

SONG VARIATION AMONG *CISTOTHORUS* WRENS, WITH A FOCUS ON THE MÉRIDA WREN

DONALD E. KROODSMA^{1,4}, KRISTA WILDA^{1,5}, VIVIANA SALAS² AND ROLDAN MURADIAN^{3,6}

¹Department of Biology, University of Massachusetts, Amherst, MA 01003

²Sociedad Conservacionista Audubon de Venezuela, Apdo. 80.450, Caracas 1080-A, Venezuela

³Departamento de Biología de Organismos, Universidad Simón Bolívar, Caracas, Venezuela

Abstract. Evidence from two *Cistothorus* wrens (*C. palustris*, *C. platensis*) has suggested that repertoire size increases with population density and that song imitators are more likely to be site faithful than are song improvisers. We tested these two ideas on a third species, *C. meridae*, an endemic to the Venezuelan Andes. Of the three *Cistothorus* wrens, song repertoire sizes of male Mérida Wrens are the smallest, ranging from 18 to 27 song types per male; Mérida Wrens are also most likely to repeat each type several times before switching to a new type. Density of Mérida Wrens was also lowest, from 0.4 to 2.0 territories per 10 ha. These wrens are highly site faithful, with marked microgeographic song variation. Female Mérida Wrens also sing. Overall, data from the Mérida Wren support the ideas that, among *Cistothorus* wrens, song reper-

toire sizes increase with population density and site faithfulness promotes song imitation.

Key words: *Cistothorus*, dialect, repertoire, song, Venezuela, vocalization, wren.

Variación en el Canto en *Cistothorus*, con Énfasis en *C. meridae*

Resumen. La evidencia proveniente de dos especies del género *Cistothorus* (*C. palustris*, *C. platensis*) sugiere que el tamaño del repertorio aumenta con la densidad poblacional y que los imitadores de cantos tienen una mayor probabilidad de ser territoriales que los que improvisan. Estas dos ideas fueron probadas en una tercera especie endémica de los Andes venezolanos, *C. meridae*. El tamaño del repertorio del canto de esta especie, con 18 a 27 tipos de canto por macho, es el más pequeño de estas tres especies. *C. meridae* también tiene una mayor probabilidad de repetir cada tipo de canto varias veces antes de cambiar a un tipo nuevo. La densidad de *C. meridae* también fue la menor, con 0.4 a 2.0 territorios por cada 10 hectáreas. *C. meridae* es muy territorial, con una marcada variación microgeográfica en las cantos. Las hembras de esta especie también cantan. En resumen, estos datos apoyan las ideas de que en el género *Cistothorus*, el tamaño del repertorio del canto aumenta con la densidad

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⁴ E-mail: kroodsma@bio.umass.edu

⁵ Present address: P.O. Box 349, El Prado, NM 87529.

⁶ Present address: Universitat Autònoma de Barcelona, Departament d'economia i d'Història Econòmica, Edifici B, 08193 Bellaterra, Barcelona, Spain.

poblacional y que la territorialidad promueve la imitación de cantos.

Cistothorus wrens have provided support for two general ideas about the evolution of vocal variation in songbirds. One idea is that male song repertoire size increases with population density and the intensity of interactions among neighboring males (Kroodsmas 1999). Among North American wrens, the density of Marsh Wrens (*C. palustris*) and Sedge Wrens (*C. platensis*) is high, for example, and repertoire sizes are relatively large, too, numbering well over 100 songs per male for both Sedge Wrens and western Marsh Wrens (Verner 1976, Kroodsmas 1977, Kroodsmas and Verner 1978, Kroodsmas, Liu et al. 1999). The trend among Marsh Wren populations is also consistent with this proposed relationship (Kroodsmas and Verner 1987). The second idea relates the style of song development to population stability. Males in sedentary or site-faithful populations of both species tend to imitate each other, whereas males of the less site-faithful, North American populations of the Sedge Wren largely improvise their songs (Kroodsmas and Verner 1978, Kroodsmas, Liu et al. 1999, Kroodsmas, Sánchez et al. 1999).

