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18 May 1979

Cross-fostering of a Wood Warbler

Abstract. Based on results with a related species, cross-fostering can  
be used to produce young of the endangered Kirtland's warbler, Dendroica  
kirtlandii, in seemingly suitable areas where it does not now occur. Eggs  
of yellow warblers, Dendroica petechia, were substituted for clutches of  
3 other species. Four of 6 chipping sparrow, Spizella passerina, nests  
produced yellow warbler young that were fed by adults to independence.

## Cross-fostering of a wood warbler

Transplanting eggs of the endangered Kirtland's warbler, Dendroica kirtlandii, to nests of other species has been suggested as a means of introducing the species to new areas (1). Renesting by parents whose eggs are stolen would maintain production on existing sites while the transplanted eggs were used to establish populations on seemingly suitable but unoccupied areas. Rearing of experimental fosterlings has been reported for several species of birds (2) but the few successful cases in which passerines have been experimentally cross-fostered in the wild involved transfer between closely related species (3). Other attempts with little or no success (4) suggested that before the technique is attempted on Kirtland's warblers it should be assessed on a similar species.

Another member of the genus Dendroica, the yellow warbler, D. petechia, was chosen as a model (5). Criteria for foster parents were 1) similarities to yellow and Kirtland's warblers in size and diet; 2) no close genetic relationship to avoid the possibility of generating undesirable hybridization (6); and 3) widespread occurrence at fairly high densities in the jack-pine habitats typical of Kirtland's warblers (7). On these bases together with local availability, 3 species were selected: chipping sparrow, Spizella passerina; field sparrow, S. pusilla; and house wren, Troglodytes aedon.

During the spring of 1978, 17 complete clutches of yellow warblers were substituted for entire clutches of these host species (8). Nest-to-nest transport was in insulated cups and took 60-90 minutes. Transfers were made among 7 localities in Kalamazoo County, Michigan, between 26 May and 8 June. Clutches varied in age from fresh to about 2 days pre-hatching.

The failure to recognize one's own young, leading to parental care of aliens, would seem to be disadvantageous if it occurred under natural conditions (13). Such failure occurs naturally, of course, in nest parasitism (14). Many species of birds reject foreign eggs, evidently by learning the appearance of their own eggs (15). Chipping and field sparrows are among the species which, as frequent hosts of the brown-headed cowbird, Molothrus ater (16), seem not to have evolved the ability to reject foreign eggs; consequently, it is not surprising that they also accepted yellow warbler eggs. House wrens are rarely victims of cowbird parasitism, presumably because the entrance holes of most of their nests are too small for the cowbird to enter (17). There was no evidence that the wrens rejected the warbler eggs; perhaps the low hatching success arose from inability of the wrens to cover the larger eggs satisfactorily.

Because the transfer of nestlings between nests is probably exceedingly rare in nature, the advantage in being able to recognize one's own nestlings would be slight. Likely causes of cross-fostering failure at this stage could be predicted to be either 1) failure of parental care to meet the requirements of the alien young (the diet provided does not supply adequate nutrition, for example) or 2) failure of young to provide appropriate stimuli for essential aspects of parental care (for example, lacking signals to trigger food-bringing). The house wren evidently fell in the second category. During observations totaling 78 minutes at 2 nests each containing a single young about 8 days old, no feedings were observed. The normal feeding rate should be about 5 feedings in this time period (11), and at contemporaneous house wren nests containing house wren young such feeding rates were observed. Exactly how the cues provided by the yellow warbler nestlings were insufficient is not known.

For many birds, the proximity of other fledged broods of the same and different species probably allows frequent opportunities for mistakes in parental care at the fledgling stage. Although some birds have been shown to restrict feeding to their own young (13) a number of reports exist of adults feeding heterospecific fledglings (18). In this context, the willingness of chipping and field sparrows to care for young so different from their own in appearance, voice, and actions is less surprising.

Based on the results presented here, it seems likely that cross-fostering can be used to produce Kirtland's warbler young in seemingly suitable areas where Kirtland's warblers do not now nest (19). It is possible that the technique could be used to increase production on current nesting grounds but, because the delay resulting from forced renesting might decrease numbers of pairs which attempt second broods (20) and because of the effectiveness of cowbird control in raising nesting success (21), this use of cross-fostering seems less attractive.

The chipping sparrow is the foster parent of choice; however, the field sparrow might do as well if protection from predation is given (22). For example, predator-proof fences might be erected around the nest. The fact that in only one case in 5 were more than 3 young reared to fledging by the foster parents suggests that clutches of 4-5 Kirtland's warbler eggs should be divided between 2 foster nests. It might even be desirable to place only a single Kirtland's warbler egg in each host nest to eliminate intra-brood competition; in this case artificial eggs might be added to maintain the clutch at the size of the host

Two additional questions important in deciding whether to use cross-fostering as a management tool are yet to be answered: will the cross-fostered young return to the area where they were reared (23) and will their sexual activities be directed toward members of their own or their foster parents' species (24)?

Cross-fostering, in addition to its management potential, should prove an important tool in the experimental study of geographical distribution, reproductive isolation, and many aspects of parent-offspring relationships.

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24. The experiments of K. Immelmann, *Die Naturwissenschaften* 7, 169 (1965) and P. Sonnemann and S. Sjölander, *Z. Tierpsychol.* 43, 344 (1977) suggest that sexual imprinting on the foster parent might occur in both sexes; whether the practical result would be to prevent the formation of warbler warbler pairs requires field testing.
25. Supported by Michigan Endangered and Threatened Species Program, Michigan Department of Natural Resources, Project No. E/T--1, Job No. 601.9 and by a Western Michigan University Research Fellowship and Grant. M. T. McCann, M. Reed, R. C. Roberts and S. I. Rothstein provided helpful comments on the manuscript. Invaluable field assistance was provided by M. Reed. J. Scott kindly allowed me to use her notes on activities at several nests. I am indebted also for help from R. J. Adams, Jr., L. G. Brewer, and G. Shy, and to the various landowners for access to the study areas.

## ABSTRACT

Habitat descriptions were made on a portion of the breeding range of Kirtland's warbler (Dendroica kirtlandij). Jack pine (Pinus banksiana), regenerated either by wildfire or grown from a non-serotinous cone source, was the dominant tree species. Contrasts of habitat parameters, according to stages of warbler use, revealed age and site differences. Comparisons between used and unused areas by warblers on sites of comparable origin show that both tree and ground cover components appear to be used as proximate cues by breeding birds. There is an inverse relationship between territory size and interspersions, the number changes between tree cover and openings. The highest density of territorial males occurs when the interspersions ratio is high and the amount of tree cover and openings is nearly equal.

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The concern for endangered species has been aptly demonstrated by the efforts made to secure the survival of a rare songbird, the Kirtland's warbler (Mayfield 1963, Shake and Mattsson 1975). The direction these efforts will take has been outlined in the Kirtland's Warbler Recovery Plan (Byelich et al. 1976), prepared by a team of qualified individuals representing private interests and state and federal agencies. The emphasis of the plan is on managing the special breeding habitat that is known to be required by the warbler.

