COEXISTENCE OF BEWICK'S WRENS AND HOUSE WRENS IN OREGON

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ECOLOGICAL investigations of closely related, sympatric species have usually revealed that each species exploits the environment differently. One mode of resource partitioning involves the defense of interspecific territories in habitats where competing species co-occur (Orians and Willson, 1964). Although Root (1969) found that the Bewick's Wren (*Thryomanes bewickii*) and the House Wren (*Troglodytes aedon*) may practice territorial exclusion in California, in Oregon the territories of these two wren species frequently overlap. In this paper I discuss the relationships and interactions between the resident Bewick's and the migratory House Wren in the Willamette Valley of Oregon.

ASPECTS OF COEXISTENCE

TERRITORY

I found extensive territorial overlap between House and Bewick's Wrens at two locations in the William L. Finley National Wildlife Refuge near Corvallis, Oregon. The first site was in a fairly open pasture with dense tangles of wild blackberry (*Rubus macropetalus*) and nutka rose (*Rosa nutkana*). Mixed stands of Douglas fir (*Pseudotsuga menzsii*) and Oregon white oak (*Quercus garryana*) with dense underbrush bordered this pasture to the north and west. I began studying three color-banded male Bewick's Wrens here during March 1969, and stable territorial boundaries existed when House Wrens arrived in late April. During my many visits to this area, only twice did I see any interspecific aggression: a Bewick's male on one occasion momentarily chased a courting House Wren male and at another time uttered the "spzz" note (Miller, 1941) when approached by a family flock of House Wrens. Such occasional interspecific interactions are common among most small passerines. On the other hand, intraspecific aggression and territorial conflicts among the wrens were often intense. On one occasion, two House Wren males were engaged in a boundary dispute that continued for several minutes, but 20 m overhead a Bewick's Wren remained undisturbed and continued countersinging with his conspecific neighbor.

Foraging locations and song posts of the male wrens were plotted on aerial photographs. I also used tape-recorded songs to draw the males to their territorial boundaries. Six House Wren males eventually estab-
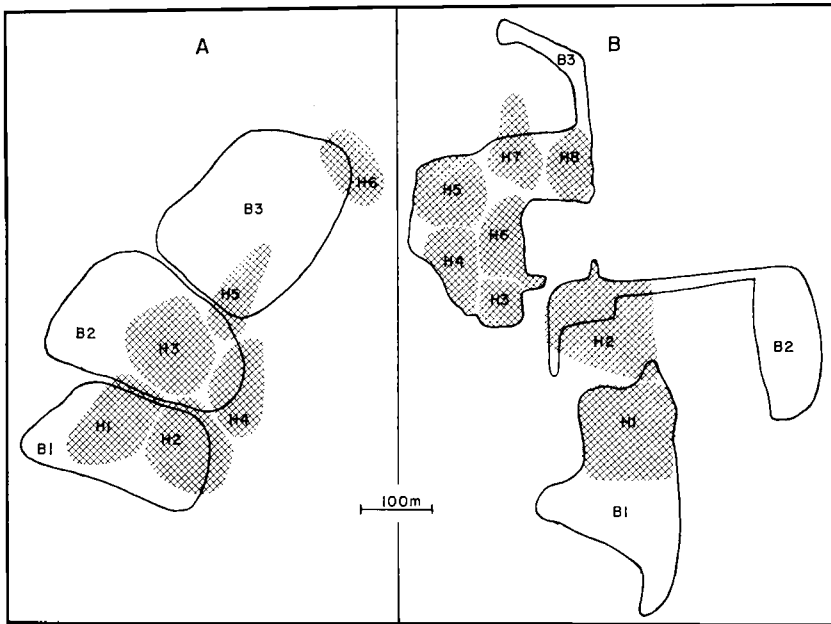
Figure 1. Territorial overlap between Bewick's (B) and House (H) Wrens at two locations on the William Finley Refuge. Territories of Bewick's Wrens are contained within solid black lines; those of House Wrens are crosshatched.

lished territories on this study site in 1969, and of these, three entire territories and portions of the other three lay within Bewick's Wren territories (Figure 1A). Portions of the Bewick's Wren territories extended to the west into the bordering woodlands, and these portions were not shared with the House Wrens. Both species were again present in 1970, but I failed to determine the exact territorial relationships. In 1971 one pair of each species bred at this locality; the House Wren's territory lay completely within that of the Bewick's Wren.