These two ideas have emerged from many studies on other species (Catchpole 1980, Baker and Cunningham 1985, Beecher 1996), but are still best treated as hypotheses to be falsified by studying additional species. Among *Cistothorus* wrens, one good test species is the Mérida Wren (*C. meridae*), an endemic to the páramo in the Andes Mountains of Venezuela. This highly differentiated species provides a good test regardless of the phylogenetic history of the *Cistothorus* wrens (which is unknown), because the two properties in question, repertoire size and developmental style, vary even among populations of currently described *Cistothorus* species.

To test these ideas, we studied the Mérida Wren at three locations in the Venezuelan Andes, between 1995 and 1997. We color-banded birds and then collected basic information on their biology, including four key items: territory size, song repertoire size, site fidelity, and the extent of microgeographic song variation (as an index of whether birds imitate).

METHODS

Fieldwork was accomplished during two main periods. The first was 14–19 August 1995, when we searched for the Mérida Wren at several locations in the state of Mérida, Venezuela, along the road from Santo Domingo to Apartaderos, and from Apartaderos to Pico El Aguila towards Piñango in the Sierra de la Culata National Park. Despite considerable searching using song playback, we heard only one male sing briefly at the Hotel Los Frailes (8°49'N, 70°47'W; 3000 m) and only one pair near Lake Mucubaji (8°48'N, 70°50'W; 3600 m). In contrast, the wren appeared to be relatively abundant in appropriate habitat above El Aguila (8°51'N, 70°50'W; 4100 m); beginning about 5 km from El Aguila on the road towards Piñango, we found the wrens along the road and especially in the valleys toward the east. During this 1995 trip, we color-banded the one male at Mucubaji and 12 males at the El Aguila

site and tape-recorded songs at both sites. Males were identified by abundant song, aggressive response to playback, and occasionally by presence of cloacal protuberance.

We resumed fieldwork almost two years later, from 26 May through 8 June 1997. Wrens in the Los Frailes population were more active than they had been in 1995, so we focused on the more convenient Los Frailes birds, color-banding 11 and extensively tape-recording and observing several pairs. Birds sang spontaneously, but we occasionally played back songs of the local population to stimulate singing; we detected no differences in songs recorded under the two conditions. To census these wrens, colleagues David W. Stemple and Gustavo Rodriguez also used song playback about six months later, during 15–18 January 1998.

The habitats at El Aguila and Los Frailes were considerably different, given the 1100-m difference in elevation (for details, see van der Hammen and Clef 1986). At El Aguila, the habitat is a transition zone between the upper bunchgrass páramo and lower superpáramo; dominant plants are the large rosettes *Espeletia timontensis* and *E. moritziana*. The Los Frailes habitat is shrubpáramo, dominated by a different rosette, *E. schultzii*, and more heavily vegetated than the higher elevation. The more sparse vegetation at El Aguila undoubtedly accounted for the larger territories there, too.

We used a variety of equipment to tape-record the wrens. Recorders were the Sony ProWalkman WMD6, Sony TC-D5 PROII, Marantz PMD222, and Nagra ISDT. Microphones were the Sennheiser MKH816, Dan Gibson parabolas with Sennheiser ME62 and MKH106 microphones, and a Telinga II parabola. We have no reason to believe that differences in our equipment caused any noticeable variation in our analyses.

To analyze the recordings, we used standard techniques to identify song types and estimate repertoire sizes. We first documented the variety of different songs (i.e., song types) that each male sang. We did so by listening to the tapes and monitoring the variety of songs on a Kay Elemetrics DSP 5500 Sona-Graph. We printed one or two complete renditions from each series of a given song type. Later, we assembled all sonograms for each male and sorted them, readily recognizing a discrete number of song types in each male's repertoire. After totaling the number of different song types and the number of series (i.e., bouts) in which they occurred, we could then estimate the sample coverage and the male's total repertoire size for the 10 males from which we had the largest samples (Table 1; see also Canady et al. 1984).

