NESTING MORTALITY IN THE
RED-WINGED BLACKBIRD[1]

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BECAUSE the ultimate success of a species is determined by its ability to reproduce, breeding success often has been used as an indicator of a species' vitality under various environmental conditions. Comparisons of breeding success in birds by such factors as latitude (Orians 1973), colony size (Darling 1938; Smith 1943; Coulson and White 1956, 1960), and colony configuration (Horn 1968) have led to many generalizations about the adaptive significance of certain breeding systems.

Because the various patterns and processes of mortality and productivity determine particular levels of breeding success, these prior events form the actual selective framework for an individual breeding system. Therefore the patterns of reproductive success within a breeding system should be indicative of the mechanisms that provide for and maintain the success of that particular breeding system.

In the current study an analysis of the breeding success in the Red-winged Blackbird (*Agelaius phoeniceus*) was undertaken, incorporating a temporal and spatial analysis of egg and nesting mortality. The contribution of each source of mortality was assessed relative to the progression of the breeding season, the development stage of the young, and the spatial relationships within the colony.

STUDY AREA AND METHODS

Nesting surveys were conducted on a tidal marsh in Ocean County, New Jersey. The lowest elevations on the marsh are dominated by two grasses, *Spartina alterniflora* and *S. patens*. With increasing elevation and a concomitant decrease in tidal flooding, several shrub species appear, the more important of them being, in order of increasing elevation, *Iva frutescens*, *Baccharis halimifolia*, and *Myrica pensylvanica*. At the higher elevations several small tree species are interspersed sparsely among the shrubs; these include *Prunus serotina*, *Chamaecyparis thyoides*, and *Rhus copallina*.

The study site was along a dead-end road that traverses 5 miles of salt marsh. Typically in such places shrub habitat occurs as a border between the low grasses of the marsh itself and higher tree-dominated inland tracts (Moul 1973). The landfill added for road construction raises the road borders slightly above the surrounding marsh, providing ground suitable for the typical shrubs and trees of the habitat. The Red-winged Blackbirds use these roadside shrubs for nesting.

TABLE 1

Breeding Success

	Clutch size					
	1	2	3	4	5	Total
No. of nests	10	22	86	45	1	164
No. of eggs	10	44	258	180	5	497
No. hatched	0	19	168	129	3	319
% hatched	0	43.2	65.1	71.7	60.0	64.2
Hatch/nest	0	0.86	1.95	2.87	3.00	1.94
No. fledged	0	12	103	77	3	195
% fledged	0	63.2	61.3	61.6	100.0	61.1
Fledged/nest	0	0.54	1.20	1.71	3.00	1.19

Nest surveys were conducted during the spring and summer of 1973. Nests were marked as they were discovered through the nesting season. Except for the early portion of the nesting season, nests were visited every other day. In chronicling the nests, the onset of egg-laying was considered day 1. Events were detected as differences in nest contents on alternate days. These events were assigned to the date between the two visits. At each visit data were recorded on the number of eggs, number of young, and the condition of the nest. Following fledging, measurements were made of nest site characteristics. Nest chronology was determined directly when nests were discovered prior to or during egg-laying or indirectly by backdating from either hatching or fledging dates.

Results and Interpretations

Breeding Success

The standard information on breeding success is presented in Table 1. At this study site three-egg clutches were most common. The relatively large number of one-egg clutches was largely the result of abandonment prior to clutch completion.

Robertson (1973b) noted that the number of young fledged per egg laid was consistently higher for Red-wings breeding in marsh rather than in upland habitats. The values in Table 1 are intermediate between those reported by Robertson for clutch sizes 3 and 4, while for clutch size 2 the value is well below that obtained in either habitat.

