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Relating Kirtland's warbler population to changing landscape composition and structure

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Abstract

The population of male Kirtland's warbler (*Dendroica kirtlandii*) in the breeding season has averaged 206 from 1971 to 1987. The Kirtland's warbler occupies dense jack pine (*Pinus banksiana*) barrens from 5 to 23 years old and from 1.4 to 5.0 m high, formerly of wildfire origin. In 1984, 73% of the males censused were found in habitat naturally regenerated from wildfire or prescribed burning. The rest were in plantations (11%) or in harvested, unburned jack pine stands stocked by natural regeneration (16%). Twenty-two percent (630 of 2,886) of the Kirtland's warbler males counted in the annual censuses from 1971 through 1984 were found in 26 stands that were unburned and naturally regenerated following harvest. From 1982 to 1987, suitable regenerating areas were barely sufficient to replace currently occupied maturing stands, so population growth was impeded. Ecosystems of suitable size and regeneration characteristics (wildfire and plantation) doubled in area by 1989. In response, the population of Kirtland's warblers increased from 167 to 398 males between 1987 and 1992, but they withdrew almost entirely from the unburned, unplanted barrens by 1989 when the area of more suitable regeneration types increased. Minimum (368 males) and maximum (542 males) population estimates for 1996 were calculated based on 1984 average density (1.9 males per 40 ha) and peak population in burns (2.8 males per 40 ha).

Introduction

The known nesting range of the Kirtland's warbler (*Dendroica kirtlandii*) is restricted to an area about 120 by 160 km in northern Lower Michigan, although there is indirect evidence of breeding in other areas of the Upper Midwest. In 1951, Harold Mayfield (1953) organized the first census of the entire population of singing males within the Michigan nesting range, which totaled 432. In the second decennial census, 502 male Kirtland's warblers were counted (Mayfield 1962). By 1971, the male population decreased to 201 (Mayfield 1972). As a result, the Kirtland's warbler was classified as an Endangered Species under the Endangered Species Act of 1973. The principal reason for this population decrease appeared to have been nest parasitism by the brown-headed cowbird (*Molothrus ater*) (Ryel 1981a). Since cowbird control was initiated (Kelly and DeCapita 1982), the warbler population has stabilized. Winter mortality (Ryel 1981a), habitat maturation, pairing success, fledgling mortality, and yearling dispersal (Probst 1986) may now limit population growth. Landscape structure may have been a limiting factor in recent times because the amount and distribution of suitable breeding areas available to the Kirtland's warbler has changed since 1961 (Ryel 1981b, Probst 1986). In recent years, Kirtland's warblers have occupied only 3 to 6 large breeding areas, each of which provides habitat for only 10 to 16 years. Thus, Kirtland's warblers are influenced by rapidly changing landscape dynamics.

Typically, this warbler occupies dense, 1.4- to 5.0-m high jack pine (*Pinus banksiana*) barrens established after wildfire (Mayfield 1960, Walkinshaw 1983). Kirtland's warbler populations in jack pine burns generally build for 3 to 5 years after colonization, level off for 5 to 7 years, and then decline rapidly (Probst 1986). The vegetation in a few active nesting areas has been described (Smith 1979, Buech 1980), but no data are available for the complete range of stand ages, tree heights, and tree stocking densities within pine barrens communities at ages (5 to 23 years) when stands have been occupied by Kirtland's warbler historically. These ecosystems are comprised of three regeneration types derived from three distinct origins or disturbance regimes: 1. forest regeneration following wildfire, 2. plantation, and 3. unburned-natural regeneration following timber harvest.

Traditional wildlife habitat evaluations have related local populations to local, multi-variate habitat characteristics. More recently, biologists have taken a broader view of regional versus local population interactions (*e.g.* Askins and Philbrick 1987, Probst 1988, Pulliam 1988) that emphasizes a step-wise filling of habitats in rank order of quality (Fretwell 1969). This paper takes a regional view of habitat and its dynamic availability and utilization considering 1) changes in the relative area of three landscape components utilized by Kirtland's warbler; 2) changes in landscape composition of Kirtland's warbler as well as the breeding male distribution response; and 3) increase in the regional population size as the landscape structure and the male warbler distribution changes. Kirtland's warblers are highly suited to studies of population regulation by landscape change because of their restricted breeding range, their concentration into 16 to 30 stands within any one year, and the ease with which the entire known male population may be censused each year.

As a result, the Kirtland's warbler represent an excellent study subject for tests of some general ecological theories: 1) population growth and size are limited by area and distribution of particular landscape components; 2) less favored landscape components are only used when more suitable areas are filled; 3) estimates of future populations can be made based on current population and the dynamic changes in distribution of Kirtland's warbler relative to landscape structure.

An analysis of regional area available to a species must first delineate the full range of suitable ecosystems before conducting detailed sampling within categories or gradients. Aerial photographs and aerial surveys revealed a striking difference in tree cover between densely-stocked areas occupied by Kirtland's warbler and sparsely-stocked unoccupied areas. Thus, we defined suitable ecosystems by the bivariate limits of tree height and tree percent cover on stands below site index 55 for jack pine within the known breeding range. (Site index is a species-specific ranking of sites by height growth over time.) Data reported here integrate the tree percent cover factor with a quantification of the stand age and tree height factors identified by previous researchers (see above). This hypothesis was tested indirectly by predicting total Kirland's warbler populations for the near-term based on area of landscape components in three general regeneration types. A tree cover and tree density hypothesis was tested directly at the local, site-specific level (Nelson 1992) and in experimental plantations. Only when a sufficient sample of plantations have been occupied by Kirtland's warblers through the complete range of suitable seral stages (there have been only four currently) will more detailed variables be appropriate as supplements to the current bivariate explanation of Kirtland's warbler habitat suitability.

1.1 Limits to population projections based on ecosystem area

Some evidence suggests that area of suitable landscape components limit Kirtland's warblers (Probst 1986). From 1982 to 1986 the proportion of males increased in marginal areas where their density (see Results) and pairing success were lower than in more suitable areas (Probst and Hayes 1987). Population projections assume predictable densities when at or near carrying capacity. If suitable area is limiting the population of Kirtland's warblers appreciably, a sudden increase in suitably-stocked, regenerating pine forest may not be matched by constant Kirtland's warblers densities because survivorship and productivity may be insufficient to fill all areas of suitable size and site characteristics. In such a situation, carrying capacity cannot be realized by short-term population growth.

