

THE ECOLOGY OF SONG IMPROVISATION AS ILLUSTRATED BY NORTH AMERICAN SEDGE WRENS

DONALD E. KROODSMA,^{1,3} WAN-CHUN LIU,¹ ELIJAH GOODWIN,¹ AND PAUL A. BEDELL²

¹Department of Biology, University of Massachusetts, Amherst, Massachusetts 01003, USA; and

²10120 Silverleaf Terrace, Richmond, Virginia 23236, USA

ABSTRACT.—Can the diverse styles of song development in songbirds be understood in an evolutionary context? Are song imitation and song improvisation strategies that evolved in identifiable ecological circumstances? Differences among *Cistothorus* wrens suggested that song imitation was used in stable, resident populations by Marsh Wrens (*Cistothorus palustris*), but that song improvisation evolved in the more nomadic populations of North American Sedge Wrens (*C. platensis*). Toward understanding this seemingly unique strategy of improvisation by North American Sedge Wrens, we reexamined song development in the laboratory and singing behavior and population movements among free-ranging males. Nestling Sedge Wrens were collected in North Dakota and during their first year of life tutored with 10 Sedge Wren song types; throughout the experiment, males were in adjacent cages and could both hear and see each other. Songs of the laboratory birds were not close imitations of songs from the training tape or immediate neighbors; rather, songs were either improvised (different from but most likely derived from training songs) or invented (no similarity to other songs in their environment). In nature, males at a Nebraska site also had unique song repertoires, a pattern that is consistent with the improvisational mode of song development. Our field surveys also verified that Sedge Wren populations are highly mobile, arriving at or departing from breeding sites at seemingly odd times of the summer breeding season. These data, together with evidence of song imitation among sedentary populations of Sedge Wrens in Central and South America, reinforce the idea that song improvisation among North American Sedge Wrens is a developmental strategy. Because songs are improvised, each male is unique, but songs do not vary geographically; hence, it seems likely that males and females can communicate with one another no matter where they find themselves in the geographic range of the species. Received 30 January 1998, accepted 14 August 1998.

WHEN THE BEHAVIORS of closely related species differ in some fundamental way, we expect that close examination of life histories will help us understand how these species' differences have evolved. Mating systems, for example, can be related to the distribution of resources (Crook 1964, Verner 1964). Foraging behaviors and cognitive abilities differ as a consequence of prey distribution and abundance (Balda et al. 1996). Among songbird species, we expect song repertoire sizes to be related to some life-history factor, such as the intensity of sexual selection (Catchpole 1980) or the density of singing competitors (Kroodsma 1983). Duetting occurs more frequently among birds that are resident and paired year-round, as in the tropics (Farabaugh 1982), and song dialects must have some ecological basis (Baker and Cunningham 1985). Perhaps overproduction of song during development is related to migratory habits

(Nelson et al. 1996). Other aspects of development, too, must be related to some fundamental features of life histories (Catchpole and Slatyer 1995, Kroodsma 1996).

In this comparative framework, the apparent differences between two North American *Cistothorus* wrens, as reported by Kroodsma and Verner (1978), have become even more intriguing. The three male Sedge Wrens (*Cistothorus platensis*) in that study imitated few songs from a training tape; instead, they produced a sizeable repertoire of seemingly normal songs, most of which were apparently "improvised" (i.e. different, but probably derived from the training songs) or "invented" (different from all songs in the training environment; see Marler and Peters 1982 for definition of terms). Marsh Wrens (*C. palustris*), in contrast, had imitated details of many songs from the same training tape (Kroodsma and Pickert 1984a). In nature, territorial male Marsh Wrens countersing with similar songs (see especially Verner 1976), but neighboring Sedge Wrens were re-

³ E-mail: kroodsma@bio.umass.edu

ported to have repertoires of dissimilar songs, so that males could not countersing with like songs (Kroodsma and Verner 1978). The proposed explanation for these differences lay in the seemingly unpredictable population movements characteristic of Sedge Wrens. Specifically, by developing generalized, species-typical songs, males would have functional songs anywhere throughout the geographic range of the species. In contrast, Marsh Wrens were more site faithful, and neighborhoods were therefore more stable, so that imitated songs could be used in countersinging duels with familiar neighbors (Kroodsma 1979).

Additional data have accentuated the apparent uniqueness of the North American Sedge Wren (Kroodsma and Verner 1978). In a variety of experiments since that early report, Marsh Wrens have consistently learned details of songs from either tutor tapes or live tutors (Kroodsma 1978, 1979, 1986; Kroodsma and Pickert 1980, 1984b; Kroodsma and Canady 1985; Brenowitz et al. 1995). Furthermore, in Central and South American populations of Sedge Wrens, most of which are believed to be sedentary, neighboring males share many song types and sometimes even countersing like North American Marsh Wrens, thus revealing that Sedge Wrens in these populations do imitate the details of songs from their neighbors (Kroodsma et al. 1999). The contrast thus intensified between the apparent song-improvising populations of the North American Sedge Wren and the song-imitating populations of other *Cistothorus*, including the endemic *C. meridae* in Venezuela (Kroodsma, Muradian, and Salas, unpubl. data). Consequently, questions and doubts arose. For example, could North American Sedge Wrens really be that different from those elsewhere? If young Sedge Wrens were provided with a simple training tape, as opposed to the more complex one used by Kroodsma and Verner (1978), might North American Sedge Wrens not also imitate like the Marsh Wren? Or, if provided with social partners, might they not imitate from those live birds? In the field, perhaps additional study of song variation among free-ranging, neighboring males, in another population, would reveal sharing of songs, thus implicating vocal imitation.