The jack pine community is most often associated with the Kirtland's warbler and characterizes this special habitat. The birds typically occupy large tracts of even-aged jack pine stands that are interspersed with openings (Mayfield 1960). The trees may range in age from 8 to 20 years and as a stand proceeds through this successional period, warbler populations increase to a peak for 3 to 5 years, then decline and, finally, disappear.

Fire is the most important environmental influence that sets back succession in this community type. Historically, wildfires burning over vast areas may have provided the specialized habitat required by the Kirtland's warbler. Recently, management practices have included prescribed burning and planting programs to create this habitat. The amount of young jack pine, however, is in short supply, and it has been suggested by the members of the Recovery Team that this is the most

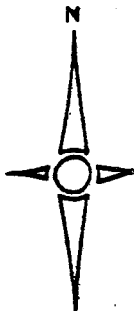
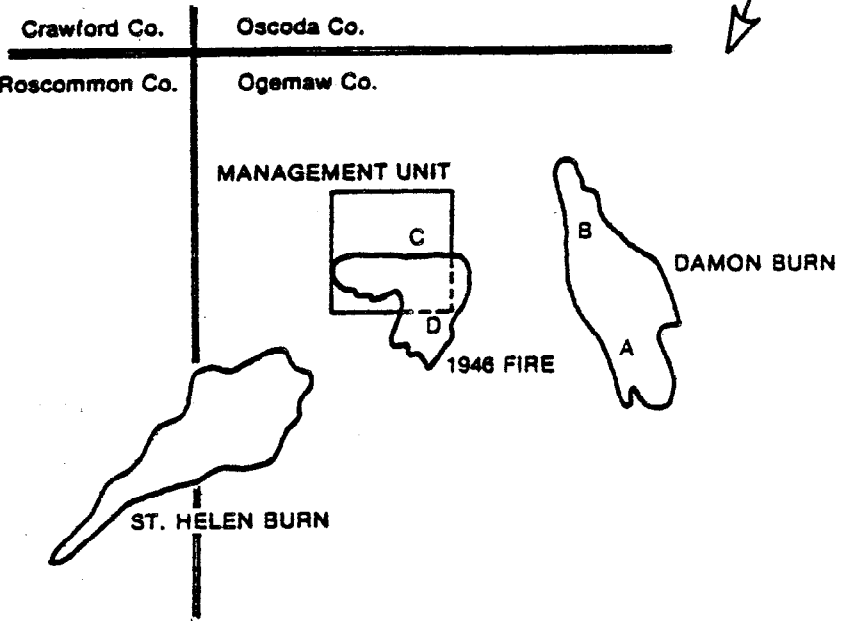
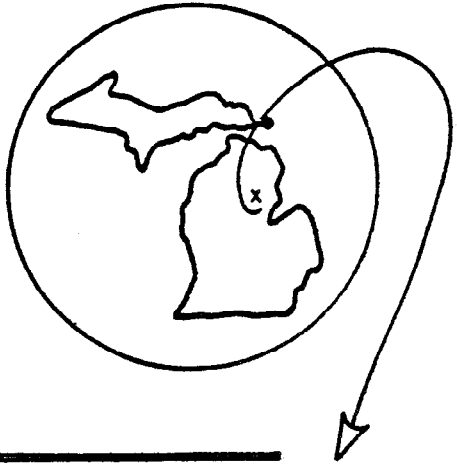
important factor that limits breeding populations of Kirtland's warblers. The uniqueness of the habitat is not well understood and quantitative information is lacking. This study was designed to describe and evaluate certain habitat parameters associated with Kirtland's warblers on a portion of its breeding range.

## METHODS AND MATERIALS

The study area is located in the northwest corner of Ogemaw County and in a small part of the adjacent Roscommon County in Michigan's lower peninsula (Fig. 1). Jack pine is the predominant cover type on glacial outwash plains of dry, pervious, sandy soils. The topography is relatively level, broken by gently rolling hills.

Kirtland's warblers have been known to occupy habitat in this general vicinity since 1961. Their use of the area is related, for the most part, to specific sites, the boundaries of which are shown in Fig. 1. These areas have, at least in part, a common history of wildfire. In May 1966, approximately 1200 hectares (ha) of mature jack pine and some hardwoods burned near the small town of Damon, Michigan. A wildfire in April 1964, near St. Helen, Michigan, straddled the Roscommon and Ogemaw County lines and burned approximately 1200 ha of jack pine and hardwoods. On another site between these two burns, a fire in May 1946, consumed approximately 790 ha of jack pine. Part of the latter was incorporated into the Ogemaw County Kirtland's Warbler Management Unit, designated in 1957 and totaling approximately 1030 ha (Radtke and Byelich 1963). The site that is presently used by warblers and is a focus for this study consists primarily of jack pine released by a commercial cutting and grown by open cone regeneration, natural seed dispersal from nonserotinous cones.





KIRTLAND'S WARBLER USE AREA

- A RECENT
- B PEAK
- C DECLINING
- D PAST



Four stages of use by Kirtland's warblers on the Ogemaw County sites were classified by reviewing annual census data (Table 1). A southern portion of the Damon burn (Area A in Fig. 1) attracted warblers for the first time in 1976 and was characterized as the most recent warbler use area. To the north, in this same burn (Area B), habitat has been used since at least 1975 and, perhaps, earlier. Counts in recent years suggest that peak numbers of warblers are presently occupying the site. In the northern part of the Ogemaw Management Unit (Area C), an increase in Kirtland's numbers in the early '70's followed by a gradual decrease in recent years indicates that use in this area is declining. Although habitat resulting from the 1946 fire was used by warblers in 1961, it is no longer occupied and was classified past use (Area D).

Field observations on the study area revealed two other warbler use areas. A site within the Damon burn adjacent to the area of recent use has had no occupation but appears to be likely habitat (J. Weinrich, pers. commun.). Adjoining or within 2 km of the Ogemaw Management Unit, areas were located that had been used intermittently. Male Kirtland's warblers have been observed on these sites, but the birds were neither noted consistently on a daily basis nor during the formal June census.

Habitat variables were measured in August and September 1977 and 1978, and were contrasted among the recent, peak, declining, and past use areas. The study was expanded after the first field season, and two additional contrasts involving warbler use sites were made: recent versus likely habitat; and, declining versus intermittent use areas. Sampling in 1978 also included Kirtland's warbler nest sites that had

Table 1. Kirtland's warbler use, expressed as the number of singing males per 100 hectares, on study areas in Ogemaw County.<sup>a</sup>

Year	Damon Burn Area A (Recent)	Damon Burn Area B (Peak)	Management Unit Area C (Declining)	1946 Fire Area D (Past)
1961	0	0	0	14
1971	0	0	10	0
1972	0	0	17	0
1973	0	0	25	0
1974	0	0 <sup>b</sup>	17	0
1975	0	14	10	0
1976	1	12	9	0
1977	6	25	3	0
1978	4	11	3	0

<sup>a</sup>Based on census results from Ryel (1978).

<sup>b</sup>Census in this area in 1974 was incomplete.

been located by Dr. L. Walkinshaw and Dr. N. Cuthbert. Those sites found in the Damon burn (Area B) were compared to those found in the Management Unit and the St. Helen burn.

