SEASONAL PATTERNS OF NESTING MORTALITY IN THE RED-WINGED BLACKBIRD

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It is likely that birds adjust their reproductive period to that time when nesting is most successful, in terms of both the immediate success in fledging young and the later success of the offspring after parental care ends. Such adjustment is selectively influenced by numerous ultimate factors (Baker 1938, Thomson 1950), which together favor those individuals who tend to breed under optimum conditions. Selection is shown by a decreasing productivity of offspring progressively earlier or later than the optimum nesting period.

While such a conceptual framework is generally accepted, little information is available on the sources, timing or magnitude of the seasonal variations in the mortality of eggs and nestlings. Analysis of the average rate of loss from each cause of mortality upon individual reproductive units throughout the reproductive period should provide insight into the mechanisms that determine and maintain the periodicity of the breeding season.

Patterns of nesting mortality can readily be studied in the Red-winged Blackbird (*Agelaius phoeniceus*), thanks to the colonial nesting habit in this species. I have analyzed nesting mortality of Red-winged Blackbirds for two nesting seasons. The role of nesting mortality in seasonally adjusting the reproductive period was evaluated by determining the average mortality rate per nest for each source of mortality.

STUDY SITE AND METHODS

This study was conducted on a tidal salt marsh in southern Ocean Co., New Jersey, during the breeding seasons of 1973 and 1974. Field methods were the same for both years and are reported elsewhere, along with a description of the study site (Caccamise 1976, 1977). Weather data were recorded about 6.4 km from the study site at the U.S. Weather Bureau Station, Tuckerton, N.J. Nests were located, tagged and subsequently visited on alternate days throughout the nesting cycle.

Nests were aged beginning with the onset of egg laying (Day-1). Because of early loss some nests could not be accurately aged and were not included in the mortality analysis. Egg and nestling losses were assigned to each category of mortality according to predetermined criteria. These included differences in nest contents between visits as well as changes in the physical conditions of the nest. *Abandonment* included those eggs which remained unhatched beyond the normal incubation period. *Egg-disappearance* constituted those otherwise unaccountable single losses that occurred without obvious changes in the

physical condition of the nest. *Unhatched eggs* included both embryo mortality and infertility and was detected when one or sometimes two eggs remained in the bottom of the nest after the other eggs in the clutch hatched. These losses ware assigned alternately to the laying days. *Clutch-loss* included mortality of all eggs in a nest and often was accompanied by partial or total nest destruction. Clutch-loss was primarily caused by predation but occasionally may have resulted from destruction by storms. The *death-in-nest* category comprised those cases in which a single nestling either was found dead or disappeared while the remaining brood members and the nest appeared otherwise normal. These losses were primarily due to nestling starvation (Robertson 1973a, Caccamise 1976) but also may have been caused by accidental eviction of the nestling from the nest. *Nestling predation* was characterized by the loss of all nestlings, generally on a single day, or in a few cases over a period of two days. Signs of nest tampering usually were evident.

Because the timing of reproductive events differed somewhat between 1973 and 1974, I used the onset of oviposition in the colonies as the starting date for chronicling reproductive events. This reduced the effect of seasonal differences between years and allowed data from both years to be pooled. Mean mortality rates per nest were calculated separately for each cause of egg and nestling loss occurring within each 10-day interval. Individual sources of mortality were later combined within each 10-day interval to assess seasonal patterns of egg and nestling mortality.

RESULTS

TEMPORAL ASPECTS OF REPRODUCTION

In 1973, egg laying began on 16 May and extended through 2 July, totaling 50 days (Fig. 1). In 1974 it began five days earlier and extended through 6 July (56 days). The weather was considerably milder early in the breeding season of 1974 than during the same period in 1973. During April and May 1974 there was a total of 529 degree-days and 11.2 cm of precipitation, while in 1973 there were 623 degree-days and 25.8 cm of precipitation. The colder and wetter conditions during early spring in 1973 probably contributed to the later onset of reproduction during that year.

