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STRUCTURE AND CONTEXT OF FEMALE SONG IN A NORTH-TEMPERATE POPULATION OF HOUSE WRENS

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Abstract.—We describe the structure and context of songs sung by females in a population of House Wrens (*Troglodytes aedon*) in north-central Wyoming. Most females in this population sing at some point during each breeding cycle. The similarity to male songs varied both in the acoustic structure of elements comprising the song and in the tendency to organize the song into the two main sections typical of male songs. To the human ear, female songs ranged from those sounding like a short human squeal to those indistinguishable from complex male songs. Female song occurred primarily when females lost contact with mates in contexts where male and female behavior is usually well-integrated. A female's song appeared to quickly redirect her mate's attention back to herself. Our findings indicate that female song in House Wrens is not restricted to tropical populations as previously suggested.

ESTRUCTURA Y CONTEXTO DE LA CANCIÓN DE UNA POBLACIÓN NORTEÑA DE HEMBRAS DE *TROGLODYTES AEDON*

Sinopsis.—Describimos la estructura y contexto de canciones vocalizadas por hembras de una población de *Troglodytes aedon* localizada en la parte norte-central de Wyoming. La gran mayoría de las hembras de esta población vocalizan durante el ciclo reproductivo. La similitud al canto de los machos varía tanto en la estructura acústica de los elementos que componen la canción, como en la tendencia de organizar el canto en dos secciones principales, que es lo típico en los machos. Para el oído humano, la canción de las aves hembras varía desde patrones complejos indistinguibles de la canción de los machos hasta sonidos parecidos a cortos alaridos de humanos. El canto de las hembras se lleva a cabo particularmente cuando éstas pierden el contacto adecuado con sus parejas, en donde la conducta de la hembra y el macho están bien integradas. Por ejemplo, las hembras cantaron cuando sus parejas interrumpieron el patrón normal de conducta asociado a la copulación. La canción de las hembras parece tener como función el lograr que los machos redirijan su atención nuevamente a éstas. Los hallazgos de este trabajo indican que el canto en las hembras de *T. aedon* no está restringido a poblaciones tropicales.

Females of many species in the family Troglodytidae sing and duet with their mates. However, most of these species are tropical and maintain permanent territories and prolonged pair-bonds in which mates remain together for more than one breeding season (Farabaugh 1982). The House Wren (*Troglodytes aedon*) has both migratory, temperate-zone populations in which pair-bonds are seasonal, and tropical populations with long-term pair-bonds and permanent territories (Drilling and Thompson 1988, Freed 1987, Kendeigh 1941). Singing by female House Wrens has been reported only in tropical populations (Chapman 1929, Farabaugh 1982, Kendeigh 1941, Skutch 1953). Farabaugh (1982) interpreted this as evidence that permanent territories and long-term pair-bonds select for the development of song in female birds. We studied a north-temperate House Wren population in which many females sing. Here we describe the structure and context of female songs in this population.

METHODS

We studied wrens from 1985 through 1989 at the Helen Brinton Bird Reserve on the Quarter-circle A Ranch and Reverse E4 Ranch 5 km S of Big Horn, Sheridan Co., Wyoming, USA.

We made most observations and all recordings of female song opportunistically during a study of the singing behavior of seven male House Wrens. We systematically recorded each song sung by a male and associated behavior for 30 continuous min between 0530 and 0900 h nearly every morning from the time of territory establishment until the fledging of young. We made no systematic effort to record female songs, rather, we obtained recordings coincidentally when recording males. In the five years of study we also observed over 250 other pairs of wrens every one to four days for 10 to 60 min each day.

We used Nakamichi CM-100 or CM-300 microphones with C-4 shotgun capsules and Sony WM-D6 or Marantz PMD 430 cassette tape recorders to record songs. Recordings were analyzed using a Kay Ele-metrics model 6061A or model 7800 Sona-Graph at the narrow band setting. Original sonograms are presented unless they were obscured by ambient noise, in which case we present tracings. We use the term "element" to refer to one or more continuous tracings clumped in time on a sonograph.