During May 1971 I mapped the territories of eight House Wrens and three Bewick's Wrens at a second location, near the headquarters of the refuge (Figure 1B). Here the habitat consisted of hedges and fencerows about the buildings (House Wren territories 1 and 2), oak woodland (House Wren territories 3–6), and an open hillside with large oaks and Douglas firs, some rose tangles, and bordering fence rows (House Wren territories 7 and 8). Extensive overlap of territories was evident. The three territories of the color-banded Bewick's Wrens were stable throughout the summer, but some exchange of territories and disappearance of birds occurred among four color-banded House Wrens. Such behaviors

are typical for House Wrens (Kendeigh, 1941) and are not necessarily attributable to interference by the Bewick's Wrens.

Further study in habitats utilized by only one of the two species revealed an apparent habitat separation. During the summer of 1970 I mapped the territories of 28 Bewick's Wrens in the dense riparian habitat of a nearby river bottom; the territories averaged 4.9 acres (range 3.1 to 9.4) and were characterized largely by oak or ash overstory with dense underbrush. I found no House Wrens here. Where the denser understory of the woodland was replaced by a grassy substrate, I usually found only House Wrens. If denser vegetation was nearby though, Bewick's Wrens might also include such open areas within their relatively large territories. House Wrens also established territories in open pastures where a single tree stump might provide a nest site and several rose thickets sufficient vegetation for foraging. Thus it appears that Bewick's Wrens prefer the thicker vegetation while House Wrens prefer the more open areas; territories may overlap in intermediate habitat types, but utilization (e.g., in foraging) of different patch types by the two species in such habitats again reflects a difference in habitat preference.

This is further suggested by territory sizes in the two areas of territorial overlap (Figure 1). The mean territory size for the 14 House Wrens was 2.3 acres (range 1.1 to 4.4), that of the six Bewick's Wrens was 9.4 acres (range 6.1 to 11.8). Territory size in several species is known to be correlated with density of preferred habitat type (see Schoener, 1968 for review), and the large mean territory size for the Bewick's Wrens here (9.4 acres as opposed to 4.9 acres in the denser woodland) was due probably to the extensive open areas between suitable habitat patches. I measured no territory sizes for House Wrens where they occurred alone; in Ohio, Kendeigh (1941) found a mean territory size of 1.0 acre, but several factors, most notably perhaps population numbers, do not allow a direct comparison of territory sizes. One other factor could lead to an increase in territory size where territories of the two species overlap; if House and Bewick's Wrens take similar prey items, both species would have to expand territory size to maintain a food supply comparable to that in nonoverlapping territories. Detection of this form of interaction requires further study.

BREEDING SEASON

The breeding season for these two species at the Finley Refuge overlaps, but the peak of the season occurs considerably earlier for the resident Bewick's Wren. In a study of 30 Bewick's Wren pairs during 1970, I determined approximate fledging dates for 19 successful nests
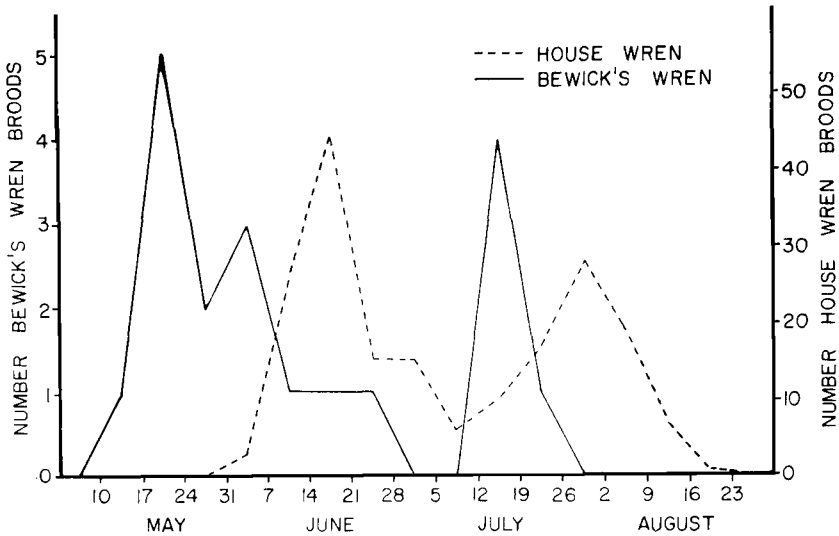
Figure 2. Number of fledged broods for Bewick's Wrens (n = 19) and House Wrens (n = 207) during weekly intervals, May-August. The House Wren ordinate is reduced to 19/207 = 0.092 percent of the Bewick's Wren ordinate to make the two graphs directly comparable. Data on House Wrens are from Kendeigh (1941).

