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SONG SHARING AND REPERTOIRES AMONG MIGRATORY AND RESIDENT RUFOUS-SIDED TOWHEES[1]

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Abstract. Among oscines, song sharing with neighbors and large song repertoires may be enhanced in resident populations. This idea was explored with the Rufous-sided Towhee (*Pipilo erythrophthalmus*) by studying singing behavior in a resident Florida and a migratory New York population. Florida males ($n = 15$) sang an average of eight song types per male, but New York males ($n = 15$) sang only 3.5. Furthermore, unlike the New York males, the Florida males shared most song types in their larger repertoires with immediate neighbors. These marked differences in sharing and repertoires need further study in the towhees and other species in order to understand more clearly the processes that lead to such population differences.

Key words: Dialect; (Pipilo erythrophthalmus); *migratory; repertoire; resident; Rufous-sided Towhee; song.*

INTRODUCTION

The evolution of vocal learning (Nottebohm 1972) has led to large song repertoires and cultural traditions among many songbird species, but the sizes of repertoires and extent of song sharing among neighbors vary considerably among species (Krebs and Kroodsma 1980). These vocal features also vary among populations of certain widespread species, and an intraspecific comparative approach can be useful in identifying ecological situations that are correlated with such population differences in vocal behaviors.

In this study, we examined the idea that resident populations of a species have larger song repertoires and more song sharing with neighbors than do migratory populations. The Rufous-sided Towhee (*Pipilo erythrophthalmus*) is a good species for study, because it is distributed across North America, and previous studies indicated more song sharing among neighbors and perhaps larger song repertoires in a resident Oregon population (Kroodsma 1971) than in a migratory Ohio population (Borror 1959, 1975). We therefore chose two eastern populations, one migratory population in New York and one resident population in Florida, to explore this question further. Our data are consistent with the idea that residency is correlated with both larger repertoires and a greater degree of song sharing with neighbors (Ewert 1978, Krebs and Kroodsma 1980, Morton 1986, Austen and Handford 1991).

METHODS

Ewert recorded males from a migratory population of *P. e. erythrophthalmus* on Long Island, New York, throughout the breeding season (late April through July) from 1969 to 1975. Towhees at Huntington, in Suffolk County, established territories in oak woodlands and adjacent old fields. At nearby (within 20 km) Connetquot State Park, towhees occurred in oak and pitch pine (*Pinus rigida*) forest and those at Tobay Beach (also within 20 km of Huntington) inhabited dense thickets of wild cherry (*Prunus serotina*), chokeberry (*Pyrus* sp.), bayberry (*Myrica pensylvanica*), and poison ivy (*Toxidendron radicans*) that grow between the leeward side of a barrier beach and a salt marsh. Ewert used a Uher 4000-L tape recorder, a Uher M512 microphone, a Uher microphone preamplifier, and a 61.5 cm fiberglass parabolic reflector. Sonagrams were made with a Kay Elemetrics 6061-B Sonagraph using the FL-1 filter.

Kroodsma recorded males from two populations of the resident *P. e. alleni* in southern Florida during March and April 1987. The towhees at the Archbold Biological Station were almost entirely within the southern ridge sandhill com-

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TABLE 1. Sampling effort and song type repertoire size for Rufous-sided Towhees from Huntington, Long Island, New York (Birds 1–15); Archbold Biological Station, Florida (16–25); and Corkscrew Swamp Sanctuary, Florida (26–30).

