

Wilson Bull., 99(4), 1987, pp. 708–712

Relaying interval after nest failure in Gray Catbirds and Northern Cardinals.—Nest failures, followed by renesting, occur frequently among passerines. The rate at which a bird re-nests can affect its productivity by influencing the number of its nesting attempts (Ricklefs 1973, Finch 1984). Quick re-nesting need not increase the number of re-nesting attempts, as some individuals might re-nest only once a season. If re-nesting followed a failure quickly it would provide, however, a longer time to care for fledglings, should they be produced. Quick re-nesting would be particularly important in a species with a short laying season. For such a species, time saved in re-nesting would have a proportionately greater effect than would be so for a species with a long laying season.

We present extensive data on re-nesting following nest failure for two species that breed in the same macrohabitat at London, Ontario: the Gray Catbird (*Dumetella carolinensis*), a migrant species, and the Northern Cardinal (*Cardinalis cardinalis*), a resident species. At London, Ontario, the laying season of catbirds extends about 50 days between mid-May and early July (Darley et al. 1971), but that of cardinals is about 120 days from mid-April to mid-August (Scott 1963).

Here we (1) compare the length of the interval between nest failure and relaying between catbirds and cardinals, and (2) relate the length of this interval to the minimum time required for rapid yolk deposition in the development of a new clutch.

Methods.—We observed cardinal nests from 1955 to 1961, and catbird nests in 1963, 1964, and 1969. The data are those used by Scott and Ankney (1980:682) to support their argument that female passerines can quickly obtain nutrients for egg production. All replacement nests of catbirds, and about 75% of those of cardinals, belonged to uniquely color-marked females that were being studied on the campus of the University of Western Ontario, London, Ontario.

We recorded the time between a failed nest and its replacement as the number of days (interval) between the day on which we recorded nest failure and the day when the first egg was laid in the next nest. We visited most nests daily, presumably after the laying hour. Thus, the observed interval was about one-half day *shorter* than the actual interval because failure occurred sometime during the 24 h preceding observation of nest failure. Parenthetically, we wish to stress that some investigators have recorded the interval between the last day a nest was active and the day that the first replacement egg was laid. In these cases, the observed interval would be about one-half day *longer* than the actual interval between failure and relaying. Thus, the two ways of recording the interval would yield a difference of 1 day for a particular case.

About 10% of our visits were made at longer than a daily interval, and when nest failure occurred during 2 days between visits we estimated the day of nest failure as occurring on one or the other of 2 days. Such intervals have been plotted in Fig. 1 for the mid-point of the two possible intervals (e.g., if the interval was either 3 or 4 days it has been plotted as 3.5 days). In Table 1, such an interval has been indicated as 3–4 days.

We usually treated the first nest found after nest failure as the replacement. In two cases, however, one involving each species, each female built two nests simultaneously but laid in only one, which we regarded as the replacement nest. This unusual behavior caused two long intervals: 7 days for the catbird (the second longest recorded in this study) and 10 days for the cardinal. Unusually long intervals could have resulted, however, if we failed to find the first replacement nest. We excluded from analysis six intervals, ranging from 14 to 31 days, because we had no record of the activities of the birds during those periods and, thus, we could have missed earlier nests.

Two exceptionally short intervals of 3 days, in cardinals, although plotted in Fig. 1, have

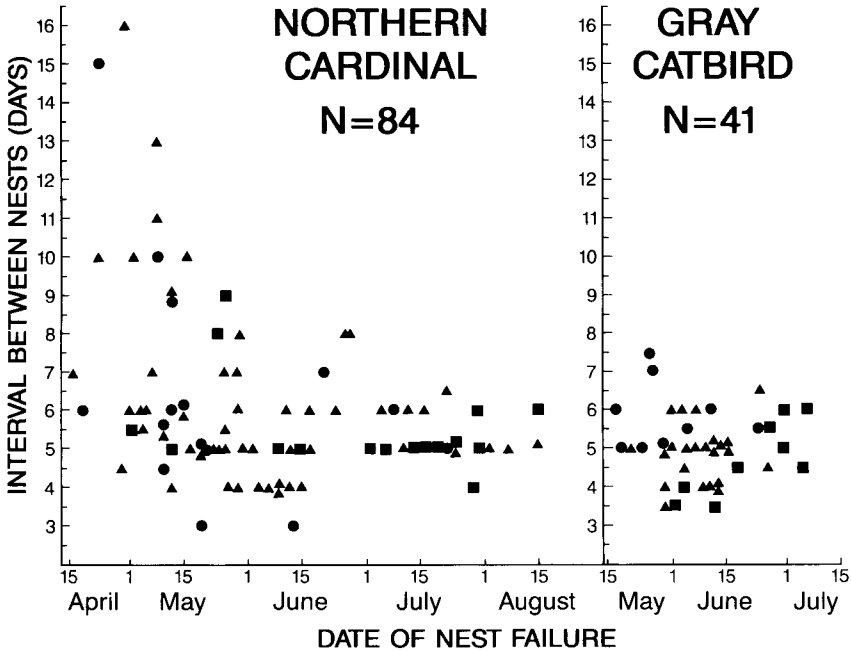


FIG. 1. Variation in the length of intervals between nest failure and first replacement egg by cardinals and catbirds. Stages of the nesting cycle when failure occurred are indicated by circles (laying), triangles (incubating), and squares (brooding).

been omitted from all analyses because they are not comparable with other intervals. Each 3-day interval followed the loss within a few hours of the only egg laid in that nest. As almost all cardinals here lay only 3 eggs, each of these two females on the day of nest failure almost certainly had one large yolky oocyte, unlike birds which lost nests later in the cycle.