We used two approaches to study geographic variation in the songs. In 1995, after establishing song repertoires for males at the El Aguila site, DEK compared each song type of each male to all of the other songs in the population and to the songs of the one male recorded at Mucubaji, 5 km distant and 500 m lower in elevation. More song sharing occurred within than between locations, but to determine how widespread this song sharing was required a second approach, which involved comparing songs of our El Aguila site with the extensive series of songs recorded in 1997 at

TABLE 1. Estimated song repertoire sizes for Mérida Wrens, from most to least thoroughly sampled males. Mérida Wren repertoire size is small compared with other *Cistothorus* wrens, which have repertoires of nearly 100 to >300 song types.

Male	Number of song bouts in sample ^a	Number of song types in sample (types occurring in only one bout)	Estimated repertoire (sample coverage) ^b
1	78	25 (2)	26 (0.97)
2	114	25 (5)	26 (0.96)
3	45	16 (6)	18 (0.87)
4	44	19 (6)	22 (0.86)
5	52	22 (8)	25 (0.85)
6	53	23 (8)	27 (0.85)
7	28	16 (7)	21 (0.75)
8	40	22 (10)	29 (0.75)
9	39	21 (10)	28 (0.74)
10	16	11 (6)	18 (0.62)

^a A bout is a series of renditions of the same song type.

^b Estimated repertoire size = (number of song types in sample) (sample coverage)⁻¹, where sample coverage is the estimated fraction of the total repertoire that has appeared in the sample, calculated as $1 - (\text{number of types occurring in only one bout} / (\text{number of song bouts in sample}))^{-1}$; see Canady et al. 1984 for details.

the Los Frailes site, again about 5 km distant. We chose for analysis a total of 148 sonagrams, 65 from El Aguila and 83 from Los Frailes. All identifying information on these sonagrams was concealed, and, after mixing them thoroughly, we numbered them from 1 to 148. One of us (KW) then took each of the 148 sonagrams, in turn, and searched the other 147 sonagrams for the best match to that particular song. We then compared the number of songs whose best match was recorded at the same site to the number whose best match was recorded at the distant site.

RESULTS

POPULATIONS

Our surveys revealed that annual survival for these wrens was relatively high and that they were most likely resident the year round. During August 1995, for example, we banded 12 males at our El Aguila study site; almost two years later, during June 1997, four of five males that we saw in our core study area were banded. We cannot be certain that the other banded wrens were absent, because all wrens were relatively unresponsive to playback and therefore difficult to find. At Los Frailes, from May–June 1997 to January 1998, three pairs remained together and retained their territories; in a fourth pair, the male was present, but his mate had apparently been replaced. The fifth banded pair was not seen, but their territory was not thoroughly checked. Thus, many wrens survived at least two years at our study sites, and they were present during June and August at El Aguila and during January, May–June, and August at Los Frailes.

Territories of these wrens were large and actively defended during all seasons. At El Aguila in 1995, territories were sufficiently large that we rarely heard two males simultaneously. A 2-km stretch of the road spanned only four territories; if territories were in fact 500 m across, the total area per territory would be roughly 25 ha. Territory sizes seemed smaller in the

more lushly vegetated valleys at El Aguila, but we did not estimate territory sizes there. At our lower elevation site, at Los Frailes in 1997, we could often hear two birds singing simultaneously, and territory sizes were clearly smaller. In one roughly 20-ha portion of the study area were four territories, an average territory size of about 5 ha. Territory sizes are clearly many times larger than are the territories of grassland or marsh-dwelling *Cistothorus* wrens in North America, for whom territories are typically only a fraction of a hectare (Kroodsma and Verner 1997).

SOCIAL SYSTEM

In each territory we found what appeared to be an adult male and an adult female. They typically foraged close together, and they also displayed jointly, perching within a meter of each other, each throwing its head back, opening the bill wide, and vocalizing vigorously. When not singing, the male and female often foraged together, typically within several meters of one another. Apparently to maintain contact, each individual would occasionally utter a few brief contact calls (Fig. 1L); if they had become separated by 10 m or more, one bird would often fly to join the other and the pair would then display jointly.

