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THE POSSIBLE INFLUENCE OF NESTBOX SIZE ON
NESTING BEHAVIOR AND REPRODUCTIVE SUCCESS
IN THE HOUSE WREN (TROGLODYTES AEDON).

by

Mary Anne Sydlik

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Western Michigan University
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THE POSSIBLE INFLUENCE OF NESTBOX SIZE ON NESTING
BEHAVIOR AND REPRODUCTIVE SUCCESS IN THE
HOUSE WREN (TROGLODYTES AEDON)

Mary Anne Sydlik, M.A.

Western Michigan University, 1980

Recent studies (Löhrl 1973, Karlsson and Nilsson 1977) have shown that there may be a relationship between nestbox size and clutch size in several passerine species. The present study was designed to determine whether nestbox size influences the clutch size and reproductive success of House Wrens (Troglodytes aedon) and to test possible cues a female might utilize to assess the size of a given nestbox. Four types of nestboxes were used in the study; they varied in floor surface from 3 inches by 3 inches to 8 inches by 8 inches. No statistically significant differences in clutch size or reproductive success were found, but this might be an artifact of a small data base. Possible differences in nest building (type of nest built, time taken to build the nest, weight of the nest, etc.) may be related to nestbox type and this in turn may influence nestbox choice in House Wrens.

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Mary Anne Sydlik

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CHAPTER I

INTRODUCTION

The debate over exactly which environmental and physiological factors might be involved in the determination of avian clutch size has been explored in depth in the literature (Lack 1954, Royama 1969, Charnov and Krebs 1974, Brockelman 1975, Ricklefs 1968, Cody 1966; see Klomp 1970 for an extensive review). Factors such as food availability, age of female, date of laying, habitat quality, territorial quality, population density, inherited differences, and to some extent mating system have been implicated in the determination of clutch size (Lack 1954, Klomp 1970, Perrins and Moss 1975, Brewer and Swander 1977, Orians 1969, Martin 1974).

A recent development in this debate is the possibility that in hole-nesting birds the size of the nestbox may have a significant influence on the size of the clutch laid and, therefore, on total reproductive output (Löhrl 1973, Nilsson 1975, Karlsson and Nilsson 1977, Mertens 1977b). Studies with the Great Tit (Parus major) have indicated that these birds prefer larger cavities when given a choice (Löhrl 1970, Nilsson 1975) and that more eggs are laid in and more young fledged from large (20 cm diam.) than from smaller (9 cm diam.) cavities (Löhrl 1973).

Karlsson and Nilsson (1977), analyzing clutch sizes of Great Tits, Pied Flycatchers (Ficedula hypoleuca), Starlings (Sturnus vulgaris), Marsh Tits (Parus palustris), and Willow Tits (Parus montanus), found that all but the Starlings responded to an increase in nestbox bottom area with a corresponding increase in clutch size.

Why should a bird adjust its clutch size with the size of its nestbox? It has been suggested that the ultimate factor involved is increased survival of nestlings due to the combined effects of the insulative qualities of the nest environment, the energetic efficiency of both parents and young, and optimal nestling temperatures (Löhrl 1973; Mertens 1969, 1977a,b; Dunn 1976; Royama 1966; O'Connor 1975a). Karlsson and Nilsson (1977), while supporting the general concept involved, have objected to the ultimate importance of optimal thermoregulatory conditions for the young. The argument in favor of this view of the importance of nestbox size is that the parents nesting in larger cavities or boxes are better able to meet both the thermal and nutritional needs of a larger brood with less effort owing to the insulative qualities of the nest environment (Löhrl 1973).

Parents with altricial young in the nest must divide their attention between fulfilling their own daily needs (food, rest, grooming, etc.), providing sufficient food for the developing young, and meeting

the thermal requirements of the young through brooding behavior. The allocation of reproductive time and energy should be made in such a way that the young are maintained at the best temperature (i.e., maximum growth, minimum maintenance costs) for the least amount of food, and resulting in the maximum number of fit offspring produced. In this framework it seems logical to expect that any factor which reduces the amount of time and energy which must be expended in feeding and/or brooding the young would be favored by natural selection, provided of course that it did not in some way prove detrimental to the parents or young. It could also be argued that a female who was capable of assessing the thermal characteristics of her nestbox or cavity and then adjusting her clutch size to take advantage of those proximate thermal conditions should be favored in terms of fitness over a female who lacked this ability.

Passerine nestlings are maintained within a fairly narrow range of temperatures ($34-36^{\circ}\text{C}$), with their body temperatures rarely falling below 30°C and actually reaching as high as 39°C in very young birds while being brooded (Ricklefs 1974). Three main factors operate to protect the ectothermic young from fluctuating ambient temperatures: parental behavior (mainly brooding rates), the insulative qualities of the nest environment (both nest and brood size), and the continually improving

thermoregulatory abilities of the young. Parental brooding is the main source of heat for the young early in the nestling period. Brooding is time-consuming and may attract predators to the nest; accordingly, modifications of the nest environment which reduce the amount of time required for brooding would be beneficial.

Nestbox size and the insulative qualities of the nest are two factors which can help to reduce the amount of time spent brooding since they can reduce the heat loss of a brood in a cold environment (Royama 1966, Løhr 1973, Mertens 1977a, b). Nest insulation can influence egg temperatures in a similar manner and thus reduce the amount of time spent incubating (White and Kinney 1974). Birds nesting in larger cavities or nestboxes build larger and presumably better insulated nests (Løhr 1973, the present study). Great Tits build larger (7.0 cm versus 1.5 cm diam.) and thicker nests in larger cavities, a fact which led Løhr (1973) to conclude that the ectothermic eggs and young in these nests may have better insulative protection against hypothermia than those found in smaller cavities.

Another factor influencing the amount of time spent brooding may be brood size, with brooding rates tending to decline as brood size increases (Royama 1966, Yarbrough 1970, Mertens 1969, O'Connor 1975a, Dunn 1976). This is generally considered to be the result of decreased heat

loss due to a lowered surface to volume ratio in the larger broods. If this is true, it would seem to indicate that adults raising a larger brood in a larger nestbox may be able to reduce the amount of time spent brooding their young.

Nestbox size may have a direct influence on nestling temperatures as the young grow and improve their ability to maintain a constant body temperature. It is generally accepted that nestling temperatures increase and become more narrowly regulated as the young mature (Ricklefs 1974). This trend is believed to be a reflection of the fact that the (lower) temperatures which are probably appropriate for embryonic development are slowly giving way to the higher temperatures which are more appropriate for adult physiological processes (O'Connor 1975b). In hole-nesting species, these higher body temperatures may increase the threat of hyperthermia (Mertens 1969, 1977a,b; Løhr1 1973; O'Connor 1975a). Løhr1 (1973) has reported that as the Great Tit nestlings grow, they tend to move apart, presumably to facilitate heat dissipation and to lower the risk of hyperthermia. Blue Tit (Parus caeruleus) nests tend to become trampled down to a flat base as the young grow, giving them more room in which to move apart (O'Connor 1975a). In larger nest cavities, these older nestlings would have more space in which to move apart as over-heating became more of a problem

and would mean that young in large nest cavities have a lower risk of hyperthermia than those found in smaller cavities (Løhr 1973).

Decreased thermal threat to the young and lowered brooding rates may not be the only benefits associated with raising a larger brood in a larger cavity. Adults with young in the nest must also provide sufficient food to their offspring. Without sufficient food, the young may lag in growth and may eventually die. Food supply, as a matter of fact, has been accepted as being the most important environmental factor limiting clutch sizes (Lack 1954). Parents who are able to decrease their brooding rates due to reduced heat loss provided by the nest environment will be free to collect more food for their young. In addition, there is evidence that a larger brood size may reduce the food requirement per young, especially in well-insulated hole nests, by reducing overall heat loss (Royama 1966). This can be interpreted to mean that adults raising a larger brood in a larger cavity may not have to expend as much energy in collecting food for each nestling as would have been expected if there were no so-called "brood effect".

