THE EFFECTS OF DISTANCE AND ISOLATION ON SONG-TYPE SHARING IN THE CAROLINA WREN

Eugene S. Morton[1]

Abstract.—I describe the geographic distribution of song types in the Carolina Wren (*Thryothorus ludovicianus*) in continuous and discontinuous populations along the eastern shore of the Chesapeake Bay and adjacent islands. On average, individuals at the same site held 66% of their songs in common (range = 49.5–89.5%). At sites in continuous mainland populations, I found a negative linear correlation between the distance separating individuals and the percentage of songs shared. Wrens on isolated island sites shared less than 20% of their song types with individuals on the nearest mainland areas. Song sharing among males separated by 3 km of water was equivalent to that found in males separated by 145 km of continuous mainland habitat. Of the 309 song types in the total sample, 78% were restricted to one site. The percentage of songs shared among neighboring free-ranging wrens found in this study is compared to the percentage of undegraded songs learned by naive young males in a laboratory experiment. *Received 16 Feb. 1987, accepted 25 May 1987.*

Many recent studies of the functional significance of song sharing among neighboring male oscines focus on distance assessment as an important source of selection on the evolution of song types and song repertoires (McGregor and Krebs 1984; Morton 1982, 1986; Shy and Morton 1986), and on the song types learned by individual birds (Morton et al. 1986). In the Carolina Wren (*Thryothorus ludovicianus*), a male hearing a conspecific song uses degradation in the perceived song to assess its distance from the singer (Richards 1981, Wiley and Richards 1982, Shy and Morton 1986). This ranging of distance is possible only if the listener has the song type it perceives stored in its memory (i.e., it has an undegraded replica of what it hears) (Morton 1986, Shy and Morton 1986). Young males base their choice of songs to learn on the amount of degradation in songs they hear, at least in the laboratory (Morton et al. 1986). This finding supports Hansen's (1979) hypothesis that local acoustic environments, in conjunction with choice during song learning, act as a "filter" selecting song types adapted to local acoustic conditions. This preferential learning of relatively undegraded songs also would result in songs being shared by neighbors because of the close proximity of neighbors relative to other conspecific singers. Close proximity would result in less degradation in perceived songs and these would, therefore, be learned preferentially. This is supported by a field study showing that the ca 32 songs learned by each Carolina Wren (range = 17–42 [Chu 1979], 25–43 [Simp-

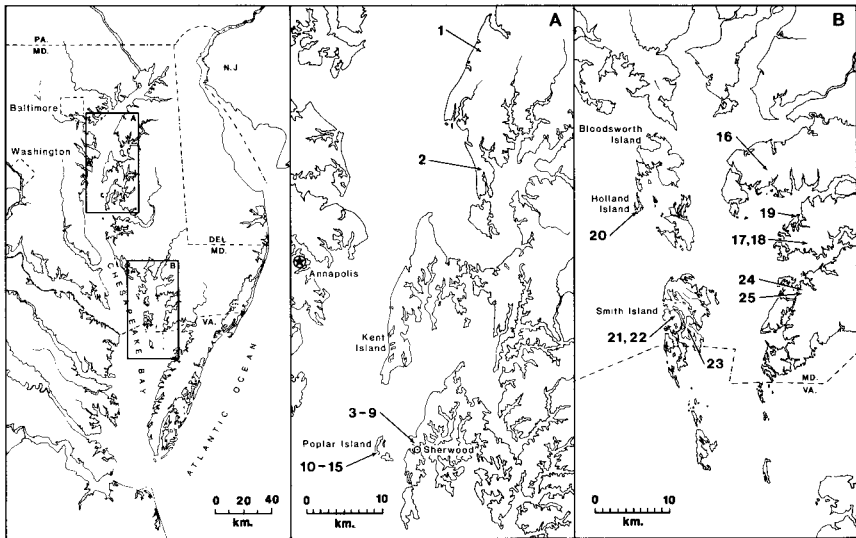[1] National Zoological Park, Smithsonian Institution, Washington, D.C. 20008.

FIG. 1. Map of the Chesapeake Bay study area with enlargements (A and B) showing locations of the 25 male Carolina Wrens whose song types were analyzed.

son 1985]) are chiefly those that degrade less (when tape recordings are played and recorded 50 m away) in their native habitat than in foreign habitats (Gish and Morton 1981).

Although we can predict the basis upon which an individual learns particular song types, we know little about the larger distribution of song types in Carolina Wrens. Over how large an area does a particular song type occur? Are song types grouped geographically or is each distributed independently? Here we describe the effects of isolation, either by distance or water barriers, on the geographic distribution of Carolina Wren song types and on the extent to which they are shared by males separated to various degrees. This provides a base from which to compare naturally occurring song sharing with data from a laboratory experiment on the effects of degradation on songs learned (Morton et al. 1986).

