The Condor 94:72–82

HABITAT USE BY THREE BREEDING INSECTIVOROUS BIRDS IN DECLINING MAPLE FORESTS[1]

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Abstract. We studied population variability and habitat use of the Least Flycatcher (*Empidonax minimus*), the Red-eyed Vireo (*Vireo olivaceus*), and the Black-throated Blue Warbler (*Dendroica caerulescens*) in sugar maple (*Acer saccharum*) forests of southern Québec in various state of decline. The Least Flycatcher was the most abundant species (1.7 pairs/ha) over the three-year study, although numbers were lower and showed higher interannual variability in declining stands compared to healthy stands. The flycatcher established its territory in areas where trees were tallest, sugar maple was in nearly pure stand, and sub-canopy was sparse. The Red-eyed Vireo (1.2 pairs/ha) was ubiquitous and populations were stable in all study sites regardless of decline. The Black-throated Blue Warbler, less abundant (0.4 pairs/ha), colonized areas of the stand that offered a high density of shrub growth under a closed canopy in both declining and healthy sites. Except perhaps for the flycatcher, there was no clear association between population change or pattern of habitat use and the level of forest decline in these three species. Confounding factors such as predisposing life-history characteristics and large scale population changes may explain some of our results.

Key words: Empidonax minimus; Vireo olivaceus; Dendroica caerulescens; *habitat selection; population stability; abundance; disturbance.*

INTRODUCTION

Temperate forests are complex habitats that support diversified communities. Several aspects of the ecology of the birds inhabiting these forests, such as community structure (Holmes and Sturges 1975, Keast 1988), population dynamics (Holmes et al. 1986, Leck et al. 1988), competition (Barlow and Rice 1977, Robinson 1981) or habitat selection (Hespenheide 1971, Sherry and Holmes 1985) have been investigated. However, relatively few studies have addressed the impacts of disturbances such as forest fragmentation (Wilcove 1985, Askins et al. 1990), forestry practices (Webb et al. 1977, DeGraaf and Chadwick 1987) and cottage development (Clark et al. 1983) on bird populations in this habitat.

Since the late 1970s birds breeding in Québec's deciduous forests have been faced with a moderate, chronic perturbation caused by sugar maple (*Acer saccharum*) decline. Trees have on average lost 20% of their crown foliage (Bordeleau and Gagnon 1988), a medium intensity perturbation comparable to some extent to sylvicultural treatments such as a 20% thinning cut (Webb et al. 1977, Freedman et al. 1981, Virkkala 1987). However, it differs in many aspects: vegetation loss is gradual, residual trees are weakened, dead branches and stems are still standing, reduction of twig growth produces tufts of foliage, etc. (Dessureault 1985). Within an ecological perspective, maple decline has numerous results such as regenerative aftergrowth (Houle 1990) and physiological imbalance of the tree leading to a loss of natural resistance to phytophagous insects (Dessureault 1985, Gregory et al. 1986).

DesGranges (1987) listed the anticipated effects of forest decline on about 25 species of birds found nesting in maple forests in Québec. He predicted that: (1) overstory and trunk species would derive temporary advantages from reduced tree growth such as reduction of twig growth producing tufts of foliage and reduction of number and size of leaves, but these advantages would be lost when trees became dessicated; and (2) species which prefer dense shrubs

[1] Received 23 May 1991. Accepted 9 October 1991.

should experience increasing benefits from the undergrowth development resulting from progressive opening of the forest. In 1986, DesGranges et al. (1987) carried out a pilot study of the effects of maple decline on bird communities and, although preliminary results supported the predictions, there was great variation in species response within any given feeding guild (canopy snatchers, canopy and shrub gleaners, and trunk and litter species).

In this study we investigated the relationships between maple decline and habitat use (sensu Hutto 1985) by three bird species which are the most abundant representatives of the three feeding guilds most likely to be affected by decline according to the predictions of DesGranges (1987) and the preliminary results of the pilot study: the Least Flycatcher (*Empidonax minimus*), a canopy snatcher, the Red-eyed Vireo (*Vireo olivaceus*), a canopy foliage gleaner, and the Black-throated Blue Warbler (*Dendroica caerulescens*), a shrub foliage gleaner. We predicted that, compared to healthy stands, declining stands should be lower quality sites for the canopy species and hence populations should be reduced and/or more variable. The opposite would be true for the shrub species which should benefit from shrub layer development resulting from opening of the canopy in affected stands. These predictions were based on the ideal-free distribution model (Fretwell and Lucas 1970) which assumes (1) that habitat selection is ideal in that each bird selects the habitat best suited to its survival and reproduction and (2) that birds are free to enter any habitat on an equal basis. Also, because affected trees are patchily distributed within the stand at intermediate levels of decline (Arseneault 1990), we predicted that affected patches should be avoided by canopy species but preferred by shrub species, the decline being an important characteristic to which birds should respond relative to other habitat features.

