

COMPARISON OF BREEDING AND POSTBREEDING MOVEMENTS AND HABITAT REQUIREMENTS FOR THE SCARLET TANAGER (*PIRANGA OLIVACEA*) IN VIRGINIA

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ABSTRACT—We investigated movements and habitat use during breeding and postbreeding periods in Scarlet Tanagers (*Piranga olivacea*) during June–September 1998 in northern Virginia deciduous forest. Nine birds (8 males and 1 female) remained on the same home range during both breeding and postbreeding periods, whereas 11 birds (9 males and 2 females) shifted home range (>300 m) between periods. Breeding season home-range size ranged from 2.6 to 5.6 ha (95% kernel), and core area from 0.61 to 0.93 ha (50% kernel). Postbreeding home ranges were similar in size to home range during the breeding period for birds that remained in the vicinity of nesting areas, but were larger for birds that moved away from the nesting area. Scarlet Tanagers occurred in both mature and successional forest during breeding and postbreeding periods, with some indication of increased use of earlier successional stages during the postbreeding period. Needs for Scarlet Tanagers during the postbreeding period (molt, premigratory fattening) differ from those during the breeding period (pair formation, nest placement, rearing of young). Those differences provide a plausible explanation that all tanagers changed focal areas between breeding and postbreeding periods. These findings confirm the need for taking the postbreeding period into account, both for understanding migrant life history and successful conservation. Received 7 December 2001, accepted 28 February 2003.

RESUMEN.—De junio a septiembre de 1998 estudiamos los movimientos y el uso del hábitat de *Piranga olivacea* durante los periodos reproductivo y post-reproductivo, en los bosques caducifolios del norte de Virginia. Nueve individuos (ocho machos y una hembra) permanecieron en el mismo ámbito hogareño durante ambos periodos, mientras que 11 individuos (nueve machos y dos hembras) cambiaron de ámbito hogareño (>300 m) entre periodos. El ámbito hogareño durante el periodo reproductivo varió entre 2.6–5.6 ha (95% kernel), y el área núcleo varió de 0.61–0.93 ha (50% kernel). Los ámbitos hogareños durante el periodo reproductivo fueron similares en tamaño a los del periodo post-reproductivo en individuos que permanecieron en la vecindad de los sitios de anidación, pero fueron mayores en aquellos individuos que se movieron fuera de los sitios de anidación. *P. olivacea* ocurrió en bosques maduros y sucesionales durante ambos periodos reproductivo y post-reproductivo, aunque la tendencia al uso de estadios sucesionales se incrementó en el periodo post-reproductivo. Las necesidades de *P. olivacea* durante el periodo reproductivo (muda, acumulación pre-migratoria de grasa) difieren de aquellas durante el periodo reproductivo (formación de parejas, localización del nido, cría de los pollos). Estas diferencias proveen de una explicación posible para el hecho que todos los individuos de *P. olivacea* cambiaran el área focal entre los periodos reproductivo y post-reproductivo. Estos hallazgos confirman la necesidad de considerar el periodo post-reproductivo para mejorar nuestro conocimiento de la historia de vida de especies migratorias e incrementar el éxito de su conservación.

POSTBREEDING BEHAVIOR, ECOLOGY, and habitat needs are poorly known for migratory birds leaving a gap of several months in our understanding of the migrant life cycle in temperate regions (Rappole 1995, Faaborg et al. 1996, Chernetsov 1998, Bayne and Hobson 2001,

Lang et al. 2002). Basic questions regarding behavior, patterns of movements in the landscape, and habitat needs during that part of the life cycle remain unanswered for nearly all species, such as minimum area of continuous habitat an individual needs to be able to molt, avoid predation, and prepare for migration. Postbreeding behavior is difficult to document, yet that information is of central importance to understanding migrant biology and conservation, particularly as alteration of the landscape

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becomes more prevalent (Faaborg et al. 1995). A few long-term, intensive banding studies have produced valuable information on postbreeding movement. For instance, Nolan (1978) was able to obtain some information on postbreeding activities for several of the birds in the Prairie Warbler (*Dendroica discolor*) population he studied. However, it is extremely difficult to detect frequency and characteristics of avian movement by observation alone (Anders et al. 1998, Vega Rivera et al. 1999, Norris and Stutchbury 2002). Advances in radiotelemetry technology offer an alternative to gather unique information on territorial behavior and habitat selection otherwise difficult or impossible to obtain using other methods (Kenward 2000).

In the early 1990s, we used radiotelemetry to study the breeding and postbreeding periods of the Wood Thrush (*Hylocichla mustelina*) in northern Virginia (Vega Rivera et al. 1998a, 1998b, 1999). Intensive molt and change of diet were hypothesized as the main factors responsible for changes on habitat use. Here, we report information on the pattern of movements and habitat use of Scarlet Tanagers (*Piranga olivacea*) during breeding and postbreeding periods. Different from Wood Thrushes, Scarlet Tanagers have a gradual molt and continue to depend strongly on insects as their main source of food. Specific questions that we expected to answer were (1) Do Scarlet Tanagers remain on breeding territories during the postbreeding period? (2) Are there differences in movement patterns and home-range size between breeding and postbreeding periods? (3) Is habitat use during the breeding season different from that during the postbreeding season?

The Scarlet Tanager is a long-distance migrant that breeds in mature deciduous woodland throughout the northeastern United States and southeastern Canada, and winters in humid forests of western South America (American Ornithologists' Union 1998, Mowbray 1999). Breeding biology for that species is relatively well known up to the time young fledge (Prescott 1965, Mowbray 1999). In the mid-Atlantic states, Scarlet Tanagers breed from early May to early August (Bushman and Therres 1988), and apparently only one brood is raised per season (Prescott 1965, Isler and Isler 1987, Senesac 1993, Mowbray 1999). We do know that after molting, departure for the wintering grounds occurs at some point during that period, in time enough

for the birds to get down into Texas and Middle American stopover habitats by late September or early October (Rappole and Blacklock 1985, Stiles and Skutch 1989, Howell and Webb 1995, Rappole et al. 1996). Arrival on the wintering grounds occurs mostly in October (Ridgely and Tudor 1989).

