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LONG-TERM TRENDS IN HABITAT SELECTION BY KENTUCKY WARBLERS

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Abstract.—Microhabitat selection of the Kentucky Warbler (*Oporornis formosus*), a forest-interior Neotropical migrant, was examined using a geographical information system. The distribution of territorial male Kentucky Warblers was mapped within a 460-ha study area in northwestern Virginia from 1979 through 1992. Each annual distribution of territories was compared, using logistic regression, to a random distribution of territories with respect to habitat features codified within a vector-based geographical information system. Kentucky Warblers selected forested areas with cove hardwoods and avoided oak/hickory overstory. The warblers also were found more often in areas that contained streams and in areas with low white-tailed deer (*Odocoileus virginianus*) densities. Since 1979 there have been significant shifts in Kentucky Warbler use of habitat at this site, resulting in fewer territories within oak/hickory and edge habitats. *Received 22 November 1993, accepted 31 August 1994.*

Kentucky Warblers (*Oporornis formosus*) are insectivorous, ground-nesting birds that breed within the interior forests of the northeastern United States and winter from southern Mexico to South America. This species is one of many wood-warblers that has shown an apparent decline over the last two decades (Robbins et al. 1989) and, therefore, is of particular interest to land managers and conservationists. In studies using multivariate analysis to describe forest bird communities, Kentucky Warblers were found to be associated with large, mature forests that possess a dense understory (Lynch and Whigham 1984, Robbins et al. 1989). As with most wood-warbler species, however, little is known of specific microhabitat requirements beyond the valuable, but anecdotal, reports from early naturalists (Chapman 1907, DeGaris 1936, Bent 1953) and annual surveys that detected population declines (Robbins et al. 1989). Declines within some unmanaged forests have been postulated to be due to an increased density of white-tailed deer (*Odocoileus virginianus;* Boone and Dowell 1986, Robbins 1991) through reduced density of understory shrubs.

Geographical information systems (GIS) have been used successfully to model habitat requirements of Sage Grouse (*Centrocercus urophasianus;* Homer et al. 1993) and Wild Turkey (*Meleagris gallopavo;* Donovan et al. 1987). These models, however, identified landscape-scale features that were associated with flocks or populations of birds and, thus, may be inappropriate for analysis of habitat use by individual birds within a forest block. Given that Kentucky Warblers inhabit mature, deciduous forests, it may be possible to determine how they are distributed within this landscape-scale habitat using a GIS.

Since 1979 extensive surveys for Kentucky Warblers have been conducted at the National Zoological Park's Conservation and Research Center (CRC). This site is a small (1,200-ha), protected area in the Blue Ridge Mountains of Virginia, 5 km south-southeast of Front Royal, Virginia. These annual surveys can be compared to vegetation and habitat attribute maps recently produced for the study area with a GIS. We examine: whether landscape level features and habitat measures derived from aerial photographs, when organized within a GIS, are suitable for quantifying habitat requirements of small forest birds; whether shifts in habitat use are detectable; and what factors might precipitate habitat shifts.

Methods

Study area.—The Natural Studies Area within the Conservation and Research Center is a 4.6-km^2 area that is 86% forested. The forests are between 20 and 100 years old, and a portion (20%) contained livestock until the 1970s. No hunting has been allowed since

Table 1. Forest types within Natural Studies Area, their percent representation of forest, and selected attributes as measured in 1989. Attributes derived from sampling forest-type polygons identified by aerial photographs (number of samples in parentheses). Species present in greater than 10% of samples are ranked in order of abundance. Cover and density measures are mean (±SE) of sample points based on ordinal scale from 0-3.

Common overstory species	Common understory species	Canopy cover	Understory density	Ground cover
	Hackberry (*n* = 50, 13%)			
Celtis occidentalis, Prunus serotina, Cornus florida, Acer negundo, Sassafras albidum	*Vitis* sp., *Rhus radicans, Parthenocissus quinquefolia*	1.44 ± 0.08	2.65 ± 0.07	2.50 ± 0.09
	Locust (*n* = 27, 11%)			
Robinia pseudoacacia, Ailanthus altissima, Diospyros virginiana	*Symphoricarpus orbiculatus, Lonicera japonica, Vitis* sp.	1.66 ± 0.13	2.36 ± 0.10	2.41 ± 0.15
	Maple (*n* = 27, 18%)			
Acer rubrum, Fraxinus americana, Ulmus rubra	*Acer rubrum, Carpinus caroliniana, Vitis* sp.	1.88 ± 0.12	2.18 ± 0.11	1.92 ± 0.13
	Oak (*n* = 118, 43%)			
Quercus spp., *Carya* spp.	*Cornus florida, Cercis canadensis*	2.40 ± 0.05	1.52 ± 0.06	2.07 ± 0.04
	Poplar (*n* = 48, 16%)			
Liriodendron tulipifera, Quercus rubra	*Lindera benzoin, Cornus florida*	2.60 ± 0.07	2.27 ± 0.07	1.79 ± 0.11

1979, and white-tailed deer densities increased from approximately 20 to 30 deer/km^2 over the period of our study (McShea et al. 1993).