METHODS

STUDY AREA

We selected 18 maple stands using a data base of sugar bushes (stands exploited for maple syrup production) compiled by Québec Ministry of Forests. We chose stands that: (1) were within a 40 km radius of Thetford Mines (lat. 46°5′N; long. 71°17′W) in the Appalachian Mountains foothills, a region particularly affected by decline (Bordeleau and Gagnon 1988); (2) belonged to the sugar maple/yellow birch (*Betula alleghaniensis*) forest type (Roy et al. 1985), accompanied by American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), or red maple (*Acer rubrum*); (3) we could access for at least three years; and (4) were of 12–20 ha each. The size of the stands chosen was representative of the area in which maple forest covers more than 60% of the land and is fragmented by numerous but small agricultural patches.

In each stand, we delimited a 12 ha (300 × 400 m) quadrat that was divided into a 50 × 50 m grid. Four points (systematically repeated) were established for bird population sampling (4 points × 18 stands = 72 points). Decline was evaluated at each point by coworkers (Arseneault et al. 1989) using the following formula:

$$D = \left[\left(\sum S_iA_i/\sum A_i\right) + 1\right] \div 2$$

where D = index of decline for the station, S_i = percentage of foliage lost by the tree i, A_i = basal area of tree i, and 1 = percentage of trees in the station which have lost at least 10% of their foliage.

The index values, ranging from 2–60, were normally distributed and the mean value for all plots was 29.0 ± 13.7 (mean ± SD). The location of each stand, the forest type, and the evaluation of the level of decline are described in Darveau et al. (1990).

Detailed observations on habitat use were carried out in six stands situated in the middle of the study network (subsequently referred to as principal stands). The index values of the 24 plots from these stands ranged from 2–34, and the mean value was 19.6 ± 9.7.

HABITAT SAMPLING

We collected data at the 63 intersects of the 50 m grid in each of the six principal stands (total $n = 378$) to describe physiography, dendrometry, shrub growth, coverage of different vegetation layers, and level of decline. Sampling was spread over three years, with one fifth of the plots sampled in 1987 and two fifths in 1988 and 1989. Physiography (topography, slope, and exposure) and drainage were evaluated following the procedure of the Groupe d'étude sur l'écologie appliquée à l'aménagement du territoire (1974).

Dendrometric measures were taken with a tape and a clinometer on four trees (diameter at breast height [DBH] > 10 cm) which were the closest to grid intersection in each of four systematically oriented quadrants (Cottam and Curtis 1956). We measured the distance from the tree center to the intersect point, the total tree height, the DBH, and the height from the ground of the first branch with leaves (defined as base of crown). Shrubs were counted in DBH classes of 0–5 and 5–10 cm (Groupe d'étude sur l'écologie appliquée à l'aménagement du territoire 1974) in a sampling area of 1 × 10 m centered on the intersect point and oriented along the small axis of the stand grid.

The percentage of ground covered by each vegetation layer was estimated in sampling areas of 10 × 10 m centered on the intersect points. Layers were identified as upper canopy layer (>20 m), intermediate canopy (10–20 m), low canopy (5–10 m), upper shrub (2.5–5 m), intermediate shrub (1.3–2.5 m), low shrub (0–1.3 m) and herb.

Decline was measured on the basis of lost foliage for each tree sampled for dendrometry (Lachance 1985), and was considered constant between years for a given plot because: (1) 14 plots re-measured did not show significant differences in foliage loss between 1987 and 1988 (Wilcoxon signed-rank test, $P = 0.60$), (2) the mean level of decline estimated from 73 plots of 1987 and 141 of 1989 did not differ (*t* test, $P = 0.40$), and (3) decline level was relatively stable in Québec from 1987–1989 (Gagnon and Bordeleau 1990).

To average observer effects on subjective measurements like vegetation cover and foliage loss, the mean between the evaluation by two separate observers stationed at opposite sides of the quadrat was always used.

