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EFFECTS OF PLOT SIZE AND HABITAT CHARACTERISTICS ON BREEDING SUCCESS OF SCARLET TANAGERS

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ABSTRACT.—We studied the effects of forest patch size and habitat characteristics on breeding success of Scarlet Tanagers (*Piranga olivacea*) in western New York in 1995 and 1996. Twenty forest stands were grouped into four size classes: Group I (<10 ha, $n = 6$), Group II (10 to 50 ha, $n = 7$), Group III (>50 to 150 ha, $n = 5$), and Group IV (>1,000 ha, $n = 2$). Group I, II, and III sites were habitat patches located in fragmented landscapes, whereas Group IV sites were located in continuous forests. Although densities of male tanagers were similar in Group II, III, and IV sites, tanagers were absent from all forest patches smaller than 10 ha. Territory size did not differ among males in Group II, III, and IV sites. Pairing success exceeded 75% in all forest size classes in 1995 and 1996, and 100% of the observed males were paired in continuous forest sites. Pairing success differed significantly among forest size classes in 1995 and approached significance in 1996. Fledging success increased significantly with area and was highest (64%) in continuous forest sites. Stepwise multiple regression and principal components analysis indicated that male tanagers breeding in forest patches with higher canopy cover and lower density of oaks had higher pairing success than males in patches with lower canopy cover and higher density of oaks, and that males breeding in larger forest patches with more surrounding forest cover had higher fledging success than males in small patches with less surrounding forest cover. Our results indicate that: (1) breeding density is not a good indicator of habitat quality for forest-interior Neotropical migrants, and (2) large tracts of continuous forest are important for maintaining populations of these species. *Received 19 March 1997, accepted 5 May 1998.*

MANY POPULATIONS of forest-interior Neotropical migrants are considered to have declined since the 1960s (Robbins et al. 1989b, Sauer and Droege 1992, but see Thomas and Martin 1996). Between 1978 and 1987, 71% of Neotropical migrant species in eastern North America displayed negative population trends, with forest-breeding species registering some of the most significant declines (Robbins et al. 1989b). Possible explanations for these population declines include the fragmentation of breeding habitat throughout North America and the loss of wintering habitat from increased tropical deforestation in South America (Robbins et al. 1989b, Rappole and McDonald 1994). Forest fragmentation, defined as the breaking up of habitat into smaller parcels, leads to a decrease in average forest patch size and an increase in the isolation of such patches (Forman 1995). During the breeding season, these fragmentation effects may reduce habitat quality and availability for migratory birds that require large areas of forest.

Forest fragmentation may adversely affect the breeding success of area-sensitive songbirds through increased nest predation and brood parasitism and/or reduced pairing success (Brittingham and Temple 1983, Wilcove 1985, Temple and Cary 1988, Gibbs and Faaborg 1990, Villard et al. 1993). Most analyses of forest fragmentation and breeding success of area-sensitive songbirds have focused on species that nest on or near the ground, such as Ovenbirds (*Seiurus aurocapillus*; Gibbs and Faaborg 1990, Villard et al. 1993, Porneluzi et al. 1993, Van Horn et al. 1995, Burke and Noll 1998), Kentucky Warblers (*Oporornis formosus*; Gibbs and Faaborg 1990), and Black-and-white Warblers (*Mniotilta varia*; Sodhi and Paskowski 1997). However, few data exist on how fragmentation and patch size affect breeding success of canopy-nesting species such as the Scarlet Tanager (*Piranga olivacea*). Scarlet Tanager numbers are estimated to have declined at an average rate of 1.2% per year from 1978 to 1987 in eastern North America (Robbins et al. 1989b)

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and at 3.1% per year from 1980 to 1994 in New York state (Sauer et al. 1996).

Although the ability to detect population declines in breeding birds varies with the statistical method used (Thomas and Martin 1996), the consistent negative trends in Scarlet Tanager numbers, and the lack of data on how forest fragmentation and patch size affect the breeding of canopy-nesting species, led us to study how the breeding success of Scarlet Tanagers varied in relation to forest patch size and local-scale isolation. Because understanding the relationship between landscape structure and breeding success is vital to the conservation of birds in fragmented forests (Lande 1988, Freemark and Collins 1992, Villard et al. 1993), we attempted to control for among-site differences in habitat quality by choosing study plots with similar vegetation characteristics, and to control for large-scale isolation effects by choosing forest patches of less than 150 ha that were approximately equal distances (20 to 30 km) from continuous forests that were larger than 1,000 ha.