Mortality

Age specific mortality.—Fig. 1 is the survivorship curve constructed from the age specific mortality of eggs and nestlings. The curve is decidedly negatively skewed indicating an increase in mortality rate as the nesting period progressed. Similar relationships were shown in mortality rates of eggs and nestlings by Young (1963) and Robertson (1972) in Red-winged Blackbirds, by Horn (1968) in Brewer's Blackbird (*Euphagus*
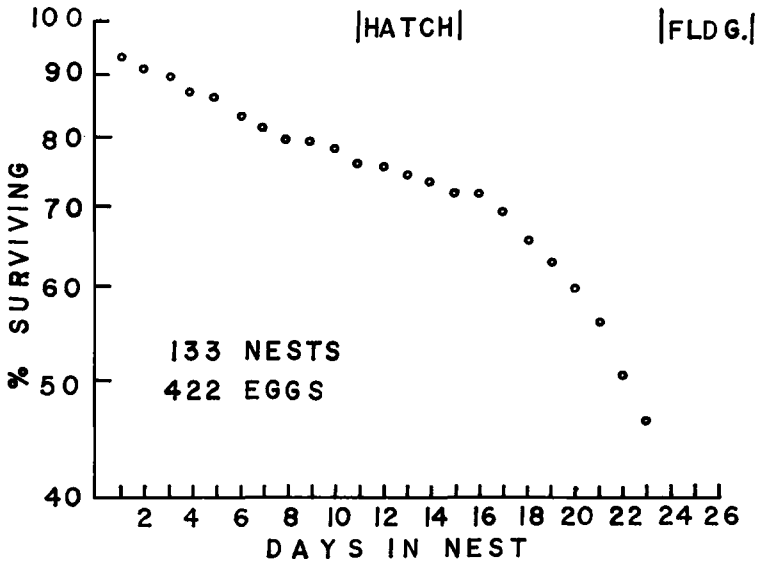
Fig. 1. Survivorship curve for eggs and nestlings. Day 1 represents the onset of laying.

cyanocephalus), and by Holcomb (1972) in the Willow Flycatcher (*Empidonax traillii*).

The initial decline in survival during the first 4 days was primarily the result of mortality from unhatched eggs. Losses from this source were assigned alternately to the laying days as a means of incorporating this source of mortality into the curve. Mortality rates from oviposition of the first egg through about day 16 were relatively low and uniform. Beyond day 16 the mortality rate increased steeply. As the nestlings develop, their demands for food increase, requiring more frequent feeding trips to the nest by the female. This, along with the continuing development of vocalizations and mobility, could contribute to the increasing predation rate during the later nestling stages (Horn 1968). Also the food demands often may exceed the female's ability to meet them under existing environmental conditions, so the young die of starvation (Robertson 1973a).

Sources and timing of mortality.—In evaluating the sources of mortality (Table 2) one must distinguish between aged and unaged nests. Those nests found after the clutch was complete and lost before hatching could not be aged. Therefore estimates of egg mortality for aged nests do not include this category of nests, and hence underestimate the actual mortality. Mortality resulting from egg abandonment and predation were

TABLE 2

SOURCES OF MORTALITY

	Eggs				Nestlings			
	Aged nests		All nests		Aged nests		All nests	
	No.	%	No.	%	No.	%	No.	%
Unhatched	37	34.6	37	20.8	–	–	–	–
Abandoned	13	12.1	67	37.6	0	0	0	0
Predation	48	44.8	65	36.5	61	50.8	61	49.2
Deaths in nest	–	–	–	–	59	49.2	59	47.6
Nest failure	0	0	0	0	0	0	4	3.2
Disappearance	9	8.4	9	5.0	–	–	–	–
Total	107		178		120		124	

most affected by this bias. This problem did not affect estimates of nestling mortality as all the nests located before hatching could be aged.

Unhatched eggs include those resulting from both infertility and embryonic death. Of 497 eggs 7.4% did not hatch. This is doubtless an underestimate of the actual value as a certain number of those eggs lost to other sources of mortality would not have hatched. Young (1963) in a similar study of Red-wing mortality found that 3% of the eggs failed to hatch. Rothstein (1973), in comparing results from several studies, reported a range of unhatched eggs from 2.7% in the Eastern Phoebe (*Sayornis phoebe*) to 26.3% in the Dickcissel (*Spiza americana*).

For both eggs and nestlings predation was the greatest source of mortality, accounting for 42% of the total mortality. Also of significance was the dead-in-nest category, which includes those nestlings found dead in the nest and those single individuals that disappeared with no sign of nest tampering. Mortality in this category resulted primarily from starvation and to a limited extent nest eviction by crowding or accident.

Abandonment was a relatively small source of mortality in the aged nests, but assumed major proportions when all nests were considered. As it was not possible to distinguish between true abandonment and those losses resulting from adult mortality, this category includes both sources.

