2000

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The Wilson Bulletin, Vol. 112, No. 2 (Jun., 2000), pp. 243-248

Wilson Bull., 112(2), 2000, pp. 243–248

BREEDING SEASON DEMOGRAPHY AND MOVEMENTS OF EASTERN TOWHEES AT THE SAVANNAH RIVER SITE, SOUTH CAROLINA

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ABSTRACT.—The Eastern Towhee (*Pipilo erythrophthalmus*) has undergone population declines across much of its range, especially in New England. Despite being a widespread and, at one time, a common species, relatively little is known about its natural history, ecology, or demographics. We conducted baseline research on Eastern Towhees at the Savannah River Site, South Carolina, in 1995 and 1996 to estimate breeding season survival rates, nest success rates, breeding densities, and daily movements. We also were interested in whether towhees had differences in survival and movement rates between young and mature managed pine stands. We found that survival rates during the breeding season of radio-marked towhees did not vary by sex or stand type. Daily nest success rates were very low [0.629 ± 0.088 (SE)] as a result of high predation levels. Abundance estimates adjusted for sampling effort differed between years. In 1995, the abundance estimate was significantly lower in mature stands (7.1 ± 0.47) than in young stands (9.6 ± 0.60) while in 1996, there was no different between mature stands (26.2 ± 5.67) and young stands (16.5 ± 3.39). Average daily movements by radio-marked towhees did not vary by sex or stand type. Movements among adjacent stands were common, and sometimes great distances. *Received 22 Sept. 1999, accepted 22 Dec. 1999.*

Eastern Towhees (*Pipilo erythrophthalmus*) were once a widespread and common breeding bird throughout Eastern North America (Greenlaw 1996). Since at least 1966, Eastern Towhee populations have declined sharply throughout most of the species' range, especially in New England (Hagan 1993, Sauer et al. 1997). The principal causes for these declines are thought to be habitat loss, habitat alteration, and increased mortality rates, especially of nesting females (Hagan 1993, Greenlaw 1996). Habitat alteration is mostly due to agriculture and forest management practices that reduce ground and mid-story cover.

Only one estimate of annual survival rate has been reported for Eastern Towhees (DeSante et al. 1996) but none during the breeding season. The propensity of towhees to forage and nest on or near the ground probably exposes them to high rates of reptilian and mammalian predation (Brawn et al. 1995). This exposure to ground dwelling predators may in part underscore the need to estimate sex-specific and breeding period survival rates (Greenlaw 1996). Baseline reproductive data are available on age at first breeding, clutch size, length of breeding season, and numbers of broods per season, but information on nest success rates is minimal (Greenlaw 1996). More importantly, conservation efforts require documentation of variation in reproductive effort across seasons, years, ages, and habitat types (Hagan 1993).

Censuses of Eastern Towhees have been conducted across various habitats based on territory mapping procedures (Greenlaw 1996). These density estimates range widely, no doubt in part because of differences in techniques used. Eastern Towhees are surveyed well by the Breeding Bird Survey (Sauer et al. 1997). Range maps suggest recent differences in densities across the range of the towhee, but no range retractions are evident (Greenlaw 1996).

Our objectives were to estimate Eastern Towhee breeding season survival rates, nest success rates, densities, and daily movement distances.

STUDY AREA AND METHODS

We studied Eastern Towhees at the Savannah River Site (SRS), a National Environmental Research Park, in western South Carolina along the Savannah River in Aiken, Barnwell and Allendale counties. Savannah

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River Site is a 770 km^2 U.S. Department of Energy facility that lies in the Upper Coastal Plain physiographic province. At the site, towhees inhabited understory grass and shrublands in mature loblolly pine (*Pinus taeda*) and longleaf pine (*P. palustris*) stands, and in replanted clearcut stands (Krementz and Christie 1999). Replanted stands were occupied by towhees until the canopy closed and the mid-story and ground cover declined after about 10–15 years. Mature pine stands were managed with periodic thinning and burning (cool and warm season) on a 3–5 yr rotation. All mature stands we monitored were burned within the previous 3 years.

In 1995, we monitored birds in 8 young longleaf pine stands and 8 mature longleaf pine stands. Young stands were 2–5 years old and from 3–26 ha. Mature stands were 32–97 years old (median = 53) and from 6–59 ha. In 1996, we used 12 young longleaf pine stands and 4 mature longleaf pine stands. Young stands were 3–6 years old and from 3–57 ha. Mature stands were 38–98 years-old (median = 57) and from 10–53 ha.

