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SUCCESSFUL INCUBATION OF EXPERIMENTALLY ENLARGED CLUTCHES BY HOUSE WRENS

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ABSTRACT.—We tested the hypothesis that clutch size is limited by the inability of female House Wrens (*Troglodytes aedon*) to incubate more eggs than they typically lay in a clutch. We studied wrens that were breeding in nestboxes placed in a forest in central Illinois. We added two eggs to clutches of seven eggs early in the breeding season and two eggs to clutches of six eggs late in the breeding season in 1986. Incubation success was measured by counting the number of chicks present in the nest four days after the first egg of the clutch had hatched. In both early- and late-season nests, incubation success of experimentally enlarged clutches was significantly higher than that of control clutches. We conclude that clutch size of House Wrens is not likely limited by the female's inability to incubate additional eggs. *Received 29 Apr. 1987, accepted 19 Aug. 1987.*

Clutch size is an important component of reproductive effort in birds, and many hypotheses have been proposed to explain how it is limited in nidicolous species (see reviews by Lack 1968, Klomp 1970, von Haartman 1971, Winkler 1985). The focus of most research has been on the nestling-fledgling stages of the breeding cycle (Lack 1947, 1954, 1968). Considerably less attention has been given to the possibilities that in nidicolous species: (1) energy or nutrient availability during egg synthesis may limit production of eggs by females, or (2) the ability to incubate the eggs may constrain clutch size.

Because previous work on our study area showed that House Wrens (*Troglodytes aedon*) were able to rear experimentally enlarged broods without apparent ill effect on the chicks or on the female within a breeding season (Finke et al. 1987), we experimentally enlarged clutches to test the hypothesis that the natural clutch size of House Wrens corresponds to the maximum number of eggs that females can incubate successfully.

MATERIALS AND METHODS

The experiment was conducted in 1986 on a 108-ha forested study area 18.5 km north and 8.5 km east of the McLean County Courthouse, Bloomington, Illinois (Section 4, T 25N, R 3E, Gridley quadrangle, McLean County), where House Wrens have been studied since 1980, when nestboxes were first placed in the forest. In 1986, wrens built 554 nests (first and second broods, as well as renests) in the 585 identical, evenly dispersed nestboxes on the study tract. The 8.4 cm × 9.0 cm floor of each nestbox was 14.6 cm below the center of the entrance hole. Additional information about the study area and nestboxes is presented in Drilling and Thompson (1984) and Finke et al. (1987).

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TABLE 1

PERCENTAGE OF DONOR EGGS FROM NESTS OF DIFFERENT CLUTCH SIZES

Season	Clutch size in donor nests										No. of clutches
	Unknown[a]	5	6	7	8	9	10	14	15	16	
Early	4.5		31.8	40.9	9.1		4.5	4.5[b]		4.5[b]	22
Late		13.6	77.3	9.1							22

[a] Nest abandoned before clutch was completed.

[b] Nests in which the female was induced to lay additional eggs by removing eggs on successive days; see text.

Nestboxes were checked twice weekly after wrens began breeding in May. The day on which the first egg was laid in a nest is referred to as the egg-1 day of the nest. Clutch size typically ranged from 3 to 8 eggs, with a modal clutch size of 7 eggs early in the season and 6 eggs late in the season (Finke et al. 1987). Only the female incubated the eggs (Kendeigh 1952, Thompson, pers. obs.). For most enlargements, we added two eggs to modal-size clutches. Thus, early in the season most enlarged clutches had 9 eggs (original clutch size = 7 eggs) and late in the season most had 8 eggs (original clutch size = 6 eggs). Unmanipulated early-season clutches of 7 eggs and late-season clutches of 6 eggs served as controls. Additional controls in which eggs were switched among clutches, but clutch size remained the same, were not employed because earlier experiments had shown that House Wrens did not reject conspecific eggs added to their nests during egg laying (D. Price, pers. comm.). A few clutches that we increased to sizes other than 8 or 9 eggs were analyzed separately.

