SONGS OF THE JAPANESE POPULATION OF THE WINTER WREN (*TROGLODYTES TROGLODYTES*)[1]

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Abstract. An evaluation of the singing behavior of the Japanese wren (*Troglodytes troglodytes fumigatus*) might help to identify the origin of Old World wren populations and the forces that have molded the remarkable songs of this species throughout the Holarctic. The Japanese wrens seem identical to European wrens: males have repertoires of 6–7 highly repeatable song types of comparable duration and complexity. Wrens of eastern North America have a similar song organization, but the internal microstructure of songs is simpler and repertoires are only 1–3 song types apiece. Both of these song populations are highly different from the wrens of western North America, which use songs with greater internal variety, more variable sequences of songs, and hence much larger repertoires of song types. These behavioral data are consistent with a hypothesis that populations in the mountainous regions of western North America were isolated before the "eastern" North American wren colonized the Old World, probably via the Bering Straits. Not knowing the malleability of these vocal behaviors under different life histories, however, makes such a phyletic conclusion highly tentative.

Key words: Japanese Winter Wren; singing behavior; song populations; phylogeny; adaptive variation.

INTRODUCTION

The singing behavior of the Winter Wren (*Troglodytes troglodytes*) might be useful for addressing two rather different, but intertwined questions. First, the wrens (Troglodytidae) are a New World family, and only this wren has colonized the Old World; vocal behaviors of Eurasian and North American populations might help to identify the origins of the Eurasian birds (for review of use of bird song in systematics, see Payne 1986). Among many nonoscines, songs are not learned from other individuals (e.g., Lade and Thorpe 1964, Kroodsma 1989a), and vocal behavior is an unambiguous genetic marker for an individual. Singing behaviors and responses to song playbacks can thus be readily used as a systematic tool at the species level (e.g., Lanyon 1978, Baptista et al. 1983, Miller et al. 1988). Even among oscines, however, in which vocal imitation and cultural evolution provide great vocal flexibility (e.g., Baker and Jenkins 1987, Payne et al. 1988, Lynch et al. 1989), some as-

pects of imitated vocal behaviors retain a clear genetic basis, and imitated behaviors may be sufficiently stable over both time and space to be used as population markers. Marsh Wrens (*Cistothorus palustris*) from populations in western North America, for example, are able to learn about three times as many songs as individuals from eastern North America (Kroodsma and Canady 1985). This genetic difference in imitative ability is mirrored in some cultural aspects of the song; birds from western and eastern populations are able to learn each others' songs, but some imitated song features seem to occur throughout only the eastern or western populations, and hybrid singers in mixed populations are relatively rare (Kroodsma 1989b and unpubl. data).

The songs of the Winter Wren may also be useful in helping us understand the role of sexual selection in shaping elaborate behaviors. The Winter Wren has one of the most complex, repeatable songs among oscine birds (Kreutzer 1974, Kroodsma 1980), and the male sings "with remarkable vehemence . . . [as if he were] trying to burst [his] lungs" (Cramp 1988, pp. 536, 526). The extent to which these songs and associated singing behaviors are crafted by selective forces

remains unknown, though, with a polygynous species (Armstrong 1955, Garson 1980, Van Horne, unpubl. data), perhaps these elaborate behaviors are the product of strong sexual selection. Two highly differentiated song populations of the Winter Wren occur in North America (Kroodsma 1980); males in western populations have larger repertoires of song types and sing more complex songs than do males of eastern populations. A third song population of this species occurs in Europe (Kreutzer 1974), and that population sings more like birds of eastern than western North America. If the forces of sexual selection have been responsible for producing such elaborate behaviors in this species, then identifying behavioral differences among populations might help to characterize those selective forces.

The one major portion of the geographic range of this wren that remains unsampled is that in Asia. With two goals in mind, we here describe the singing behavior of the Japanese wren (*T. t. fumigatus*; Ornithological Society of Japan 1975). First, we hoped that a comparison of the vocal behaviors of the Japanese wren with those of the European and the two divergent North American populations would help identify the source population(s) of the Old World wrens. Second, we wished to document the vocal behavior of this remarkable singer on a fourth subcontinent, perhaps in the process revealing the presence or absence of selective (or nonselective) forces that have affected the complex songs of this species. Our results indicate that song repertoire size and construction of songs for Japanese birds are indistinguishable from those of European birds, but we cannot determine with certainty whether phylogeny or unidentified adaptive forces might be responsible for these holarctic distributions of behaviors.