All males but only one female (OC-733) discussed in this report were individually color-banded. Other females, designated with two-letter codes, were identified by their continuous presence on a territory and uninterrupted association with one male and nest-site throughout a nesting attempt. We are confident that we were observing the same female in each case because male behavior changes dramatically after the loss of a mate (pers. obs.). There is some chance, however, that birds we assumed to be two different females breeding in separate years were instead one

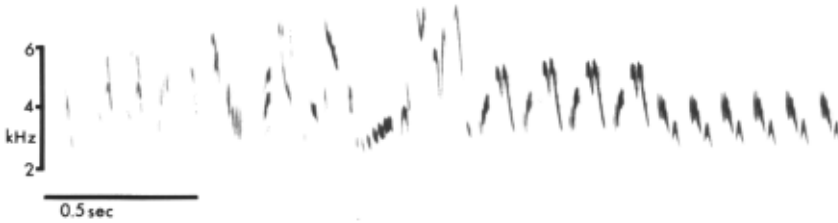


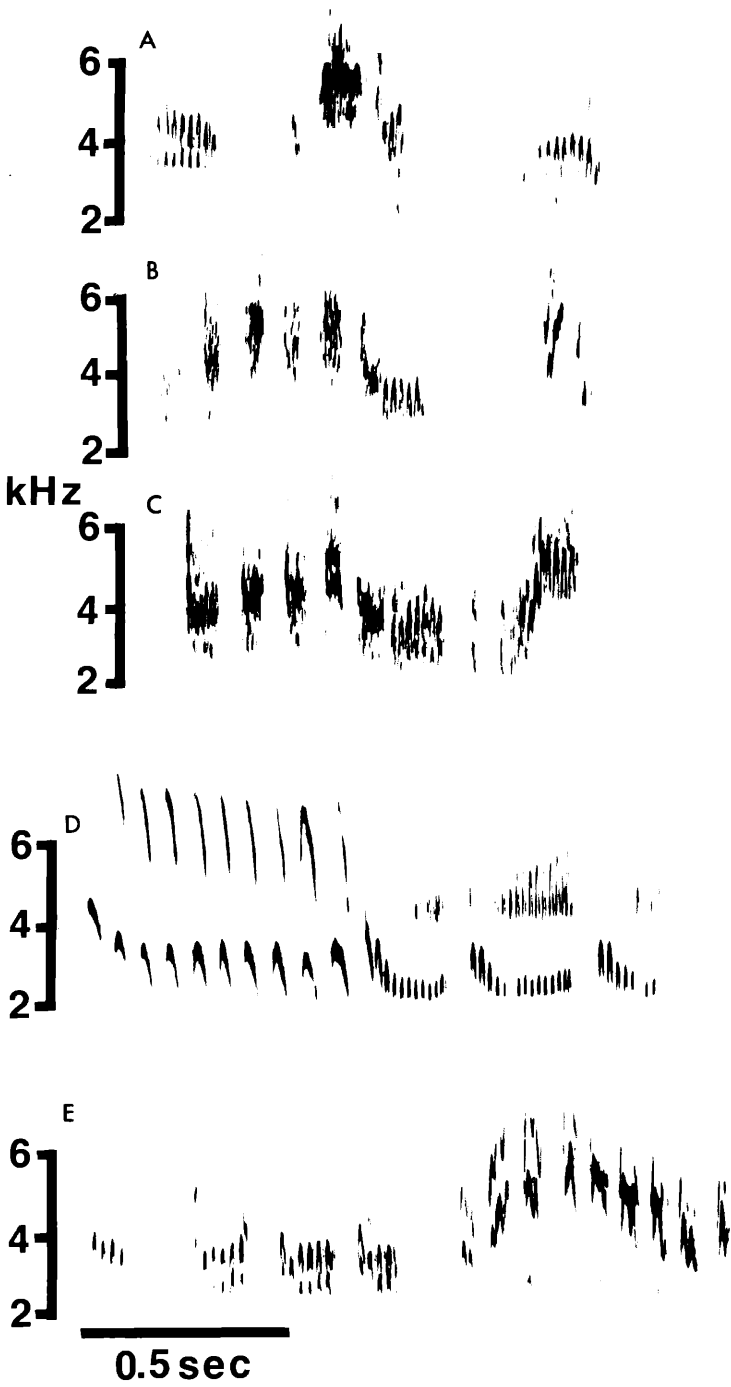
FIGURE 1. One song from a male House Wren in the Wyoming population. The normally low-amplitude introductory portion of the song was electronically enhanced to make it visible.

unbanded individual that bred on different territories or with different mates in two separate years.

