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EASTERN TOWHEE NUMBERS INCREASE FOLLOWING DEFOLIATION BY GYPSY MOTHS

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ABSTRACT.—Bird populations and habitat were monitored each year before (1984 to 1986), during (1987 to 1988), and after (1989 to 1996) a major gypsy moth (*Lymantria dispar*) outbreak in the eastern panhandle of West Virginia. Extensive tree mortality caused by repeated defoliations by gypsy moths resulted in the release of understory vegetation. Densities of Eastern Towhees (*Pipilo erythrophthalmus*) were significantly higher in the period following the gypsy moth outbreak. Both before and after the outbreak, Eastern Towhee densities were higher in areas of the forest with less overstory (particularly high canopy) and lower densities of live trees (particularly small trees). This indicates that not all forms of early successional habitat, specifically areas with a high density of small-diameter trees, are suitable for species deemed as "early successional." Although the gypsy moth outbreak resulted in an increase in the number of saplings, it also opened up the canopy and created a dense layer of shrubs in many areas. Because Eastern Towhees forage and nest on the ground and in shrubs, the outbreak increased the amount of suitable habitat for this species. Given that densities of Eastern Towhee are declining in the state, it is useful to document habitat features that are important for sustaining towhee populations. *Received 13 January 1997, accepted 13 May 1997.*

SINCE ITS INTRODUCTION around 1869, the gypsy moth (*Lymantria dispar*) has become one of the most economically and ecologically important forest pests in the United States. It has infested approximately 25% of the nation's hardwood forests, and the range of the gypsy moth eventually is expected to include most of the eastern United States (Gottschalk 1991). Despite the presence of gypsy moths in North America for more than 100 years, few studies have examined their effects on bird populations and habitats (e.g. Cooper et al. 1987, DeGraaf 1987, Thurber et al. 1994). Repeated defoliation by gypsy moths can result in widespread mortality of trees, particularly oaks (*Quercus* spp.), which are a preferred food item of the larvae. These factors can result in major changes in forest structure and species composition.

There has been concern that species of vertebrates dependent on early successional habitats have been declining, particularly in the eastern United States (Hagan 1993, Litvaitis 1993, Yahner 1995), and that these declines may be linked to forest maturation. Gypsy moths set back succession by decreasing the number of large overstory trees and increasing the amount of understory vegetation and the number of smaller trees via regeneration (Quimby 1987, Hix et al. 1991, Twery 1991). Thus, tree mortality caused by repeated defoliations by gypsy moths can create suitable habitat for early successional species, such as the Eastern Towhee (*Pipilo erythrophthalmus*). The Eastern Towhee is characterized as a forest generalist typically found in early successional habitat, edge or open areas, or in forests with a well-developed understory (James 1971, Maurer et al. 1980, Hagan 1993). Our objective was to describe the types of habitats Eastern Towhees were associated with both before and after a major outbreak of gypsy moths. We wanted to determine if more suitable habitat was created for towhees as a result of gypsy moth defoliation, and to assess how vegetation changes may affect towhee populations in our study area. These findings are of particular interest in light of recent work showing that numbers of Eastern Towhee are declining in eastern North America (Hagan 1993). Determining the habitat associations of Eastern Towhees, particularly where they are found in high numbers, may help to shed light on the causes of their decline in other areas.

STUDY AREA AND METHODS

This study was conducted within the Sleepy Creek Public Hunting and Fishing Area (hereafter Sleepy

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TABLE 1. Average defoliation values ($\bar{x}$ ± SE) from 1987 to 1996 for all trees >15.2 cm dbh. Averages based on defoliation estimates of 0 to 3 (0 = no defoliation, 1 = 1 to 33% defoliation, 2 = 34 to 67%, 3 = >67%).