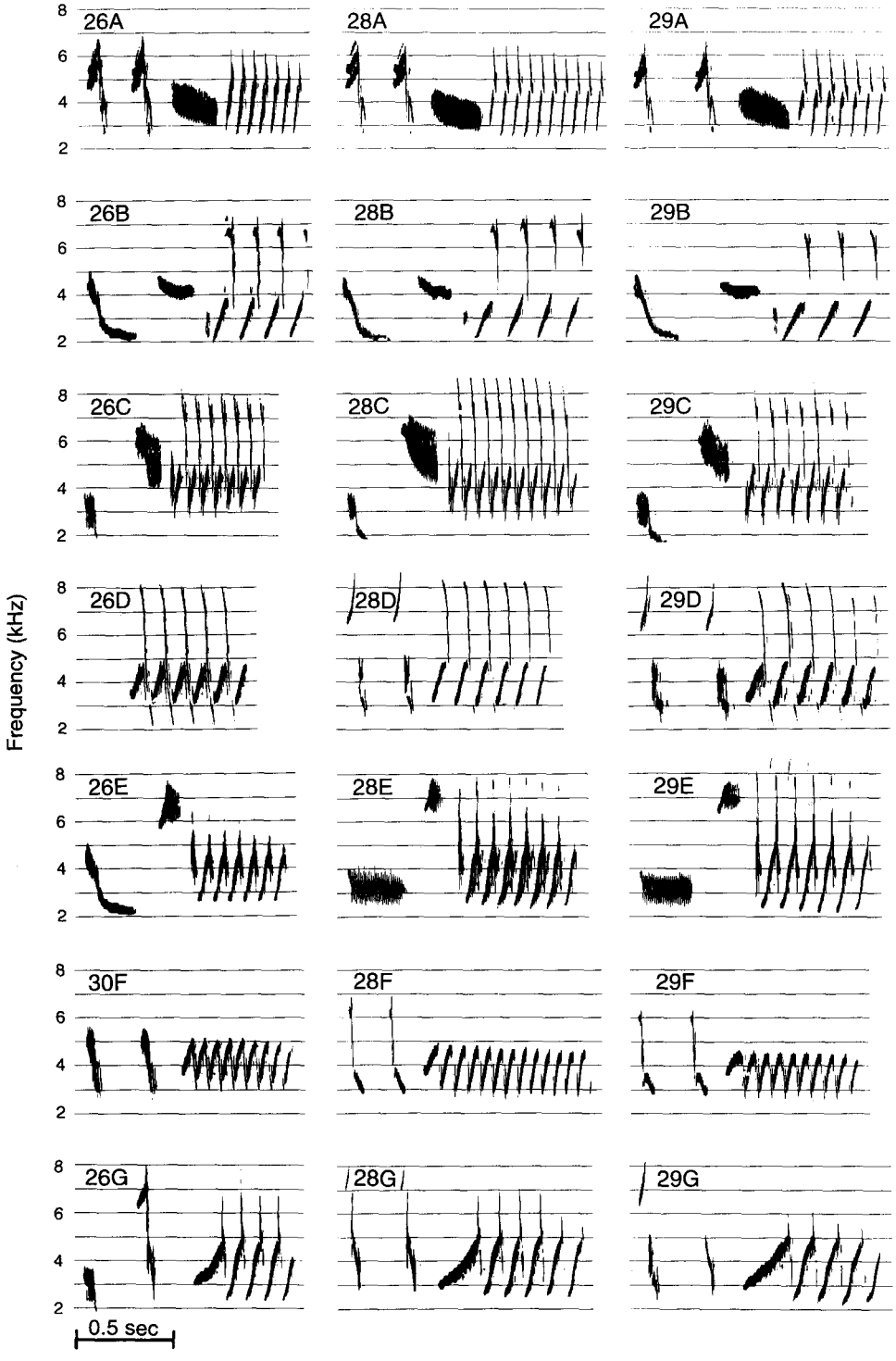
Bird[a]	Bouts/song type[b]											Types[c]	Bouts	Songs
1	20	15										2	35	1,495
2	253	196										2	449	19,172
3	12	9										2	21	897
4	—	—										2	34	1,452
5	9	6	5									3	20	854
6	12	9	5									3	26	1,110
7	—	—	—									3	29	1,238
8	6	6	2	2								4	16	598
9	71	37	36	30								4	174	7,430
10	11	4	4	2								4	21	897
11	—	—	—	—								4	24	1,025
12	—	—	—	—								4	12	512
13	11	11	6	6	4							5	38	1,623
14	—	—	—	—	—							5	34	1,452
15	—	—	—	—	—							5	14	598
16	6	4	3	3								4	16	258
17	8	6	6	5	4	4	3					7	37	434
18	5	4	4	4	4	3	3	2				8	29	209
19	7	6	6	5	4	4	4	3				8	39	289
20	8	8	8	6	6	5	3	3				8	47	824
21	4	4	3	2	2	2	1	1	1			9	21	221
22	6	3	3	3	2	2	2	2	1			9	24	673
23	7	6	6	5	5	5	4	4	3			9	46	832
24	3	2	2	2	1	1	1	1	1	1		10	15	133
25	5	4	3	3	3	3	3	3	2	2	1	11	32	218
26	8	6	5	5	3	2						6	29	256
27	5	4	3	2	2	1	1					7	18	279
28	8	6	5	5	5	5	4					7	38	413
29	11	11	10	9	8	8	6					7	63	734
30	5	5	5	5	3	3	3	3	2	1		10	35	212