In about half of the intensively observed territories at Los Frailes, during late May and early June 1997, we found a "third bird" that was clearly associated with the adults. This extra bird sang either like an adult female, sometimes displaying jointly with the pair, or else sang imperfect songs typical of what young males of other species are capable of producing between 3 and 9 months of age (e.g., Kroodsma 1974). Sometimes the three birds displayed close together, as a trio, and all three birds typically roosted in the same nest overnight. At other times, however, this third bird foraged separate from the other two; it would occasionally call (Fig. 1L), and the pair would respond with like calls or perhaps even sing. Based on the dispersal

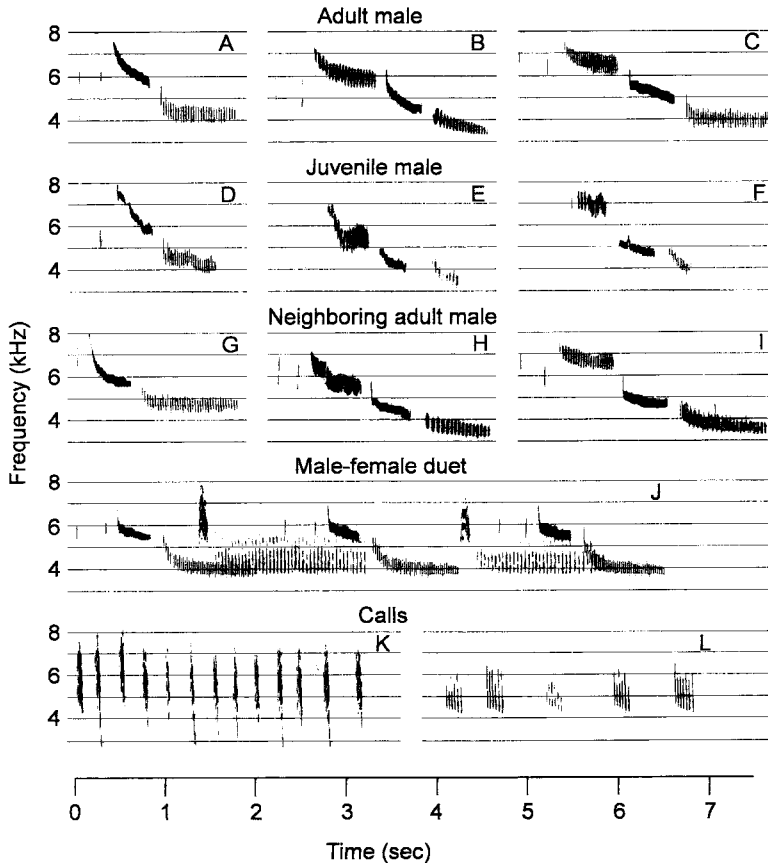


FIGURE 1. Sonograms of Mérida Wren vocalizations, revealing the major features of this wren's vocal behavior. Most male songs are two- (A, D, G; see also male's part of duet in J) or three-parted (B, C, E, F, H, I). In the first three rows, similar songs are in the same column, showing that a juvenile male (D-F) learns the songs of the adult male in his territory (A-C), songs that are similar to other males in the neighborhood (G-I). Females often "sing" with the males (J); illustrated are three identical male songs (like the song in G) and two female songs. Also heard is an aggressive "chubb" note (K) and softer contact calls (L).

behavior of other sedentary Neotropical wrens (E. S. Morton, R. N. Levin, unpubl. data), we believe that these three birds were within their first year of life and that they were simply delaying dispersal from their natal territory.