BIRD SAMPLING

At four points within each stand ($n = 72$ sampling points), we used the fixed-radius point counts technique (FRPC) (sensu Ralph 1981), a rapid method that allowed relative density estimations of bird populations present (Scherrer 1982). Three 15-min observation periods were carried out yearly (1987–1989) at each point and all birds heard or seen within a circle of 40 m (0.5 ha) were noted.

The standard method of grid mapping (Svensson 1970) was used to estimate population size in the six principal stands. From 1987 to 1989, six visits per year were carried out in these stands. During 2.5 hr, we followed the 50 m grid and mapped the positions of the three species of bird studied. Territories were later delimited independently by two observers using transparent acetates and mean values were used in analyses to minimize observer bias (method similar to Verner and Milne 1990).

All visits were conducted between 26 May and 30 June, i.e., during nest building and incubation periods. Counts were done between 04:00 and 09:00 (EDST) during clear weather with little or no wind. We rotated order of plot visit, entrance points on grids, and observers (six per year, 13 in total) to minimize bias.

DATA ANALYSIS

As intra-stand variability of the decline was comparable to inter-stand variability (Arseneault et al. 1989, M. Darveau, unpubl.), and because our three species generally have territories smaller than 1 ha (see results and Barlow and Rice 1977, Sherry 1979), we carried out the data analyses on the point count data with a regression model for nested data (Daniel and Wood 1980). This enabled us to partition intra and inter-stand variability without loss of information. The regression equation used was:

$$Y = b_0 + b_1x_1 + b_2x_2 + \ldots + b_{18}x_{18}$$

where Y = number of birds, x_1 = the level of decline, and $x_2 - x_{18}$ = 17 dummy variables for the 18 maple stands (the 18th is redundant). In each regression, we verified that assumptions of linearity, and of normality and homoscedasticity of residuals were met (Daniel and Wood 1980). When the model was significant, we tested for the significance of b_1 (the level of decline) with a *t* test and calculated the partial coefficient of correlation.

Habitat use was evaluated by counting, for the three species, the number of years a territory had been recorded in the 50 × 50 m square surrounding each of the 378 grid intersects, following a procedure inspired by Sherry and Holmes (1985, 1988). The number of years of occupation (0–3) was considered an index of preference and was used as a factor in one-way analyses of variance on habitat data (either Box-Cox or arcsine transformed to achieve normality and homogeneity of variances; Sokal and Rohlf 1981). The variable drainage was ordinal non-metric, but it was analyzed as a metric because we had no substitute for this potentially important variable. Tukey's test was used for multiple comparisons

TABLE 1. Correlations between the index of decline and the abundances of the three bird species in the 18 stands with 4 point counts each, southern Québec. Values are partial coefficients of correlation from the regression on nested data with the level of significance of the effect of decline (b_1, see methods; df = 53) in parentheses.

Variable	Least Flycatcher	Red-eyed Vireo	Black-throated Blue Warbler
1987	−0.41 (0.001)	+0.08 (0.58)	+0.14 (0.27)
1988	−0.27 (0.04)	+0.24 (0.07)	−0.09 (0.48)
1989	+0.09 (0.37)	−0.01 (0.91)	+0.05 (0.73)
3-year mean of point counts	−0.33 (0.02)	+0.08 (0.58)	+0.13 (0.31)

among means (Day and Quinn 1989). Multiple discriminant analysis was used to identify the principal variables distinguishing the four groups (number of years of occupancy). For the analyses, we retained 17 of the 29 habitat variables based on three criteria: correlations between variables, preliminary stepwise analyses, and biological relevance (see Williams et al. 1990). For instance, we kept foliage loss even if it was not significant but we dropped upper canopy layer coverage because it was difficult to normalize and it was correlated with total tree height ($r = 0.31$, $P < 0.001$). Discriminant functions were established on a random sample representing 75% of the observations, and were tested on the remaining 25% (Hair et al. 1987). For graphic representations, we stretched attribute vectors (variables) and group centroids by multiplying their structure correlations by their F value from the ANOVA (Hair et al. 1987).

RESULTS

BIRD POPULATIONS

Point counts. Thirty species of birds, including nine species observed in at least 50% of the counts, were censused. A yearly mean of 13.3 ± 2.3 pairs (mean ± SD, $n = 72$ plots) belonging to 9.3 ± 1.7 species were recorded at each site. The Least Flycatcher and the Red-eyed Vireo were the most abundant with mean counts of 2.0 ± 1.3 (mean ± SD) and 1.9 ± 0.6 pairs per site, and the Black-throated Blue Warbler was fifth with 0.9 ± 0.5 pairs. These species together represented 36% of all contacts. None of the three species showed significant change between consecutive years (Wilcoxon signed-rank tests for years two by two, $P > 0.05$).