Because of the heightened contrast between song development and singing behavior of

North American Sedge Wrens and other *Cistothorus* populations, we attempted to replicate and extend the conclusions of the earlier study (Kroodsma and Verner 1978). We obtained 20 Sedge Wrens in North Dakota (not Michigan, as in the earlier study), and during their first year of life exposed them repeatedly to 10 different Sedge Wren song types from a training tape (not 67 song types, only 9 of which were normal Sedge Wren songs). To increase the likelihood that males would reveal any tendency to imitate, we paired males in adjacent cages so that neighboring males could interact socially and learn from each other. Under these circumstances, Marsh Wrens would routinely learn all 10 and only those 10 song types (see Kroodsma 1979, Brenowitz et al. 1995). To reassess whether neighboring males shared songs, we also recorded birds in a local population in Nebraska (not Illinois). Last, to monitor population movements, we used a small army of volunteer birdwatchers; our goal was to try to learn more about the wrens' seemingly unpredictable population movements both within and between years. In the end, our results largely confirmed those of the earlier study: North American Sedge Wrens do improvise their songs, modifying in a variety of ways the songs that they hear in their environment; consequently, Sedge Wren songs are like snowflakes in that each song conforms to a general pattern, but no two of them are alike. This developmental style does seem well adapted to the highly mobile populations that were again documented throughout much of the breeding range.

METHODS

Song development in the laboratory.—The Sedge Wrens used in this study were obtained as nestlings at two sites in North Dakota on 2 July 1996. One nest (seven nestlings) was collected at Lonetree Wildlife Management Area near Harvey, Wells County. Two additional nests (13 nestlings, with 7 in one nest and 6 in the other) were collected at the J. Clark Salyer National Wildlife Refuge near Upham, McHenry County. Permission to collect was granted by both the North Dakota Game and Fish Department and the United States Fish and Wildlife Service. On the day nestlings were obtained, they were transported back to Massachusetts, where they were housed under permit 128.96SCB granted by the Massachusetts Division of Fish and Wildlife.

Each nest was placed into a single cage (30 × 40 × 50 cm), and nestlings were fed a modified "Lanyon

diet" during the nestling stage and a slightly less protein-rich diet after weaning (see Kroodsma and Verner 1978). As birds began to feed on their own, each was placed into its own cage. Initially, we maintained the nestlings on 15 h of daylight, which was reduced to 11 h over an eight-week period during October and November 1996. During late January 1997, we began increasing the daylength back to 15 h, again over an eight-week period.

To improve our chances of detecting song imitation, we housed all birds in the same room. Although any laboratory setting is highly artificial, we wanted a seminatural situation in which birds of both sexes could hear and see each other. Housing them together in a large aviary was not possible, because wrens are highly aggressive and undoubtedly would have killed each other. Young males were identified by their slightly larger size and their subsong, and during the spring of 1997, as they were beginning to sing, eight of the males were paired with another male, and the two males in each pair were placed in adjacent cages facing one another. If the young birds did not learn from the training tape, we felt that this arrangement would increase the probability that young birds would at least imitate each other. Song imitation could thus be achieved either by learning directly from the tutor tape, or by learning from the other males in the room, especially from the immediately neighboring male.

When young birds were about 20 days old, we began playing them a tutor tape of Sedge Wren songs recorded at the Jack Sinn Wildlife Area near Ceresco, Lancaster County, Nebraska. It seemed acceptable to use songs from a location other than where birds were collected, because previous surveys of Sedge Wren songs had revealed no geographic variation (Kroodsma and Verner 1978) and because other songbirds readily imitate songs even of different subspecies (e.g. Baptista 1974). The tutor tape contained 10 different song types in a natural sequence of 43 songs delivered during 3 min and 25 s, repeated as follows: 1, 2, 1, 2, 3, 2, 3, 3, 3, 3, 4, 3, 4, 4, 5, 4, 5, 5, 4, 5, 6, 7, 6, 5, 7, 6, 8, 8, 8, 8, 8, 8, 8, 9, 9, 9, 9, 10, 9, 10, 10. Thus, some song types were heard only twice in this sequence (1, 7), and others were heard as many as seven times (3, 8); some were heard with up to five renditions in succession (3, 8, 9), but others were heard only as alternated with other types. This sequence was played to the birds repeatedly, typically 16 times a day, over a 60-day period from July to September of their hatching year. The next spring, as the birds began to sing, we again played this sequence of songs in an attempt to maximize the probability that the birds would learn from the tape. Exposure to the songs was extensive, and during the first fall, when sensitive periods of songbirds typically occur, each song type was heard 2,000 to 7,000 times (which is well beyond the number required for imitation in other songbird species; e.g. Hultsch and

Todt 1989, Peters et al. 1992). Because we found no effect of the frequency of exposure to the different song types, we do not discuss this issue further.

We tape-recorded the birds during their first spring (1997 tapes 101 to 200 and 401 to 474 in the Kroodsma collection). We placed Shure or Realistic condenser microphones in front of each cage, and during 45 to 90 min, usually beginning when the lights first turned on in the room, we used Nakamichi tape decks to record onto Maxell MS-90 studio cassette tapes. Song was highly plastic during the autumn of the hatching year and early the next spring, but 8 of the 11 males eventually produced "crystallized" adult song. We stopped tape recording in early May 1997, when we felt that we had sufficient samples from the males.

To estimate the size of each male's song repertoire, we first printed hundreds of sonograms for each male (Kay Elemetrics DSP 5500 analyzer; 2 to 10 kHz, filter bandwidth analogous to 300 Hz). Each song typically consisted of a few normal introductory notes followed by a "trill" of repeated syllables, and we focused on the trill syllables in our song classification. We next measured the syllable period for each sonogram (i.e. the time from beginning of one syllable to the beginning of the next), and then arranged all the sonograms of a given male by their syllable periods. Each sonogram was then compared to others in a range of similar syllable periods, and we grouped sonograms that we felt represented the same song type. When a male sang a given song type, he typically sang several renditions of that type over a minute or so, and we counted each of those sequences as a single, independent occurrence of that song type. Typically, hundreds of songs of other types and tens of minutes would intervene before that same song type would be introduced again. The number of these independent occurrences, or "bouts," was determined for each song type in the sample, and an estimator of "sample coverage" was then calculated (1 - number of song types occurring only "once" in the sample / total number of "bouts" in the sample). As more bouts are sampled, the number of song types occurring only once typically declines, thus resulting in a higher sample coverage. The number of song types in a sample divided by the sample coverage yields an estimate of the total number of song types in a male's repertoire (see Canady et al. 1984).