METHODS

Study area.—The study was conducted at the Smithsonian Conservation and Research Center (CRC), Front Royal, Virginia (38°30'N, 77°25'W). The CRC covers an area of 1,112 ha of which ~63% is forested and the rest covered by pastures and fields. The most common forest-cover types are black locust (41% of forested area), tulip poplar (29%), mixed oak (22%), hardwood (6%), and pine (2%). The CRC is surrounded by a matrix of urban (town of Front Royal), residential, farmland, and extensive mature forest habitat (Shenandoah National Park).

Capture of birds.—We used passive mist-netting within mature deciduous forest at the CRC to capture 10 and 20 tanagers during the breeding seasons (June–August) of 1997 and 1998, respectively. Each bird was banded with a federal band, sexed, weighed, measured, and fitted immediately at point of capture with a transmitter. Although the Scarlet Tanager is principally a canopy species (Mowbray 1999), we successfully captured 8 birds in 1997 and 11 birds in 1998 using passive ground-level nets (~8,000 net hours). To increase our sample, we also captured males from 17 June to 17 July by attracting them to ground-level nets using playback of territorial song and stuffed models on their breeding territories.

Radio attachment and radiotracking.—Transmitters (Model BD-2G, Holohil Systems Ltd., Carp, Ontario; 1.5 g. [which is ~5% of the Scarlet Tanager adult body weight: $n = 20$, average 28.4, SD = 1.98], battery life >90 days, range of detection of 400–1,000 m on the ground) were attached to birds using a leg backpack harness (Rappole and Tipton 1991). During 1997, transmitters with thin antennae were used that were damaged by most birds resulting in a considerable reduction in range of transmitter detection; therefore, we excluded those birds from statistical analyses but included them in other data summaries and considerations as indicated in the text. We have no evidence that radiotagged birds were killed or scavenged. Although five birds lost their transmitters in 1997, there were no feathers or any other sign of predation where we found the transmitters. Moreover, we were able to recapture three of the birds that lost their transmitters and did not observe any abrasion or other sign of injury to the birds from transmitter attachment.

We located radiotagged tanagers at 2 day intervals using a four-element Yagi antenna and portable re-

ceiver (Telonics, Inc., Mesa, Arizona). We pinpointed locations by approaching each bird. After locating a bird, we observed it for up to 20 min and recorded any behavior that indicated reproductive activity or that molting was underway. After the observation period was complete, or when the bird moved out of sight, we marked the site where we first saw the bird and determined geographical location using a GPS (Trimble, Sunnyvale, California) receiver or we referenced it (i.e. noted compass direction and distance) to a nearby previously marked position. A minimum of 75 fixes was obtained for each location. Those positions were differentially corrected, averaged, and entered as a coverage into the CRC GIS database that included coverages for habitat type, roads, and streams.

When a bird's signal could not be found, we searched first by driving along roads using hand-held detection equipment. If the signal was not found for 3–5 days, we performed an aerial search at 350 to 500 m above ground level from a Cessna 172 equipped with two wing-mounted, four-element antennas. Upon detecting a signal, we circled to determine a location for the individual and identified a landmark. We assumed that a bird had left the study area if an aerial search covering a circle 10 km in radius centered on the bird's last known location failed to locate its signal.

Delimitation of breeding and postbreeding periods.—To demarcate the end of reproductive activities and beginning of postbreeding period, we used the date on which birds were first observed molting or moving to a new home-range site. We defined a "new home-range" site as one located >300 m from a previous site where the bird stayed for >5 days. For 6 birds that did not move and were not observed molting, we used the date of 31 July to separate breeding from postbreeding period, based on the fact that 6 birds in 1997 and 11 birds in 1998 with functional transmitters disappeared from the breeding area prior to the first week of August. Moreover, six birds in 1998 and two birds in 1997 were observed molting between 27 July and 7 August.

Analysis of movements.—For each bird, we calculated several variables to determine possible differences between breeding and postbreeding periods. We define home range as "the minimum area in which an animal has a specified probability of being located" (Worton 1995). We calculated 50 and 95% kernel home range, hereafter referred to as "core area" and "home range," respectively. We chose the kernel model for analysis because it is a nonparametric technique that depicts irregular distributions more accurately and produces home-range size with less bias relative to other home-range estimators (Seaman and Powell 1996). Smoothing parameters were determined by least squares cross-validation (Seaman and Powell 1996) and grid size was selected automatically using routines of the ANIMAL MOVEMENTS extension program for ARCVIEW (Hooge and Eichenlaub 1997).

For home-range calculations, we used only those birds with >20 telemetry locations in each period. Distance between breeding and postbreeding sites was calculated as the distance between the arithmetic centers of each site, on the basis of home-range calculations. We also calculated average distance between consecutive locations and used it as an index of mobility for an individual. Degree of overlap between two home ranges was estimated using the index of Minta (1993). Values of that index vary from 0 to 1, with 1 indicating two areas of identical size and location. All measurements were calculated using routines of the ANIMAL MOVEMENTS extension program for ARCVIEW (Hooge and Eichenlaub 1997).

We analyzed changes in the area of usage (breeding vs. postbreeding) using the multiresponse permutation procedures tests (MRPP, Mielke and Berry 1982). The MRPP is a nonparametric routine that compares observed intragroup average distances with average distances that would have resulted from all the other possible combinations of the data, under the null hypothesis that the two use distributions are the same. The program BLOSSOM (Slauson et al. 1991) was used to perform the tests.