A modified plot-transect method was used to sample the study sites. Each transect was 120m in length, this distance representing the radius of an approximate 4 ha area. The orientation of the transect was randomly chosen from eight possible compass points. In 1977, transects were run the full length in one direction and were started near the location of a singing male Kirtland's warbler that had been determined from that year's census maps and field observations. The following year, transects were centered around the locations observed and censused in 1978, and two 60m lines were run in opposite directions. In those areas where no warblers were present at the time of the study (i.e., past and likely habitats), transects originated either around male warblers located on 1961 census maps or within 16 ha blocks selected from aerial photos. A minor deviation from this scheme was used at each of the eight nest sites. Two transects were centered exactly at the site and 60m lines were run in the four cardinal directions. For each transect in the recent, peak, declining and past use areas, at least one jack pine tree characteristic of the stand was cut at its base, aged by counting annual growth rings, and measured for total height, diameter at breast height (dbh), and the last five shoot growth intervals.

The transect consisted of 12 contiguous 10m plots, 5m wide. On each plot, living and dead tree stems were counted by species in four height classes: less than 1m, 1-2m, 2-3m, and greater than 3m. Multiple tree stems resulting from suckering growth were considered as

one unit by each height class. Nested within each plot a modified cover grid, approximately 0.5m high with 25 point intercepts was used to examine, by species, the low shrub and herbaceous layer and other ground cover components. The grid was placed as close to the center of the plot as tree stems would allow and moved three more times so that 100 points were counted per plot within an approximate 1m<sup>2</sup> area. Percent cover was determined from this figure.

The 10m transect line was divided into 20-0.5m segments and at each point interval, ground cover by species, measuring less than 0.5m high, and tree cover in two height classes, 0.5m to 2m and greater than 2m, were noted. Percent tree cover was calculated by totaling the number of such points recorded and dividing by the total number of points possible. Two other parameters involving stand structure were determined from the line. An interspersion value was calculated by counting the number of times a change between jack pine and open ground cover appeared within the intermediate height class (0.5-2m). For this same height category, the average length of open spaces was determined by measuring the distances where no tree cover had been noted and dividing by the number of such openings.

Observations of 12 male Kirtland's warblers that were readily visible and audible from roads were made on the study area in May and June 1978, to determine territory size. At least one side of each defended area was measured by pacing along a road, the limits of those movements thought to be associated with territorial behavior. With the knowledge of other physical or social boundaries, a map of each territory was drawn on an aerial photo, and the approximate size was measured with a Bryant transparent grid. A transect line as described

tested at the 0.05 probability level and is noted if found otherwise

Variations about reported mean values are designated by one standard

error.

## RESULTS

Thirty-five genera of plants representing 19 families were identified on the study area (Table 2). In addition, family identification was made for specimens belonging to Gramineae and Cyperaceae. Unidentified mosses have not been included and lichen taxonomy for species noted as pixie cups, British soldiers, and reindeer moss was not determined.

The plant species were broadly classified according to their life form as either tree or ground cover components. Trees included pine, willow, oak, juneberry, hawthorn, black cherry, maple, and dogwood. All other species were classified as ground cover and some were further divided according to life form. They include grasses and sedges; shrubs-blueberry, sweet fern, and sand cherry; and, mosses and lichens.

Jack pine was the predominant tree species on all sampled sites. There was 100 percent frequency of occurrence on the 5 x 40m transect segments except in the past use area where one segment ran through a large opening.

Jack pine on the recent, peak, declining, and past use areas ranged in age from 11 to 32 years (Table 3). Height of the trees ranged from  $2.8 \pm 0.1\text{m}$  to  $7.0 \pm 0.3\text{m}$ . The mean diameter at breast height (dbh) was three times as large on the area of past use compared to the recent and peak sites while the total basal area was about 12

Table 2. List of vascular plant species<sup>a</sup> found on transects sampled in 1977 and 1978 on study areas in Ogemaw and Roscommon Counties.

Scientific name	Common name
Equisetaceae	
<u>Equisetum hyemale</u>	horsetails
Lycopodiaceae	
<u>Lycopodium</u> sp.	clubmoss
Polypodiaceae	
<u>Pteridium aquilinum</u>	bracken fern
Pinaceae	
<u>Abies balsamea</u>	balsam-fir
<u>Pinus strobus</u>	white pine
<u>Pinus resinosa</u>	red pine
<u>Pinus banksiana</u>	jack pine
Gramineae	grasses
Cyperaceae	sedges
Liliaceae	
<u>Lilium philadelphicum</u>	wood lily
Orchidaceae	
<u>Spiranthes gracilis</u>	slender ladies' tresses
Salicaceae	
<u>Salix humilis</u>	gray willow
Myricaceae	
<u>Comptonia peregrina</u>	sweet fern
Fagaceae	
<u>Quercus</u> sp.	scrub oak
Ranunculaceae	
<u>Anemone</u> sp.	anemone
Rosaceae	
<u>Spiraea alba</u>	meadow-sweet
<u>Amelanchier</u> sp.	juneberry
<u>Crataegus</u> sp.	hawthorn



Table 2. (cont'd.).

<u>Fragaria virginiana</u>	strawberry
<u>Potentilla tridentata</u>	three-toothed cinquefoil
<u>Potentilla argentea</u>	silvery cinquefoil
<u>Rubus</u> sp.	blackberry
<u>Rosa</u> sp.	wild rose
<u>Prunus pumila</u>	sand cherry
<u>Prunus serotina</u>	black cherry
<b>Aceraceae</b>	
<u>Acer rubrum</u>	red maple
<b>Rhamnaceae</b>	
<u>Ceanothus</u> sp.	New Jersey tea
<b>Violaceae</b>	
<u>Viola abunca</u>	sand violet
<b>Cornaceae</b>	
<u>Cornus racemosa</u>	gray dogwood
<b>Ericaceae</b>	
<u>Epigaea repens</u>	trailing arbutus
<u>Gaultheria procumbens</u>	wintergreen
<u>Gaultheria hispidula</u>	snowberry
<u>Arctostaphylos uva-ursi</u>	bearberry
<u>Vaccinium</u> sp.	blueberry
<b>Apocynaceae</b>	
<u>Apocynum androsaemifolium</u>	dogbane
<b>Rubiaceae</b>	
<u>Houstonia longifolia</u>	long-leaved bluet
<b>Compositae</b>	
<u>Liatris</u> sp.	blazing star
<u>Solidago</u> sp.	goldenrod
<u>Aster</u> sp.	aster
<u>Helianthus</u> sp.	sunflower
<u>Cirsium</u> sp.	thistle
<u>Hieracium aurantiacum</u>	orange hawkweed

<sup>a</sup>According to Gray's Manual of Botany compiled by Fernald (1950).

Table 3. Age, total height, dbh, total basal area, and shoot growth from 1974-1977 of 12 jack pine trees sampled within each Kirtland's warbler use area in 1977 and 1978.