STUDY AREA AND METHODS

The study was conducted at seven sites along a 145-km transect on the Eastern Shore of Maryland and four adjacent islands (Poplar, Smith [two adjacent islands], and Holland) in the Chesapeake Bay (Fig. 1). Carolina Wrens repeat an unvarying song type many times before switching to another song type (Kroodsma 1977). We call each continuous repetition of a song type a bout (="song series" of Borror 1956). We recorded bouts of song from 25 male wrens at 11 sites from March through August, using a Uher 4000 Report IC tape recorder (19.05 cm/sec recording speed) and Dan Gibson EPM model P-200 parabolic microphone.

Earlier, we determined that a minimum of 60 bouts is usually needed to guarantee that a complete repertoire has been recorded (Chu 1979). Many males, especially young ones (Simpson 1984), however, cycle through their repertoires in fewer than 60 bouts. For example, a captive male, recorded continuously for three days, reached asymptote after 45 bouts were recorded (his repertoire consisted of 27 song types). Thus, we feel that we obtained full repertoires for all of the birds for which we obtained 60 or more bouts (64% of sample), as well as most of the remaining birds sampled (number of bouts sampled per male ranged from 35 to 139 with a mean of 75).

Approximately 10 songs from each bout were recorded and analyzed. We recorded the songs of one individual at a time over one or more days. The birds were not banded, but previous work has shown that this species is sedentary and defends the same territory year-round (Morton and Shalter 1977). Morton (unpubl. data) found no territory changes among males in a color-banded population over three years (see also Simpson 1985, p. 794). Thus, our focus on one male on the same territory over a short period of time would adequately ensure that the same individual was recorded each day.

Spectrograms of songs from each male were made with a Kay Elemetrics Corp. Type 7029A sound spectrograph using the FL-1 circuit, 300 Hz "wideband" filter setting and the 80–8000 Hz analyzing range. The song consists of identical repeated syllables each composed of a variable number of elements (examples of spectrograms are found in Borror 1956, Richards 1981, Gish and Morton 1981). As the song is not complex, we were able to classify songs as the same or different based upon examination of spectrograms. When comparing one song with another the criteria used for assessing their similarity were (1) element-for-element matching, (2) approximate or exact correspondence in frequency (Hz), and (3) duration of a syllable (terms follow Gish and Morton 1981). Spectrograms of all songs and their classification are in Chu (1979). The following quantitative measures were taken for each song type: number of elements per syllable, highest and lowest frequency (kHz), syllable duration (msec), and intersyllable interval (msec). These measures were used to compare unusually widespread song types with those having a more limited distribution.

We first recorded the song repertoires of the entire wren population (6 males) on Poplar Island for comparison with wrens at the closest mainland site, a distance of 3 km. For this island-mainland comparison, we recorded 7 mainland males on adjacent territories along a 3-km transect perpendicular to the mainland to island axis. This protocol was repeated for comparisons with the two Smith Islands and Holland Island and their nearest mainlands. Only one or two wrens occurred on these islands, however, so we emphasize the Poplar Island-mainland comparison. In addition, song-type sharing was calculated within and among all sites.

Sharing is expressed as the average percentage of the song repertoire shared between two individuals. Thus if male 1 shares 60% of its song types with male 2 and male 2 shares 50% of its song types with male 1, they share an average of 55%. Site comparisons were based on similarity in composition of the pooled song types from any two localities.

Distances between recording sites were measured from a map as the shortest land distance for mainland to mainland comparisons. For island to mainland comparisons, the distance from the island to the nearest mainland was summed with the shortest land distance between this landfall and the mainland site of interest.

RESULTS

We recorded 1812 song bouts and identified 309 song types from the 25 males. The mean repertoire consisted of 29.0 ± 6.8 song types [SD] (range = 17–42). Using only birds for which 60 bouts or more were obtained (N = 16), the mean repertoire size was 32.4 song types (median =

TABLE 1

NUMBER OF SONG TYPES SHARED AMONG CAROLINA WRENS AT POPLAR ISLAND (6 MALES)
AND THE CLOSEST MAINLAND (7 MALES)

Bird no.[a]	No. in population sharing song types[b]						Song types shared/total in repertoire	% shared
	2	3	4	5	6	7		
Poplar Island								
10	4	3	8	10	8		33/36	92
11	3	3	6	11	8		31/31	100
12	0	1	3	6	8		18/19	95
13	2	5	6	10	8		31/32	97
14	0	4	1	7	8		20/20	100
15	5	2	8	11	8		34/36	94
Mainland								
3	2	1	4	2	10	4	23/23	100
4	3	3	2	4	11	4	27/35	77
5	3	1	2	0	7	4	17/17	100
6	6	3	4	4	12	4	33/34	97
7	2	3	2	2	13	4	26/26	100
8	5	2	1	4	12	4	28/29	97
9	7	2	2	4	13	4	33/34	100

[a] Same number and location of the bird as in Fig. 1.
[b] For example, bird 10 had four songs shared with one other population member, three songs shared with two, etc.