RESULTS

The prevalence of song in females.—The mates of six of the seven intensively-recorded males sang at least once during their breeding cycles. We did not keep records of song frequency in other females on the study site, but we estimate that we heard over 75% of females observed each year sing. As we made direct observations on each pair during a very small portion of the time that they were on the study site, we suspect that most females in this population use song at some point during each breeding cycle.

The structure of female songs.—The songs of male House Wrens have a low-amplitude introductory section, containing elements that are usually repeated only once, and a longer and louder terminal section that contains one to three groups of elements or pairs of elements repeated several times (Platt and Ficken 1987, also Fig. 1). Female songs varied in their degree of similarity to male songs. Songs of some females were shorter than those of males, contained few, if any, elements found in male songs, and sounded similar to a human squeal (Fig. 2A–E). The songs of other females resembled male songs in organization, element structure, or both. Female DY sang one song with a low-amplitude introductory section and a louder terminal section containing two sets of repeated elements (Fig. 3A). However, the elements of her song were much less complex than those found in male song. In contrast, female MB sang several songs containing elements also sung by males in the population, but her songs were short and lacked two-part organization (Fig. 4). Female OC-733 sang songs indistinguishable from the type of songs sung by males in the population, including her mate (Fig. 5). We also found that several females from whom we recorded more than a few songs sang two or more songs differing in structure (i.e., Figs. 2A–C, 4, 5), however, too few clear recordings were obtained to determine whether any female possessed an organized repertoire of specific song “types.”