Measure	Use Area			
	Recent	Peak	Declining	Past
Stand age (yrs)	11-12	10-12	16-32	20-31
Total height (m) $\bar{X} \pm S. E.$	2.8 $\pm$ 0.1	2.8 $\pm$ 0.1	3.7 $\pm$ 0.2	7.0 $\pm$ 0.3
dbh (cm) $\bar{X} \pm S. E.$	2.8 $\pm$ 0.2	2.8 $\pm$ 0.2	4.4 $\pm$ 0.6	10.9 $\pm$ 0.5
Total basal area (cm <sup>2</sup> )	89	86	232	1081
Shoot growth, 1974-1977 (cm) $\bar{X} \pm S. E.$	122 $\pm$ 4	120 $\pm$ 6	116 $\pm$ 6	120 $\pm$ 5

times greater. Although, the total amount of shoot growth was not significantly different between use areas, there was a significant difference in annual growth of shoots as measured by interval length between years using the Friedman analysis of variance by ranks (Siegel 1956). The greatest growth occurred in 1976 and 1977.

Ground vegetation on study sites was sampled during August and September. In order to determine the relationship between the percent cover values obtained during the sample period and the May and June period when warblers were breeding, a series of 20 semipermanent plots were measured monthly from 8 June to 5 September 1978. The plots were located near roadsides adjacent to areas used by warblers and ground cover only was sampled using the grid method of 100 point intercepts. There were no significant differences in percent cover of individual species nor total cover by month.

On transects sampled in 1977 and 1978, the number of jack pine stems differed significantly by warbler use area (Table 4). A high of 10,600 stems per ha was recorded in the recent use area. A low of 1600 stems per ha was measured in the area of past use. On sites with a higher stem density, there was relatively more jack pine in shorter height classes. Trees greater than 3m high were significantly more abundant in the areas of declining and past use. For these same use categories, this difference was also reflected in the percent tree cover over 2m high.

The number of oak stems was significantly different only in the peak use area (Table 4). Particularly on this site and in other parts of the Damon burn, oak regeneration is in the form of bushy, suckering growth. The species, however, was relatively more abundant in the past

Table 4. Means  $\pm$  S. E. <sup>a</sup> for parameters including tree, ground cover, and stand structure components measured in 1977 and 1978 on Kirtland's warbler use areas.

Parameter	Use area			
	Recent (n = 24)	Peak (n = 24)	Declining (n = 24)	Past (n = 30)
<b>Tree components</b>				
Species (No. stems/100m <sup>2</sup> )				
Jack pine (live)	106 $\pm$ 22 <sup>b</sup>	84 $\pm$ 16 <sup>bc</sup>	37 $\pm$ 4 <sup>c</sup>	16 $\pm$ 2 <sup>d</sup>
Height				
< 1m	16 $\pm$ 6 <sup>b</sup>	6 $\pm$ 1 <sup>bc</sup>	6 $\pm$ 2 <sup>bc</sup>	2 $\pm$ 1 <sup>c</sup>
1-2m	65 $\pm$ 14 <sup>b</sup>	40 $\pm$ 13 <sup>bc</sup>	6 $\pm$ 2 <sup>cd</sup>	2 $\pm$ 0.5 <sup>d</sup>
2-3m	24 $\pm$ 6 <sup>bc</sup>	38 $\pm$ 8 <sup>b</sup>	12 $\pm$ 2 <sup>cd</sup>	2 $\pm$ 0.5 <sup>d</sup>
> 3m	1 $\pm$ 0.5 <sup>b</sup>	1 $\pm$ 0.5 <sup>b</sup>	13 $\pm$ 1 <sup>c</sup>	10 $\pm$ 1 <sup>c</sup>
Jack pine (dead)	6 $\pm$ 2 <sup>b</sup>	6 $\pm$ 2 <sup>b</sup>	4 $\pm$ 0.5 <sup>b</sup>	2 $\pm$ 0.5 <sup>b</sup>
Oak	2 $\pm$ 0.5 <sup>b</sup>	16 $\pm$ 4 <sup>c</sup>	2 $\pm$ 0.5 <sup>b</sup>	8 $\pm$ 2 <sup>b</sup>
Other <sup>e</sup>	3 $\pm$ 1 <sup>b</sup>	2 $\pm$ 0.5 <sup>b</sup>	2 $\pm$ 0.5 <sup>b</sup>	5 $\pm$ 1 <sup>c</sup>
<b>Height (% cover)</b>				
0.5-2m	21 $\pm$ 2 <sup>b</sup>	32 $\pm$ 4 <sup>bc</sup>	40 $\pm$ 4 <sup>c</sup>	32 $\pm$ 2 <sup>bc</sup>
> 2m	9 $\pm$ 2 <sup>b</sup>	6 $\pm$ 1 <sup>b</sup>	46 $\pm$ 4 <sup>c</sup>	52 $\pm$ 5 <sup>c</sup>
<b>Ground cover components (%)</b>				
Total cover (live)	55 $\pm$ 2 <sup>bc</sup>	51 $\pm$ 3 <sup>b</sup>	62 $\pm$ 3 <sup>c</sup>	78 $\pm$ 2 <sup>d</sup>
Sedge-grass component	16 $\pm$ 2 <sup>b</sup>	11 $\pm$ 2 <sup>b</sup>	29 $\pm$ 3 <sup>c</sup>	28 $\pm$ 3 <sup>c</sup>
Shrub component	34 $\pm$ 3 <sup>bc</sup>	26 $\pm$ 3 <sup>c</sup>	24 $\pm$ 3 <sup>c</sup>	39 $\pm$ 2 <sup>b</sup>
Blueberry	22 $\pm$ 3 <sup>bc</sup>	17 $\pm$ 3 <sup>bc</sup>	10 $\pm$ 3 <sup>c</sup>	25 $\pm$ 3 <sup>b</sup>
Sweet fern	10 $\pm$ 2 <sup>b</sup>	7 $\pm$ 2 <sup>b</sup>	9 $\pm$ 2 <sup>b</sup>	11 $\pm$ 1 <sup>b</sup>
Sand cherry	2 $\pm$ 0.5 <sup>b</sup>	2 $\pm$ 0.5 <sup>b</sup>	5 $\pm$ 1 <sup>b</sup>	4 $\pm$ 1 <sup>b</sup>
Bearberry	1 $\pm$ 0.3 <sup>b</sup>	6 $\pm$ 2 <sup>c</sup>	0.3 $\pm$ 0.1 <sup>b</sup>	1 $\pm$ 0.3 <sup>b</sup>
Moss-lichen component	1 $\pm$ 0.8 <sup>b</sup>	5 $\pm$ 1 <sup>bc</sup>	8 $\pm$ 2 <sup>c</sup>	2 $\pm$ 0.5 <sup>b</sup>
Braken	1 $\pm$ 0.5 <sup>b</sup>	1 $\pm$ 0.5 <sup>b</sup>	0	5 $\pm$ 2 <sup>c</sup>
Other plant species <sup>f</sup>	2 $\pm$ 0.2 <sup>b</sup>	1 $\pm$ 0.2 <sup>b</sup>	1 $\pm$ 0.2 <sup>b</sup>	4 $\pm$ 0.5 <sup>c</sup>
Slash (dead wood)	10 $\pm$ 1 <sup>b</sup>	8 $\pm$ 1 <sup>b</sup>	2 $\pm$ 0.5 <sup>c</sup>	1 $\pm$ 0.5 <sup>c</sup>
Dead plant material, bare ground	34 $\pm$ 2 <sup>bc</sup>	42 $\pm$ 3 <sup>b</sup>	36 $\pm$ 2 <sup>bc</sup>	21 $\pm$ 2 <sup>d</sup>
<b>Stand structure components (based on 40m line)</b>				
Length of open spaces (m)	5 $\pm$ 1 <sup>b</sup>	4 $\pm$ 1 <sup>b</sup>	3 $\pm$ 0.4 <sup>b</sup>	6 $\pm$ 1 <sup>b</sup>
Interspersion value	13 $\pm$ 1 <sup>b</sup>	16 $\pm$ 1 <sup>b</sup>	16 $\pm$ 1 <sup>b</sup>	13 $\pm$ 1 <sup>b</sup>

<sup>a</sup>The same superscript in a row (b,c,d) indicates no significant difference between means.