METHODS

The birds we studied were seven male wrens recorded by Momose at Hoshino Hot Springs and the nearby area in Karuizawa, Nagano Prefecture, Japan (138.36°E, 36.18°N, altitude 1,000 m) from 18 April to 23 April 1989. Six of the males (birds 1–3, 5–7) were captured with a mist net and color-banded at least one day before the recording had started. A seventh male (4) was not netted and was recorded only briefly. All birds were within 4 km of each other, and the territories were in three clusters: birds 6 and 7

were immediate neighbors; birds 1, 3, and 2 formed a linear array in which immediate neighbors at their territory boundaries were often within earshot; and birds 4 and 5 were separated from each other by about 500 m and usually were not within earshot.

Tape-recording equipment included the following. In the field, a Casio DA-1 digital tape recorder with Sony DT90 digital tape, an omnidirectional Victor MU-510 microphone, and Sony PBR330 parabolic reflector were used. In the laboratory at Davis, the original tapes were copied to Realistic or Scotch reel-to-reel tapes with a Nagra III tape recorder (19 cm/sec).

Four of the birds (1, 2, 3, 7) were recorded continuously for at least 90 min beginning at sunrise. The other three birds (4, 5, 6) were recorded for only 12, 65, and 66 min, respectively, all beginning at or shortly after sunrise. At the time of recording, four of the males (2, 3, 5, 7) had at least one active nest, with the females of males 3, 5, and 7 carrying nest materials. As a result, some males did not actively sing after dawn, and occasionally playback was used to stimulate singing. Thus, though some long recordings were made in a continuous fashion with no stops (e.g., 263 songs in 1 hr, 32 min from bird 1), during some sessions the males sang discontinuously and the tape recorder was turned off during the longer silent intervals. We rarely missed more than one or two songs when the bird did resume singing, so that our recordings represent a fairly complete picture of singing activity during natural or stimulated singing sessions.

In addition to these recordings from Japan, we also had recordings from other areas that were generously loaned to us by several colleagues. Recordings by E. Davis (Aleutian Islands), D. J. Martin (British Columbia), E. H. Miller (Iceland), and B. N. Veprintsev (Soviet Union) provided valuable information on geographic variation.

The tape copies were sent to Kroodsma for spectrographic analyses. A Kay Elemetrics DSP 5500 sonagraph (transform size analogous to 300 Hz filter) was used to display the songs, and each of the 1,861 Japanese wren songs was studied for detailed sequencing of its constituent elements. We use the term "note" to refer to a continuous trace on the sonagram, "syllable" to refer to each repeated unit of identical notes or groups of notes in a "trill," and "song element" to refer in a more

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                                            Number of bouts (y-axis)
14 -| 1E | 2E |
    | 2A | 2F |
    | 2C | 2G |
12 -| 2D | 3A |              | 1D |
    | 1C | 2D | 1B | 3B | 1C | 2B |
10 -| 2A | 3D | 2A | 3B | 1F | 2E |
    | 2B | 3E | 3A | 3C | 2B | 2F |
 8 -| 2C | 3E | 3B | 3C | 2D | 3C |
    | 2G | 3E | 3E | 4B | 2G | 3D |                   | 1A |
 6 -| 3F | 4A | 3E | 5A | 3A | 6A |                   | 2C |
    | 5D | 4C | 5B | 5B | 3F | 6C |                   | 3A |
 4 -| 6C | 4D | 5B | 6A | 5A | 6E | 2A | 3C |
    | 6D | 5C | 5E | 6D | 5D | 7A | 3F | 5F |         | 1B |
 2 -| 6E | 5D | 6B | 7A | 5E | 7B | 5C | 7D |         | 1D |
    | 7C | 7F | 7E | 7F | 6E | 7D | 6F | 7E |    | 6A | 1E |    | 2E |
 0 -
      3    8   13   18   23   28   33   38   43   48   53   58   63   68
                              Songs / bout
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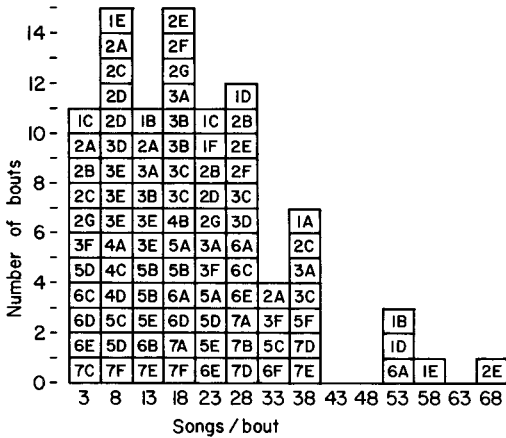
FIGURE 1. Number of songs per bout for seven Japanese wrens, in which a bout is a consecutive series of renditions of a given song type. In each cell is given the bird number and song type letter (e.g., 4A is song type A of bird 4). On the abscissa, "3" represents 1–5 songs/bout, "8" represents 6–10, etc. Thus, on 11 occasions birds sang bouts of 1–5 songs, on three occasions bouts of 51–55 songs, and so on. When interpreting this figure, remember that recordings were made under a variety of conditions, e.g., both at dawn and later in the day, under both artificially stimulated (playback) and natural singing, and in the presence or absence of an actively nest-building female. Furthermore, some bouts were incompletely recorded because a few songs may have been missed when the tape recorder was first turned on or when the bird flew to a distant location.