VOCAL BEHAVIOR

Male songs. A song was typically introduced with nearly inaudible, brief "clicks" that spanned a broad frequency range. After those notes, the male delivered a series of two, three, or less frequently, four discrete whistled or buzzy sounds (Fig. 1A-C, G-I). Most songs consisted of two main components; the first was typically a pure whistle, sweeping down in frequency, and the second was invariably a raspy or buzzy sound, often with discrete pulses. Three-parted songs also ended with raspy or buzzy sounds; the first or second components usually contained only one pure whistle, and at least one (often two) raspy elements.

The males typically sang with eventual variety, repeating one song type many times before switching to another. During natural singing (i.e., no playback), males repeated a given song type relatively few times at dawn, and then gradually, during the first 30-60 min of singing, repeated each type more frequently before switching to the next. One male, for example, was recorded at El Aguila during two long dawn sequences; the numbers of repetitions within each bout for the two mornings were 9, 8, 12, 28, 27, 21, 14, and 14, and 5, 7, 7, 20, 27, and 26. Another male, also at El Aguila during August, sang a series of bouts with the following number of renditions of each song type: 11, 12, 8, 16, 1, 13, 16, 14, 5, 21, 6, 9, 8, (playback here), 29, 27, 26, 10, and 6. Song playback promoted intensive singing (and approach to the playback speaker), with an increase in bout duration. The maximum number of renditions recorded in a bout was 33.

The song repertoire sizes of the Mérida Wren were

relatively small (Table 1), at least for *Cistothorus* wrens. For the six males that we had most thoroughly sampled (by the sample coverage estimator), repertoire sizes ranged from 18 to 27.

Female song. The female song typically consisted of an introductory, raspy sound followed by a trill of simple notes (Fig. 1J). In contrast to male repertoires of 18–27 songs, females used only this simple trill. A female often vocalized simultaneously with, or just before or after, her mate. These exchanges seemed especially frequent and intense at dawn, just after the birds emerged from their roost nest, and after song playback, when both male and female responded intensely to the apparent territorial intrusion. On these occasions, males would often sing three or even four songs back-to-back, often of two or three different song types, and females would contribute two or three songs to the joint display (see Fig. 1J).

Geographic variation. Our initial comparison of songs among the males at the El Aguila study site showed extensive sharing of song types. Two neighboring males (4 and 5 in Table 1) that we recorded thoroughly, for example, shared 17 of the 19 song types (89%) in the repertoire of the male with the smaller repertoire. Song sharing among El Aguila neighbors ranged from 38% to 89% (median 63%), far higher than the amount of song sharing between these neighbors and the one male recorded at Mucubaji, only 5 km distant (range, 13–27%, median 18%).

Our more thorough, blind comparison of songs from El Aguila and Los Frailes also confirmed that neighboring males have songs far more similar to one another than to distant males. In this comparison of 148 songs, 65 from El Aguila and 83 from Los Frailes, we found especially good, paired matches for 63 of the sonagrams. Among these matches, 32 were songs from El Aguila and most closely matched another El Aguila song; 30 songs were from Los Frailes and most closely matched another Los Frailes song. For only one El Aguila song did we find the best match at the Los Frailes site. The probability of this distribution of similar songs occurring by chance is small ($P < 10^{-12}$). Thus, not only do neighboring males share many songs with their immediate neighbors, but songs of males only 5 km distant are considerably different.

Song development. As in other songbirds, the song matching by adult neighbors and the microgeographic variation in songs must occur because males learn the songs of the local breeding population. Our first evidence of this behavior occurred during our August 1995 observations at El Aguila, where we heard two males in advanced stages of plastic song. Songs rambled and were clearly not stable, as successive songs differed from each other considerably. We had only fleeting glimpses of those males, however, and did not know if they were associated with a territorial pair or on their own newly established territory.

Better evidence of vocal learning came from the male we studied during late May and early June 1997 at Los Frailes. He, too, was in the plastic song stage, quietly singing as he foraged some distance (up to 100 m) from the adult pair. When adult males in the area sang, it seemed that this male in plastic song often tried to match the songs he heard, just as the neigh-

boring males often matched song types as they countersang. Many of this male's better efforts were clearly good matches to songs in the neighborhood (Fig. 1A–I).