The age, incubation history, and size of the donor clutch relative to that of the recipient clutch could influence the outcome of the experiment, and we attempted to match recipients and donors as closely as possible. Eggs were added on or before the day after egg laying ended in 25 of 28 (89%) early-season nests and 14 of 22 (64%) late-season nests; the age and incubation status were matched as closely as possible in the remaining nests. Some of the eggs used to create enlarged clutches came from females induced by daily egg removal to lay additional eggs beyond the normal clutch size (see Kendeigh et al. 1956); eggs used from these nests came from the first eight eggs to be laid. Nine of 22 (41%) early-season nests from which eggs were taken for addition to the experimentally enlarged clutches had clutches of 7 eggs, and 17 of 22 (77%) late-season donor nests had clutches of 6 eggs (Table 1).

Nests were checked daily as the estimated date of hatching approached, which allowed determination of the number of eggs surviving the incubation period and of the day on which the first chick hatched (brood-day 0). We used the number of chicks (brood size) present on brood-day 4 as the measure of the females' ability to incubate clutches of different sizes. This measure of incubation success combines losses from two distinct, but potentially related, sources. The first is loss caused by the failure of eggs to hatch and the second is loss caused by the death of chicks shortly after they emerge from the egg. We cannot distinguish between these sources of mortality, because parents remove dead chicks (usually) and unhatched eggs (occasionally) between our visits to the nest (Thompson, pers. obs.). Assuming that one egg is laid each day, the incubation period was estimated as the interval from the day that the last egg of the clutch was laid (calculated as egg-1 day + clutch size) to brood-day 0. Data on unmanipulated clutches from the 1984 and 1985 breeding seasons were included for some comparisons.

Statistical tests were performed using subprograms of the Statistical Analysis System (SAS 1985).

TABLE 2

FATE OF ENLARGED AND CONTROL CLUTCHES FROM MANIPULATION TO BROOD-DAY 4 IN RELATION TO SEASON

Season and treatment	No. abandoned	No. that failed for other reasons[a]	No. that did not fail
Early season			
Enlarged clutches	1 (3.6)[b]	4 (14.3)	23 (82.1)
Control clutches	7 (6.2)	14 (12.4)	92 (81.4)
Late season			
Enlarged clutches	3 (13.6)	2 (9.1)	17 (77.3)
Control clutches	7 (10.6)	9 (13.6)	50 (75.8)

[a] Includes predation and accidents.

[b] N (%).

RESULTS

Nest survival.—Of 28 early-season 7-egg clutches to which two eggs were added, 24 (85.7%) survived the incubation period and had at least one chick successfully hatch from the eggs of the clutch. Of these 24 enlarged clutches, 23 (95.8%) still had chicks on brood-day 4. In 7-egg controls, 98 of 113 clutches (86.7%) survived to hatching, with 92 of these 98 clutches (93.9%) surviving with chicks to brood-day 4. There is no significant difference in the proportion of control and enlarged clutches surviving incubation ($\chi^2 = 0.02$, df = 1, $P > 0.05$) or in the proportion of those hatching that survived to brood-day 4 ($\chi^2 = 0.14$, df = 1, $P > 0.05$).

Similarly, of 22 late-season 6-egg clutches to which two eggs were added, 19 (86.3%) survived the incubation period to hatch at least one chick. Of these 19 clutches, 17 (89.4%) had chicks present on brood-day 4. In 6-egg controls, 57 of 66 clutches (86.4%) survived to hatching, with 50 of these 57 clutches (87.7%) surviving with chicks to brood-day 4. Again, there is no significant difference in the proportion of control and enlarged clutches surviving incubation ($\chi^2 < 0.01$, df = 1, $P > 0.05$) or of those surviving from hatching to brood-day 4 ($\chi^2 = 0.15$, df = 1, $P > 0.05$).