Habitat.—Selection of habitat was analyzed at two spatial scales. For the entire radiotagged population, we determined selection of forest type by plotting each bird's radiolocations on a GIS forest-type coverage (use), recording habitat for each location, and comparing them with percentage of occurrence of those forest types in the area of coverage (availability). For that purpose, we defined boundaries of the study area as the 95% kernel home range generated using radiolocations from all birds. We used a chi-square test of goodness of fit to test the null hypothesis that usage occurs in proportion to availability, considering all habitats simultaneously (Neu et al. 1974). The chi-square test requires that the observations of an animal's location be independent. We considered consecutive locations for a given bird as independent because they were separated by a minimum of 24 h, a sufficient time for the animal to move between any two points in the area (White and Garrott 1990). On a finer scale, we determined habitat selection within the home range of each bird. We first performed a nearest-neighbor analysis test (Hooge and Eichenlaub 1997) to determine if locations of each individual within its home range were clustered or randomly spaced across the home range. We interpreted lack of spatial randomness as an indication of habitat selection. Second, we plotted each bird's radiolocations on a GIS forest-type coverage (use), registered the number of radiolocations occurring in each habitat type, and then compared those to expected values on the basis of proportion of each habitat that occurred within each home range (Neu et al. 1974).

For each bird, we determined habitat-use characteristics during the breeding and postbreeding

periods by sampling tree composition and size within four to five circular plots, 22.5 m in diameter (0.04 ha), centered at randomly chosen bird locations within each period (breeding and postbreeding). Vegetation data from a given circular plot were used to describe the site for only one bird regardless of the number of birds using the site. Tree data were averaged across sampled plots to characterize a particular site (James and Shugart 1970). All trees were identified and counted in diameter at breast height (DBH) categories (small, 4–18.4 cm; medium, 18.5–46.4 cm; large, 46.5–85 cm; and outsized, >85 cm). From those data, we generated three additional variables: basal area, density of tree species characteristic of mature forest, and density of tree species characteristic of successional forest. Segregation of tree species on the basis of "mature" versus "successional" followed Eyre (1980): "Mature" forest species = bitternut hickory (*Carya cordiformis*), pignut hickory (*C. glabra*), shagbark hickory (*C. ovata*), mockernut hickory (*C. tomentosa*), red oak (*Quercus falcata*), white oak (*Q. alba*), chestnut oak (*Q. prinus*), black oak (*Q. velutina*), tulip poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), and American basswood (*Tilia americana*); "Successional" forest species = slippery elm (*Ulmus rubra*), hackberry (*Celtis occidentalis*), ailanthus (*Ailanthus altissima*), black locust (*Robinia viscosa*), sassafras (*Sassafras albidum*), boxelder (*Acer negundo*), common persimmon (*Diospyros virginiana*), and apple (*Malus* sp.).

To analyze for differences between breeding and postbreeding sites, we compared density of trees and snags, trees in each size category, and trees characteristic of mature and successional forest. We were interested in both population and individual trends. Therefore, we tested for differences in vegetation attributes among sites for pooled data (Kruskal–Wallis test followed by a nonparametric multiple comparison for unequal samples; Zar 1996), and for each bird in paired comparisons (Wilcoxon signed-rank test).

To further analyze differences between breeding and postbreeding sites for each bird, we compared overall tree species richness (total number of species) and similarity in composition and density. We used Morosita's index of similarity because that index was formulated for counts of individuals, and it is recommended as the best overall measure of similarity for ecological use (Wolda 1981). That index ranges from 0 to 1, with 0 values representing pairs of sites with no species in common, and values of 1 representing complete overlap.

In all statistical tests, a probability of 0.1 or less was accepted as significant, but we report actual *P* values for descriptive purposes. To adjust for table-wide significance we used the sequential Bonferroni correction (Rice 1989). Unless otherwise mentioned, means are given as mean \pm standard error (SE). In

text, tables, and figures, individual identification of birds is given by a four-symbol code, with the first character being a letter representing the sex of the bird (M = male, F = female, U = unknown).

RESULTS

We obtained adequate sample sizes for home-range analysis for 20 birds (3 females and 17 males). On the basis of postbreeding movement behavior, we categorized birds into two groups: (1) birds that did not change home range during breeding and postbreeding periods (i.e. distance between breeding and postbreeding home-range arithmetic centers was <300 m); and (2) birds that changed home range between breeding and postbreeding (home ranges >300 m apart).

The first group consisted of eight males and one female. Measures for those birds averaged 6.7 ± 0.75 ha in home-range size, 0.95 ± 0.07 ha in core area size, and 103 ± 2 m in mobility. Those values exclude statistics for the female that moved over a large area throughout the breeding and postbreeding seasons (home range = 46.6 ha; core area = 3.2 ha), and might never have been mated. Departure from the study area (last recorded dates) occurred from 11 to 27 September. The MRPP test of the null hypothesis (that breeding and postbreeding radiolocations came from the same distribution) was rejected for all eight males ($P < 0.0001$). However, we did not detect differences in size of home range, core area, or mobility between breeding versus postbreeding periods (Table 1, all $P > 0.20$). Nevertheless, individually, birds in the group showed differences in home-range size (Table 1). Minta's index of overlap for that group averaged 0.62 ± 0.056 (range 0.47–0.86).

The second group consisted of nine males and two females. The group included two males that moved out of their breeding home ranges but moved back and forth between their breeding and postbreeding sites. One of those males moved to a postbreeding site on 6 July, moved back and forth 3 \times between breeding and postbreeding sites, and finally moved back to its breeding site on 11 August, and remained there until 27 September, when it was last recorded. The second male moved to postbreeding site on 19 July, moved back and forth 4 \times between breeding and postbreeding sites, and finally moved back to its postbreeding site where it

TABLE 1. Descriptive statistics for home range (ha) and movement data (m) for breeding (B) and postbreeding (PB) periods, for radiotagged Scarlet Tanagers, Northern Virginia, 1998.