The estimates of ecosystem area and carrying capacity presented here involve predictions from commonly available forestry data. These predictions cannot be improved by analysis of vegetation measurements because we cannot predict future vegetation composition at the local scale. Thus, we use the range of conditions in each of three forest regeneration types to predict the minimum and maximum populations for the landscape structure currently developing. Almost all habitat models used in wildlife biology assume habitat limitation such that a significant increase or decrease in habitat area will result in a population response.

We assembled both field data and unpublished government reports on ecosystem area and Kirtland's warbler male populations to accomplish 5 objectives: (1) describe the complete known range of ecosystems for the Kirtland's warbler during the period 1978 to 1986. Document Kirtland's warbler utilization of unburned barrens and evaluate general ecosystem characteristics influencing utilization of such stands, (2) tabulate the past and current area of suitably-aged jack pine ecosystems in northern Lower Michigan, (3) infer relative suitability of 3 regeneration types (i.e. stand origins) from differences in 1984 Kirtland's warbler distribution and density. Test hypotheses about changes in distribution of birds in 1989 relative to 1984, (4) tabulate future area of regenerating wildfires and suitable plantations available during 1989–1996. Forecast a range of Kirtland's warbler carrying capacity based on the historical range of density for suitable areas, and (5) briefly evaluate the Kirtland's warbler habitat management goals.

2. Methods

To determine historical breeding densities, and the suitability of regeneration types within an ecosystem, we used the annual Kirtland's warbler overall census results of Mayfield (1953, 1962, 1972, 1973a, 1973b, 1975); Ryel (1976a, 1976b, 1979a, 1980a, 1980b, 1981b, 1982, 1983, 1984); Burgoyne and Ryel (1978); Weise (1987); and Weinrich (1988a, 1988b, 1989, 1991a, 1991b). Kirtland's warbler population trends and area of suitable ecosystems were compiled from unpublished reports on file with the Michigan Department of Natural Resources (DNR) and the Huron-Manistee National Forest. The age limits to ecosystem suitability were based on common historical occupancy by breeding Kirtland's warblers. Ecosystems were classified as 'suitably-aged' by historical criteria if they were jack pine habitat 8 to 20 years old in wildfire, or 10 to 20 years old in plantation or unburned, unplanted stands. Areas that were actually used by warblers were termed 'occupied habitat' (subsets of suitably-aged ecosystems with few exceptions). Within occupied habitat, wildfire and plantation areas were classified as 'suitable areas' (see Results), and unburned, unplanted habitat as 'less suitable areas'. Density of Kirtland's warblers overall, or in landscape components such as regeneration types, was calculated from the Kirtland's warbler annual census in conjunction with stand area from cover type maps from the Michigan DNR or USFS. Significant differences in the availability of different regeneration types over time, or their utilization by Kirtland's warblers, were tested for random distribution with Chi-Square Tests.

Vegetation sampling was designed to document the range of conditions of suitably-aged jack pine ecosystems (objective 1), rather than average conditions. The vegetation measurements were also used to infer and interpret the relative suitability of the three regeneration types. The latter would be representative of conditions available during the study, but not useful for characterizing future landscape composition. Vegetation was measured in 35 subareas within 21 breeding areas occupied by Kirtland's warblers. Kirtland's warbler areas were divided into 3 regeneration types: natural regeneration from fire (N = 19) (including one prescribed burn) referred to as 'wildfire' areas; plantations (N = 8); and harvested, unburned, naturally regenerated stands (N = 8). The 35 subareas included all wildfire and plantation stands occupied between 1979 and 1985. Twelve breeding areas were measured during the first 2 years of utilization, and 3 areas during the last 2 years of occupation to define the lower and upper bounds of acceptable stand maturity. We measured vegetation from 1979 to 1985 between 15 April and 30 April and between 15 August and 20 September. Vegetation measurements for tree crown cover were made using the line transect method (Lindsay 1955) combining some adaptations of that technique by Buech (1980) and Probst (1976) (see below). Single 300- to 500-m transects were oriented along the long axis of a cluster of Kirtland's warbler male territories in each study area. Each transect was subdivided into 10 to 15, 30.5-m long segments. In plantations, transects were oriented 45° to planting rows.

The major differences among regeneration types in these jack pine communities are tree density and crown cover. Tree crown cover was estimated by measuring the percentage of the transect line covered by the vertical, plumb line projection of tree crowns or thicket onto the ground. Tree stems taller than 0.6 m were counted in rectangular sample units 1.5 × 15.3 m adjacent to the transect line at alternate 15 m segments of the transect. Trees taller than 0.6 m were measured to the nearest 0.3 m, because height is the major vegetation variable used to establish temporal limits to suitable jack pine ecosystems for Kirtland's warblers. The border of a tree crown or thicket was defined by those outer branches that intersected a vertical, perpendicular plane above the tape. The lower height of live jack pine foliage, which varied with forest age, was measured for each tree or thicket that intersected the transect. The lower heights were weighted by cover to calculate average lower height of foliage. In thickets, crown cover and lower heights were separated by species and overlapping cover was recorded. Thus, single species calculations could be combined or separated, but only combined covers are reported here because jack pine dominated in all but three strands [which were dominated by red

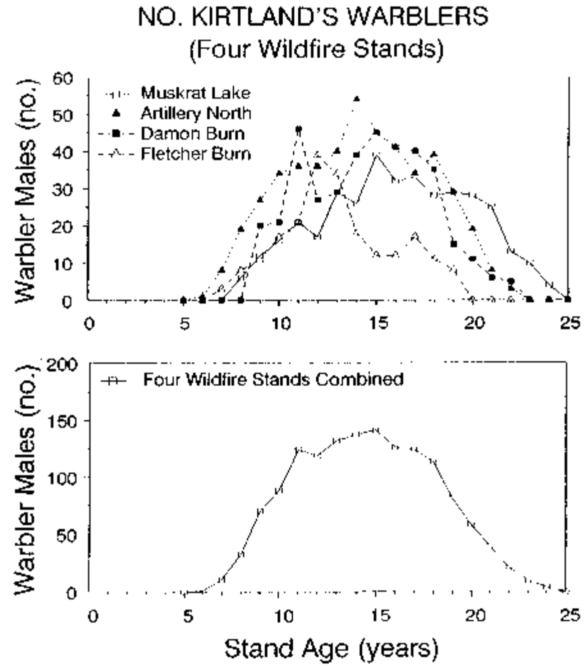

Fig. 1. Stand age population trends of Kirtland's warbler males in four wildfire-regenerated breeding areas in Michigan.

