A HISTORY, BIOLOGY AND RE-EVALUATION OF THE KIRTLAND'S WARBLER HABITAT IN THE BAHAMAS

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INTRODUCTION
Since its discovery, the Kirtland’s Warbler (Dendroica kirtlandii) has been referred to by a number of writers as America’s rarest songbird. Its breeding range is one of the most geographically-restricted of any mainland bird, and its limited wintering distribution is perhaps the smallest of any known nearctic migrant. This bird was described from a single spring migrant found near Cleveland, Ohio, in 1851 (Baird 1857). Between 1879 and 1902, and before this warbler’s breeding grounds in Lower Michigan were finally discovered, 17 records of 68 individuals collected on 10 different Bahamian islands were obtained. It is believed that its numbers declined during this period. The actual number of Kirtland’s Warblers that existed in the latter half of the 19th century is a matter of speculation, but several authors have suggested that the population may have exceeded 1000 pairs. This figure is based in part on the relatively large series of specimens collected in the Bahamas during a period of sporadic visits between 1879 and 1915. The first actual census of Kirtland’s Warblers on their breeding grounds was undertaken in 1951 when the population was found to consist of only 432 males (Mayfield 1955). The population fluctuated but continued to decline until 1987 when an all-time low count of 16/ adult males was obtained. Since 1990 there has been a marked upward trend in the number of males on the breeding grounds (Figure 1) and, although it is still considered highly-endangered, prognosis for its long-term survival now seems encouraging.

Huber (1982) lists 600 published works for this species, yet despite the considerable interest in this rare warbler and the efforts that have been made to study and manage it under the Endangered Species Act (U.S. Fish and Wildlife Service), little is known about the bird’s winter habitats (e.g. Mayfield 1996). This does not result from a lack of effort, but the Kirtland’s Warbler population was so low during the period when surveys were being conducted on its winter grounds (1972-1986) that encounters were few and little was learned. Information presented here suggests to us that many of the sightings reported in the last several decades have been from altered winter habitats, and we propose that the current interpretation of what comprises primary natural winter habitat needs to be re-evaluated. This is based on revisiting earlier reports and on sightings we made in the winters of 1990 and 1995.

OVERVIEW OF THE BIOLOGY OF WINTERING KIRTLAND’S WARBLERS
Wintering grounds of this wood warbler are essentially restricted to the Bahamas. Birds probably occur throughout the archipelago, although the majority of the records and reports are from the northern islands. The 1957 A.O.U. Checklist notes wintering Kirtland’s Warblers on the following: Little Abaco, Great Abaco, Berry, Andros, Cat Cay, New Providence, Athol, Eleuthera, Green Cay, Cat Island, Great Inagua, Watling Island (=San Salvador), and the Caicos Islands. There are also late 1800’s records from Rum Cay and the Berry Islands (Cory 1891). Reports and records from Hog Island (=Paradise Is.) and Crooked Island were made after the publication of the 1957 A.O.U. Checklist (Challinor 1962, Radabaugh 1974). Although new reports continue to appear, no additional islands have been added for the Bahamas.

Faanes and Haney (1989) reported a female Kirtland’s
Warbler in xeric scrub in the Dominican Republic. The bird was found on 14 and 15 March 1985 near Laguna Saladilla. This was the first detailed winter record of this species outside the Bahama Archipelago. Wunderle and Waide (1994) allude to a second record from the Dominican Republic attributed to Wayne Arendt, but provide no details. There is also one uncorroborated sighting from coastal east-central Mexico (Lane 1975).

Brudenell-Bruce (1975), defining the wintering period for Kirkland's Warblers in the Bahamas as October to 5 May, apparently overlooked August reports (Wallace 1968, Hundley 1967). Numbers of Kirkland's Warblers are clearly in winter residence in the Bahamas prior to October as there are scattered reports of fall migrants from the southeastern United States between late August and the third week in September. There is an unaccepted but not necessarily erroneous report from Florida for 1 August 1981 (Stevenson and Anderson 1994), and Robertson (1971) reports one seen in Nassau by two excellent observers on 20 August 1970. Additionally, we present here reports from Abaco for 17 and 25 August 1990.

**POPULATION DECLINE**

It is now recognized that the species exhibited a continual decline between the turn of the century and 1987, when the Kirkland's Warbler breeding population reached an all-time low (Mayfield 1992; Figure 1). This decline was well documented in that the annual census consisted of actual counts of singing adult males. The factors attributed to the decline were the shrinkage of suitable habitat, and the adverse effect of brood parasitism by the Brown-headed Cowbird (*Molothrus ater*), a species that in the middle part of this century underwent a massive population explosion and range expansion. It is likely that Brown-headed Cowbirds, originating in the grasslands of the central plains, did not reach the pine forest of northern Michigan until the forest had been opened by lumbering in the 1870s and 1880s. Mayfield (1961) documented that cowbirds parasitized 55% of all Kirkland's Warbler nests in the 1940's and 1950's, and that unparasitized nests produced four times as many young as ones occupied by cowbirds. In the early 1970's, parasitism rates reached 70 to 83% (Walkinshaw 1972).

The additional problem possibly threatening the survival of the Kirkland's Warbler was identified as the habitat on the wintering grounds in the Bahamas. Radabaugh (1974) investigated this but, because of his inability to locate a significant number of wintering birds (his studies were during a period when the male population was down to 200 pairs), the results were inconclusive. Mayfield (1973, 1996) concluded that the wintering habitat in the Bahamas "seems to have changed remarkably little in the last century" and that cowbirds were the chief factor for the continued decline of the warbler.