Egg disappearance accounted for only nine losses. The exact cause of this source of mortality was not clear, but conceivably it resulted from several sources. As no cowbird eggs were found during this study, losses from this source were unlikely. Eggs could have been broken either accidently by the female or through structural weakness of the egg. During windstorms, which are common in this region, a single egg could be dumped from the nest as the supporting plant bent under the wind's force. Finally, predators might have removed single eggs while not disturbing the nest or the remaining contents.
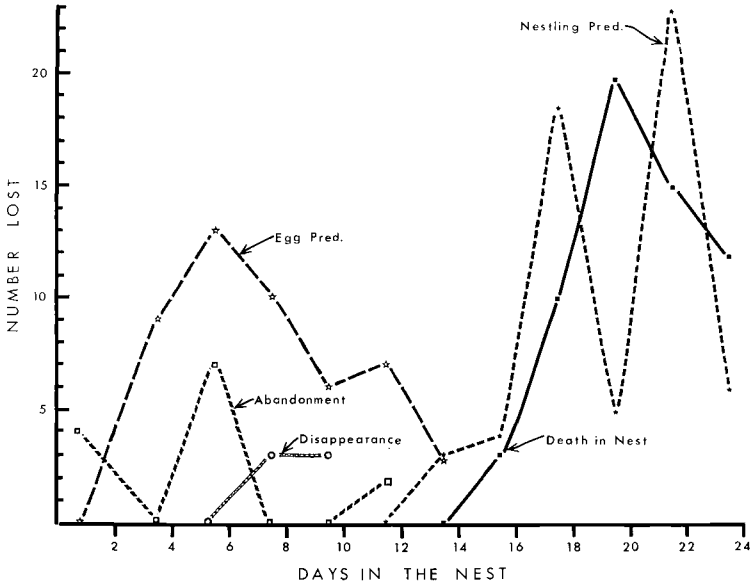
Fig. 2. Age specific mortality of each mortality source.

Structural failure of nests was uncommon, accounting for a loss of only four nestlings. At this study site nest substrate and nesting material were plentiful, so nest site selection and nest construction may have been effective enough to withstand the local environmental conditions.

Fig. 2 shows the number of losses from each source of mortality relative to the progression of the nest cycle. As these data include only aged nests, egg mortality is somewhat underestimated, as indicated earlier, but the relative timing should be unaffected.

A general decrease in abandonment as the nest cycle progresses is to be expected if nest tenacity increases with the nest's age. These data show such a relationship.

There is no apparent relationship between the levels of egg and nestling predation and the amount of time spent in the nest. As both are quite variable throughout the development period, this suggests that predation was independent of the developmental state of the young either in the egg or nestling stage. Conversely the dead-in-nest category showed a marked increase from hatching until about day 19.

Fig. 3 shows the seasonal changes in mortality. The nesting activity is represented as the percentage of the total nests active on each of the dates. The number of nests with eggs reached its maximum just prior to the time when the number of active nests peaked, while the maximum number of nests with nestlings reached its maximum slightly later.
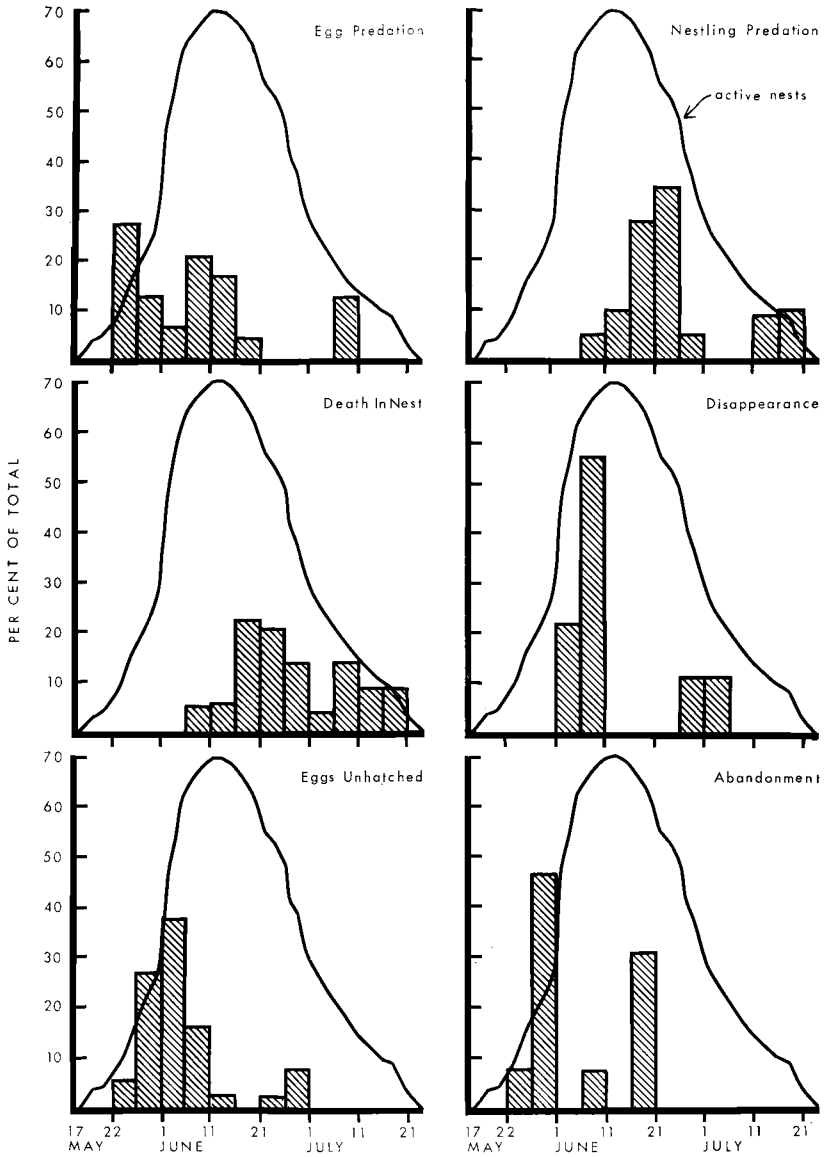
Fig. 3.   Seasonal distribution of mortality and nest abundance.

