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THE HOUSE WREN BREEDING IN GEORGIA: AN ANALYSIS OF A RANGE EXTENSION

BY EUGENE P. ODUM AND DAVID W. JOHNSTON

To US, the appearance of the House Wren, *Troglodytes aëdon*, as a nesting bird in Georgia has significance beyond the addition of a new species to the list of breeding birds for the state. In the first place, the phenomenon of southward invasion has been a subject of special interest to Georgia bird students for the past ten years. Secondly, the appearance of the House Wren fulfills the last of three predictions ventured by Odum and Burleigh in 1946. Finally, as a result of the work of Kendeigh and his associates at Cleveland, the physiological tolerances of the House Wren to temperature and other factors are known—enabling us to base a discussion of the limiting factors upon something more than pure theory. The writers are indebted to Mr. Chandler Robbins and Dr. John W. Aldrich for checking distribution records and to Dr. S. Charles Kendeigh for reading the manuscript.

The Georgia Record: On June 20, 1950, Odum heard the unmistakable song of the House Wren and was able to observe the bird for several minutes near the Veterinary Clinic Building on the Agricultural Campus of the University of Georgia. The next day, the authors found a pair of birds at this location and watched the female

carrying nesting material into the end of a pipe which formed part of a series of fenced enclosures for animals undergoing treatment at the clinic. The particular pipe selected by the birds was a brace set at an angle to the corner post. The pipe was just under two inches in inside diameter, and the bolt at the top constricted the entrance to about one inch. The nest was about nine inches down from the opening, and was designated as nest No. 1. On June 23, Johnston discovered another female and nest (nest No. 2) about 150 feet from nest No. 1; it was located also in a slanting brace pipe. This nest contained five nestlings which appeared nearly ready to leave the nest. Subsequent observation revealed conclusively that, while there were two females, there was only one male present. Of course there might have been a second male before we discovered the group. On June 26 the first egg was laid in nest No. 1, and on the same day the five young left nest No. 2; both the male and female were observed caring for these young. Two of the nestlings were converted into study skins after we failed to raise them in captivity. Only four eggs were laid in nest No. 1, the last being laid on June 29. All these eggs hatched between July 11 and 13.

In the meanwhile, on July 10, Johnston observed all three adults together near old nest No. 2, and saw a female (probably the one from nest No. 2) go into another pipe near by. This pipe was found to contain a nest (No. 3) with five eggs and was located between nests 1 and 2. Since the eggs began hatching on July 18, it is evident that this set was started about July 2, only about six days after the young had left nest 2. Only three of the five eggs in nest No. 3 hatched. These three young, together with the four in nest 1, were banded and, as far as we know, successfully left the nest. Female No. 2 was also banded. The male was observed to be active at both nests.

The pens in which all nests were located cover about one-half acre and are shaded by a grove of large, old, pecan trees. A number of pens were unused and were overgrown with tall weeds and bushes. Nests 2 and 3 were located among these weeds, but No. 1 was in the center of the used pens. The grove was surrounded by lawns or open grassy areas. The wrens were able to get their food and to carry on other activities mostly within the pen area, but the male was observed on a number of occasions to cross the lawn and a road to shrubbery around two nearby houses. Nest 1 was completely shaded throughout the day, but nests 2 and 3 were both located in pipes on the outermost fence row and were exposed to full sunlight most of the day.

To summarize, the two females and one male built three known nests. Since the House Wren is normally double-brooded, nest No. 2

may be regarded as belonging to the first nesting period; five eggs were laid and five young were fledged. The other two nests may be regarded as second nestings and contained four and five eggs, or an average of 4.5 eggs. Presumably, female No. 1 had a nest in the first period which was completed before the colony was discovered. The total known production, however, was 14 eggs with 12 birds fledged (including the two that were collected) and two eggs which failed to hatch.