In the last decade the population has been slowly recovering. This increase is primarily attributed to a recovery program on the nesting grounds that combines clear-cutting, controlled burning and replanting, and a strong cowbird removal effort. In 1994 alone nearly 16 hundred hectares of land were replanted with jack pines, and future plantings will be on a rotation basis in order to maintain the successional conditions necessary for the welfare of this warbler (Ashcraft 1995). Based on informa-
tion we present here we believe this recovery also results, in part, from the regrowth of the pine forests in the northern parts of the Bahama archipelago.

HISTORICAL SUMMARY OF KIRTLAND’S WARBLERS IN THE BAHAMAS

The first specimen of a Kirtland’s Warbler was actually collected at sea near Abaco 10 years prior to the species’ description. It was obtained aboard ship by Samuel Cabot, Jr. on his voyage to Yucatan in 1841 (Baird 1865). By the turn of the century, and before the discovery of the species’ breeding grounds, 55 of the 75 total specimens of these warblers known at the time were collected in the Bahamas (Chapman 1899).

The historic abundance of Kirtland’s Warblers on their wintering grounds is unknown, but based on statements of collectors they were “not uncommon” or “fairly numerous” between the 1860’s and 1890’s (Mayfield 1960). Cory (1896) noted these warblers as common in winter on New Providence and Andros and he suspected they bred in the Bahamas. By the turn of the century, the number of reports in the Bahamas decreased despite sporadic field efforts.

Previous Surveys

Through most of this century, searches for Kirtland’s Warblers in the Bahamas have been largely unsuccessful. James Bond spent about 100 field days in the Bahamas in the mid-1930’s and saw only one individual. In 1949 Mayfield and Van Tyne spent 59 man-days searching without success for the warbler on New Providence and Eleuthera. Additionally, Mayfield made brief trips in the 1960’s to Great Abaco, Grand Bahama and Inagua and never found this warbler (Mayfield 1972). Mayr (1953) reported no Kirtland’s Warblers were observed on Bimini despite a diligent search. In 1960 Walkinshaw caught no Kirtland’s Warblers in 305 net hours at Mastic Point, Andros. Radabaugh (1974) found one bird in 800 hours of field work on 11 islands between 1972 and 1973. Emlen (1977), in his extensive censusing of land birds on Grand Bahama Island, found none in 500 hours between 1968 and 1971. His field efforts exceeded 200 days. Mary Clench (Carnegie Museum, Pittsburgh, PA) led a team of biologists through 21 islands and cays, many of which were remote and uninhabited, in 1976 and found no Kirtland’s Warblers. Dr. Budden surveyed Bahamian birds, with a focus on the southern islands during the 1970’s and 1980’s, and found no Kirtland’s Warblers. Wunderle and Waide (1993) failed to detect any of these warblers during 411 point counts and 787 net hours on Andros, Great Inagua and New Providence in 1986. Additionally, King et al. (1979) and others conducted intensive field studies on Abaco while working on Bahama Parrots (Amazona leucophrasia bahamensis) and all failed to report a single sighting of Kirtland’s Warblers.

The U.S. Fish and Wildlife Service conducted winter surveys for the Kirtland’s Warblers in mid-1980’s. Most of their activities were on the southern islands. Reports from these surveys are included in Table I (C. Faanes pers. comm.)

Recent Records

Our recent sightings of Kirtland’s Warblers in Caribbean Pine forest (Pinus caribaea) were made on southern Great Abaco (1990, 1995) and Grand Bahama (1995). Additionally, P. W. Smith and Susan Smith reported records on New Providence in 1989 and 1992 at the edge of a Carib-

Figure 2. The Kirtland’s warbler in its habitat. (Photo: VIKTO, Philadelphia Academy of Sciences)
<table>
<thead>
<tr>
<th>Northern Island Groups</th>
<th>Approximate area sq mi</th>
<th>Population (1990)</th>
<th>Density per sq mi</th>
<th># reports</th>
<th># individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bimini</td>
<td>9</td>
<td>1,630</td>
<td>102</td>
<td>3 (3%)</td>
<td>3 (2%)</td>
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<tr>
<td>Grand Bahama*</td>
<td>530</td>
<td>41,010</td>
<td>77</td>
<td>7 (7%)</td>
<td>57 (30%)</td>
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<tr>
<td>Abaco*</td>
<td>649</td>
<td>10,061</td>
<td>16</td>
<td>1 (1%)</td>
<td>6 (3%)</td>
</tr>
<tr>
<td>Berry*</td>
<td>14</td>
<td>634</td>
<td>53</td>
<td>3 (3%)</td>
<td>5 (3%)</td>
</tr>
<tr>
<td>Andros*</td>
<td>2,300</td>
<td>8,755</td>
<td>4</td>
<td>6 (6%)</td>
<td>8 (4%)</td>
</tr>
<tr>
<td>New Providence*</td>
<td>80</td>
<td>1,711,542</td>
<td>2,144</td>
<td>20 (20%)</td>
<td>62 (33%)</td>
</tr>
<tr>
<td>Eleuthera</td>
<td>200</td>
<td>10,524</td>
<td>5</td>
<td>9 (9%)</td>
<td>18 (9%)</td>
</tr>
<tr>
<td>Cat</td>
<td>150</td>
<td>1,678</td>
<td>11</td>
<td>3 (3%)</td>
<td>3 (2%)</td>
</tr>
<tr>
<td><strong>Subtotal</strong></td>
<td><strong>3,932</strong></td>
<td><strong>245,867</strong></td>
<td><strong>62</strong></td>
<td><strong>82 (83%)</strong></td>
<td><strong>166 (85%)</strong></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Southern Island Groups</th>
<th>Approximate area sq mi</th>
<th>Population (1990)</th>
<th>Density per sq mi</th>
<th># reports</th>
<th># individuals</th>
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</thead>
<tbody>
<tr>
<td>Exuma</td>
<td>112</td>
<td>35,394</td>
<td>32</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Long</td>
<td>230</td>
<td>3,107</td>
<td>14</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Rum Cay</td>
<td>30</td>
<td>380</td>
<td>2</td>
<td>1 (1%)</td>
<td>1 (0.5%)</td>
</tr>
<tr>
<td>San Salvador</td>
<td>63</td>
<td>486</td>
<td>8</td>
<td>3 (3%)</td>
<td>6 (3%)</td>
</tr>
<tr>
<td>Crooked</td>
<td>70</td>
<td>423</td>
<td>5</td>
<td>1 (1%)</td>
<td>1 (0.5%)</td>
</tr>
<tr>
<td>Acklins</td>
<td>110</td>
<td>428</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mayaguana</td>
<td>110</td>
<td>308</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Great Inagua</td>
<td>599</td>
<td>985</td>
<td>2</td>
<td>5 (5%)</td>
<td>6 (3%)</td>
</tr>
<tr>
<td>Little Inagua</td>
<td>49</td>
<td>—</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Caicos Bank*</td>
<td>103</td>
<td>12,400</td>
<td>64</td>
<td>7 (7%)</td>
<td>10 (5%)</td>
</tr>
<tr>
<td><strong>Subtotal</strong></td>
<td><strong>1,260</strong></td>
<td><strong>21,729</strong></td>
<td><strong>17</strong></td>
<td><strong>17 (17%)</strong></td>
<td><strong>24 (13%)</strong></td>
</tr>
</tbody>
</table>