(Figure 2). I visited each of the 30 territories weekly, listening for fledgling calls; the young were usually quite vocal throughout the morning, but several fledgling flocks remained unnoticed for at least 1 week. Such errors suggest a slightly later breeding schedule than is actually the case.

House Wrens are migratory, and during 1969-1971 the first males arrived at the Finley Refuge about 20 April. I have no information on fledging dates for the House Wren, but Kendeigh's (1941) data are useful. In Ohio the median date for the first male activity is 1 May, about 10 days later than in Oregon. If 207 fledging dates given by Kendeigh are then advanced 10 days, those dates may be comparable to fledging dates of House Wrens in Oregon (Figure 2). House Wrens are characteristically double brooded, and fledge 50 percent of their young in July and August (Kendeigh, 1941).

Only two of 30 Bewick's males raised two broods, one with the same female consecutively and one apparently with two females simultaneously (Kroodsma, 1972). The young Bewick's Wrens fledged in July are largely those of first-year males and a few older birds that were unsuccessful in their first nesting attempt. The majority (here 11 of 19, or 58 percent) of Bewick's broods probably leave the nest before an appre-

ciable number of House Wren broods appear, and the peaks of the breeding seasons for these two wren species are well separated. As late as 16 August 1971 Zeillemaker (pers. comm.) reported nestling House Wrens, and I found three family flocks on the Finley Refuge. The breeding season may extend longer for the House Wren, but the basic differences are revealed by Figure 2. The greatest strain on the food supply is undoubtedly during the nestling-fledgling periods, and the staggered breeding periods may diminish competition.

SONGS

Interspecific recognition is facilitated by similarities in morphology or behavior, and if natural selection favors interspecific territorial defense, a convergence of recognition marks might be expected (Cody, 1969). The evolution of learned songs may facilitate interspecific recognition and territorial defense. Thus Treecreepers (*Certhia familiaris*) that learn songs of conspecifics as well as of Short-toed Treecreepers (*C. brachydactyla*) defend territories against both species (Thielcke, 1970). Many wren species apparently learn their songs (House and Bewick's Wrens— see below, as well as the Rock Wren, *Salpinctes obsoletus*, and Winter Wren, *Troglodytes troglodytes*, pers. observ.; Long-billed Marsh Wren, *Telmatodytes palustris*, Jared Verner, pers. comm.); interspecific song learning is therefore a distinct possibility among wrens.

Grant (1966) was unable to distinguish the songs of *Thryothorus sinaloa* from those of *T. felix*, two wrens that defend mutually exclusive territories where sympatric in Mexico. This may be an example of song convergence, but it needs further study. Murray (1944) heard a House Wren with an unusual song, suggesting that of either a Carolina Wren (*Thryothorus ludovicianus*) or a Kentucky Warbler (*Oporornis formusus*), and Thomas (1943) reported what appeared to be a typical Bewick's Wren singing both Bewick's and House Wren songs.