Our main objectives were to quantify how Scarlet Tanager density, pairing success, and fledging success varied with forest area and isolation, both of which are positively correlated with increases in habitat fragmentation (Forman 1995). Previous studies of the response of Scarlet Tanagers to forest fragmentation either ignored breeding biology or found too few nests to accurately estimate breeding success (Robinson 1992, Bollinger and Linder 1994).

STUDY SITES AND METHODS

Study species.—Scarlet Tanagers are foliage-gleaning insectivores during the breeding season and nest between 2 and 20 m off the ground (Ehrlich et al. 1988). Tanagers are socially monogamous (Ehrlich et al. 1988); males arrive and establish territories in mid-May, and females arrive in late May. Adult males may feed incubating females or watch the nest while the female forages (pers. obs.). Young fledge 9 to 11 days after hatching (Ehrlich et al. 1988) and follow adults for at least two weeks after fledging (pers. obs.).

Study sites.—We selected 20 study sites and grouped them into four forest size classes: Group I (<10 ha; $n = 6$), Group II (10 to 50 ha; $n = 7$), Group III (>50 to 150 ha; $n = 5$), and Group IV (>1,000 ha; $n = 2$). Study plots of 50 ha each were established within Group IV sites. The number of Group IV plots was limited by the lack of continuous forest within a 100-km radius of Brockport, New York. To at least partially control for "large-scale" isolation effects, forest patches <150 ha were located approximately equal distances (20 to 30 km) from continuous forest. However, fragmented forest plots differed in isolation at the local scale, defined as the amount of forest within 1 km of the plot (Table 1).

Methods.—Territory boundaries were mapped on 1:660 aerial photographs using song playback (Falls 1981). Male Scarlet Tanagers respond to conspecific song by countersinging and moving closer to the source of the song until reaching the territorial boundary (pers. obs.). We did not mark individual males and can only assume that the same males were observed in a territory on subsequent visits. Our assumption is supported by the fact that territorial boundaries remained static during the nesting season, suggesting that we were observing the same individuals (see also Prescott 1965). For purposes of territory mapping, each forest patch was visited at least twice, with a minimum of five days between visits. A planimeter was used to trace territory boundaries and estimate territory size. Tanager densities were calculated by counting the number of males in each study site and dividing by forest area or sample plot size (Wenny et al. 1993).

Territorial males were classified as paired if they were seen interacting with a female, defending a nest, or carrying food (Porneluzi et al. 1993). Song playback was helpful in determining pairing status early in the breeding season because females often followed males as they approached the song source. Unpaired males responded aggressively to song playback late in the breeding season and could frequently be heard in full song during July. In contrast, paired males were less responsive to song playback during July. Only males whose pairing status was positively determined were used in subsequent analyses. Because there was no obvious difference in the tendency of males classified as paired or unpaired to abandon territories, we assumed that territory fidelity in the two groups of males was equivalent.

We estimated individual nesting success by counting the number of fledglings that accompanied the male or female (Vickery et al. 1992). We used this method because counting nestlings was difficult given that Scarlet Tanagers nest relatively high off the ground, and locating nests was too time consuming. We spent long periods of time searching for and following tanagers to determine fledging success. Song playback helped determine fledging status because males without fledged young responded to taped songs, whereas males with young generally did not. Territorial birds were checked about every four days from late June through late July. A pair was considered successful if it was accompanied by at least one fledgling. Only pairs in which both adults were seen clearly alone for at least 15 min, or with fledglings,

TABLE 1. Mean values for vegetation and landscape variables at study sites larger than 10 ha. See text for details of measurements and calculations.

