THE INFLUENCE OF NEST BUILDING AND EGG LAYING BEHAVIOR ON CLUTCH SIZE IN RENESTS OF THE WILLOW FLYCATCHER

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INTRODUCTION

The number of eggs within a clutch of a bird species in different years can sometimes be ascribed to food supply (Lack, 1947, 1954, 1966, 1969). If there is an obvious change in food supply on a seasonal basis within a year, one might also account for a seasonal change in clutch size. It is more difficult to explain a significant decline in mean clutch size of a species from a first nest to a renest when ecological factors do not appear altered.

Many factors aside from food could influence a clutch size change. Among these are inter- and intraspecific social interactions, photoperiod changes, physiological fluctuations, and temperature. The factors that I studied were nest building and egg laying behavior, and the way in which these behaviors affect (1) the interval between beginning and completion of a nest and (2) the interval between nest completion and deposition of the first egg. These intervals and clutch sizes may be compared in first nests and renests (nests constructed after nest failure).

I assumed that if there were a significant decrease in clutch size, there would be a concurrent decrease in the time intervals of nest building and egg laying. Thus there would be a decrease in the time in which a female would have to prepare for egg laying. Food availability for nutrition to convert to egg mass would have a role but would be modified by a time element affected by nest building behavior.

METHODS

My plan was to determine (1) any differences in clutch size of first nests and renests of Willow Flycatchers (*Empidonax traillii*), (2) the time interval required in stages of nest building and in the interval between nest completion and deposition of the first egg in first nests and renests and (3) the time interval between loss of a first nest and appearance of a first egg in a renest.

These studies were over a five-year period from 1963-1967: Toledo, Ohio, 1963-65; Fremont, Nebraska, 1966; and Wooster, Ohio, 1967. The birds nested in shrubs and small trees in old fields, marshes, or ditch banks. I searched for nests each day and attempted to find nests before construction was complete. Stages in nest building were (1) just started; a few loose pieces of nest material, (2) platform; a solid mat of nest materials ready for beginning of bowl construction, (3) bowl complete; the entire outer shell of the nest complete but with no lining and (4) nest complete; bowl of nest lined with fine grasses.

Nests were visited each day throughout nest building, egg laying, incubation, and nestling care. From 1964-1967, movements of some pairs were followed to determine the time interval between

predation on eggs or young and laying of the first egg in a renest. Several reports indicate that Willow Flycatchers are single-brooded and thus a renest cannot be confused with a second nesting (Berger, 1967; Holcomb, 1972; McCabe, 1963; Walkinshaw, 1966).

Willow Flycatchers are territorial and monogamous (McCabe, 1963; Stein, 1958; Walkinshaw, 1966). As I found every nest within the study areas I could identify individual females without color-marking. One female was color-marked. All first nests were begun before 20 June and all known renests 20 June or after. Thus, I have grouped nests into first nests and renests on the basis of date when building began

Differences between mean values were considered significant if $P < 0.05$ using a 2-tailed Student's *t*-test. Results are shown as means and standard error of the mean.

RESULTS

A significant decline in mean clutch size was found from first nests to renests (3.68 ± 0.1, $n = 31$; 3.14 ± 0.1, $n = 29$). Mean clutch size for all nests was 3.41 ± 0.1 and is similar to the values reported by Walkinshaw (1966) and Berger (1967). Most clutches were three or four eggs; there was one of five eggs in a first nest and one of two eggs in a renest. Fresh egg mean weights for 81 eggs in first nests and 87 eggs in renests was 1.7 g for both. Thus there was a mean of 0.92 g additional mass of eggs in first nests than renests (3.68 eggs $\times$ 1.7 g = 6.26 g; 3.14 eggs $\times$ 1.7 g = 5.34 g). Walkinshaw (1966) reported a mean weight of 1.67 g for 83 eggs.

In first nests there were 12 three-egg clutches, 18 four-egg clutches, and one five-egg clutch. In renests there were 22 three-egg clutches, 4 four-egg clutches, and one two-egg clutch. Of eight pairs that had two clutches each, three females laid 6 eggs (2 clutches of 3 eggs each) and five females laid 7 eggs (one clutch of four eggs and one clutch of 3 eggs. Four of the five females laid their four-egg clutch in the first nest.

Table 1 reveals no difference in the time needed to complete stages of nest building in first nests or renests. However, a significantly longer interval occurs between nest completion and egg laying in first nests than in renests.

Table 2 shows a mean of 6.6 days for the interval between the time of removal of eggs and/or nestlings by predators and the day of initial egg laying in a second nest for 18 females. There was no difference in length of the delay relative to time in the egg laying, incubation or nestling periods of the nest at the time of predation. The greatest delay was 12 days. This female was captured, marked and released but her first nest and eggs remained intact.