We used meteorological summaries for London obtained from Environment Canada, Atmospheric Environment Service, in our analysis of a relationship between interval length and weather. Statistical procedures followed those of Sokal and Rohlf (1981).

Results.—During 17 May–6 July, when both species were laying, 41 catbirds renested 5.05 ± 0.92 days [SD] and 37 cardinals 5.53 ± 1.36 days (two-tailed test with unequal variances, $t = 1.833$, $df = 76$, $0.10 > P > 0.05$) after nest failures (Fig. 1). Variability of the interval length for cardinals was significantly greater than that of catbirds ($F = 2.195$, $P < 0.01$).

Renesting intervals for cardinals were longest and most variable in April and May, and, like catbirds, were shortest in early June and later increased slightly (Fig. 1).

We divided the 25 intervals recorded for cardinals before 17 May, when interval length was the most variable (Fig. 1), into two groups: (1) those associated with below average temperatures on the day of nest failure and on the next 2 days (i.e., the days when a female usually begins to rebuild and when oocytes for the next clutch could begin rapid yolk deposition) and (2) those associated with above average temperatures on those days. Only 3 of the cold weather renestings ($N = 11$), but 12 of the other renestings ($N = 14$) occurred within 6 days (G -test with Yates' correction, $G = 6.752$, $df = 1$, $P < 0.01$).

TABLE 1
 FREQUENCY OF DIFFERENT INTERVALS BETWEEN NEST FAILURE AND THE FIRST
 REPLACEMENT EGG RELATED TO NESTING STAGE WHEN NEST FAILED

| Nesting stage and species | Interval (days) | | | | | | | | | | |
|------------------------------|------------------|---|-----|----|-----|---|-----|---|-----|---|---|
| | 3-4 ^a | 4 | 4-5 | 5 | 5-6 | 6 | 6-7 | 7 | 7-8 | 8 | 9 |
| Laying | | | | | | | | | | | |
| Catbird | | | | 3 | 2 | 2 | | 1 | 1 | | |
| Cardinal ^b | | | | 3 | | 1 | | 1 | | | |
| Incubating | | | | | | | | | | | |
| Catbird | 2 | 5 | 2 | 10 | | 3 | 1 | | | | |
| Cardinal | | 8 | | 14 | 1 | 7 | 1 | 2 | | 3 | |
| Brooding | | | | | | | | | | | |
| Catbird | 1 | 1 | 2 | 2 | 1 | 2 | | | | | |
| Cardinal | | 1 | | 9 | | 2 | | | | 1 | 1 |

^a Indicates that interval could have been 1 of 2 days (e.g., 3-4 indicates interval of 3 or 4 days).

^b Only cardinal nests that failed between 17 May and 15 August were used to exclude extreme variability of intervals in April and May.

Interval lengths following loss during incubating or brooding by catbirds did not differ significantly (Wilcoxon two-sample test, $t = 0.266$, $P > 0.5$). Intervals were longer following loss during the laying stage (laying vs incubating, Wilcoxon two-sample test, $t = 2.399$, $P < 0.02$; laying vs brooding, Mann-Whitney U -test, $U = 62$, $0.10 > P > 0.05$) (Table 1). The length of intervals for cardinals was not significantly affected by the stage at nest failure (Kruskal-Wallis test, adjusted $H = 0.3677$, $df = 2$, $P > 0.8$).

Discussion.—Our observations agree with those of Mousley (1917) and Chance (1940) who reported that many species of north-temperate-zone passerines relay within 5 to 7 days of nest failure.

The retarding effect of cold weather on reproductive activity, noted in female cardinals, is known for other species (e.g., Nolan 1978:185) and causes much variability in nesting activity early in the breeding season. Finch (1984), who studied another species with a long nesting season, also noted that the greatest range in length of renesting intervals occurred early in the season, as in cardinals.

Catbirds had a marginally shorter renesting interval than did cardinals. The difference, although significant only at $P = 0.10$, suggests that shorter intervals may distinguish species with short nesting seasons from those with long nesting seasons. The noted difference and the significant difference in variances, however, may simply have resulted from biased sampling, as our data on catbirds were collected in summers from which we have no cardinal data.