<sup>e</sup>Includes: balsam-fir, white pine, red pine, willow, junberry, hawthorn, black cherry, red maple, dogwood.

<sup>f</sup>Includes: horsetails, clubmoss, wood lily, ladies' tresses, anemone, strawberry, cinquefoil, blackberry, rose, sand violet, trailing arbutus, wintergreen, snowberry, dogbane, bluet, blazing star, goldenrod, aster, sunflower, thistle, hawkweed.

use area. Approximately 26 percent of all living stems in this area were oak (8 of 29) versus about 16 percent (16 of 102) in the peak use area. The majority of the oak stems in the older stand were individual seedlings less than 1m high.

The number of stems of other tree species in the past use area differed significantly from those in the other areas (Table 4). All of the nine species noted occurred on this older site and the majority were also less than 1m in height.

Significant differences by use area were found for ground cover components (Table 4). The amount of the total live cover increased from the recent to the past use areas. The sedge-grass component was higher in the older stands (i.e., declining and past use), yet the percent cover of blueberry was lowest in the area of declining use and highest on the past use site. A higher incidence of bearberry was only found in the peak use area. Bracken did not appear in the declining use category and is significantly more abundant in the oldest stand. On this same site, more variety of other ground cover species occurred and a significant increase in this parameter over the other use areas was found. Species such as goldenrod and blackberry, however, were relatively frequent throughout all use categories.

In 1978, on 20 percent of the plots (12 of 60) in the past use area, additional bracken was encountered that stood taller than the grid sampler (over 0.5m high). The individual plants were cut and removed prior to taking ground cover measurements. In 1977, in this same area, such bracken growth did not occur and it was not necessary to cut plants on any of the sampled sites. Hard killing frosts in June of that year may have set back the species growth. A more

moderate growing season was experienced in 1978.

Deadwood from fallen snags was more apparent in the recent and peak use areas than in the area of past use. Cutting debris was spotty throughout the area of declining use. The amount of dead plant material exceeded that of bare ground which was usually encountered only when the transect line crossed a road or trail. The significant differences in this ground cover component (Table 4) were appropriately patterned after the amount of total live ground cover in the same use category. Less dead plant material implied greater total live ground coverage.

Certain parameters differed significantly by warbler use area but did not show any consistent trends. They include: the percent tree cover in the 0.5 - 2m height category, and the percent cover of the shrub and the moss-lichen components. No differences were found in the percent cover of sweet fern and of sand cherry nor in either of the stand structure components (Table 4).

The parameters discussed above exclusive of the percent cover of sand cherry, bracken, other plant species, slash, and dead plant material were used in the discriminant function analysis contrasting the recent, peak, declining, and past use areas. A discriminant coefficient was calculated for each variable used and ranked according to its order in the statistical analysis. The relative contribution of those variables to a particular function was determined by summing the absolute values of the actual coefficients, dividing that sum into the coefficient of interest, and expressing the result as a percentage.

The three possible mathematical functions were all highly significant ( $P < 0.01$ ). The results of the first and second are

Table 5. Summary of the first and second discriminant functions including the means  $\pm$  S.E. and the discriminant coefficients for the top three parameters measured in 1977 and 1978 on Kirtland's warbler use areas.

Parameter	Discriminant Function I			Discriminant coefficient <sup>a</sup>	
	Recent (n = 24)	Peak (n = 24)	Declining (n = 24)		Past (n = 30)
Tree cover > 2m (%)	9 $\pm$ 2	6 $\pm$ 1	46 $\pm$ 4	52 $\pm$ 5	26
Total live jack pine (No. stems/100m <sup>2</sup> )	106 $\pm$ 22	84 $\pm$ 16	37 $\pm$ 4	16 $\pm$ 2	18
Total live ground cover (%)	55 $\pm$ 2	51 $\pm$ 3	62 $\pm$ 3	78 $\pm$ 3	10
Discriminant Function II					
Blueberry (% cover)	22 $\pm$ 3	17 $\pm$ 3	10 $\pm$ 3	25 $\pm$ 3	19
Shrub component (% cover)	34 $\pm$ 3	26 $\pm$ 3	24 $\pm$ 3	39 $\pm$ 2	17
Bearberry (% cover)	1 $\pm$ 0.3	6 $\pm$ 2	0.3 $\pm$ 0.1	1 $\pm$ 0.3	14

<sup>a</sup>Relative contribution (%) of the parameter to the discriminant function.

Table 6. Discriminant coefficients for top ranked parameters and means  $\pm$  S. E. for all parameters measured in 1978 on areas of most recent Kirtland's warbler use and likely, but unused, warbler habitat.

Parameter <sup>a</sup>	Recent (n = 9)	Likely (n = 15)	Discriminant coefficient
<b>Tree components</b>			
Species (No. stems/100m <sup>2</sup> )			
<u>Jack pine (live)*</u>	96 $\pm$ 37	38 $\pm$ 10	25
Height			
< 1m	14 $\pm$ 8	4 $\pm$ 1	
<u>1-2m*</u>	50 $\pm$ 18	14 $\pm$ 4	27
<u>2-3m*</u>	30 $\pm$ 12	17 $\pm$ 6	23
> 3m	1 $\pm$ 0.5	2 $\pm$ 1	
Jack pine (dead)	10 $\pm$ 6	2 $\pm$ 1	
Oak	0.4 $\pm$ 0.2	10 $\pm$ 4	
Other <sup>c</sup>	5 $\pm$ 2	2 $\pm$ 1	
Height (% cover)			
<u>0.5-2m*</u>	19 $\pm$ 5	20 $\pm$ 3	
> 2m	1 $\pm$ 0.5	5 $\pm$ 3	
<b>Ground cover components</b>			
Total cover (live)*	56 $\pm$ 2	62 $\pm$ 2	
Sedge-grass component	16 $\pm$ 3	22 $\pm$ 4	
Shrub component	35 $\pm$ 4	35 $\pm$ 5	
Blueberry	28 $\pm$ 4	28 $\pm$ 6	
Sweet fern	5 $\pm$ 1	5 $\pm$ 1	
Sand cherry	2 $\pm$ 1	2 $\pm$ 0.5	
Bearberry	1 $\pm$ 0.5	2 $\pm$ 1	
Moss-lichen component	0.2 $\pm$ 0.1	1 $\pm$ 0.5	
Braken	1 $\pm$ 1	1 $\pm$ 1	
Other plant species <sup>d</sup>	2 $\pm$ 0.2	3 $\pm$ 1	
Slash (dead wood)	10 $\pm$ 1	3 $\pm$ 1	
Dead plant material, bare ground	34 $\pm$ 2	35 $\pm$ 2	
<b>Stand structure components (based on 40m line)</b>			
Length of open spaces (m)*	5 $\pm$ 1	6 $\pm$ 1	
Interspersion value	13 $\pm$ 2	12 $\pm$ 1	

<sup>a</sup>An asterisk (\*) indicates parameters used in the discriminant function analysis. Underscored parameters are those that ranked in the top three.