Subspecific Identity: We felt it was important to know the subspecies of our birds in order to have definite information as to the probable racial stock from which the invading birds came. Accordingly, on July 18, after the young had hatched and could be cared for by the females, the male was collected. The skins of the male and the two nestlings were sent to Dr. John W. Aldrich, to whom we are indebted for making careful comparisons with specimens in the United States National Museum collection. The following is a direct quotation from his letter of August 4, 1950: "The Georgia breeding specimens of the house wren which you forwarded for identification, turned out to be referable to *baldwini*. As might be expected they most closely resemble the Appalachian mountain birds further north which are to a certain extent intermediate between typical *baldwini* and typical *aëdon*. As you guessed, your Georgia adult specimen is identical with West Virginia specimens. Unfortunately, our material of nestling *baldwini* is nil but your nestlings do not resemble at all comparable specimens from the northeastern seaboard." Breeding House Wrens collected in North Carolina by Burleigh have also been identified as *baldwini*, including a male taken at the extreme eastern section at Beaufort (Pearson, Brimley, and Brimley, 1942; Burleigh, 1937).

Analysis of the Invasion: As pointed out by Odum and Burleigh (1946), the amount and distribution of suitable habitat, as well as climate, may be direct limiting factors. In their paper, the southward invasion of three species, the Robin, *Turdus migratorius*, Song Sparrow, *Melospiza melodia*, and Chestnut-sided Warbler, *Dendroica pensylvanica*, was discussed and the conclusion reached that climate could not have been a limiting factor in establishing the southern boundary of the original range. On the other hand, an increase in suitable habitat plus an increase in population within the original range, and perhaps other biotic factors, were believed responsible for the invasions as observed. All these species, and most others which have shown marked range extensions in recent years, are either species of the forest-edge (*i. e.*, species requiring both trees and vegeta-

tion of grass or grass-shrub life form intermixed) or species of early seral stages of vegetation. White man's land-use practices have increased these types of vegetation greatly, giving species which are adapted to these types and which have inherently wide tolerance for climate a chance to spread. In the above mentioned paper it was suggested that the Blue-headed Vireo, *Vireo solitarius*, House Wren, and Horned Lark, *Eremophila alpestris*, might be expected to extend their breeding ranges in the Georgia region. These predictions were based on the fact that all three species had at that time (1945) become established as breeding birds on the Piedmont Region of North Carolina (for the first two species) and Alabama and Tennessee (for the lark), and there seemed to be no barriers, either climatic or of habitat, to prevent continued spread until they at least occupied all the Piedmont. The spectacular advance of the Blue-headed Vireo deep into the Georgia Piedmont in 1946–48 has already been reported (Odum, 1948). In the spring of 1950, William W. Griffin found the Horned Lark nesting for the first time in Georgia at Rome (personal correspondence). Thus, the nesting of the House Wren at Athens completes the picture in less than five years. In each of these cases, there was enough observation by bird students prior to the discovery of birds in new territory to make it certain that a real range extension was involved and not merely the discovery of previously overlooked breeding birds.

Prior to 1920 the House Wren was apparently unknown as a breeder south of Virginia or Kentucky (except possibly in extreme northeast Tennessee). There are several old records, including one of young birds at Greenville, S. C. in 1888 ("C. M. F.", 1888), but they are not well-documented and must be regarded as questionable. About 1922 the House Wren suddenly began to appear in the North Carolina Piedmont (Pearson, 1934), and within a few years it was recorded as breeding in widely scattered towns (Fig. 1) from Statesville near the mountains to Englehard and Beaufort on the coast (Pearson, Brimley, and Brimley, 1942). While Sprunt and Chamberlain (1949) did not list the House Wren as breeding anywhere in South Carolina, we have well-documented reports which indicate that the species has recently become established, at least on the upper Piedmont of the state. In the vicinity of Greenville, Mr. P. M. Jenness (personal correspondence) stated that he "had no record outside the normal spring migration period until July 5, 1942." At that time he observed a singing male enter a bird box. Conclusive evidence of breeding was obtained in 1945 when a pair nested in a box near his home and, since 1948, one or two pairs have been found nesting at each of two separate localities

in the city of Greenville. At Spartanburg, Mr. Gabriel Cannon wrote that no nesting House Wrens were seen "by the best informed members of the bird group" prior to 1949 when a singing bird was observed in July. In 1950, House Wrens were found in several localities within the city and conclusive evidence of nesting was