Bird	Home range ^a		Core area ^b		Mobility ^c		Overlap ^d	DHR ^e	Last recorded
	B	PB	B	PB	B	PB			
	Birds that stayed^f								
M443	4.4	4.3	0.64	0.36	101	106	0.53	80	22 September
M491	3.3	6.6	0.48	0.56	83	167	0.48	91	22 September
M818	6.2	7.3	0.75	0.70	312	208	0.54	147	11 September
M820	4.4	4.4	0.59	0.64	101	154	0.65	64	27 September
M891	4.8	4.5	0.95	0.50	100	77	0.86	21	22 September
M895	5.5	4.9	0.88	0.54	85	169	0.54	81	27 September
M900	7.7	4.0	0.63	0.45	96	116	0.48	85	18 September
M988	8.3	6.9	0.81	1.2	121	77	0.86	91	22 September
	5.6 ± 0.61	5.4 ± 0.47	0.72 ± 0.06	0.62 ± 0.09	125 ± 27	134 ± 17	0.62 ± 0.06	83 ± 12	
	Birds that moved								
M894	2.6	89.3	0.67	11.7	59	257	0.17	370	25 September
M990	2.7	23.6	0.46	4.90	80	366	0.24	1,100	27 September
F819	3.9	6.14	0.57	0.68	75	111	0	11,100	11 September
M893	4.4	38.5	0.44	7.86	97	277	0	3,900	24 September
M898	6.9	—	1.50	—	113	—	0	3,300	6 August
M899	7.3	14.9	0.96	3.89	137	161	0	7,100	27 September
F896	2.5	—	0.38	—	30	—	0	—	29 July
M148	8.5	—	2.18	—	127	—	0	—	14 August
M468	4.7	—	1.27	—	87	—	0	—	20 August
M897	3.8	—	0.35	—	70	—	0	—	14 July
M989	16.4	—	1.50	—	111	—	0	—	13 August
	5.8 ± 1.2	34.5 ± 14.7	0.93 ± 0.18	5.8 ± 1.9	90 ± 10	234 ± 45			

^a Calculated as 95% kernel home range.

^b Calculated as 50% kernel home range.

^c Mean distance between consecutive locations.

^d Minta's index of overlap.

^e Distance between arithmetic centers of nesting and postnesting home ranges.

^f Birds whose nesting and postnesting home ranges were separated by <300 m.

stayed until 18 September when it was last recorded (Fig. 1). Because of those movements, home range, core area, and mobility during the postbreeding period for those birds were much larger than breeding values (birds M894 and M990; Table 1).

Four birds (one female and three males) moved beyond the CRC boundaries after the breeding period, establishing new home ranges located >3 km from their breeding home ranges (Fig. 2). Departure dates from their breeding sites were 17 June, 8 and 16 July, and 3 August. One of the males moved back to his breeding site on 14 September and disappeared 10 days later (see Table 1 for individual statistics: F819, M893, M898, M899). For three of those birds, values of home range, core area, or mobility were significantly larger during the postbreeding period (all $P < 0.01$).

Five birds, one female and four males, disappeared from their breeding site between 14 July

and 20 August and they were not relocated. Breeding home ranges and core areas for those birds are shown in Table 1.

Habitat selection.—Scarlet Tanager radiolocations within the study area were in black locust forest (36%), tulip poplar forest (26%), mixed oak forest (26%), and hardwood forest (12%). Chi-square tests of habitat preference on pooled data showed a significant difference between observed locations and habitat availability ($P < 0.0001$). Subsequent calculation of confidence limits showed significantly more frequent than expected use of mixed oak and hardwood forests and less frequent than expected use of tulip poplar forest; black locust use was proportional to its availability. Analysis of data segregated by periods (breeding and postbreeding) rendered similar results, except for mixed oak forest, which was used equal to or more than its availability during the breeding and postbreeding periods, respectively (Table 2).

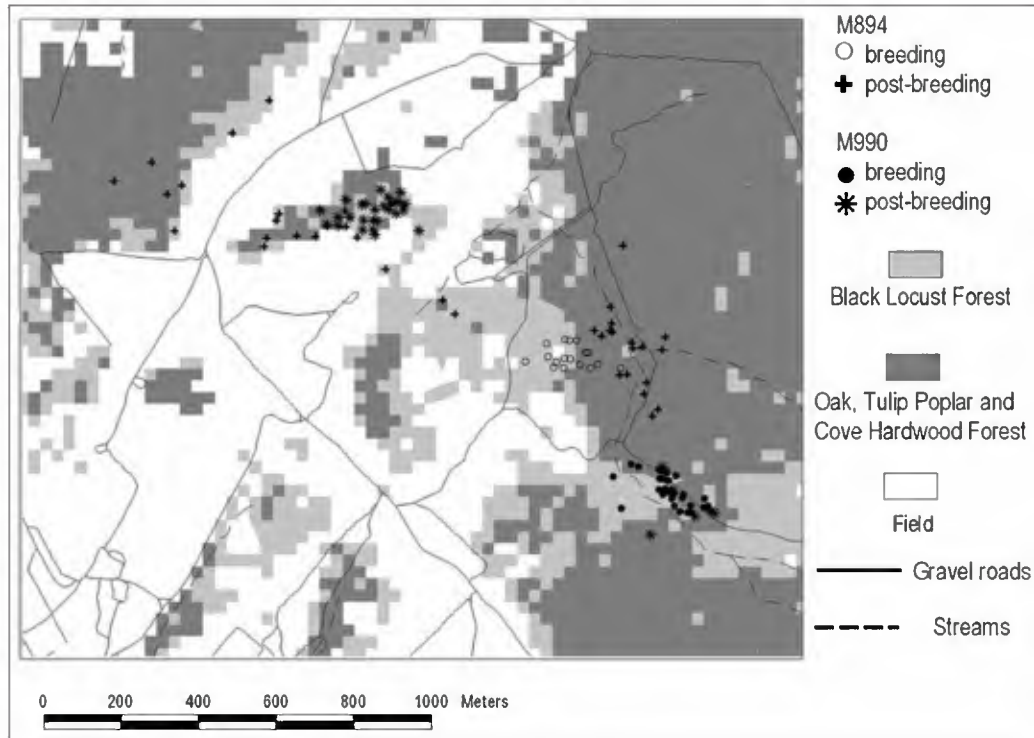


FIG. 1. Radiolocations of two adult Scarlet Tanager during breeding and postbreeding seasons, CRC, Virginia, 1998.