Year	Average defoliation
1987	1.0 ± 0.1
1988	1.2 ± 0.1
1989	0.3 ± 0.0
1990	0.7 ± 0.1
1991	0.4 ± 0.0
1992	1.0 ± 0.1
1993	0.7 ± 0.1
1994	0.0 ± 0.0
1995	0.0 ± 0.0
1996	0.0 ± 0.0

Creek), an 8,000-ha area located on Sleepy Creek and Third Hill mountains (elevation 240 to 662 m) in Morgan and Berkeley counties, West Virginia. This area lies within the Ridge and Valley province and is typical of the oak-hickory forests of the region. Sleepy Creek is maintained by the West Virginia Division of Natural Resources, and no efforts were taken to control gypsy moths during the course of our study. Bird populations and habitat were monitored before (1984 to 1986), during (1987 to 1988), and after (1989 to 1996) a severe gypsy moth outbreak. Some of the study plots on the low valley and midslope areas received defoliation in 1986 as gypsy moth numbers were increasing (Cooper et al. 1987). Two consecutive years of heavy defoliation occurred in 1987 and 1988 as gypsy moth numbers reached outbreak levels (Cooper et al. 1993; Table 1). Defoliation returned to low levels until another outbreak occurred in 1992, and then were low from 1992 through 1996 (Table 1).

Six transects, each approximately 2 km in length, were established on Sleepy Creek Mountain in 1984. (Fig. 1). Two transects were placed along each elevational gradient (ridgetop, midslope, and valley) to represent a uniform sample of locations on the mountain. In 1985, a seventh transect was added along the midslope of Third Hill Mountain, which lies parallel to Sleepy Creek Mountain (Fig. 1). Six circular (125-m radius) plots were placed along each transect, for a total of 42 plots. The centers of these plots were used as bird sampling points and were at least 325 m from the nearest adjacent plot center. This placement maximized independence among plots while minimizing geographic variation in vegetation structure and composition. Five 0.04-ha (1/10 acre) subplots were placed within each plot, for a total of 210 subplots. One subplot was always located at the plot center, and one was randomly located within each of the four quadrants of the 125-m plot (see Fig. 1). These subplots were used as vegetation sampling plots to be associated with the bird counts done at the plot centers. Values for each vegetation variable at each plot were based on the mean of the five subplots. A tree in the center of each plot and subplot was permanently marked with paint

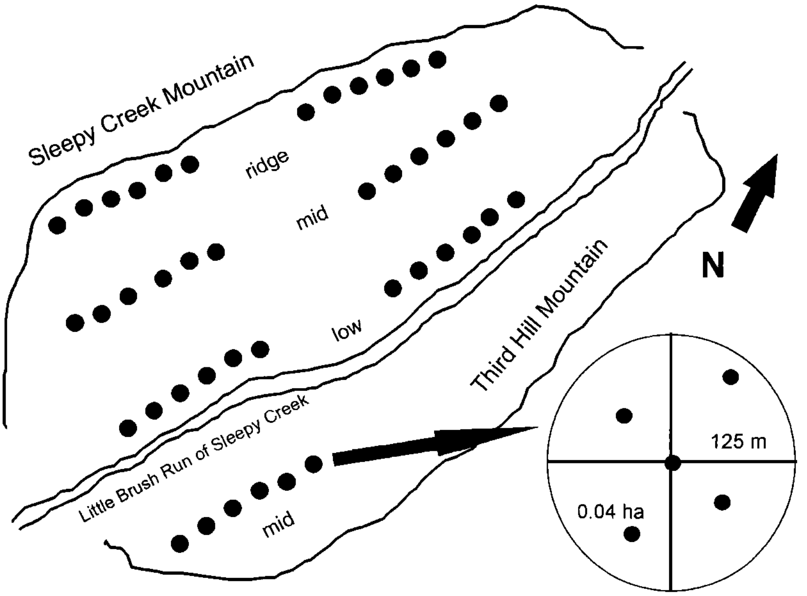

FIG. 1. Plot layout on the ridgetop, midslope, and low valley of Sleepy Creek and Third Hill mountains. Dots are 125-m radius plots, each of which contained five 0.04-ha vegetation sampling subplots (inset).

and aluminum tags to facilitate relocation. The same plots and subplots were maintained throughout the duration of the study.