I recorded and analyzed the song repertoires of 30 Bewick's Wrens at the Finley Refuge, and in addition listened carefully to thousands of songs while studying the behavior of this species. Individual males are highly variable songsters, having from 13 to 20 song types each. Juvenile males learn their songs from adult males, but I have heard no clear mimicry of other species. House Wrens are also highly variable songsters; a normal song "begins with a chatter of rapid notes and then, without pause, runs down the scale in a cascade of seemingly doubled notes"(Bent, 1948). This is evident from the spectrograms of two typical House Wren songs in Figure 3. The chatter is composed of rapidly repeated syllables (for terminology see Mulligan, 1966) of a broad frequency spectrum; the last half of the song usually consists of several
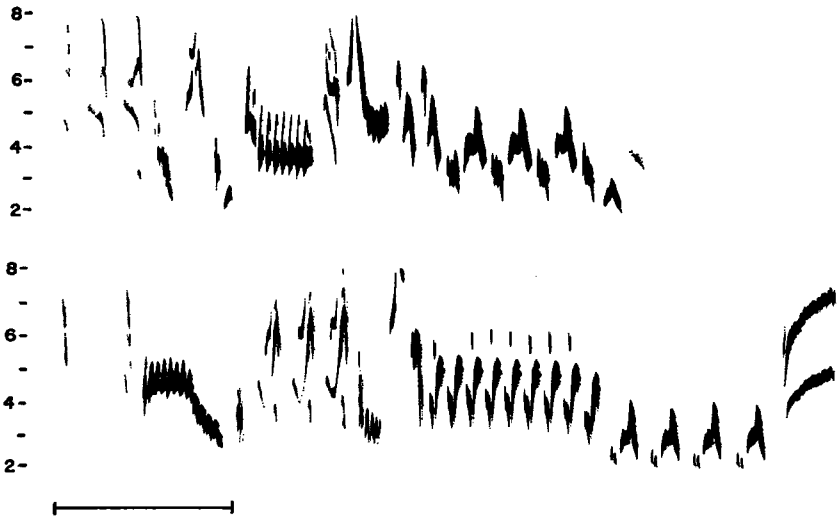
Figure 3. Spectrograms of two typical House Wren songs from the William Finley Refuge. The vertical scale is marked in Khz, and the time marker indicates 0.5 second.

trills of progressively lower frequency. When stimulated (here by song playback), the song frequently ends with a high frequency note type as in the lower spectrogram of Figure 3. The syllable types in the songs of neighboring territorial males are very similar. This suggests, and the interspecific mimicry described below confirms, that juvenile House Wrens also learn songs.

The field ornithologist has no difficulty distinguishing the normal rippling "voluble gabble" of the House Wren from the "fine, clear, bold song" of the Bewick's Wren (Bent, 1948). Yet I have extensive recordings from two House Wren males that copied songs from Bewick's Wrens. Some overlap in song structure among normal songs of the two species does occur, and might be expected among such variable songsters. But one House Wren (Figure 4, Bird A) at the Finley Refuge included in his repertoire portions of at least eight song types (18 notes or syllables) of Bewick's Wrens. Six of those songs are compared with Bewick's Wren songs in Figure 4. Some songs are exact duplicates; the differences in others are no greater than the intraspecific variations that occur in the Bewick's Wren population. These 18 note or syllable types were combined with 19 typical House Wren notes or syllables in a variety of song combinations. Of 3,574 songs studied from this individual, 1,183 (33.1 percent) were unmistakably Bewick's Wren songs, and only 266 (7.5 percent) were typical House Wren songs. The remainder

(2,125, or 59.5 percent) were combinations of the two, but consisted largely of components derived from Bewick's Wren songs.

No other House Wrens were nearby, but three Bewick's Wrens had adjacent territories. During early April 1971 I watched a Bewick's Wren pair here, but their territory had shifted about 50 m when I discovered this House Wren in early June. One Bewick's Wren male foraged occasionally in a fence row the House Wren also frequented. The House Wren did on one occasion supplant this male from a song perch, although I saw no intense aggression like that described below for other portions of the breeding range. The Bewick's Wrens frequently countersang with the House Wren, singing the song type in their repertoire matching the one that the House Wren was singing. Despite a repertoire consisting of an approximately equal number of notes or syllables from Bewick's and House Wren songs (18 and 19, respectively), about 75 percent of the House Wren's singing efforts were of Bewick's songs. This is probably explained by the absence of House Wrens with which to countersing. As has been shown with Chaffinches (*Fringilla coelebs*), the songs an individual uses most frequently are those that also occur in repertoires of neighboring males (Thorpe, 1958); here the House Wren was probably matching song types with the Bewick's Wrens.

