REGULATION OF NESTING TIME AND DISTRIBUTION IN THE HOUSE WREN

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AT the Baldwin Bird Research Laboratory, near Cleveland, Ohio, where this study was carried on between 1921 and 1938, House Wrens (*Troglodytes aedon baldwini*) commonly begin their first clutches in the latter half of May, and individuals that nest a second time lay their second clutches in late June or early July. Considerable variation, however, occurs. The first clutch of the year was started on 7 May in 1921 but not until 4 June in 1926. What regulates the time of nesting in a species and why it varies from year to year are interesting questions and may give information on what controls the breeding distribution of the species. Doubtless a number of internal physiological and external environmental factors are involved (Wagner, 1960; Marshall, 1961). The present study, supported by a grant from the National Science Foundation, attempts to analyze some aspects of the problem.

That most birds in high latitudes nest in the spring or early summer, rather than in the autumn or winter, depends in large part on the stimulating effect of increasing photoperiods for the development of the gonads. The House Wren winters principally in the Gulf states and hence is subjected to increasing photoperiods after the winter solstice in late December. Although no study has been made of the gonad cycle in this species throughout the year, there is reason to believe that the gonads are in full functional condition at the time of the birds' arrival on their nesting territories in the northern states and southern Canada.

The median date for activity of the *first* males at nest boxes in northern Ohio is 1 May, of females, 11 May. The median date for *all* males to begin nesting activities is 11 May, for females, 20 May (Kendeigh, 1941*a*). Late arriving birds may, however, continue to establish nesting activities throughout June and the first half of July. Differences in beginning of nesting activities any year must obviously depend, in part, on the time of the birds' arrival.

For species in desert regions, the coming of rains may initiate nesting activities. In arctic regions, areas free from snow may be required by ground-nesting species. Differences between localities and from one year to another in time of nesting activities often agree with first availability of food. None of these factors appears to be critical for the House Wren.

Temperature, however, may be important. In her work with the Song Sparrow (*Melospiza melodia*), Nice (1937) indicated that first eggs in early April were laid five days after three days averaging 18.2 C, and general laying began five days after three days averaging 22.9 C. If egg laying was delayed,

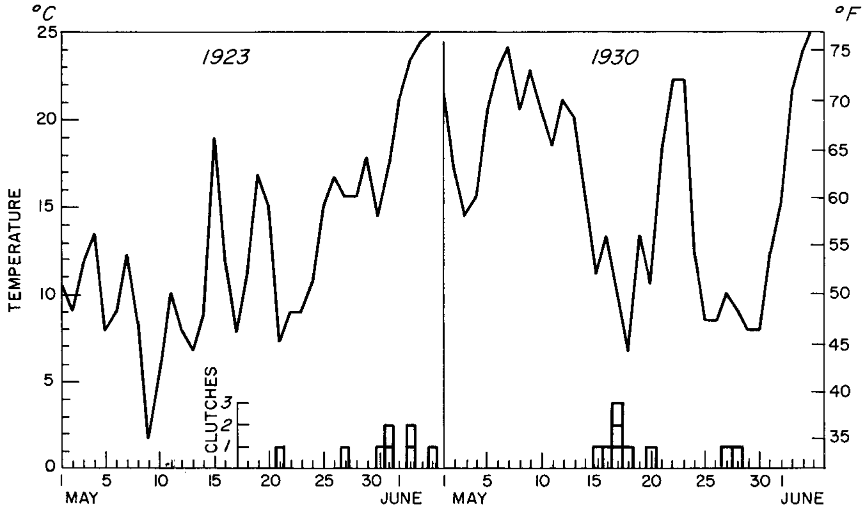

FIG. 1. Dates on which clutches were started and mean daily temperatures during May and early June 1923 and 1930.

the temperature threshold decreased 0.87 C per day thereafter for two weeks.