Study site	TRDN	SHDN	PECC	CAHT	AGST	SPRI	SPDI	QUDN	ACDN	BAAR	LOAR	PECO	FOKM
						Variable[a]							
						Group II							
Brockport	502.0	25,200	92	27.2	77	13	2.88	0.0	156.0	42.56	1.33	33	26
Vroom Street	804.0	21,700	86	31.6	72	8	1.09	10.0	638.0	61.34	1.51	65	197
Iron Bay East	426.0	15,400	88	32.9	115	18	3.41	30.0	102.0	51.90	1.65	62	81
Iron Bay West	386.0	18,000	94	28.9	115	17	2.80	40.0	178.0	68.34	1.62	37	117
Genesee Country	558.4	15,000	93	20.1	61	16	3.13	65.8	137.6	38.36	1.66	63	124
Island Cottage	448.8	27,625	89	31.5	62	17	3.14	61.0	6.6	44.19	1.16	5	33
Cobbs Hill	294.0	55,300	93	31.4	139	13	2.59	38.4	8.5	59.14	1.15	20	16
						Group III							
Mendon Ponds	509.6	31,214	87	33.2	107	19	2.69	78.4	250.6	78.55	1.78	7	181
Powdermill	673.6	15,083	85	33.8	117	17	2.99	68.8	308.8	59.65	1.70	61	228
Thousand Acre	618.0	9,100	93	26.4	80	14	3.81	6.0	393.0	38.21	1.95	13	96
Kendall	661.1	14,167	88	27.9	76	17	2.94	29.7	269.5	87.35	2.03	61	147
Rush Rotary	502.7	19,333	93	25.4	71	15	2.48	9.9	240.9	87.35	2.14	65	55
						Group IV							
Letchworth	620.0	20,150	97	33.8	134	23	3.87	43.0	108.0	139.82	>3.00	100	544
HiTor	611.0	19,450	88	26.9	70	22	3.37	84.0	161.0	89.05	>3.00	100	

[a] TRDN, tree density (trees/ha); SHDN, shrub density (shrubs/ha); PECC, percent canopy cover; CAHT, canopy height (m); AGST, age of stand (years); SPRI, tree species richness; SPDI, tree species diversity; QUDN, *Quercus* density (trees/ha); ACDN, *Acer* density (trees/ha); BAAR, total basal area (m^2); LOAR, log of area; PECO, percent core area; FOKM, amount of forest cover within 1 km of study site (ha).

TABLE 2. Vegetation and landscape factors generated by principal components analysis. Only factors with eigenvalues >1.0 are shown.

	PC1	PC2	PC3	PC4
	Factor			
Eigenvalue	4.453	3.125	1.949	1.300
Proportion of total variance	0.343	0.240	0.150	0.100
Cumulative variance	0.343	0.583	0.733	0.833
	Variable			
Total forest area	0.443	−0.063	−0.113	0.116
Tree density	0.193	−0.458	0.179	−0.010
Shrub density	−0.183	0.363	0.252	0.159
Canopy cover	0.044	0.210	−0.454	0.539
Canopy height	0.063	0.212	0.570	0.052
Stand age	0.085	0.378	0.296	0.312
Tree species richness	0.376	0.212	−0.119	−0.288
Tree species diversity	0.219	0.230	−0.407	−0.174
Quercus density	0.201	0.228	0.148	−0.575
Total basal area	0.395	0.117	0.168	0.281
Acer density	0.054	−0.485	0.177	0.152
Percent core area	0.369	−0.153	0.001	0.153
Forest cover within 1 km	0.440	−0.026	0.109	0.027

were included in our analyses. If paired birds were seen without fledglings, we returned for a second visit to confirm their fledging status. Unpaired males defending territories throughout the breeding season were classified as unsuccessful breeders. We used the average number of young fledged by males at each site to compare fledging success among sites.

We used the 0.04-ha circle sampling method (James and Shugart 1970) to describe vegetation in forest patches with tanagers (Group II, III, and IV sites; Table 1). We chose forest patches to minimize among-site variation in vegetation structure. Vegetation characteristics measured in randomly located plots within each forest patch included: tree species richness and frequency, % canopy cover, basal area, diameter at breast height, tree density, canopy height, and shrub density. We recorded all tree species in each plot and used the Shannon-Wiener index to describe tree species diversity. Stand age was estimated from increment borer samples from the five largest trees in each patch. In addition to estimating total tree density, we estimated maple (*Acer* spp.) and oak (*Quercus* spp.) densities. We considered the number of plots necessary to describe the vegetation at each site to be adequate when total tree density did not differ by more than 25 trees per ha between consecutive plots, and no new tree species were recorded.