| **Totals**             | **5,192**              | **267,596**      | **52**            | **99**    | **190**       |

1Skeailey and Burrows 1982

bean Pine woodland (P. W. Smith, pers. comm.). Our Abaco records are from the Abaco National Park. One was seen on 17 August 1990 near the intersection of the main highway and the eastern side of logging road BM 10 (MW-M, R. Gnam, I. Lothian). Another was seen in this same general area on 25 August 1990 (RG, IL). A 1 December 1995 Abaco record is of an immature 0.6 mi SSE of the same highway intersection along the road leading to Hole in the Wall (DSL). This bird (or at least one in the same location) was seen again on 3 December. All three Abaco sites are all within several kilometres of each other, and the habitat was identical. The 1995 Grand Bahama record is of an adult male from 25 November in the Lucayan National Park along the trail leading east from the parking lot, and about 30 meters before Ben’s Cave (C. Faanes, JCH, DSL). The bird was relocated on 27 November (DSL). All the Abaco sightings, as well as the Grand Bahama ones, are from open-canopy Pine forest with a low, open, 0.5-2 m understory. The habitats and behaviour of the birds are described below.

Geographical Distribution Within the Bahamas

The three records and reports from Bimini are questionable. Bond (1957) states there are no records of this warbler from Bimini. Perhaps these early century reports are from Cat Island and not Cat Cay but most authors have considered these as Bimini records. Of the 99 winter reports, two-thirds (67) are from the northern pine islands (Andros, Grand Bahama, Abaco and New Providence) or their associated cays, and nearly all reports (83%) are from the northern Bahamas. The Berry Islands should be included in the list of northern pine islands. There are reliable reports of pine from the Berry Islands (e.g. Gardiner and Brace 1889), but they were logged out early in this century (Campbell 1978). Interestingly there are three 1891 specimen records for these islands (Cory 1891) and only two reports for this century. Cory reports the Berry Islands were still forested in 1891. In terms of individual birds the percentage is even higher: 166 of 190 individuals (86%) are from these pine islands and their associated offshore cays. Eleuthera had 9% of the reports and individuals while of the remaining 19 reports, 16 are from various other Bahama Islands, two are from the Dominican Republic and one is from Mexico. Nearly all multiple records (more than one bird per report) are from the northern Bahama, and most multiple records are from the northern islands that support forest of Caribbean Pine. To some extent it is obvious that the large number of records compiled from the pine islands may reflect as much the activity of bird students as it does the winter distribution of Kirland’s Warblers. Nonetheless, it is also clear that these islands have been, and are, important to the winter survival of these warblers. This fact becomes even more pronounced when the size of these four islands is compared to the area of the entire Bahama archipelago. The northern pine islands (Abaco 649 mi²; Grand Bahama...
validity of the records, but clearly he is not familiar with all the problems museums have in tracking early specimens.

RE-EVALUATION OF KIRTLAND’S WARBLER WINTERING HABITAT

Early literature reports, field studies conducted by Radabaugh (1974), the U.S. Fish and Wildlife Service surveys (1985-86) (especially the birds found by Paul Sykes on Eleuthera), and chance observations that were given detailed reports in literature (i.e., Challinor 1962) all lead to the conclusion that Kirtland’s Warbler’s winter habitat is primarily low, broadleaf scrub (low-coppice). In fact, this conclusion gradually dictated which habitats received priority for surveys - the results of which further confirmed that low scrub was the warbler’s preferred habitat (Faanes pers. comm.). In the only detailed published study of Kirtland’s Warbler winter habitat, Radabaugh (1974) provided a list of plants associated with the single bird he found in coastal scrub on Crooked Island. Prior to Radabaugh’s study, Mayfield (1972) reviewed what was known about the winter habitat of Kirtland’s Warblers. He notes from all reports “old and modern” I conclude that the Kirtland's Warbler usually inhabits low, broad-leaved scrub in the Bahamas.” This interpretation of the birds’ winter habitat is still current (Mayfield 1996). Mary Clench after looking at known sites of former occurrence found them to be distinctly different habitats that were of little value in determining habitat preference (Campbell 1978). Authors have not attempted to relate their descriptions of plant communities with existing botanical community profiles.