Bird counts were conducted using the variable circular plot technique (Reynolds et al. 1980). Each transect (and thus each plot) was surveyed five times over the course of the breeding season, from late May to mid-July each year. Approximately five transects were surveyed each week over a period of roughly seven weeks. All transects were surveyed once before any transect was sampled a second time, all transects were surveyed a second time before any transect was sampled a third time, and so on until all transects were surveyed five times. The order the plots were surveyed within a transect and the order of the transects within each sampling bout were decided by random drawing. Observers were switched among transects to avoid an observer/transect bias, i.e. having the same observer sampling the same transect each time.

Bird counts began just after sunrise and were completed by approximately 0830 EDT. To reduce observer variability, all field technicians were trained in bird identification (by sight and sound) and distance estimation prior to actual data collection (Kepler and Scott 1981). Practice of distance estimation was aided with the use of a measuring tape so that observers became familiar with birdsong at different distances at sampling plots. An eight-minute survey was conducted at each plot, during which all birds seen or heard were recorded. Distance was estimated from where the observer was standing to a point on the ground directly below the bird. Detection cutoff values were calculated according to Reynolds et al. (1980) with all observations from all years pooled (ca. 2,400 observations of towhees made from 42 plots over 13 years). The calculated detection cutoff value for the Eastern Towhee on our study plots was 70 m, and this was used as the cutoff value for all plots within the study area. The number of towhees counted at each plot was averaged over the five visits and is expressed as number of towhees per 70-m plot (i.e. 15,394 m^2). Each plot was considered separately for statistical purposes.

Vegetation was sampled at each subplot following a modification of the methods of James and Shugart (1970). There were 5 sampling points in each cardinal compass direction spaced 2.26 m apart, for a total of 20 sampling points per 0.04-ha subplot. At each sampling point, ground cover and vegetation were recorded using a sighting tube with a wire crosshair at the end. The observer sighted vertically through the tube (first down, then up), and vegetation that intersected the crosshairs was recorded by height class from the ground up through the canopy. Observers sometimes had to step back to observe canopy cover that was obscured by lower canopy. Each "hit" or intersection of the vegetation with the crosshair counted as 5%, so values for each variable ranged from 0 to 100% at each subplot. If foliage from any woody-stemmed plant less than 3 m in height was intercepted by the crosshairs, it was recorded by species or species group and counted as shrub cover. Foliage greater than 3 m in height was classified as canopy cover. Presence (as opposed to absence) of canopy cover was recorded as total canopy cover. If the highest layer of canopy present was between 3 and 12 m, it was recorded as maximum low canopy cover. If the highest layer of canopy present was greater than 12 m, it was recorded as maximum high canopy cover. Observers were trained to estimate canopy heights with the use of a clinometer, and premeasured reference trees were recorded at each plot. Cover and canopy variables were measured each year during late May and June to assess the effects of defoliation prior to refoliation, which sometimes occurs after heavy (i.e. >60%) defoliation. The subplots were revisited and the number, and diameter at breast height (dbh) of each species of tree (any woody plant >3 m in height) within the subplots were measured using a modified Biltmore stick (James and Shugart 1970, Husch et al. 1972). Each tree >15.2 cm dbh was assigned to a defoliation level (0 = no defoliation, 1 = 1 to 33% defoliation, 2 = 34 to 67%, 3 = >67%). A defoliation value was calculated for each year based on the average of all defoliation classes for all trees assigned a value (Table 1).

Eighteen habitat variables were included in the analyses (see Table 4): number of live trees (all species) in six size classes (0 to 7.6 cm dbh, >7.6 to 15.2 cm, >15.2 to 22.8 cm, >22.8 to 30.4 cm, >30.4 to 38.1 cm, and >38.1 cm); number of dead trees in the same six size classes; total number of live trees; total number of dead trees; percent cover of woody-stemmed vegetation <3 m in height (i.e. shrub cover); percent total canopy cover (percent of canopy present vs. absent); percent cover of maximum high canopy (when the uppermost canopy was >12 m high); and percent cover of maximum low canopy (when the uppermost canopy was 3 to 12 m high). Habitat variables were measured at each subplot, and the values were averaged over the five subplots to get a plot value (n = 42) to be tested against the number of birds counted at each plot.