general way to either notes, syllables, or both. Although the songs were long and complex, a male repeated each song form with remarkable consistency. We therefore graphed the longest or best quality songs in a given sequence and indicated on that one sonagram the stopping points or peculiarities of other renditions of that particular song type.

RESULTS

The songs of a male Japanese wren consisted of a series of highly predictable and repeatable sequences of note or syllable types. He typically sang with "eventual variety," i.e., successive songs were highly similar to one another and eventually, after typically 20–30 songs (Fig. 1), the male switched to a series of a different song type. Occasional songs deviated from these regular series of renditions, and these deviations revealed the basic process by which the wren constructed and managed his repertoire of songs. We illustrate

these general statements with detailed descriptions of the singing behavior, especially of bird 2, a male from which we recorded seven different song types in 394 songs.

THE SONG TYPE

To illustrate how the wrens packaged their song elements into repeatable sequences that we called song types, we first examine one of those song types in detail. Song type 2A (bird 2, song type A; Fig. 2A) occurred in four different series (i.e., "bouts") in our recordings; those series consisted of 13, 32, 8 (+4 AF hybrids–see below), and 6 renditions of song type 2A (see Fig. 1), separated by 80, 108, and 143 songs of other song types, respectively. The number of songs/bout is a minimum, because only the third bout (of 8 + 4 hybrid AF songs) was bounded by continuous singing of songs of other types, rather than by the beginning or ending of a recording session in which a few songs may have been missed.

Like the other song types of bird 2 (see Fig. 2), song type 2A consisted of an introductory phrase and what we have called a "repeated unit." The song began with a series of introductory notes that frequently were only faintly recorded; song amplitude seemed to increase gradually during the first half second or so, and we could not always be certain whether the male omitted some of the first notes or whether they were just too weakly recorded. After about 1.4 sec, the male began the repeated unit. The longer renditions (23 out of the 59 pure 2A renditions) of this song type would double back to this point, as if this repeated unit of about 4.4 sec, but not the introductory phrase, were a loop that could be sung as many as two to three times. The longer songs were thus generated by repetition of a large portion of the song.