Figure 3. The Caribbean pine forest of Grand Bahama.

530 mi²; Andros 2,300 mi²; and New Providence 80 mi²) make up 3,559 square miles and 66% of the total land area of the Bahamas. Other large islands, which are devoid of pines, account for very few reports. Although it is clear that the greatest number of reports are from the islands most frequently visited by naturalists we should point out that San Salvador, a relatively large island in the southern Bahamas has a marine research station and is therefore frequently visited by bird students, yet accounts for only two records. Conversely, several of the Caicos Bank also support extensive stands of Caribbean Pine (Correll and Correll 1982) and although these islands are only 193 mi² and seldom visited, they account for at least seven reports (not all from pine communities) while a number of the larger southern, pineless islands have no reports (Table 1). The early number of records from the Caicos must be greater than two in that Cory (1892) reports them as occurring on North Caicos, Grand Caicos and East Caicos, but the documentation for this has subsequently been lost and only one of Cory’s specimens is still extant (Buden 1987). Buden thought that somehow this lessened the As a rule early natural historians were not ecologically minded and, prior to the 1950’s, habitat descriptions for any species were seldom precise and often misleading. Based on our observations, and after re-examining the available literature, we conclude that pine woodlands are an important, perhaps major, element of wintering habitat. This is reinforced by the fact that 80% of all known wintering individuals are from island groups dominated by Caribbean Pine forest. Most of the winter habitat descriptions from these islands that do not mention pine are vague to the point that one cannot rule out the possibility that the shrub/scrub vegetation described was actually pine forest understory. Many of the published records are clearly from open canopy pine forest, as are ours.

Habitat Characterization

We would characterize the habitat in which we observed Kirtland’s Warblers on Grand Bahama, Greater Abaco and the site on New Providence where P. W. Smith reported these birds in 1989 and 1992 as barren tertiary
pine lands. The characteristic flora of dry barren community (New Providence) as described by Correll and Correll (1982) consist of an open overstory of *Pinus caribaea* and an understory of *Petitia domingensis*, *Duranta repens*, *Acacia choriophylla*, *Tetraxagia bicolor*, *Zanthoxylum Hugh*, *Corida bahamensis*, *Ernodia littoralis*, *Hypericum hypericoides*, *Turnera ulmifolia*, *Vernonia bahamensis* and *Pteridium aquilinum*. Our Grand Bahama and Abaco sites, based on the presence of *Salal palmetto*, are probably best considered wet barrens or ones that are intermixed. Correll and Correll (1987) list the following species as typical understory plants in wet barrens: *Metopium toxiferum*, *Byronima lucida*, *Erestoma caribaea*, *Coccoloba diversifolia*, *Guapira discolor*, *Petrecellitrum kegense*, *Corchorus hirsuta*, *Bourreria ovata* and *Lantana involucrata*. Characteristic vines and herbs in the wet barrens include *Rajania hastata*, *Smilax auriculata*, *S. baumannii*, *Rhabdodendron biflorum*, *Dichromena colorata*, *Fusculia petraea*, and *Andropogon spp.* A detailed study of the Abaco site was prepared by Gnam (1991). She examined the shrub layer and determined the relative dominance of the 10 most common shrubs in her research area. Shrub density is expressed in number of shrubs per 0.48 ha (1 acre), and species identified in order of dominance were *Metopium toxiferum* (42%), *Lantana denuilata* (26%), *Tabebuia bahamensis* (21%), *Guetardia longiflora* (13%), *Tetrapia bicolor* (87), *Ilex krugiana* (87), *Morinda rossii* (81), *Duranta repens* (59), *Myrica cerifera* (47), *Acacia choriophylla* (36), *Thuina discolor* (36), *Petitia domingensis* (35), *Salal palmetto* (30), *Myrsine floridana* (21), *Concorpus erectus* (19), *Eugenia axillaris* (17), *Zania pumila* (12), and *Barreria ovata* (8).

Vegetation identified at our Lucayan National Park site include (those also occurring at the Abaco site are marked with an *): *Boseria simaruba*, *Pinus caribea*, *Metopium toxiferum*, *Thraxmax mornris*, *Cassia americana*, *Tabebuia bahamensis*, *Smilax auriculata*, *Coccoloba diversifolia*, *Tetrapia bicolor*, *Tremam larcaneri*, *Corchorus hirsutus*, *Salal palmetto*, *Cocotririxa argentea*, *Psidium longipes*, *Lantana involucrata*, *Cassytha filiformis*, and *Ipomea indica*. Both the Abaco and Grand Bahama sites had a rich herb layer composed largely of *Andropogon virginicus*, and *Heterotheca gramnifolia*, and *Pteridium aquilinum*. Unlike our sites on Abaco, the Grand Bahama site was immediately adjacent to several acres of tall copice.

Where we can find descriptive reports of the scrub occupied by Kirkland's Warblers, it is always stated to be low and/or sparse. This was true for our records as well. The one bird we watched for 30 minutes flew from one shrub to another, pausing to forage around each. The shrub layer was not uniform in height nor density, and there were many open areas throughout. One could easily walk through the habitat by maneuvering around the palms and larger denser shrubs. This was true at our Abaco sites also. We suspect that this is a key aspect for the wintering habitat. These shrub understories are quite unlike the green impenetrable walls of shrubs found in tall copice, wind-banneled coastal scrub, or mature shrub thickets. Other than early-stage disturbed landscapes where the shrubs reoccupy land at different rates, the fire subclimax pine forest may provide not only consistently available sparse, open, habitat of this type in the Bahamas. Except for recently disturbed areas or plant communities dominated by exotics (West End, Grand Bahama: Paradise Is.), nearly all records where the plant community is described are from pine habitats.