32, range = 19–42). The mean repertoire size for birds for which less than 60 bouts were recorded (N = 9) was 23.0, which was also the median value (range = 17–29). These values are comparable to data from North Carolina (Simpson 1985).

The percentage of repertoires shared by males holding adjacent territories averaged 64.3% (males 3–9), 64.8% (males 17, 18), 64.2% (males 24, 25) for 3 mainland sites, and 68.9% (males 10–15) for Poplar Island. The extent of song sharing among males within two sites, Poplar Island and the mainland adjacent to Poplar Island, is given in Table 1. From 95–96% of the pooled song types for each site occur in the repertoires of two or more males at that site. Thus, while a group of males having contiguous territorial boundaries share about 64–69% on average of their repertoires of song types (range = 49.5–89.5%) in pairwise comparisons, the likelihood of a given song type occurring among at least two males in a small population of males at the same site (only some of which have contiguous territories) is much greater. Thus, immediate neighbors may share fewer song types than is possible, indicating a possible preference for learning some songs not the repertoire of contiguous neighbors (Morton et al. 1986).
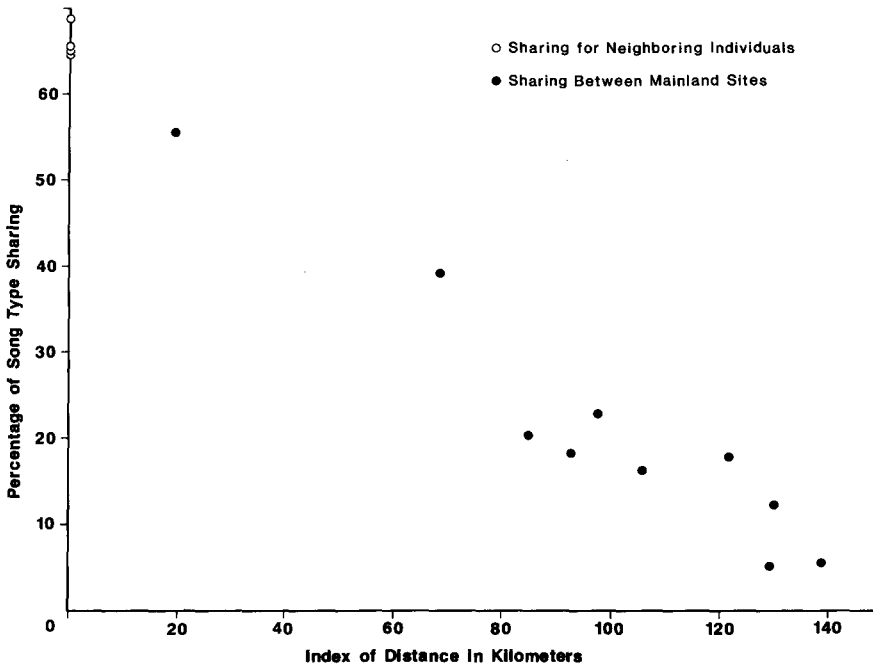
FIG. 2. Song sharing in percentage between neighboring individuals at the same site (open circles) and between mainland sites with no water barriers separating them (closed circles), as a function of distance separating them.

There was a highly significant negative correlation between distance and the percentage of song types shared ($r = -0.98$, $P < 0.001$) (Fig. 2). Removing males on adjacent territories (0 distance in Fig. 2) from the analysis still results in a highly significant negative correlation ($r = -0.95$, $P < 0.001$). In contrast, sites separated by water (island to mainland and island to island comparisons, $r = -0.21$ and $r = -0.04$, respectively, $P > 0.1$ for both) show no correlation with distance and percentage song sharing (Fig. 3).