Pied Flycatchers (*Muscicapa hypoleuca*) do not begin laying until mean daily temperatures exceed 10 C, and a later drop in temperature to 6 C may interrupt the beginning of new clutches in the species (Curio, 1959). That temperature also affects the initiation of egg laying in the House Wren is evident in comparing the two years, 1923 and 1930 (Fig. 1).

It has been suggested that the onset of egg laying is induced by the accumulation of heat since the beginning of spring. Kluijver (1952) summed the daily mean temperatures above 0 C each year, 1912 to 1951, for the period from 16 March, when nest-building activities began in the Great Tit (*Parus major*), to 20 April, the mean "determinant" date for egg laying, and found a high inverse correlation with the onset of egg laying. Laying did not always start, however, as soon as a fixed "warmth–sum" was reached. Cold weather, prevalent at the time, would delay laying, and other factors, such as relative humidity, appeared to exert an influence. The accumulation of heat may have been more important in developing the birds' food of moth caterpillars, upon which they depend almost entirely for feeding their young, than because of any direct effect of the heat upon the gonads (Kluijver, personal communication; Lack, 1956). It is not practical to correlate the accumulation of heat during the spring which the House Wren experiences with the onset of laying, as the location of individual birds in their wintering range and at various times during their migration northward is unknown. The effect of temperature on the initiation of egg laying, however, may be more direct.

The egg is mostly formed a few days before it is laid. The yolk material is deposited around the oocyte while it is still in the ovary, then ovulation occurs as the oocyte bursts out of the ovarian follicle and enters the oviduct. Albumen, shell membranes, and the hard shell are added as the egg moves down the oviduct. The passage down the oviduct in the domestic fowl, and presumably also in other birds, involves approximately the last 24 hours before the egg is laid.

Riddle (1916) showed for the Domestic Fowl that the rate of growth of the oocyte in the ovary is very slow until five to eight days before ovulation, but then it increases nearly 26 times; the transition from one rate to the other occurring in a single day. Romanoff (1943) verified this sudden outburst of growth not only for the fowl but also for the pheasant, quail, and duck, with the change in rate beginning in all species five or six days before ovulation. These are all nidifugous species.

In the nidicolous Starling (*Sturnus vulgaris*), Bissonnette and Zujko (1936) showed that the increase in diameter of ovarian follicles was slow until late March, then increased 32 times in rate, being most rapid during the five days before ovulation. In the Jackdaw (*Corvus monedula*), rapid enlargement begins four days before ovulation (Stieve, 1919). During the four and one-half days before ovulation in the pigeon (Riddle, 1927), coincident with the onset of rapid growth of the oocyte, the oviduct increases in weight by 1,000 per cent, the suprarenals hypertrophy, blood sugar is raised 20 per cent, blood calcium by 100 per cent, blood fat by 35 per cent, and blood phosphorus by 50 per cent. Blood phosphorus reaches its peak three days before ovulation; blood fat, blood calcium, and sugar two days before; the suprarenal size at the time of ovulation; and the oviduct a day after ovulation as the egg passes through it and is laid. Any factor that affects the energy resources of a bird, such as temperature, would conceivably be of vital importance on the deposition of yolk and these other changes and, consequently, on the time of laying.

As far as I am aware, little or nothing is known as to what determines the time for the sudden increase in growth of the oocyte in the ovary four to five days before it is ovulated and five to six days before it is laid as an egg. Since the changes involved affect not only the oocyte but the accessory sex organs and the blood chemistry as well, they are probably under hormonal control. Copulation with the male appears not to be the releasing stimulus in the domestic fowl that continues to lay eggs almost daily without cocks present. However, it may be important in wild species. Copulation, in the House Wren, although seldom observed, was believed to occur immediately after the female chose her nest box and a male. Nest building by the female generally begins on the same day, and the first egg is laid three to five days later.