During prior field studies Craig Faanes (pers. comm.) found *Wild Sage* (Big Sage), *Lantana involucrata*, [Verbenaceae] to be important to foraging Kirkland's Warblers. Sykes (1989) reported that 59% of the food items were small fruits, 83% of which were of a [this] single species. It is a two meter tall, erect, aromatic, woody shrub with blue or purple drupes. This species grows throughout the Bahamas and is characteristic of open habitats. In successional profiles studied by Byrne (1980) this *Lantana* achieves maximum density at 5-14 years after land clearing and persistent low densities for up to 50 years after disturbance. Nearly all of the records obtained by US Fish and Wildlife Service teams between 1985 and 1986 were associated with *Lantana*, and the warblers were observed feeding on the drupes (C. Faanes, pers. comm.). We found *Lantana* present at both our Grand Bahama and Abaco sites. The dominant species at our Abaco site was *Bosleria sedgebrush L. demutata*. Sykes reported that the birds he found in 1985 on Eleuthera were associated with a bush known locally as sage, and in addition to insects, they ate its small 'berries'. Frank Chapman found Kirkland's Warblers eating these same 'berries' on Cat Cay in late April 1907 (Chapman 1908).

It is probably not the pines *per se* that are important to their winter habitat and foraging ecology. Nevertheless, Caribbean Pine may contribute to the community in a number of ways. First, the combination of an open pine overstory and herb-shrub understory closely mimics the breeding habitat of these warblers. This in itself may provide important visual cues for the birds' selection of winter habitat. Second, the pines partially shade out understory, slowing its development and retard the formation of a tree-height copice, a habitat that is apparently avoided by these warblers. The partial shade may also contribute to a non-uniform spacing and growth of individual shrubs. Pines may also give key foraging plants such as *Lantana* a long-term competitive edge against more vigorous taller copice species. Third, the pines shed needles that contribute to the accumulation of fuel, resulting in frequent low intensity burns that help maintain suitable understory habitat. Finally, and perhaps most importantly, mature pines dictate the structure of the bird community. At least 13 other species of wood warblers occur in Bahama pine communities in the winter and, of these, 8 are in the genus *Dendroica*. During Emelien's (1977) studies on Grand Bahama, when the regenerating pine forest was just 9 to 20 years of age, Palm Warblers (*Dendroica palmarum*) were ranked number one in dominance (214.8/km²). In Lee's (1996) surveys on Greater Abaco, when the pine forest
was 25 to 36 years of age, Palm Warblers ranked number 5 in dominance and were half as abundant (110.2/km²). Additionally, on Abaco a large percentage of the Palm Warblers foraged in the open pine canopy, and not just on the ground and understory. The maturing of the pines changes not only the structure of the avian community, but it also contributes to the stratification of wood warblers and other songbirds, and thereby possibly helps to limit competition. This would be particularly true in ground and low shrub foraging microhabitats.

History of Pine Forest

Paleo-zoogeography suggests that during the Pleistocene Kirkland’s Warblers were short range migrants breeding in the coastal plain of the southeastern United States and wintering in pine forest in the Bahamas. At the height of the Wisconsin glaciation 17,000 yr BP extensive jack pine forests that presently provide the breeding habitat for these warblers in Lower Michigan were confined to the southeastern United States. The jack pine stands moved north and west within the past ten thousand years (Mengel 1964, Mayfield 1988b). Fossil material from New Providence shows arboreal birds to be present on the Great Bahama Bank during the last glacial stage of the Wisconsin (Brodkorb 1959, Olson and Hilgartner 1982). Of the 15 species Brodkorb identified six are extinct species that occur today in the pine forest (Lee 1996) suggesting these forests were on the northern Bahama Islands since at least the late Pleistocene. Conversely, fossil pollen samples indicate that pines were uncommon in southern Florida until about 5,000 yr BP (Watts 1971), further suggesting that the northern Bahamas has a long history of regional importance for avian species preferring, or achieving maximum densities in pine habitats. The long history of pine forest in this area is also implied by a number of endemic races of woodland birds known from these islands. At least four of these are pine obligates (see Lee 1996) as is the endemic Bahama Swallow, Callisichlidon cyanomaviridis.

Massive lumbering of pines in the Bahamas has occurred at least twice in historic times. What remained of the original pine forest after the colonial period was cut in the early part of this century (i.e., sawmill constructed in 1905 near Wilson City, Abaco that ran for 20 years, Campbell 1978) but the history of this period of lumbering is scant. By 1943 nearly all the mature pines on Abaco (and presumably other islands) had been cut, forcing the industry to turn to immature secondary trees for pulp (Campbell 1978). The islands were lumbered again from the late 1940’s through the early 1970’s. Radabaugh’s (1974) surveys were conducted toward the end of the second cutting, and he documented what occurred. The Abaco Lumber Company ran a pulpwood operation on Grand Bahama from about 1948 to 1955, and between 1956 and 1959 Owens-Illinois also lumbered pulpwood there. Jointly, these companies lumbered off about 53,000 ha of the 111,000 ha island. This was clearly most of the pine woodlands as a significant percentage of the island is mangrove. There are no pines on the western end, and the pine forest starts about 6 km west of Freeport. Owens-Illinois moved to Abaco, lumbering through the 1960’s. After a 1967 trip to the south end of Great Abaco C. R. Mason reported that in areas that were unbroken pines a few years ago “Most of the land is cut over, burned over, much of it being planted in cane” (Audubon Field Notes 22(1):30). King et al. (1979) state that all the pines, save for a 1620 ha tract on Little Abaco, and a smaller area at the southern end of Great Abaco, were removed. In 1968, pulpwood cutting began on Andros and activities were completed there in 1973. Owens-Illinois removed all trees over 10 cm dbh (4 inches) and five “seed trees” per acre were left standing for regeneration. By the time of Radabaugh’s 1972 visit, most of Abaco had been lumbered, regeneration was slow and he estimated 20,000 ha to be virtually treeless. He observed unattended forest fires burning for days on both Grand Bahama and Andros. Radabaugh concludes “to the extent that the Kirkland’s Warbler, as a species, relies on pinelands in winter, lumbering could have been detrimental to the point of having contributed to the recent decline in their numbers.”