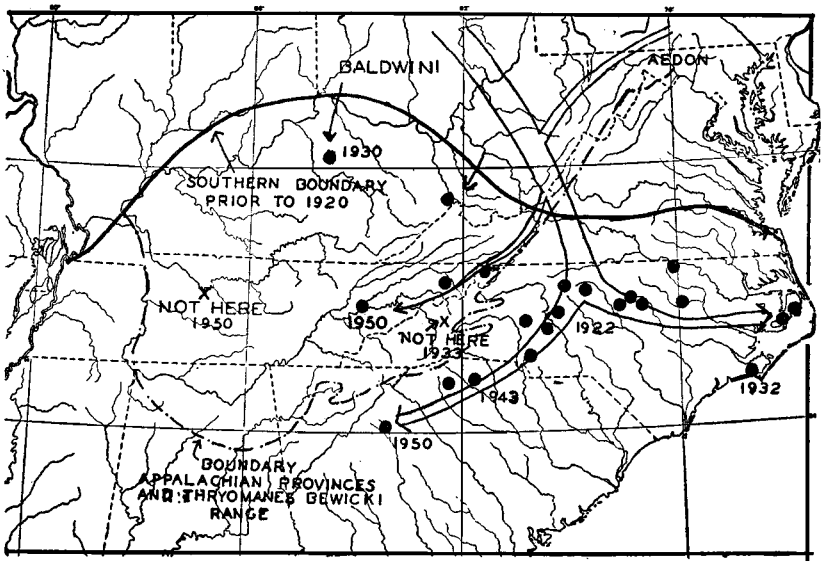

FIGURE 1. Distribution of the House Wren showing the southward extension of breeding range of the Ohio subspecies, *Troglodytes aedon baldwini*. Solid dots are localities where the House Wren has been recorded breeding since 1920, the dates being the first dates of authentic breeding in the indicated regions.

obtained at several places (Crick, 1950). Pickens (1927) reported that a friend found a House Wren nesting on his porch at Greenwood in 1925, but since the Carolina Wren, *Thryothorus ludovicianus*, so often nests on porches and is so often confused with the House Wren, this record may be considered questionable.

In Kentucky, the House Wren apparently did not nest in Lexington until 1930 (Allen, 1946). In Tennessee, it has been reported breeding at least as early as 1934 in the extreme northeast corner (Johnson City region). However, at Knoxville the House Wren nested "for the first time on record" in 1950. Dr. J. C. Howell found three pairs present in one area (Regional Reports, Aud. Field Notes, 4 (5): 276). Up to August, 1950, there was no evidence that the House Wren had yet bred in Nashville, or middle Tennessee generally, according to a letter received from Mr. A. F. Ganier.

With the above information on range extension to the north and the data on racial status, we may at least obtain a rough outline of the probable course of the southward invasion (Fig. 1). The birds which have reached Georgia are evidently of midwestern stock originating in the region of West Virginia where some mixing has occurred with the eastern stock, *aëdon*. Once east of the Appalachian mountains the bird has spread rapidly down the Piedmont region east to the North Carolina coast and south to Georgia. It is interesting, and perhaps significant, that the invasion has been more rapid east of the Appalachians than either within or west of them. The Bewick's Wren, *Thryomanes bewicki*, a competitor, is absent as a breeding bird in the Carolina and Georgia Piedmont and Coastal Plain, but breeds at least sparingly in the Appalachian Provinces as outlined by the dotted line in Figure 1. Just how important the competition between these species is and what the final outcome will be can only be determined in the years to come. It is not likely that the Bewick's Wren is numerous enough or vigorous enough to prevent the House Wren from entering a locality, but even a small amount of competition could slow down the invasion and thus account for the unequal southward progress on the two sides of the mountains. Referring to the two species in the region of Johnson City, Tennessee, Tyler and Lyle (1947) state, "when these two wrens meet, they fight to the death. It may be that time will replace the Bewick's with the House Wren in this locality."

Another noteworthy feature of the invasion is that progression appears to be in "jumps," rather than by steady, gradual expansion. The southward invasions of the Robin and the Blue-headed Vireo were definitely of this "paratrooper" type; that is, birds appeared at a considerable distance beyond the last known point and colonized locally, usually more than one pair appearing simultaneously. Indeed, this may actually be a common invasion pattern. In Georgia, the Robin, Blue-headed Vireo, and the Song Sparrow suddenly nested at points 100 miles from their former range without appearing at intermediate points. In the case of the House Wren, groups of birds have appeared rather suddenly at Spartanburg, Knoxville, and Athens, where bird students are active; to what extent intervening points are occupied has not been determined.