It is possible that the apparent relationship between nest hole size and clutch size could be explained by either differences in the ages of the females involved in the studies and/or variation in the time of occupation

of the cavity, which could lead to significant differences in egg laying dates and clutch sizes. There is evidence to suggest that within a given species younger females lay smaller clutches than older females (Klomp 1970). Fortunately, the birds Löhrl (1973) worked with were banded and some of the females nested on the same territories during both years of his study. Since he switched nest hole types for each location in the second year of the study, he was able to compare clutch sizes for females which had initially laid large clutches in large cavities in the first year and then nested in small cavities the second year; these females laid smaller clutches the second year (from 12-14 eggs to 9-10 eggs). Another general trend in avian clutch size is for the number of eggs per clutch to decline during the breeding season (Klomp 1970); Great Tits apparently fall into this category (Klomp 1970). One concern, then, is that perhaps the larger nest holes were occupied earlier in the breeding season and that as a result the females laying in these holes were able to begin laying sooner than those in the small cavities. Löhrl (1973) stated that all nest holes were occupied all year round and that there were no significant differences in the average laying dates for the two nest hole types in either year of the study.

If it is accepted that cavity size influences the

clutch size of some hole-nesting birds, then the females must have some means of assessing the size of the cavity. Løhr (1973) has suggested that one of the following types of information might be used: 1. optical information concerning the actual size of the cavity; 2. tactile information obtained by moving around inside the cavity; or, 3. indirect information acquired in relation to the amount of energy expended to build a larger nest in a larger cavity.

The present study was undertaken in an attempt to test several hypotheses concerning the influence of nestbox size on the nesting activities, clutch size, and reproductive success of the hole-nesting House Wren (Troglodytes aedon). The first question addressed was whether or not nestbox size influenced the clutch size and reproductive success of House Wrens. The second question involved trying to resolve the problem of how a female might be determining the size of her nestbox. Last of all, data were collected on the types of nests built in varying nestbox types and the amount of effort (in terms of time) spent building these nests. Some attention was given to the possibility of nestbox size preferences.

CHAPTER II

MATERIALS AND METHODS

Nestboxes

Four nestbox types were used. The only nestbox dimension that varied was the size of the floor surface. Type A nestboxes had a floor surface of 4 inches by 4 inches (area 16 sq.in. and volume 86.4 cu.in.); this was considered to be the normal size for a House Wren nestbox. Type B nestboxes had a floor surface of 8 inches by 8 inches (area 64 sq.in. and volume 358.4 cu.in.). Type C nestboxes had the same external dimensions as the type B nestboxes, but were actually smaller on the inside. This affect was achieved by lining the back and two sides of the nestbox with sections of wood at the height where the top of the nest is usually found. Since the female, once she accepts the nest base the male has built, lines the nest, the idea was to limit the actual area available to her while she was lining the nest and laying her eggs. Valume in these nestboxes was 250.8 cu.in. Type D nestboxes were very small, with a floor surface of 3 inches by 3 inches (area 9 sq.in. and volume 49.5 cu.in.). The back panels of the nestboxes were constructed to open downward to make data collection easier. Nestbox types A, B, and C were used in 1975; the 1976 study involved nestbox

types B and D.

Study Areas

The study was conducted in Kalamazoo County, Michigan, during the summers of 1975 and 1976. During the first year of the study 118 nestboxes (40 type A, 39 type B, and 39 type C) were put up around the county, mostly in residential areas. Yards with large trees and an abundance of bushes were used as often as possible, since House Wrens prefer this type of habitat. Each nestbox was nailed to a tree (with one exception) at a height of 6 feet off the ground. The nestboxes were put up between 12-27 April 1975.

Twenty nestboxes (10 type B, 10 type D) were used in 1976. They were put up on Kalamazoo Nature Center property, in or near areas where House Wrens had nested in previous years. Each nestbox was nailed to a tree or fence post at a height of $4\frac{1}{2}$ feet off the ground; the lower height was chosen to facilitate observations of nestbox contents. Nestboxes were put up 15-28 April 1976.

Procedures

The following routine was utilized during the 1975 breeding season. Nestboxes were checked for signs of nesting activity at four-day intervals from early May to

late July. A record was kept of House Wrens singing in the study areas. When a male began to build a nest the nestbox was checked every other day for signs that the female had begun to line the nest; when this happened, the nest was checked every day. During the nest building stage the height of the nest base and the depth of the nest cup were recorded to give an indication of the size of the nests built in the different nestbox types. Daily visits continued through the egg laying, incubation and nestling periods. Eggs were numbered as they were laid. The daily visits made it possible to keep accurate records of the number of eggs laid, the number of young hatched, and the number of young surviving to leave the nest. At the end of the breeding season the nests which were still intact were collected and weighed as a further comparison of the nests built in the three nestbox types.

The 1976 study involved checking the nestboxes for signs of nesting activity and for eggs at intervals of seven to eight days. At first, nests were checked daily during the egg laying and incubation stages, but egg laying was very erratic and many of the eggs were removed from the nests. Visits were then dropped back to three- to seven-day intervals. Nesting behavior was followed only during the first breeding period, from May to late June. Clutch size and hatching success

were recorded, along with an estimated number of fledglings per nest.

CHAPTER III

RESULTS AND DISCUSSION

1975 Clutch Size Data

There are three components to clutch size data: number of eggs laid, number of hatchlings produced, and number of young surviving to leave the nest. The data collected in 1975 included all three types of data for both the first and second breeding periods.

House Wren clutch size varies from 3 to 9 eggs, but is usually 5 or 6 (Kendeigh 1952). Clutches laid in the first breeding period are normally larger than in the second breeding period (Kendeigh 1941). My limited data do not show this trend, except perhaps for type A nestboxes (Table 1). Mean clutch size for this nestbox type was 7.3 for the first breeding period, while the one clutch laid in a type A nestbox during the second breeding period had only 5 eggs. Mean clutch size for types B and C nestboxes for both periods were similar (Table 1).

A comparison between the number of eggs laid per nest in the three nestbox types using analysis of variance showed no statistically significant differences. The mean number of eggs laid per clutch during the first breeding period were as follows: 7.3 (range 6-9) in type

Table 1. The number of eggs, nestlings, and fledglings per nest according to nestbox type for the first and second breeding periods, 1975.

Box #	FIRST BREEDING PERIOD			SECOND BREEDING PERIOD		
	Eggs	Nestlings	Fledglings	Eggs	Nestlings	Fledglings
Type A						
12	7	5	0			
13	7	6	6			
23	9	6	6			
24	8	6	6			
60	6	5	5	5	5	5
69	7	7	0			
Means	7.3	5.8	5.75	5.0	5.0	5.0
Type B						
7				6	6	6
34	7	6	6			
36				7	6	5
61				7	7	7
114	6	6	6			
Means	6.5	6.0	6.0	6.7	6.3	6.0
Type C						
76	6	6	6	6	6	6
94	6	0	0			
98	7	5	5	6	6	6
Means	6.3	5.5	5.5	6.0	6.0	6.0

A nestboxes, 6.5 (range 6-7) in type B nestboxes, and 6.3 (range 6-7) in type C nestboxes. The apparent trend of larger clutches in smaller type A nestboxes was not statistically significant. Mean clutch sizes for the second breeding period were: 5.0 (only one nest) in type A nestboxes, 6.7 in type B nestboxes, and 6.0 (no variation) in type C nestboxes.

There were two instances of disturbance during the laying sequence. Egg laying began at nestbox 98 (type C) on 12 May, and five eggs were laid in the next five days. On 17 May three of the eggs had disappeared and a sixth had been laid. The next day another egg had been laid, but by 19 May all but one egg was gone (#2). There was then a ten day period during which no eggs were laid. By 31 May the nest had been re-lined and egg laying resumed; seven eggs were laid in the next seven days and there was no further disturbance at this nestbox.

The second instance of disturbance involved nestbox 23 (type A), where egg laying began on 15 May. Eggs were laid on 15, 16, and 17 May, but on 17 May the first two eggs were found on the ground broken. In this case egg laying continued without a break until 24 May, when the ninth egg was laid. There was no further evidence of disturbance at this nestbox.