Data analysis.—Pre-outbreak values were the average of each of the 18 variables plus Eastern Towhee density estimates for each plot over the period from 1984 to 1986 (n = 42 for the pre-outbreak period). Because the seventh transect was established in 1985, the values for this transect in the pre-outbreak period represent the average of 1985 and 1986 only. Post-outbreak values were the average for each plot over the period from 1989 to 1996. The years 1987 and 1988 were left out of the analyses because we were interested primarily in the periods before and after this major disturbance. The disturbance years were left in for repeated-measures trend analysis only. An α of 0.05 was used for all tests.

To account for correlation among years due to repeated sampling of the same plots, we used repeated-measures analysis of variance (Hatcher and Stepanski 1994) to determine if Eastern Towhee density estimates increased over time. This was done for the 36 plots on Sleepy Creek Mountain. Due to an unbalanced design (measured for 12 and not 13 years), a separate ANOVA was performed on the six plots on Third Hill Mountain.

A matched-pairs t-test on before and after values at each plot was used to determine if Eastern Towhee numbers were higher in our study area after the gypsy moth outbreak. Paired t-tests also were used to determine if values for the vegetation variables were significantly different before and after the outbreak for the study area as a whole. Principal components analysis (Isebrands and Crow 1975, Johnson 1981) was used to describe the vegetational gradients in the habitat data set. Pearson correlation was used to determine the degree of association between density estimates of towhees and the major vegetational gradients in the study area as determined by PCA. Because our objectives were to explain habitat associations of Eastern Towhees, in this paper we describe only the vegetational gradients that were significantly correlated with towhee densities. Eastern Towhee density estimates also were correlated with percent cover of 11 common species of plants within the shrub layer, which were indicative of different habitat conditions within the study area. All variables were transformed prior to analysis. Percentage data were subjected to an arcsine square-root transformation (Krebs 1989); the transformation $\log_{10}$ (variable+1) was used for all other variables (Dowdy and Weardon 1991).

To examine the degree of predation and Brown-headed Cowbird (*Molothrus ater*) parasitism at Sleepy Creek, we searched for nests in and around the 42 sampling plots in 1995 and 1996. Nests were monitored following guidelines suggested by the Breeding Biology Research and Monitoring Database (i.e. BBIRD) sampling protocol (Martin et al. 1996), and contents of nests were recorded. Care was taken not to disturb vegetation surrounding the nest. Parasitism was indicated by the presence of a Brown-headed Cowbird egg or nestling in a towhee nest. Nests were considered successful if they fledged at least one host young.

RESULTS

Estimates of density ranged from an average of 0.2 birds per plot (i.e. 15,394 m^2) in 1986 to 1.8 birds per plot in 1994 (Table 2). The abundance of Eastern Towhees increased significantly across all years ($F = 211.1$, $P = 0.0001$). The estimated regression slope of number of towhees against time was 0.13 ± SE of 0.01. The trend was not linear, although in the linear analysis time accounted for 73% of the total variance in towhee numbers. Towhee numbers increased significantly on Third Hill Mountain ($F = 18.85$, $P = 0.0073$). Again, a linear trend accounted for most of the total variance (53%). Density estimates were significantly higher after the outbreak than before over all 42 plots (paired $t = 14.99$, $P = 0.0001$).

TABLE 2. Abundance of Eastern Towhees (no. per 70-m radius plot) in Berkeley and Morgan counties, West Virginia, 1984 to 1996. Density estimates were calculated using variable circular plots with a cutoff distance of 70 m at each plot.