Limiting Factors: Kendeigh (1934) felt that on the basis of information then available, "the southward distribution appears to be controlled by high daily maximum temperatures and competition with the Bewick Wren." Experimentally, 93° F. was found to be a critical temperature for *T. a. baldwini* and the 86° F. average daily maximum

temperature isotherm was suggested as a limiting point beyond which the House Wren did not nest commonly. It is important to note that the former temperature was determined by actual experimentation, the latter being merely a correlation with the then existing southern range boundary. Recent climatic changes, if any, have tended towards increasing mildness which would aid northward invasions but which would actually discourage southward invasions. Biotic factors, therefore, rather than climatic factors were the probable factors limiting the original southern range boundary at Virginia and Kentucky. This conclusion, of course, assumes that there has been no fundamental change in the morphology and physiology of the species itself which would enable it to become more tolerant of southern climates. In any event, there has been an appreciable lag between the time of extensive habitat change and the occurrence of the invasion. Since a population buildup would likely occur within the original range first, this lag would be expected if environmental changes were the basic cause of the invasion. Thus, after the House Wren became an abundant species within its range as a result of man-made changes in the environment (that is, production of a vast amount of forest-edge habitat with suitable nesting sites) it then began to spread southward to occupy territory the climate of which it could tolerate. An interesting feature of the invasion is that the Ohio House Wren, *baldwini*, has reached Georgia and the east coast of North Carolina, and not the Eastern House Wren, *aëdon*, as one might assume and as did Pearson (1934). As previously indicated, future observation and study will be required to determine if the absence of the Bewick's Wren east of the Appalachians has anything to do with this distributional pattern. The present situation should provide an unusual opportunity to study further the relationship between these two species which occupy a similar niche.

While climate might not have been the absolute limiting factor in southward distribution in the original range (prior to 1920), it is quite possible that the species may now be approaching a point where climate will be more and more important in determining ultimate success and more of a barrier to further spread. The House Wren is believed to be relatively stenothermic as compared with the Robin and Song Sparrow, to mention two other species invading in the same territory. At least we now have an opportunity to analyze the situation and perhaps to venture predictions for the future.

Weather conditions during the months of May, June, and July, 1950, at Athens, where the species is at least starting to get a foothold, were about as normal as one could possibly expect. Average monthly

temperatures were no more than a degree from normal and precipitation was likewise near normal. There were no bad storms or unusually hot or cold periods. The first appearance of birds here, therefore, was not during an unusual breeding season, although the early spring and winter preceding had been unusually warm and dry. In Figure 2

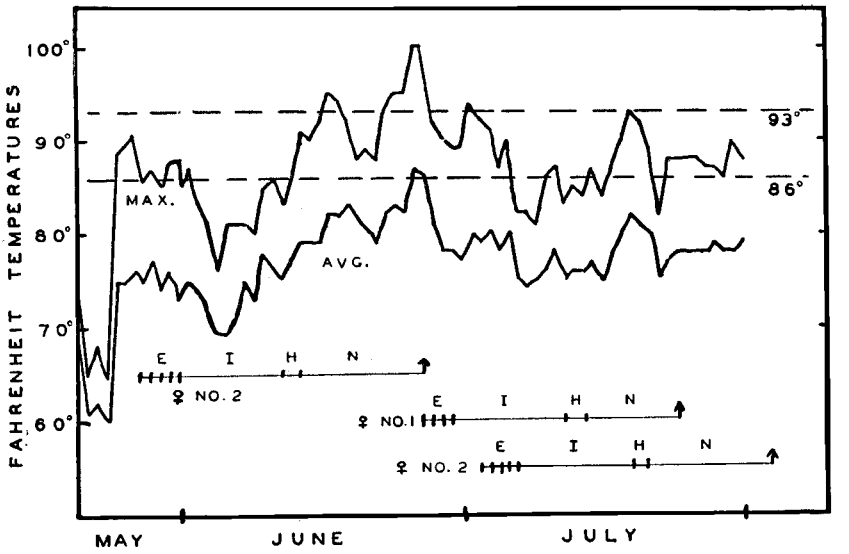

FIGURE 2. Daily maximum and average temperatures during egg-laying (E), incubation (I), hatching (H), and nestling period (N) of three broods of House Wrens at Athens, Georgia, in 1950. See text for explanation.