Dominant forest types were identified in 1986 through analysis of color-infrared aerial photographs with a minimum resolution of 1 ha (Teetor 1988). The composition of forest-type polygons were verified by surveying one 0.04-ha circular plot for every 1,000-m^2 block within each polygon ($n = 270$ plots). At each circular plot, the first- and second-most-abundant canopy and understory species were identified, and the density of canopy cover, understory shrubs, and ground cover was estimated on a scale from 0 to 3 (Table 1). Our analyses concentrate on bird associations with canopy species, because this measure is obtainable from the aerial photographs. Each forest type, however, appears to occur in conjunction with a unique understory composition and vegetation density (Table 1).

Territory determination.—The study area was surveyed for singing males and other evidence of breeding activity from 1 May through 31 July during 1979 through 1992. An exception was 1984 when no surveys were conducted. The forest was searched by walking transects, trails and roads throughout the Natural Studies Area, with no part of the study area farther than 150 m from the survey trails (i.e. all within easy aural-detection range). From 1,000 to 5,000 h were expended on searches for and observations of Kentucky Warblers each breeding season. We are confident all territorial males were located. Most (92%) of the located males were color-banded after capture using mist nets and recorded calls, and the territory occupancy of all males was visually confirmed. Males that occupied a site with boundaries, defined by regular singing activity for greater than two weeks, were considered territorial. The analysis included territorial, unmated males (5%), but did not include the few males that did not appear to hold a territory. Males that shifted territories between early and midseason were not counted twice, but instead assigned the location of their midseason territories. The center of each male's territory was located on a map, and each of these points became the center of a 50-m-diameter circle representing an idealized (circular) territory. This average size was determined by repeated location of color-banded individuals and represents a minimum estimate of territory size (McDonald unpubl. data).

GIS.—PC ARCINFO, a vector-based GIS, was used to create map layers for forest type, streams and ponds, forest age, deer densities, bird territories, and random territories. The forest-type layer was derived from infrared aerial photographs. Fields were not included for this analysis because Kentucky Warblers do not use this habitat. Streams were deliniated from aerial photographs taken in 1986. Two forest ages were determined based on comparison of digitized maps created from aerial photographs taken in 1937 and 1986.