Successive songs of 2A typically varied in two ways: overall duration and the number of repeated syllables in the trills. Bird 2 terminated renditions of this song type at 20 different locations in the basic sequence of song elements. The three favored locations (with 7, 16, and 7 renditions stopping at that point) were either after a single loud note at about 4 kHz or after a frequency sweep from about 6.5 to 4 kHz; in other song types, too, those types of locations were often stopping points or transition points at which hybrid song types might be formed (see Figs. 2B–G). Renditions of 2A also differed in
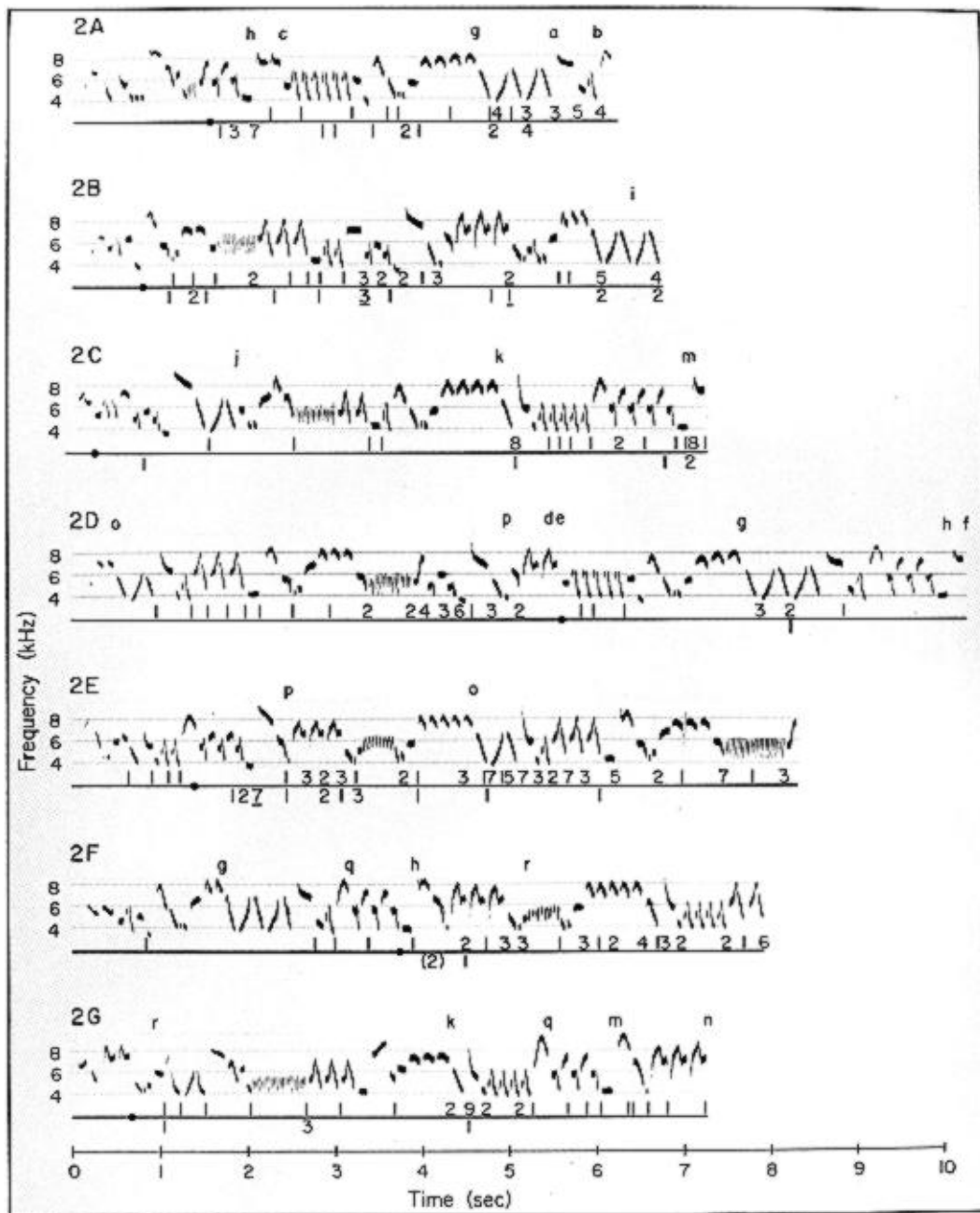
FIGURE 2.   Song type repertoire of bird 2. The baseline at 2 kHz is bisected by a solid disc to mark the end of the introductory notes and the beginning of the repeated unit (see text). The number of renditions that stopped at different places in this sequence of song elements is marked along the baseline; numbers above the baseline are for songs that stopped during the first singing of the repeated unit, those below during the second (or third, as with two songs of B and two of E, indicated by the underlined numbers). Two songs of F ended during the second singing of the repeated unit, but recordings were of insufficient quality to determine the exact location (indicated by "2" in parentheses). Lowercase letters identify particular notes or sections of the songs that are discussed in the text (see Results).

the number of repeated syllables in each of the trills, but by convention we classified that as "within song type" variation (which is not to claim, of course, that such variation is behaviorally unimportant).