Other calls. These wrens also used a number of other vocalizations, only one of which was recorded well. The "chubb" call, so named because of its harsh quality, seemed to occur during aggressive encounters, such as when territorial pairs (or trios) encountered each other at territorial boundaries. This call was also heard just after birds emerged from the nest in the morning. Never were we able to identify the sex or age of the calling individual.

DISCUSSION

Two extreme features of the biology of the Mérida Wren support the idea that, among *Cistothorus* wrens, male repertoire size is positively correlated with population density. First, the repertoire size of the Mérida Wren is exceptionally small, averaging about 25 songs per male. In contrast, Sedge Wren males in Costa Rica and North America typically have hundreds of song types in their repertoires (range for seven males, 85 to 330, Kroodsma and Verner 1978, Kroodsma, Liu et al. 1999, Kroodsma, Sánchez et al. 1999). Marsh Wren repertoires are also large, ranging from estimates of 109 to 211 (median 150) for four populations of western North America, down to estimates of 33 to 63 (median 48) in five populations of eastern North America (Kroodsma and Verner 1997).

Second, population density for the Mérida Wren is exceptionally low relative to that of other *Cistothorus* wrens. At El Aguila and Los Frailes, we estimated densities at 0.4 and 2.0 territories per 10 ha. Marsh Wren densities are much greater, with typical densities of 50 to 100 territories per 10 ha (range 4.2 to 1770; Kale 1965, Tintle 1982, review in Kroodsma and Verner 1997). Sedge Wren populations can also be very dense, estimated at 68 and 78 territories per 10 ha in two studies in which Sedge Wrens were the focus (Walkinshaw 1935, Burns 1982; Herkert et al., in press).

Population density appears correlated not only with repertoire size but also with the style of song presentation routinely used by singing males. Among *Cistothorus* wrens, the male Mérida Wren not only has the smallest repertoire but is also most likely to present his repertoire in such a way that successive songs are typically of the same type; only when highly agitated does he sing different song types in succession. Sedge Wrens vary their style of presentation considerably, but they usually alternate song types so that successive songs are different; on occasion, when singing is less intense, they repeat the same type several times before switching to another (Kroodsma and Verner 1978). Among Marsh Wrens, males of especially dense western populations race through their large song repertoires, typically presenting 50 or more song types before repeating any of them. Eastern Marsh Wrens often alternate two or more song types before introducing new types, and in some coastal populations (e.g., North Carolina, Texas), males sometimes sing the same song type several times before switching to another (Kroodsma and Verner 1997). Overall, the data are

consistent with the idea that larger repertoire sizes co-evolved with the behavior of presenting different songs in rapid succession, as might occur between intensely countersinging males on small territories in dense populations (Kroodsma 1999).

The biology of the Mérida Wren is also consistent with a proposed relationship between relative site-fidelity and how young males develop their songs. The adult Mérida Wrens are highly site faithful, if not permanently resident in these populations, and young males in the population apparently learn the songs of local adults. Learning of local songs causes microgeographic differences in songs to accumulate over only a few kilometers. Among *Cistothorus* wrens, then, the Mérida Wren is another site-faithful species that imitates, much like the Marsh Wren and Neotropical Sedge Wrens, but unlike the song-improvising, less site-faithful Sedge Wren of North America (Kroodsma and Verner 1997, Kroodsma, Liu et al. 1999, Kroodsma, Sánchez et al. 1999).

The biology of the Mérida Wren is intriguing in yet another way: the female sings. Her song is far simpler than the male's, but she perches with him high in the vegetation in their joint display. In neither the Sedge nor Marsh Wrens do the females display with the males. New data from a Colombian endemic (*Cistothorus apolinari*), however, reveal that the female also vocalizes in that species as the male sings; her song also consists of repetition of a simple note (P. Caycedo, unpubl. data).