Early- and late-season enlarged clutches that failed before brood-day 4 and control clutches that failed were equally likely to have been abandoned as to have failed from other causes (Early, $\chi^2 = 0.34$, df = 1, $P > 0.05$; Late, $\chi^2 = 0.40$, df = 1, $P > 0.05$) (Table 2).

Incubation success in unmanipulated clutches.—The number of chicks present on brood-day 4 (incubation success) in unmanipulated early- and late-season nests in 1984–1986 generally increased as clutch size increased (Fig. 1), and there was not a marked decrease in the proportion of eggs

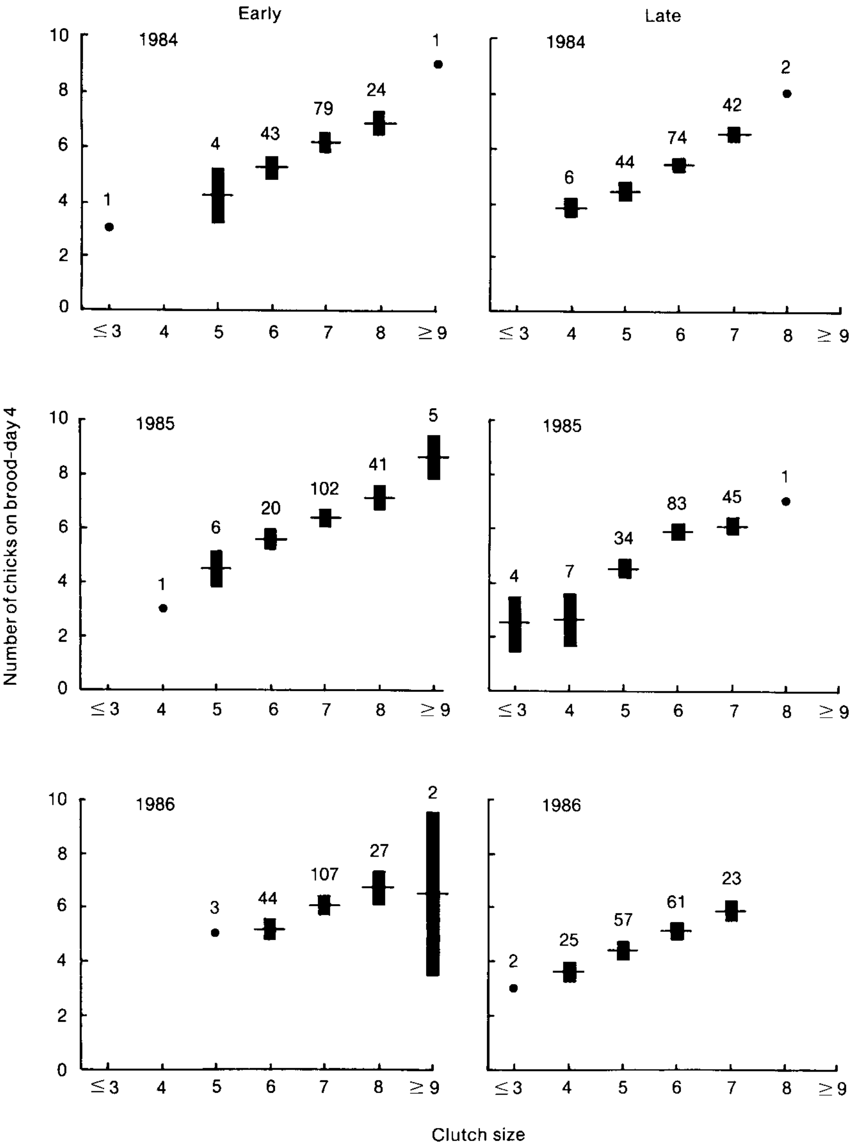

Fig. 1. Number of chicks present on brood-day 4 (incubation success) of unmanipulated clutches in 1984, 1985, and 1986, in relation to clutch size. Horizontal bar is the mean; filled rectangle is ±2 SE. Sample size for each clutch size is given above the rectangle.

that hatched or neonates that died between hatching and brood-day 4 over the range of natural variation in clutch sizes.