[a] Birds within a location are listed in increasing order of repertoire size.
[b] Numbers of bouts for each male's song type (i.e., the number of independent occurrences for each type) listed in decreasing order. Bird 1 thus sang one of his two song types on 20 occasions and the other one on 15 occasions. For several New York birds (4, 7, 11, 12, 14, 15) the number of bouts/song type was not recorded.
[c] The total number of different song types from the male, followed by the total number of sampled bouts and total number of songs recorded. The total number of songs for several New York birds (4, 7, 11, 12, 14, 15) is estimated based on mean duration of song bout and mean song rate.

munity, the dominant tree species being slash pine (*Pinus elliottii*), turkey oak (*Quercus laevis*), and scrub hickory (*Carva floridana*) (see Fig. 2 in Abrahamson et al. 1984; see also Woolfenden 1970). The study site at Archbold began about 1 km east of the main station building and was a roughly 1 × 1.25 km area. At Corkscrew Swamp National Wildlife Sanctuary, about 95 km south-southwest of Archbold, towhees were recorded in slash pine and saw palmetto (*Serenoa repens*) near the Sanctuary headquarters.

In addition, Kroodsma recorded three neighboring male towhees in an oak woodland in western Massachusetts during July 1992. This smaller sample was used to provide additional data on song variation for the northern, migratory towhees. In both Florida and Massachusetts, Kroodsma used a Nagra IS-DT recorder and a Sennheiser MKH106 microphone in a 61.5 cm aluminum parabola. Each recorded song was viewed on a Kay DSP 5500 Sonagraph, and representative songs of each type were printed.

For analyses of repertoire size, we selected 15 towhees from New York (Huntington) and 15 from Florida (ten from Archbold, five from Corkscrew). These 30 individuals had been intensively tape-recorded and monitored, and we felt confident we had recorded an adequate sample of their repertoires (Table 1). Ewert tape-recorded or monitored by ear 11 of the 15 towhees at Huntington two or more years (range 2–6 years), and repertoires did not change from year to year. He also recorded an additional 151 towhees at his three sites and Kroodsma recorded another 14 towhees at Archbold and Corkscrew Swamp. These birds provided additional


Frequency (kHz)
8
6
4
2
26A
28A
29A
26B
28B
29B
26C
28C
29C
26D
28D
29D
26E
28E
29E
30F
28F
29F
26G
28G
29G
0.5 sec

data on the distribution of song types and syllables.

The songs that we recorded from each individual were catalogued by "song type." Like many other songbirds in which individuals have a repertoire of different songs, towhees repeat each type several times before switching to another. Omission of an introductory note or different numbers of repeated syllables in the terminal phrase occurs in successive renditions of the same song type, but such variation, though perhaps biologically significant, is minor compared to the extent of variation that occurs between bouts. Each bout of a given song type is thus considered one "independent" occurrence of that song type; given a sufficient sample size of bouts, identifying the song repertoire for each individual is straightforward (see also Borror 1959, 1975; Kroodsma 1971; Ewert 1978).

After identifying repertoires of the towhees, we searched for evidence of geographic variation in the songs. For the New York males, Ewert searched for entire song types or portions of song types (e.g., syllables of trills) that were identical in different males. For the Florida birds, Kroodsma numbered all sonagrams and, without knowing the singer's identity, searched for identical song types or syllables among the different birds. To verify that our strikingly different results reflected location and not investigator differences, Kroodsma also sorted sonagrams of the nine towhees that nested at Huntington in 1971, and Ewert examined the Florida sonagrams. We were in complete agreement about the song classifications.

RESULTS

Florida towhees had significantly larger repertoires than did New York towhees (2-tailed t-test, $P < 0.001$), with all but one Florida male having a larger repertoire than any of the 15 New York males (Table 1). The mean number of song types per individual on Long Island was only 3.5 (n = 15 males, 13 of which were banded; range two to five song types). At Archbold, one male (16) sang only four song types, but the other 14 males in the Florida sample sang from six to 11 different songs ($\bar{x}$ = 8.0). Seven of these males (17–18, 20–23, 25) were banded, and singing locations and behaviors of all birds were highly consistent between sample periods. Furthermore, repertoires from many of the males were recorded in one session, so we are confident that the listed repertoires represent the singing of only one male.