To determine the source of the songs that each male developed, we first selected a distinctive subset of the 10 tutor songs. The syllable periods in the trills of the 10 tutor songs were 60, 67, 87, 87, 109, 125, 125, 136, 146, and 149 msec. Because syllables with longer periods are more complex and have more distinctive features, we chose to study most carefully the five tutor songs with the longest syllable periods. We next took each song type from six laboratory-reared males who were paired off with another singing

TABLE 1. Eight male Sedge Wrens improvised large repertoire sizes (E). Repertoire sizes are estimated from the formula $E = B/D$, where $D = 1 - C/A$, and D is an estimator of sample coverage, or the fraction of the male's song repertoire that has been revealed in the sample. Males 1 and 2, 3 and 4, and 5 and 6 were paired with each other in adjacent cages; males 7 and 8 were paired with other males for whom we could not estimate repertoire size.^a

Bird	(A) ^b Total bouts sam- pled	(B) No. song types in sam- ple	(C) No. song types occur- ing only once	(D) Sample cover- age	(E)	
					Esti- mated reper- toire size	No. song types >130 msec ^c
1	70	41	17	0.76	54	25
2	53	26	6	0.89	29	15
3	56	31	12	0.79	39	14
4	59	31	8	0.86	36	6
5	75	43	18	0.76	57	28
6	193	48	2	0.99	49	29
7	102	41	9	0.91	45	— ^d
8	106	50	22	0.79	63	—

^a Testes of two additional birds (9 and 10) were relatively small when birds were sacrificed at the end of the experiment, and their songs were not sufficiently stable for us to estimate song repertoires. Another bird (11) sang relatively little, and we did not attempt to determine his repertoire.

^b A bout is defined as an independent occurrence of a given song type (see text).

^c The sample of songs (with syllable periods >130 msec) that was used to compare songs of these males to songs of each other and of the tutor tape.

^d Because males 7 and 8 were not paired with another singing male, we did not compare their songs to the songs of other males; hence, we did not partition their repertoire into songs with briefer or longer syllable periods.

male (males 1 to 6; Table 1) and compared these song types with each of those five distinctive tutor songs. Each male's song was rated 1, 2, or 3 (with occasional intermediate ratings estimated to the nearest quarter point, e.g. 1.25, 1.50, 1.75), depending on the quality of the match with the tutor song: 1, nearly perfect match, and clearly imitated from the tutor song; 2, songs somewhat similar, with the male's song sharing enough features with the tutor song so that one could imagine how the male improvised upon the tutor song to derive his own song; and 3, male's song unlike any tutor song. Although we initially used all song types developed by the males, our final comparisons are based only on those song types with the longer syllable periods (see Table 1). Using the same rating system, we next compared the songs of each of the six males with the songs of the other five males. We again selected the more distinctive songs in each male's repertoire and compared only those songs with syllable periods >130 msec. We tried to be consistent in our comparisons. Initially, three of

us (Goodwin, Kroodsma, and Soares; see Acknowledgments) worked together to develop an appropriate way of comparing songs; Goodwin then finished the laboratory comparisons.

Singing behavior of free-ranging males.—We complemented our laboratory approach with an analysis of the singing behavior of free-ranging males at the Nebraska field site. During 11 to 13 July 1995, we intensively recorded two neighboring males (A and B) and then obtained smaller samples from several other males nearby (within ca. 500 m). To make these recordings (1995 tapes 73 to 79 in the Kroodsma collection), we used a Sony TC-D5ProII cassette recorder with a Sennheiser ME62 microphone mounted in a Dan Gibson parabola.

We estimated song repertoires for the A and B males from Nebraska as follows. First, for 60 min of recordings from each male, we made sonograms of all songs. We then sorted all 813 songs of male A and 670 songs of male B into different song types. Because many song types occurred in only one sequence in our initial sample, we realized that our samples were not adequate for estimating song repertoires. We therefore augmented this initial sample as follows. The syllable periods for the initial song types ranged from 46 to 161 msec, but we chose to focus on song types with longer syllable periods (>130 msec). In additional recordings from these two birds (about 85 min for male A, 30 min for male B), we searched on the spectrum analyzer for examples of all song types with these larger syllable periods. With this augmented sample in hand, we then used simple proportions to estimate how the sample of songs with shorter syllable periods would have changed if we had increased that sample, too (see Results). After calculating the estimator of sample coverage, we could then estimate the repertoire size of these two males.

To determine the amount of song sharing among neighboring Sedge Wrens at the Nebraska site, we again focused on those detail-rich song types with syllable periods >130 msec. We first compared those portions of the song repertoire from males A and B and then searched the smaller samples from other birds in the area for matches with the songs of males A and B.