The period of greatest egg predation occurred prior to the peak in the number of nests with eggs. Conversely the distribution of nestling predation assumed the general shape of the curve for abundance of active nests. The maximum levels of nest predation occurred about 10 days after

the peak in the number of active nests. This coincided with the period of maximum number of nests containing nestlings.

Young found dead in the nest were much more evenly dispersed than any other mortality source. A minor peak occurred slightly after the peak in the number of active nests, but this peak was small compared to those from the other mortality sources. Comparative information on the level of mortality resulting from this source may provide some insight into the general quality of the environment relative to the needs of nesting Red-wings. A preponderance of the mortality in this category is related, either directly or indirectly, to the female's ability to supply her young's needs adequately. Changes in such factors as food supply, weather, and levels of inter- and intraspecific interactions should be reflected as changes in the levels of mortality resulting from this source.

Mortality from unhatched eggs was assigned to day 1 for that particular nest. The distribution of mortality from this source closely followed the distribution of the numbers of nests at day 1. In both distributions the primary peak occurred during the first week in June, with a smaller peak during the last week in June. This suggests that the probability of producing unhatchable eggs was relatively constant through the breeding season, with the changes in the levels of mortality resulting from changes in egg production.

Most abandonment occurred at the end of May, just before the peak in the number of nests at day 1. About 19 June a second abandonment peak coincided with a decided lull in egg-laying.

NESTING SYNCHRONY

Horn (1970) quantified nesting synchrony in Brewer's Blackbirds by using the mean square of the dates when the first eggs were laid. As very few data at the extremes of the distribution can produce disproportionate increases in this measure, certain of these data must be eliminated subjectively. For this reason, this measure may have some disadvantages in making comparisons between studies. Robertson (1973b) used the same measure, but also quantified nesting synchrony in Red-wings using a version of the quartile method. In this, the minimum number of consecutive days that includes 50% of the nests is taken as the index to nesting synchrony. Although Robertson (1973b) used the date of clutch completion to chronicle nesting dates, it seems more appropriate to use the laying date of the first egg, as Horn (1970) did. This not only reflects the actual onset of the production of young more accurately, but also eliminates the variation resulting from differences in clutch size.

Using this latter method for measuring synchrony, 50% of the nests were included within a period of 10 days. Robertson (1973b) found that

most marsh colonies with high nest densities (96.1–108.3 nests/ha) were more synchronous than the low density upland colonies (4.2–12.7 nests/ha). Nest density at my study site (10.5 nests/ha) was low by Robertson's criteria, but nest synchrony was greater than at most of the high density colonies he studied. Apparently nest density alone may not be a good predictor of nesting synchrony as measured by this method.

The advantages of synchronized nesting are not entirely clear. Orians (1973) suggested that the nesting season for Red-wings in both tropical and temperate climates ends long before the food supply diminishes. Thus length of the nesting season and hence the degree of nesting synchrony apparently are not limited by the temporal availability of food. As the number of Red-wings breeding within a particular habitat may be limited by the availability of nesting space (Orians 1961b, Willson and Pianka 1963), synchronized nesting may tend to lower the total number of breeding birds at any colony site. Because of its tendency to restrict the number of breeding birds in a colony, synchronized nesting must encourage greater nesting productivity per individual. Although the mechanisms that accomplish this are obscure, suggestions will be made below as to how predation may contribute to the development and maintenance of synchrony in colonially nesting Red-winged Blackbirds.

PREDATION

Nest density.—Nests in this colony were arranged in clumps with individual aggregates varying considerably in size and number of nests. Clumps contained from one to several males, and thus were not necessarily the result of polygamous pairing between a single male and two or more females. The relationship of nest density to predation was assessed by comparing the proportions of predatory losses of nests in different nest density categories.