The timing of the logging operations, combined with the slow regeneration of mature pine forest, compares rather favourably with the limited number of sightings of Kirkland’s Warblers on the northern islands in the middle 2/3 of this century. The relatively large number of records from the 1900’s come from a period prior to the massive systematic removal of trees. Despite survey attempts by Bond in the 1930’s and Mayfield and Van Tyne 1949 there is an absence of any records on these pine islands from earlier in this century until the late 1950’s. This corresponds with lumbering and protracted periods of regrowth. A consistent number of reports are available between 1959 and 1969 for Grand Bahama (Hundley 1967). As most reports are for pine forest, it is clear that observers were returning annually to specific small isolated pockets of forest that had not been removed by the 1956-59 Owens-Illinois operation. Radabaugh found no Kirkland’s Warblers on these islands in 1972 and Emlen (1977) found none on Grand Bahama between 1968 and 1971. The 1969-74 Grand Bahama reports by Fluck (in Radabaugh 1974) were from sites with young pines. By 1989, 16 to 30 years after the termination of lumbering, there has been a small resurgence of sighting in the northern islands, and our recent records are from tertiary regrowth pine forest which are at least 25 to 30 years in age.

We should point out that we are not the first to equate large-scale lumbering of pines in the Bahamas with the decline of Kirkland’s Warblers. Radabaugh (1974) expressed obvious misgivings, but his statements were guarded as a result of inadequate winter habitat information and his own inability to locate these warblers in pine forest. Terbough (1974, 1980) discussed the adverse effects to wintering Kirkland’s Warblers because of clearing
of pines from the northern islands. Andrew Paterson (1972), writing near the completion of the mid-1900's lumbering operations, was highly concerned about the effects of pulpwood operations on Kirtland's Warblers. While he provided no supportive information, Radabaugh (1974) mentioned that Paterson saw three on Andros during a 3.5 year residence ending in May 1971. Therefore, we assume his 1972 reference to these birds and pines is from personal experience.

Fire Ecology
While it is clear that fire is an important contributing element in the pine woodlands and other habitats of the Northern Bahamas, the natural frequency and seasonality of fires, and how they effect suitability of Kirtland's Warbler habitat is unknown. The Lucayan National Park sites had been burned 3.5 years prior to our 1995 observation. Our Abaco sites (1990 and 1995) looked to have also been burned on a similar time frame. Lightning is the only non-anthropogenic source of fire ignition, and its primary occurrence in rainy seasons would insure that, in the past, most fires would be contained in small areas. In South Florida pine sands it takes two to three years for sufficient fuel to accumulate for natural burns, and in 10 to 15 years herbaceous plants become shaded out by the development of a closed hardwood layer (Snyder et al. 1990). Prolonged intervals between fires result in high fuel loads that cause intense fires that in turn often kill canopy trees.

It would appear that fire is required for the maintenance of open Caribbean Pine forest, and that fire dictates the growth, diversity, and relative dominance of understory plants. Fires on the northern islands typically consume only litter and some understory, and the open canopy does not normally support crown fires. Additionally, the drying of fuel is accelerated by the open canopy, allowing fires to sweep through the forest in rainy seasons. This is key for lightning-induced fires. Pine needles accumulate on the ground and decompose slowly, and the grassy herb layer contributes to fuel loads. The pine islands have obvious adaptation to fire. Caribbean Pine's long needles shield vulnerable buds, and thick insulating bark protects the trunks. While hardwood shrubs are 'killed' by fire, most resprout from below ground. Herbs respond with rapid regrowth. Thus, it would appear that fire is not only a natural element of the Bahama pine forest, but that it is a necessary process. In South Florida similarly-structured Slash Pine (Pinus elliottii var. densa) forest becomes tropical hardwood hammocks with a reticent overstory of pine within just two or three decades of fire exclusion (Robertson 1953). In areas surveyed by Lee (1996) on Abaco, where hot fires apparently killed the pine canopy, dense stands of young (estimate 8-15 years) Caribbean Pines formed solid monocultures of closely-spaced, heavily-foliaged trees. Few birds used these stands and structurally they were quite different than the sites where we observed Kirtland's Warblers. If this regrowth is also typical of regeneration of cut-over forest in the Bahamas, much of the pine area would have been unsuitable to Kirtland's Warbler for 1.5 to 2 decades after lumbering and again after the pulpwood operations. Emlen (1977), who did not find the species on Grand Bahama, referred to most of his study sites as sub-mature pine forest. Old stumps at his sites indicated that pines had previously achieved maximum growth at about 35 cm diameter. However, it is obvious that pines of this size represented secondary growth. Campbell (1978) reported some virgin pines to have achieved diameters exceeding 30 inches (76 cm). In the forest Emlen studied canopy cover varied from 19.4% to more than 60% in 0.5 ha patches. Older trees in Emlen's study areas provided a 10-20% canopy. This lower density cover is consistent with the intermediate aged pine forest at our 1990 and 1995 observation sites where the pines were widely spaced.