Population surveys.—To monitor population movements of Sedge Wrens in North America, we enlisted the aid of numerous volunteers, most of them members of the Cornell Laboratory of Ornithology or the American Birding Association, or both (see Acknowledgments). Volunteers were asked to visit a convenient field site every 10 days or so throughout the breeding season and estimate the number of singing birds that they heard during a standard visit of 10 to 15 min. We were especially interested in documenting the first arrival and the final departure of wrens at each location, as well as any dramatic change in numbers throughout the season. It was

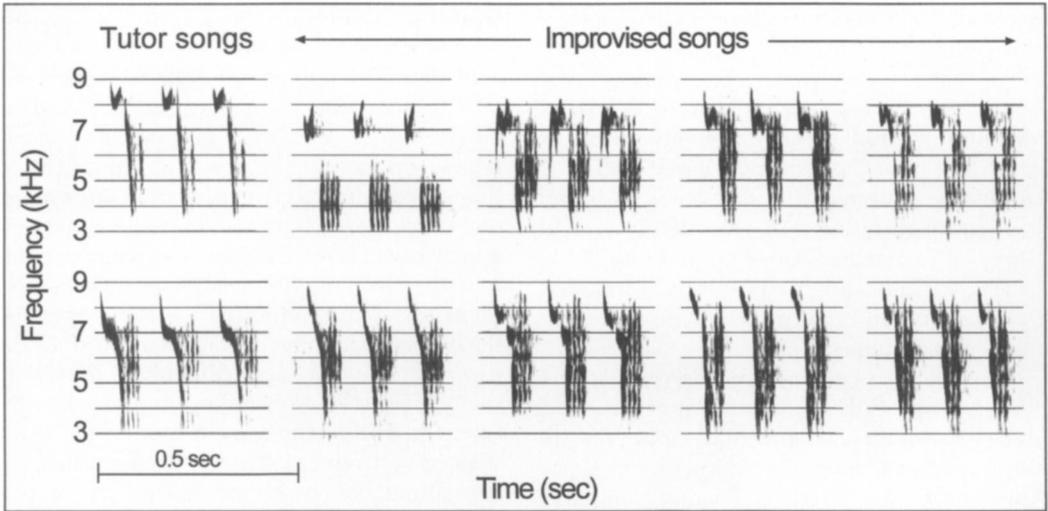


FIG. 1. Sedge Wrens from North America improvise songs. Each song is about 1.5 s in duration and consists of two to four introductory notes and a trill of repeated syllables; here are displayed only three trill syllables from each song. On the left are sonograms of 2 of 10 tutor songs heard by laboratory-reared males; on the right are the syllable portions of four song types that we classified as improvisations of the tutor song on the left. Tutor songs are numbers 3 (top) and 5 (bottom; see Methods), and all improvisations are from the songs of male 1 (see Table 1).

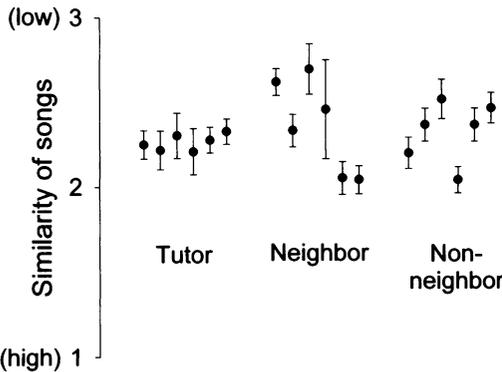


FIG. 2. The songs developed by six laboratory-reared Sedge Wrens were consistently poor copies of the tape-tutor songs (average rating, 2.2 to 2.3) but were usually better copies than of the songs of singing neighbors or non-neighbors. Within each subset of the figure, mean and standard error for males 1 to 6 are given from left to right. Best copies, though still only improvisations (mean rating = 2.0), were by neighboring males 5 and 6 of each other. Because only six songs were included in this analysis for male 4 (Table 1), the relatively high match (mean = 2.0) of his songs to those of non-neighbors could be an artifact of the small sample.

hoped that this range-wide monitoring might reveal birds departing from some locations as they arrived at others.

RESULTS

VOCAL BEHAVIOR

We first describe how young males in the laboratory developed their songs. For comparison, we then describe repertoires and song sharing among singing males at our Nebraska field site. Last, we summarize the results of our field survey of Sedge Wren populations.

Song development in the laboratory.—The song repertoire size of male Sedge Wrens ranged from 29 to 63 and was thus considerably larger than 10, the number of types heard from the training tapes (Table 1). Clearly, unlike the Marsh Wren’s approach to this same task (see Brenowitz et al. 1995), the males did not acquire their song repertoires by simply imitating the 10 songs from the training tape.

A comparison of each male’s songs with the songs from the training tapes showed poor imitation, but extensive improvisation (Figs. 1 and 2). All together, males 1 to 6 developed 117 song types with syllable periods >130 msec (Table 1), but we rated only two of those songs

as reasonable imitations of a song on the tutor tape (rating 1.25 for each song). Another seven songs that were similar to the training songs were rated 1.75. For another 52 of the 117 songs, we felt we could identify the tutor song on which the improvisation was based (rating of 2), but the source of the remaining 56 songs was less clear (rating >2). Overall, the average rating for each male's songs ranged from 2.2 to 2.3 (Fig. 2), indicating that the typical song was a poor imitation but a probable improvisation based on the tutor songs.

Males did not converge extensively on each others' songs (Fig. 2), again suggesting that precise imitation of singing males is not the primary mode of song development for North American Sedge Wrens. When we compared each of the 117 songs with songs of the immediate neighbor, we rated 100 songs as improvisations (rating 2) or worse (rating >2). Of the 17 songs that most closely matched the songs of neighbors, not one was a perfect match, but seven were fairly good copies (rating 1.25). The other 10 songs (four with rating 1.5, six with rating 1.75) also suggested that males could have derived some of their songs from each other. Males 5 and 6 accounted for 15 of these 17 relatively close matches and were the two neighbors who had the largest number of songs with syllable periods >130 msec (Table 1); but again, most of their 57 songs were, at best, rated as improvisations (rating ≥ 2). Males who were not immediate neighbors had less influence on each other; only 10 songs of non-neighbors had a rating of <2 .