In analysis of habitat use at a home-range scale, we tested first the null hypothesis that radiolocations were randomly spaced across home ranges. Of 14 birds analyzed, the null hypothesis was rejected for 11 birds during the breeding period and 12 during the postbreeding period (nearest neighbor analysis test, $0.05 < P < 0.1$; Bonferroni $\alpha_{adj} = 0.007$). Analysis of preference for habitat type within each bird's home

range (14 birds analyzed) showed significant differences for four birds during the breeding period and three birds during the postbreeding period ($0.006 < P < 0.05$; Bonferroni $\alpha_{adj} = 0.006$). However, there was not a clear pattern of preference-avoidance of habitat type among those birds.

Kruskal-Wallis tests on pooled data for habitat variables comparing breeding (B,

TABLE 2. Habitat use by radiotagged Scarlet Tanagers ($n = 18$) and proportion of area of forest types. Equal, less, and more indicate results of chi-square test of goodness-of-fit for the null hypothesis that each forest type was used in proportion to its occurrence, northern Virginia, 1998.

	Forest type			
	Black locust	Tulip poplar	Mixed oak	Hardwood
Pooled data	Equal 320 (36%) ^a	Less 234 (26%)	More 234 (26%)	More 105 (12%)
Breeding	Equal 204 (35%)	Less 169 (29%)	Equal 137 (24%)	More 65 (11%)
Postbreeding	Equal 116 (36%)	Less 66 (20%)	More 97 (30%)	More 40 (13%)
Area available (%)	38	34	21	7

^a Number of radiolocations and percentage.

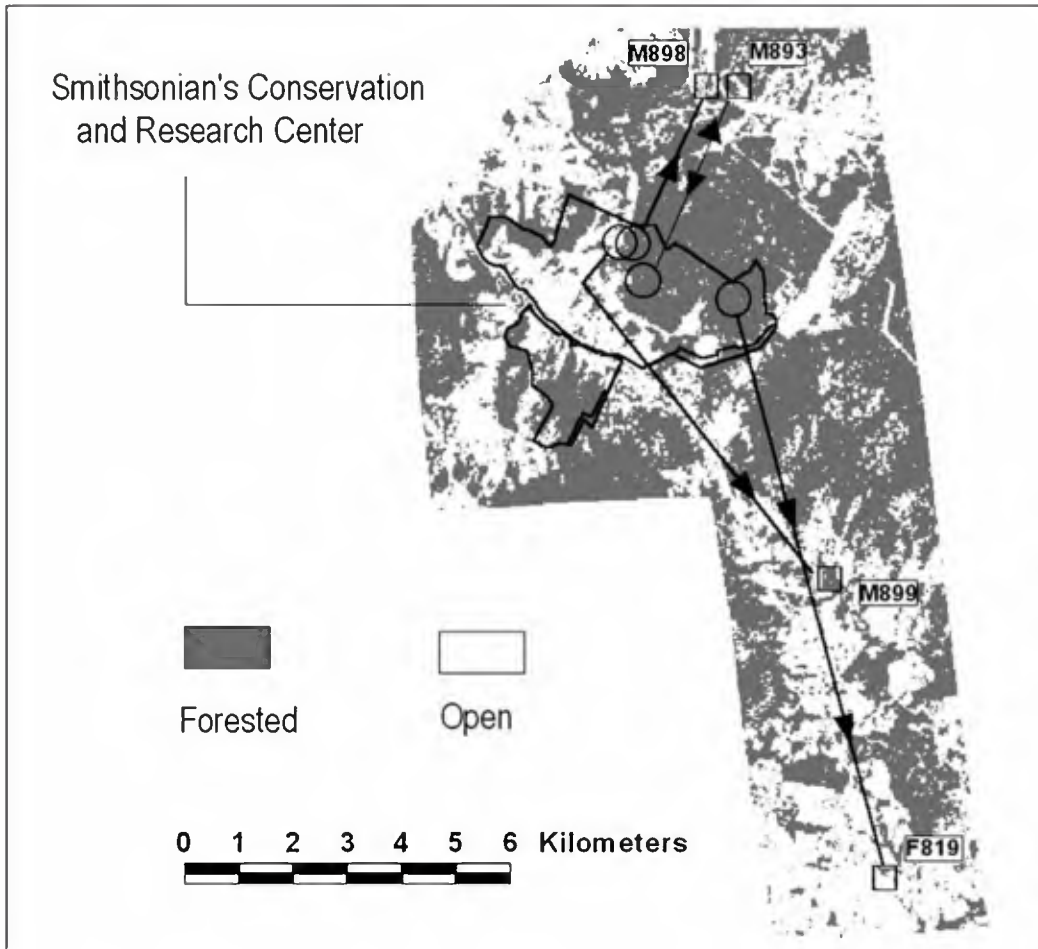


FIG. 2. Breeding (open circles) and postbreeding (open squares) of four adult Scarlet Tanagers that nested and molted in areas separated by >3 km, CRC, Virginia, 1998.