We used a planimeter and aerial photographs (1:660) to estimate several landscape variables for each study site (Table 1): total forest area, amount of forest within 1 km of each forest patch, and core area size. We defined core area as the amount of habitat >100 m from the forest edge (Forman and Godron 1986).

Vegetation and landscape measurements produced sets of 10 and 3 variables, respectively. Because many variables were highly correlated with one another, we used principal components analysis (PCA) to simplify the structure of the data sets by reducing them to a smaller set of uncorrelated variables that accounted for a large part of the variation in the original data set. Before the PCA was completed, area was log-transformed, and *Acer* and *Quercus* densities were square-root transformed. PCA was performed on correlation matrices, and resulting factors (axes) with eigenvalues >1.0 were used in analyses of habitat characteristics and breeding variables (Pearson 1993). The extent to which the original variables were correlated with the components (factor loadings) was used to interpret each axis. New variables produced by PCA were then used to analyze bird-habitat relationships. PCA created four new variables (Table 2). Although loadings generally were less than ± 0.50, we interpreted the first axis (PC1) to represent forest area/surrounding forest cover within 1 km; tree species richness, total basal area, and percent core area also had relatively high loadings on this axis. We interpreted the other three axes to represent tree density (PC2), forest development (PC3; which involved canopy height and tree species diversity), and canopy cover/*Quercus* density (PC4). Stepwise multiple regression was then used to examine the relationship between vegetation and landscape variables and Scarlet Tanager breeding success.

We used chi-square tests to compare pairing success among forest size classes. We used Blossom (a distribution-free software package for data sets with many zero values that uses a multi-response permutation procedure [MRPP]) to test for differences

TABLE 3. Density (males per ha) and territory size (ha) of male Scarlet Tanagers among forest size classes in 1995 and 1996. Values are $\bar{x}$ ± SD.

	1995		1996	
Forest size class	Density	Territory size	Density	Territory size
Group I (<10 ha)[a]	0	—	0	—
Group II (10 to 50 ha)	0.11 ± 0.05	6.79 ± 1.63	0.09 ± 0.04	7.60 ± 0.99
Group III (>50 to 150 ha)	0.09 ± 0.02	6.13 ± 1.54	0.09 ± 0.03	7.19 ± 0.68
Group IV (>1,000 ha)	0.15 ± 0.01	6.36 ± 2.22	0.15 ± 0.01	7.39 ± 2.12

[a] No tanagers were present in Group I forest patches.

in fledging success among forest size classes (Slauson et al. 1991). ANOVA was used to test for within-year differences in tanager density and territory size among forest size classes. We also tested for between-year differences in dependent variables using the appropriate parametric (paired *t*-test) or nonparametric (Wilcoxon paired sample test) procedure. If no significant between-year differences existed, we tested for area effects on dependent variables using average values for each forest patch (Diggle et al. 1994). We used data from all forest size classes in analyses of tanager density. For all other tests, we used only data from Groups II to IV because tanagers were absent from all Group I forest patches, and it would have been inappropriate to include these patches in analyses of territory size and reproductive success.