Whether the tutor tape or the immediate singing neighbor had more influence on song development seemed to differ among birds (Fig. 2). For birds 1 to 4, the songs that each male acquired were more like the tutor songs than like the songs of the immediate neighbor. For example, 18 of the 25 songs that we evaluated for male 1 were rated as more similar to a tutor song than to a neighbor's song, and only four were rated as more similar to the neighbor's song (two-tailed sign test, $P = 0.004$). The trend for males 2 to 4 was similar (male 2, $P = 0.18$; male 3, $P = 0.04$; male 4, $P = 0.38$). In contrast, for birds 5 and 6, most songs were more like the songs of the neighbor than like the tutor tape (male 5, $P = 0.08$; male 6, $P = 0.002$). This pair of males probably derived their rela-

tively large repertoires by improvising on each other's songs.

In these developmental data, we tend to report trends rather than rigorous statistical analyses. Trends seem more appropriate, because the comparison of songs was so subjective; although we tried to be consistent in our ratings, our effort was a continual guessing game as to which features of the songs to compare and how the birds might have derived their songs. More important, although we could establish the observed number of songs with various ratings, we found it more difficult to determine the "expected" number of songs for each rating category. For example, even though the males seemed to produce better copies (i.e. rating <2) from immediate neighbors than from the tutor tape (9 total "copies" from tape, 17 from neighbors), one cannot conclude that social partners are a better source of songs than a training tape. The difficulty with this conclusion is that the more songs that two individuals improvise from the same training tape, the more likely it is that some of those independent improvisations will, by chance, be like one another. For three of the males (1, 3, 4), for example, the average rating of songs showed that their songs tended to be more similar to the songs of non-neighbors than to songs of neighbors (Fig. 2). The pool of songs from the four non-neighbors was much larger than the pool of the one neighbor's songs, however, so one cannot be sure if songs of non-neighbors were similar because the two males influenced each other, or because each male independently improvised a similar song based on the training tape.

Singing behavior of free-ranging males.—The song repertoire sizes of the free-living males in Nebraska were far larger, and therefore more difficult to estimate, than were those of the laboratory-reared males. In 60 min, for example, male A sang 105 different song types in 813 songs. On average, 6.2 renditions of a song type occurred on each occasion (i.e. in a bout) that it was used. Among the 105 song types in this initial sample, 82 occurred in only one bout, indicating that the male had a much larger repertoire that included song types we had not yet recorded. Similarly, for male B we recorded 96 song types in our initial sample, but 81 of them occurred only once.

Using our augmented sample of songs with syllable periods >130 msec, we continued to

discover new song types for males A and B. In 45 additional bouts, male A revealed 24 new types, making a total of 54 song types with syllable periods >130 msec. Using simple proportions, we calculated that in our tape-recorded sample of about 1,700 songs, male A sang 189 different song types (54 with syllable period >130 msec, 135 <130 msec), but 112 of those occurred only once. Using our estimator of sample coverage (Table 1), we calculated that we had recorded only about 59% of male A's total song repertoire. For male B, an additional 13 bouts of songs with syllable periods >130 msec revealed only three new song types. We estimated that male B sang 128 song types in our sample of 973 recorded songs, but 69 of those song types occurred only once; sample coverage was again low, about 58%. Dividing the total song types in the sample by the estimator of sample coverage yields a total song repertoire estimate of 320 types for male A and 220 types for male B, but the relatively low sample coverage for both males reduces our confidence in the accuracy of these estimates.

As in the laboratory, our comparisons of the song types used by these neighboring males in Nebraska revealed little song sharing. We first compared male B's 28 song types with syllable periods >130 msec with the songs of his immediate neighbor, male A. If birds A and B had had identical repertoires, we would have expected about 17 of those 28 songs to be found in our incomplete sample of bird A's repertoire (sample coverage of male A was 59%; $0.59 \times 28 = 17$). Only two songs were matched at less than 2, however (both at 1.75); the other 26 were rated 2 or higher ($\bar{x} = 2.2$). Another 20 song types with syllable periods >130 msec were recorded from six other males near males A and B. When we compared those songs with the songs of males A and B, we found a similarly low level of sharing (rating of 2.2 compared with songs of male A, 2.3 with male B). Thus, the similarity of songs among neighboring males in nature (2.2 to 2.3) was comparable to the similarity found between tutor songs and the songs of laboratory-reared males (2.2 to 2.3) and between songs of laboratory-reared males and their immediate neighbors (2.0 to 2.7). Neither our laboratory data nor our field data revealed evidence of accurate song imitation.

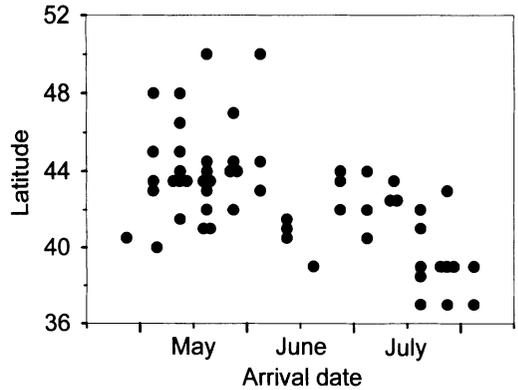


FIG. 3. Arrival date of Sedge Wrens at breeding sites. Most arrive slightly later at more northern latitudes; unlike other songbirds, Sedge Wrens continue to arrive in mid and southern latitudes from mid-June into August. Each disc represents the arrival date at a particular field site monitored by volunteers.

POPULATION SURVEYS

The data collected by our field volunteers reconfirm the Sedge Wren's reputation as a rather sporadic and unpredictable breeder (Fig. 3). In northern provinces and states, birds tend to arrive in May and depart in August or September, but in the more southern locations, birds more typically arrive in mid-July or even later. At some locations in any province or state, however, birds may be present one year but absent the next, or they may arrive or depart at times of the year that are atypical for other songbirds.