In both years, egg-laying began later at my colony than at other colonies of similar latitude. This was true both for inland marsh colonies (Smith 1943, Beer and Tibbitts 1950, Robertson 1973b, Dolbeer 1976) and tidal marsh colonies (Meanley and Webb 1963) near the upper Chesapeake Bay. However, these colonies were all essentially inland, while mine was on the ocean shore. The difference
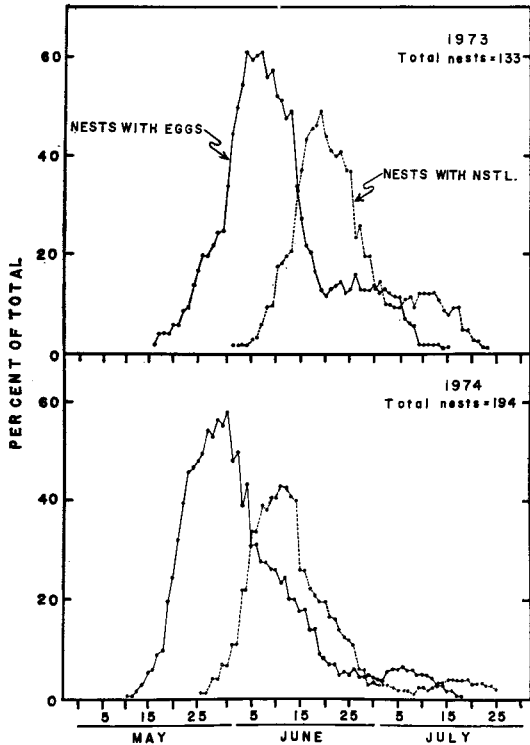
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FIGURE 1.   Seasonal patterns of nesting chronology for 1973 and 1974. Each point represents the percent of the total aged nests that contained eggs or nestlings at each date.

FIGURE 3.   Mean clutch size for each 5-day interval throughout the laying periods of 1973 and 1974. Sample size is given next to each point on the graph.

ence between years in the occurrence of these peaks, the shapes of the curves were similar indicating that nesting synchrony was essentially the same for both years.

Mean clutch size decreased during the season (Fig. 3). An analysis of variance performed on these data indicated a highly significant difference ($P < 0.01$, F $= 4.607$, d.f. $= 11/307$) in mean clutch size among 5-day intervals. A similar decrease in mean clutch size was suggested for Red-winged Blackbirds by Meanley and Webb (1963) and Dolbeer (1976).

NESTING MORTALITY

In 1973 and 1974, respectively, I found 164 and 242 active nests, of which 133 and 191 could be accurately aged. Breeding success and the sources of mortality for all the aged nests are presented in Table 1. Causes and relative magnitudes of the losses are similar to

likely reflected the retarded spring warming typical of temperate shore areas. The cooling influence of the ocean would be expected to delay vegetational development as well as the resurgence of insect populations.

The number of active nests increased more rapidly in 1974 than in 1973, coinciding with an earlier peak in the percent of total nests at Day-1 (Fig. 2). Notwithstanding the differ-
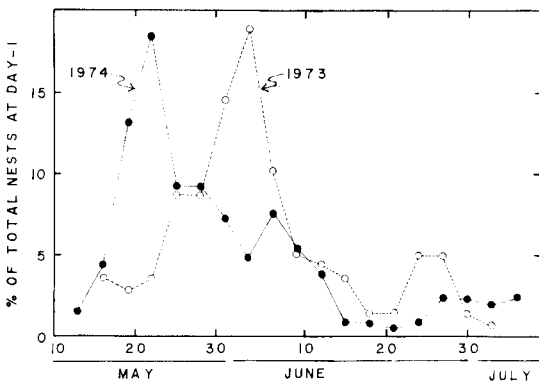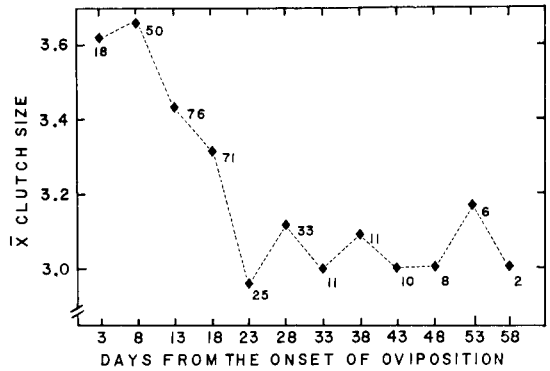