Kendeigh, Kramer, and Hamerstrom (1956) reported several similar instances of interrupted egg laying and

disappearance of eggs from House Wren nests. They suggested that the wrens removed the eggs from the nest, but gave no possible explanation for this behavior. It is possible in the two instances described above that either a period of cold, rainy weather or my daily visits to the nests--or the combination--could have been involved in the loss of eggs. Predation by neighboring House Wrens could also explain the systematic disappearance of eggs from a nest. Since only a few eggs were lost at a time, it seems unlikely that another predator (squirrels, raccoons, domestic cats, etc.) was removing the eggs.

Hatching success for the three nestbox types is listed in Table 1. The mean number of nestlings produced during the first and second breeding periods, respectively, was as follows: 5.8 (range 5-7) and 5.0 (only one nest) in type A nestboxes; 6.0 (no variation) and 6.3 (range 6-7) in type B nestboxes; and 5.5 (range 5-6) and 6.0 (no variation) in type C nestboxes. A one-way analysis of variance showed no significant differences in hatching success between the three nestbox types.

The third and final consideration is fledging success. The 1975 fledging success means are very similar, ranging from 5.5 in type C nestboxes to only 5.75 in type A nestboxes and 6.0 in type B nestboxes during the first breeding period (Table 1). A one-way analysis of variance

showed no significant difference between the nestbox types.

1976 Clutch Size Data

Data collection during the 1976 breeding season was limited to the first breeding period (Table 2). The purpose of using type D nestboxes was to test the idea that in a very small nestbox House Wrens might lay significantly smaller clutches than those laid in the larger type B nestboxes. This did not happen. Clutches laid in type D nestboxes were either 6 or 7 eggs per clutch (mean 6.6). This mean was larger than that for the type B nestboxes (Table 2), but this trend is not statistically significant using a one-way analysis of variance. Neither hatching success or number of fledglings per nest were significantly different (one-way analysis of variance). There appears to be a trend toward higher reproductive success in the smaller type D nestboxes, but with such a small sample it is impossible to say that this trend is significant.

During the 1976 breeding season there were several incidents of interrupted egg laying and of eggs disappearing from nests. In nestbox 9 (type B) egg laying apparently began on 17 May, but no other eggs were laid until 22 May (nest was checked daily). By 31 May 7 eggs had been laid, but they all disappeared sometime in the next eight days. There was no direct evidence of what had happened to the eggs, but there was a bluebird nestbox

Table 2. The number of eggs, nestlings, and fledglings per nest according to nestbox type for the first breeding period, 1976.

Box #	TYPE B			Box #	TYPE D		
	Eggs	Nestlings	Fledglings		Eggs	Nestlings	Fledglings
8	5	4	4	6	6	6	6
9	7	0	0	7	7	7	7
10	6	6	6	12	7	6	6
15	5	0	0	16	7	0	0
				19	6	0	0
Mean	5.75	5.0	5.0		6.6	6.3	6.3

nearby with another House Wren nest in it. Eggs were being laid in this nest at the same time the clutch was laid in the House Wren nestbox. It is possible that either a single female was laying eggs in both nestboxes (which seems unlikely) or there were two female House Wrens in the area at the same time. In the latter case, it would be possible that the female nesting in the bluebird nestbox removed the eggs from nestbox 9. As far as I could determine, there was only one male House Wren singing in the area.

Another incident of nest disturbance occurred in nestbox 15 (type B). Egg laying began around 17 May; by 21 May there were five eggs in the nest, but on 22 May

four of the eggs had disappeared and by 24 May they were all gone. There was no indication that a predator had removed the eggs.

Nestbox 16 (type D) was also involved in egg loss. Egg laying began on 18 May. The next day that egg was gone and a new one had been laid. Egg laying continued until 25 May, when there were six eggs in the nest. When I returned eight days later all of the eggs had been removed and the nest itself was disrupted, which seemed to indicate that a predator (probably a raccoon, Procyon lotor) had taken the eggs.

Nesting Losses

In evaluating clutch size data it is important to examine the various types of nesting losses and the type of nestboxes involved and try to relate these factors to the overall nesting success. In view of Lohr's (1973) theory that temperature in the nest during the nestling period is a vital factor in the survival rate of the young, it is notable that that only one out of 41 nesting losses occurred during this period (Table 3). A nestling died between 12:00 on 11 July (1975) and 15:00 12 July in a type B nestbox. The nest contained six young which were seven or eight days old. Ambient temperatures had been high during this period and it is possible that the nestling died from hyperthermia, even though nestling House Wrens

Table 3. 1975 nest losses according to nestbox type and reason for loss.

Box type	Eggs lost during laying	Eggs never hatched	Eggs abandoned	Nestling period *	Predators **
A	2	5	0	0	14
B	0	2	4	1	0
C	7	6	0	0	0
Totals	9	13	4	1	14

* One nestling disappeared from a nest during a spell of hot weather (see text).

**A squirrel destroyed one nest of 7 and a racoon another nest of 7.

are not fully homeothermic until about the ninth day of the nestling period (Baldwin and Kendeigh 1932).

Most nesting losses occurred during the egg laying period or at the time of hatching (Table 3). In 1975 a total of 13 eggs failed to hatch. The fact that I was handling the eggs every day and that I had numbered them could have contributed to the number of eggs lost at this stage. Another 14 young were taken by predators on or near the day of hatching. In both cases the nests were in type A nestboxes. The nest in nestbox 12 (type A) was abandoned by the parents on the day of hatching, probably

due to the fact that a red squirrel (Tamiasciurus hudsonicus) had been gnawing at the entrance hole; the young died shortly afterwards due to neglect. A racoon apparently took the young in nestbox 69 (type A). There were six eggs and one nestling in the box on 5 June, but by 6 June they had all been removed and the nest had been disrupted.

There was only one case of parental abandonment of a nest during egg laying. It occurred in a type B nestbox (31) during the first breeding period. Four eggs were laid from 7-10 June. Abandonment of the nest could have been related to severe storms during the last two days of egg laying. Since there was a male singing in the area even after the nest was abandoned, it may be that the female abandoned or was killed during the storm.

Loss of eggs during the egg laying periods has already been discussed. During 1975 this was an uncommon occurrence. There were only two cases, one in a type A nestbox and one in a type C nestbox, and both occurred early in the first breeding period.

Nesting losses in 1976 were mainly the result of eggs disappearing from the nests. A total of 25 eggs (out of 56 laid) were lost in this manner. Of the remaining thirty-one eggs, only two did not hatch. To my knowledge, there was no predation on nests during the nestling periods and all young that hatched survived at least

until the thirteenth or fourteenth day of the nestling period and presumably to leave the nest.

One question which arises is whether my daily visits to the nests increased the probability of abandonment by the parents and the probability of the nests being taken by predators. It is apparent from the previous discussion that once egg laying began, parents did not tend to abandon their nests. This was true in 1975, when the nests were visited daily from egg laying through fledging of the young (approximately 5 weeks). The two incidents of predation in 1975 seem to have been related to the hatching of the young, a point at which the nests became more noticeable to human observers due to the loud cries of the young. Roseberry and Klimstra (1970) examined the possible effects of human visits to the nests of Meadowlarks (Sturnella magna); they found that careful visits to the nests did not increase the incidence of abandonment or predation for this species. No statistical relationship was found between human visits to the nest and predation rates in the Bicolored Antbird (Gymnopithys bicolor) (Willis 1973) and in a variety of species nesting in old-fields (Gottfried and Thompson 1978).

Nest Building

Löhrl (1973) found that thicker nests were constructed by Great Tits in the larger nestboxes he provided them

with than in the smaller ones. In the type A nestboxes (diam. 20 cm or 7.87 in.) Great Tits built nest depressions with an average of about 7 cm (2.76 in.) of moss and other material on all sides. Type B nestboxes (diam. 9 cm or 3.54 in.) had nest depressions with an average of only 1.5 cm (0.59 in.) nest edges. The nest depression apparently remained at a constant 6 cm (2.36 in.) diameter. Lohrl (1973) felt that the size of the nest was a reflection of its insulative properties and that these insulative properties were important during incubation and the early nestling period, prior to the development of homeothermy in the young. He postulated that in times of low ambient temperatures, young would survive better in the thicker nests due to the greater insulative properties of these nests.