The distribution of the 309 song types was highly skewed (Table 2); most (242, 78.3%) were found at only one site. Most (95%) of these unique song types were found in the repertoire of at least two birds at the site. Although there was no difference between wrens at the island and mainland sites in the uniqueness of their repertoires ($\chi^2 = 8.6$, df $= 6$, $P > 0.1$), it was our impression that island-inhabiting birds had more atypical songs. For example, the only song in our sample that was clearly mimicked (a Pine Warbler [*Dendroica pinus*]) was sung by two wrens on Poplar Island.
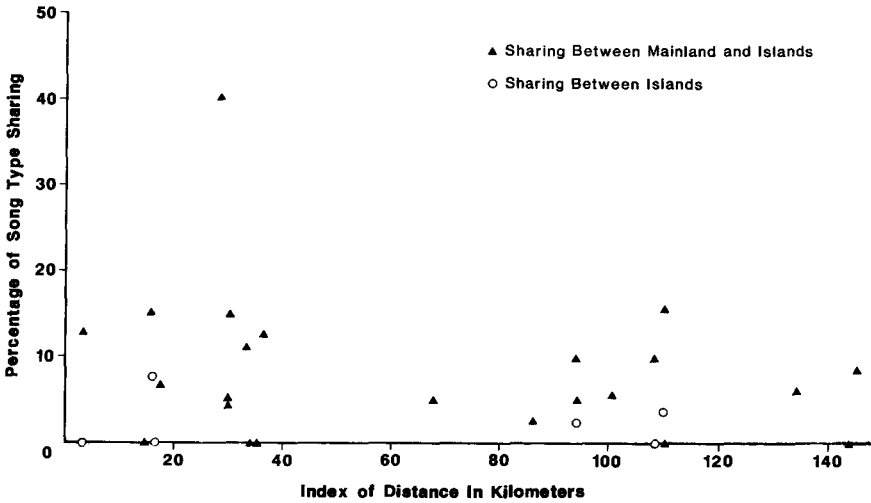
FIG. 3. Percentage song sharing between sites separated by water barriers as a function of distance separating them.

DISCUSSION

Song-type distribution. — The distribution of song types we observed for the Carolina Wren is similar to that reported for other species of oscines with repertoires. For example, Bitterbaum and Baptista (1979) examined syllable repertoires of male House Finches (*Carpodacus mexicanus*) up to 5-km apart and found a significant negative correlation (−0.95) between the extent of syllable sharing and distance. Kroodsma (1974) suggested a similar relationship for Bewick's Wrens (*Thryomanes bewickii*) up to about 6-km apart. In sedentary species, especially those occupying permanent territories such as the Carolina Wren, geographic isolation appears to be equivalent to acoustic isolation. That is, in our study, a water barrier sufficient to keep birds at two sites from hearing one another resulted in a divergence of song types similar to that noted in males a much greater distance apart on mainland sites with continuous populations.

The extent of song sharing between wrens on islands and mainland sites indicates that a water barrier reduces, but does not completely prevent dispersal (Table 2). The percentage of sharing between wrens on Poplar Island and the adjacent mainland, 3-km distant, was 12.4%; equivalent to wrens separated by 145 km on continuous mainland sites. One mainland individual (Table 1, No. 4), however, had 8 song types not found in the repertoires of any of the other mainland males. Of these, 3 were found only in Poplar Island males, indicating probable emigration from the island to the adjacent mainland.

TABLE 2

SONG-TYPE SHARING BETWEEN SITES FOR 309 TOTAL SONG TYPES AT FOUR ISLAND AND
SEVEN MAINLAND SITES

Song type found at:	Number types	%
One site	242	78
Mainland	116	38
Island	126	41
Two sites	39	13
Mainland	11	4
Island	8	3
Both	20	7
Three sites	16	5
Mainland	3	1
One mainland and two island	3	1
Two mainland and one island	10	3
Four sites	6	2
Three mainland and one island	5	2
Two mainland and two island	1	<1
Five sites	2	1
Three mainland and two island	1	<1
Four mainland and one island	1	<1
Six sites	3	1
Four mainland and two island	3	1
Seven sites	1	<1
Five mainland and two island	1	<1

The sharing of song types is an indicator of continuity or connectivity between individuals in a population. Individuals in disjunct or separated populations are expected to share song types only if an exchange of individuals has occurred at some time in the past. As adult Carolina Wrens are sedentary, this exchange likely is due to natal dispersal. Song learning takes place during the first 3 months of life (Helgeson 1980, Morton et al. 1986). Adults do not add new song types even if they are artificially moved to sites where they interact with live songsters using different songs (Morton et al. 1986). Thus dispersing juveniles can carry song types learned before dispersal to new areas. Still, most song types (242 or 78% of the total sample of 309) were restricted to single sites. In contrast, four types (1%) were found nearly everywhere (Table 2); this cannot be accounted for by the natal dispersal argument.