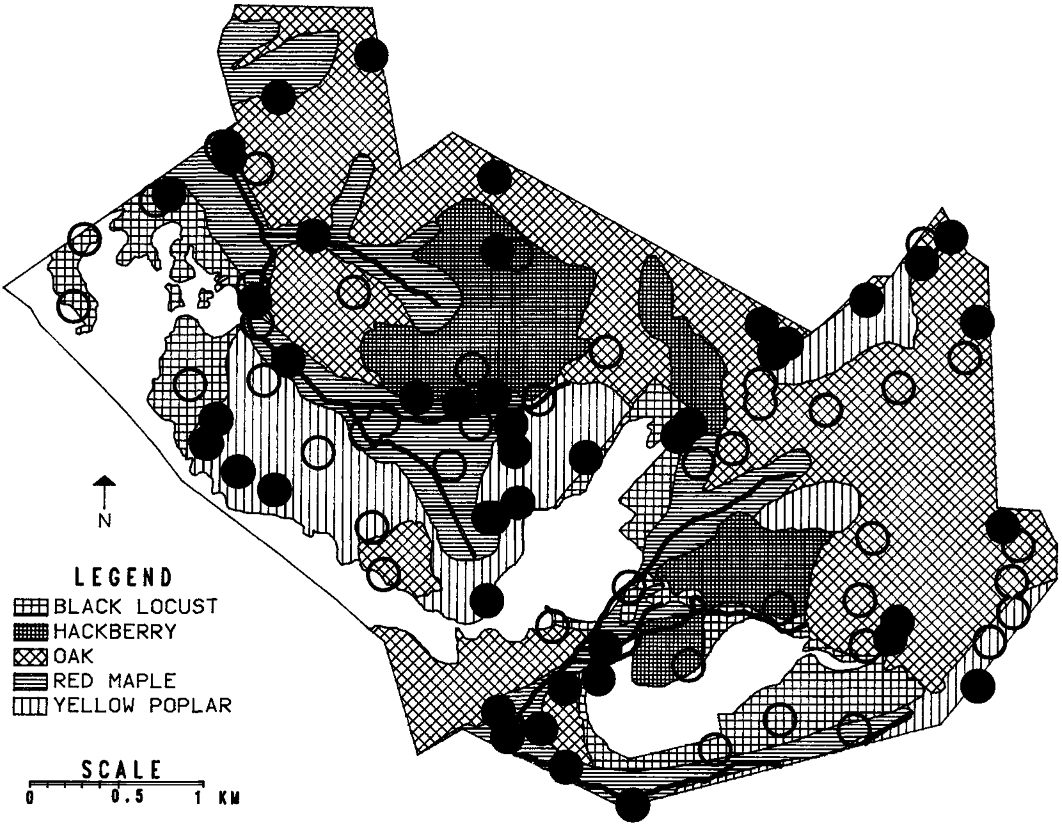

Fig. 1. Map of forest types within Natural Studies Area at Conservation and Research Center, Front Royal, Virginia. Actual (closed circles) and random-generated (open circles) territories for 1988 are shown.

Forest habitat before 1937 was categorized as "old," and forests that had been pasture in 1937 considered "new." Most open pastures in the area were abandoned in the 1960s.

Deer densities were estimated throughout the study period by repeatedly driving a 2-km census loop that passes through most of the study area. We counted the number of marked and unmarked deer along the loop (for details, see Stuwe 1986). Densities increased over the course of the study from 20 to 30 deer/km^2 (McShea et al. 1993). A small portion of the study area (15%) was fenced and, annually, deer were driven out into the larger study area, and/or hunting restrictions were not enforced. No formal census was taken of the fenced area due to its small size, but annual line-transect censuses (Anderson et al. 1979) report on average one-fourth the number of deer per kilometer walked in the fenced area, compared to the larger study area (39 km walked in 1993).

For our analyses, the GIS was queried for each territory as to forest type, age of forest, and deer density. We viewed map layers on the computer screen to determine if a territory encompassed forest-type boundaries or streams. Forest type was assigned according to the largest polygon within the territory, with territories that encompass more than a single forest type scored as containing a habitat boundary. Boundaries included an additional habitat type (field) that was not included in the forest-type analysis.

For each of the 13 years of Kentucky Warbler data, an equal number of random territories were produced using UTM coordinates generated by the random-number algorithm in LOTUS 123. The program was given the boundary coordinates for the Natural Studies Area and, using the last digits of the computer's clock as a seed value, it generated a number of random points for each year. These points became the center of 50-m-diameter circles to produce idealized territories, just as were the actual bird locations (Fig. 1). We determined the habitat features of these random-generated territories in the same way as actual territories.

Analysis.—For this vector-based GIS, most of the information is categorical, with only presence/absence coded for a specific feature. A logistical-regression model within CATMOD (SAS/STAT; SAS Insti-

TABLE 2. Number of territorial male Kentucky Warblers mapped each year, and attributes of their territories as determined from GIS. "Boundary" indicates birds whose territory crossed forest-type boundaries. For forest type, distribution of territories relative to random territories was compared for each census year.

						Forest type				
Year	No. territories	Mature forest	Stream present	Low deer density	Boundary	Locust	Maple	Oak	Poplar	Hackberry
1979	27	21	7	2	18	10	7	5	4	1
1980	31	24	12	7	19	7	11	6	4	3
1981	38	30	14	5	27	9	11	13	3	2
1982	48	34	15	6	26	5	14	16	8	5
1983	44	40	17	11	26	4	16	13	9	2
1985	40	31	10	9	27	4	13	13	5	5
1986	39	30	12	13	26	6	12	8	5	8
1987	29	21	9	12	21	6	6	5	6	6
1988	39	27	19	17	22	6	16	5	7	5
1989	51	42	20	24	36	1[a]	23	8[a]	10[a]	9
1990	50	41	15	27	39	5	15	4[a]	17[a]	9
1991	35	29	11	21	23	4	9	2	17[a]	3
1992	37	30	20	25	32	2	17	1[a]	13[a]	4
Summary	508	400	181	179	342	69	170	99	108	62
Random	508	432	44	54	268	47	89	227	88	57

[a] Distribution of bird territories significantly different from random territories ($P < 0.05$).

tute 1987) was used to determine if habitat features of Kentucky Warbler territories were significantly different from random-generated territories. Tests of each model produced a chi-square value (a maximum-likelihood estimation) for each variable, as well as parameter estimates and standard-error values (Feinberg 1970, Schoener and Adler 1991).