$n = 9$), postbreeding (PB, $n = 6$), and breeding–postbreeding sites (B/PB, $n = 9$; sites used for birds during breeding and postbreeding periods) were significant for density of trees (>4 cm DBH, $P = 0.084$), large trees (46–85 cm DBH, $P = 0.035$), and outsized trees (>85 cm DBH, $P = 0.026$). Subsequent nonparametric multiple comparison tests for unequal samples for those variables are shown in Figure 3. Although those differences are not significant using Bonferroni adjusted alpha (0.011), it is important to note that postbreeding sites had more trees and basal area (because of larger density of small trees, 4–46 cm DBH), more snags, and more trees characteristic of successional habitats. On the other hand, breeding and breeding–postbreeding

sites had more big trees (>46 cm DBH), and more trees characteristic of mature habitats. Note also in Figure 3 that for most variables, the range of values for sites used during breeding–postbreeding periods tended to be intermediate between sites only used during breeding or during postbreeding periods.

Statistical tests for individual birds examining differences in vegetation attributes between breeding and postbreeding sites are shown in Table 3. In general, results of analyses were in agreement with those obtained in pooled data (Fig. 3). However, as expected, there was individual variation (i.e. nonsignificant individual differences for variables that were significant when data were combined across individuals).

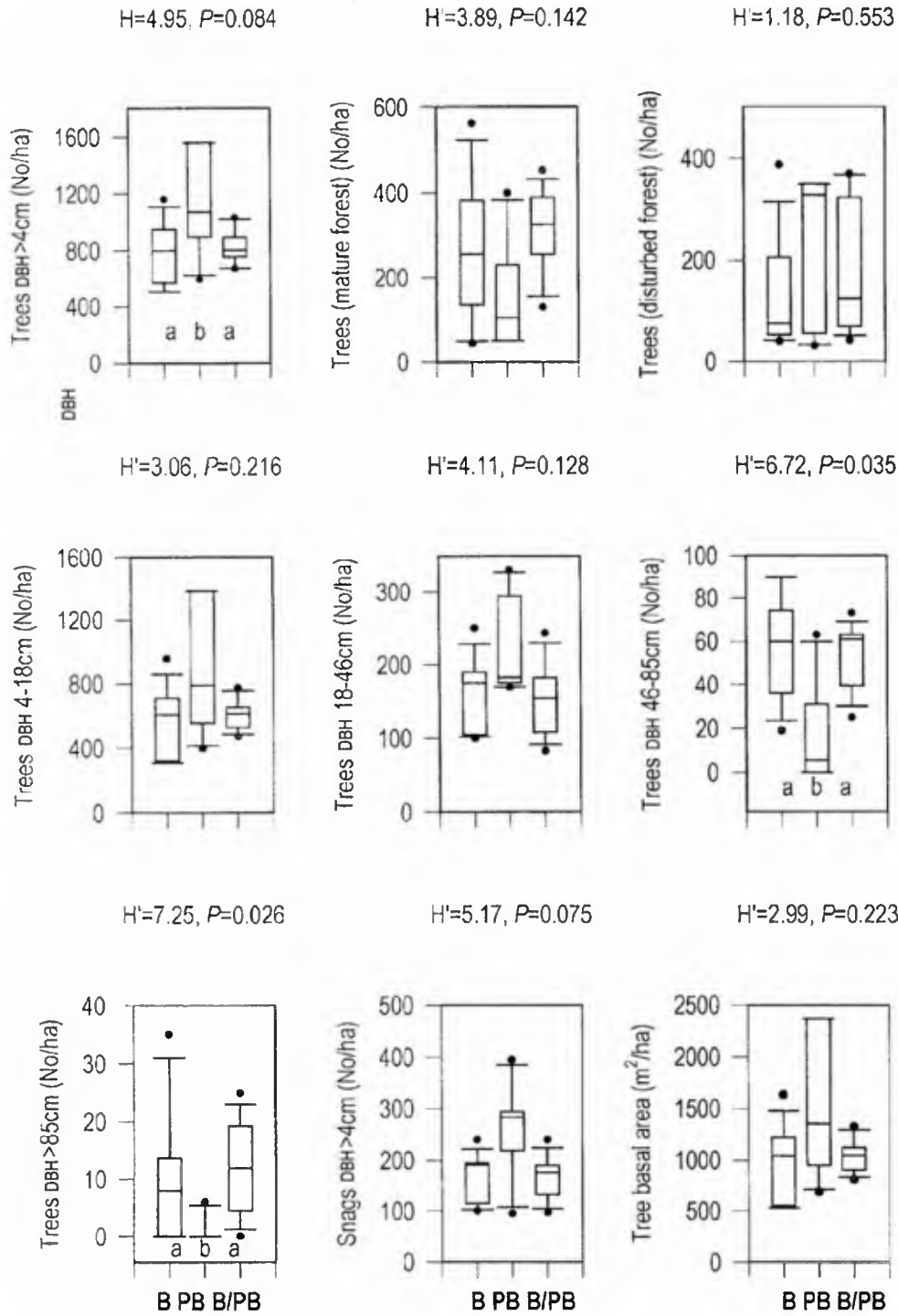


FIG. 3. Comparison of habitat variables among breeding (B, $n = 9$), postbreeding (PB, $n = 6$), and breeding-postbreeding (B/PB, $n = 6$) sites for radiotagged adult Scarlet Tanagers. Box plots with the same letter were not significantly different ($P > 0.05$, nonparametric multiple comparison for unequal samples, Zar 1996). CRC, Virginia, 1998.

TABLE 3. Results of statistical tests (paired comparisons, Wilcoxon signed-rank test) examining differences in vegetation attributes between breeding and postbreeding sites for 13 radiotagged adult Scarlet Tanagers. Breeding (B) and postbreeding (PB) indicate the site where a higher value occurred, "=" indicates equal density (number per hectare) of trees, northern Virginia, 1998.