Three of the 59 2A songs differed in the basic sequence of note or syllable types. For one song (beginning at "a" in Fig. 2A), after singing about 6/7 of the repeated unit the male returned to the beginning of the song and began again. A second song skipped the introductory notes and began with the repeated unit. A third song illustrates how song variations or song hybrids (relatively rare songs that consist of a combination of two more commonly used song types) were often generated by the use of similar or related sequences of elements from other song types; the male substituted note "d" from song type 2D (Fig. 2D) for the section "b–c" in the repeated unit of Figure 2A. Careful study of song type 2D reveals that section "e–f," which immediately follows note "d" (Fig. 2D), contains the same sequence of song elements as does the repeated unit of 2A, though with a different starting and ending point. Thus, in one of 23 longer 2A songs when this male launched into the second singing of the repeated unit, he simply used a transition with some shared features from another of his song types.

That song with characteristics of types A and D might be called an AD hybrid, just as four additional songs were clearly hybrid song types that began with song type A and concluded with song type F. As with most hybrid songs, the "parent" song types for the four hybrids shared a sequence of song elements (in Fig. 2A and 2F, see section "g–h"), and after singing that shared section the male had the option of finishing that particular song with either song type without violating his commonly used sequences of song elements. Songs of Bird 2 that deviated from one of the commonly used song types illustrated in Figure 2 were usually based on such shared sequences of song elements. Conversely, songs that deviated from these common sequences often stopped abruptly, as if the male realized that his attempted novel sequence were "in error."

Of 331 other songs recorded from bird 2, the majority (317, or 96%) matched the basic sequence of element types illustrated in Figure 2. Those 14 songs of bird 2 that differed from types B–G (Fig. 2) also provide some insight into how the wrens managed their large repertoire of song elements and sequences. Three of the 14 songs, for example, added or omitted a single note, thus generating a sequence not routinely used among song types A–G; those songs then abruptly stopped. Three other songs also omitted (2) or added (1) a single note, but in two of the three cases the new sequence was identical to a commonly used sequence in other songs, and the songs continued without further incident.

The other eight of these 14 songs from bird 2 illustrate again how shared sequences of song units between songs were sometimes used to generate song variations. One song branched at "i" in 2B to "j" in 2C; the three notes before "i" and "j" are shared by song types 2B and 2C, and this hybrid song was therefore based on a brief sequence of song elements shared by the two parent song types. Seven other hybrid songs were based on the shared section "k–m" in 2C and 2G (see Fig. 2). On these seven occasions during a bout of 2C songs, the male followed section "k–m" with section "m–n" from 2G; on four of those occasions the male returned to the beginning of the repeated unit of 2C, on one occasion he stopped within the section m–n, and on two occasions he continued with song type 2G.

Hybrid songs, such as these AF and CG hybrids, sometimes occurred during seemingly undisturbed singing as a natural transition between the two parent song types. About half of bird 2's song hybrids, however, occurred just after the male had moved far upstream and had begun relatively intense countersinging with his immediate neighbor. During this natural interaction, the male sang eight A songs intermingled with four AF hybrids, then one C song, two CG hybrids, and two G songs, before settling down to singing a bout of normal duration, 25 F songs. High motivation during this confrontation undoubtedly led to the reduced bout lengths (compare bout lengths of Fig. 1) and the increased song variation (i.e., hybrids) here.

THE SONG REPERTOIRE

Different song types in a male's repertoire were generated by reusing many of the same song elements and element sequences. In the most extreme case for bird 2, song type 2D was largely a composite of types 2E and 2A: section "o–p" of 2D was part of the repeated unit of 2E and section "e–f" was the repeated unit of 2A, though the repeated unit began at a different point (see Fig. 2). Two song types of bird 1 (not illustrated— see Table 1, footnote c) were essentially identical to each other except for consistently different introductions of 0.9 and 2.0 sec, respectively. Many

TABLE 1.   Summary of recording samples and song repertoire sizes for 7 Japanese wrens.

Bird	Repertoire of song types	Bouts sampled[a]	Total songs	Hybrid songs[b]
1	6[c]	1-2-2-2-2-1 = 10 (3)	300	2
2	7	4-3-3-3-3-2-3 = 21 (12)	394	6
3	6	4-3-4-2-5-3 = 21 (15)	407	9
4	4	1-1-1-1 = 4 (0)	44	0
5	6	2-3-2-3-2-1 = 13 (7)	216	0
6	6	3-1-2-2-3-1 = 12 (6)	252	2
7	6 (or 7)[d]	2-1-1-2-2-2 = 10 (4)	248	21