Least Flycatcher numbers showed a negative correlation with the index of decline for 1987, 1988, and with the three-year mean while the Red-eyed Vireo and the Black-throated Blue Warbler did not (Table 1). There was no relationship between interannual population variability (coefficient of variation for the three-year mean point count for each station) and the level of decline except perhaps for the Least Flycatcher populations which tended to fluctuate more in declining sites (partial correlation, $r = 0.23$, $P = 0.08$).

Grid maps in the six principal stands. The three studied species had very different abundance/distribution patterns. The flycatcher was abundant (20.3 pairs/12 ha; extreme values = 7–44) but concentrated in 1–3 dense clusters per stand and on average occupied only 47% of a stand. The vireo was less abundant (14.5 pairs/12 ha; ext. = 9–22) but was more uniformly distributed and occupied 57% of a stand. The warbler was less common, with 4.6 pairs/12 ha (ext. = 1–12) and occupied only 28% of a stand.

Bird densities showed no significant relation with foliage loss either on a yearly basis or for the 3-year mean (Spearman correlation, $n = 6$, $P > 0.10$) (Fig. 1). Interannual population variability was correlated with foliage loss for the Least Flycatcher ($r = 0.88$, $n = 6$, $P = 0.02$) but not for the Red-eyed Vireo or Black-throated Blue Warbler ($P > 0.10$). From 1987 to 1989, flycatcher numbers dropped from 44 to 10 pairs in one of the two most affected stands whereas in the other numbers increased from 13 to 32 pairs.

HABITAT SELECTION

Univariate comparisons. We compared, for each species, habitat characteristics of plots grouped according to the number of years (0–3) they had been used by territorial individuals. For the Least Flycatcher, the 378 plots were distributed, among the four groups, in 115, 78, 96, and 89 plots occupied 0, 1, 2, and 3 years respectively. Univariate analyses of variance showed significant

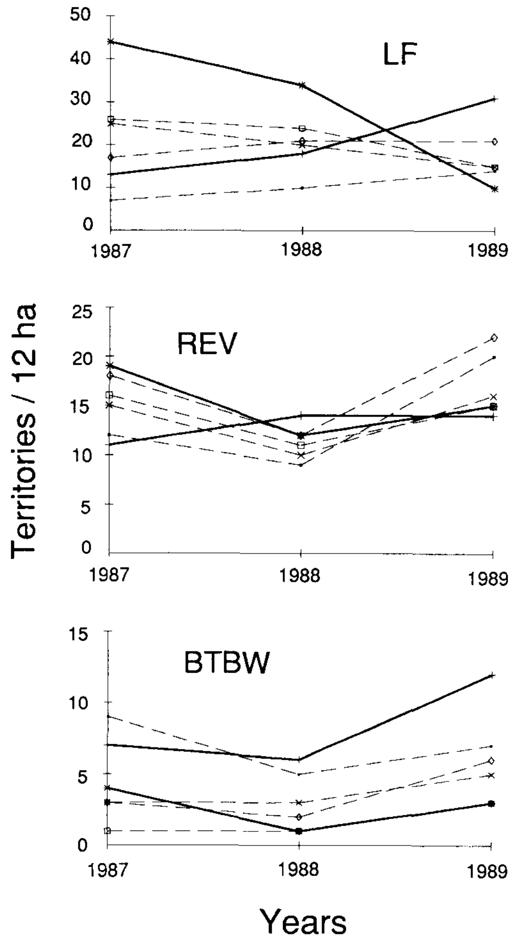

FIGURE 1. Annual variation of the number of territories for the Least Flycatcher (LF), Red-eyed Vireo (REV), and Black-throated Blue Warbler (BTBW) in six maple stands, southern Québec. Thick solid lines emphasize the two most affected stands (decline index >20).

differences ($P < 0.05$) for six of the 17 habitat variables (Table 2). Tests of comparison on means showed consistent results, respecting the gradient of the number of years of occupation and systematically disassociating the areas never used by flycatchers from those used in at least one year. The Least Flycatcher was most often associated with areas of the stand where canopy was high and well developed and contained a higher proportion of sugar maple than other areas of the stand, and as a result also had a low coverage of herbaceous plants. The variable "loss of foliage" (decline) did not affect use of plots by flycatchers at this spatial scale.