In the present study it was found that nests varied in size and shape between the four nestbox types. Nest building often began with the appearance of ten or eleven sticks in a nestbox. This seemed to be the minimum number of sticks a male House Wren put into a nestbox in adding it to his territory. Male House Wrens claim a larger number of nestboxes or natural cavities than are actually used to raise broods (Kendeigh 1941); in the present study the placement of this basic number of sticks in a nestbox was frequently as far as nest building went. In other cases, the male went on to build a nest base of

about 1 to 2 inches. If a female accepted the nestbox and nest base, a cup of thin, weedy material was built. The depth of the cup was not as variable as total nest height (Tables 4 and 5). Cup depth in 1975 was between 2.0 to 2.5 inches during the first breeding period and around 3 inches during the second breeding period (Table 4). Limited data collected during the first breeding period of 1976 indicated that a slightly deeper cup was being built, ranging from 2.5 to 3 inches (Table 5). Analysis of variance indicated no significant differences between mean cup depths in nestbox types A through C in 1975, between mean cup depths in nestbox types B and D in 1976, or between all four nestbox types when the data were pooled for the two years of the study. Mean cup depth in these cases is designated by the average of the range for an individual nestbox (i.e., for box 12 the range in cup depth was 2.0 to 2.5 inches and the mean was taken as 2.25 inches). The relative constancy of nest depression or cup depth is similar to Löhrl's (1973) observations with Great Tit nests.

The total height of the finished nest varied even within the same nestbox type (Tables 4 and 5). The smallest nest heights were found in the type C nestboxes during the first breeding period of 1975, where mean nest height was only 2.33 to 2.55 inches. Nests built in type B nestboxes during both of the breeding periods in

Table 4. 1975 nest building data by nestbox type, length of time (in days) taken to complete the nest, total nest height (in inches), length of time (in days) taken to build the nest cup and line it, and the depth of the finished nest cup.

Box #	Type	FIRST BREEDING PERIOD				SECOND BREEDING PERIOD			
		Nest building	Nest height	Cup building	Cup depth	Nest building	Nest height	Cup building	Cup depth
12	A	12-15	5.5	6-7	2.0-2.5				
13	A	14-16	2.5	3-7	1.5				
23	A	7-10	3.5	3-5	--				
24	A	19-20	3.75-4.0	2-3	2.5				
60	A	4-6	3.0-3.25	4-6	2.5	3-7	3.5	3-7	3.0
69	A	12-17	4.0	5-7	2.5-3.0				
Means		11.3-14.2	3.7-3.8	3.8-5.8	2.2-2.4				
7	B					31	3.0	1-2	3.0
31	B	21-25	2.75-3.0	1-2	2.5				
34	B	20-27	3.0	4-6	2.0-2.5				
36	B					29-33	3.0	1-3	2.0
61	B					16-20	4.5	2-3	3.0
114	B	8-12	3.5	2-4	3.0				
Means		16.3-21.3	3.1-3.2	2.3-4.0	2.5-2.7	25.3-28.0	3.5	2.0-2.67	2.7
76	C	8-11	2.0-2.5	2-4	--	3-7	3.5	3-7	3.0
94	C	11-14	--	3-4	--				
98	C	8-11	2.0	1-4	2.0				
98	C*	6-8	3.0	3-5	2.0	3-5	4.5	2-3	3.5
Means		8.3-11.0	2.33-2.5	2.25-4.25	2.0	3.0-6.0	4.0	2.5-5.0	3.25

* Re-nested

1975 and the first breeding period of 1976 were remarkably similar, ranging only from 3.1 to 3.5 inches (Tables 4 and 5). Type A nestboxes reached a mean height of 3.7 to 3.8 inches during the first breeding period of 1975 (Table 4), which is still lower than the nest heights for the type D nestboxes used in 1976. In this case the mean nest height ranged from 4.2 to 4.3 inches (Table 5). The apparent trend in nest heights for House Wrens is to build higher nests in smaller nestboxes. Nest heights among the four nestbox types were found to be significantly different ($F=4.24$, $\text{prob.} < 0.05$) when data for the two years were pooled and tested using analysis of variance.

Data were collected in 1975 concerning the amount of time taken to build nests in nestbox types A, B, and C (Table 4). The range in number of days taken to complete a nest was from 4 to 6 days for nestbox 60 (type A) to 29 to 33 days for nestbox 36 (type B) (Table 4). These data were tested for differences in amount of time taken to build a nest in the three nestbox types but, perhaps owing to the small amount of data, no significant differences were found.

The longest mean period of days taken to build a complete nest was found in type B nestboxes, where it took an average of 25.3 to 28.0 days to build a nest used in the second breeding period and an average of 16.3 to 21.3 days to build a nest used in the first breeding

Table 5. 1976 nest building data with reference to type of nestbox used, total height of the nest and nest cup depth (in inches).

Box #	Type	Nest height	Cup depth	Box #	Type
8	B	3.0	--	12	D
9	B	4.0	3.0	16	D
10	B	2.5	--	19	D
15	B	3.0	2.5; 2.5*		
Means		3.1	2.75		

* Two cups built in nestbox at the same time

period (Table 4). Although nests built in types are similar in height to the nests built in types (Table 4), they were significantly heavier (see discussion of nest weights). Several populations for the heavier nests built in type B the length of time taken to build these nests discussed in a later section.

Figure 1 shows the general shape of most nests. A large, flat base filled the bottom with the nest cup (mean depth 2.5 to 2.7 in. 4 and 5) placed in one of the rear corners. occasionally placed in the center back or in front corner. Female House Wrens did not ap

Figure 1. Typical nest for a type B nestbox.



a clearly defined preference for cup placement in this large nestbox type, which agrees with observations by Preston (1958).

Nest built in type A nestboxes during the first breeding period had the next longest mean nest building period, an average of 11.3 to 14.2 days (Table 4). These nests were variable in both height and shape. In nestbox 12 the nest completely filled the nestbox; at the other extreme, a very small nest was built in nestbox 13 (Figure 2 and Table 4). Both nests were built in the same general time period (12 May to 23 May for 12 and 13 May to 26 May for 13) and clutches of 7 eggs were laid in both nestboxes (Table 1). Unfortunately

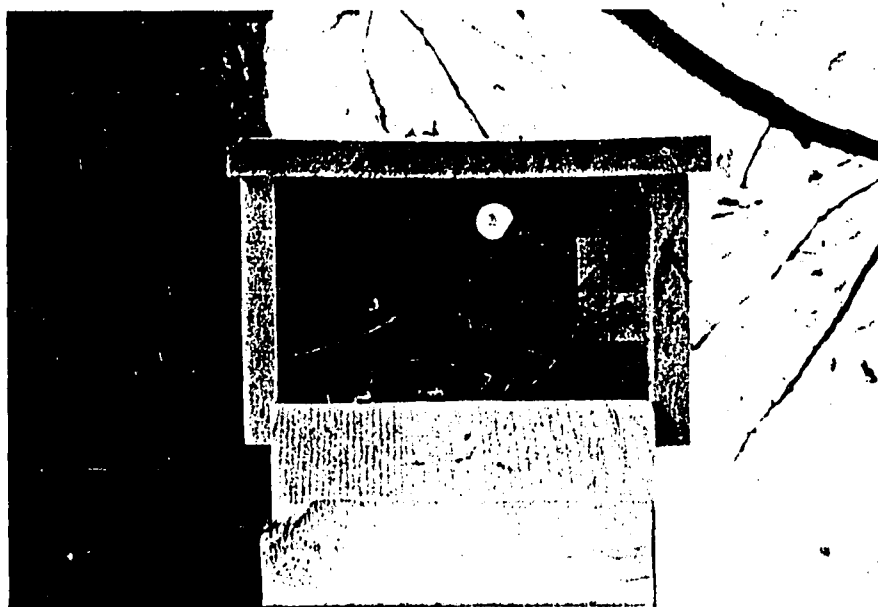
Figure 2. Nest built in nestbox 13 (type A) in 1975.



a predator disrupted the nesting cycle in nestbox 12, so a comparison of fledgling success cannot be made. It is interesting to note that although nest height in in type A nestboxes ranged from 2.5 to 5.5 inches, the range of cup depths was only 1.5 to 3.0 inches (mean 2.2 to 2.4 inches).