In his study of the Swift (*Apus apus*), Lack (1956) believed that the first egg of clutches was laid five days after an improvement in the weather, as did Nice (1937) for the Song Sparrow. In the Great Tit, Kluijver (1951) places the "determinant date" for the laying of the first egg four days previous (i.e., three days before ovulation). In an earlier study with the House Wren (Kendeigh, 1941*b*), a correlation was obtained between the average temperature during the three days before the egg was laid and its weight. Likewise, a correlation was found between the mean temperature 24 hours before time of ovulation (i.e., the second day before laying) and the size of the clutch.

Kluijver (1951) assumes that four days is the time required for the rapid deposition of yolk and other changes, since this was the usual interval observed between a significant temperature change and the laying of the first egg of a clutch. Once this yolk deposition was started, the first egg was invariably laid, and an additional egg was laid each day until the clutch was completed, regardless of intervening unfavorable weather. This is not the case in all species, however. Kluijver states that egg laying in the Blue Tit (*Parus caeruleus*) is often interrupted by a fall in temperature. In the Swift, the interval between eggs is longer in bad weather (Lack, 1956). Missed days in egg laying are not infrequent with the House Wren, and, as indicated above, the size of eggs and the number in a clutch appear to be influenced by temperature even after the clutch has been started. By using a special stain introduced with the food, Riddle (1911) was able to measure the daily deposition of yolk around the oocyte in the domestic fowl and found that it often fell to one-half the maximum, and occasionally was lacking for 24 hours. For these various reasons, therefore, we do not accept a "determinant" date four or five days before laying but believe that temperature may influence the egg laying up at least to the time of ovulation and possibly up to the actual deposition of the egg into the nest.

TEMPERATURE THRESHOLDS

The average air temperature was first determined for the fifth day before the laying of the first egg, following the practice of previous investigators, in each of 122 first clutches for the 18 years involved in this study. This was 15.1 C with a wide standard deviation of ± 5.1 C. The average temperature was then determined for the three days preceding the laying of the first egg, the same interval as used in our previous study (Kendeigh, 1941*b*). This temperature was 14.8 C ± 2.7 C. The two average temperatures are not significantly different, but the smaller standard deviation for the three-day period

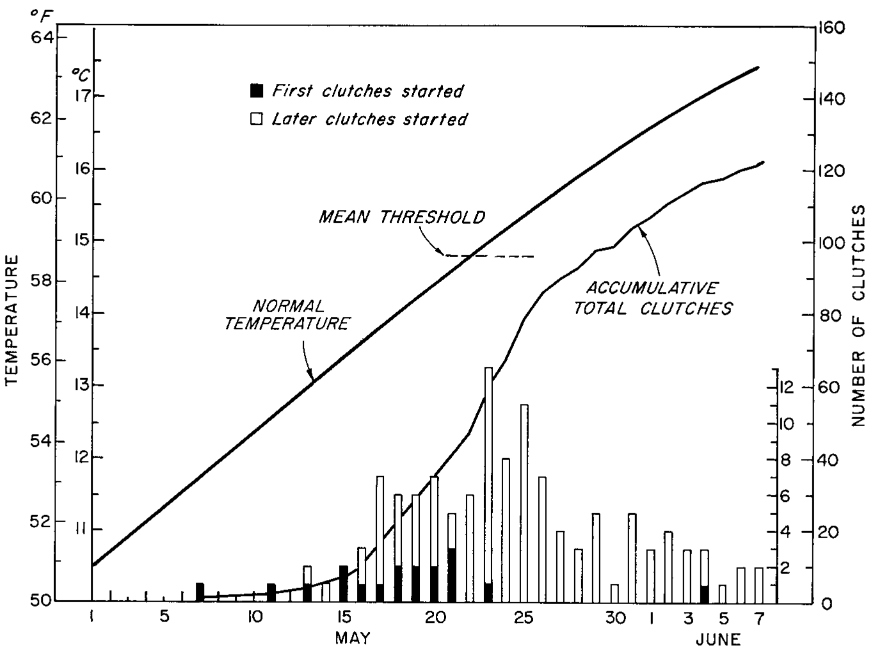

Fig. 2. Number of clutches started each day, accumulative number started, and normal air temperatures, during years 1921 to 1938, inclusive.

of about one-half of the standard deviation for the fifth day before laying may indicate that the three-day period is of greater significance.