I tested the recognition of these atypical House Wren songs by both House and Bewick's Wrens in an area of territorial overlap (Figure 1B). The interspecific song learning undoubtedly caused some dispersion of breeding pairs, for Bewick's Wrens invariably responded very aggressively to these songs. House Wrens were often completely undisturbed, but they exploded into song and approached the tape recorder at the slightest trace of a typical House Wren song.

A second House Wren (Figure 4, Bird B) 8 km northwest of the Finley Refuge mimicked at least 11 song types of Bewick's Wrens. Of 90 note or syllable types I identified in his repertoire, 38 were typical of Bewick's Wren songs. Eight of those song types are shown in Figure 4. As no other wrens were within 0.5 km, behavioral interactions were not studied.

Interspecific song learning may occur in the laboratory when juvenile males are insufficiently exposed to songs of conspecifics (Lanyon, 1960; Thorpe, 1961). A secondary preference for relatively similar songs of other species may then be expressed. Analogous situations may occur in the field, especially where singing conspecifics are not plentiful. This is especially true with the House Wren in the Willamette Valley of Oregon, where isolated pairs or bachelor males are quite common. The two House Wren males that mimicked Bewick's Wrens were both relatively isolated during the breeding season; no other singing conspecifics were
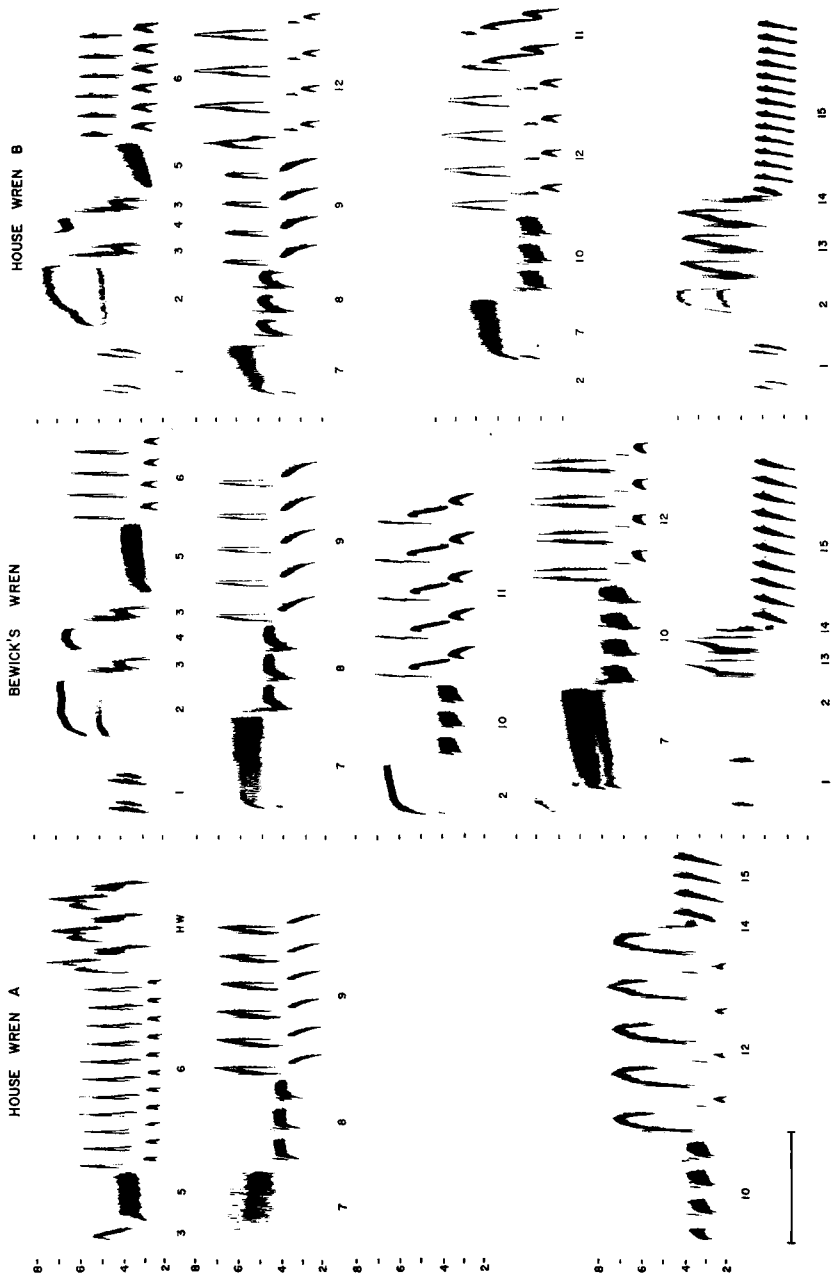
Figure 4A. Spectrograms of songs of two House Wrens compared to those of the Bewick's Wren. Typical House Wren song components are labeled "HW"; portions of House Wren songs that are of Bewick's Wren origin are numbered and indicate the corresponding portion of the Bewick's Wren song.
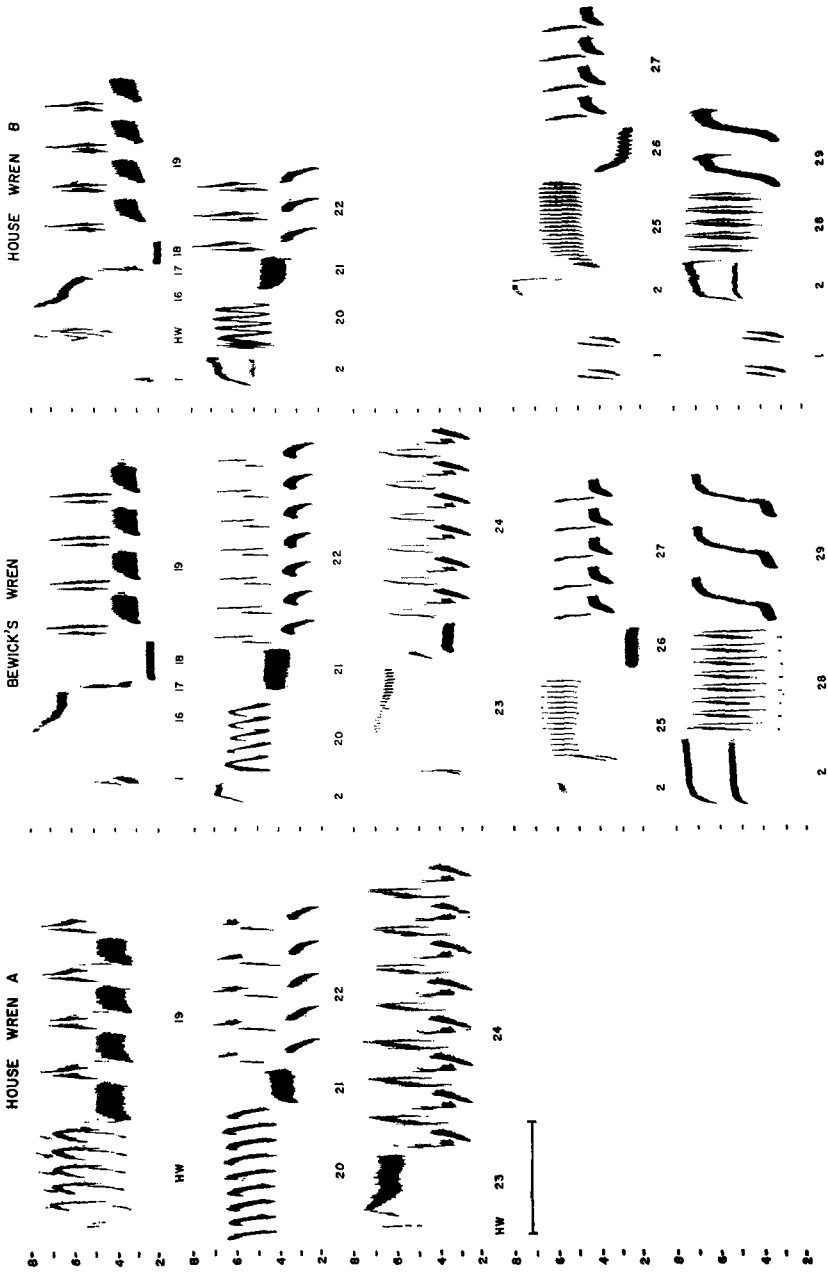
Figure 4B. Similar songs are placed in rows as far as is possible; House Wren spectrograms placed between rows contain elements from two Bewick's Wren songs. The Bewick's Wren songs are from three individuals. The vertical scale is marked in Khz; the time marker indicates 0.5 second.