Bird ID	Vegetation traits ^a								
	Total trees	Mature forest trees	Successional forest trees	Snags	Small trees	Medium trees	Large trees	Outsized trees	Basal area
Birds that stayed									
M443	PB*	PB	PB	PB	PB	PB	PB	B	PB
M491	B	B	B	B	B	B	B	=	B
F815	PB	PB	B	PB	PB	PB*	PB	B	PB
M891	PB	PB	PB**	PB	PB	=	PB	B	PB
M895	PB	B	B	B	PB	B	PB	B	PB
M900	B	PB	B	B	B	B	PB	=	B
M988	B**	B**	PB	PB	B*	PB	B	B	B*
Birds that moved									
M894	PB*	B	PB	PB	PB	=	B	B	PB
M990	B	PB**	B	PB*	B**	PB	PB*	B	B**
F819	B	B**	B	PB*	B	PB	B**	B	B
M893	PB**	B*	PB**	PB	PB**	PB	B**	=	PB**
M898	PB	B*	PB*	PB	PB*	PB	B**	B*	PB*
M899	B	B	B	B	B*	B	B**	B**	B*

* $P < 0.10$; ** $P < 0.05$; (Bonferroni adjustment, $\alpha_{adj} = 0.0008$, rendered no significant all tests).

^a Vegetation traits were total trees (trees DBH > 4 cm); mature forest trees (DBH > 4 cm, characteristic of mature forest); successional forest trees (DBH > 4 cm, characteristic of successional forest); snags (dead trees DBH > 4 cm); small trees (DBH 4–18.4 cm); medium trees (DBH 18.5–46.4 cm); large trees (DBH 46.5–85 cm); outsized trees (DBH > 85 cm); basal area.

We recorded 48 tree species within sampled sites. Of those, hickories, oaks, flowering dogwood (*Cornus florida*), slippery elm, red maple (*Acer rubrum*), and tulip poplar constituted 70% of all detections. Birds that established breeding and postbreeding home ranges on the same site included on average more tree species per site (21 ± 1.2) than birds that established postbreeding home ranges distant from breeding home ranges (16 ± 1.6) ($W = 222$, $P = 0.006$). Within each group (i.e. birds that stayed and birds that moved), differences in the average number of tree species between breeding and postbreeding sites were not significant ($P = 0.85$ and 0.75 , respectively). As expected, Morosita's index of similarity (breeding vs. postbreeding sites) was larger for birds that stayed (0.61 ± 0.37) than for birds that moved (0.30 ± 0.08). Considering only the three more abundant species at each site, species such as hickories, slippery elms, and flowering dogwoods were recorded in breeding and postbreeding sites; whereas pignut hickory was the only species restricted to breeding sites, and ailanthus, sassafras, and red maple were recorded only on postbreeding sites.

Among the noteworthy pieces of anecdotal information of individual movements are the

following: (1) Four adult male birds returned to their breeding home ranges for periods of hours or days after establishing postbreeding home ranges elsewhere >300 m from the breeding home range. (2) Four second-year males were radiotagged, none of which appeared to have been mated. Three of those moved considerable distances around the study area, whereas the fourth (M443) remained in a relatively restricted home range over the entire summer season. (3) During the postbreeding period, three adult males visited the same forest fragment located 0.6–1.1 km from their breeding home ranges, and two adult males moved to the same site located 3.3 and 3.9 km from their breeding home ranges. (4) One pair (F896, M897), the only family on which we were able to obtain observations, split care of two fledglings between them, with one fledgling accompanying the female, and one accompanying the male.

DISCUSSION

During the breeding season, our marked population of Scarlet Tanagers moved over an area of 2.6–5.6 ha. Postbreeding home ranges were similar in size to home range during the

breeding period for birds that remained in the vicinity of nesting areas but were larger for birds that moved away from the nesting area. Unfortunately, there is no published information to compare our estimates of area used for Scarlet Tanagers. In Maryland, Bushman and Therres (1988) found Scarlet Tanagers absent from tracts of forest less than 1–5 ha. In New York, Roberts and Norment (1999) found that Scarlet Tanagers were absent from forest patches <10 ha. In the Appalachian region, Rosenberg et al. (1999a) mentioned that Scarlet Tanagers “are predicted to occur in virtually any size forest patch within landscape blocks that are at least 50% forested” and “even small patches of roughly 10 ha located in landscapes that are only 30% forested provide moderately suitable habitat for breeding tanagers.” However, the initial question asked by Rosenberg et al. (1999a), “how much mature forest is necessary to sustain a breeding population of that Neotropical migratory songbird?” is only partially answered. Bushman and Therres (1988) concluded that block sizes of 3,100 ha are probably necessary for maximum densities or population sizes of Scarlet Tanagers. Rosenberg et al. (1999b) used an area of 1,000 ha to describe landscape characteristics surrounding census points. Roberts and Norment’s (1999) analysis included the amount of forest within 1 km of the plot. In our study, radiotagged individuals moved up to 11 km from the nesting territory, which implies that Scarlet Tanagers may be scouting over an area of ~38,000 ha or even larger because some individuals were not located within that area.

Certain aspects of observed postbreeding behavior of adult Scarlet Tanagers are similar to postbreeding behavior recorded in other studies for that and other migrants that breed in mature Appalachian forest. For instance, Vega Rivera et al. (1999) found that 31 of 61 radiotagged adult Wood Thrushes moved at least 10 km away from the study area prior to molting, a pattern comparable to that documented for Scarlet Tanagers in which 11 adult birds evidently left the study area prior to molt (i.e. before 1 August). In addition, Rappole and Ballard (1987) captured a molting female Scarlet Tanager on 21 Aug at a study area in Athens, Georgia, a site located 100 km south of the nearest breeding population for that species in the Appalachian forest of the mountains of

Georgia. Members of other Appalachian forest-breeding species were also captured at that site in July and August (e.g. Northern Parula [*Parula americana*], Ovenbird [*Seiurus aurocapillus*], Black-and-white Warbler [*Mniotilta varia*], American Redstart [*Setophaga ruticilla*], and Canada Warbler [*Wilsonia canadensis*]), several of them also in molt. A similar behavior (i.e. individuals abandoning their territories after reproduction and before starting molt or during early stages of molt) has been reported for other species (e.g. Nolan 1978, Sealy 1979, Cherry 1985, Chernetsov 1998).