[a] Number of independent series of each song type in the repertoire, an index of how thoroughly the repetoire has been sampled. For a repertoire of six song types for wren 1 (indicated 1-2-2-2-2-1), for example, two song types occurred in only one series (one bout), and four song types occurred twice. The number of bouts recorded for each bird is totaled. Also, in parentheses is given the number of bouts in the recordings since the last new song type was introduced; during early morning singing, four males (3, 5–7) sang a bout of each of their six song types before repeating any bouts, and such regular rather than random use of song types helped in documenting repertoire size.
[b] A hybrid song is a relatively rare song (about 2% of all songs) that consists of a combination of two more commonly sung song types.
[c] Two song types (A and E) of bird 1 differed only in the introductory notes of the song (0.9 sec for A, 2.0 sec for E), but the bird used A and E as if they were two independent song types.
[d] We have counted 14 songs as song hybrids of song types A and B; those 14 songs occurred between a bout of A and a bout of B songs. Additional recordings might have revealed that this male regularly sang this hybrid AB pattern, in which case we would have classified it as a seventh song type.

briefer sections were also shared among song types. For bird 2 (see Fig. 2), section "g–h" of 2A and 2D was also shared by 2F, and section "q–r" was shared by 2F and 2G. Section "g–a" of 2A, consisting of 3–5 notes, was clearly represented in all of the song types except 2G. A detailed analysis would undoubtedly reveal that most song elements and sequences were shared among the song types, and that it was those shared song elements and sequences that formed the building blocks for the repertoire of different song types that each male used.

Our data suggested that a typical repertoire size for males in this population was six or seven song types (Table 1). One male (4) was recorded for only 12 min and only four song types were found, but the other six males were sampled more thoroughly. Birds 2 and 3 had been recorded most intensively, with a total of 21 bouts for each, and each song type occurred in two to five bouts (each bout is an "independent occurrence" of that particular song type). Furthermore, during the fairly continuous singing of the early morning, the males tended to sing a bout of each song type before repeating any bouts (Table 1, footnote a), so that the entire song type repertoire could be confidently recorded in a minimum of time. Birds 2 and 3 thus had seven and six commonly used song types, respectively. The other four birds, even though recorded less intensively than birds 2 and 3, also used six or seven song types (Table 1). The regular singing behaviors of these males made it relatively unlikely that additional song types would have been revealed in more recordings, and we estimate that the mean repertoire size for the population was between six and seven.

SONG SHARING AMONG INDIVIDUALS

Males within the population also shared many of the same song sequences and song elements. Birds 2 and 3 were immediate neighbors, and song 2E, for example, was almost identical to song type 3E (compare songs in Figs. 2 and 3). Most of 2F can be found, with slight variation, in song 3A. Song type 3F is perhaps more typical in that it shares many song elements and only shorter sequences of those elements with the song types of male 2. Such similar song types among neighboring individuals reveals that they are learning their songs from conspecifics in the population.

DISCUSSION

The repertoire size of the Japanese wrens that we studied is most like that of the wrens in France that Kreutzer (1974) described. Kreutzer tabulated the repertoire size for nine males as 4–7 song types, but his estimates of repertoire size depended on his sampling effort: four males from which he had examined 180 songs all had either six or seven song types, but the five males from which he had sampled only 100–140 songs had only four or five song types. Because males sing long sequences of songs of the same song type, the number of sampled songs is not as accurate a reflection of sampling effort as is the number of bouts of each song type (see Table 1). Nevertheless, three of Kreutzer's four wrens that had been most thoroughly sampled had six song types and the other had seven song types; these repertoire sizes are identical to the repertoire sizes of six and seven that we found in our six more thoroughly sampled Japanese wrens. Wrens of
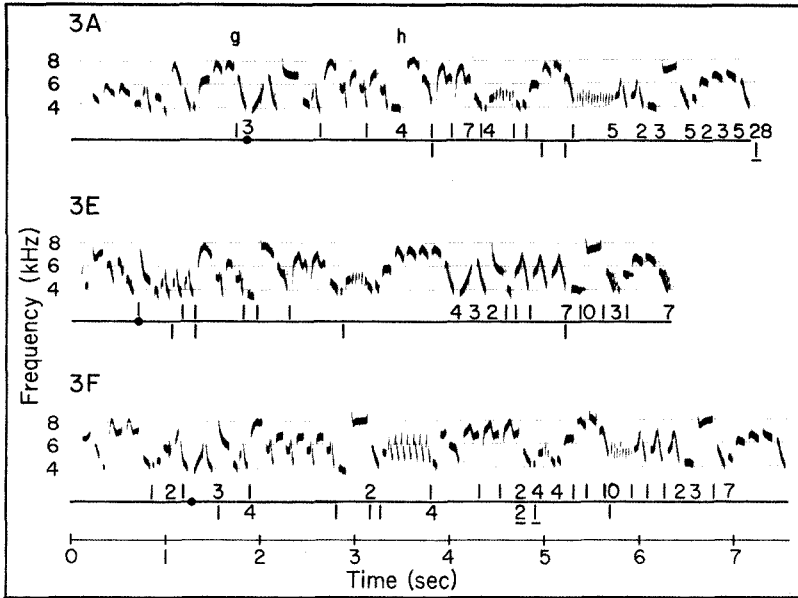
FIGURE 3.   Three song types (A, E, F) of Japanese wren 3. Three songs (1 of A, 2 of F) ended during or after the third singing of the repeated unit. See Fig. 2 legend for additional details. Song types were labelled A, B, . . . G independently for each bird, so "A" songs of different birds bear no special resemblance to one another.