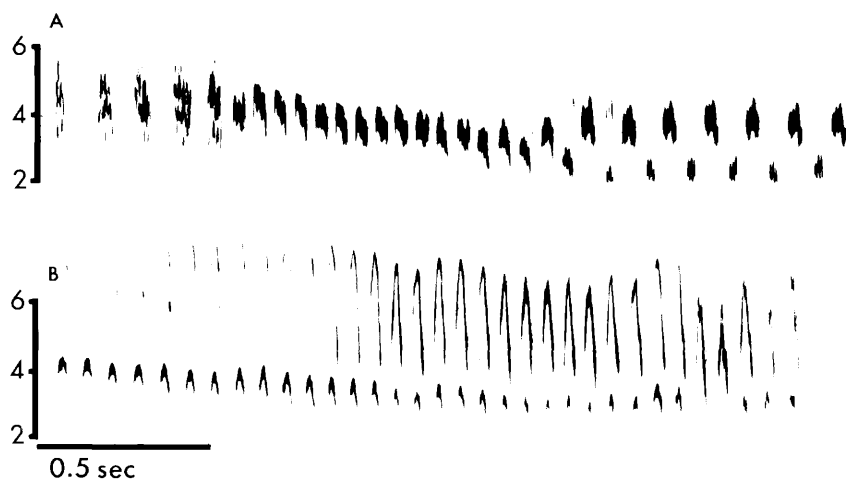


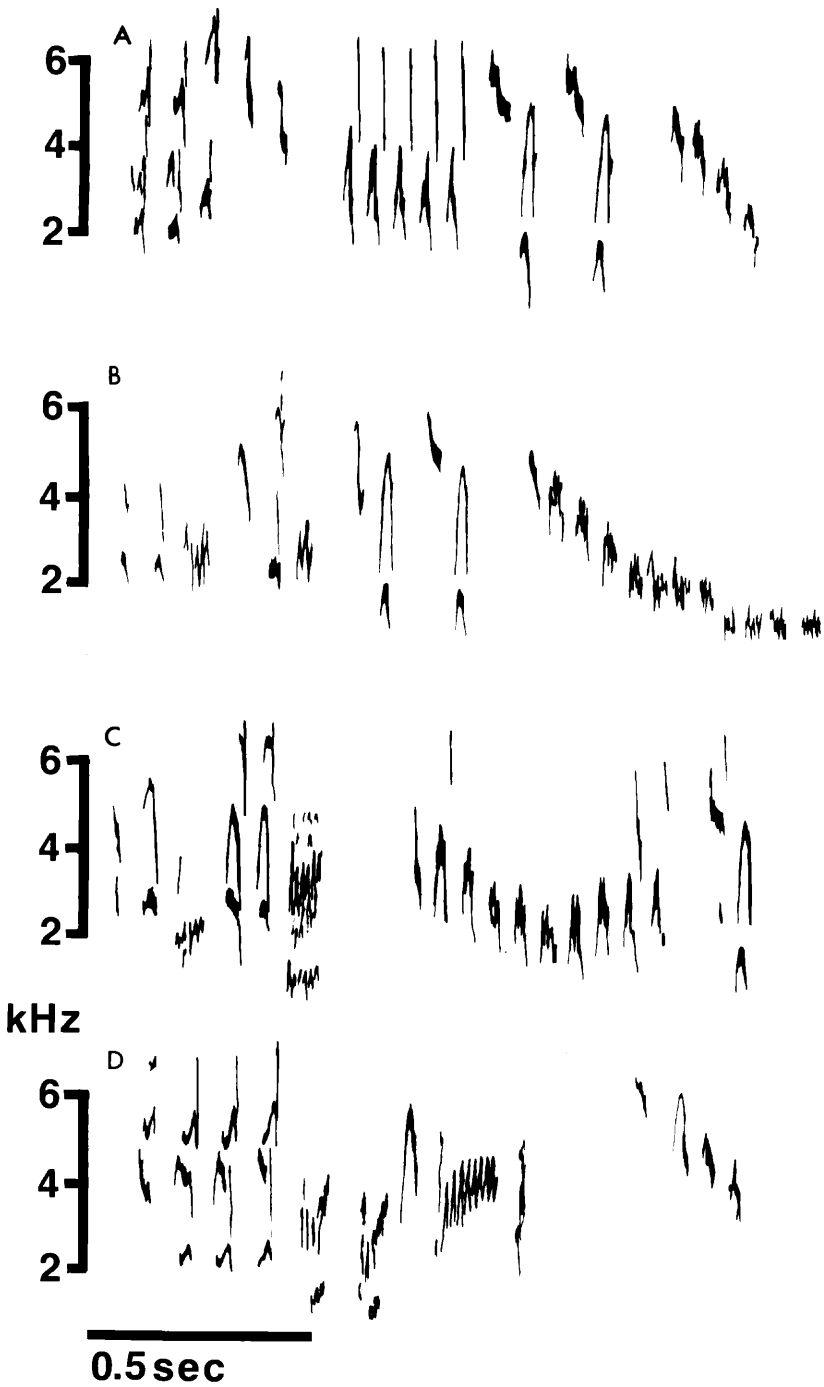
FIGURE 3. Two songs from female DY. Song A possessed the two-part structure found in male songs. The first five elements of this song were sung at a lower amplitude than the remainder of the song and were electronically enhanced so that they were visible. Song B resembles songs sung by female House Wrens in Panama (Farabaugh 1982: 105).

Songs of individual females did not appear to change in structure during a breeding season. However, in one instance where we startled a female as she returned to her nest, the female first gave two male-like songs and then after her mate sang, she sang two cruder squeal-like songs.

Contexts of female song.—Before discussing contexts in which females sang, we describe three normal patterns of interaction between mates during a breeding cycle. First, during nest-building, a male usually escorts his female as she makes trips to gather nest material. At some point during each trip, he returns to the nest and sings until she returns. Second, pairs begin copulating when the nest is nearly complete and continue copulating until most eggs are laid. On days that copulation occurs, a male moves very little, sings at a barely audible volume, and constantly performs a copulation-associated display, the “tail-raise” (Johnson and Kermott 1989). Third, while the female incubates, the male periodically approaches the nest and sings. This song appears to be a signal to the female as she usually exits the nest immediately after the male begins singing. The male often continues singing until the female returns. Females sometimes appear reluctant to enter or leave the nest unless their mate is singing.