FIGURE 2.   Nesting synchrony during 1973 and 1974. Each point represents the percent of the total nests in which the first egg was laid (Day-1) during each 5-day interval (total nests 1973 = 133, 1974 = 194).

TABLE 1.   Nesting success and sources of mortality.

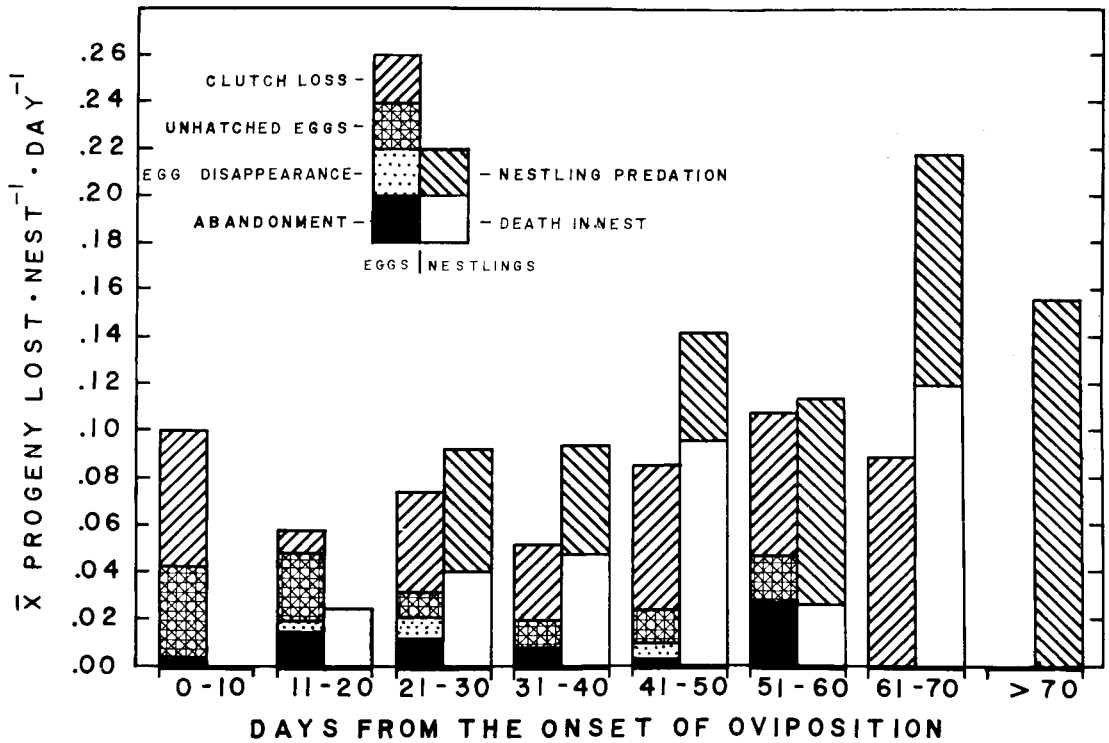|	1973		1974	
	No.	%	No.	%
Nests	133		191	
Eggs	422		623	
Egg mortality				
Abandonment	13	5.7	36	10.5
Egg disappearance	9	4.0	13	3.8
Eggs unhatched	37	16.3	42	12.2
Clutch loss	48	21.1	87	25.3
Total egg mortality	107	47.1	178	51.8
Nestling mortality				
Death in nest	59	26.0	78	22.7
Nestling predation	61	26.9	88	25.6
Total nestling mortality	120	52.9	166	48.3
Total young fledged	195		276	

FIGURE 4.   Mortality rates for individual sources of mortality throughout the nesting period.

those reported in other studies (Smith 1943, Robertson 1972, Holm 1973).