within earshot. In addition, both males were unpaired. Their isolation and perhaps atypical singing behaviors could both have been factors contributing to their lack of reproductive success.

DISCUSSION

Strong competition between two species is a prerequisite to selection for interspecific territoriality (Cody, 1969; but see Murray, 1971 for a discussion of nonadaptive interspecific territoriality). In my study areas competition appears to be diminished by differences in habitat preference and timing of the breeding season. Interspecific song learning increases aggression and may disperse breeding pairs.

Considerable aggression occurs between these two species in other portions of their breeding ranges. Roads (1929) wrote that these two species in Ohio "never occupy the same territory," and that hostilities were "most bitter." Tyler and Lyle (1947) remarked that "when these two wrens meet, they fight to the death." In northern Ohio, Newman (1961) reported intense fighting between a male of each species; the two pairs eventually coexisted by resorting to territories apparently exclusive of the other species. Sutton (1930) and Brooks (1934, 1947) have offered similar comments from the eastern United States. Unfortunately a recent range expansion of the House Wren complicates interpretation, as closely related species are often quite aggressive during initial contact (Odum and Johnston, 1951).

Sympatric populations of these two wrens have existed in Oregon (Gabrielson and Jewett, 1940) and in California (Root, 1969) for longer periods, and were described by the early naturalists (e.g., Audubon, 1839). In California, Root (1969) found that interspecific territories were well-defined and stable; the migratory House Wren normally displaced the resident Bewick's Wrens from habitats the former had occupied the previous year. The Bewick's Wrens remained at these localities only if the House Wren population was low.

Interactions between populations of these two wren species in California and Oregon appear very different. Competition for nest sites among hole-nesters may lead to aggression (see Kendeigh, 1941 for examples), but probably would not lead to the well-defined, stable interspecific territorial boundaries described by Root (1969). Kendeigh (pers. comm.) relates that House Wrens are more aggressive when breeding populations are high. Similarly Arnold (1966) found that the territorial relationships between *Thryothorus* wren species in Costa Rica could vary with different population densities. In Oregon Bewick's Wrens are more numerous than House Wrens, although Gabrielson and Jewett (1940) considered the latter "abundant." Thus, differences in the local breeding

densities of Bewick's and House Wrens might contribute to the absence of interspecific territorial interactions.

Both wren species occupy a variety of habitat types throughout the West. In California and Oregon alone, although only one subspecies of the migratory House Wren is recognized, nine subspecies of the more sedentary Bewick's Wren are currently recognized (A.O.U., 1957). Presumably the morphological features on which the subspecific taxonomy of the Bewick's Wren is based reflect ecological and behavioral differences as well. In this light, behavioral interactions between the Bewick's Wrens and House Wrens might also be expected to vary in different portions of their breeding ranges.

SUMMARY

The territories of Bewick's and House Wrens overlap extensively at two locations on the William Finley National Wildlife Refuge in the Willamette Valley of Oregon. Intense competition appears to be diminished largely by differences in habitat preference and timing of the breeding season. Interspecific song learning among House Wrens may increase dispersion of breeding pairs of the two species. These two species interact aggressively where sympatric in other portions of their breeding range. The nature of their coexistence in Oregon may be due to low breeding densities of House Wrens or to subspecific divergence in the more sedentary Bewick's Wren.

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