Use of Other Habitations
We recognize that Kirtland's Warblers do winter in scrub and low coppice. While there are no published records of birds in high scrub (trees 15 feet or more in height (Mayfield 1972), a habitat that abounds throughout the Bahamas) our Grand Bahama bird retreated into high scrub. Maynard noted on New Providence that these warblers "retire at night to roost in higher dense shrubbery" near the overgrown old fields where he collected them. We should also note that other major natural terrestrial communities in the Bahamas [coastal rock, sand strand and Umbilia white sand, Sabal palmetto flats (a freshwater community), salt marshlands, and mangrove; Correll and Correll 1982] have never been reported as wintering habitats for these warblers despite the fact that other migrant Parulidae commonly occur in all of them. Little mature tropical hardwood forest remains in the Bahamas, and while there are no reports of Kirtland's Warblers from this habitat, we are not aware of any winter bird surveys in this habitat type. However, these forests generally lack the type of understory characteristic to pine forest and we assume they are for the most part unsuitable. Sandy Sprunt (pers. comm.) reports a Kirtland's Warbler that he and Noel and Helen Snyder found on Inagua in an open woodland with an overstory of Buicida bucerus (locally called "Inagua Oak"). The understory was fairly open as well and comprised of Crabwood (Chermisus lucidus and/or Coccoloba frugii), Strongback (Krugiodendron forrestum and/or Bourreria currita) and tear coat. We should also point out that there is little indication that Kirtland's Warblers are edge species.

While the decline of the Kirtland's Warblers after 1890 was linked to the loss of breeding habitat and the invasion of Brown headed Cowbirds into Northern Michigan, this decline also occurred in the same general time that pines were systematically and repeatedly removed from the Bahamas. (To this time scale should be added the lag time necessary for forest regeneration.) During lumbering and regeneration followed by pulp wood harvest and regeneration, the number of Kirtland's Warblers reported from the Bahamas (the northern islands in particular) was...
minimal when compared to the documented field efforts of qualified observers (see above). As best we can determine, 74 (75%) of the 99 winter reports come from pine islands or their offshore cays, and at least 33 (33%) [60% where habitat is discussed] of these reports were associated with pines. Hundley (1967) states that, of the number of records that came from Grand Bahama in the late 1950's and 60's, "almost all birds were seen in areas of Caribbean Pine (Pinus caribaea) with an understory of Poison Wood (Metopium toxiferum) and Palmetto (Sesneroa repens)." Only two of 57 individuals reported from Grand Bahama are from the western end where pine forest does not occur. At this time, there is strong documentation for Kirtland's Warblers using the low understory vegetation in open canopy Caribbean Pine forest. In fact, Kirtland's Warblers use of low scrub may, in part, be a response to deforestation and degradation of winter habitat. Minimally this information should be taken into account during future winter survey efforts.

From a historical perspective it appears that much of the scrub habitat in which Kirtland’s Warblers occur is an artifact of past land use. Byrne (1980) studied the vegetation of Cat Island and traced the change in plant communities. From his studies it is clear that the non-pine islands were dominated by hardwood forests prior to colonization. Furthermore, it is apparent that much of the timber was removed prior to the late 1800's. Wood exploitation began in the sixteenth century and continued into present times. Several quotes will illustrate the intensity of early lumbering.

"Wood cutting is gradually becoming more difficult and less lucrative. On the islands lying next to Providence the best wood is always cut off, and thus there must be recourse to islands lying farther away, or the woods must be more deeply gone into" (Schoepf 1778).

On Cat Island it was necessary to have a man on guard at the northeastern part of the island to prevent men from Eleuthera from cutting wood (Stiles 1836). By the mid-1800's the wood on Cat Island closest to settlements had been removed but elsewhere the forest was still intact. Harvey, a surveyor who visited the island in 1855, wrote "The timber on St. Salvador (Cat) is fine and large and might be made a profitable branch of commerce; madiera, mahogany, casada, prince-wood and brazeletta, yellow wood and lignum vitae are found in every part but in greatest abundance on the east side" (Harvey 1858).

From the early reports it appears that scrub habitats in non-pine areas in the Bahamas would be much more restricted prior to the mid-1800's than from the late 1800's to present. The natural shrub communities would for the most part be limited to coastal areas and these are generally too tall or too dense to provide what is considered as good habitat for Kirtland's Warblers.

The shrub/scrub in which Kirtland's Warblers now occur result from lumbering and a series of agricultural failures which left a patchwork of abandoned fields. Small scale cotton farming occurred in the early 1700's followed by extensive cotton growing from the late 1700's through the Civil War. The short-lived but extensive sisal industry (1887-1896) was followed by the even less successful culture of bowstring hemp (1887-1940).

Unresolved Factors
There are three major obstacles preventing us from presenting a unquestionably sound case for wintering Kirtland’s Warblers being primarily pine woodland specialists. Unfortunately none of these obstacles can be overcome with the amount of information presently available. While these factors decrease the strength of our belief that pine woodlands are essential to these warblers they do not negate them.

First, there are no records of wintering Kirtland's Warblers prior to extensive, and essentially complete, habitat modification. This modification results from nearly complete hardwood timber removal, continuous lumbering, agriculture, and man-induced fire. The magnitude of these activities can not be overstated. Therefore, what has been reported is the response of these warblers to man's activities and occurrence records are at best only suggestive of pre-Columbian habitat needs.