Nest building activity in type C nestboxes for the first breeding period of 1975 took an average of only 8.3 to 11.0 days. As in type B nestboxes, a base of from 1 to 2 inches filled the bottom of the nestbox. But in this type of nestbox, the cup was always placed in the center of the nestbox, between the wood blocks which reduced the actual interior area available for

Figure 3. Typical nest for a type C nestbox, with nest cup placed between the wood blocks which reduced the actual interior area available for nesting.



nesting (Figure 3). Nests built in type C nestboxes were lower in height than the nests built in the other two nestbox types (Table 4).

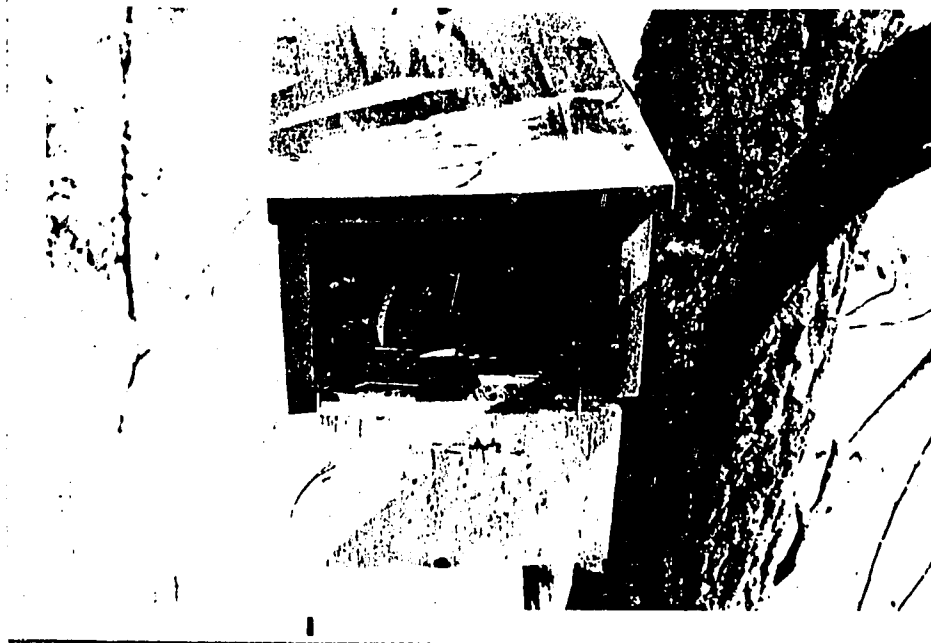
In 1975 three nestboxes were used for both breeding periods (two type C and one type A). There was usually a period of inactivity at the nests between the fledging of the first brood and the resumption of activity at the nest. Kendeigh (1941) reported that a period of about 13 days is spent caring for the first brood outside of the nest and that it was about 11 days after fledging before the male begins to re-build the nest. In my study this period of inactivity at the

nestbox ranged from no more than 2 or 3 days in nestbox 98 (type C) to a total of 16 to 20 days in nestbox 76 (type C). Nestbox 60 (type A) was intermediate, with a non-active period of between 6 to 9 days. Re-building the nest for the second brood took only about 3 to 7 days, presumably because most of the original nest was left intact.

Preston (1958) reported what he felt was an unusual case of a House Wren nest with two cups. The nestbox involved was six square inches inside. The nest cups were placed in each of the two rear corners of the nestbox. Only one of the cups was lined; six eggs were laid in this cup. Preston then removed the eggs as part of the study he was doing, along with all of the nest material. A new nest was begun immediately, again with two cups. This time, though, both cups were lined and both were used for egg laying. Two eggs were laid in one of the cups, four in the other. The female apparently tried to incubate both clutches, but seemed to keep the larger clutch warmer and only these eggs hatched.

Double cup nests occurred in both years of my study, always in the large, empty type B nestboxes (8 in. square inside). The first case occurred during the first breeding period of 1975 in nestbox 7. The two cup depressions were present in this nestbox from the beginning of nest building, when presumably only the male

Figure 4. Type B nestbox with a double cup nest.



was building the nest. Nest building began around 22 May and continued until 22 June, when the first egg was laid. One cup was placed in the front right corner of the nestbox, while the other was located in the back left corner. The rear cup was eventually filled with sticks while the front cup was lined and used for egg laying. Six young were fledged from this nest (Table 1).

The second case of double cup nesting occurred in 1976, in nestbox 15. Once again the two cups were present from the beginning of nest building, between 27 April and 7 May. Egg laying had begun by 18 May, when two eggs were found in the back right cup (Figure 4). The two cups were located in the rear corners of the nestbox and both

had been lined. On 21 May there were five eggs in the back right cup, but by 22 May all but egg #5 had disappeared. This egg was also gone by 24 May, along with the nest cups. Both cups had been re-built and re-lined by 2 June, but when I returned the next day there was a mouse (species unknown) in the front of the nestbox. There was no further activity of either the House Wrens or the mouse in this nestbox through the end of June, when the study was terminated.

Since the eggs laid in the nestbox Preston observed were split between the two cups and since only the eggs in the larger clutch hatched, Preston (1958) concluded that the "split personality" which led to the building of two nest cups was a lethal mutation which resulted in a reduced reproductive output. Contrary to his results, there was no reduced reproductive output in the first double cup nest I observed. In both of my observations and in one of Preston's two observations, all of the eggs were laid in one of the two cups. I see no way in which this behavior would necessarily lead to a reduced reproductive output.

It is interesting that this behavior has been reported only in relatively large nestboxes (6 in. square in Preston's study, 8 in. square in mine). Extended observations at the 1975 nest and casual observation at the 1976 nest did not indicate the presence of more than

one female. Besides, since it is the male who initiates nest building and since this behavior occurs generally before mate selection has occurred, the number of females present does not explain what stimulates the male to build a double cup nest. Perhaps the male has some sense of how large a typical cavity should be, whether this is an inborn or a learned trait, and is responding to his perception of the size of the nestbox by building the equivalent of two nests in one cavity. This perception of cavity size could be visual or related to the amount of effort expended in building some minimum amount of floor covering or a combination of the two sensory inputs.

Nest Weights

Nests were collected at the end of the 1975 breeding season. Not all nests were recoverable. The results of these measurements are listed in Table 6, where the data have been listed according to nestbox type and whether or not the nest made it as far as egg laying.

Nest weights varied from 0.45 to 86.8 g (mean 20.31 g) in type A nestboxes to 1.0 to 111.85 g (mean 69.58 g) in type B and 1.05 to 137.75 g (mean 36.93 g) in type C nestboxes for all nests (Table 6). One-way analysis of variance indicated that nest weights were significantly different ($F=6.75$, $\text{prob.}=0.004$). Further analysis, using the Student's t-test, showed that nests built in types

Table 6. 1975 nest weights (in grams) according to nestbox type. An * indicates a nest which was used at least for egg laying.

Box #	TYPE A Nest weight	Box #	TYPE B Nest weight	Box #	TYPE C Nest weight
10	0.45	7	107.8 *	4	7.25
12	86.8 *	8	1.1	16	46.5
13	16.95*	26	1.0	18	10.05
14	14.6	29	102.4	75	1.05
15	11.7	31	53.9 *	76	70.3 *
24	55.5 *	34	111.85*	94	25.5 *
25	0.7	35	57.4	96	8.7
44	30.35	36	86.25*	97	25.3
46	24.3	50	71.1	98	137.75*
49	1.05	61	102.8 *		
51	18.1	114	69.75*		
53	5.65				
54	0.75				
79	36.6				
100	3.8				
112	17.65				
Means	20.31		69.58		36.93
Ranges	0.45-86.8		1.0-111.85		1.05-137.75
* Nests used for egg laying					
* Means	53.08		88.73		77.85
* Ranges	16.95-86.8		53.9-111.85		25.5-137.75

A and B nestboxes were significantly different in weight ($t=4.087$, $\text{prob.}<0.0001$) and so were nests built in types B and C nestboxes ($t=1.76$, $\text{prob.}<0.01$); nests built in types A and C nestboxes were not significantly different

in weight ($t=1.248$, $\text{prob.}<0.3$).