We captured towhees by placing 20 12-m (30-mm) mist nets in a 5 × 5 grid (1995, 4 ha) or a 5 × 4 grid (1996, 3 ha) with nets 50 m apart. Birds were captured during 3 sampling rounds in 1995 (25 April–24 May, 25 May–23 June, and 26 June–21 July) and 1996 (1 May–30 May, 1–28 June, and 1–30 July). We sampled all stands once per round.

Each day, beginning 30 min before sunrise, we opened mist nets for 4 h and closed them earlier only when precipitation exceeded 0.5 cm/h or temperatures exceeded 30° C. We checked nets at 30–45-min intervals, more often when weather conditions threatened the health of netted birds. For each captured bird, we recorded age and sex (Pyle et al. 1987), and banded each bird with a USGS-Biological Resources Division leg band. We also treated recaptures at different stands within the year as new individuals because our telemetry observations indicated that movement among monitored stands was low, and we had no comparable checks for unmarked birds moving among stands.

Beginning on 7 May 1996, we attached radio transmitters to 20 towhees (9 M, 11 F) using a thigh harness (Rappole and Tipton 1991, Powell et al. 1998). The radio with harness weighed 1.3–1.4 grams, or about 3% of body mass. We monitored each bird's status (dead, alive, censored) and location (UTM ± 20 m) daily until either radio failure or the end of the study period (18 July). Birds alive on 18 July were considered to have survived the breeding season. We did not begin tracking until 13 May after which time we estimated a 10 week survival rate.

At the end of each week's monitoring, every radio-tagged bird was categorized as survived, censored, or dead. Mortality was assigned to individuals when the recovered radio or radio harness was disfigured or the carcass was found. Survival was assigned if the bird was seen alive or if the radio signal was lost shortly after an indication of battery failure (e.g., variable pulse rate). An individual was censored if the radio failed prematurely without warning or if the harness and radio were found under conditions for which neither mortality nor survival of the individual could be determined. We identified predators by examining physical evidence at the recovery site.

Cohorts of radio-marked towhees were used to estimate weekly survival probabilities using the program SURVIV (White 1983). We tested for both sex-specific and stand type specific (young/mature pine stand) effects on survival rates by comparing general (specific survival rate estimates) and constrained (combined estimates of survival rate) models using Aikike's Information Criteria (AIC; Burnham and Anderson 1998). If the AIC values for competing models were less than 2 units different, we relied on the Likelihood Ratio Test to determine which model the data fit better (Burnham and Anderson 1998). Finally, we estimated an overall weekly survival rate combining sexes and stand types.

In 1996, nests were found by monitoring radio-tagged females. We used at least 5 consecutive daily readings at the same location as evidence of nesting. We began looking for nests of radio-tagged females on 16 May. Occasionally nests were located by flushing unmarked towhees from a nest. Once located, nests were monitored every 2–4 days until the nest failed or nestlings fledged. Date, number of eggs or nestlings, and number of Brown-headed Cowbird (*Molothrus ater*) eggs were noted at each nest.

Nests that fledged at least one young were considered successful. Nest survival rates were estimated using a modified Mayfield (1975) approach incorporating the exact number of days between nest checks for increased survival rate precision (Bart and Robson 1982).

We estimated abundance for the mist net grids in each stand type. If a bird was captured once during any 2-day monthly capture period, it was recorded as present, otherwise it was categorized as absent. Only capture histories for adults were used for analyses. Abundance was estimated using the program MARK (White 1999). In 1996, these abundance estimates were not comparable between stand types because we sampled different numbers of stands per stand type (12 young, 4 mature). To correct for the differential sampling effort, we estimated an adjusted relative abundance ($\hat{N}_i'$) by dividing the abundance ($\hat{N}_i$) of stand type i (where i = mature or young stands) by the number of stands sampled (n_i). Variance for this estimate was derived as:

$$v(\hat{N}_i') = v(\hat{N}_i) \times \left(\frac{1}{n_i}\right)^2$$

where n = the number of stands sampled. Relative abundance ($\hat{N}_i'$) between stand types was compared using a 95% confidence interval (CI).

We measured daily distances moved based on consecutive daily radio tracking locations. Because Krementz and Pendleton (1994) found that differences in daily distances moved among individual American

TABLE 1. Sample sizes, cumulative number of weeks tracked, numbers survived, censored, and died of radio-marked Eastern Towhees by stand type and sex at Savannah River Site, South Carolina.