Here we summarize, by province and state, the primary observations of our volunteers. Interpreting presence and absence in such a survey must be done with some care. When birds are breeding, males sing throughout the day and, often, the night, so breeding birds are easily detected. Absence of singing means either that the birds are truly absent or, if they are present, that they are no longer breeding (i.e. the males do not have additional breeding opportunities and hence do not sing); quiet fall birds are difficult to observe.

Manitoba.—Birds typically arrive during mid-May and leave by mid-September, based on a survey from 1970 to 1995, mostly at the Oak Hammock Marsh near Winnipeg (Rudolf Koes). For 19 of 25 years, birds arrived during the 2nd and 3rd weeks of May; for 11 of 19 years, birds departed in the 2nd and 3rd weeks

of September, although birds had been seen as late as the third week of October. Our two Manitoba surveys at Balmoral during 1994 and 1995 were consistent with this pattern. Another observer described these wrens as "unpredictable," failing "to find them in the same location . . . two years in a row" (Mary Krueger, near Gretna).

North Dakota.—According to Stewart (1975), the peak of breeding is mid-June to early August. In our survey, wrens typically arrived in early to mid-May; singing stopped by August, but some birds were seen into mid-October. During 1994 to 1996, North Dakota received more than normal precipitation, and Sedge Wrens were especially abundant.

Minnesota.—At most sites, wrens arrived during May and departed during August or early September, but were seen as late as the 2nd week of October (Jon Little). At St. Paul Park in Dakota County, however, during both 1995 and 1996, birds did not inhabit reestablished prairie until late June or early July, apparently breeding throughout July and August; birds shifted locally, too, during late summer as uplands dried out (Tom Bell). Overall, the bulk of migration occurs during mid- to late May and mid- to late September (Janssen 1987).

Wisconsin.—Wrens typically arrive in May and are last seen in August. At two sites, however, arrivals were in midseason, during July; one location was an upland field in the southwestern part of the state, the other a restored prairie in Dane County. During 1997, the wrens appeared on 31 July at a site where they had not been during 1995 or 1996, and they were seen through September (Vernon County, John A. Shillinglaw). Sedge Wrens in Wisconsin sing through July and become quiet in August, long after most other passerines have become quiet (Robbins 1991).

Michigan.—Wrens typically arrive during mid-May and depart in mid-August, according to the volunteer surveys and to 20 years of records from Arcadia, Manistee County (Keith Westphal). Additionally, at Houghton Lake, Roscommon County, arrival dates were the 3rd week of May in 1993, the 1st week of May in 1994, and the 2nd week of May in 1995 (Michael Petrucha). When most songbirds have become silent during August, Sedge Wrens often remain persistent singers, even throughout the night; songs have been heard at dawn as late as

22 October (Walkinshaw 1935; see also Brewer et al. 1991).

South Dakota.—Status apparently differs by region. In the southeastern corner of the state, wrens arrive in early to mid-May. They are opportunistic, leaving a flooded area during May and recolonizing that site during July, then singing and presumably breeding throughout August. They have been observed during migration until the 3rd week of October (see Peterson 1995). In the south-central part of state, however, during a period of 25 years, singing males have never been heard before 20 July at LaCreek National Wildlife Refuge, Bennett County (Richard C. Rosche).

Nebraska.—Sedge Wren populations apparently are highly responsive to rainfall; 1995 was "the weirdest year ever." Wrens arrived in May and were everywhere, undoubtedly because 1995 was a very wet year (Gary Lingle, Hall County). Wrens were heard from the 2nd week of May to the 3rd week of June near Ames, Dodge County (Janis Paseka). More typically, many populations are late-season nesters, arriving during July or August (see Lingle and Bedell 1989, Bedell 1996).

Iowa.—Arrival and departure depends on annual and local conditions. In some areas, arrivals are typically late summer; at Shenandoah (Page County), for example, 11 of 15 annual first sightings ranged from the 3rd week of July to the 4th week of August, with records of singing males as late as the 4th week of August and the 1st week of September (Jean B. Braley). In other areas, such as Zirbel Slough (Cerro Cordo County), birds were present from May through August. At several locations, use of habitat shifted during the season. Our survey data are typical for Iowa (Jackson et al. 1996).

Illinois.—Similar to the situation in Iowa, arrival and departure are dependent on annual and local conditions. During a wet 1995 spring, for example, birds appeared at Carlock (McLean County) early in spring where they typically had not appeared until August in other years (Thomas A. Marquardt). Late arrivals, from mid-June to mid-July, are typical of several sites in Boone, Lee, Ogle, Iroquois, and Jasper counties.

Indiana.—Arrival and departure dates are variable. Sedge Wrens are present earlier in the summer in northern Indiana (LaPorte, Starke, and Fulton counties) but arrived in late July at

a more southern site in Jackson County for two consecutive years.

Ohio.—No surveys conducted. The occurrence of Sedge Wrens is sporadic; most nestings occur in late July and August (Trautman and Trautman 1968). Breeding can begin in mid-May or mid-July, with young fledging as late as the 3rd week of September. Wrens seldom occupy the same nesting areas in two consecutive years (Peterjohn 1989).

Kansas.—Sedge Wrens arrive in mid- to late July most years and appear to breed in late summer, although the single breeding record documented in the state was in the 1st week of September (D. Rintoul pers. comm., Schwillig 1982, Thompson and Ely 1992). Field data from 1992 to 1997 for the Breeding Bird Atlas show that the breeding range is primarily in northeastern Kansas, but some years wrens are also found in the southeastern and central parts of the state (W. Busby pers. comm.). Birds are opportunistic: 1995 was wet and atypical, and observers had more June sightings on 1995 BBS routes than during 1966 to 1992 combined (Paul Bedell, Chris Smith, Dave Rintoul). In our survey, birds also arrived during July and August (e.g. 3rd week of July 1995 in Baldwin City, Douglas County, Cal Cink; and at Konza Prairie, Riley County, Dave Rintoul; 4th week of July, Perry Lake and Valley Falls, Jefferson County, Dan LaShelle).