The Red-eyed Vireo was found 0, 1, 2, and 3 years in 42, 108, 143, and 85 plots respectively. None of the 17 univariate analyses on habitat variables showed significance at the 0.05 level (Table 3).

The Black-throated Blue Warbler was found 0, 1, 2, and 3 years in 173, 118, 59, and 28 plots respectively. Because of the small numbers of plots where the warbler was seen for more than one year, we combined groups 2 and 3 (Table 4). Two of the 17 habitat variables showed significant differences using ANOVAs: the number of shrubs 0–5 cm DBH and the cover of deciduous shrubs less than 1.3 m in height. The Black-throated Blue Warbler is thus associated with areas of thick undergrowth without respect to foliage loss.

Discriminant analyses. For the Least Flycatcher, two axes of the discriminant analysis performed on the 17 habitat variables were significant at the 0.05 level and totaled 88% of the explained variance (Table 5). The classification ratio was 0.35, superior to the minimum acceptable value of 0.25 based on the proportional chance criteria (Hair et al. 1987). The discriminant analysis performed poorly on the plots occupied one year, with only 10% of these cases correctly classified. This suggests that these plots were the most difficult to characterize.

The bi-dimensional representation of the group centroids and variable-vectors shows the importance of discriminating variables (Fig. 2). The first axis ordered the groups by number of years of occupation. The most discriminant variables were, in decreasing order of importance, height of the first leafed branch, the total crown height, proportion of sugar maple trees, and the coverage of medium and tall tree strata, all being positively correlated with the first axis. Only herb cover was significantly negatively correlated with this axis.

For the Red-eyed Vireo, the discriminant analysis was not significant. For the Black-throated Blue Warbler, one discriminant axis was significant and comprised 77% of explained variance (Table 5). The model correctly classified 47% of the observations; e.g., 11% more than the acceptable minimum. As with the flycatcher, it was mostly areas occupied only one year that were not correctly classified by the model. Five discriminant variables were significant, three positively correlated with the axis and two negatively correlated (Fig. 3). Plots occupied two or

TABLE 2. Habitat characteristics of plots used 0, 1, 2, or 3 years by the Least Flycatcher in six maple forest stands from southern Québec.

Variable	Number of years of occupation 0	1	2	3	ANOVA[A]	Tukey[B]
n	115	78	96	89		
Drainage[C]	2.9[D]	2.8	2.9	3.0	0.22	
Upper canopy layer (>20 m)[E]	2.7	6.9	5.9	4.9	0.002	0–12
Interm. can. layer (10–20 m)	47.1	48.4	50.7	56.4	0.0003	01–3
Lower canopy layer (5–10 m)	30.1	33.1	30.5	34.3	0.10	
Sugar maple (stems/plot)[F]	2.6	2.9	3.2	3.3	0.0001	0–23
American beech (stems/plot)	0.5	0.4	0.4	0.3	0.34	
Yellow birch (stems/plot)	0.3	0.2	0.2	0.2	0.35	
Distance to closest tree (m)[G]	5.7	5.5	5.7	5.5	0.76	
DBH (cm)	25.3	28.0	27.0	28.9	0.06	0–3
Tree height (m)	14.9	15.9	17.0	16.7	0.0001	0–23
First branch height (m)[H]	5.6	6.3	6.8	6.9	0.0001	0–123
Foliage loss (%)	17.9	14.3	15.6	18.1	0.27	
Shrubs 0–5 cm DBH[I]	6.1	5.4	6.4	5.7	0.40	
Shrubs 5–10 cm DBH	0.5	0.4	0.4	0.3	0.49	
Low deciduous shrubs[J]	14.5	14.8	17.9	16.2	0.49	
Low coniferous shrubs	2.4	3.0	2.0	2.3	0.32	
Herbs	23.6	14.9	12.4	14.1	0.001	0–123

[A] Probability level for 1W-ANOVA on Box-Cox or arcsine transformed data (Sokal and Rohlf 1981).
[B] Multiple comparisons among means (Tukey's test) on transformed data. A dash separates group significantly differents ($P > 0.05$).
[C] 2 = good, 3 = fairly good, and 4 = imperfect (Groupe d'étude sur l'écologie appliquée à l'aménagement du territoire 1974).
[D] Means from raw data.
[E] Ground cover (%) of the upper canopy layer.
[F] Plot of four trees (Cottam and Curtis 1956).
[G] Distance between the sampling point and the heart of the closest tree (Cottam and Curtis 1956).
[H] Height from the ground of the first leaved branch.
[I] Number of shrubs of 0–5 cm DBH in a plot of 10 m^2.
[J] Ground cover (%) of deciduous shrubs with less 1.3 m high in a plot of 10 m^2.