The proportion of song types shared among birds also differed strikingly between the New York and Florida sites. In New York, only 21 (5%) of 409 song types recorded from all birds in Huntington, Connetquot, and Tobay Beach were shared. Of the 15 intensively sampled birds at Huntington (Table 1), only two of 51 song types (4%) were shared among birds, i.e., two males shared one song type and all 50 other song types were unique. This low degree of song sharing among neighboring males contrasts sharply with the Florida samples (Fig. 1). At Archbold, in an area about 50% larger than the Huntington site, 59 (45%) of 130 song types were shared. At Corkscrew Swamp, 29 (71%) of 41 song types were shared with other males, and two neighboring males even shared their complete repertoires of seven song types apiece (males 28 and 29 in Fig. 1). Even though repertoires are relatively small in New York, during seven years of field work Ewert found no birds on Long Island that shared identical song repertoires.

In both Florida and New York, songs were more likely to be shared within a site than between sites. One Corkscrew male sang two song types that were identical to songs in repertoires of two different males at Archbold, but all other shared songs were found at only one site. Similarly, 19 of the 21 shared songs in New York occurred at only one site. Within each New York site, however, song sharing seemed no more likely to occur among neighbors than among nonneighbors.

To examine more closely the extent of vocal sharing among birds, we also determined the de-

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FIGURE 1. Highly similar songs in the repertoires of neighboring male Rufous-sided Towhees from Corkscrew Swamp Sanctuary, Florida. Column 1 contains all six songs (A–E, G) of male 26 and one of male 30 (F), column 2 all seven songs of male 28 (A–G), and column 3 all seven songs of male 29 (A–G). Terminal trills of each row are identical, and the entire song repertoires of birds 28 and 29 are considered identical to each other. Songs 28A–C and 29A–C are also shared with male 26; songs 26D, 26E, 30F, and 26G are unique because of different (or a lack of) song introductory notes.

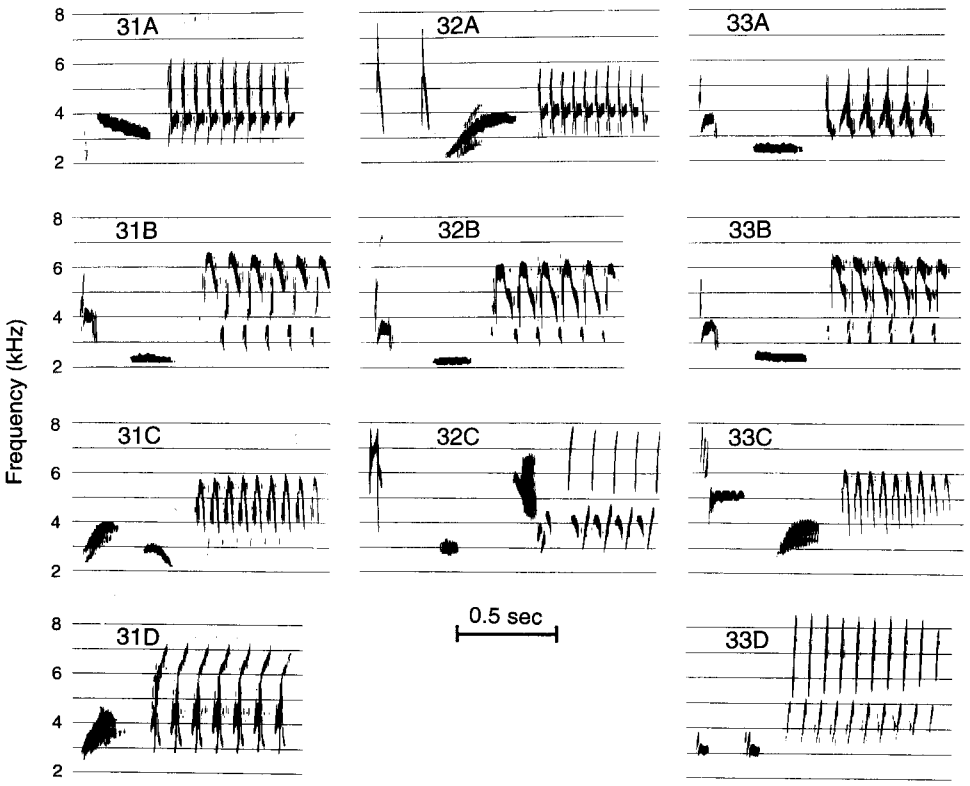

FIGURE 2. Representative song repertoires and degree of song sharing in New England, as recorded from three males in western Massachusetts. Males 31–33 have smaller repertoires than do Florida birds; shared, identical trill syllables are relatively rare (31A = 32A; 32B = 33B; 31C = 33C), and only one pair of identical songs (32B = 33B) was found among these neighboring males.