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FIGURE 2. Songs from female BW (A-C), female BR (D) and female LG (E). All songs lack the two-part organization found in male songs. Only the first type of element in song D shows any resemblance to elements found in male songs.



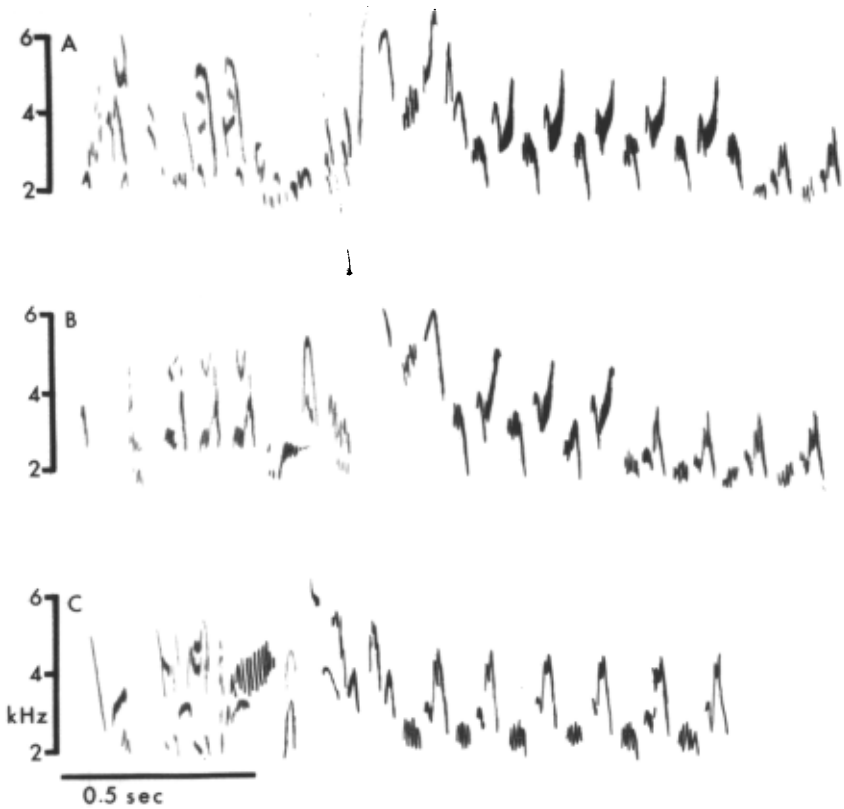


FIGURE 5. Two songs from female OC-733 (songs B and C) that were identical in organization and element structure to the songs of males, including her mate (song A).

The behavior of males and females suggests that male song at the nest during incubation and nest-building may function as an "all-clear" signal to the female.

Several females sang while soliciting copulation from their mates. However, most female song occurred when contact with their mate was interrupted in contexts where male and female behavior is usually well-integrated. For example, females sang when mates failed to lead them to and from the nest during nest-building and when mates broke from the normal pattern of behavior associated with copulation. We provide two specific examples.

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FIGURE 4. Four songs from female MB. These songs lacked the two-part organization found in male songs but most of the elements in these songs resembled those found in male songs.

In 1986, female MB sang approximately 2–4 songs/min the day after arrival on her mate's territory. It appeared that she sang most of her songs in immediate response to those of her mate. Both male and female behaved atypically this day. The female made trips to the nest-box, but never carried nest material. On several occasions, the male sang from the nest area as though trying to lead her to the nest, but when the female approached to within a few meters, he chased her vigorously throughout the territory. The female constantly approached the male and answered his songs at all locations in the territory and he frequently chased her long distances in these situations as well. The female often sang several songs in rapid succession following a chase. On several occasions both male and female were silent for several minutes and then when the male sang, the female immediately answered. We saw no chases and heard very little song from the female the next morning. The pair began normal nest-building activity a week later.