The location of each nest was mapped on aerial photos of the study site. A circle including 1810 m², roughly equivalent to the largest of Red-wing territories (Orians 1961a, Case and Hewitt 1963, Holm 1973), was centered around each nest site. Individual nests were then placed within a nest density category corresponding to the number of nests within that circle. This provided for relatively similar numbers of nests in the five nest density categories.

If no relationship exists between nest density and the level of protection from predation, then the proportion of nests lost by predation within each nest density category should be about the same as the proportion of the total nests in that category. A Chi-square test for such a relationship indicated that the observed levels of predation did not deviate significantly

from those expected ($\chi^2 = 2.45, P > 0.05$). Thus the clumped distribution of the nests within the colony evidently provides no protection from predation beyond that generally attributable to colonial nesting. This does not preclude the possibility that the location of the clump within the colony or the location of the nest within the clump could effect a nest's susceptibility to predation.

Nest dispersion.—Because at this study tract suitable nest sites were situated relatively close to the road, the actual nest dispersion was a linear array of clumps varying in size and density. If predation pressure is a function of prey availability then the numbers of predatory losses should vary with nest density along this linear array. Conversely, if predation pressure is subject to amelioration through variations in the physical environment or through particular spatial relationships within the colony, then no close relationship between nest availability and predation would be expected.

A test for such relationships was made by dividing the linear nesting array into 480-m segments along the road that forms the main axis of the study site. Compilations of the total number of nests and the number of nests lost to predation were made for each of the 14 segments. A Chi-square test indicated that the observed frequency of predation in each segment did not vary significantly from the expected frequency ($\chi^2 = 10.8$, $P > 0.05$), based on the proportion of the total nests in each segment. Thus on a per nest basis, predation pressure was similar throughout the colony, irrespective of the nest location or the number of nests in the immediate vicinity. These results again suggest that, if indeed colonial nesting does provide some protection from predation, the effect is generalized and dispersed throughout the colony.

Horn (1968) found that in Brewer's Blackbirds variations in colony configuration and nest spacing resulted in a tendency for differential predation during the period of egg-laying and incubation. In Horn's linear colonies, which were similar in configuration to my colony, predation was more intense on nests closer than the median distance between nests and less intense on nests farther apart. This he considered to be selection for dispersal. When a similar comparison was made on the numbers of predatory losses in my study, no significant differences were detected between nests nearer or farther than the median nest distance. This again supports the thesis that any protection from predation afforded by aggregated nesting in this colony is dispersed throughout the colony and is not a function of the nest dispersion within the colony.

Predation pressure.—An estimate of predation pressure was obtained by calculating the average number of nests preyed upon per nest per day for each nest density interval (Robertson 1973b).

Two peaks in predation pressure occurred (Fig. 4), the largest at low
nest densities and a smaller peak at high nest densities. At intermediate
nest densities predation pressure was at its lowest levels.

The number of nests preyed on relative to the number of nests present
in the colony showed a distinct bimodality, which is reflected in the low
predation pressure at intermediate nest densities in Fig. 4. These inter-
mediate nest densities encompass a period of 15 days, which would seem
to be long enough to minimize the chances of sampling error in the day
component of predation pressure.

DISCUSSION

MORTALITY

Temporal patterns.—The reproductive potential of a species is seldom
realized under natural conditions. Various random or probabilistic events
tend to reduce this potential in many ways including mortality in the
offspring. In altricial birds the commitment by the parents, in terms of
time and energy, increases continuously from the onset of the reproductive
condition until all parental care ceases. Because such birds are generally
limited to a specific breeding season and because the amount of energy
that can be devoted to reproduction is finite, the amount of time and
energy wasted through the loss of an offspring depends on when in the
nesting season and at what developmental stage the loss occurs.

From the standpoint of selection such considerations can be of great
importance. In the Red-winged Blackbird the loss of a clutch of eggs to
predation early in the season should have far less impact on the potential
reproductive output of an individual than loss of a clutch of nestlings
late in the season. Not only would the total energy commitment be far
less for the eggs, but the female's chances for renesting would be far
greater. With the nestling losses sufficient time could have elapsed for
seasonal constraints to prevent renesting.