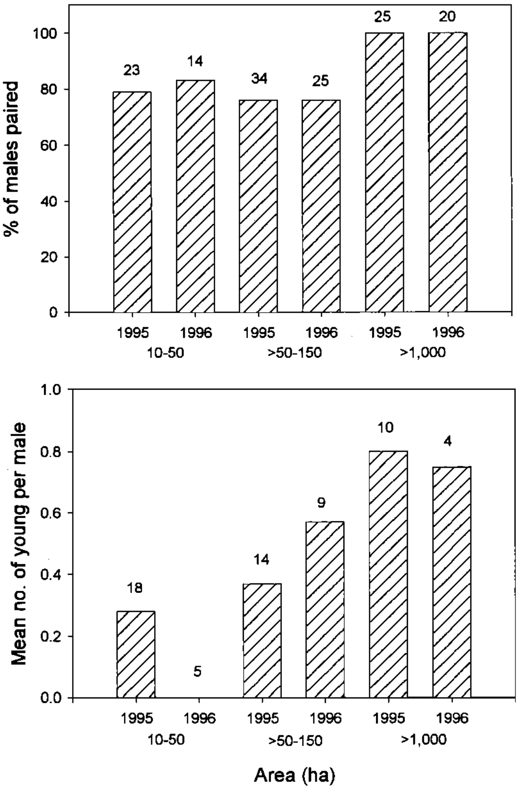

FIG. 1. Pairing success (top) and fledging success (bottom) of male Scarlet Tanagers among forest size classes in 1995 and 1996. Numbers above bars are the number of males in each size class for which pairing or fledging success was determined.

RESULTS

Breeding variables versus area.—Pairing success, fledging success, and density varied significantly with forest area; values generally were higher in larger forest patches. Male Scarlet Tanager density differed significantly among forest size classes in 1995 ($F = 6.11$, df = 3 and 14, $P = 0.007$) and 1996 ($F = 15.42$, df = 3 and 14, $P < 0.0001$), and no territorial males occurred in Group I (<10 ha) forest patches (Table 3). Density also differed significantly after averaging 1995 and 1996 data for each forest patch ($F = 8.32$, df = 3 and 15, $P < 0.002$). Male territory sizes did not differ among forest size classes with tanagers (Group II, III, IV) in 1995 ($F = 0.22$, df = 2 and 10, $P = 0.809$) or 1996 ($F = 0.21$, df = 2 and 10, $P = 0.816$; Table 3). Also, tanager territory size did not differ significantly among forest size classes based on average values for 1995 and 1996 ($F = 0.20$, df = 2 and 11, $P = 0.819$).

Pairing success was high (>75%) in all forest size classes that contained tanagers and was 100% in continuous forest plots (Group IV) in 1995 and 1996 (Fig. 1). In 1995, pairing success differed significantly among forest size classes ($\chi^2 = 6.58$, df = 2, $P = 0.04$), whereas differences in pairing success among forest size classes in 1996 approached statistical significance ($\chi^2 = 5.49$, df = 2, $P = 0.07$). Pairing success differed significantly among forest size classes after combining data from 1995 and 1996 ($\chi^2 = 11.98$, df = 2, $P = 0.003$). However, univariate regression showed no significant relationship between forest patch area and mean pairing

TABLE 4. Stepwise multiple regression analyses of principal components scores against 1995–1996 average Scarlet Tanager breeding variables within each forest patch. See Methods for further description of principal component variables.

PCA variable	Pairing success	Fledging success
PC1 (forest patch area, forest within 1 km of patch)	0.12	0.44**[a]
PC2 (tree density)	0.06	0.10
PC3 (forest development)	0.04	0.07
PC4 (canopy height, *Quercus* density)	0.31*[a]	0.03

*, $P < 0.05$; **, $P < 0.01$.

[a] No other variables entered the model.

success in each forest patch in 1995 and 1996 ($r^2 = 0.159$, $P = 0.157$).

Fledging success increased significantly with area, using 1995 and 1996 average values for each forest patch ($r^2 = 0.565$, $P = 0.002$). Fledging success differed significantly among forest patch size classes in 1996 (MRPP, $P = 0.06$; Fig. 1); no males ($n = 5$) in Group II sites fledged young compared with 44% of the males ($n = 9$) in Group III sites and 75% of the males ($n = 4$) in continuous forest (Group IV) sites. Similar, although nonsignificant, trends in fledging success occurred in 1995 (MRPP, $P = 0.19$; Fig. 1). Fledging success differed significantly among forest size classes after combining data from 1995 and 1996 (MRPP, $P = 0.034$); combined fledging success was 22% in Group II patches, 39% in Group III patches, and 64% in continuous forest sites.

Vegetation analyses.—We attempted to minimize among-site differences in vegetation to reduce effects on tanager reproductive performance. However, two variables differed among forest size classes: total basal area and species richness were significantly higher in continuous forest than in smaller forest patches ($H = 6.22$, df = 2, $P = 0.045$; $H = 5.90$, df = 2, $P = 0.053$).