Year	No. plots surveyed	% plots with towhees	Mean no. towhees[a]	Minimum no. towhees	Maximum no. towhees	SE
1984	36	52.8	0.3	0	1.2	0.06
1985	42	47.6	0.3	0	1.2	0.05
1986	42	50.0	0.2	0	1.0	0.04
1987	42	52.3	0.4	0	1.8	0.08
1988	42	88.1	0.9	0	2.8	0.10
1989	42	83.3	1.2	0	2.8	0.12
1990	42	95.2	1.5	0	3.4	0.12
1991	42	95.2	1.7	0	4.0	0.16
1992	42	92.9	1.6	0	4.0	0.16
1993	42	97.6	1.7	0	4.0	0.14
1994	42	95.2	1.8	0	4.4	0.17
1995	42	95.2	1.7	0	4.4	0.17
1996	42	85.7	1.2	0	3.4	0.14

[a] Values for density estimates were made for each plot/year combination and then averaged for each year. Maximum and minimum values are combined across plots within years.

Prior to the outbreak, the first three principal components accounted for 61.1% of the variation in the vegetation data set (Table 3). During this period, Eastern Towhee density estimates were significantly correlated only with PC II ($r = -0.34$, $P = 0.0295$), which represented a gradient from plots with a high density of trees (particularly trees of small diameter) and a high canopy structure to plots with lower densities of live trees, i.e. plots of sparse vegetation.

After the outbreak, the first three principal components accounted for 73.8% of the variation in the vegetation data set (Table 3). During this period, Eastern Towhee density estimates were significantly correlated with PC III ($r = -0.51$, $P < 0.0005$), which represented a gradient from a high density of trees (particularly small-diameter trees) and thus a closed canopy, to plots with more canopy gaps and lower densities of live trees (due to high numbers of medium and large dead trees; Table 4).

Table 3. Results of principal components analysis on Eastern Towhee habitat variables before (1984 to 1986) and after (1989 to 1996) an outbreak of gypsy moths.

	Pre-outbreak			Post-outbreak		
	PC I	PC II	PC III	PC I	PC II	PC III
Eigenvalue	5.7	2.8	2.3	5.6	4.7	2.8
% Relative total variance	32.0	16.0	12.9	31.4	26.6	15.7
% Cumulative total variance	32.0	48.1	61.1	31.4	58.0	73.8

After the gypsy moth outbreak, the study area as a whole had greater percentage of shrub cover and low canopy cover, a greater number of live trees 0 to 7.6 cm dbh, a greater number of total live trees, and a greater number of dead trees in the four largest size classes (Table 5). The study area had a smaller percentage of canopy cover and high canopy cover, fewer dead trees in the 0 to 7.6 cm size class, and a smaller number of live trees in the four largest size classes. Because the decrease in numbers of small dead trees offset the increase in numbers of medium and large dead trees, the total number of dead trees did not change significantly. The number of live trees >7.6 to 15.2 cm and >15.2 to 22.8 cm, and the number of dead trees >7.6 to 15.2 cm also did not change significantly from the pre- to post-outbreak periods. Results of the correlation analysis between towhee density estimates with common shrub-level plant species before and after the outbreak are given in Table 6.

We found 41 Eastern Towhee nests in 1995 and 1996. Fourteen nests failed during the egg stage, 12 failed during the nestling stage, and 15 fledged at least one Eastern Towhee. Three of the 41 nests were parasitized by Brown-headed Cowbirds. One nest that failed in the nestling stage contained one unhatched cowbird egg, whereas two successful nests fledged one cowbird each. One of these nests fledged three host young and one cowbird young, and the other fledged one host young and one cowbird young. Successful nests fledged an average of 2.73 young.

Discussion

The Sleepy Creek site as a whole became more attractive to towhees after the influence of

Table 4. Pearson correlations between statistically significant vegetational gradients from principal components analysis and Eastern Towhee density estimates (*n* = 42) before (1984 to 1986) and after (1989 to 1996) an outbreak of gypsy moths.