Mean daily temperatures of 14.8 C and above, lasting one to several days, may occur repeatedly throughout May, being separated by periods when the temperature falls below this level. Such periods of high temperature, if they come before the middle of the month, are often not followed by egg laying; but after 15 May they are almost invariably followed by the deposition of eggs within the average of 2.8 days (1–5 days). The year 1926 is an exception. Heavy mortality of birds over the preceding winter so reduced the wren population that first eggs were not recorded until 4 June. There is no evidence at hand to determine whether this temperature threshold becomes lower with the progress of the season, as found by Nice (1937) for the Song Sparrow.

When the number of first clutches started each day during May and early June of the 18-year period is plotted (Fig. 2), the peak comes about 23 May. It is significant that the normal temperature at this time is very close to the mean threshold of 14.8 C. The decline in number of new clutches started at temperatures above 14.8 C is not because these temperatures are unfavorable

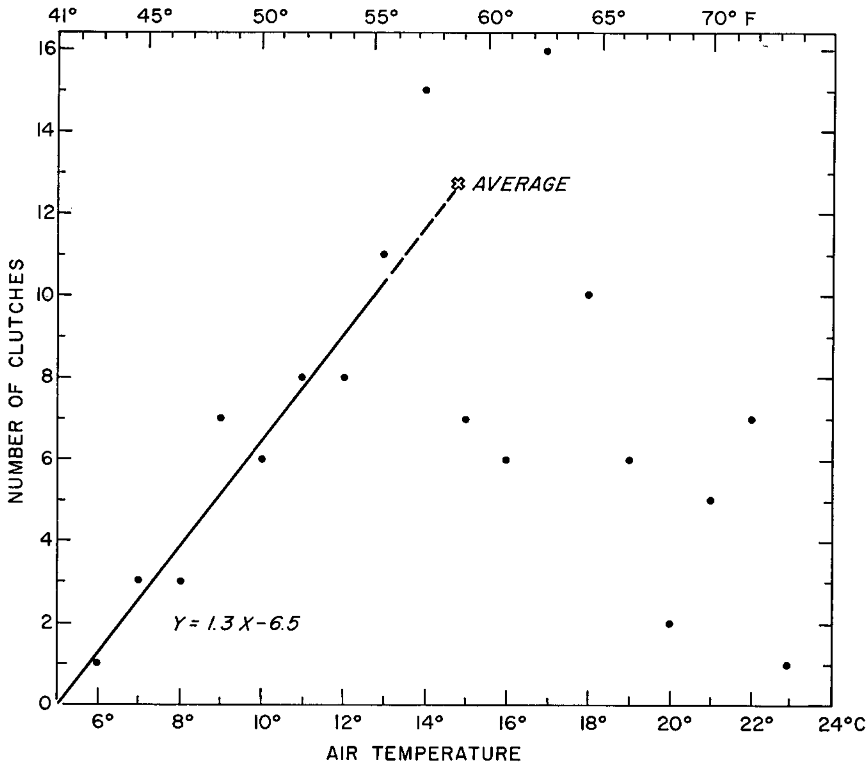

Fig. 3. Correlation between number of clutches started and mean air temperatures for the three preceding days.

but because of the decrease in arrival of new birds from the south and of the nesting area becoming saturated with territories.

When the number of clutches started is plotted against average air temperatures for the three days preceding the first egg (Fig. 3), it is evident that hardy birds can begin laying at temperatures well below the average threshold of 14.8 C. However, the number of such clutches started decreases linearly with drop in temperature, and an absolute threshold of 5 C is indicated. The seven clutches started at temperatures of 6 C, 7 C, and 8 C were scattered through the month, viz., 13, 14, 16, 22, and 24 May.