pine (*Pinus resinosa*)]. Stand ages and lower foliage heights of different habitat classes were compared using the Mann-Whitney test. Tree density among the three habitat classes was analyzed with a nested analysis of variance (SYSTAT). Because of unequal subplot sizes, sequential subplots within a study area were combined until an area of 93 m^2 was achieved. The square root transformation of number of trees in each subplot was used to normalize the data.

The minimum carrying capacity of Kirtland's warbler males was predicted by using average male densities from 1984 in all stands in the two primary regenerations types (wildfire and plantation). Estimates of area within those same landscape components were used to project future carrying capacity. The 1984 Kirtland's warbler male densities were used as the basis for predicting minimum carrying capacity because populations were well distributed among landscape components at that time (see results). Also, Kirtland's warblers use stands for 8 years or more (Probst 1986, 1988; Walkinshaw 1983) so habitat turnover from stand maturation is low in almost all years. Thus, the overall 1984

Table 1. Pine tree heights, percent cover, and lower foliage heights of occupied Kirtland's warbler breeding areas in Michigan.

	Average tree height (ranges) (m)	% Tree cover (ranges and means)	Average lower height of foliage[a] (ranges and means)
Recently occupied habitat (N = 10)	1.4–2.3	15.8–38% ($\bar{x}$ = 27.3%)	0.1–0.9 m ($\bar{x}$ = 0.3 m)
Habitat with established populations (N = 16)	2.4–3.8	21–67.5% ($\bar{x}$ = 43.2%)	0.2–1.1 m ($\bar{x}$ = 0.6 m)
Habitat with declining populations (N = 5)	3.9–5.6 m	36[b]–86% ($\bar{x}$ = 61.0%)	0.7–1.5 m ($\bar{x}$ = 1.2 m)

[a] Weighted by tree cover.
[b] Includes unplanted area between planted strips at one site. Excluding unplanted space within this plantation, range = 54–86%, x = 69.8%.

Kirtland's warbler densities should be representative of the period 1982 to 1985, when the birds were at low densities in less-suitable habitat and at higher densities in suitable habitat. Such a distribution is typical, and appropriate for predictions based on habitat-limited populations, because we excluded years when Kirtland's warblers were below carrying capacity in suitable habitat. Maximum carrying capacity was estimated from peak male densities (13 to 15 years stand age) in 4 major wildfire areas only (See Fig. 1). No comparable plantation data was available. We predicted future populations for 'overmature', occupied breeding areas based on published rates of mortality and population decline (Probst 1986). The predictions of population decline in specific habitats were compared to the actual populations observed through 1987. Thus, future carrying capacities were estimated using data on historical rates of population build-up and decline, after testing them in the near term. The estimates of future Kirtland's warbler populations will only be valid if populations are strongly regulated by quantity of suitable breeding areas and if non-habitat limiting factors remain constant.

We use range rather than confidence limits on estimates of future carrying capacity for the following reasons: (1) annual censuses of Kirtland's warbler males are comprehensive, and average male density is essentially a population mean rather than a sample within a population for a given year; (2) the future distribution of Kirtland's warbler across landscapes is changing markedly because of the higher proportion of more suitable ecosystems that is becoming available from 1988 to 1998 (see Results); (3) the distribution of landscape components, stand sizes and stand ages of occupied areas will change in the coming decade; and (4) it is likely the Kirtland's warbler density of specific breeding areas depends on the context and interaction of overall population size and area of suitable ecosystems. As a result, the application of confidence limits from one population to a very different population and set of conditions would be inappropriate.

3. Results

3.1 Stand suitability

The annual censuses recorded Kirtland's warblers in ecosystems ranging from 5 to 24 years age since date of origin. Populations increase during early periods of occupancy, stabilize during the middle period of occupancy, and decline as areas become overmature for Kirtland's warblers. This is illustrated (Fig. 1) by four large wildfire areas for which there were large enough populations to track stand age population trends. (Other breeding areas did not have complete stand age records, large populations, or regular, sustained warbler occupancy.) We have arbitrarily divided the stand age continuum