An analysis using CATMOD is based on a contingency table containing all combinations of categorical variables found in the sample set, and we refer to each unique combination of variables as a subset. All subsets with fewer than five entries were deleted before analysis.

A sufficient sample size for logistic regression was achieved only after pooling the 13 years of census data. We assumed each year included a period of habitat selection for each migratory bird, based on preliminary data of territory shifts by marked individuals (McDonald pers. obs.). We provide an analysis using only the first capture year of each marked bird to show the significant habitat variables do not change with the reduced sample size. Pooling years also may infer significance to habitat features based on a single year that strongly deviates from random; a single variable (i.e. forest type) was tested for each individual year to assess the consistency of trends seen in the cumulative data set.

Temporal changes were tested by dividing the data in half, with 1979 through 1986 as an early group, and 1987 through 1992 as a late group. The random and actual territories then were tested separately using time as the dependent variable. We assumed that habitat shifts would not be evident when comparing random territories before and after January 1987, but would be evident for actual territories.

RESULTS

During 13 years of surveys, 278 territorial male Kentucky Warblers were banded within the study area. With the return of some marked males on subsequent years, and the presence of a few territorial but unmarked males each year, we located 508 territories during the study period ($\bar{x} = 39.0 \pm$ SE of 2.1 territories/year; Table 2).

Kentucky Warbler territories were not randomly distributed (Table 3). Forest type, streams, and density of deer were significant variables, but forest age and the presence of a habitat boundary did not contribute significantly to territory locations. The first three variables are significant both when examining all territories mapped, and when examining only the first territory established by each marked male during his residency within the study area (Table 3). Using each census year separately to examine selection for forest type, only the last four years showed preferences which were significantly different from the random territories (Table 2).

The logistic-regression model produced a likelihood-ratio value indicating a significant

TABLE 3. Importance of habitat features in logistic-regression model differentiating actual and random-generated territories of Kentucky Warblers over 13-year period. First two columns show results using all territories mapped, while third column based on mapping only first territory for each marked male.

		All territories		
Source	df	35 subsets ($n = 960$)	19 subsets[a] ($n = 1{,}014$)	First territory (14 subsets[a], $n = 508$)
Intercept	1	47.6***	68.4***	25.9***
Forest age	1	1.7	—	—
Forest type	4	27.9***	33.7***	9.3*
Stream	1	44.5***	55.2***	21.4***
Boundary	1	0.7	—	—
Deer density	1	49.8***	53.6***	23.9***
Likelihood ratio		44.0*	26.1*	16.2*

*, $P < 0.05$; ***, $P < 0.001$.

[a] Logistic-regression model without forest age and boundary as independent variables.

correlation between some of the independent variables (Table 3). Two variables, forest type and presence of a stream, were significantly correlated ($r = 0.52$, $n = 1014$, $P < 0.001$), as the maple-forest type was often associated with moist soil conditions.

By analyzing each variable separately, we found that Kentucky Warblers territories ($n = 507$) occurred more often than expected in maple-forest type ($X^2 = 19.95$, $P < 0.001$), and possibly locust-forest type ($X^2 = 3.3$, $P = 0.06$; Table 4). Territories often encompassed a stream ($X^2 = 97.53$, $P < 0.001$) and often were found within areas of low deer densities ($X^2 = 79.31$, $P < 0.001$). The birds avoided oak-forest types ($X^2 = 62.8$, $P < 0.001$).

Since 1979 there have been significant shifts in the birds' use of habitat (Table 5). Kentucky Warbler territories have increased within hackberry- and poplar-forest types ($X^2 = 4.57$ and 16.5, respectively, $P < 0.05$), and have decreased in oak- and locust-forest types ($X^2 = 21.1$ and 4.9, respectively, $P < 0.05$). There has also been a significant shift into the low-deer-density areas, whereas no shift in territory proximity to streams has occurred (Table 5). No shifts in the variables measured were evident for the random-generated territories (Table 5).

TABLE 4. Maximum-likelihood estimates (±SE) for habitat variables statistically significant in logistic-regression model. Sign of estimate indicates association of parameter with bird territories relative to random-generated territories.