TABLE 3. Habitat characteristics of plots used 0, 1, 2 or 3 years by the Red-eyed Vireo in six maple forest stands from southern Québec. Variables and statistical tests are described in Table 2.

Variable	Number of years of occupation 0	1	2	3	ANOVA	Tukey
n	42	108	143	85		
Drainage	3.0	2.8	2.9	3.0	0.38	
Upper canopy layer (>20 m)	2.7	5.2	5.3	4.9	0.07	0–2
Interm. can. layer (10–20 m)	48.6	47.9	51.7	52.6	0.13	
Lower canopy layer (5–10 m)	31.6	32.9	32.3	30.6	0.71	
Sugar maple (stems/plot)	2.7	3.1	2.9	3.2	0.17	
American beech (stems/plot)	0.4	0.4	1.2	0.3	0.22	
Yellow birch (stems/plot)	0.2	0.2	0.3	0.2	0.90	
Distance to closest tree (m)	5.4	5.6	5.6	5.6	0.88	
DBH (cm)	25.8	27.6	26.7	28.1	0.60	
Tree height (m)	15.5	15.8	16.2	14.5	0.20	
First branch height (m)	6.1	6.2	6.5	6.5	0.44	
Foliage loss (%)	16.3	17.4	15.3	18.0	0.29	
Shrubs 0–5 cm DBH	6.6	6.6	5.9	4.9	0.73	
Shrubs 5–10 cm DBH	0.8	0.4	0.3	0.4	0.07	
Low deciduous shrubs	16.3	16.7	15.4	15.2	0.86	
Low coniferous shrubs	2.4	2.4	1.4	4.2	0.16	
Herbs	19.8	16.7	15.6	17.2	0.75	

TABLE 4. Habitat characteristics of plots used 0, 1, 2 or 3 years by the Black-throated Blue Warbler in six maple forest stands from southern Québec. Variables and statistical tests are described in Table 2.

Variable	Number of years of occupation 0	1	2–3	ANOVA	Tukey
n	173	117	87		
Drainage	2.9	3.1	2.9	0.19	
Upper canopy layer (>20 m)	4.7	6.0	3.7	0.17	
Interm. can. layer (10–20 m)	52.5	48.9	48.6	0.12	
Lower canopy layer (5–10 m)	33.4	30.7	31.1	0.19	
Sugar maple (stems/plot)	3.1	2.9	2.8	0.09	
American beech (stems/plot)	0.4	0.5	0.4	0.23	
Yellow birch (stems/plot)	0.2	0.2	0.4	0.11	
Distance to closest tree (m)	5.5	5.7	5.6	0.53	
DBH (cm)	27.6	27.5	25.9	0.39	
Tree height (m)	16.2	16.3	15.6	0.31	
First branch height (m)	6.6	6.3	6.0	0.07	
Foliage loss (%)	17.3	15.2	17.2	0.57	
Shrubs 0–5 cm DBH	4.8	6.1	8.0	0.0001	01–2
Shrubs 5–10 cm DBH	0.4	0.4	0.5	0.79	
Low deciduous shrubs	13.8	16.4	19.1	0.01	0–2
Low coniferous shrubs	1.9	2.4	3.5	0.14	
Herbs	15.5	17.2	18.5	0.55	

three years had more shrubs of 0–5 cm DBH and showed a higher cover of deciduous and coniferous low (<1.3 m high) shrubs, whereas unoccupied plots had a higher proportion of sugar maple and a lower crown base.

DISCUSSION

Our data lead to the conclusion that numbers of two of the three species studied, the Red-eyed Vireo and Black-throated Blue Warbler, are not directly affected at the observed intensity of decline, and hence do not conform to our predictions. The Least Flycatcher was affected by decline: populations were negatively correlated with decline in point counts and populations fluctuated more in affected stands using both grid maps and point counts, although the trend in the latter case was not quite significant ($P = 0.08$). This supports our predictions based on the ideal-free distribution model (Fretwell and Lucas 1970) that healthy sites are higher quality sites for the Least Flycatcher compared to affected sites; i.e., they

TABLE 5. Result of discriminant analyses on habitat characteristics of plots used 0, 1, 2, and 3 years by the three insectivorous bird species in maple forests of southern Québec.