eastern North America have smaller repertoires, only 1–3 song types, and wrens of western North America have a far greater variety of song forms, generated largely by a different style of singing (see below and Kroodsma 1980).

The songs of the Japanese wrens are also constructed in much the same way that songs from Europe and eastern North America are constructed. Each song type consists of a highly repeatable sequence of song elements, and successive renditions of that song type occur in long bouts. For two New York males, only six out of 299 songs (2%) were hybrid songs that began with elements of one song type and ended with those of another. For the seven Japanese wrens, 40 of 1,861 songs (also 2%) were considered to be hybrid song types. Similar data do not seem to be available from Kreutzer's (1974) work in France.

Winter wrens of western North America generate a great diversity of song types by recombining favored sequences of song elements into different songs (Kroodsma 1980, Van Horne and Waterman 1990). Two males in Oregon had 8–10 introductory phrases of about a half second in duration. Long bouts of songs (up to 80) were sung with a given introductory phrase, but concluding portions of successive songs in these bouts often differed markedly, and one male sang 66 different song types in 518 songs (see Table 2 in

Kroodsma 1980). We analyzed the songs of a third male from western North America for this study. D. S. Martin kindly recorded for us, during 21 and 22 April 1990, 447 songs from one male in the Queen Charlotte Islands of British Columbia. On 21 April, this male sang seven different song introductions in seven bouts, and on 22 April the male introduced three additional song introductions in seven more recorded bouts. Additional sampling would probably have revealed a repertoire larger than 10 song introductions. As with the Oregon males (Kroodsma 1980), each song introduction was used with several different song conclusions to generate many additional "song types" (e.g., Fig. 4). These western Winter Wrens seem to sing as if they have been selected to perform highly varied or stimulating sequences of songs under especially intense motivational levels (Kroodsma 1977).

The song data from admittedly small samples in different portions of the Holarctic suggest that there exist three continental song populations of the Winter Wren. The two most divergent song populations are in western and eastern North America. Oregon and British Columbia males have a large repertoire of song forms generated by recombination of complex song units and favored sequences of those song units (Kroodsma 1980, Van Horne and Waterman 1990, this

study); these behaviors are undoubtedly typical of much of western North America. New York and Maine males have only 1–3 song types, each of which is sung in a highly repeatable fashion, and the detailed microstructure of song elements is also simplest in this population. Recordings from Michigan are similar to those from New York and Maine (D. E. Kroodsma, unpubl. data). Wrens from France and Japan, about 10 thousand kilometers apart on the Eurasian continent, have repertoire sizes of 6–7 song types; these songs are repeated with the same degree of stereotypy as found among wrens from eastern North America, and internal complexity is intermediate between that of wrens from eastern and western North America. Brief recordings from locations such as Morocco and throughout Europe, including Iceland (Kreutzer 1974, analyses of Veprintsev and Miller recordings in this study), suggest a relatively homogeneous singing behavior of this wren throughout the Old World. Wren songs from the Aleutian and Commander Islands (E. Davis and B. N. Veprintsev, unpubl. data) have a distinctive, harsher tonal quality, perhaps as a consequence of the relatively windy, treeless habitats, but data on repertoire sizes and stereotypy of successive songs are unavailable.