<sup>b</sup>Relative contribution (%) of the parameter to the discriminant function.

<sup>c</sup>Includes: willow, juneberry, and black cherry.

<sup>d</sup>Includes: strawberry, cinquefoil, blackberry, sand violet, dogbane, goldenrod, aster, sunflower, and hawkweed.



Table 7. Discriminant coefficients for top ranked parameters and means  $\pm$  S. E. for all parameters measured in 1978 on areas of declining warbler use and intermittently used habitat.

Parameter <sup>a</sup>	Declining (n = 9)	Intermittent (n = 9)	Discriminant coefficient <sup>b</sup>
<b>Tree components</b>			
Species (No. stems/100m <sup>2</sup> )			
Jack pine (live)	36 $\pm$ 6	32 $\pm$ 8	
Height			
< 1m*	12 $\pm$ 4	2 $\pm$ 1	
1-2m	6 $\pm$ 2	4 $\pm$ 1	
2-3m	7 $\pm$ 3	19 $\pm$ 6	
> 3m	10 $\pm$ 2	8 $\pm$ 2	
Jack pine (dead)*	4 $\pm$ 0.5	2 $\pm$ 0.5	
Oak	2 $\pm$ 0.5	2 $\pm$ 0.5	
Other <sup>c</sup>	4 $\pm$ 1	3 $\pm$ 1	
Height (% cover)			
0.5-2m	36 $\pm$ 5	32 $\pm$ 5	
> 2m	51 $\pm$ 6	34 $\pm$ 4	
<b>Ground cover components (%)</b>			
<u>Total cover (live)*</u>	<u>60 <math>\pm</math> 4</u>	<u>48 <math>\pm</math> 4</u>	<u>31</u>
<u>Sedge-grass component*</u>	<u>23 <math>\pm</math> 4</u>	<u>35 <math>\pm</math> 1</u>	<u>30</u>
<u>Shrub component*</u>	<u>32 <math>\pm</math> 4</u>	<u>9 <math>\pm</math> 2</u>	<u>13</u>
<u>Blueberry*</u>	<u>16 <math>\pm</math> 5</u>	<u>1 <math>\pm</math> 0.5</u>	
Sweet fern	8 $\pm$ 2	4 $\pm$ 2	
Sand cherry	8 $\pm$ 2	4 $\pm$ 2	
Bearberry	0.5 $\pm$ 0.2	0.1 $\pm$ 0.1	
Moss-lichen component	3 $\pm$ 1	2 $\pm$ 1	
Braken	0	0.1 $\pm$ 0.1	
Other plant species <sup>d</sup>	2 $\pm$ 0.5	1 $\pm$ 0.5	
Slash (dead wood)	2 $\pm$ 0.5	8 $\pm$ 2	
Dead plant material, bare ground	38 $\pm$ 2	44 $\pm$ 3	
<b>Stand structure components (based on 40m line)</b>			
Length of open spaces (m)	3 $\pm$ 0.5	4 $\pm$ 1	
Interspersion value	18 $\pm$ 2	14 $\pm$ 2	

<sup>a</sup>An asterisk (\*) indicates parameters used in the discriminant function analysis. Underscored parameters are those that ranked in the top three.

<sup>b</sup>Relative contribution (%) of the parameter to the discriminant function.

<sup>c</sup>Includes: white pine, red pine, juneberry, black cherry.

<sup>d</sup>Includes: wood lily, ladies tresses, strawberry, blackberry, rose, trailing arbutus, goldenrod, sunflower, hawkweed.

abundant in the area of declining use while the sedge-grass component accounted for 74 percent (35 of 48) of the total live ground cover in the intermittent use area.

The composition and structure of vegetation around Kirtland's warbler nest sites found in the peak use area of the Damon burn and on other occupied study areas (i.e., the Management Unit and the St. Helen burn) was measured in 1978 (Table 8). Although the total number of jack pine stems was not significantly different between the two groups, more jack pine stems less than 2m high and fewer stems greater than 3m high in the Damon burn reflects a younger stand. The values for the number of stems of other tree species and the percent tree cover over 2m high, both of which are significantly higher in the other areas, support this same notion. Clumped, bushy oak was present on the Damon burn nest sites and was not present on other areas.

Although the total amount of live ground cover is similar for both nest site groups, differences appear in the composition (Table 8). There was a greater percent coverage by shrubs (especially, blueberry) and bearberry on transects around the Damon nest sites while a greater amount of the sedge-grass component was present in other areas. Nest site data were compared with those data of associated territories and no significant differences were found for any parameter.

Of the 12 male Kirtland's warblers that were observed on territory, five were associated with nests as mentioned; three were seen with females; and, one male was observed feeding warbler fledglings. It was not known if the three remaining birds had secured or attracted mates. The size of the territories ranged between 1.0 and 5.6 ha and averaged  $2.4 \pm 0.4$  ha.

Table 8. Means  $\pm$  S. E. <sup>a</sup> for parameters measured in 1978 around nest sites in the Damon burn and nest sites located in other areas