daily maximum and daily average temperatures for the known breeding period are plotted. The time of egg-laying of the first brood of female No. 2 was calculated from the known time of nest-leaving, assuming a nestling period of 15 days and an incubation period of 13 days (Kendeigh, 1941). As can be seen in this figure, there were about five periods during which maximum temperatures were above 86° F. (the limit originally suggested by Kendeigh) for several days at a time. Since Kendeigh (1934) has shown that the time of egg-laying is a critical period, it is important to note that egg-laying occurred in one of these hot spells in each of the three known clutches. In May the nights were cool and average temperatures lower than during other egg-laying periods, but the week during which female No. 1 was laying was the hottest of the breeding periods, the maximum temperatures being well above the 93° F. found by Kendeigh to produce physiological distress. It is important to note that only four eggs were laid at this time. Thus, egg-laying at Athens in 1950 occurred at about the most

unfavorable times possible as far as maximum temperatures were concerned. In spite of this and the fact that two nests were in the direct sunlight, nestlings were successfully raised, but their number was reduced. Thus, five eggs were laid in the nest of the first nesting period and an average of 4.5 in the two second nestings. This may be compared with a 6.5 average of the first set and 5.2 for the second set as found by Kendeigh and Baldwin (1937) for *T. a. baldwini* at Cleveland, Ohio. Also, two eggs of one of the second sets failed to hatch. Again Kendeigh has shown that the number of eggs decreases and the percentage of unhatched eggs increases with an increase in temperature.

Thus, it would seem that the Ohio House Wren can tolerate conditions on the Georgia Piedmont in an average year, but its reproductive potential is likely to be less than that farther north; in other words, temperature is exerting a limiting effect. Accordingly, climate appears to be more and more a barrier as the species spreads southward. In time, of course, a small, more heat-tolerant race might become selected or evolved, or lower mortality might counterbalance the lower reproductive potential. Perhaps for the first time in the history of North American ornithology we have a good opportunity to watch the interaction of climatic and biotic factors on a species expanding its range, and moreover, a species which has been well-studied both in the field and in the laboratory. It is hoped that this paper will stimulate bird students in southeastern United States to record all possible details on the species. Absence or failure of the species in a given locality is just as important for the records as is the converse.

SUMMARY

1. In June, and July, 1950, the first nests of the House Wren known in Georgia were observed at Athens. One male and two females constructed three nests. The first nest found (nest No. 1) was believed to be a second nesting and contained four eggs all of which hatched and fledged. The other female had two broods, the first of which contained five young (two were collected) and the second contained five eggs of which only three hatched and fledged. All nests were located in metal fence posts within a one-half acre grove containing fenced enclosures for domestic animals. Only one nest, however, was well-shaded by the pecan trees. The male of the colony was collected and proved to be *Troglodytes aëdon baldwini;* it was identical with West Virginia specimens.

2. Since the House Wren was not known to nest south of Virginia and Kentucky prior to 1920 but has since appeared in many points of

North Carolina, upper South Carolina, and western Tennessee, it is clear that a well-marked southward invasion of the southeast by birds of mid-western stock (*baldwini*) is occurring. Progress has been most rapid in the Piedmont Region, east of the Appalachians, where Bewick's Wren is rare or absent as a breeding bird. The invasion resembles that of the Robin and the Blue-headed Vireo recently documented, in that it has occurred by "jumps"—groups of birds colonizing locally, often at some distance from the last known point of their southern range.

3. Analysis of climatic conditions and known physiological tolerances of the species leads to the conclusion that biotic rather than climatic factors limited the southern boundary of the range as it existed prior to 1920. However, since the amount of reproduction (as judged by the number of eggs laid and hatched) by the Athens colony was definitely decreased by high temperatures during the egg-laying periods, it is thought that climate, particularly maximum daily temperatures during the breeding season, will exert an increasingly important limiting effect as the species moves southward.

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