Missouri.—Sedge Wrens are typical late-season nesters. In all six surveys, wrens arrived in mid-July or later (Boone, Franklin, and Newton counties; see Robbins and Easterla 1992). Reports before 15 July are concentrated in the northwestern part of state, but after 15 July, birds seem to be distributed throughout the state, especially in the glaciated and osage plains (based on data for the Missouri Breeding Bird Atlas, Brad Jacobs); numbers of singing males continue to increase until mid-August (Robbins and Easterla 1992).

Kentucky.—Sedge Wrens are late-season nesters, with young fledging as late as 9 October. Spring migrants during April and May, but all confirmed breeding records are later, mostly in July and August. Wrens seldom nest in any one area for more than a year or two (Palmer-Ball 1996).

Elsewhere.—The Sedge Wren is unpredictable elsewhere in its range, too. In Arkansas, for example, wrens arrived in rice fields during July

and had nestlings as late as the 2nd week of September (Meanley 1952). In New York, the Sedge Wren numbers fluctuate with the water table, and territories can also be established late (e.g. into July; Andrlé and Carroll 1988), as also occurs in Vermont (Laughlin and Kibbe 1985).

DISCUSSION

Given the same kind of experimental training, male Marsh Wrens and Sedge Wrens in North America develop their song repertoires differently. Marsh Wrens faithfully imitate songs from their tutor environment. In nature, for example, a New England male has a repertoire of about 50 different song types, but if he hears only five songs in his laboratory environment, he will learn only five or six (Brenowitz et al. 1995). If he hears nine, however, he will learn nine (Kroodsma 1979), or if he hears 45, he will develop a sizeable repertoire of about 40 songs (Brenowitz et al. 1995). Other experiments, too, have repeatedly revealed how Marsh Wrens copy the details of songs to which they are exposed (Kroodsma and Pickert 1980, 1984a, 1984b; Kroodsma 1981, 1986).

Male Sedge Wrens approach this developmental task differently. When exposed to 10 song types, they do not imitate those 10 types. Instead, they generate a far larger song repertoire, apparently based largely on improvisations of the songs that they have heard. Although a few of the developed songs in this study were fairly good matches to the tutor songs, perhaps comparable to what Marsh Wrens would do, the vast majority were only "somewhat similar." For many of those new songs, one could imagine how a given tutor song might have been modified to produce the song of the young wren, but other songs appeared to be outright "inventions," bearing no resemblance to any of the tutor songs (for discussion of terms, see Marler and Peters 1982). Even those inventions, however, fell within the considerable range of variation that one encounters among free-ranging Sedge Wrens. The young Sedge Wren thus appears to take songs that he hears, and then modifies them in subtle to striking ways, thereby generating a considerable repertoire size of seemingly normal Sedge Wren songs.

The developmental scenario for these two

wren species, as determined in the laboratory, is consistent with patterns of microgeographic variation of song in nature. Male Marsh Wrens on neighboring territories share large portions of their song repertoires, especially where males remain at or return faithfully to the same breeding site year after year (e.g. Verner 1976; see also Kroodsma and Verner 1997). Such song sharing among songbirds (Kroodsma and Konishi 1991) can occur only when males imitate their large song repertoires from one another. Sedge Wrens, however, share few song types with either immediate neighbors or more distant individuals. In a previous study (Kroodsma and Verner 1978), neighboring male Sedge Wrens in Illinois were estimated to share about 5% of their song types with each other. In our Nebraska sample, we used a different approach, but again found few songs among neighboring males that we considered good imitations. Although such a geographic distribution of song types could arise by song imitation and then considerable dispersal from the site of learning, so that both birds and their imitated songs were dispersed widely in space, our laboratory studies suggest otherwise. Dispersal movements of Sedge Wrens undoubtedly help to disperse both individuals and their songs, but the laboratory studies reveal that it is their improvising and inventing style of song development that is the primary cause of both the highly individualistic nature of Sedge Wren repertoires and the low song sharing among neighboring and more distant individuals.

To what extent might these conclusions be distorted because the developmental studies were done in the highly artificial laboratory environment? This issue is important, because natural social conditions simply cannot be simulated in the laboratory, and absolute statements about song development must be made cautiously (Beecher 1996, Kroodsma 1996, Baptista and Gaunt 1997, Payne and Payne 1997). Critical here, we believe, is that our conclusions are based largely on a comparison of how males of two closely related species respond to essentially the same developmental environment. For both wren species, males were housed in separate cages in the same room, with females present in adjacent cages, so that birds could see and hear each other. In this setting, male Marsh Wrens have repeatedly re-

sponded to a tape-tutored, small song repertoire of conspecific songs by imitating only those songs, but male Sedge Wrens responded very differently, by improvising or inventing a much larger song repertoire than was heard. In a previous experiment, male Sedge Wrens also improvised their songs, based on hearing a diverse array of 67 different songs, only nine of which were normal Sedge Wren songs. Marsh Wrens hearing the same tape imitated many songs (Kroodsma and Pickert 1984a). The difference between species in the response to learning opportunities is consistent and striking, thus revealing a non-subtle difference in how males of these two wrens face their developmental task.