Little information is available (Smith 1943) on the proportion of
female Red-wings that renest following loss of a nest, nor on how this
proportion changes as the season advances. For those females that do
renest, the likelihood of nesting success can be estimated from the date
egg-laying is initiated. Fig. 5 shows the average number of young produced
per nest relative to the date when egg-laying began for each nest. Except
for the very early and late nests, the fledging success is relatively constant
for nests started throughout the egg-laying period. This rather broad
plateau of similar levels of fledging success provides a considerable time
span during which egg-laying can be initiated without an overall lowering
of the chances for success. The length of this plateau period far exceeds
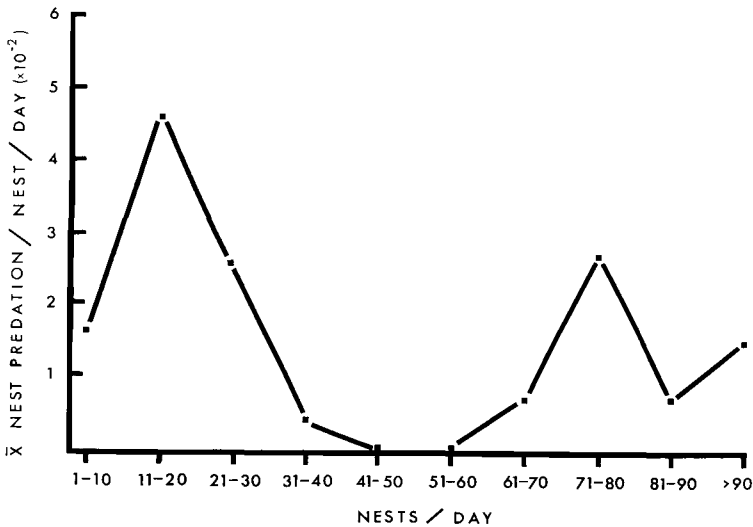
Fig. 4. Predation pressure relative to nest density.

the period when most egg-laying occurs. Therefore renesting attempts are not necessarily exposed to a greater likelihood of loss by starting later in the season. This pattern may be contrary to that reported by Patterson (1965) for the Black-headed Gull (*Larus ridibundus*). He found a correlation between the proportion of nests started in a given 5-day period and the surviving fraction of eggs laid during that period. Because the proportion of successful eggs declined with the number of nests started, a renesting individual would be at a serious disadvantage if breeding was even somewhat synchronized.

The length of time egg-laying can be started without causing an overall decrease in the chances for nesting success may be related to the Red-wing's propensity for renesting. The question whether the plateau effect in the Red-wing (Fig. 5) is the result of persistent renesting or whether it allows for renesting could easily lead to circular reasoning. Additional information is necessary on both the proportion of individuals that renest following nest loss, and how this changes through the laying period.

Spatial patterns.—Analyses of predation for this colony have shown that predation pressure apparently was not directly related to variations in nest density or to differences in the spatial arrangement of nests within the colony. In work to be reported elsewhere (Caccamise MS) nests where young died in the nest showed a significantly greater mean nest density and a significantly smaller mean distance to the nearest nest than those nests not suffering such losses. Thus while nest dispersion within the
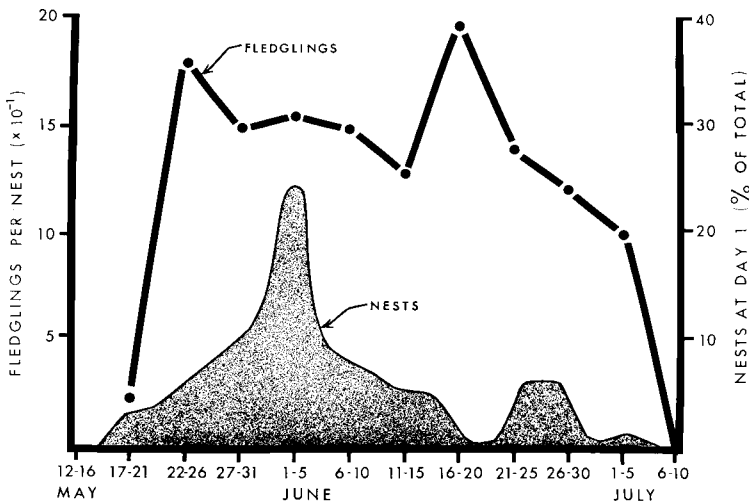
Fig. 5. Fledgling productivity per nest and percentage of the nests in which laying was initiated during each indicated 5-day interval.

colony may not serve as a basis for selection by predation, there may be selection against individuals with a propensity for highly aggregated nesting when nest density exceeds optimum levels.

Although most mortality in this category probably results from nestling starvation, it seems unlikely that these greater losses in high density areas result from direct competition between females for a limited food supply. A more plausible but less direct cause could be the modification of time and energy budgets resulting from the increased social interactions in the high density areas. Although Red-wings are polygamous and the females maintain territories within the larger territories of males, the factors controlling territory size are not well understood (Orians 1961a). Where nest densities are high, increased aggressive interactions between females could well be sufficiently disruptive to increase mortality of young in the nest.