Examination of the nest weights for nests used for egg laying indicated that there was less variation among nestbox types (Table 6). Weights ranged from 16.95 to 86.8 g in type A nestboxes to 25.5 to 137.75 g in type C and to 53.9 to 111.85 g in type B nestboxes. The mean weights were not as far apart as they had been for all nests: 53.08 g (type A), 77.85 g (type C), and 88.73 g (type B). Perhaps owing to the small sample size, one-way analysis of variance indicated no significant difference ($F=0.99$, $\text{prob.}<0.4$).

Nestbox Selection in Wrens

Bent (1964) described the House Wren as "one of the most eccentric" birds in terms of its choice of nest sites. It was his opinion that while the original nest sites used by House Wrens were probably natural cavities in trees or stumps, they have now reached a state of "semidomesticity" and appear to prefer nestboxes put up for their use or some other hollow object found near human settlements (Bent 1964). Some of the unusual nest sites reported by Bent include empty cow skulls, hornet and wasp nests, and holes in brick walls. No indication was given as to their relative success in these unusual nest cavities.

It was not the original purpose of the present study to determine whether or not House Wrens were choosing

Table 7. 1975 nestbox usage according to nestbox type. Figures include pooled data for both breeding periods.

Box type	Eggs/ young	Sticks in box	TOTAL USED	Wrens in area, box unused	No wrens, box not used	Box lost, stolen	TOTAL NOT USED
A	7	14	21	9	10	--	19
B	6	7	13	14	8	4	26
C	5	4	9	13	16	1	30
TOTAL			43				75

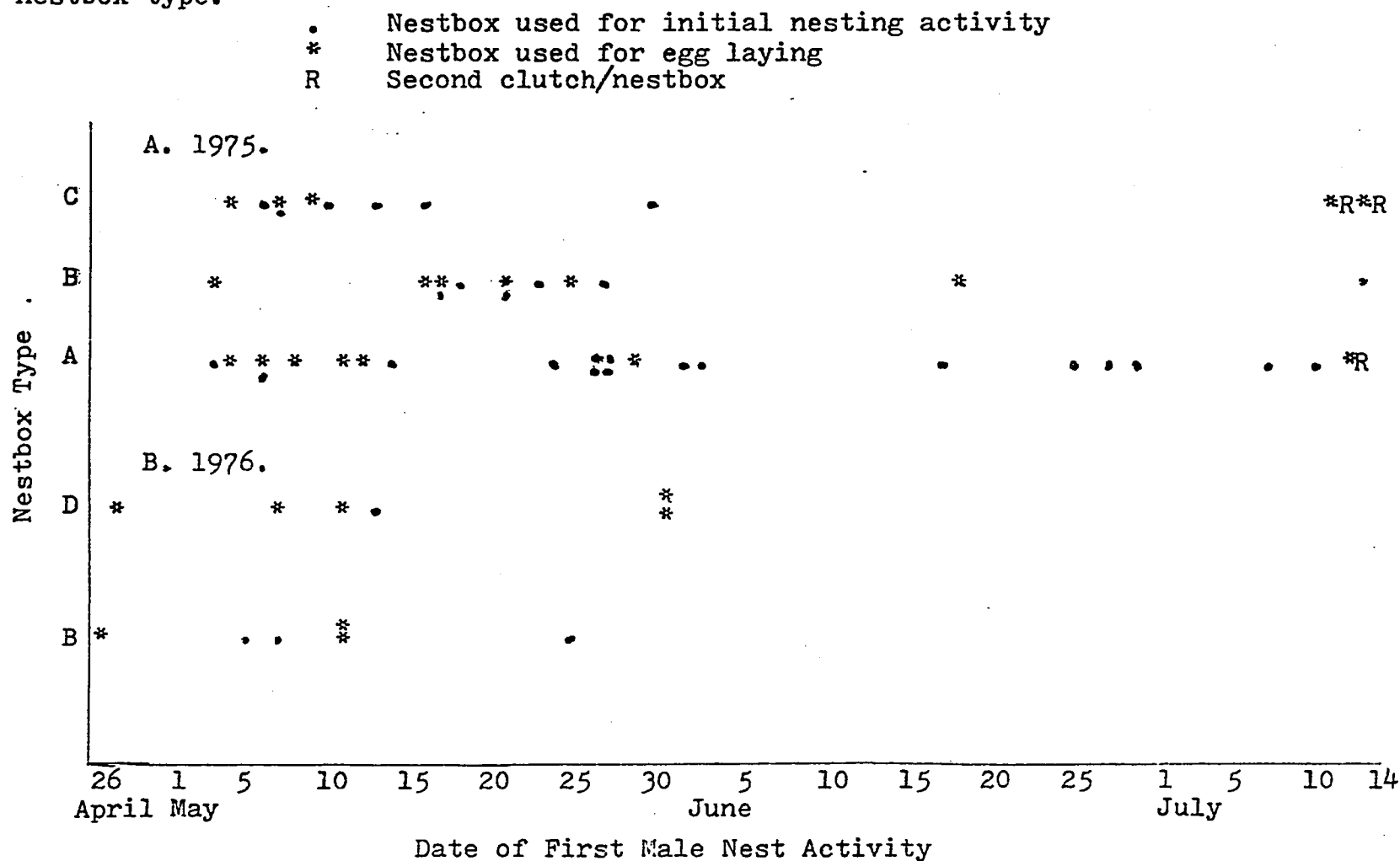
between large and small nestboxes; as a matter of fact, the nestboxes were placed far enough apart that an individual male should not have had to make a choice between a large and a small nestbox in his territory. As the study progressed, however, it became apparent that the males were probably exercising some sort of choice in occupying the nestboxes. To explore further the possibility that the males were preferentially occupying one nestbox type over the others, the data were grouped into the following categories for further analysis: date of first activity at a nestbox, total number of nestboxes used, and orientation of nestbox entrance.

In 1975 there did seem to be a pattern to the occupation of nestboxes. Nestbox types A and C were the

first to be claimed by males (3 May to 15 May, Figure 5a); this period of activity was followed by two weeks (15 May to 27 May, Figure 5a) when type B nestboxes were added to territories. Only type A nestboxes were used for "new" nest construction throughout the breeding season (Figure 5a). The pattern of nestbox choice is especially interesting since Kendeigh (1941) has reported that House Wrens tend to avoid cavities of too great a size and since it is the older males who tend to arrive earliest on the breeding grounds (Kendeigh 1941). It would seem possible, then, that the older males claimed the available small interior nestboxes (types A and C) and that by the time the younger males arrived, they were forced to make use of the less desirable, large interior nestboxes (type B). It is somewhat disappointing, then, to find that there was no apparent pattern in nestbox choice in 1976, when both the very small and the very large nestboxes (types D and B, respectively) were picked at about the same rate (Figure 5b).

The data for nestbox usage are listed in Table 7. The 1975 breakdown is as follows: 21 type A nestboxes were used for nesting activity, 13 type B, and 9 type C (Table 7). The differences in nestbox usage are significant ($\chi^2 = 7.68$, d.f. 2, prob. < 0.05). This would seem to confirm the earlier reference to Kendeigh's (1941) statement that House Wrens seem to shun nestboxes

Figure 5. Date of first male nest activity (sticks in nestbox) for each nestbox type.



which are too large, except that there was not a significant difference in the following year's usage data. Twenty nestboxes were put up in 1976; of these, 6 type B and 6 type D nestboxes were used for nest activity. This is particularly confusing since the difference in nestbox floor area was even greater (9 sq.in. and 64 sq.in.) in 1976 than it had been in 1975 (16 sq.in. and 64 sq.in.). One fundamental difference in the two years of the study was that in the second year nestboxes were placed in a high density House Wren breeding area (the Kalamazoo Nature Center), whereas in the first year the nestboxes were more scattered geographically around Kalamazoo County. It is possible that in high density area there was a shortage of appropriate nest sites and that this led to the use of most of the available nestboxes, irrespective of floor area. It is of further interest that the marked difference in nestbox choice in 1975 did not seem to affect the final number of nestboxes which made it as far as the egg laying stage: 7 type A, 6 type B, and 5 type C (Table 7).