To determine if incubation success varied seasonally among years, the effects of clutch size, year, and their interaction on brood size were investigated using a 2-way analysis of variance. For both early- and late-season nests, there is a significant effect on brood size of clutch size (early: $F_{6,493} = 23.0$, $P < 0.001$; late: $F_{6,494} = 54.7$, $P < 0.001$), but not of year (early: $F_{2,493} = 2.1$, $P > 0.05$; late: $F_{2,494} = 1.9$, $P > 0.05$) (Type III sum of squares) (SAS 1985). Neither interaction is significant ($P > 0.05$). Thus, incubation success of unmanipulated clutches did not vary significantly among the 1984–1986 breeding seasons. Another comparison among these three breeding seasons was made by considering the incubation success of unmanipulated early-season, 7-egg clutches and late-season, 6-egg clutches. Incubation success is not significantly different among years in early-season, 7-egg clutches (Kruskal-Wallis test, $\chi^2 = 2.88$, $P > 0.05$), but it is significantly different in late-season, 6-egg clutches (K-W test, $\chi^2 = 6.08$, $P < 0.05$). Incubation success of late-season unmanipulated clutches was lower in 1986 ($\bar{x} = 5.1$ chicks) than it was in 1984 ($\bar{x} = 5.4$ chicks) and in 1985 ($\bar{x} = 5.5$ chicks).

Incubation success in enlarged clutches.—In both early- and late-season nests, enlarged clutches produced significantly more chicks on brood-day 4 than did control clutches (Fig. 2). In early-season clutches, the median brood size produced by enlarged clutches was 8 chicks ($\bar{x} = 7.5$) and by control clutches it was 7 chicks ($\bar{x} = 6.2$) (Wilcoxon 2-sample test, $Z = 4.22$, $P < 0.0001$) (Fig. 2A, B); in late-season clutches, the median brood size produced by enlarged clutches was 7 chicks ($\bar{x} = 6.9$) and by control clutches it was 5 chicks ($\bar{x} = 5.1$) ($Z = 4.61$, $P < 0.0001$) (Fig. 2C, D).

Four early-season clutches of 7 eggs and five early-season clutches of 8 eggs were increased to 10 eggs (Table 3). In five of these nine clutches, the number of chicks present on brood-day 4 was greater than the original clutch size laid by the female. One early-season clutch of 9 eggs was increased to 11 eggs, producing 10 chicks on brood-day 4.

Incubation period.—Incubation periods of enlarged early-season clutches ($\bar{x} = 12.3$ days ± 0.19 [SE]) were significantly longer than those of controls ($\bar{x} = 11.7 \pm 0.08$ days) ($t = 3.54$, df $= 120$, $P < 0.001$). For late-season clutches, the incubation periods are not significantly different: enlarged clutches, $\bar{x} = 11.2 \pm 0.14$ days; control clutches, $\bar{x} = 11.4 \pm 0.11$ days ($t = 0.92$, df $= 74$, $P > 0.05$).

DISCUSSION

The addition of two eggs to nests containing the most common clutch size in both early and late seasons resulted in significantly more chicks