DISCUSSION

Reports by Berger (1967), Berger and Hofslund (1950) and Walkinshaw (1966) show more four-egg clutches than three-egg clutches in the Willow Flycatcher although my data and that of King (1955) show fewer four-egg clutches. I suggest that the per-

TABLE 1.
Mean time intervals required for stages in nest building and egg laying periods (days)

		Nest start to platform stage	Platform to nest bowl complete	Nest bowl completion to nest complete	Nest complete to first egg laid
Before 20 June-First nests	n	9	11	25	28
	$\bar{x}$	1.0	1.3 ± 0.1	1.5 ± 0.1	3.1 ± 0.3
	Range	—	1–2	1–3	1–6
20 June and after-renests	n	7	9	25	33
	$\bar{x}$	1.3 ± 0.2	1.6 ± 0.2	1.3 ± 0.1	1.4 ± 0.1
	Range	1–2	1–3	1–2	1–3
Combined data on all nests	n	16	20	50	61
	$\bar{x}$	1.1 ± 0.1	1.4 ± 0.1	1.4 ± 0.1	2.2 ± 0.2
	Range	1–2	1–3	1–3	1–6

TABLE 2.
Mean interval (days) between removal of eggs or nestlings by predators and deposition of a first egg in a renest

Time in nesting cycle[1]	No. of nests	Distribution of intervals	Mean interval
Egg laying or nest complete before egg laying	4	6, 6, 8, 8	7.0
Day 1-7 Incubation	8	4, 5, 6, 6, 7, 7, 7, 8	6.3
Day 8-14 Incubation	2	6, 7	6.5
Special[2]	1	12	12.0
Day 0-7 Nestlings	3	5, 5, 6	5.3
Totals	18	—	6.6

[1]Incubation requires 12-15 days and nestling periods are 11-15 days.
[2]A female abandoned eggs in early incubation after she was captured for color-banding and marking.

centage of three-egg clutches in a sample over many studies may reflect the percentage of renests occurring in the sample. Berger (1967) suggested a higher proportion of four-egg clutches to three-egg clutches and that the ratio may be 2:1. However, my sample shows 34 three-egg clutches and 22 four-egg clutches. I may have a high proportion of renests.

Walkinshaw (1966) reported only two of 23 females that had more than one nest. One laid seven eggs and one laid eight eggs. My data showed only 4 four-egg clutches in 27 renests. Furthermore, from the limited data available for females that were identified in a first nest and renesting, all laid six or seven eggs altogether with one female laying the larger clutch in her second nest. These data suggest that most Willow Flycatchers do not lay more than seven eggs in a nesting season in which they have two nests.

The data available on determinate species show that they lay a set number of eggs and that the number is determined prior to the onset of egg laying (Davis, 1955; Holcomb, 1971). If the first clutch of eggs in a nesting season is determinate, is there a predetermined number of ova that will develop into eggs for the entire nesting season? Are these determined prior to laying of the first clutch or is renest clutch size determined after the laying of the first clutch? These and many other questions remain to be answered by future investigations.

In Willow Flycatchers a significant decrease in clutch size is found from the first clutches to later clutches as well as a reduction in total egg mass. Furthermore, no difference occurs in the length of time needed to build a nest, but there is a shorter interval between nest completion and egg laying in renests. A mean interval of 6.6 days is a short time in which to build a nest and begin laying, allowing little or no time for building body reserves.

On the basis of these data I suggest that clutch size is not reduced due to food shortage but may be due to a shortage of time in which to take in sufficient nutrients for development of a larger clutch. The short time interval may be due to a change in behavior. The first nest is constructed only after the female has been in the nesting habitat for at least two weeks and perhaps as many as four weeks. Females generally began arriving the second week in May although most nest building began the first two weeks in June. During the interval a pair formation and delay before nest building a female may consume sufficient food to replenish body reserves lost in migration. She pairs with a male and becomes familiar with a territory. The primary reproductive stimulus is a mate. It may take several days to select a nest site for a first nest.

Willow Flycatchers begin nesting moderately late in the season compared to most other passerine species at the same latitude. Because they are insectivorous, the proximate factors of temperature and rainfall may influence the onset of reproductive activity as modified by food supply. The ultimate factor regulating onset of reproduction is probably photoperiod (Holcomb, 1972).

When the female loses her first clutch, she is more familiar with the territory, the male, and possible nest sites than at the time of her first nest construction. The sight and tactile influences of eggs, nest or nestlings and auditory influence of nestlings are lost as sources of stimulation.

It requires between four and five days to build a nest, and an interval of about 1.5 days occurs between nest completion and egg laying. Because there was only a mean of 6.6 days available, the female probably selects a nest site to begin building within one day after loss of a first nest.

It is important to note that the length of the nest building interval was not different in first nests and renests even though ovaries must have developed more rapidly in the renest situations. Ovarian production of estrogen does influence nest building (Lehrman, 1961; Hinde, 1967). In American Goldfinches (*Spinus tristis*) a difference is found in interval from nest completion to egg laying and a decrease in clutch size between early and late nests (Holcomb, 1969).

Most nesting occurs in June and July. If a female is to raise young, she must be capable of laying a second clutch very rapidly if a first clutch is destroyed. Ricklefs (1969) summarized 17 studies for temperate region songbirds and reported a mean of 7.8 days for initiation of a new clutch after losing an earlier clutch. Thus several passerine species may lay a second clutch rapidly at the expense of laying fewer eggs. The factors such as temperature influence on clutch size in first nests and renests as discussed by Kendeigh et al. (1956) for the House Wren (*Troglodytes aëdon*) and Holcomb (1972) for the Willow Flycatcher are not discounted. However, these may be secondary in importance to the behavior as it is modified by reproductive physiological mechanisms.

SUMMARY

Willow Flycatchers lay fewer eggs in renests than in first nests. The time required for nest building is the same in first nests and renests but the interval between nest completion and egg laying is greater in first nests. The number of days required between loss of eggs or young in a first nest and egg laying in a renest is only 6.6 days.

Nest site selection must be rapid after loss of a first nest. Female behavior is probably influenced by her familiarity with the environment and rapid ovarian growth. The acceleration of behavior as influenced by endogenous and exogenous stimuli possibly leaves no time for building body energy reserves for egg laying and thus mean clutch size is reduced in renests.

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