Combining the results from 1973 and 1974, the average rate of loss per nest was assessed for each source of mortality relative to the progression of the nesting season. The relative importance of the sources of mortality changed during the season (Fig. 4). Predation (egg and nestling) and death in the nest accounted for less total mortality early in the season than they did later. Conversely, the proportions of losses from unhatched eggs and abandonment diminished during the season.
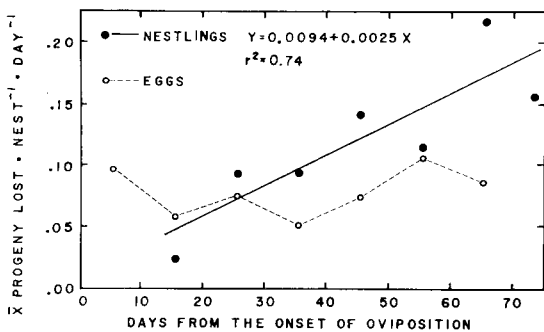

FIGURE 5.   Seasonal patterns of the rates of egg and nestling mortality. The regression equation relates mean number of nestlings lost per nest per day (Y) and days from the onset of oviposition in the colony (X).

A significant linear regression ($P < 0.05$) was found between the number of days from the onset of egg-laying in the colony and total nestling mortality (Fig. 5). A similar relationship was not apparent between season and total egg mortality.

DISCUSSION

Because egg and nestling mortality were determined as average daily rates over the entire season, they indicate the likelihood of mortality occurring on a per nest basis for each day of the season. As nests were active for a series of days, the total mortality over an entire nest cycle can be estimated by summing the daily rates of egg and nestling mortality over those days when a typical nest was occupied. In a complete cycle a nest usually gained an egg on each of three consecutive days; eggs were incubated the next 12 days; nestlings were present for the following 10 days.

Since there was no apparent relationship between the rate of egg mortality and seasonal advance (Fig. 5), calculation of the average rate of egg mortality over the entire season was justified. The seasonal average was 0.0812 deaths·nest^{-1}·day^{-1}. A typical nest contained eggs for 15 days. Therefore the average total egg mortality was 1.218 deaths/nest.

The rate of nestling mortality was not constant but increased as the season progressed (Fig. 5). The average total nestling mortality is the sum of the individual daily mortalities over each 10-day period that nests contained nestlings. Thus the total average nestling mortality increased as Day-1 occurred later in the season.

Summing the average total mortality of eggs and nestlings for each day during the season provided a function (Fig. 6) depicting the expected cumulative mortality (ECM) per nest relative to the date when laying began. The function increased linearly with a slope equal to that for the regression between the rate of nestling mortality and relative date (Fig. 5).

Early in the season, when ECM was relatively low, mean clutch size was greatest. Thus average productivity per nest (clutch size minus ECM) was greatest early in the season, when most eggs were laid. As total ECM approached the mean clutch size, the expected fledgling productivity became zero. This coincided approximately with the termination of egg-laying.

Selection appeared to favor early nesting. Dolbeer (1976) suggested that in his Ohio study the number of young fledged per nest declined during the season largely because of increasing predation. Likewise, Robertson (1973b) and Caccamise (1976) showed that predation rates per nest were highest when colony size was well below the maximum. Such selection pressure would be expected to produce a highly synchronized breeding system, temporally compressed. However, during my study and in other similar studies (Smith 1943, Case and Hewitt 1963, Robertson 1973b, Dolbeer 1976) breeding was protracted, continuing well beyond what appeared to be the optimum time.

The fitness of an individual is determined by its ability to rear offspring successfully, not only during one breeding season but also in subsequent seasons. Thus, the chances of a late breeding attempt having a negative impact on fitness must be small compared to the chances of that individual breeding successfully in the future. Selection would otherwise tend to eliminate those individuals who breed late in the season when there is little chance for success. Since some Red-winged Blackbirds initiate new nests long after the best period, these late nesting attempts must have little or no effect on the future breeding success of these individuals.