Relationships between habitat characteristics and breeding success.—We explored relationships between tanager breeding variables and habitat characteristics using PCA and stepwise multiple regression (Table 4). Site scores for PCA variables were regressed against 1995/1996 mean fledging success and mean pairing success in each forest patch. Stepwise multiple regression showed a significant positive correlation between average patch values for 1995/1996 pairing success and site scores for PC4 (increased canopy height/lower *Quercus* density; $r^2 = 0.31$, $P = 0.04$); no other variables entered into the model. Male tanagers breeding in forest patches with increased canopy cover and lower *Quercus* density had higher pairing success than males in patches with reduced canopy cover and higher *Quercus* density. Stepwise multiple regression also showed a significant positive correlation between average fledging success for 1995/1996 and site scores for PC1 (forest area/surrounding forest within 1 km; $r^2 = 0.44$, $P = 0.01$); no other variables entered into the model. Males breeding in larger forest patches with more surrounding forest cover had higher fledging success than males in small patches with less surrounding forest cover.

DISCUSSION

Breeding biology.—The absence of breeding Scarlet Tanagers in forest plots smaller than 10 ha indicates that tanagers are area sensitive and is consistent with other studies of minimum-area requirements for forest-interior Neotropical migrants. Minimum-area requirements for Scarlet Tanagers vary regionally, with few tanagers occurring in forest plots <5 to 24 ha (Galli et al. 1976, Blake and Karr 1987, Lynch 1987, Tilghman 1987, Dawson et al. 1993). Although we found no Scarlet Tanagers in forest patches smaller than 10 ha, densities and territory sizes of males were similar across other forest size classes. These results are similar to those of Ambuel and Temple (1983), who found no difference in Scarlet Tanager densities in Wisconsin forest patches ranging from <12 to >500 ha. Although density and territory size were similar across the range of forest patch sizes larger than 10 ha, our data suggest that birds breeding in fragmented forest habitat had significantly lower fledging success than those breeding in continuous forest, as occurs in Ovenbirds in Pennsylvania (Porneluzi et al. 1993). In our study, pairing success was higher in continuous forests than in small forest plots; a similar pattern occurs in Ovenbirds (Villard et al. 1993, Van Horn et al. 1995, Burke and Noll 1998). These results emphasize the idea that density may be a misleading indicator of breeding success or habitat quality (Van Horne 1983, Vickery et al. 1992). Populations with relatively high territorial densities may have reduced breeding success owing to increased numbers of unpaired males or from complications caused by social factors (Vickery et al. 1992). For example, preliminary mist-netting data suggest that many male Scarlet Tanagers in small forest patches are second-year birds that are less likely to attract a female (pers. obs.).

Factors affecting habitat selection.—Our data suggest that the amount of forest area and surrounding forest cover within 1 km influence Scarlet Tanager breeding success. Likewise, forest patch occupancy by Scarlet Tanagers in Ontario was influenced by forest patch area and distance to the nearest occupied forest patch (Villard et al. 1995). Thus, the breeding success of Scarlet Tanagers should decline with increasing forest fragmentation. However, we cannot determine whether fragmentation effects demonstrated in our study were due to area effects per se, local isolation (related to the amount of surrounding forest cover within 1 km of the forest patch), or some interaction between these variables. In our study, forest patch area appeared to affect both fledging success and pairing success. However, total forest area and forest area within 1 km of the forest patch were highly correlated ($r = 0.874$) and had relatively high loadings on PC1, which was positively correlated with fledging success. Also, there was a significant positive relationship between 1995–1996 fledging success and forest area within 1 km of the forest patch ($P = 0.049$), although the relationship was not significant for pairing success.

Although we attempted to minimize among-site vegetational differences, some differences existed, and our data suggest that canopy cover, basal area, and tree species richness affect tanager breeding success. Our results generally are consistent with previous studies of habitat selection by Scarlet Tanagers, which suggest that tanagers prefer mature forest habitat, despite geographic variation in habitat selection (Shy 1984). Scarlet Tanager abundance in Illinois was positively associated with forest area and decreasing shrub vegetation (Blake and Karr 1987), whereas Scarlet Tanagers in Michigan had a higher probability of occurrence in forests with high tree density and increased basal area (Porter 1996). Tanager densities were highest in Wisconsin forest patches with increased canopy height, and tanagers chose territories within forest stands containing relatively dense canopy and subcanopy foliage (Ambuel and Temple 1983). However, the positive relationship between tanager pairing success and PC4 (a variable related to decreased *Quercus* density) was unexpected, because Scarlet Tanagers are thought to exhibit a preference for oak woodlands (Bent 1958, Shy 1984, Pinkowski 1991).