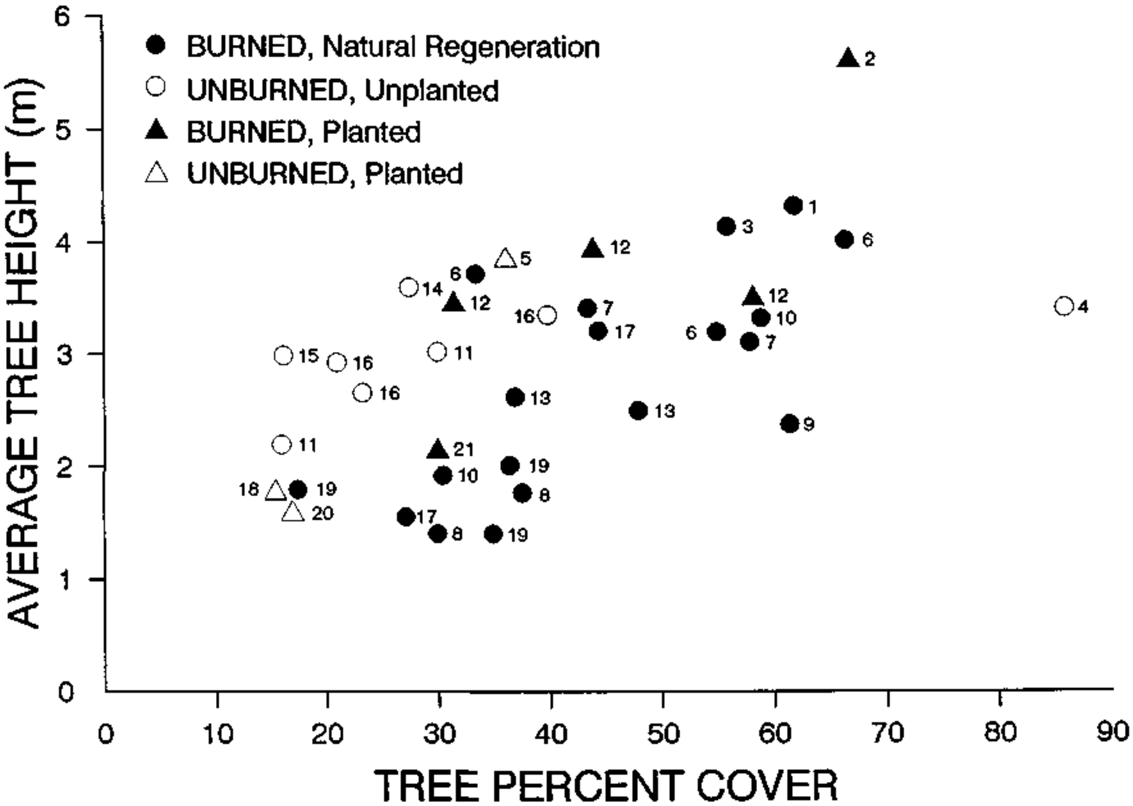

Fig. 2. Ranges of average tree height and percent tree canopy of stands sampled within habitat occupied by Kirtland's warblers in Michigan. Classification of habitats into marginal or suitable follows the categories defined for contrasting pairing success (Probst and Hayes, 1987). (Young marginal habitat matures into suitable.) 1. Artillery South; 2. Mack L. Red Pine #1; 3. Pere Cheney; 4. Ogemaw Management*; 5. Lovells N. (S.5); 6. Muskrat Lake (S.7, S.13N, S.13S); 7. Artillery North (S.8 and 9, S.9 South); 8. Damon* (North, South); 9. Fletcher Burn; 10. Mack L. Prescribed Burn (1978, 1983); 11. Mack L. Unburned (1980, 1983); 12. Mack L. Plantation (S.3) (Jack Pine, Red Pine); 13. Lovells South; 14. Monument; 15. McKinley #1; 16. McKinley (Area #2, Area #3, Area #4); 17. Rayburn; 18. Lovells North #2 (S.6); 19. Bald Hill (1982 S.20, 1983 S.20, 1983 S.14); 20. Mack Lake, Red Pine #2; 21. McKinley #5 ('77 Plantation). (*Data from Smith (1979).)

into 'young', 'established' and 'declining'. Stands are not colonized by Kirtland's warblers until the average tree height reaches 1.4 to 2.3 m (Table 1). The tree cover in young, recently colonized stands was at least 15% to 20% in all occupied stands (Table 1). During the middle years of highest Kirtland's warbler density, stands range between 2.4 and 3.8 tree height and up to 60% tree cover (Table 1). Kirtland's warbler populations begin to decrease when tree heights reach about 3.8 m and the lower height of live foliage reaches about 1.0 m (Table 1). At this stage of regeneration, tree cover typically exceeds 60%.

Tree canopy cover is more useful for evaluating habitat quality than stocking frequency or stem density because it integrates the stocking, spacing, and height factors. In any stand, the stocking should have from 20% to 25% tree cover for successful warbler colonization (Fig. 2). During the period of established populations, tree cover is between 27% and 60% (Table 1). When such conditions are found in fire-regenerated areas, they typically have more than 5,000 stems per ha (Table 2). More suitable wildfire and plantation areas (Table 3) have more tree cover than unburned, unplanted clearcuts (Fig. 2). Because trees are evenly distributed in plantations, optimal tree canopy cover (27%–60%) can be achieved with a lower tree den-

Table 2. Stand age and pine stem density of three occupied Kirtland's warbler habitat classes in Michigan.

	Subarea age first year occupied	Pine density (stems/ha)
Wildfire habitat (N = 19)	(7–10)	(1,680–43,751)
	$\bar{x}$ = 8.3 A[a]	$\bar{x}$ = 11,222.5 A[a]
Plantation habitat (N = 8)	(7–12)	(1,272–4,296)
	$\bar{x}$ = 9.2 A	$\bar{x}$ = 2565 B
Unburned, nat. regen. (N = 8)	(11–15)	(1,272–3,705)
	$\bar{x}$ = 12.8 B	$\bar{x}$ = 2131.5 B

[a] Significant differences (P < 0.01) among means (Mann-Whitney Test) in a column are indicated by different capital letters.

Table 3. Distribution and density of Kirtland's warblers among occupied habitat types in Michigan, 1984 and 1989.

Location	Area ha		No. males		Density (No. males per 40 ha)	
	1984	1989	1984	1989	1984	1989
Wildfire	3,451	4,164	158	163	1.8	1.6
Plantation (Burned and unburned)	329	1,106	23	48	2.8	1.7
Subtotal	3,780	5,270	181	211	1.9	1.6
Unburned, Natural Regeneration	1,643	14	34	1	0.8	–
	5,423	5,284	215	212	1.6	1.6

This includes a small proportion of birds outside the defined range of suitably-aged habitat.

sity. However, unplanted areas with less than 2,500 stems/ha have not been used consistently (*i.e.* intermittent use), if at all (see below). Unburned, unplanted areas with less than 20% canopy cover that are occupied by males (Fig. 2), may have significantly fewer female Kirtland's warblers (Probst and Hayes, 1987). Warbler populations in burns decline rapidly after 7 to 10 years of occupancy (Fig. 1). During population decline average tree height of habitat reaches from 4.0 to 4.5 m (4.5 to 5.6 m in plantations) and low, live foliage is absent below about 1.2 m in height (Table 1).