Also important to consider is how young Sedge Wrens might respond to adult social tutors in a laboratory setting. If a young male were paired with an adult singer during his first two to three months of life, for example, would the young male learn extensively or even exclusively from that male? In other species, including the Marsh Wren (Kroodsma 1978, Kroodsma and Pickert 1984b), social tutoring by adults can certainly enhance learning (Pepperberg 1985, Baptista and Gaunt 1997; but see Nelson 1997), or can even enable learning when tape-tutoring was insufficient (see Zann 1997). For two reasons, we do not believe that adult social tutoring would have made a major difference in our overall conclusions. First, for species in which adult social tutoring is required for song development, as with the Zebra Finch (*Taeniopygia guttata*), songs of young birds are abnormal in the absence of such social tutoring (e.g. Clayton 1988, Slater et al. 1988, Bohner 1990). The songs of our Sedge Wrens, however, seem to be entirely normal and instantly recognizable as Sedge Wren songs, thus indicating that adult social tutoring is not essential for normal song development. Second, these young wrens served as their own reciprocal social tutors, and we would have expected them to learn from each other if social interactions were important in song development. Young male Black-capped Chickadees (*Poecile atricapillus*), for example, do not learn well from tape recordings, but they do learn from each other in a social setting, so that cohorts within a group converge on the same abnormal songs (Shackleton and Ratcliffe 1993, Kroodsma et al. 1995). The songs of neighbor-

ing Sedge Wrens in our developmental study, however, were not especially similar; song repertoires of individuals did not significantly converge on one another, and they remained highly individualistic. Overall, then, we do not believe that using adult social tutors would significantly change the basic conclusion of our study: i.e. young male Sedge Wrens improvise rather than imitate their songs.

This unusual form of song development by North American Sedge Wrens occurs in a correspondingly unique ecological context. Throughout their North American range, these wrens occur in moist meadows and grasslands, the suitability of which is highly dependent upon rainfall (e.g. Wiens 1974, Rotenberry and Wiens 1991, Rotenberry et al. 1995). Both within and among years, these wrens appear highly opportunistic, taking advantage of habitat as it becomes available from May to as late as October. During May, migrants arrive in the appropriately moist locations, especially throughout the northern part of the breeding range. During midseason, however, after birds have had sufficient time to raise one brood, considerable shifting of breeding territories seems to occur. This shifting of territories can occur on a local scale, such as within a field, as birds seem to track a moisture gradient. But the shifts can also be non-local, as birds arrive in geographic areas where they had not yet occurred that year.

Exactly what strategies Sedge Wrens use in making these movements is unknown. One possibility is that they can somehow monitor local conditions and then use first whatever second breeding opportunities occur locally. Alternatively, individuals of some populations may be preprogrammed to fly considerable distances (see Gwinner 1977), taking the first leg of the southward migratory journey before making a second breeding attempt. Such individuals might arrive, then, in the southern parts of the geographic range, such as Missouri, Kansas, or southern Indiana.

These opportunistic movements, which must lead to considerable mixing of populations, could have coevolved with the Sedge Wren's unique mode of song development. Because males probably never have the same countersinging neighbor for more than one breeding attempt, selection for precise imitation of neighbors must be absent, or at least relaxed

(unlike what occurs in the Marsh Wren; see Verner 1976). Instead, each Sedge Wren seems to follow some inborn rules as he improvises his own large set of songs, thereby generating a unique but large song repertoire of "typical" Sedge Wren songs. With considerable movements of individuals, the populations of this monotypic species (AOU 1957) must be relatively homogeneous genetically, and male Sedge Wrens everywhere must therefore use the same improvisational program to generate their songs. Females, too, would share the essence of this song program, so that they could decode the behaviors of the males. As a consequence of the population movements and the style of song development, neighboring male Sedge Wrens in nature have songs no more like one another than like more distant males. By maximizing individual variation in their large song repertoires, these wrens have actually minimized geographic variation, thereby enabling communication among Sedge Wrens irrespective of their population of origin.

Unpublished data from other populations of *Cistothorus* wrens in Central and South America suggest that the improvising nature of the North American Sedge Wren is truly unique and adapted to its semi-nomadic life style. In *Cistothorus meridae*, an endemic in the Andes of Venezuela, for example, territorial relationships of males are relatively stable over a few years. Males learn the songs in a given neighborhood and therefore share songs with immediate neighbors such that songs of males only a few kilometers distant are distinctive (Kroodsma, Muradian, and Salas unpubl. data). Even males in sedentary populations of the Sedge Wren, the same species that occurs in North America, imitate. In Costa Rica, for example, neighboring males share many song types with each other, and songs differ between neighboring locations (i.e. "dialects" occur), revealing that imitation must play a key role in song development (Kroodsma et al. 1999). Neighboring males of the sedentary *C. platensis* in the Falkland Islands also share songs with one another (Kroodsma and Woods unpubl. data). Furthermore, neighboring *C. platensis* in Brazil, at Brasilia National Park, were recorded countersinging with like songs (Kroodsma et al. 1999), much like sedentary Marsh Wrens do, especially in western North America (Verner 1976). Sedentary Sedge Wrens

in Central and South America thus seem to develop their songs more like North American Marsh Wrens than like their conspecific, but semi-nomadic Sedge Wrens.

Conclusions.—We have hope that future studies will reveal an ecological, evolutionary basis for the diverse array of song developmental styles among songbirds. Here, we confirmed that North American Sedge Wrens improvise their songs and that songs of free-ranging males are diverse and dissimilar. Like snowflakes, songs are apparently constructed based on a set of design rules, but within those prescribed limits the diversity seems almost infinite. Such a developmental style seems well adapted to a semi-nomadic life style, in which song neighborhoods are unstable and males (and females) from extensive areas of the geographic range must be able to communicate with a large song repertoire that conforms to a common vocal code. The contrast is striking between this song-improvising developmental style of the North American Sedge Wren and the song-imitating style of apparently all other *Cistothorus* populations (even other Sedge Wren populations), all of which appear to be more sedentary or site faithful. Among songbirds, perhaps site fidelity promotes imitation, and neighborhood instability either reduces selection for imitation or actually promotes improvisation; whether or not this rule is general among songbirds must await other studies that search for ecological correlates of song developmental styles.

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