Second, while the Northern Pine Islands (particularly New Providence and Grand Bahama) account for a large proportion of the available records, it is also clear that this is where most of the human activity is, and has been, centred. Therefore, the records reflect the frequency of reported encounters and not necessarily the actual distribution of the birds throughout their wintering range. Statistically, human population size on islands accounts for 70% of the variability. However, even with this bias recognized over 60% of the sightings where habitat is mentioned are from pine forest, while significant areas of all these islands do not support pine forest. In addition to observer effort, these islands were the most extensively altered for agriculture and thereby had a history of abandoned fields that were attractive to Kirtland's Warblers.

Third, we are not comfortable with the accuracy of identification for all reports. Anthony White (pers comm.), for example, is aware of 10-12 reports additional for last year (1995), but only one of them was accompanied with enough details to determine it was probably a Kirtland's Warbler. These reports are not included in this survey. To partly offset this problem we chose to include only records that were supported by specimens, were in published accounts in referred journals, or were obtained by bird students we personally know to have the skills to correctly identify this species. Obviously because of this many good records were excluded, but even some of the published ones are suspect.

Anthony White (pers comm.) points out that the yellow underparts of the resident race of Yellow-throated Warbler (Dendroica dominica flavescens) are a major source of
confusion with the Kirtland’s Warblers on Grand Bahama. He cites an example of a group of bird watchers lead by a well-known ornithologist who watched a bird they believed to be a Kirtland’s for 30 minutes. Everyone was convinced of the identification, but a review of photographs and video tapes later proved it to be a Yellow-throated Warbler!

Records made by short term visitors who are unfamiliar with the countries avifauna should be examined carefully. In the Florida Audubon trips to Grand Bahama (Hundley 1967, Blanchard 1965) reports indicate that some birds were seen working their way up the sides of trees like a nuthatch or a Black-and-White Warbler. This behaviour is well known for Yellow-throated Warblers in the Bahamas and is, except for these reports, unknown for Kirtland’s Warblers. Thus, some unknown percentage of the early to mid-1960’s Grand Bahamas reports are highly suspect but clearly not all are erroneous. Emlen (1977) recorded densities of 14 individuals of the resident race per km² on Grand Bahama. Thus, anyone spending any time at all on the island would quickly discover their error or be reporting large numbers of Kirtland’s Warblers. P. Funk, for example, banded two and reported 5 others between 1969-72 (Radabaugh 1994) and surely his sightings were identified correctly. However, if we exclude the reports from the period Florida Audubon visited the island then Grand Bahama would have only 7 reports (9% of total) and 13 (7%) individuals. Still the number of reports from the northern islands (60 [78%]) and from the pine islands (45 [58%]) is still high, and even if all the reports from Abaco and Grand Bahama are excluded, the northern pine islands still account for a statistically significant number of records and reports when compared to available land mass.

This potential for mis-identification is exacerbated by the fact that there are no adequate illustrations of flavescens in any available field guides. In reality, however, the different foraging heights of the two species in Caribbean Pine forest, and complete eye ring and the tail-wagging behaviour of Kirtland’s Warblers should minimize any confusion once field workers are armed with information.

We recognize that we have only hints as to the preferred habitat use of Kirtland’s Warblers. All information comes from a period after which the natural plant communities of the Bahamas have been totally altered by man’s activities. It is clear that wintering Kirtland’s Warblers are adapted to successional windows just as they are on their breeding grounds. Fire and possibly cyclones are the apparent natural regulatory agents for these windows. Present day conditions in Caribbean Pine forest provide the only extensive areas of “natural” habitat, but these too have been greatly modified by man. It is not clear if large mature stands of Caribbean Pine once provided near continuous blocks of suitable understory shrub habitat or if the warblers focused activities in the shrub communities of mid-age pine stands as we see today.

Because of the ability of large mature shrubs (tall coppice) to sprout after fire or cyclones it would appear that these communities probably offered only short-lived shrub habitat prior to agriculture and this would not provide conditions stable enough to meet long term needs of wintering Kirtland’s Warblers. Minimally our biogeographic sketch dictates that Caribbean Pine communities can not be overlooked when developing conservation strategies for these warblers, and suggests that they have been key to the birds’ pre-colonial winter habitat needs. We conclude that wintering Kirtland’s Warblers tolerate a range of shrub habitat types. They occur in old abandoned fields (Maynard in Mayfield 1972) and other man-disturbed habitat. The large number of records from the late 1800’s, many from abandoned fields, may stem from the agricultural failure of the short lived sisal hemp (Agave mexicana) industry. The records from Eleuthera are from one of the most heavily-disturbed islands in the Bahamas. At the site where Sykes found two birds near Governor’s Harbour in 1985 the birds foraged in a small area that had been cleared several years before. Except for the pine islands, available habitat is limited even in the wake of agricultural practices. Sykes (1989) determined that “at least 2%” of Eleuthera’s uplands were potential winter habitat for Kirtland’s Warblers. Prior to pre-colonial deforestation we suspect that there was little to no habitat for this bird on Eleuthera or most other non-pine islands. Natural habitats are limited to low-scrub (Radabaugh 1974, Mayfield 1972, 1996), xeric scrub (Dominican Republic; Faanes and Haney 1989), and the shrub understory of open-canopy free climate woodlands of Caribbean Pine forest (this study). In all likelihood these warblers are not responding to specific plant communities per se but to natural or man-influenced conditions that provide a successful opening favourable to their low-scrub requirements. Under certain circumstances hurricanes might contribute to successional communities that could temporarily benefit these birds. Hurricanes not only blow down trees but cause flooding in low lying areas that kill pines (Hurricane Betsy killed large tracks of pines in 1965 [Campbell 1978]). The intermediate aged pine forests of the northern Bahama islands provide extensive, natural, fire-maintained stands of shrub understory habitat, and are therefore today important to wintering Kirtland’s Warblers. Their occurrence on pine islands is statistically significant while other factors size of islands and latitude is not.

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