	Pre-outbreak (PC II)		Post-outbreak (PC III)	
Variable	*r*	*P*	*r*	*P*
Towhee density estimate	−0.34	0.0295	−0.51	0.0005
% vegetation <3 m height	0.54	0.0002	0.15	0.3381
% total canopy cover	0.24	0.1230	0.83	0.0001
% max. low canopy cover	−0.51	0.0005	0.30	0.0557
% max. high canopy cover	0.60	0.0001	0.45	0.0025
No. live trees (0 to 7.6 cm dbh)	0.84	0.0001	0.40	0.0079
No. live trees (>7.6 to 15.2 cm)	0.42	0.0057	0.68	0.0001
No. live trees (>15.2 to 22.8 cm)	−0.15	0.3424	0.37	0.0145
No. live trees (>22.8 to 30.4 cm)	−0.16	0.3247	0.01	0.9726
No. live trees (>30.4 to 38.1 cm)	−0.05	0.7334	0.14	0.3807
No. live trees (>38.1 cm)	0.09	0.5716	0.15	0.3437
Total no. live trees	0.79	0.0001	0.57	0.0001
No. dead trees (0 to 7.6 cm)	0.44	0.0037	0.01	0.9628
No. dead trees (>7.6 to 15.2 cm)	−0.05	0.7543	0.01	0.9757
No. dead trees (>15.2 to 22.8 cm)	−0.03	0.8578	−0.40	0.0082
No. dead trees (>22.8 to 30.4 cm)	0.11	0.4809	−0.55	0.0001
No. dead trees (>30.4 to 38.1 cm)	0.23	0.1438	−0.37	0.0147
No. dead trees (>38.1 cm)	−0.04	0.7804	−0.27	0.0797
Total no. dead trees	0.27	0.0851	−0.14	0.3859

TABLE 5. Means (± SE) for habitat variables and Eastern Towhee density before (1984 to 1986) and after (1989 to 1996) an outbreak of gypsy moths. *P*-values are from paired *t*-tests comparing pre- and post-outbreak values.

Variable	Pre-outbreak	Post-outbreak	*t*	*P*
Towhee density estimate	0.3 ± 0.0	1.5 ± 0.1	−14.84	0.0001
% total canopy cover	88.8 ± 0.6	75.8 ± 0.6	10.31	0.0001
% shrub cover (<3 m high)	41.5 ± 0.6	67.7 ± 0.7	−14.82	0.0001
% max. low canopy cover	23.7 ± 1.6	44.5 ± 0.8	−8.23	0.0001
% max. high canopy cover	65.7 ± 1.7	31.7 ± 1.0	12.57	0.0001
No. live trees (0 to 7.6 cm dbh)	256.1 ± 15.8	394.4 ± 20.7	−7.66	0.0001
No. live trees (>7.6 to 15.2 cm)	101.5 ± 5.8	110.0 ± 4.2	−2.01	0.0522
No. live trees (>15.2 to 22.8 cm)	47.7 ± 4.5	39.0 ± 3.5	2.73	0.0093
No. live trees (>22.8 to 30.4 cm)	22.7 ± 1.2	17.5 ± 1.6	4.76	0.0001
No. live trees (>30.4 to 38.1 cm)	17.3 ± 1.0	9.5 ± 0.8	6.59	0.0001
No. live trees (>38.1 cm)	20.9 ± 1.6	10.8 ± 1.0	6.40	0.0001
Total no. live trees	466.5 ± 20.1	581.3 ± 21.9	−5.86	0.0001
No. dead trees (0 to 7.6 cm)	70.9 ± 4.8	40.4 ± 2.4	9.85	0.0001
No. dead trees (>7.6 to 15.2 cm)	45.9 ± 3.9	43.2 ± 4.2	1.77	0.0835
No. dead trees (>15.2 to 22.8 cm)	9.0 ± 0.8	18.1 ± 1.6	−6.23	0.0001
No. dead trees (>22.8 to 30.4 cm)	2.7 ± 0.3	10.2 ± 0.8	−9.25	0.0001
No. dead trees (>30.4 to 38.1 cm)	2.0 ± 0.3	7.9 ± 0.7	−8.78	0.0001
No. dead trees (>38.1 cm)	1.0 ± 1.6	9.3 ± 0.9	−15.63	0.0001
Total no. dead trees	131.3 ± 7.3	129.0 ± 7.1	1.99	0.0522

the gypsy moth outbreak. Mortality of overstory trees and subsequent opening of forest canopy caused increases in understory vegetation due to increased light penetration and nutrient-laden gypsy moth frass reaching the forest floor (see Collins 1961). Because a gypsy moth outbreak can set back succession (i.e. decrease the number of large- and medium-sized trees and increase the amount understory vegetation), it is beneficial for Eastern Towhees. The increases in understory vegetation (particularly shrubs) increased nesting cover and foraging opportunities for this species.