Parameter	Estimate	Chi-square
	Intercept	
	-1.02 ± 0.12	68.4***
	Forest type	
Hackberry	0.35 ± 0.17	4.4**
Locust	0.33 ± 0.17	3.7
Maple	-0.17 ± 0.16	1.2
Oak	-0.67 ± 0.12	29.2***
Poplar	0.15 ± 0.14	1.2
	Stream	
Present	0.83 ± 0.11	55.2***
	Deer density	
Low	0.67 ± 0.09	53.6***

**, $P < 0.01$; ***, $P < 0.001$.

DISCUSSION

Kentucky Warblers selected specific habitats within forest blocks. Favored habitats were cove hardwoods that contained a relatively dense understory. Within our study area, cove-hardwood habitat is dominated by a red maple (*Acer*

TABLE 5. Comparison of chi-square values from logistic-regression model examining changes in habitat variables from first half (1981–1987) to second half (1988–1992) of study period for actual and random-generated territories.

Source	df	Random-generated territories (subsets = 13, $n = 503$)	Territories (subsets = 15, $n = 484$)
Intercept	1	1.77	2.3
Forest type	4	3.60	35.8***
Stream	1	0.07	0.5
Deer density	1	2.84	58.8***
Likelihood ratio	8	7.87	26.5***

***, $P < 0.001$.

rubrum) overstory and an understory composed of red maple, American hornbeam (*Carpinus caroliniana*) and grape (*Vitus* sp.; Table 1). Kentucky Warbler preference for cove hardwoods also was evident from our direct field observations of the warblers.

The presence of streams within many Kentucky Warbler territories may be due to either the plant community associated with the increased moisture, or to the fact that the moister soil and leaf litter support higher densities of the invertebrates consumed by these insectivorous birds. Prey densities were correlated with nesting success and recruitment for similar forest insectivorous species (Sherry and Holmes 1992).

The concentration of Kentucky Warblers within low-deer-density areas also indicates that understory characteristics are important in the warbler's habitat selection. Because deer are primarily browsers, they can significantly affect understory composition and density (Alverson et al. 1988, Tilghman 1989). Deer density increased by approximately 30% over the 13 years of this study within a large portion of the study area; during this period Kentucky Warblers shifted into the area where deer densities were annually reduced. Within the study area, forest types with low understory densities (i.e. oak-forest type) showed a decrease in Kentucky Warbler territory establishment.

The apparent influence of deer densities on Kentucky Warbler distributions has significant management implications. White-tailed deer densities are increasing throughout the eastern United States, especially in public lands that have prohibited hunting (Warren 1991). We hypothesize that high densities of deer have resulted in a decrease in suitable habitat for Kentucky Warblers at the Conservation and Research Center. High deer densities have been postulated to cause declines of forest birds in several protected areas (Casey and Hein 1983, Boone and Dowell 1986), but our findings are the first quantitative evidence that deer densities are correlated with a shift in the distribution of forest birds.

A second hypothesis is that the habitat shift is not the result of increasing deer densities, but rather an indirect result of the apparent decrease in Kentucky Warbler populations throughout the eastern United States. There are several regional studies that document declining Kentucky Warbler densities over the same years as our study (Robbins 1980, Robbins et al. 1989). If fewer warblers are breeding each year, several models predict that less favorable habitats will cease to be used by territorial males (Krohn 1992). This would explain the decrease in breeding males within dry, but dense, habitats, such as the locust-forest type. Territory shifts in response to habitat changes have been documented in Kirkland's Warbler (*Dendroica kirklandii*), where brood parasitism by the Brown-headed Cowbird (*Molothus ater*) may be limiting the populations (Probst and Weinrich 1993). For our study, the locust-forest type composed most of the forest edge; higher rates of predation and brood parasitism by Brown-headed Cowbirds may make this habitat less favorable. Recent evidence, however, does not indicate higher nest-failure rates along these forest edges (McDonald unpubl. data).

These two hypotheses are not mutually exclusive, as higher deer densities may reduce the quality of otherwise suitable forest types. However, if the second hypothesis is true, we predict no shift in Kentucky Warblers into the recently vacated forest types if deer densities were reduced.

Although the resolution of forest types possible in this study was larger than territory size, the microhabitat differences within a forest type were not sufficiently distinctive to mask completely Kentucky Warbler habitat preferences. However, we were limited by the sample size of any single year, and most of our analyses were possible only because of the availability of long-term data. This is true not only for the test of temporal shifts in habitat use, but also for the evaluation of habitat selection. No single, annual census produced sample sizes sufficient for analysis of more than a single variable using logistic regression. The shifts in habitat use indicate that single-year surveys may not provide a reliable index of habitat availability, as habitat suitability is a dynamic process that can be influenced by both biotic and abiotic factors.

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