Historically, Kirtland's warblers have been found in large (> 32 ha), 8- to 20-year-old barrens that have been regenerated by wildfire. In the past 2 decades, a different type of habitat has become available: clearcut pine stands stocked by natural, nonserotinous seeding; and rarely, by planting. Twenty-two percent (630 of 2,886) of the Kirtland's warbler males counted on the annual censuses from 1971 through 1984 were found in 26 areas (distributed among 16 surveyed sections) that were unburned following harvest (data on file). Females or nests were found in at least 18 of the 26 areas. Two of these breeding areas in unburned, unplanted barrens supported more than 66% of the males in that regeneration type during the period 1971 to 1984. A third unburned habitat that was planted held another 16% of the males during that period. These 3 areas were characterized by denser tree regeneration (stands 4, 15, 16, Fig. 2) than most other unburned jack pine areas (aerial observation), and one of the 3 was planted for Kirtland's warbler.

Unburned, unplanted jack pine barrens are characterized by lower tree density (Table 2) and more open canopy cover than wildfire areas (Fig. 2); therefore few of them develop the characteristics of more suitable areas. When unburned, unplanted barrens are first colonized, they are older than plantations (p < 0.01) or wildfire stands (P < 0.001, Table 2 and Fig. 2) and average about 3.3 m in height at this threshold. Unburned areas

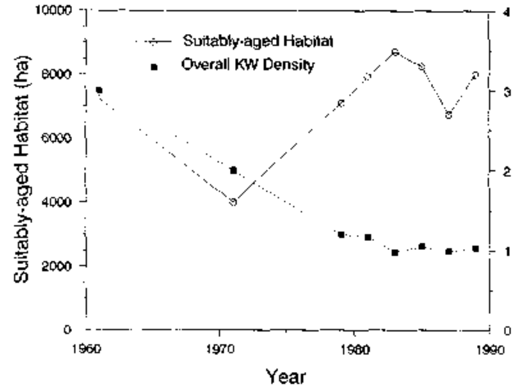

Fig. 3. Area of jack pine ecosystems in lower Michigan suitably-aged (see Table 5) for Kirtland's warbler and overall density of males between 1960 and 1990. Sources; Data from unpublished reports by J. Weinrich (Michigan DNR) and D. Sorenson (USDA Forest Service).

planted for Kirtland's warbler (stands 5, 18 and 20 in Fig. 2) can produce adequate tree cover at the usual 2 to 3 m height (Fig. 2), and plantations (burned or unburned) can support high (2.8 males per 40 ha) Kirtland's warbler populations (Table 3).

3.2 Landscape composition and population distribution

In 1984, the known breeding population of Kirtland's warblers was located on 5,420 ha (Table 3) of 8,760 ha of suitably-aged jack pine ecosystems within the known breeding range in northern lower Michigan (Fig. 3). From 1977 to 1983 three-fourths of the male population (from 155 to 180 birds) was located in 5 or 6 major breeding areas (Ryel 1981b, Probst 1986) whose combined total area represented only about one-third the entire occupied areas. Further, from 1979 to 1989, 77% of the male Kirtland's warblers were censused in areas larger than 200 ha, so patch size of landscape components is an important attribute. Male Kirtland's warbler density in all suitably-aged stands fell from 3.0 males per 40 ha in 1961 to 1.0 males per 40 ha in 1984 (Fig. 3). This decrease is probably due to a degradation in average habitat suitability because dense plantations and wildfires had declined in the previous 2 decades (Probst 1986). Further, overall Kirtland's

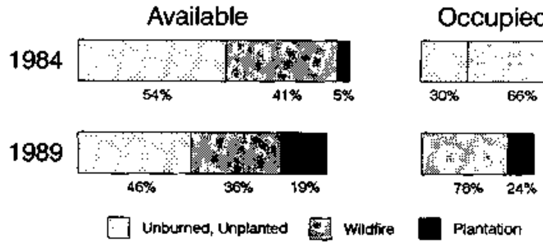

Fig. 4. Change in landscape composition of jack pine ecosystems (greater than 31 ha) and Kirtland's warbler distribution between 1984 and 1989.

warbler densities between 1975 and 1990 were declining to stable despite a doubling in area of suitably-aged barrens at that time (Fig. 3). But in occupied areas only, Kirtland's warbler densities were 1.9 males per 40 ha in 1984 within wildfire and plantation together and 1.6 males per 40 ha in 1989 (Table 3), suggesting preference for these two landscape components.

These observations lead to tests for nonrandom distribution of Kirtland's warblers among the three regeneration types within the years 1984 and 1989, as well as the period 1979 to 1989 as a whole (Fig. 4). For the 11 year period as a whole, the distribution was non-random ($P < .001$). Kirtland's warblers used suitably-aged regeneration types nonrandomly (Fig. 4) in 1984 and 1989 ($P < .001$; both years). In both years, unburned, unplanted areas were substantially under-utilized ($P < .001$; both years). Considering only wildfire and plantation types, in 1984 there was no deviation from random utilization ($P = .48$), but in 1989 there was a bias in favor of wildfire areas ($P < .001$). Comparing the 1989 warbler distribution to the 1984 distribution (Fig. 5), there were shifts in utilization of landscape components ($P < .001$). The warbler occurance in unburned, unplanted areas was lower in 1989 than 1984 ($P < .001$), as was the occurance in plantation habitat ($P = .023$), compensated by increased utilization of wildfire habitat ($P = .016$). Thus, we interpreted warbler occurance in unburned, unplanted areas before 1987 to be a consequence of saturation or overmaturity of major colonies in the two more suitable regeneration types (Probst 1986). The above comparisons were based on patterns of occupancy within barrens defined as suitably-aged

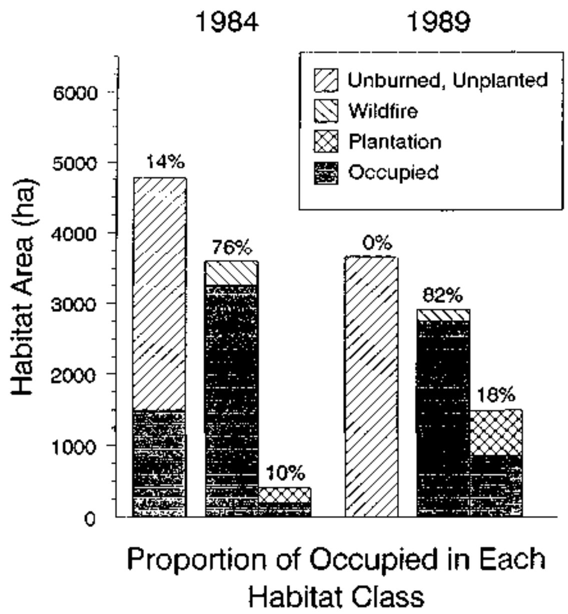

Fig. 5. Changes in availability of regeneration types and bird distribution between 1984 and 1989. The distribution of Kirtland's warblers within a year is indicated above each bar. Chi-square Tests were used for significant differences in proportions of total acres or males in occupied habitat in a regeneration type relative to the proportion of suitably-aged habitat in that type.