According to Mayr (1946; see also Armstrong 1955), this wren was more likely to colonize the Old World via the Bering Straits than by the North Atlantic and Iceland. In this scenario, the wren then spread across Asia, to Europe, and finally to Iceland. In North America, during successive Pleistocene glaciations, one population of this wren may have been isolated among the western mountain ranges, much as Mengel (1964) proposes for the history of species formation among North American warblers. Then it was not this isolated western population, but rather the parental population, with its transcontinental range in boreal coniferous or mixed forests, that colonized the Old World via the Bering Straits during one of the interglacial periods. The similarity of Eurasian and eastern North American vocal behaviors in this species is consistent with the hypothesis that colonization of the Old World is a more recent event than the isolation of the populations in western North America.

Other phyletic hypotheses might also be considered, of course, though none seems quite as plausible as does that derived from the Mayr (1946) and Mengel (1964) proposals. An ancestral wren with relatively simple vocal behaviors may have achieved a holarctic distribution, via
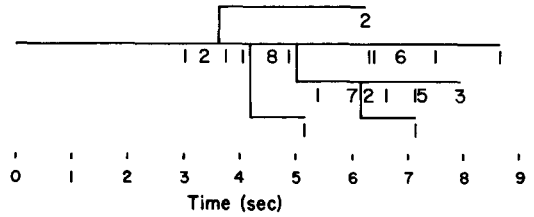

FIGURE 4. Representation of five "song types," all of which were based on a common introduction, from a male wren in the Queen Charlotte Islands of British Columbia. The horizontal line from 0.0 to 8.6 secs represents one type. At 3.6 sec, 4.1 sec, and 5.0 sec, other types diverge, with a fifth type diverging from one of these branches at 6.1 sec. All 66 renditions thus began with the same approximately 3.6 sec introductory phrase, but five different concluding phrases were used. The number of song renditions that stopped at different points is indicated.

either the Bering Straits or the North Atlantic, and then developed into what appears now to be three continental song populations. Perhaps less likely is that European and Asian wrens originated from two separate invasions by eastern and western North American forms, respectively, because then highly divergent forms would have had to converge on identical repertoire sizes and singing styles in France and Japan.

We cannot be certain which of many possibilities is correct, partly because we do not know the relative times of the North American divergence and Old World colonization, but also because we do not know the relative stability of different vocal behaviors over evolutionary time. During high motivation, wrens are especially prone to use more complex singing behaviors (e.g., Kroodsma 1977). Wren 2 in this study, for example, produced a more complex series of songs by using short bouts of 1–2 renditions of a song type and by forming hybrid songs when he was countersinging with a neighboring male. Differing motivational levels among populations may be a consequence of territorial density or mating system and could lead to rapid convergence or divergence of vocal characters among geographically isolated populations. We simply do not know to what extent highly different singers might converge, over evolutionary time, if they were placed under similar environmental conditions. Nor do we know how much of the sometimes extreme vocal variation among populations or species, such as that observed among the North American Winter Wrens or Marsh Wrens (e.g., Kroodsma and Canady, 1985), is exactly

crafted by ubiquitous selective forces and how much is crafted by chance events. Although we believe that the data suggest an early isolation of western North American wrens, followed by colonization of Eurasia from ancestors of the wrens now in eastern North America, other adaptive hypotheses that involve differing rates of vocal change are also possible.

The vocal behavior of *Troglodytes troglodytes* suggests an affinity to the Timberline Wren, classified by some authorities as *Thryorchilus browni* (AOU 1983), but by others as *Troglodytes browni* (Peters 1960, Howard and Moore 1980). This wren occupies montane habitats in Central America, and the songs of this species are also long and reasonably complex. Like the Winter Wren of eastern North America and Japan, it creates its longer songs by repeating a portion of its songs several times (Kroodsma, unpubl. data). Unfortunately, as is the case among populations of what is currently classified as *Troglodytes troglodytes,* we cannot know whether the similarities in song structure between the Timberline Wren and the Winter Wren are due to chance, convergence because of similar selection pressures, or taxonomic affinity. Only with a more thorough understanding of life history phenomena and the forces molding these complex songs, together with genetic data revealing phyletic affinities of different wren groups, will we be able to distinguish among these different possibilities.

ACKNOWLEDGMENTS

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