Parameter	Damon burn (n = 24)	Other areas (n = 24)
Tree components		
Species (No. stems/100m <sup>2</sup> )		
Jack pine (live)	76 $\pm$ 18 <sup>b</sup>	39 $\pm$ 4 <sup>b</sup>
Height		
< 1m	14 $\pm$ 3 <sup>b</sup>	5 $\pm$ 2 <sup>c</sup>
1-2m	41 $\pm$ 10 <sup>b</sup>	10 $\pm$ 2 <sup>e</sup>
2-3m	20 $\pm$ 5 <sup>b</sup>	14 $\pm$ 2 <sup>c</sup>
> 3m	1 $\pm$ 0.2 <sup>b</sup>	10 $\pm$ 2 <sup>c</sup>
Jack pine (dead)	4 $\pm$ 2 <sup>b</sup>	2 $\pm$ 0.5 <sup>b</sup>
Oak	28 $\pm$ 3 <sup>b</sup>	0.5 $\pm$ 0.1 <sup>c</sup>
Other <sup>d</sup>	0.5 $\pm$ 0.2 <sup>b</sup>	4 $\pm$ 2 <sup>c</sup>
Height (% cover)		
0.5-2m	29 $\pm$ 2 <sup>b</sup>	35 $\pm$ 2 <sup>b</sup>
> 2m	11 $\pm$ 2 <sup>b</sup>	30 $\pm$ 4 <sup>c</sup>
Ground cover components (%)		
Total cover (live)	60 $\pm$ 2 <sup>b</sup>	54 $\pm$ 3 <sup>b</sup>
Sedge-grass component	11 $\pm$ 1 <sup>b</sup>	26 $\pm$ 2 <sup>c</sup>
Shrub component	36 $\pm$ 3 <sup>b</sup>	21 $\pm$ 2 <sup>c</sup>
Blueberry	30 $\pm$ 3 <sup>b</sup>	13 $\pm$ 2 <sup>c</sup>
Sweet fern	4 $\pm$ 1 <sup>b</sup>	6 $\pm$ 2 <sup>b</sup>
Sand cherry	1 $\pm$ 0.5 <sup>b</sup>	2 $\pm$ 1 <sup>b</sup>
Bearberry	5 $\pm$ 1 <sup>b</sup>	2 $\pm$ 1 <sup>c</sup>
Moss-lichen component	3 $\pm$ 1 <sup>b</sup>	4 $\pm$ 1 <sup>b</sup>
Braken	2 $\pm$ 1 <sup>b</sup>	0.5 $\pm$ 0.2 <sup>c</sup>
Other plant species <sup>e</sup>	2 $\pm$ 0.2 <sup>b</sup>	1 $\pm$ 0.2 <sup>c</sup>
Slash (dead wood)	3 $\pm$ 1 <sup>b</sup>	3 $\pm$ 0.5 <sup>b</sup>
Dead plant material, bare ground	36 $\pm$ 2 <sup>b</sup>	43 $\pm$ 3 <sup>b</sup>
Stand structure components (based on 40m line)		
Length of open spaces (m)	4 $\pm$ 1 <sup>b</sup>	4 $\pm$ 1 <sup>b</sup>
Interspersion value	16 $\pm$ 2 <sup>b</sup>	16 $\pm$ 1 <sup>b</sup>

<sup>a</sup>The same superscript in a row, (b,c) indicates no significant difference between means.

<sup>d</sup>Includes: white pine, red pine, willow, juneberry, hawthorn, black cherry.

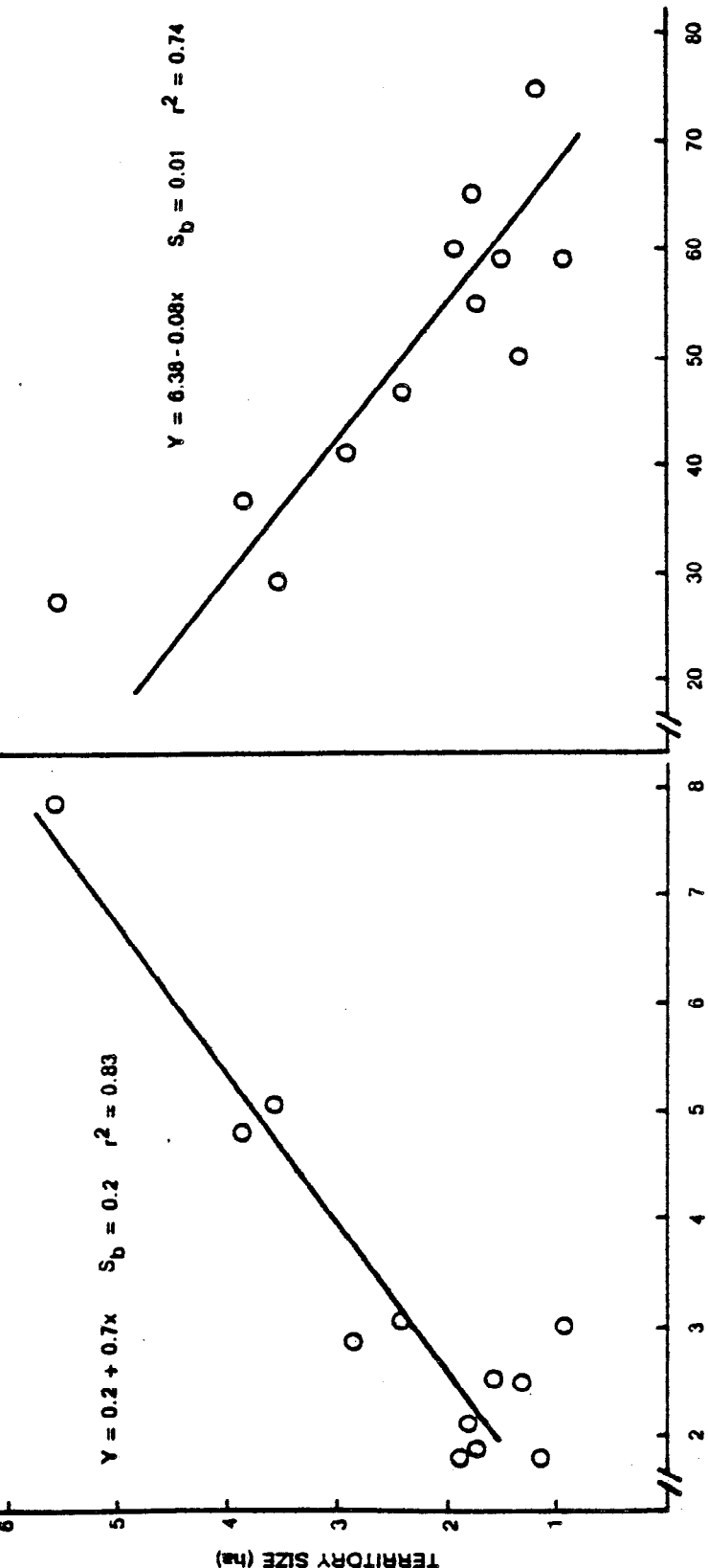
<sup>e</sup>Includes: clubmoss, blackberry, blazing star, goldenrod, aster, sunflower, hawkweed.

Measurements of all the habitat variables were made on these territories with the plot-transect method. Seven of the parameters were used as independent variables in a stepwise regression analysis on territory size. They include: the number of jack pine stems 1-2m, 2-3m, and greater than 3m high, the total number of live jack pine stems, the percent cover of the sedge-grass component and blueberry, and the interspersion value. The stepwise analysis resulted in a significant ( $P < 0.01$ ) linear equation inversely relating the interspersion value to territory size (Fig. 2).

The other stand structure component, average length of the open spaces on a 40m line, was then examined in greater detail. This parameter and the interspersion value are correlated ( $r = 0.86$ , d.f. = 10). Within the territory used by male Kirtland's warblers, the variances of the length measurements were heterogeneous (Bartlett's  $q$ -statistic = 17.8,  $X^2_{0.2,1}=1.6$ ). Thus the length of these openings being highly variable created a patchy environment. The relationship between territory size and the average length of open spaces was determined by regression analysis. The significant ( $P < 0.01$ ) equation showed that with increasing territory size, the average length of the open spaces increased (Fig. 2).