(8–20 years of age). However, about 8% of the birds in 1984 and 1989 occurred in habitat younger or older than previously defined as suitably-aged for predictive purposes. The occurances were both infrequent and limited enough to not warrent changing the suitable age limit to jack pine ecosystems.

3.3 Testing the carrying capacity estimate

We tested the prediction that habitat lost in declining, more suitable areas could be replaced by colonization in developing, more suitable areas (wildfire and plantation). In 1980, we attempted to predict the rate of decline of 5 major breeding areas (Table 4) based on 0.75 survivorship estimate (Probst 1986, Probst and Hayes 1987). The number of males in the 5 major colonies fell from 180 males in 1982 (Probst 1986) to 43 males (53 predicted) in 1987 (Table 4).

Because the distribution of birds among regeneration types can vary (Fig. 5), it is not possible to predict Kirtland's warbler populations in regenerating ecosystems based on projections of 'suitably-aged' area alone. However, if we separate suitably stocked ecosystems (*i.e.* plantations and wildfire areas) from less suitable ones, we can calculate minimal estimates of carrying capacity by applying the 1984 Kirtland's warbler density figures (1.9 males per 40 ha) to wildfires and plantations. In 1980, we predicted a maximum of 125 males would be in 2630 ha of young barrens (not occupied before 1980) in 1987. The number of males in new suitable barrens in 1987 turned out to be 123 males. Thus, the prediction of 1987 carrying capacity in declining (43 males) plus new habitat (125 males) totaled 168 males, versus 160 males actually censused (less than 5% error) in wildfire and plantation habitat. (Seven males were also found in unburned, unplanted areas in 1987, bringing the total to 167 males.) For

Table 4. Observed and projected populations (males per 40 ha) in declining major Kirtland's warbler colonies in Michigan.

Location	Year of Origin	Observed					
		1984	1985	1986	1987	1988	1989
Fletcher	1968	12	17	9	6(5)[a]	0	0
Muskrat	1964	28	24	11	10(12)	4	0
Artillery N.	1966	38	32	16	14(15)	3	0
Damon Burn	1966	35	15	11	6(15)	5	1
Mack L. (S.3)	1967	17	12	14	7(6)	1	0
		130	100	61	43(53)	13	1

[a] 1980 prediction based on 0.75 survivorship (Probst 1986).

Table 5. Carrying capacity for 1987, 1989 and 1996 in new[a] suitably stocked plantation and wildfire stands for Kirtland's warbler in Michigan.

Habitat category	1987 Area (ha)	1987 Carrying capacity[b]	1989 Area (ha)	1989 Carrying capacity[b]	1996 Area (ha)	1996 Carrying capacity[b]
Wildfire	1,134	54	2,878	137	1,891	90
Plantation[c]	1,496	71	1,569	75	6,008	285
Total	2,630	125	4,447	211	7,899	375

[a] Not colonized before 1980.
[b] Calculated from 1984 densities 1.9 males per 40 ha 8 to 20 years age (wildfire stands), or from 10 to 20 years age (plantations).
[c] Suitably-stocked plantations (> 2500 stems per ha) managed for Kirtland's warbler.

these projections of male population we assumed that all *suitably stocked* stands of the appropriate age would be colonized and occupied at the same approximate male densities found in 1984, which proved to be a reasonable assumption. We also assumed that the area of the Mack Lake Burn was so large that we could not ignore the very low density of colonists occasionally observed in regenerating burns before age 8 (Table 2). Therefore, we included 700 ha as suitable at stand age 7 instead of the usual 8 years (see above).

By 1989, the suitable area in the Mack Lake Burn of 1980 exceeded 1,745 ha and supported 106 male Kirtland's warblers. Between 83 (at 1.9 males per 40 ha) and 122 (at 2.8 males per 40 ha) males were predicted. M. Aili, M. Nelson and J. Probst predicted an overall 1989 minimum carrying capacity in lower Michigan of 211 to 311 males (based on 1.9 and 2.8 males per 40 ha, respectively) in 'new areas' (not colonized before 1980). The 1989 census counted 212 males – all but one in more recent breeding areas.

4. Discussion

4.1 Future habitat quantity and carrying capacity

Between 1957 and 1961, 4 areas totalling 4,676 ha – one in the Huron National Forest and 3 on State land in Michigan – were set aside specifically for preserving the Kirtland's warbler (Mayfield 1963). The state areas were to be planted, and the federal areas were to be burned and planted as necessary (Radtke and Byelich 1963). With one exception (stand #10, Fig. 2), all prescribed burning has failed to provide natural regeneration. The current area targeted for Kirtland's warbler management has increased to 55,900+ ha (including 2,000 ha U.S. Fish and Wildlife Service ownership). The Kirtland's Warbler Recovery Plan (developed under authority of the Endangered Species Act of 1973) calls for regenerating jack pine ecosystems through harvest followed by burning on State (31,400 ha) and U.S. Forest Service (24,300 ha) land so that about 11,180 ha of suitably aged habitat will be available every year. The areas will be regenerated at the rate of about 1,120 ha per year in 17 State forest and 7 federal management areas (Fig. 6), plus some small U.S. Fish and Wildlife Service parcels. These stands are usually managed on a 50-year Kirtland's warbler management and commercial timber rotation; Kirtland's warblers are the primary resource objective. Prescribed burning usually has failed to provide the dense tree stocking required by the Kirtland's warbler, primarily because jack pine regeneration has been de-emphasized as an objective of fire prescriptions. Land managers have been seeking alternatives to burning without sacrificing any secondary habitat requirements (Probst 1988).