gree to which males at each site shared trill syllables. At Corkscrew and Archbold, 78% and 72% of recorded trill syllables were shared with other males, respectively. Sharing of trill syllables among Huntington males in any given year was considerably lower, and ranged from 18% to 56% (median, 33%) for Ewert's seven-year study period. Thus, although complete songs were rarely shared among the migratory birds, components of those songs were shared more often (illustrated with songs from Massachusetts in Fig. 2).

DISCUSSION

These data suggest that males in resident populations of Rufous-sided Towhees share more songs with their neighbors than do males in migratory populations. In the resident populations of Oregon (Kroodsma 1971) and Florida (this study), males shared most of their song repertoires with immediate neighbors. In migratory populations of the northeastern part of North America, however, sharing is rare. Borror (1959, 1975), working primarily in Ohio but also sampling other locations in the eastern United States, found that most song patterns were unique to a single bird. Likewise, we found little sharing of song types among towhees in New York or Massachusetts.

Song repertoires of resident populations in Oregon (Kroodsma 1971) and Florida also appear to be larger than those in migratory populations, such as those intensively sampled in New Jersey (Molnar 1977), New York, or Massachusetts. Although Borror (1975) found a large number of "song patterns" in some of his migratory Ohio birds (22 and 18 for two birds listed in his Table 4), we are not certain that his method of classifying songs is comparable to ours. We used the "bout" behavior of the birds to identify "song types," i.e., renditions of one basic pattern repeated many times in a row were considered one

song type. It seems likely, however, that the minor variations of a particular song type we saw within bouts were classified by Borror as different song types.

How these population differences develop is largely unknown. One possibility is that the degree of song sharing and the size of song repertoires are simply proximate consequences of population processes. In resident populations, turnover of territory holders may be reduced, with resident towhees spending more time on a single territory and associating for longer periods with the same neighbors. Young males in Oregon apparently establish life-long territories in such stable neighborhoods (Kroodsma 1971), and they would consequently learn to sing the songs of the local neighborhood. Territorial defense may occur year-round, providing a longer season for both adult song and juvenile practice than in more migratory populations, where, at least at Huntington, few nestlings (none of 11 banded) or juveniles (only 7.8% of 357 banded) return as adults (Ewert 1978). A second possibility is that genetic differences exist among these populations (e.g., Kroodsma and Canady 1985), such that males in resident populations have a greater tendency to match songs of their neighbors and to develop larger song repertoires than do males in migratory populations. Additional populations could be sampled to verify the correlation of song sharing and repertoire size with resident and migratory status, and studies of song development would help to determine whether ontogenetic differences occur among these populations. Exactly why residency would promote selection for more sharing or for larger repertoires must await a better functional understanding of these two aspects of songbird behaviors.

Data from other species also suggest that more sedentary populations develop a greater degree of geographic song variation (e.g., Brown-headed Cowbird (*Molothrus ater*), Rothstein and Fleischer 1987, Eastzer et al. 1985, Dufty 1985; Vesper Sparrow (*Pooecetes gramineus*), Kroodsma 1972, Ritchison 1981; White-crowned Sparrow (*Zonotrichia leucothrys*), Baptista 1975, Heinemann 1981, DeWolfe et al. 1974, Austen and Handford 1991). Although migratory populations can certainly maintain localized distributions of songs (e.g., Adret-Hausberger and Güttinger 1984), we know of no good examples of species in which migratory populations have more localized distributions of learned songs than do more sedentary populations (although the House Finch, *Carpodacus mexicanus,* is worth closer study; Mundinger 1975, Bitterbaum and Baptista 1979). The correlation between local song variation and sedentary populations thus seems rather well established, though the causal relationship between the song distribution and the population processes continues to be debated (e.g., Baker and Cunningham 1985, Greenwood 1985).

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