Red-winged Blackbirds are known to be persistent renesters. However, Nero (1956) suggested that females maintain territories
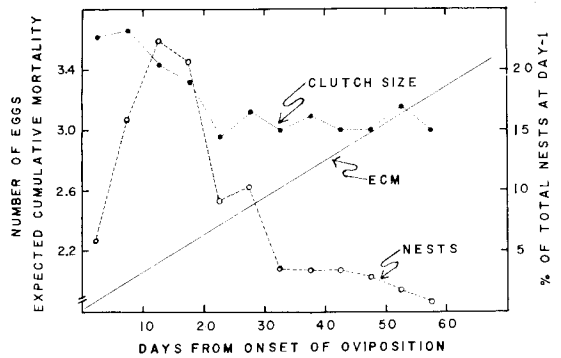

FIGURE 6. Seasonal patterns in the relationship between clutch size, nest starts (Day-1) and expected cumulative mortality. The expected cumulative mortality is estimated for nests begun on each successive day of the season.

within larger male territories when in polygynous associations. If true, there may be a number of surplus nonbreeding females during part of the season (Jackson 1971). While some evidence refuting the hypothesis has been presented (Brown 1969, Holcomb 1974, Dolbeer 1976), the question remains open. In either case, if a nesting attempt has little impact on fitness, nearly any chance for rearing young successfully would appear to be worth the attempt. This would be true whether a female were nesting for the first time or renesting.

The breeding season of the Red-winged Blackbird is synchronized with the abundance of insect prey (Wilson and Orians 1963, Orians 1973). While the proximate factors that initiate reproduction in Red-winged Blackbirds are poorly understood, it seems likely that ultimate control for the onset of reproduction is influenced by the seasonal patterns of food abundance. Because breeding ends when food is most abundant, proximate control for the termination of reproduction is probably not related directly to food abundance. Orians (1973) suggested two possible explanations for why reproduction ceases under these conditions: (1) Young from late nests might become independent during periods of diminishing food supplies; (2) Predation rates on later nests might be high enough to make further attempts at reproduction unprofitable. The first of these explanations has not been tested; however, the second is compatible with the results obtained in my study. Over the breeding season, the proportion of mortality due to predation increased. However other causes of death, particularly death in the nest, also made sizeable contributions to the total mortality through all but the very end of the

breeding season (Fig. 4). As indicated by the increasing expected cumulative mortality (Fig. 6), later nesting attempts became increasingly unprofitable, but this resulted from a decrease in average clutch size as well as an increase in the mortality rate.

Seasonal adjustment of the termination of reproduction probably results from the interaction of many ultimate factors. My data suggest that in the Red-winged Blackbird the increasing rate of nesting mortality with seasonal advance may be of some ultimate importance in ending the breeding season.

SUMMARY

The seasonal distribution of egg and nestling mortality was studied in the Red-winged Blackbird. The relative contribution of individual sources of mortality changed during the season. Deaths from nest abandonment and unhatched eggs decreased in relative contribution to the total mortality while predation and nestling starvation increased. The mean progeny lost per nest per day was calculated for eggs and nestlings through the season. The rate of egg mortality remained relatively constant with a seasonal mean of 0.0812 egg losses·nest^{-1}·day^{-1}. The rate of nestling mortality increased seasonally yielding a significant linear regression with the number of days beyond the onset of egg-laying in the colony. Clutch size decreased significantly from 3.7 eggs per nest at the beginning of the season to about 3.0 eggs per nest at the end of the egg-laying period. Based on the mean rate of egg mortality and the regression relating the rate of nestling mortality with season, the expected cumulative mortality was calculated for nests begun on each laying date of the season. This increasing function approximated clutch size at about the time when egg laying ceased in the colony. Because many individuals began nesting late in the season when chances for success were small, there appeared to be little selective pressure against late nesting attempts. Evidence suggests that increasing nesting mortality with seasonal advance may be an important ultimate factor in establishing the termination of the breeding season.

ACKNOWLEDGMENTS

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