Such early disappearance of migrants from their breeding areas is sometimes assumed to be evidence of migration. However, there are three reasons why we believe that early departure from the breeding territory does not represent the initiation of migration for the Scarlet Tanager: (1) several birds (15, or 75%) remained on ($n = 9$) or near ($n = 6$) the breeding area after 1 August, and those birds did not depart until mid-September; (2) timing (July) for those that left the study area indicates departure prior to molt, a condition not favorable for overlap with migration; (3) television tower kill data from northern Florida do not show evidence of migration in that species until September (Crawford 1981), comparable to when the bird appears as a migrant along the Texas Gulf Coast (Rappole and Blacklock 1985). We suggest that Scarlet Tanagers leave their breeding sites prior to migration to find high-quality habitats (i.e. abundant food resources, low predator pressure) in which they can spend the 4–8 week interim between completion of breeding and initiation of southward migration.

We do not know why some birds remained on or near nesting areas throughout the molting period and some birds left. In the Wood Thrush, early departure by some individuals appears to reflect insufficiency or absence of preferred molting habitat on or near nesting sites as evidenced by a significant shift in Wood Thrush habitat preference between breeding and postbreeding periods, with many birds choosing to move to earlier successional stages in apparent search for higher vegetation density and fruits (Vega Rivera et al. 1999). A similar explanation may apply to Scarlet Tanagers. We found evidence that tanagers shifted focal areas between breeding and postbreeding periods, even for those that did not change home-range location.

However, we did not find an obvious trend indicating a change in habitat type use, although we did find slight differences in vegetation attributes between breeding and postbreeding sites (Table 3). A possible explanation for that absence of a strong and evident habitat change may be the scale at which we were able to measure habitat variables, and difficulty of tying specific variables to tanager habitat use. During the postbreeding period, tanagers are much more difficult to track than Wood Thrushes. Wood Thrushes tend to forage low in dense shrubs, remaining in the same small area, often for several days. We hypothesized that switch of habitat and decreased activity were the result of an intensive molt and a largely frugivorous diet (Vega Rivera et al. 1998b). According to our observations, Scarlet Tanagers had a gradual molt and never seemed to lose their flying capabilities. They forage higher in the canopy, tend to move longer distances between sightings, and continue depending strongly on insects as their main source of food.

That at least four adult male Scarlet Tanagers returned on occasion to their breeding home ranges after establishing postbreeding home ranges elsewhere would seem to indicate that there is a value of some importance in maintaining a presence on the breeding site, perhaps affecting ability to retain control of the site in subsequent breeding seasons as it has been proposed for tropical passerines (Lefebvre et al. 1992). If that is true, the conflicting needs for remaining on the breeding territory to maintain ownership during the postbreeding period versus the need to locate the best possible molting habitat could explain the variety of movement patterns observed in that species, as well as in the Wood Thrush where similar patterns are observed (Vega Rivera et al. 1999). At one end of the spectrum, one could expect to see individuals that have both good breeding and good molting habitat on their breeding territories remaining on their breeding territories throughout the entire breeding-to-postbreeding period, whereas at the other end of the spectrum would be those individuals that have no good molting habitat on the breeding site. Those birds presumably are those that depart the area altogether. Intermediate strategies involving movements over various intervals back and forth between breeding and molting sites during the postbreeding period then could be explained on the basis of the amount of available

molting habitat on the breeding home range. That explanation introduces the possibility of intraspecific competition as an additional factor affecting postbreeding movement patterns, although to date we have seen no evidence of such interactions in either the Scarlet Tanager or Wood Thrush.

Adult male tanagers occasionally disappeared from their territories during the breeding period, but we have no data on where they went. Stutchbury (1998) found that male Hooded Warblers left their territories during the breeding period and invaded the territories of other males for the apparent purpose of copulating with mated females. J. M. Meyers (pers. comm.) found that radiotagged male Painted Buntings (*Passerina ciris*) left their pine-oak forest territories in coastal Georgia during the breeding period for the purpose of foraging in marshland habitat, traveling as far as 700 m, a habit alluded to by Lanyon and Thompson (1986) as well. Either or both explanations could apply to tanagers.

We had four second-year males in our study area, none of which appeared to be mated. Three of those birds moved in ways typical of floaters, covering relatively large distances, and showing little attachment to any particular site (Hensley and Cope 1951, Rappole et al. 1977). One bird, however (M443) stayed in one area from June to September. That bird may have been a "lurker," that is, a category of unmated male first described by M. V. McDonald for Kentucky Warblers (*Oporornis formosus*) in which the bird remains throughout the season in apparent interstices of existing male breeding territories (Rappole and McDonald 1994).

CONSERVATION IMPLICATIONS

Our data indicate that breeding period and postbreeding period requirements for Scarlet Tanagers are somehow different, and sites with different characteristics often are needed to meet those needs. Six of our birds left their breeding territories to move at least 300 m to molting areas and five disappeared from the study area. Those that established postbreeding home ranges on our study area spent the remainder of their postbreeding period on those new home ranges until apparent departure on migration in mid-September. Although habitat use at a macro level (i.e. forest type) did not ap-

pear to change significantly between breeding and postbreeding periods, it is apparent that some factor or combination of factors, presumably related to habitat, favored those home-range shifts. Clearly the 4–8 week postbreeding period that extends from the time when the young reach independence until departure on migration is an important stage when complete, prebasic molt and premigratory fattening must be accomplished. Conservation strategies for the Scarlet Tanager and other species of migrants will have to incorporate those different needs during the different phases of the annual cycle to be successful.

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