Variable	Least Flycatcher	Red-eyed Vireo	Black-throated Blue Warbler
Probability of level of discriminant functions (% explained variance)[A]			
DFI	0.0001 (63%)	n.s.	0.01 (77%)
DFII	0.04 (25%)	n.s.	n.s.
Classification results[B]			
Classification ratio	0.35	—	0.47
Acceptable minimum	0.25	0.29	0.36
Classification results by group			
0 yr	0.37	—	0.79
1 yr	0.10	—	0.10
2 yrs	0.40	—	0.32[A]
3 yrs	0.53	—	—

[A] Significance level of the *F* value. Between parentheses: contribution (%) of the axis to the total explained variance.
[B] Proportion of observations from the holdout sample (25% of cases) correctly classified by the model. The acceptable minimum corresponds to the group size proportional chance criteria (Hair et al. 1987).

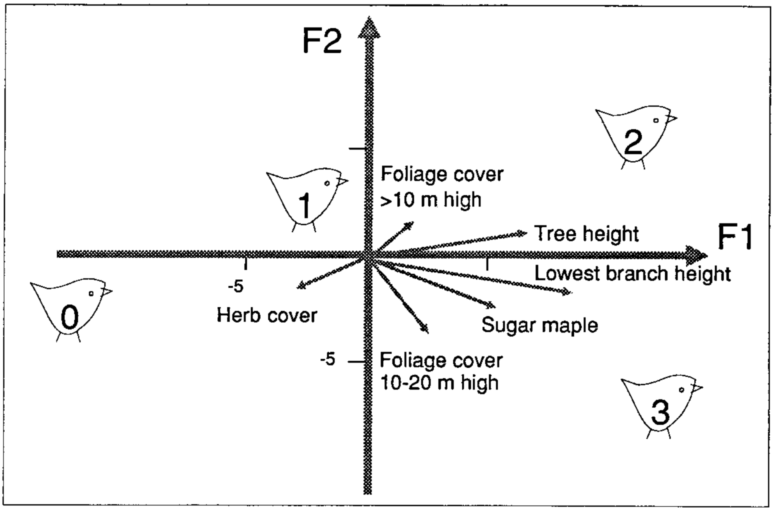

FIGURE 2. Bi-dimensional representation of variables discriminating the Least Flycatcher habitat in southern Québec. Variables are described in Table 2. Numbers show group centroids for plots used 0, 1, 2, or 3 years by flycatchers.

are more heavily used and hold stable populations whereas poorer quality habitats are more variable. However, the absence of significant negative correlation between population numbers of the Least Flycatcher and the level of decline in the grid maps data set could mitigate this conclusion. The discrepancy between results from the two data sets may originate from (1) lower amplitude of decline in the six stands selected for the detailed study compared to the 18 studied with point counts (see methods), (2) differences in precision or accuracy of the two bird sampling methods (Shields 1979, Verner and Ritter 1985), and (3) statistical type I or II error (Sokal and Rohlf 1981).

The 246% population increase in one of our two most affected stands (Fig. 1) is remarkable even when considering that population stability may be a better indication of habitat quality than population size (Fretwell and Lucas 1970; see Van Horne 1983, Pulliam 1988). Based on studies of the effects of disturbances like thinning cuts, we expected that canopy opening resulting from decline could have had either no effect or a negative effect on Least Flycatcher populations, but not a positive effect (Webb et al. 1977, Freed-

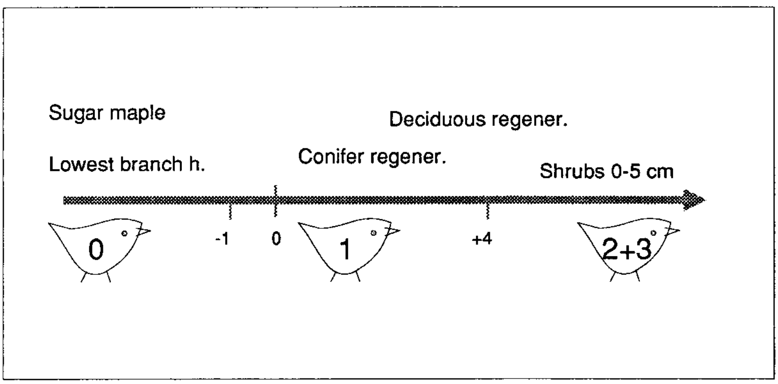

FIGURE 3. Uni-dimensional representation of variables discriminating the Black-throated Blue Warbler habitat in southern Québec. Variables are described in Table 2. Numbers show group centroids for plots used 0, 1, or 2–3 years by warblers.