RELATION TO NORTHWARD DISTRIBUTION

Cleveland, Ohio, is near the center of the distributional range of *T. a. baldwini.* This subspecies is uncommon at Quebec, in Quebec Province, and absent at White River, Ontario (Kendeigh, 1934). The *A.O.U. Check-list of North American Birds* (1957) indicates, however, that *T. a. parkmanii* has spread from the west around the north side of Lake Superior, northward to a line extending from Minaki in western Ontario to Lake Abitibi on the eastern boundary of the province. This invasion may have been relatively recent.

If the temperature of 14.8 C is taken as the threshold for initiation of general egg laying, the later rise in temperature would delay general nesting until early June at Quebec and until middle June at White River (Fig. 4). This would agree roughly with the formula suggested by Baker (1938) that, with passerine species, the start of the egg season gets later and later northward at a rate of about 18 days per 10° of latitude, although between 32°N and 46°N there is a general tendency for breeding to start later than would be necessary to conform with this rule. Cleveland lies at about 41.5°N, Quebec close to 47°N, and White River at about 48.5°N. That no nesting of *T. a. baldwini* is reported at White River may be due to the very late date at which temperatures become favorable, fully a month or a month and a half after the bird's gonads have matured. This is not to gainsay that a few hardy birds might attempt nesting as soon as temperatures went above 5 C. It is possible that the population of *T. a. parkmanii* has more of these hardy individuals than does *T. a. baldwini*, since this subspecies occurs still farther to the north.

Egg laying and incubation are about equally energy-demanding processes (Kendeigh, 1962), and inability of the bird to mobilize sufficient energy at the prevailing temperatures may be the direct factor that limits northward dispersal. At 14.8 C, my calculations indicate that the heat energy the incubating bird would need to apply to the eggs in order to maintain them at the proper incubation temperature would amount to 44 to 68 per cent of the productive energy that the bird had available. Productive energy is the energy that a bird can produce for various activities over and above what it requires for existence. The lower value would be sufficient were the next box fully exposed to the sun throughout the day; the higher value would be required if the nest box were continuously in the shade. As air temperatures drop, the bird can spare less from the maintenance of its body temperature, yet the eggs require the application of more heat to keep them at the proper incubation temperature. At 5 C, the amount of heat that would need to be applied to the eggs in nest boxes in the sun and shade would require 1.5 to 2 times the amount that a bird of average capacity could accumulate at this temperature. Energy reserves in the body would need to be drawn upon and the situation would have to be very temporary. The amount required for egg laying at these temperatures would be within the same range. Since the bird must use productive energy for other activities as well as incubation, only individuals of unusual energy-mobilizing capacities would be able to carry on