Overall, our data from the Mérida Wren, an endemic to the páramo of the Venezuelan Andes, are consistent with two main ideas on the evolution of vocal variation among *Cistothorus* wrens. The small song repertoires, the eventual variety mode of presenting the repertoire, and the low population density of the Mérida Wren support the idea that song repertoire size and versatile singing (i.e., successive songs more likely to be different) increase with population density. Mérida Wrens are also resident, or at least highly site faithful, and young males learn the local dialect, thus supporting the idea that site-faithful *Cistothorus* wrens are more likely to acquire songs by imitation than are populations that breed more opportunistically, such as the Sedge Wrens of North America.

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LITERATURE CITED

- BAKER, M. C., AND M. A. CUNNINGHAM. 1985. The biology of bird-song dialects. *The Behavioral and Brain Sciences* 8:85-133.
- BEFCHER, M. D. 1996. Birdsong learning in the laboratory and field, p. 61-78. *In* D. E. Kroodsma and E. H. Miller [EDS.], *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, NY.
- BURNS, J. T. 1982. Nests, territories, and reproduction of Sedge Wrens (*Cistothorus platensis*). *Wilson Bulletin* 94:338-349.
- CANADY, R. A., D. E. KROODSMA, AND F. NOTTEBOHM. 1984. Population differences in complexity of a learned skill are correlated with the brain space involved. *Proceedings of the National Academy of Sciences* 81:6232-6234.
- CATCHPOLE, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour* 74: 149-166.
- HERKERT, J., D. E. KROODSMA, AND J. P. GIBBS. *In press*. Sedge Wren (*Cistothorus platensis*). *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia, PA.
- KALE, H. W., II. 1965. Ecology and bioenergetics of the Long-billed Marsh Wren *Telmatorhynchus palustris griseus* (Brewster) in Georgia salt marshes. Publication of the Nuttall Ornithological Club, No. 5, Cambridge, MA.
- KROODSMA, D. E. 1974. Song learning, dialects, and dispersal in the Bewick's Wren. *Zeitschrift für Tierpsychologie* 35:352-380.
- KROODSMA, D. E. 1977. Correlates of song organization among North American wrens. *American Naturalist* 111:995-1008.
- KROODSMA, D. E. 1999. Making ecological sense of song development by songbirds, p. 319-342. *In* M. D. Hauser and M. Konishi [EDS.], *The design of animal communication*. Massachusetts Institute of Technology, Cambridge, MA.
- KROODSMA, D. E., W.-C. LIU, E. GOODWIN, AND P. A. BEDELL. 1999. The ecology of song improvisation as illustrated by North American Sedge Wrens. *Auk* 116:373-386.
- KROODSMA, D. E., J. SÁNCHEZ, D. W. STEMPLE, E. GOODWIN, M. L. DA SILVA, AND J. M. E. VIELLIARD. 1999. Sedentary life style of Neotropical Sedge Wrens promotes song imitation. *Animal Behaviour* 57:855-863.
- KROODSMA, D. E., AND J. VERNER. 1978. Complex singing behaviors among *Cistothorus* wrens. *Auk* 95:703-716.
- KROODSMA, D. E., AND J. VERNER. 1987. Use of song repertoires among Marsh Wren populations. *Auk* 104:63-72.
- KROODSMA, D. E., AND J. VERNER. 1997. Marsh Wren

(*Cistothorus palustris*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 308. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

TINTLE, R. F. 1982. Relationship of multiple nest building to female mate choice in Long-billed Marsh Wrens, *Cistothorus palustris*. M. A. thesis, State University of New York at Stony Brook, Stony Brook, NY.

VAN DER HAMMEN, T., AND A. M. CLEEF. 1986. Development of the high Andean páramo flora and vegetation, p. 153–201. In F. Vuilleumier and M. Monastreio [EDS.], High altitude tropical biogeography. Oxford University Press, Oxford, UK.

VERNER, J. 1976. Complex song repertoire of male Long-billed Marsh Wrens in eastern Washington. Living Bird 14:263–300.

WALKINSHAW, L. H. 1935. Studies of the Short-billed Marsh Wren (*Cistothorus stellaris*) in Michigan. Auk 52:362–369.