Our results suggest that the term "early successional" may be too vague to properly describe optimal towhee habitat, and that the structure and/or composition of early successional habitat must be considered. Among other things, "early successional" can indicate a dense stand of sapling trees. Both before and after the outbreak, towhee densities consistently were negatively associated with high densities of live trees, particularly when a large number of the trees were of a small diameter. However, although Eastern Towhees nest and forage on the ground and in shrubs, we did not find a positive association between estimates of towhee density and the amount of vegetation <3 m in height at

TABLE 6. Pearson correlations between Eastern Towhee density estimates (no. per 70-m radius plot) and percent cover of 11 common plant species in the shrub layer (<3 m high) before (1984 to 1986) and after (1989 to 1996) an outbreak of gypsy moths (n = 42).

	Pre-outbreak		Post-outbreak	
Species	*r*	*P*	*r*	*P*
Blackberry (*Rubus* spp.)	0.37	0.0171	0.68	0.0001
Black birch (*Betula lenta*)	−0.10	0.5490	−0.39	0.0097
Black cherry (*Prunus serotina*)	0.49	0.0010	0.39	0.0011
Black gum (*Nyssa sylvatica*)	−0.42	0.0059	−0.47	0.0019
Black locust (*Robinia pseudoacacia*)	0.32	0.0396	0.41	0.0064
Grapevine (*Vitis* spp.)	0.23	0.1503	0.50	0.0007
Hickory (*Carya* spp.)	0.16	0.32	0.53	0.0004
Red maple (*Acer rubrum*)	−0.54	0.0003	−0.58	0.0001
Spicebush (*Lindera benzoin*)	−0.27	0.0887	−0.35	0.0242
Witch hazel (*Hamamelis virginiana*)	−0.37	0.0295	−0.44	0.0036
Yellow poplar (*Liriodendron tulipifera*)	−0.22	0.1576	−0.34	0.0281

our site. This result may have occurred because "% shrub cover" encompassed all vegetation <3 m in height, regardless of species or height within the category. For example, tree saplings and shrubs were lumped as "shrub cover." When towhee densities were correlated with individual plant species, however, several patterns of association emerged.

Towhees were positively associated with plant species that were most abundant on the drier ridgetop and midslope plots at Sleepy Creek. The highest densities of towhees occurred on the ridgetops, and these plots were associated with the most open canopy, lowest tree density, and the lowest small-tree density, particularly in the post-outbreak period. In canopy gaps on the drier upland sites, vegetation such as *Vitis* spp. and particularly *Rubus* spp. grew in abundance. The ability of shade-intolerant seedlings and saplings such as black cherry, black locust, and certain hickory species (see Table 6 for scientific names of plants) to grow on these upland sites further indicates the degree of openness (i.e. density of low trees) of the stands.

Towhee density estimates were negatively associated with many plant species that grow primarily in the moister coves and valley areas of the site. Both before and after the outbreak, towhees were negatively associated with red maple and black gum, and after the outbreak, they were negatively associated with other plant species such as spicebush and witch hazel. These species are shade tolerant and were found more often on wet soils at Sleepy Creek. After the outbreak, towhees also were negatively associated with certain shade-intolerant species, such as yellow poplar and black birch. However, saplings of these species were found primarily in canopy gaps in the moist valley of the study site and were not abundant on the drier ridgetop and midslope plots.

Because towhees nest and forage on or near the ground, a high density of trees may indicate that there is less space to carry out daily activities, and towhees therefore may prefer areas with lower tree densities. Dense stands of saplings may not provide suitable nesting cover or foraging habitat for towhees. Shrubs such as *Rubus* and *Vitis* may provide more appropriate dense cover close to the ground and better structure in which to place nests. After the outbreak, some of the study plots had increased numbers of small trees. If towhee numbers are lower in areas with more small trees, then defoliation actually may make the habitat less suitable for towhees. However, shrub cover also increased after defoliation. Thus, defoliation would be detrimental to towhees only if shrub cover declined as a result of the increase in small trees.