Stand type Sex	*n*	Weeks tracked	Survived	Censored	Died
Mature					
Male	3	16	1	2	0
Female	5	30	3	1	1[a]
Young					
Male	6	46	3	3	0
Female	6	43	4	2	0

[a] Source of mortality was an unidentified mammal.

Woodcock (*Scolopax minor*) often overwhelmed the effects of sex and age on movements, we used the average distance moved per day per individual as a response variable. We excluded all individuals with less than 10 daily movements to reduce the effects of individual birds with small sample sizes. We investigated whether sex, stand type, or the interaction of sex and stand type explained variation in daily movements using a linear model (PROC GLM; SAS version 6.02 on an IBM PC; SAS Instit. 1990).

All means presented are ±1 SE.

RESULTS

We radio-tagged 20 towhees between 7 May, and 13 June 1996. Half of the sample was marked by 16 May and only one death was documented (Table 1). More males were censored (4 of 9) than females (3 of 11). Censoring occurred throughout the study period and was not related to any weather events.

We found no differences in survival rates between sexes or stand types (Table 2). Therefore we estimated a combined overall weekly survival rate (Table 2).

Nests were located in grape (*Vitis* spp., 3), sparkleberry (*Vaccinium arboreum,* 2), oaks (*Quercus* spp., 2), common persimmon (*Diospyros virginiana,* 1), wax-myrtle (*Myrica cerifera,* 1), and broomsedge (*Andropogon virginicus,* 1). All marked females either had developed brood patches when captured or were observed being courted, nest-building, feeding young, or all of the above. While under observation, 5 females exhibited nesting behavior once, 2 females twice, and 3 females three times. We located 1 nest for one

TABLE 2. Weekly survival rate (±1 SE) estimates and test statistics by sex, stand type, and pooled for radio-marked adult Eastern Towhees during the breeding season at Savannah River Site, South Carolina

Factor				Likelihood Ratio Test		
	ϕ	SE	Akaike's Information Criteria	χ^2	*n*	*P*
Pine stand age						
Young	1.000	0.1060				
Mature	0.979	0.0206	10.502[a]			
Pooled stand data	0.993	0.0073	10.613[b]	2.11[c]	1	0.15
Sex						
Male	1.000	0.1259				
Female	0.986	0.0134	10.436[a]			
Pooled sex data	0.993	0.0073	9.674[b]	1.24[c]	1	0.26
Pooled survival rate	0.993	0.0069				

[a] General model test fit statistic (e.g., whether habitat specific survival rates were necessary to model the data).
[b] Constrained model test fit statistic (e.g., whether a combined habitat survival rate was sufficient to model the data).
[c] Likelihood ratio test for fit between models (e.g., analogous to the constrained AIC test statistic).

female, 2 nests for two females and 3 nests for one female. Overall, we monitored 10 nests (9 during egg/nestling period, 1 during the nestling period). Only 3 egg clutches were found. Two nests were parasitized by Brown-headed Cowbirds with 1 cowbird egg per nest. The shortest time between the young fledging from one nest and the start of nest construction on the next nest for an individual female was one week. Of 10 nests monitored, only 1 nest fledged young. On separate occasions, three marked males were observed with fledglings. All other nests were destroyed by unknown predators. Across stand types (7 young and 3 mature), the daily survival rate during egg stage was 0.661 (±0.0875). For the egg and nestling periods combined, the estimated daily survival rate was 0.619 (±0.0811).

We captured 51 towhees (33 in young stands and 18 in mature stands) in 1995 with 11 recaptured at least once. The adjusted abundance estimate ($\hat{N}_i'$) in the 4 ha plots was 9.6 (±0.60) for young stands and 7.1 (±0.47) for mature stands; respective densities were 2.4 and 1.8 birds per ha. We estimated that more towhees were found in young pine stands than in mature stands because the 95% CI's for ($\hat{N}_i'$) did not overlap (young: 8.5–10.8; mature: 6.2–8.0). We captured 60 towhees (49 in young stands and 11 in mature stands) in 1996 with 7 recaptured at least once. The adjusted abundance estimate ($\hat{N}_i'$) in the 3 ha plots was 16.5 (±3.39) for young stands, and 26.2 (±5.67) for mature stands; respective densities were 5.5 and 8.7 birds per ha. There was no difference in the relative abundance of towhees in mature and young pine stands as the 95% CI's for ($\hat{N}_i'$) overlapped (young: 9.9–23.2, mature: 15.1–37.3).