From the transect line run through each of these 12 territories, totals for live jack pine stems, live ground cover components, and lengths of open spaces where no tree cover over 0.5m high was noted were determined. Coefficients of variation of 0.82, 0.15, and 0.22, respectively, were calculated. Using the coefficients as relative indices, the number of jack pine stems on the transects sampling these territories was highly variable while the amount of total live

At the same time, the fact that the company is not a public company is a significant factor in determining the company's value. The company's value is determined by the company's performance, the company's growth prospects, and the company's risk profile. The company's value is also determined by the company's financial position, the company's management team, and the company's competitive advantage. The company's value is also determined by the company's industry, the company's market position, and the company's overall reputation. The company's value is also determined by the company's financial performance, the company's growth prospects, and the company's risk profile. The company's value is also determined by the company's financial position, the company's management team, and the company's competitive advantage. The company's value is also determined by the company's industry, the company's market position, and the company's overall reputation.



LENGTH OF OPEN SPACES (m)

INTERSPERSION VALUE

ground cover and the amount of open space appeared to be less variable. On the average for any one transect, 55 percent of the line was open (i.e., there was no tree cover over 0.05m high) and about 59 percent of the ground cover was living material.

## DISCUSSION

Jack pine stands used by Kirtland's warblers during this study were, for the most part, within the generalized age limits of 8 to 20 years reported by Mayfield (1960). The wide range in age of the declining use area may be an artifact of silvicultural treatments. Various selective cuttings, for instance, and the release of seeds from a nonserotinous cone source would yield an uneven-aged stand (Rudolf 1958). The wide range in age of the past use area suggests that there was some lag in jack pine regeneration after the 1946 fire, assuming that the majority of the seed is released from serotinous cones within a few days. Some trees, aged 31 years, did appear within one year but as much as an 11 year time interval has been spanned for regeneration efforts. The sample size of 12 may not adequately reflect the overall age structure of either of these sites.

The differential rate of shoot growth by year was similar in the four sampled stands. This suggests that environmental factors such as the amount of precipitation or temperature extremes acting within the general study area are responsible for the yearly variations.

Although differences found among the four use areas in parameters such as the number of jack pine stems greater than 3m high and the percent tree cover over 2m high reflect age, most of the distinctions may be attributable to site differences. For instance, on the declining use area, that without a history of fire, there is a



predominance of the sedge-grass component suggesting that this life form will dominate in the absence of fire. The density of jack pine in the past use area is relatively low. As a jack pine stand matures, an exponential rate of decline in stem density is expected as competition for water, space, and sunlight intensifies (Miller and Schneider 1971, Yarranton and Yarranton 1975). Even if the original loss of young stock was 50 percent, the stem density on this site in 1961, when it was occupied by Kirtland's warblers, would be considerably less than that measured on the Damon burn. This suggests that conditions prior to the fire were different for these two stands and that Kirtland's warbler use of an area may be somewhat independent of absolute stand density. The highly variable figures for the number of jack pine stems on known territories lends support to the latter notion.

Within, rather than among, site differences can be evaluated by the comparisons involving stages of warbler use. The dissimilarities between the recent and peak use areas are in the shrubby oak component and bearberry, a ground cover plant with a very patchy distribution. Differences between the recent and likely habitats involve oak and jack pine stems, in essence, the amount of tree coverage. Declining and intermittent use areas, though sites not of the same origin, have comparable stand histories and show differences in ground cover components, notably, total live ground cover. These comparisons suggest that both tree and ground coverage factors are involved in habitat selection by Kirtland's warblers.

The oak is unique to parts of the Damon burn and its form resembles that of young bushy jack pine (J. Byelich, pers. commun.).

On the peak site, the oak and pine configuration provides adequate tree coverage for use by breeding Kirtland's warblers. The oak is also present in the likely use area, but with jack pine being two and one half times less abundant, the visual impression is more open and may not release a settling response (Hilden 1965) in the birds. Other factors that relate to the evaluation of a nonused site should also be considered. It is possible that if there were more warblers, more such habitat may be exploited. Influences from intraspecific social interactions may affect the choice of an area. Habitat parameters that were not measured in this study, such as the relationship between use and stand size and shape, edaphic factors, the effect of terrain and the surrounding habitat types or a more detailed analysis of burned versus unburned sites may add further insights.

In the recent use area the factors of tree and ground cover involved in habitat selection appear to be present; however, warbler densities are low. This suggests that the arrangement of the tree cover and openness is important and that it may predict the ability of a habitat to attract and hold more warblers. The area of recent use should not be construed as suboptimal, but rather that it may be at its peak warbler density for the resources available.

The structural importance of Kirtland's warbler habitat is further enhanced by the relationships between territory size, the interspersion value, and the average length of open spaces on the transect line. Interspersion appears to be a proximate factor used by males to select appropriate habitat. As smaller territories imply increased interspersion, it follows that optimizing an area for potential Kirtland's warbler use is maximizing the interspersion of

tree cover and open spaces. The specific resources provided by each of these components have not yet been identified.

As suggested, ground cover factors are also involved in habitat selection. On known territories, live material accounted for an average of 59 percent of the total ground cover and a relative amount of coverage may be another proximate cue. No species-specific patterns that did not relate to site differences could be identified. The higher incidence of bearberry on the peak use site may have been a consequence of sampling due to its patchy distribution. It does provide additional bare ground coverage but its contribution to the total is still relatively low. On the intermittently used areas, where males had been observed, there may be an acceptable tree and open cover arrangement but decreased ground coverage may make it less attractive, particularly for a ground nesting species.

As habitat parameters were similar on territories and around nest sites, there appears to be no unique feature associated with the latter. Nesting materials analyzed by Southern (1961) were thought to be typical sweepings from the general area (Mayfield 1960). The most frequent coverage over nests was blueberry in one study (Orr 1975) while sedges and grasses were found to be more abundant in another (Mayfield 1960). It appears that a particular plant species is not selected but rather that choice is determined by, and consistent with, overall site conditions as the nest site comparisons in this study suggest. If the broad habitat requirements of tree and ground coverage factors are met, nest site locations would probably not be limited.

Presently, management efforts for the Kirtland's warbler are aimed at increasing the acreage of young jack pine. For a potential warbler use area, attention should also be paid to the amount of naturally occurring ground coverage and consideration given on how to encourage its growth. It could be very desirable, for instance, to enhance blueberry where it is the predominant ground cover type by prescribed burning. This could be one of the most economical methods to promote desirable ground coverage and may more closely approximate natural conditions.

Considering that sampled territories had a relatively consistent open cover value of 55 percent, an approximate 50:50 to 60:40 ratio of open spaces to tree cover might be used as a management goal. Data from this study suggest that the proportionate scale is provided by numerous small openings. Supplemental plantings or appropriately timed thinnings might be useful on some sites. The practical and economical feasibility of both of these methods should be carefully considered and pose further research questions. A jack pine planting with an opposing wave configuration (J. Byelich, pers. commun.) might be used. An alternative suggestion would be broken and staggered strips of jack pine. Either scheme should provide increased interspersion compared to conventional planting practices. How best to achieve the desirable interspersion where the reliance of jack pine regeneration is on prescribed burning should be one of the immediate management related research concerns.

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