Female BW paired on 29 Apr. 1987 and began building a nest in a cavity 20 m off the ground in a large exposed snag. At one point on 4 May, she arrived in the brush at the base of the nest tree with nest material. However, the male was not present and she sat for about 20 s and then sang three songs. The male immediately returned and perched near the nest entrance and sang, at which point the female moved to the nest. On 5 and 6 May, the male was quiet, stayed near the female most of the time, and copulated with her several times. Between 7 and 11 May, however, four males settled on neighboring territories and made repeated intrusions into the focal pair's territory. The focal male appeared agitated on these days and flew repeatedly back and forth through his territory, singing loud songs. The female followed him, constantly answering his songs. Several times she approached to within 0.5 m of him and sang, sometimes while soliciting copulation. In each case he flew away. On 12 and 13 May, the male redirected most of his attention towards the female and she sang much less. On 14 May, she began regular incubation and sang very little thereafter.

Female song also occurred during the incubation stage if a male failed to sing near the nest while the female waited to exit or re-enter the nest. In most instances, the male returned to the nest area and sang immediately after the female sang. Females also sang when their mates attempted to attract or actively courted other females. While their mates incubated, over 50% of males in this population attempted to attract a second mate by singing near an unoccupied cavity on their territories. Most females sang from the nest entrance when their mates started singing at an alternate nest site. Some females interspersed song with flights between the nest site and their mate's alternate nest site.

Females were also heard to sing repeatedly on the first few days after their mates paired with a second female. For example, on 23 May 1986, female MB's mate paired with a second female at a nest box 30 m from her own. Normally, female MB would have been incubating. However, she remained in the nest for only a few minutes at a time before exiting

and giving several songs. Her mate, who was escorting his second female to and from the other nest, only responded to some of her songs. When he flew to her, she would flutter her wings, hunch over and sing vigorously. He usually flew immediately back to his second mate. Female MB's song output gradually decreased over the next few days as she returned to a normal pattern of incubation.

Finally, we witnessed one incident where one female attempted to evict a second, paired female from a territory. Non-resident males challenge resident males for territories during more than 7% of all breeding cycles in this population. During these takeover attempts, residents repeatedly pursue challengers for 20 to 60 s in tight circles throughout the territory, pausing only 10 to 30 s between chases. Residents sing frequently between chases and initiate each new chase as soon as the challenger sings. In the female-female takeover attempt, the resident also pursued the challenger in short chases each time the challenger sang her crude squeal-like song. The resident female also sang her own squeal-like song at regular intervals between each chase.

The unusual singing and breeding behavior of female OC-733.—We first observed female OC-733 on 13 Jun. 1986 when she inspected the nest box of her eventual mate. Between inspections, she sat near the male and sang male-like songs (see above). Later, she sang loudly each time she left the box during nest-building. After forming a cup of twigs, most females spend 2–4 d lining the nest with grass and feathers before beginning to lay eggs. Female OC-733, however, put feathers in her nest for at least 2 weeks without laying any eggs and continued singing during this time. She sang most of her songs when sitting within 1 m of the male, alternating her songs with his. Both birds appeared to answer each other's songs when singing was more sporadic. On several occasions, the female moved to the edge of the territory alone and sang for several minutes. From 28 to 30 Jun., her mate moved near an unoccupied next box on the territory and sang loud, long bouts of song in a manner similar to that seen when he was unpaired. Female OC-733 sang very little on these days and was not seen from 1 to 4 Jul. On 4 Jul., the male removed the feathers from the original nest leaving only the base of sticks. On 5 Jul., female OC-733 had returned and was relining her original nest and singing sporadically. She continued lining the nest until 18 Jul. when both birds disappeared for the season. Female OC-733 returned and bred successfully in 1987 and 1988. We never heard her sing in either of these years.