man et al. 1981, DellaSala and Rabe 1987). This may result from two factors. First, the parameters used to evaluate habitat quality may not always reflect those used by the Least Flycatcher. Second, flycatchers may settle in a stand in response to factors other than habitat quality; e.g., social factors. In some bird species, the presence of already settled individuals is a strong incentive to settlement (Morse 1985, Slobodchikoff and Shields 1988). This could be especially important for the Least Flycatcher whose territories occur in dense clusters in a non saturated habitat (see Sherry and Holmes 1985, Briskie and Sealy 1989).

Our analysis showed that decline itself is an important habitat characteristic affecting habitat use by the three species, although other habitat features were important. It is still possible that some of the characteristics affecting habitat use in the flycatcher or the warbler such as canopy height may be indirectly related to decline. The observed pattern that the vireo did not select parts of the stands whereas the flycatcher and, to a lesser extent, the warbler did, agree with previous studies showing that the Red-eyed Vireo is less sensitive to changes in vegetation structure than the two latter species (Webb et al. 1977, Holmes et al. 1979, Darveau et al. 1982, Clark et al. 1983, Morgan and Freedman 1986, Thompson and Capen 1988).

Large scale population changes may confuse some of our results. Disturbances like forest fragmentation (see Brittingham and Temple 1983) or forest management (see Virkkala 1987), either on breeding or wintering grounds, are known to induce large scale changes in bird populations. Habitat use within a region is dependent upon population variation occurring at larger scales (Fretwell and Lucas 1970, Wiens 1985, Holmes et al. 1986, Holmes and Sherry 1988), and observed regional population patterns may grossly reflect those more widespread phenomena. In the last decades, Breeding Bird Survey (BBS) trends for south-eastern Canada and north-eastern United States (our southernmost studied stand was 25 km from New Hampshire) showed that the Least Flycatcher was decreasing in the latter region (1978–1987; n = 2,000 census routes; Robbins et al. 1989) but was stable in south-eastern Canada (1966–1988; n = 150 census routes; Erskine et al. 1990) whereas the Red-eyed Vireo and the Black-throated Blue Warbler were increasing in both regions. These trends suggest that the flycatcher populations should actually be at a lower level compared to previous years and that low quality habitats may not be used. On the other hand, declining stands, even if they are lower quality sites for the vireo and the warbler, may be colonized by immigrants from more productive areas nearby (see Pulliam 1988).

At moderate levels of disturbance, behavioral mechanisms and dispersal may compensate for the negative impact and mask any effect. At the present level of decline (10–30% loss of foliage), we conclude that there are no drastic changes in habitat use and that birds are able to adjust behaviorally and maintain population densities. However, the case of the Least Flycatcher suggests that disturbances like maple decline, even at medium intensity, may accelerate a decrease in population of a species which has already begun to drop across major parts of its range.

ACKNOWLEDGMENTS

We thank Yves Mauffette, Jeremy N. McNeil, Michael L. Morrison, and an anonymous reviewer for their comments on earlier drafts of the manuscript. We are grateful to the field assistants, François Bolduc, Martine Caron, Gaétan Filion, Patrick Gadbois, Hélène Gaulin, Suzanne Guimond, Natalie Hamel, Benoit Jobin, Michelle Landry, Claire Lépine, Christian Marcotte, Claude Nadeau, and Monique Salathé who also worked on laboratory analyses and data compilation. We thank Jack Hughes and Janet Wyman for editorial assistance, and Nathalie Plante for advice concerning statistical analyses.

This study was carried out within contract KA313-8-4131/01-XSK of Supplies and Services Canada and Environment Canada (Can. Wildl. Serv., Québec Region), following initial support from Wildlife Toxfund (a cooperative fund of Environment Canada, the World Wildlife Fund Canada, and Noranda Inc.). Employment and Immigration Canada and the Fédération des producteurs acéricoles du Québec also contributed to the financing of this project. Finally, M. Darveau benefited from grants of the Fonds F.C.A.R. du Québec, the Société zoologique de Québec and the Fonds de soutien au doctorat de l'Université Laval. This study is a part of a larger program of the analysis of the impacts of forest decline on the sugar maple forest ecosystem.

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