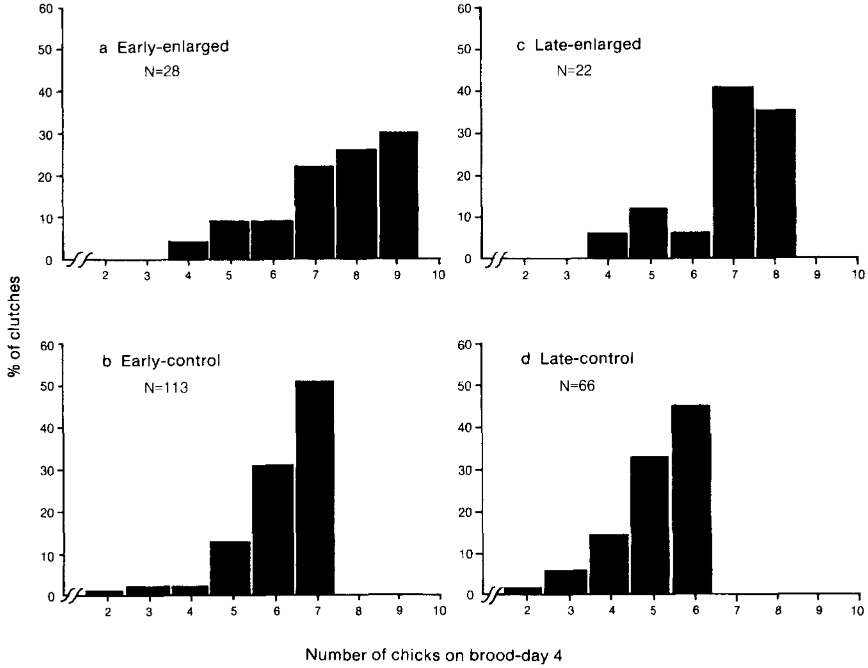

FIG. 2. The distribution of number of chicks present on brood-day 4 (incubation success) for enlarged and control early-season nests with an original clutch size of 7 eggs (A and B, respectively) and for enlarged and control late-season nests with an original clutch size of 6 eggs (C and D, respectively).

hatching and surviving to brood-day 4. Thus, House Wrens laying modal-size clutches were able to incubate more eggs than they laid, suggesting that clutch size was not limited by incubation ability. Two problems, however, need to be considered when interpreting our results. The first is the use of artificial nest sites, and the second is the lower hatching success of late-season control clutches in 1986 compared with that of unmanipulated clutches in earlier years.

The use of nestboxes rather than natural cavities may have influenced the outcome of the experiment, as our nestboxes are probably larger than most natural cavities (pers. obs.). The effect, if any, of this difference is unknown, but clutch sizes in our nestboxes are similar to those reported from nests in natural cavities (e.g., Sage et al. 1913, Trautman 1940). Nonetheless, the effect of the use of artificial nest sites on incubation success cannot be directly assessed and must await studies of House Wrens nesting in natural cavities.

The lower incubation success of late-season controls in 1986 compared

TABLE 3
DISTRIBUTION OF NUMBER OF CHICKS PRESENT ON BROOD-DAY 4 (INCUBATION SUCCESS) IN OTHER EXPERIMENTAL ENLARGEMENTS

No. eggs laid in enlarged clutches	No. eggs added	No. chicks on brood-day 4							No. clutches
		0	5	6	7	8	9	10	
7	3	1[a]	1				2		4
8	2			1		1	2	1	5
9	2							1	1

[a] Clutch depredated by raccoon (*Procyon lotor*) during incubation.

with that in late-season unmanipulated clutches in 1984 and 1985 raises the question of the generality of conclusions based on results from 1986. The difference, however, occurred during the latter half of the breeding season only and is not great (≤ 0.4 chicks). Furthermore, whatever was responsible for the decrease in the incubation success of late-season controls in 1986 may well have decreased concomitantly the incubation success of enlarged clutches. If conditions in late 1986 were unfavorable, they should have affected enlarged clutches more severely than controls. That this did not happen suggests that the significant differences between enlarged and control clutches in late 1986 are not a product of unusual conditions at that time.

Klomp (1970) summarized results of early studies on the ability of females to incubate additional eggs, and Winkler and Walters (1983) discussed the evidence for incubation-limitation in precocial species. In general, many species seem to be able to incubate enlarged clutches successfully. For example, both American Avocets (*Recurvirostra americana*) (Shipley 1984) and Fieldfares (*Turdus pilaris*) (Slagsvold 1982) incubate enlarged clutches successfully. In contrast, inability to incubate additional eggs has not been frequently reported, although Andersson (1976) and Tarburton (1987) demonstrated that parents given enlarged clutches failed to produce as many hatchlings as parents incubating unmanipulated clutches in Long-tailed Jaegers (*Stercorarius longicaudus*) and in White-rumped Swiftlets (*Aerodramus spodiopygius*), respectively.