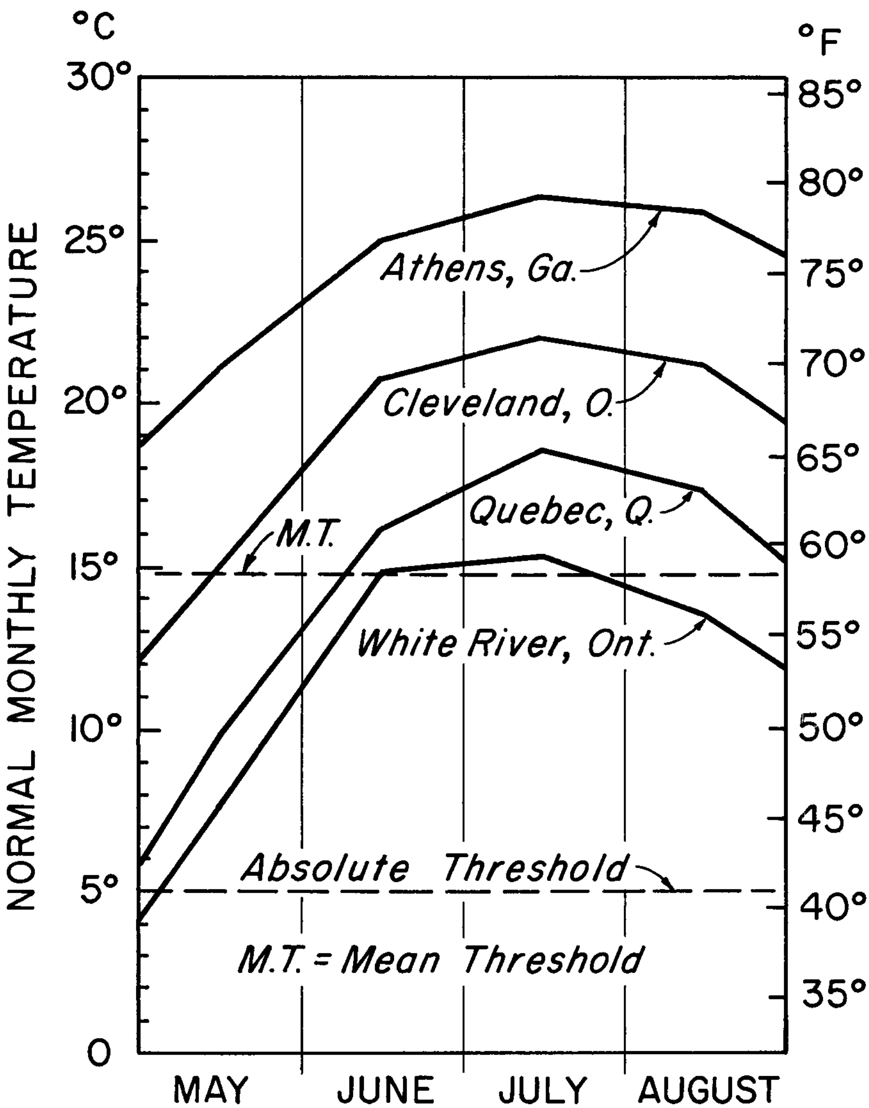

FIG. 4. Progress of normal air temperatures at four localities from May through August.

nesting activities at this temperature. At still lower temperatures it would become impossible.

RELATION TO SOUTHWARD DISTRIBUTION

The farthest south that the House Wren has penetrated, and this only in recent years, is in the vicinity of Athens, Georgia (34°N). Temperatures are suitable for egg laying at Athens in April (Fig. 4), but the birds are probably not then ready to do so because of the undeveloped gonads. At this time of year, photoperiods increase in length less rapidly in the south than in the north. Odum and Johnston (1951) found nesting at Athens beginning in late May and continuing into July. Of three known nests, one contained five nestlings, one had five eggs of which only three hatched, and one had only four eggs. In northern Ohio, seven eggs per clutch are common in May and early June, six eggs from early June to middle July, five eggs from early to late July, and four eggs from middle July to August. There is evidence that high temperatures tend to curtail the laying of large clutches of eggs (Kendeigh, 1941*b*). It is of interest that normal temperatures during May at Athens are similar to those during June and July at Cleveland (Fig. 4). The four-egg clutch at Athens was laid during and immediately following the highest temperatures during the entire summer (30.6 C). There is doubtless a limit southward where temperatures become so high during May as to discourage egg laying altogether.

SUMMARY

Onset of egg laying in the House Wren is regulated to the general time of year by the development of the gonads under the stimulus of changing photoperiods, to the time of month by their return to the breeding grounds from spring migration, and to the precise day by temperature. Low temperatures, particularly during May when the development of the gonads puts the birds in breeding condition, may limit the breeding range northward and high temperatures may limit the breeding range southward. Limitation of the breeding range appears thus to be determined by the lack of synchronization between the occurrence of favorable temperatures and photoperiods—northward because the onset of favorable temperatures is too slow, southward because it is too fast.

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