One possible variable which might have influenced nestbox choice is orientation of the nest entrance. Ricklefs and Hainsworth (1969) made the observation that Cactus Wrens (Campylorhynchus brunneicapillus) used nest cavities which faced out of the wind early in the breeding season when it was colder and into the

Table 8. Orientation of nestboxes in 1975.

Box type	DIRECTION							
	N	NE	E	SE	S	SW	W	NW
A	13	1	2	3	8	1	11	1
B	10	1	7	1	9	1	6	-
C	9	3	5	-	14	2	5	-
Totals	32	5	14	4	31	4	22	1

wind later on when it had become hotter. The advantage to this switch in orientation is that when the entrance faces into the wind, air can circulate through the nest and thus reduce the difference between ambient and nest temperatures (Ricklefs and Hainsworth 1969). A similar change in nest entrance orientation with climatic changes was confirmed for another desert species, the Verdin (Auriparus flaviceps), by Austin (1974, 1976); he was also able to show that almost all criteria of success were higher for nests with entrance holes oriented in the predominant direction (Austin 1976). Another study indicated that Yellow-bellied Sapsuckers (Sphyrapicus varius) and Common Flickers (Colaptes auratus) had mean nest orientations of due south (Inouye 1976). In this case the author, pointing out the lack of much wind in the area, felt that the predominant southerly orienta-

Table 9. Numbers of nestboxes used in 1975 according to nestbox type and nest entrance orientation.

Box type	ORIENTATION							
	N	NE	E	SE	S	SW	W	NW
A	7	1	2	1	2	1	7	-
B	3	-	3	-	2	1	4	-
C	-	1	3	-	4	-	1	-
Totals	10	2	8	1	8	2	12	-

B. Nestboxes used to successfully fledge young.								
A	-	-	1	-	1	1	1	-
B	2	-	2	-	1	-	-	-
C	-	-	-	-	2	-	-	-
Totals	2	-	3	-	4	1	1	-

tion was associated with the position of the sun and that it permitted maximum use of solar radiation to assist the parents in warming the young (Inouye 1976). Northern Orioles (Icterus galbula) and Orchard Orioles (I. spurius), on the other hand, do not seem to share this preference for a particular compass direction in nest orientation (Schaefer 1976).

Nestbox orientation data generated by the present

Table 10. Number of nestboxes not used for nest activity and orientation of nest entrances, according to nestbox type, in areas where House Wrens were heard or seen.

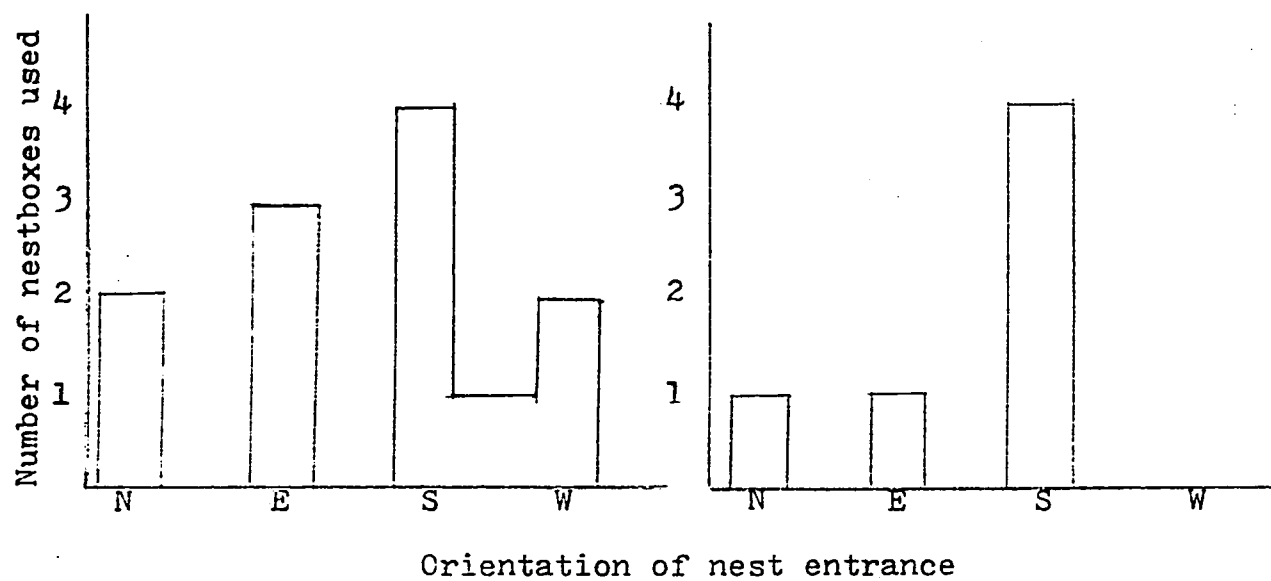
Box type	ORIENTATION							
	N	NE	E	SE	S	SW	W	NW
A	3	-	-	1	3	1	3	-
B	3	1	4	-	4	-	2	-
C	4	1	1	-	2	-	4	-
Totals	10	2	5	1	9	1	9	-

study were examined from two points of view: the general tendency to choose one direction over all others irrespective of nestbox type (Figure 6a, b) in the two breeding periods in 1975 and the possibility that orientation biased the preference for one nestbox type over the others (Tables 8, 9, and 10).

As stated earlier in this paper, in Kalamazoo County the House Wren breeding season begins in late April and continues until mid-July; the two breeding periods are roughly April to mid-June and late June to late July. Predominant wind directions during these two breeding periods apparently do change, from predominantly westerly winds in April and May to southwesterly in June and July (Henry 1906). It is difficult to make statements based on small samples, but the data presented

Figure 6. Nestbox orientation and usage.

A. First breeding period 1975. B. Second breeding period 1975.



in Figures 6a and 6b seem to fit the predicted pattern. In the first breeding period of 1975 the nest entrance orientations were pretty well scattered, but mostly in a southerly or easterly direction; winds at this time tend to come from the west. The predominant direction of nest entrance during the second breeding period was once again southerly, but since the winds shift and come from the southwest during this time most of the nests were oriented in the general direction of the predominant winds. It is important to point out that of the 118 nestboxes available in this study, only 4 faced in a southwestern direction (Table 8) and therefore that particular orientation of nestbox entrance was not really a choice that was available to the wrens utilizing my nestboxes. This is one aspect of House Wren nest site selection which should be studied further.

Data relating nest entrance orientation, type of nestbox, and nestbox usage have been arranged in Tables 9 and 10. In Table 9a orientation and nestbox type have been related to numbers of nestboxes used for preliminary nest activity; when the total numbers of the various nestbox types facing in a given direction are taken into account (Table 8), there is no apparent trend in choice of nestbox type and orientation of nestbox entrance. This lack of relationship between size of nestbox and nest orientation is even more striking when

related to the number of nestboxes used to successfully fledge young (Table 9b). It is important to take into account the number of nestboxes of a given size which are not used for nesting in relationship to the orientation of their entrance holes. As can be seen from a comparison of the number available in a given direction (Table 8) and the number unused which faced in that direction and were located in areas where House Wrens were present (Table 10), the orientation of nestbox entrance does not seem to have influenced the type of nestbox avoided by male House Wrens.

CHAPTER IV

CONCLUSIONS

The main objective of this study was to determine whether or not nestbox size had a significant effect on the clutch size and reproductive success of House Wrens. The data collected during two summers of research do not indicate a statistically significant relationship between nestbox size and reproductive success in this species (Table 1). These results are in agreement with those of Karlsson and Nilsson (1977) for Starlings, but do not fit data collected for Great Tits, Pied Flycatchers, Marsh Tits, and Willow Tits (Löhr 1973, Karlsson and Nilsson 1977). There is no obvious relationship between House Wrens and Starlings which would explain the lack of response to nestbox size in terms of clutch size laid. It is possible, as a matter of fact, that House Wrens show an inverse relationship between nestbox size and clutch size (Tables 1 and 2), but that with the small sample collected in the present study it was not possible to discern this relationship statistically.