The possibility that clutch size may be limited ultimately by an inability to incubate additional eggs has been considered unlikely because (1) hatching success typically does not decrease proportionately with increasing clutch size over the natural range of clutch sizes and (2) clutch size, which has been determined by other selective forces, and the ability to incubate a specific number of eggs have evolved in parallel (Klomp 1970:37). The first is inapplicable if each female's clutch size is adjusted to her incubation ability, resulting in either no correlation or in a positive correlation between clutch size and hatching success; there is no reason to expect a negative correlation. Perrins (1965) and Nur (1984, 1986) have emphasized this with regard to individual variation in ability to rear additional chicks during the nestling stage, and the same argument applies for ability to incubate additional eggs. As House Wrens were clearly able to incubate additional eggs successfully, clutch size was not individually adjusted to the maximum number of eggs that a female could incubate. The second point needs to be considered further only if it can be demonstrated that females are *not* able to incubate successfully clutches larger than those they initially attempt. This is clearly not the case in the House Wren under the conditions of our experiment.

The possibility remains that although females can incubate additional eggs, females doing so would experience reduced survival or reduced future reproductive success, or both (i.e., they would incur a cost of reproduction). Although there is no general agreement as to the energetic demands of incubation, it is unlikely to be so great as that of other stages of the breeding cycle (see summary by Walsberg 1983). Haftorn and Reinertsen (1985) concluded that, even at the northern limit of the Blue Tit's (*Parus caeruleus*) breeding range, females in nestboxes are easily able to maintain egg temperatures well above the temperature below which no embryonic development occurs. House Wrens incubate their eggs in well-insulated cavities, and there is little reason to suspect that incubation is so energetically demanding for House Wrens that it is necessary for them to decrease their clutch size to save energy or to maintain egg temperature. Costs, however, may be exacted in other ways.

One possible cost incurred by females incubating enlarged clutches was the extension of incubation by half a day early in the season. Length of the House Wren's incubation period is directly related to ambient temperature, which exerts its influence by affecting female attentiveness (Kendeigh 1952). At low ambient temperatures unattended eggs cool rapidly, and Kendeigh (1963) showed that heat energy applied to eggs by incubating females decreases as air temperature decreases. Furthermore, the amount of heat applied to the eggs is a function of the number of eggs in the clutch (Kendeigh 1963). In our study, early-season ambient temperatures averaged about 7.5°C lower than they were later when incubation periods of controls and enlarged clutches were not significantly different. A prolonged incubation period in enlarged clutches early in the breeding season suggests that females with enlarged clutches were unable to maintain egg temperatures as high as those maintained by females with smaller control clutches. The importance of a half-day's delay in hatching is unknown; however, this effect in 1986, a year in which May temperatures were 1.3°C above the long-term average, raises the possibility that in unusually cold springs, females laying clutches much larger than the modal size may experience some difficulty during incubation.

In conclusion, House Wrens were able to incubate enlarged clutches in our nestboxes in 1986, and it is unlikely that inability to incubate additional eggs has been an important selective force limiting clutch size in this species.

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MEETING OF THE ASSOCIATION OF FIELD ORNITHOLOGISTS

The Association of Field Ornithologists (formerly NEBBA) will hold its annual meeting 13–15 May 1988 at the Vermont Institute of Natural Sciences, Woodstock, Vermont. Housing and the Saturday evening banquet will be at the nearby Kedron Valley Inn. The meeting will include invited and contributed papers, workshops and field trips. For information about the meeting, contact: SARAH B. LOUGHLIN, AFO Local Committee Chair, Vermont Institute of Natural Science, Woodstock, VT 05091 (802/457-2779). For information about the scientific program, contact: PETER F. CANNELL, Program Committee Chair, Division of Birds, NHB 116, Smithsonian Institution, Washington, DC 20560 (202/357-2334).