Seventeen individuals met our minimum requirements for analysis of daily movements. Except for the incubation period when females were always on their nests, both sexes typically moved over the entire stand where they were captured. Only 2 birds, both females, remained in the stands where they were captured. The remaining 15 birds moved among adjacent stands. Stand types used included pine stands from just replanted to those over 75 yr old. Towhees marked in young pine stands used either middle aged (ca 20–35 yr) or mature stands, whereas towhees marked in mature stands also used middle-aged stands. No towhees moved from either a young or mature stand to a young stand. These movements were not permanent movements, but represented daily activities. Daily movement averaged 99 m/day (±10.46), with daily movements ranging from 39–173 m/day. The maximum distance moved per marked bird over each individual's sampling period averaged 464 m (±64.18), with maximum distances ranging from 110–1250 m. We found no effect of sex ($F_{1,16}$ = 0.99, $P > 0.05$), stand type ($F_{1,16}$ = 0.12, $P > 0.05$) or interaction between sex and stand type ($F_{1,16}$ = 0.74, $P > 0.05$) on daily distances moved.

DISCUSSION

Weekly breeding season survival rates of towhees in 1996 (0.993 ± 0.0069) did not vary by habitat type. Stober and Krementz (unpubl. data) did not find any differences between breeding season survival rates for Bachman's Sparrows (*Aimophila aestivalis*), another scrub species that uses young and mature longleaf pine stands at our study site. The absence of any difference in survival rates for either of these scrub birds between such seemingly different seral stages is surprising. One interpretation of this similarity in habitat-specific survival rates is that these scrub birds rely only on the mid-story and ground cover for their needs, that is, they do not 'see' the forest overhead.

Our estimates on nest success during the egg stage and for the entire nest stage were quite low compared to most passerines (Martin and Li 1992), but may be representative of Eastern Towhees from the Northeast (J. S. Greenlaw, pers. comm.). We suspect that nest success during 1996 was low based on the findings of Stober and Krementz (unpubl. data) who worked at the same study site on nesting success of Bachman's Sparrow (*Aimophila aestivalis*). Bachman's Sparrows are an appropriate bird to compare with towhees because they use similar microhabitats within the pine sere. The daily nest survival rate in Bachman's Sparrows in 1995 was 0.952 (±0.013, n = 26), while in 1996, it was 0.889 (±0.027, n = 15). Daily nest survival was significantly lower in 1996 than in 1995, when only 1 of 15 sparrow nests fledged one individual (Stober and Krementz, unpubl. data).

Caine and Marion (1991) reported towhee densities in middle aged (20–25 yr-old) pine plantations in north-central Florida from 2.1–4.2 pairs/km^2 (0.02–0.04 pairs/ha). From their descriptions, the stands of Caine and Marion (1991) most closely resembled our mature stands. Our density estimates of 2.4–8.7 birds/ha far exceeded those of Caine and Marion (1991). This again supports Greenlaw's hypothesis that towhee densities vary within habitat types.

Our sampling methods were not designed to monitor within day movements but instead were set up to monitor movements within the breeding season. Of those birds not censored (13 of 20), among-day movements during the breeding season were short (ca 100 m/day). In most cases, all birds had an area of central activity as was found by Greenlaw (1969). In addition, we found that excursions away from the central activity area were common, sometimes long (1250 m), and crossed through different aged pine stands. Middle aged pine stands were the usual target of these movements. Why towhees did not move to young stands is perplexing.

Our findings indicate that towhee breeding season survival rates are high, but that nest success rates are low. These low nest success rates, if occurring elsewhere, may be contributing to the observed population declines. Towhees appear flexible in their habitat requirements as long as there is a well developed mid-story and ground cover. Therefore, we recommend that land managers concerned with scrub-successional species like the towhee take appropriate management actions (e.g., selective harvests and prescribed burning) to produce optimal habitat.

ACKNOWLEDGMENTS

We acknowledge the assistance of J. S. Christie, C. E. Moorman, C. E. Richter, P. A. Moritz, J. M. Stober, T. N. Grigorieff, K. M. Hartke, D. P. McGowan, Jr., and H. McPherson with data collection. We are indebted to J. Blake, B. Jarvis, J. B. Dunning, and J. M. Stober for their scientific and logistical advice. Funding was provided by the U.S. Forest Service (Cooperative Research Agreements 12-11-008-876), SRS Biodiversity Research Program, U.S. Geological Survey Patuxent Wildlife Research Center, and The University of Georgia Warnell School of Forest Resources.

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