A follow-up study with banded individuals and a larger sample base could shed more light on the true relationship between nestbox size, age of breeding individuals, type of nest built and amount of time taken to build it,

and clutch size. It is possible that since they arrive at the breeding grounds earlier, older and more experienced males tended to claim the smaller nestboxes; since it is easier and quicker to fill this type of nestbox, these males could begin advertising for mates earlier in the season. In this way egg laying by the mate could begin sooner, which in itself might lead to a larger clutch size (Kendeigh 1941). It is also possible that it is more important to House Wrens that the young be well insulated early in the nestling stage than that they have room to move apart later on; in this case it may be that it is less expensive in time and energy to completely fill a small nestbox and, thereby, provide tight insulation for the nestlings than it is to build a nest with an equivalent amount of insulation surrounding the young in a larger nestbox. The results of the analysis of nest building data agree with this view of House Wren nest building behavior. The smaller nestboxes were preferred (Table 7) and had significantly higher nests (Table 4) while it took longer (although the difference was not statistically significant) in general to build the nests in the larger nestboxes (Table 4). A young, inexperienced male who arrived at the breeding grounds, then, might either pick a large nestbox out of inexperience or because it was the only choice left to him. This would be detrimental for

several reasons. First, it would take him longer to build a sufficiently well-insulated nest; the need for more insulation in larger nestboxes may explain why the nests found in these nestboxes weighed more than the others (Table 6). The delay in mate attraction and subsequent egg laying could decrease his chances of attracting a good mate and, since House Wren clutch size decreases during the breeding season (Kendeigh 1941), could also lead to a lowered clutch size.

Further studies should also examine the relationship between nestbox size, clutch and brood sizes, and the trade off between brooding and feeding rates. Dunn (1976) has shown that the larger the brood size in House Wrens, the lower the age of "effective endothermy" or the age at which the parent can cease brooding the young. It will also be important to determine the conductance values for nests built in different size nestboxes; this type of data could be valuable in determining the ultimate importance of nestbox size in general with respect to clutch size.

Another main objective was to collect data which might indicate what type of cues female House Wrens use to determine the size of their nestboxes. Two nestbox types were used to collect these data: the large, empty type B nestboxes and the large type C nestboxes with reduced interior volumes. Since there were no statisti-

cally significant differences in the clutch sizes or reproductive success of females nesting in these two nestbox types or in the smaller type A nestboxes, it is not possible to make any statements concerning the cues used to determine nestbox size on the basis of this study. It is an important aspect of the whole question of nestbox size and the determination of clutch size and should be pursued further. It might be more rewarding to collect data using similar nestbox types and a species of bird where a pronounced difference in clutch size has already been correlated with nestbox size.

Finally, the relationship between wind direction, nest entrance orientation, and reproductive success should be studied in more depth in the House Wren. Data presented here hint at the fact that this may be an important factor in choice of nestbox in this species. Perhaps they compensate for using smaller nestboxes by attempting to choose a nestbox which will face into the wind and might therefore aid in cooling the young later in the nestling cycle, when they have reached homeothermic condition and hyperthermia is a threat.

BIBLIOGRAPHY

- Austin, G. T. 1974. Nesting success of the Cactus Wren in relation to nest orientation. Condor 76: 216-217.
- , 1976. Behavioral adaptations of the Verdin to the desert. Auk 93: 245-262.
- Baldwin, S. P. and S. C. Kendeigh. 1932. Physiology of the temperature of birds. Sci. Publ. Cleveland Mus. Nat. Hist. 3: 1-196.
- Bent, A. C. 1964. Life histories of North American Nuthatches, Wrens, Thrashers, and their allies. New York: Dover Publications.
- Brewer, R. and L. Swander. 1977. Life history factors affecting the intrinsic rate of increase of birds of the deciduous forest biome. Wilson Bull. 89: 211-232.
- Brockelman, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. Amer. Natur. 109: 677-699.
- Charnov, E. L. and J. R. Krebs. 1974. On clutch-size and fitness. Ibis 116: 217-219.
- Cody, M. L. 1966. A general theory of clutch size. Evolution 20: 174-184.
- Dunn, E. H. 1976. The relationship between brood size and age of effective endothermy in nestling House Wrens. Wilson Bull. 88: 478-482.
- Gottfried, B. M. and C. F. Thompson. 1978. Experimental analysis of nest predation in an old-field habitat. Auk 95: 304-312.
- Henry, A. J. 1906. Climatology of the United States. U. S. Department of Agriculture, Weather Bureau Bulletin. Q.
- Inouye, D. W. 1976. Nonrandom orientation of entrance holes to woodpecker nests in aspen trees. Condor 78: 101-102.
- Karlsson, J. and S. G. Nilsson. 1977. The influence of nest-box area on clutch size in some hole-nesting

- passerines. Ibis 119: 207-211.
- Kendeigh, S. C. 1941. Territorial and mating behavior of the House Wren. Ill. Biol. Monogr. Vol. 18, No. 3.
- , 1952. Parental care and its evolution in birds. Ill. Biol. Monogr. Vol. 22, Nos. 1-3.
- , T. C. Kramer, and F. Hamerstrom. 1956. Variations in egg characteristics of the House Wren. Auk 73: 42-65.
- Klomp, H. 1970. The determination of clutch size in birds. A review. Ardea 55: 1-174.
- Lack, D. 1954. Natural regulation of animal numbers. London: Oxford University Press.
- Löhrl, H. 1970. Unterschiedliche bruthöhlenansprüche von meisenarten und kleibern als beitrag zum nischenproblem. Verh. Deutsch. Zool. Ges. 64: 344-347 (Cited in Löhrl 1973).
- , 1973. Einflub der brutraumfläche auf die gelegröbe der kohlmeise (Parus major). J. Ornith. 114: 339-347.
- Martin, S. G. 1974. Adaptations for polygynous breeding in the Bobolink. Amer. Zool. 14: 109-119.
- Mertens, J. A. 1969. Influence of brood size on the energy metabolism and water loss of nestling Great Tits, Parus major major. Ibis 111: 11-16.
- , 1977a. Thermal conditions for successful breeding in Great Tits (Parus major L.). I. Relation of growth and development of temperature regulation in nestling Great Tits. Oecologia 28: 1-29.
- , 1977b. Thermal conditions for successful breeding in Great Tits (Parus major L.). II. Thermal properties of nests and nestboxes and their implications for the range of temperature tolerance of Great Tit broods. Oecologia 28: 31-56.
- Nilsson, S. G. 1975. Clutch size and breeding success of birds in nestboxes and natural cavities. Vår Fågelvärld 34: 207-211.
- O'Connor, R. J. 1975a. The influence of brood size upon metabolic rate and body temperature in nestling

- Blue Tits Parus caerulus and House Sparrows Passer domesticus. J. Zool. (London) 175: 391-403.
- , 1975b. Nestling thermolysis and developmental change in body temperature. Comp. Biochem. Physiol. 52A: 419-422.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. Amer. Natur. 103: 589-603.
- Perrins, C. M. and D. Moss. 1975. Reproductive rates in the Great Tit. J. Anim. Ecol. 44: 695-706.
- Preston, F. W. 1958. House Wren attempts incubation in two nests simultaneously. Wilson Bull. 70: 193-194.
- Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis 110: 419-451.
- , 1974. "Energetics of reproduction in birds." In Avian energetics (R. A. Paynter, Ed.), Publ. Nuttall Ornithol. Club No. 15.
- , and F. R. Hainsworth. 1969. Temperature regulation in nestling Cactus Wrens: the nest environment. Condor 71: 32-37.
- Roseberry, J. L. and W. D. Klimstra. 1970. The nesting ecology and reproductive performance of the Eastern Meadowlark. Wilson Bull. 82: 243-267.
- Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits Parus major. Ibis 108: 313-347.
- , 1969. A model for the global variation of clutch size in birds. Oikos 20: 562-567.
- Schaefer, V. H. 1976. Geographical variation in the placement and structure of oriole nests. Condor 78: 443-448.
- White, F. N. and J. L. Kinney. 1974. Interactions among behavior, environment, nest, and eggs result in regulation of egg temperature. Science 186: 107-115.
- Willis, E. O. 1973. Survival rates for visited and unvisited nests of Bicolored Antbirds. Auk 90: 263-267.
- Yarbrough, C. G. 1970. The development of endothermy

in nestling Gray-crowned Rosy Finches, Leucosticte
tephrocotis griseonucha. Comp. Biochem. Physiol.
34: 917-925.