DISCUSSION

Skutch (1953: 122) described the song of female House Wrens in one Costa Rican population as "a low, rapid twitting, followed at times by a slight clear trill. Exceptionally, the female has a rich, full resonant trill. . . ." He also noted that "the female House Wren sings her little song chiefly in response to the richer, fuller verses of her mate, rarely when alone." Chapman (1929: 67–68) described the song of female House

Wrens at Barro Colorado, Panama as a "twit-twit-twit-twit-tee-tee-tee." He also wrote: "She is not a soloist and, as a rule, gives voice only when she hears the song of her mate." Farabaugh (1982) described the songs of female House Wrens in Panama as consisting of long series of different "chip-type" notes, with each note repeated 4–12 times before a switch to another note. The two songs that she presented were each at least 7 s long and one song completely overlapped two male songs. Farabaugh (1982) also suggested that females in her population were territorial because they responded strongly to playbacks of other females' songs.

Songs of female House Wrens in Wyoming varied in their similarity to male songs. The elements comprising some female songs appeared underdeveloped, unmelodic, and indistinct, whereas others resembled or were identical to those found in male songs. Most songs of male House Wrens contain two main sections, a low-volume introductory chatter followed by a louder terminal trill. Only a few female songs appeared to be organized into two sections. Skutch's (1953) descriptions suggest that the songs of female House Wrens in Costa Rica also vary in their similarity to male songs, both in the acoustic structure of elements and the tendency to be organized into two parts.

Why do songs of females in our population vary so widely among individuals and in their similarity to male songs? Brenowitz et al. (1985) examined the degree of sexual dimorphism in the neural vocal control systems of a thrush and two species of wrens in which females sing regularly, but in which the song repertoires of females vary in size relative to those of males. The degree of sexual dimorphism in the brain decreased as the relative repertoire size of females increased across species. It would be interesting to compare the degree of dimorphism in the brains of individual females in our population with the structure (i.e., "maleness") of their songs.

We cannot explain the relationship between female OC-733's male-like songs, her frequent singing in unusual contexts, and her failure to breed in 1986, or her change to normal breeding behavior and producing little, if any, song in the two years that followed. Abnormal hormone levels during the first year may have been involved.

The context and possible functions of female song.—Female song occurs primarily when contact with the male is broken in contexts where male and female behavior is usually well-integrated. In some situations, the female's song clearly appears to function in coordinating the male's behavior with her own. For example, if the male fails to provide what appears to be an "all-clear" signal to the female when she intends to move to or from the nest during nest-building or incubation, song from the female often brings the male immediately to the nest where he sings and she then moves. Contrary to the suggestions of Farabaugh (1982), we have no evidence that female song is normally directed off the territory.

We are uncertain as to why females engage in "song-answering" with their mates in certain contexts. Song-answering of mates by females occurs in several species of birds (see Beletsky 1985). Beletsky and Corral (1983)

suggested that a female Red-winged Blackbird (*Agelaius phoeniceus*) may sing immediately after her mate to indicate she is directing her song specifically at him. They proposed that song-answering conveys information to the male regarding the female's identity, her physiological state including readiness to breed and/or some other pair-bond specific information. The large majority of female song that we observed in House Wrens occurred immediately after pair formation and may serve similar functions in this species.

In conclusion, female House Wrens sing in one north-temperate House Wren population, and this song appears to function in communication among mates. We are not suggesting that females sing in all northern House Wren populations. Indeed, Kendeigh (1941) never noted female song during two decades of observations on a population of House Wrens in Ohio. However, we recommend that the House Wren no longer be used as an example of a species in which female song is primarily associated with prolonged pair-bonds, year-round territoriality and tropical residence (Farabaugh 1982: 103–104). Further research into the proximate and ultimate causes of intrapopulation and interpopulation variation in the songs of female House Wrens should shed some light on the evolution of female song in other species.

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NOTICE TO AUTHORS—CHANGE OF EDITORS

The association of Field Ornithologists is pleased to announce the election of Dr. Ken Yasukawa as the next editor of the *Journal of Field Ornithology*. All new manuscripts submitted for possible publication in the *Journal* should be submitted to the editor-elect:

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