PREDATION

By far the greatest source of mortality to eggs and nestlings in Red-wings is predation (Smith 1943, Young 1963, Robertson 1972, Holm 1973). Of particular importance, in terms of selection and survival value of certain prey characteristics, is the timing and intensity of predation pressures.

Holling (1959) presented a series of predation models based on the relationship between the number of prey consumed per predator and prey

density. In these models the total predation response had two components (Solomon 1949). The first, a functional response, represented the change in number of prey consumed by individual predators. The second, a numerical response, resulted from a change in the total number of predators. These responses occur either in concert or independently such that the "proportion of prey destroyed increases from zero to some finite prey density and thereafter decreases" (Holling 1959).

Robertson (1973b) interpreted the results of his study and those of Smith (1943) in terms of model 3b as presented by Holling (1959). In applying this model the range of prey abundance was represented both by colonies of different sizes and by the variation in colony size between years. Comparisons were made in the levels of predation between these different prey densities. As Fautin (1941) showed in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and Cullen (1960), Kruuk (1964), and Patterson (1965) in various colonial nesting seabirds, the proportion of nests preyed on decreased with increasing colony size.

In colonial nesting species that exhibit only moderate levels of nesting synchrony, colony size is dynamic through the course of a nesting season. With the development and subsequent decline of a colony during a nesting season, colony size assumes values from zero at the onset of nesting through a maximum at the greatest nest density, and again approaches zero as the season ends. This colony size continuum, if viewed as a series of colony size intervals, is analogous to the series of different colonies that have been used to test for the relationships between colony size and predation. Therefore as a colony passes through these successive size intervals, the relationships between colony size and predation should follow a pattern similar to that shown for comparisons between colonies.

A quite different relationship was evident in the current study (Fig. 4); the very low levels of predation pressure at intermediate population sizes resulted in a bimodal distribution. It is significant that within each nest density interval the level of predation pressure is a composite of two distinct time periods, one before and one after maximum nest density. This would minimize the effect on predation pressure of progressive factors, i.e. search image formation, that tend to develop with the progression of the breeding season. Therefore of those factors that can affect the mortality of a prey species by a particular species of predator (Leopold 1933, Errington 1946, Holling 1959), those related to prey abundance would be expected to have the most pronounced effect on the levels of predation pressure when analyzed in this way.

Interpretations of the results from this study are facilitated by combining models similar to two of those presented by Holling (1959). For both models I have assumed that the numerical response is negligible. This
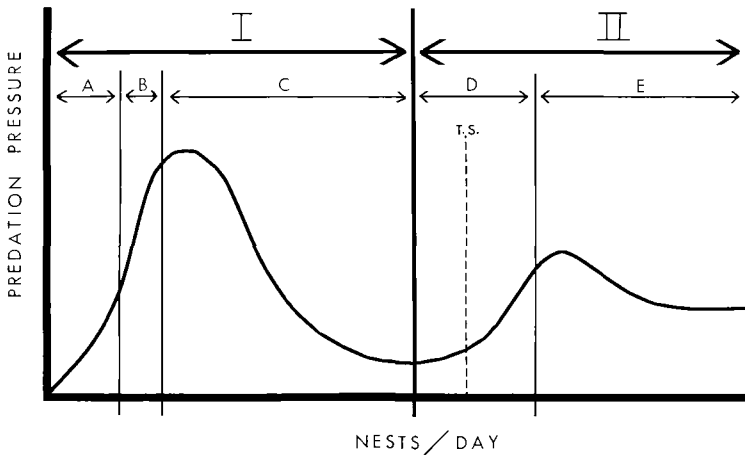
Fig. 6. A model of the relationship between colony size and predation pressure.

would appear justifiable in view of the relatively short time span of nesting, the comparatively small part of the total salt marsh the Red-wing colony occupied, and the relatively small amount of biomass available in the form of eggs and nestlings. Part 1 of the curve in Fig. 6 is similar to type 3b as presented by Holling (1959). The second portion of the curve (Fig. 6-II) is a modification of model 3b, incorporating compensatory predation (Errington 1946). By combining these models a relationship emerges between predation pressure and prey abundance that is very similar to that shown by the data in Fig. 4.

At very low prey densities (Fig. 6-A) the probability of a predator encountering a Red-wing nest is minimal. There is also little opportunity for a predator to specialize on a prey of such low density; thus predation pressure at these very low prey densities also is quite low. When prey densities are higher (Fig. 6-B) the chances of a predator-prey encounter are greater. Also a certain amount of prey specialization might be possible, as prey could become sufficiently plentiful to allow search images to form.