By 1993 all suitably stocked Mack Lake Burn acreage will be old enough to support Kirtland's warbler breeding, and 3,360 ha of State of Michigan and USDA Forest Service Kirtland's warbler plantations will be old enough to be utilized. These new areas will be offset by maturation of the Bald

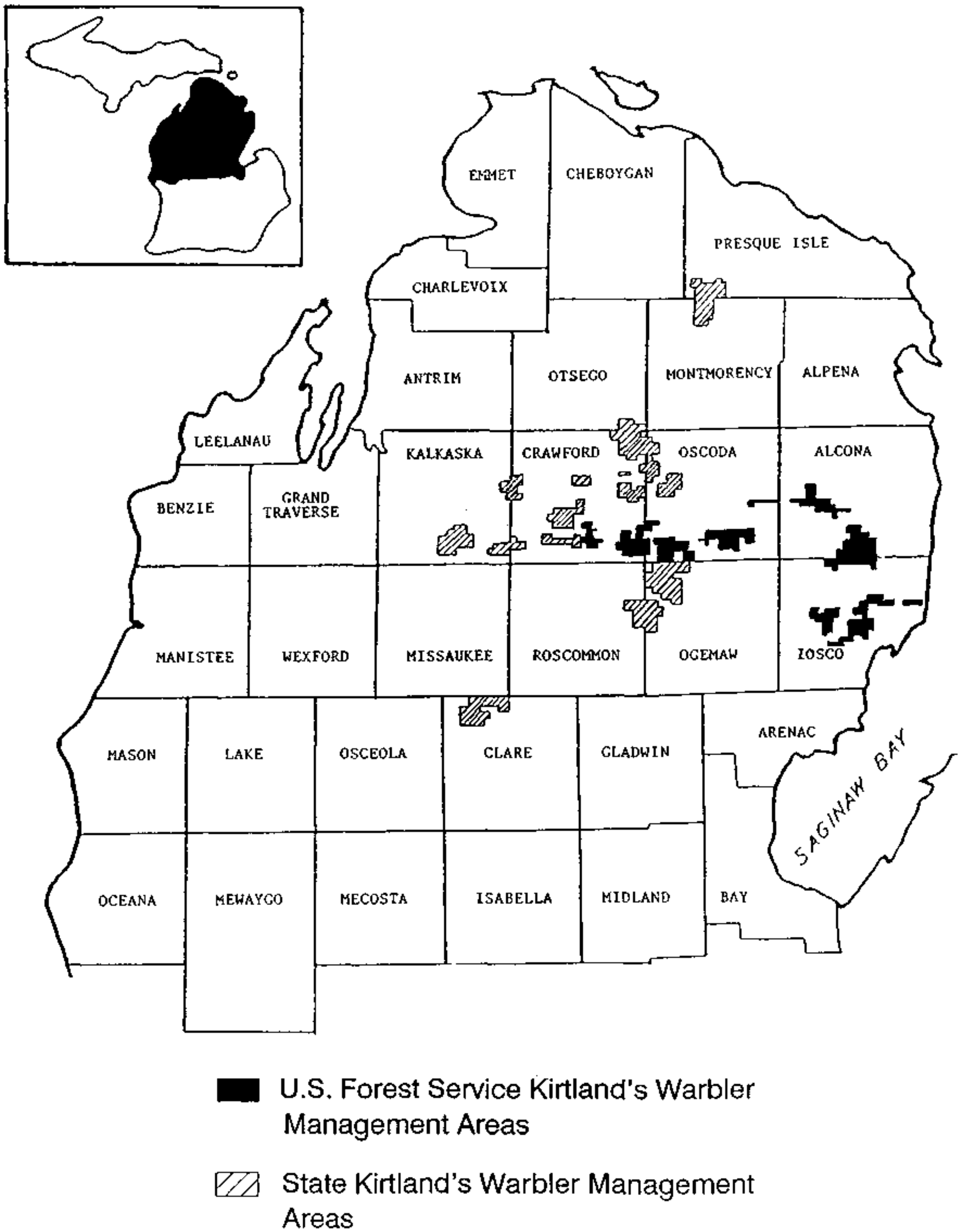

Fig. 6. State and federal Kirtland's warbler management areas in Michigan.

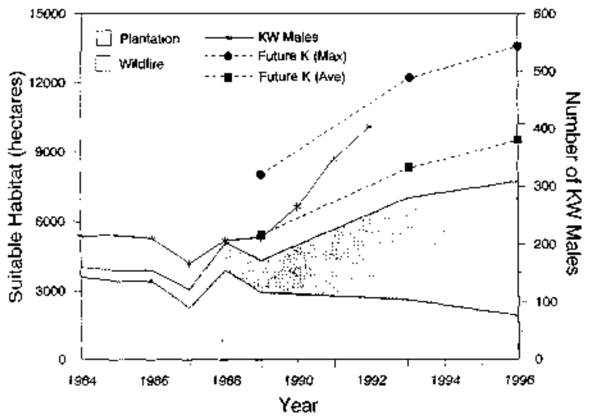

Fig. 7. Quantity of suitably-stocked habitat and proportion in plantation and wildfire for Kirtland's warbler in Michigan (1984–1996). Past populations (1984–1992) and estimated carrying capacity (1989–1996) of male Kirtland's warblers are also shown. The lower carrying capacity estimate is based on the 1984 average male density (1.9 males per 40 ha) in wildfire plus plantation habitat. The higher estimate (2.8 males per 40 ha) was derived from peak populations during the middle years of habitat occupancy (see Fig. 1). Sources: Habitat area from unpublished reports by J. Weinrich (Michigan DNR) and D. Sorenson (USDA Forest Service).

Hill Burn area, which should begin a slow decline in Kirtland's warbler numbers about 1992 and will have few birds after 1996. We estimated minimum carrying capacity for 328 male Kirtland's warblers in 1993 and 368 males in 1996 (Fig. 7) based on the 1984 average male density among all wildfire and plantation stands. A maximum estimate of 483 males in 1993 and 542 in 1996 is based on peak densities (2.8 males/40 ha) in wildlife habitat. A higher resolution study of the Mack Lake Burn area (Nelson 1992) suggests that our estimates of suitably-stocked habitat there may have been too conservative, increasing carrying capacity by 40-60 male Kirtland's warblers by the mid-1990's.