Our data suggest that large tracts of continuous, late-successional forest are sources of high productivity for maintaining Scarlet Tanager populations in small forest patches with lower productivity. Scarlet Tanager assemblages in fragmented forest landscapes may consist of a mixture of source and sink populations, which may be influenced by changes in surrounding landscape, resource availability, or population density (Pulliam 1996, Burke and Noll 1998). Thus, for canopy-nesting species such as the Scarlet Tanager, it is more advantageous to preserve a single large forest plot rather than several small plots, even though the amount of area protected is the same (Ambuel and Temple 1983, Wilcove 1985, Temple and Cary 1988, Yahner 1988, Robbins et al. 1989a).

Although our data strongly suggest that Scarlet Tanager breeding success is higher in continuous forest than in smaller, more isolated forest patches, two methodological problems could have influenced our results. First, we determined fledging success of a greater proportion of males in Group II forest patches (62%, $n = 37$ birds) than in Group III patches (39%, $n = 59$ birds) and the Group IV continuous plots (31%, $n = 45$ birds). If there was a bias toward being unable to determine the fledging success of unsuccessful pairs, more unsuccessful pairs would have gone unreported in larger forest size classes. This would have resulted in more data being lost from larger forest plots, and larger forests having higher rates of fledging success than smaller forest patches. However, it was easier to determine fledging status of birds *without* fledged young because they responded more to song playback. Thus, if anything, pairs that successfully fledged young were underrepresented in Group IV plots, and fledging success in continuous forest habitat may have been even higher than our data indicate. Second, tanagers may have been more reluctant to respond to song playback in smaller forest patches, perhaps because of higher predation risk. We cannot directly evaluate this hypothesis, although lack of any clear differences in song rates among forest size classes (Roberts 1996) suggests that at least one behavioral trait potentially related to susceptibility to predation was not affected by area.

Land-use change and management implications.—It is difficult to identify the number and size of forest plots needed to conserve area-sensitive bird species (Freemark and Collins 1992). Even though forest cover in the northeastern United States is increasing, with average cover values currently at 65 to 85% (Foster 1995), large forest tracts in some parts of the region are being fragmented (Villard et al. 1992, Roth and Johnson 1993, Foster 1995). In addition, increases in total forest cover in an area may not necessarily be accompanied by increases in the amount of suitable habitat for area-sensitive birds. Analysis of aerial photographs indicated that forest cover within 1 km of our study sites increased by a median of 129% between 1966 and 1990 owing to withdrawal of land from agricultural use (Roberts 1996). These results parallel land-use changes across western New York, where hayfield area has decreased by 17% since 1967 (Bollinger and Gavin 1992). Although land-use changes may lead to increased forest cover through succession, newly forested areas may not represent high-quality breeding habitat for tanagers because they are not large enough, are too isolated from other large forest patches, or are too young. Although succession may lead to mature forest habitat capable of supporting breeding Scarlet Tanagers, current management may preclude successful breeding. For example, two of our study sites underwent a selective timber harvest in 1994 that resulted in the removal of the largest trees from parts of the sites. This change appeared to result in increased territory size of males and reduced pairing success in the partially cleared regions (unpubl. data).

Our data suggest that density is not the best indicator of habitat quality for area-sensitive songbirds and that decisions on management of forest fragments in eastern North America must consider characteristics of the surrounding landscape and patterns of land-use history, as well as characteristics of the habitat patches themselves. For example, successional change, which is influenced by land-use history at local and regional scales, affects bird distribution and abundance (Litwin and Smith 1992). Data on return rates to habitat patches with different areas and connectivity to other patches (Villard et al. 1995), and on current forest fragmentation rates and successional patterns, would also be valuable in formulating land management plans involving area-sensitive forest birds in eastern North America.

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