The stage at which nest failure occurs may influence the length of the subsequent interval before renesting. The relationship, however, is by no means clear. We found no effect in cardinals, but in catbirds the interval was slightly longer following nest failure during laying. Nolan (1978:117) concluded that the interval shown by Prairie Warblers (*Dendroica discolor*) did not vary upon the nesting stage at loss. For other species, however, Delius (1965) and Anderson (1979) noted that the nesting stage at loss influenced the length of the renesting interval.

TABLE 2
DIAMETERS (MM) OF LARGEST OOCYTES AND WEIGHTS (MG) OF OVIDUCTS RELATED TO THE
NESTING STAGE OF GRAY CATBIRDS

| Egg in oviduct | Eggs laid | Range of diameters of largest oocytes | Range of weights of oviducts | Nesting stage |
|-------------------------------------|------------|--|------------------------------|--------------------------------------|
| Penultimate ^a (N = 3) | 2, 2, 2 | 8.80–10.55 1.85 ^b –2.25 ^b | — | Laying |
| Last ^a (N = 2) | 3, 4 | 1.80–2.30 | 1310–1890 | Laying |
| None (N = 3) | 3, 4, 4 | 2.00–2.60 | 390–445 | Incubation (day 2 or 3) ^c |
| None (N = 4) | 3, 4, 4, 4 | 2.10–2.25 | 210–290 | Incubation (day 4 or 5) ^c |
| None (N = 2) | — | 2.30–2.45 | — | Incubation (day 12) ^c |

^a Judged from size of largest oocyte.

^b Second largest oocyte.

^c Inferred from known nesting history of birds.

When a small passerine has completed laying, she will typically have only small oocytes (Payne 1969) (Table 2). Such oocytes can attain maximum size within 4 days (e.g., Krementz and Ankney 1986). The *minimum* possible interval, measured from the day when a nest was last active, preceding the day of the first replacement egg is 5 days (4 days of rapid yolk deposition plus one day in the oviduct). However, as we calculated the interval beginning probably well after nest failure, the 4-day interval in cardinals and catbirds is the minimum possible interval. Some 5-day intervals may also be the minimum possible. Nest failure may occur too late in the day for the largest oocyte to complete its growth in time to be laid after a 4-day interval. Clearly, most catbirds and cardinals cannot renest faster than they do from late May onwards.

The oviduct of a catbird does not reach minimum breeding weight, following laying, until midincubation (Table 2). Thus, if a nest were lost early in the nesting cycle, little renewed growth of the oviduct would be necessary, and this would aid rapid relaying.

When nest loss occurs during early laying, intervals may be 3 days, as in cardinals, or even shorter in other species (Delius 1965, Leinonen 1973). What is the fate of the oviducal egg or the large yolky oocytes that would normally have completed the clutch? Three answers seem possible, other than that of laying the oviducal egg on the ground. (1) The oviducal egg present at the time of nest loss might be retained for several days. This is unlikely as it would be maladaptive. (2) Large yolky oocytes present at the time of nest loss might become atretic. The reabsorption of nutrients might accelerate, exceptionally, the growth of a small oocyte as Barry's data (1962) suggest. (3) The largest mature oocyte might be retained, without growth or atresia, for a few days beyond its expected day of ovulation (see Gilbert and Wood-Gush 1971) and, thus, could be used to initiate the replacement clutch. That is, what might have been the last egg of one clutch becomes the first egg of the next clutch.

Acknowledgments.—We are indebted to the late N. K. Taylor who made many observations on catbird nests, to A. L. A. Middleton who observed many cardinal nests, and to A. V. Newsome who kindly provided the measurements of reproductive organs of catbirds from her unpublished study of the ovaries of catbirds and Brown-headed Cowbirds (*Molothrus ater*). We are particularly grateful to J. D. Delius who took great pains to answer questions about skylarks. R. Bailey gave generously of his time in providing help in statistical matters. B. Kessel and R. E. Ricklefs graciously provided information on replacement nests.

We appreciate comments made on earlier drafts of this paper by C. D. Ankney, K. L. Bildstein, P. A. Gowaty, H. Mayfield, and J. L. Zimmerman.

The National Engineering and Science Research Council of Canada and the Ontario Research Council provided financial support for our broader studies of catbirds and cardinals.

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- DAVID M. SCOTT, ROBERT E. LEMON, AND JAMES A. DARLEY, *Dept. Zoology, Univ. Western Ontario, London, Ontario N6A 5B7, Canada.* (Present address of REL: *Dept. Biology, McGill Univ., Montreal, Quebec, H3A 1B1, Canada*; JAD: *Dept. Psychology, St. Mary's Univ., Halifax, Nova Scotia B3H 3C3, Canada.*) Received 4 Dec. 1986, accepted 23 Mar. 1987.

Wilson Bull., 99(4), 1987, pp. 712-717

Influence of nest-box placement and density on abundance and productivity of American Kestrels in central Missouri.—When extra nest sites are provided by man, an increase in raptor breeding densities often follows (Newton 1976, 1979). The scarcity of suitable cavities probably limits nesting populations of American Kestrels (*Falco sparverius*) (Cade 1982).