4.2 Primary habitat factors

Some evidence suggests that tree height and percent cover (*i.e.* foliage volume) is the primary factor controlling habitat suitability for Kirtland's warblers. In typical wildfire areas, barrens with dense regeneration are occupied first, but no areas were occupied with less than 16% cover (Table 1). Nelson (1992) successfully tested this tree-stocking variable in 3 tree-density classes as a hypothesis determining Kirtland's warbler utilization in the Make Lake Burn. Further, stands of intermediate tree density were older than dense stands when first used (Buech 1980) and usually support fewer birds (Smith 1979 and unpublished data). Territory sizes were larger in the more open areas of a stand (Mayfield 1960, Smith 1979, and pers. obs.). The average density of male Kirtland's warblers was higher in suitably-stocked plantations (whether burned or unburned) or wildfire areas, relative to unburned, unplanted areas (Table 3). Only 25 to 67% of males in young or poorly stocked areas obtain mates compared to 95% pairing success in more suitable areas (Probst and Hayes 1987). Thus, it is a reasonable hypothesis that tree density has been more limiting to Kirtland's warblers in unburned stands than lack of fire *per se*, but the number of unburned plantations available during the study was too small for statistical comparison. At the least, unburned stands have been under-managed, and therefore under-utilized by Kirtland's warblers.

Previous explanations of Kirtland's warbler habitat suitability centered about the bird's nesting biology (Mayfield 1960, Walkinshaw 1983), and the U.S. Department of Interior Kirtland's Warbler Recovery Team has emphasized the importance of fire influencing ground cover requirements for suitable nest sites (Byelich *et al.* 1976). However, it is unlikely that this ground-nesting bird is limited by nest sites. The threshold for initial occupancy may be related to minimal foliage volume necessary for Kirtland's warblers foraging requirements. The decline of suitability at older stand ages could be related to a lack of live lower branches (Table 1) for fledgling cover and for the foraging of the female Kirtland's warbler. If tree foliage volume (in appropriate ecosystems) is of primary importance to Kirtland's warbler habitat suitability, the occupied areas can be described by tree height and tree cover (Fig. 2). The composition and height of ground cover (Probst, unpubl. MS) may only become limiting in more mesic sites (site index greater than 55) not considered suitable for the species at present.

4.3 Habitat and population projections

It is possible to predict Kirtland's warbler population response to major changes in landscape composition. We predicted that the high proportion of Kirtland's warblers in young or less suitable areas between 1984 and 1987 could impede population growth enough that the 10,000 ha Mack Lake Burn would not be densely occupied initially (reflected in Fig. 3), even within the suitably stocked patches. The Kirtland's warbler population increased substantially starting in 1990 (including the Mack Lake Burn), but we also predicted that population growth would moderate in 1992 because of declining populations in the Bald Hill Burn. Also, a higher proportion of birds were in suitable areas between 1988–1991 than existed between 1982 and 1987. Thus, we predicted that the shift in nesting distribution across the landscape would increase annual productivity enough to allow full occupation of new jack pine barrens that became suitable for Kirtland's warbler from 1990 through 1993. Kirtland's warbler numbers may increase or be maintained around the turn of the century in plantation areas which will equal the area of the suitable Mack Lake Burn habitat. If this positive trend is to continue into the next century it will be necessary to keep management objectives on schedule.

We can evaluate the adequacy of the areas designated for Kirtland's warbler management using the density estimates in Table 3 and the minimum carrying capacity estimates (Fig. 7). The most pessimistic prediction uses the current overall density of 1.9 males per 40 ha in wildfire and plantation areas combined. Habitat area of 11,180 ha would only support 531 male Kirtland's warblers based on 1984 densities and habitat considerations alone. However, the quality of the managed habitat and new wildfires may be sufficient to allow an average of 3 or more males per 40 ha in most stands, which would yield 839 male Kirtland's warblers. Such densities may occur in favorable landscapes such as the Mack Lake Burn (Zou, *et al.* 1992) or managed areas with aggregations of large suitable patches. As more samples of occupied plantation become available, it may be possible to project higher Kirtland's warbler densities in managed versus wildfire areas. A higher average male density, of over 4 males per 40 ha would be required to achieve the recovery goal of more than 1,000 male warblers on existing dedicated areas. This goal may be attainable on the area set aside for management, but it will require full implementation of the management program as well as suggested improvements in landscape design and stand attributes (Probst 1988) to achieve the established objectives.

Finally, biologists must understand the mechanisms determining landscape dynamics and metapopulation interactions if they are to estimate area required for viable populations. In the case of the Kirtland's warbler, we have suggested that population regulation through landscape composition and structure may be related to nonbreeding birds and dispersal among fragmented areas of marginal quality – not from reduced average nesting success of most breeding pairs (Probst 1988). A shortage of quality landscape components and less suitable landscape structure may result in more birds abandoning their territories to search for better nesting areas. In addition, stand size and biogeography of stands may affect colonization success (Fritz 1979), arrival dates (Probst 1988), territorial settlement, and fledging dates. Delays in the initiation of breeding may cause birds to miss food resource peaks and sacrifice opportunities for renesting or second nesting.

It is possible to investigate the influence of variable carrying capacity on the entire known population of the Kirtland's warbler because the landscape composition and structure has varied substantially during the past two decades. When the regional population was at or above carrying capacity, the annual censuses were stable and males expanded their habitat selection to include less suitable areas. The area of suitable ecosystems doubled by 1988 and 1989. We presumed that the Kirtland's warbler population was well below carrying capacity beginning in 1988 and increased its overall productivity beginning about 1989. Thus, we predicted a rapid population increase between 1990 and 1995 based on landscape change including aggregate stand area and chronology. The 1990 through 1992 census results confirm that a 88% increase has already occurred (Fig. 7).

If the Kirtland's warbler population was at or above carrying capacity, the period from 1979 to 1986 may have been a fortuitous time to study Kirtland's warbler landscape dynamics. More generally, if density limitation relative to landscape composition varies in intensity over time, then habitat-based, local population predictions will be inaccurate unless they are coupled to metapopulation processes. Thus, geographic and annual population variability may restrict the utility of traditional local habitat modeling in wildlife biology.

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