There is no obvious morphological similarity in the widespread song types that might correlate with their broad distribution (Chu 1979, Table

TABLE 3

MEASUREMENTS (MEAN ± SD) OF THE FOUR WIDESPREAD SONG TYPES COMPARED TO THE
SAME MEASURES ON THE REMAINING SAMPLE (305 SONG TYPES)

Song type[a]	Elements per syllable	Highest frequency (kHz)	Lowest frequency (kHz)	Syllable duration (msec)	Intersyllable duration (msec)	Freq. range (kHz)	N
18	5.2 ± 0.7	6.0 ± 0.4	1.6 ± 0.2	334 ± 18	53 ± 7	4.3 ± 0.5	12
35	4.2 ± 0.5	5.4 ± 0.7	1.9 ± 0.1	222 ± 25	43 ± 11	3.5 ± 0.6	12
50	4.8 ± 0.8	5.0 ± 0.5	1.3 ± 0.1	320 ± 39	46 ± 13	3.7 ± 0.5	15
67	3.9 ± 0.6	5.3 ± 0.5	1.5 ± 0.2	207 ± 23	46 ± 10	3.8 ± 0.5	15
$\bar{x}$[b]	4.6 ± 0.8	5.4 ± 0.6	1.6 ± 0.3	276 ± 70[d]	48 ± 11[d]	3.9 ± 0.6	54
$\bar{y}$[c]	4.8 ± 0.2	5.5 ± 0.2	1.6 ± 0.1	333 ± 74	59 ± 23	3.9 ± 0.2	679

[a] Refers to the number assigned to song types in Chu (1979).
[b] Means for the four widespread song types, calculated from the entire sample of 54 song examples rather than as the mean of the four means.
[c] Refers to the means for the 679 song examples of the remaining 305 song types.
[d] Significantly different from the grand mean ($\bar{y}$) using a one-tailed *t*-test, $P < 0.0005$. The remaining values do not differ.

3). Syllable duration and intersyllable intervals in our four most wide-spread songs, however, are significantly shorter than the rest of the sample (Table 3). Perhaps these songs are widespread because they suffer little degradation in many habitats (Gish and Morton 1981). If Northern Mockingbirds (*Mimus polyglottus*) mimic these preferentially, Carolina Wrens might learn them. This might explain how these songs reach the islands so readily since mockingbirds regularly leave the islands in the winter and return to them in the spring (pers. obs.).

The distribution of song types in Carolina Wrens indicates a tendency for songs to be restricted to a single site, akin to dialects, but some (22%) songs are widespread to varying degrees. A small percentage of the song types (1% in this study) were found at all sites. Songs shared between individuals at different sites likely result from natal dispersal. Still, the restricted geographic range of most song types indicates a strong tendency for males to copy songs from others, with whom, after natal dispersal, they will compete territorially.

Song sharing among neighbors. — The advantage of sharing songs with neighbors has been discussed elsewhere (Shy and Morton 1986, Morton 1982, 1986). Morton et al. (1986) showed that 4 naive young wrens preferentially learn undegraded songs, acquiring repertoires largely consisting of such songs (71–89%). Undegraded song is equivalent to neighbor song, as mentioned above (see also McGregor and Krebs 1984, Shy and Morton 1986). If 71–89% of a wren's song repertoire results from an innate predisposition to learn undegraded songs, then a bird with an

average repertoire size of 32 song types is predicted to learn from 23 to 28 songs from neighbors and from 4 to 9 song types from nonneighbors. These latter song types would either be unique to the individual (i.e., learned at its natal site and not found in its breeding site or through mimicry of other species) or not shared with immediate neighbors.

If the average preference for undegraded songs of 80% found by Morton et al. (1986) is multiplied by the total number of song types noted in the present study, 309, we obtain a value of 247. This is the number of song types that should be limited to immediate neighbors and, therefore, to one site. As we reported above, 242 of the 309 song types were restricted to one site, only 2% different from the predicted value. In other words, our site ("population") data may be explained at the level of individual birds exposed only to song types heard from different distances (i.e., more or less degraded). Thus, data showing that 78% of the song types are restricted to a single site may be the result of individual interactions among birds within hearing distance of one another. An alternate idea, that site-restricted songs serve to restrict gene flow (e.g., Baker 1975), has not been tested.

The ranging hypothesis (Morton 1986) predicts that the extent to which song types are shared will increase with increased neighborhood stability. With such stability there will be less selective pressure favoring the acquisition of unshared song types. This prediction is testable because the Carolina Wren ranges into warmer climates where the large, unpredictable, winter die offs found in our Maryland study site do not occur (Morton and Shalter 1977).

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