The large increase in Eastern Towhee densities after the gypsy moth outbreak suggests that the habitat became more suitable. This conclusion is based on the assumption that density of towhees reflects habitat suitability. The association between density and habitat suitability has been debated elsewhere (Wray et al. 1982, VanHorne 1983, Vickery et al. 1992). The fact that habitat associations were similar both before and after outbreak, and that before the outbreak 31% of the plots had no towhees, supports the idea that higher densities of towhees indicate suitable habitat in our study area. Similarly, Holmes et al. (1996) found that plots with high densities of Black-throated Blue Warblers (*Dendroica caerulescens*) were more suitable than plots with low densities of warblers. Eastern Towhee numbers likely did not result from increased food through the temporary abundance of gypsy moths. Although many birds, including Eastern Towhees, eat gypsy moth larvae, this food source makes up only a small proportion of total diet (Smith 1985, Cooper et al. 1987, Smith and Lautenschlager 1981). Indeed, most species of birds (except *Coccyzus* cuckoos) that eat lepidopteran larvae prefer smooth, hairless species over hairy larvae such as gypsy moths (Smith 1985, Whelan et al. 1989). Although other factors could have influenced towhee numbers, we believe that the dramatic habitat changes after the gypsy moth outbreak provide the most plausible explanation for the increases in towhees that we observed.

In order to better understand the influence of gypsy moth-induced tree mortality on Eastern Towhees, further work needs to be done on pairing and reproductive success within outbreak areas. Concern has been raised that trees killed by defoliation may make better vantage points avian nest predators and Brown-headed Cowbirds (Robbins 1979, Yahner and Wright 1985). However, only three of the 41 nests that we monitored were parasitized by cowbirds, despite the many standing dead trees in the area. Predation was the major cause of nest failure at Sleepy Creek, but this is typical for many populations of passerines (Martin 1993).

Using a combination of sources, Hagan (1993) reported a major decline in Eastern Towhees in the northeastern United States from 1966 to 1989. Moreover, he reported an annual decrease in towhees of 1.2% per year in West Virginia. Although data from our study area indicate that Eastern Towhees are increasing rather then declining, they support Hagan's assertion that declines in Eastern Towhees probably are related to forest succession. Breeding Bird Survey data from the region surrounding our study area (Maryland routes 6 and 7; Pennsylvania routes 92 and 194; Virginia routes 1, 5, 7, and 8; and West Virginia routes 48, 49, 50, and 51) indicate no significant trend (overall trend for all routes was 0.698, $P > 0.05$) in Eastern Towhee numbers from 1984 to 1995 (Droege and Peterjohn pers. comm). Since 1980, much of the area surrounding the Sleepy Creek site has been heavily treated with pesticides to control gypsy moths (USDA 1994). Thus, the vegetation changes in the areas where the surveys were conducted would not be the same as those that occurred at Sleepy Creek. Our data also support the idea that Eastern Towhees can respond immediately to newly created habitat (e.g. areas subject to gypsy moth defoliation and subsequent understory release) that formerly occurred only rarely in a heavily forested state such as West Virginia. This ability to rapidly colonize new areas would seem to be especially adaptive in bird species restricted to ephemeral habitats. In the absence of marked individuals, it is impossible to determine where the towhees from our study area originated.

Eastern Towhee populations may benefit from events that are likely to occur (particularly in West Virginia) over the next decade or so. Much of the forest that replaced timber cut earlier this century is reaching maturity and is likely to be harvested soon. Approximately 89% of the forested area in West Virginia is privately owned, and more than half of the privately owned forest is expected to be cut over the next 10 years (Birch et al. 1992). Populations of vertebrates frequently reflect land-use practices (Litvaitis 1993); prospective land-use changes may create more suitable habitat for Eastern Towhees and other early successional species, and we may once again see generalized increases in their populations in eastern North America.

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