At moderate prey densities (Fig. 6-C) predation pressure per nest decreases. At these intermediate nest densities mutual protection from predators is possible. Considerable evidence supports the idea that synchronized colonial nesting does provide some protection from predators (Stresemann 1928, Kruuk 1964, Patterson 1965, Horn 1968, Robertson 1973b). Thus apparently predation pressure can be lessened by the mutual protection provided by colonial nesting.

At nest densities above the threshold of security (Fig. 6-TS) predation pressure increases sharply (Fig. 6-D). This increase may occur because,

at these high prey densities, a segment of the prey population is forced to occupy suboptimal nest site locations. These nest sites are more susceptible to predation by virtue of such factors as quality of nest substrate, proximity to food sources, placement relative to the colony, and distances to neighboring nests. Once these high susceptibility nests are removed by predation, the predation pressure on the remaining nests falls to levels set by other factors.

Finally during the periods of highest nest densities predation pressure is somewhat lower (Fig. 6-E). In the absence of a numerical response, satiation of the predators (Tinbergen 1960, Robertson 1973b) has been suggested as a possible factor in limiting increases in predation rate. The number of nests lost during periods D and E are about the same, but the proportionate loss is lower during E because of the greater number of nests present. As the total amount of biomass lost to predation is relatively small, factors other than predator satiation may be responsible for the decline in predation pressure at high nest densities.

Robertson (1973b) found that predation pressure on one of his marsh study sites varied in a fashion very similar to that presented in Fig. 4 and thus may also be interpreted in terms of the models presented in Fig. 6. This similarity was apparent during the two years of largest colony size (1969, 202 nests; 1970, 167 nests). During the year of smallest colony size (1968, 133 nests) the increase in predation pressure during the periods of high nest density was considerably smaller than in the other 2 years. Thus possibly the high predation pressure during the years of high nest density resulted from the presence of a proportionately greater number of nests built in low suitability locations.

Interpretation of these data in terms of the models presented illustrates how predation can contribute to the development and maintenance of nesting synchrony, while incorporating a mechanism for counterselection at high nest densities. This is not to suggest that predation is the only selective force influencing nesting synchrony, but rather it illustrates how, under particular conditions of population pressures and habitat characteristics, predation can contribute to the selective processes yielding the levels of nesting synchrony characteristic of Red-winged Blackbirds. If the quality of the nest site is in some way related to susceptibility to predation, and if high suitability nest sites are in limited supply, then at periods of high nest density a maximum of the nests present should be built in low suitability locations. Increases in nesting synchrony tend to increase this kind of predation pressure, while nesting over a broad time span tends to decrease it. Thus the degree of nesting synchrony, at least in part, may ultimately be determined by the availability of high quality nest site locations.

Under such a system high predation pressure is to be expected both in large colonies when nest densities are low, i.e. at the beginning and the end of the nesting season, and in small colonies with too few individuals to provide for mutual protection from predators. Robertson (1973b) found a greater proportion of nests preyed on in small colonies (32–41 nests) than in large colonies (108–202 nests), but Smith (1943) found similar levels of predation between colony sizes. As suggested by Robertson (1973b), most of Smith's small colonies (1–3 males) may have had too few nests to allow predator specialization, thereby precluding the expected high predation pressure.

Predation can be expected to select for asynchronous nesting only when the vagaries of local environmental conditions and population pressures coincide to produce conditions under which a segment of the population is forced to use nest sites with an increased potential for predatory loss. That differences in the quality of nest sites are recognized and preferentially selected by Red-wings was observed by Orians (1961a). He found (1961b) "Peripheral territories that are most advantageously located with respect to feeding grounds are most fiercely contested and are occupied first during the breeding season." It seems likely that a process similar to that providing for nest sites advantageous in terms of food supply could operate to produce nest sites minimizing susceptibility to predation.

Summary

Mortality of eggs and nestlings was monitored in a colony of Red-winged Blackbirds nesting on a salt marsh in southern New Jersey. Sources of mortality, age specific mortality, and seasonal distribution of mortality were evaluated. Predation was the greatest source of mortality in both eggs and nestlings, with egg abandonment and death of nestlings in the nest the next greatest sources of loss. The survivorship curve was negatively skewed indicating an increasing mortality rate with the progression of the nesting cycle. The seasonal distribution of mortality was distinctive for each of the six mortality categories. Nesting synchrony was high compared to what has been shown in other low density colonies of Red-winged Blackbirds. Predation pressure, on a per nest basis, remained constant throughout the colony irrespective of the number of nests within a nesting aggregate or the spatial distribution of nests relative to the colony axis. Predation pressure was shown to vary with changes in nest density through the nesting season. A model of these relationships is presented with sug-

gestions as to how the interrelationships between nest density, predation pressure, and nesting synchrony may contribute to the maintenance of the colonial nesting habit.

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