievert	xeric scrub	C. Faanes, pers.
Great Inamia		10	1 4 1005		-	comm.
Ulvai Illagua	ł	± 1	1 Apr. 1903	C. Faanes	xeric scrub	C. Faanes, pers.
Great Inagua		1ð	2 Apr. 1985	C. Faanes	xeric scrub	comm. C. Faanes, pers.
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;						comm.
Hog (Paradise)	Paradise Beach	19	27 Aug. 1967	G. J. Wallace	pine	Wallace 1968
Hog		10*	27 Mar. 1957	D. Challinor	scrub ^c	Challinor 1962
Mexico	Lazario	13	11 Nov. 1974	J. Lane	thick brush	Lane 1975
Middle Caicos	-	2*	9 Jan. 1891	C. L. Winch		Cory 1891
New Providence		4*	10 Jan. 1884	C. B. Cory		Mayfield 1960
New Providence	≤3 km Nassau	24*	10 Jan29 Mar. 1884	C. J. Maynard	low scrub	Maynard 1896
New Prov. (Green Cay)		2*	12 Apr. 1886	-	1	Ridgway 1891
New Providence	near Nassau	4*	21 Mar.–25 Apr.	C. B. Cory		Van Tyne 1951
New Providence		8* (23.32)	100/ 18–25 Anr. 1887	A H Tennings	1	Chanman 1800
New Providence		10*	² Anr. 1887	A H lennings(?)		11SNM 274850
New Providence	Nassau	2* (19)	25 Mar2 Apr. 1893	C. J. Mavnard		Chanman 1898
New Providence	Nassau	5* (23, 19)	4 Mar6 Apr. 1897	C. J. Maynard		Chapman 1898, Bangs
	-			i		1900
New Providence	Athol	* *	5 May 1897	C. J. Maynard	Ι	Chapman 1898
New Providence	Nassau	*	Apr. 1902	J. L. Bonhote	1	Bonhote 1903
New Providence	Nassau	12*	5 Mar. 1913	C. J. Maynard		MCZ 63660

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APPENDIX 1. Continued.

		Mission	Date	Okonite	Unkited	Courseb
Island	TOCATION	Valiable Vac	Date	OUSEI VEI	TaUtat	20000
New Providence		1*	1915	C. J. Maynard		Van Tyne 1951
New Providence		ŝ	26 Feb. 1941	P. B. Street		Hundley 1967
New Providence	near aimort		20 Aug. 1970	G. Woolfenden	voung pine	Am. Birds 25:48.
New Providence		19	30 Jan. 1985	C. Faanes, P. Sievert	pine edge	C. Faanes, pers.
						comm.
New Providence	Coral Harbor Road	1	13 Dec. 1989	S. and P. W. Smith	pine edge	P. W. Smith, pers.
					1	comm.
New Providence	Coral Harbor Road	1	13 Dec. 1991	S. and P. W. Smith	pine edge	Am. Birds 47:304.
North Caicos	Bellefield Landing	12	10 Feb. 1978	M. Clench	sparse vegetation	Clench 1978
Paradise	next to golf course	13	2 Feb. 1985	J. Gerwin	shrub edge	J. Gerwin, pers.
)					comm.
Rum Cay		×]	1891?	C. L. Winch	1	Cory 1891
San Salvador (Watling)	1	4* (13, 29)	4–9 Apr. 1886	-		Ridgway 1891
San Salvador	I	1*	27 Dec. 1963	D. Paulson	dense low coppice	TSU
San Salvador		1*	27 Dec. 1965	D. Paulson	scrub forest	Mayfield 1972
South Caicos	1	1ð	6 Feb. 1985	D. Faanes, P. Sievert	xeric scrub	C. Faanes, pers.
						comm.
South Caicos	ł	1ð	10 Feb. 1985	C. Faanes	L	USFWS memo, 1995
Subtotal: Bahamas		196^{d}				
Subtotal: Mexico						
Subtotal: Dominican Republic		2				
Total individuals		199				
a Becords and remote known to authors as c	of 30 November 1997 Total de	es not include undat	ed reports from Caicos Island	ls (Sanderson 1982) or recent sigh	ntings (December 1997) from r	ine islands in the Caicos Islands

APPENDIX 1. Continued.

L Precords and reports any availability of the second state of the s