AGE-SPECIFIC MORTALITY IN THE EGGS AND NESTLINGS OF BLACKBIRDS

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STUDIES of population dynamics are recognized as an important component of modern biology, and such studies have been made on many forms, both vertebrate and invertebrate.

At the present time one of the needed forms of information for these studies is life curves for the various animal types. In ornithology some data for this use have been gathered by banding, but these relate primarily to adult and subadult segments of the populations. Vertebrate population studies in general have been handicapped by a shortage of data on age-specific mortality, particularly that occurring at early ages (Deevey, 1947; Hickey, 1952). Most ornithological data of this sort have pertained to precocial game species, where the early survival of young is extremely difficult to determine. Estimates can be made by observing brood-shrinkage over a period of time (Randall, 1940; Leedy and Hicks, 1945), but it is seldom possible to determine when specific individuals are lost. Studies on the breeding success of altricial birds can be particularly useful in gaining information on early mortality in certain natural populations. Age-specific mortality rates can be approximated by keeping careful records of the appearance and disappearance of eggs and young in the nest. For comparison with mammals, egg-loss can be considered equivalent to intrauterine mortality.

Studies of avian breeding success have occupied many ornithologists, and excellent papers on this topic are abundant. However, these have concerned themselves mainly with what has come to be considered as standard information on breeding success: per cent of nests successful (fledging at least one young), per cent of eggs hatching, and per cent of young fledging.

Aside from the papers of Paynter (1949), Petersen and Young (1950), and Young (1955), there does not appear to have been much effort to gather age-specific mortality data for the early stages of avian life cycles in altricial species. This paper presents such information for these early stages (egg and nestling) of the Red-winged Blackbird, *Agelaius phoeniceus,* and the Yellow-headed Blackbird, *Xanthocephalus xanthocephalus.*

METHODS

Studies were made during the spring and summer of 1959 and 1960 in a cat-tail (*Typha*) marsh in the lowlands of the Mississippi River near Stoddard, Wisconsin.

As each nest was found it was marked by a stake to which a numbered

TABLE 1
BASIC NESTING DATA

Year	*Total nests*	*Active nests*[1]	*Per cent successful*[2]	*Number of eggs*	*Per cent hatched*	*Number of young*	*Per cent fledged*	*Per cent of eggs producing fledglings*
				Red-winged Blackbird				
1959	381	238	35	730	54	393	53	28
1960	416	280	24	902	45	402	40	18
Total or per cent	797	518	29	1,632	49	795	46	23
				Yellow-headed Blackbird				
1959	105	60	40	197	53	105	60	32
1960	66	56	39	172	35	60	78	27
Total or per cent	171	116	41	369	45	165	67	30

[1] Containing at least one egg.
[2] Fledging at least one young.

tag was attached, and a record of the contents of the nest was made. On each subsequent visit the contents of the nest were checked until the young fledged or the nesting attempt failed.

An attempt was made to visit each nest at least every two days. During the height of the nesting season this proved physically impossible. Conversely, when the nesting population was low, each nest could be visited daily. A sample of 125 nests proved to have been examined an average of 8.6 times per nest, with about 1.9 days as the usual interval between visits. This included many nests that failed; since successful nests were followed to completion they were obviously visited more frequently.

In some nests it was possible to mark the eggs individually as laid. In many other cases this was not possible. However, it was often possible to mark at least part of the clutch, the first egg for example, or the last two, etc. Successful marking of the very young was not accomplished, but nestlings were banded as they reached a suitable age.

In all, 432 Red-wing nests containing 1,372 eggs, and 98 Yellow-head nests containing 323 eggs, had a history permitting an accurate check of the survival of eggs and young until fledging, or abortion of the nesting attempt.

Records were not all based on marked eggs. If, for example, a nest had three eggs when first found, and four the following day, they could then be aged, provisionally, as 1, 2, 3, and 4 days old, since eggs were almost invariably laid at the rate of one per day. If all the young fledged 24 days later we would know that their respective days in the nest, including time in the eggs, ranged from 25 to 28 days, even though they were not marked. When eggs disappeared from unmarked clutches they were alternately as-

TABLE 2
TIME SPENT IN NEST

Days	Red-winged Blackbird		Yellow-headed Blackbird	
	Eggs[1]	*Young*[2]	*Eggs*[1]	*Young*[2]
9	0	0	0	0
10	0	1	0	0
11	10	37	4	0
12	33	46	5	4
13	41	46	7	14
14	27	0	5	0
15	9	0	2	0
16	0	0	2	0
17	0	0	0	0
Totals	120	130	25	18
and averages	12.6	12.1	13.1	12.8

[1] From oviposition to hatching.
[2] From hatching to fledging.

signed specific positions in the laying order. Thus one egg disappearing from a three-egg clutch was first considered to be the first egg, in the next case it was recorded as the second egg, etc.

Additional nests (86 Red-wing and 18 Yellow-head) were found in which it was not possible to plot the egg/nesting survival with any accuracy. If a nest had four eggs when first found, and was destroyed before any of these hatched, there would be no way of determining the age of the eggs, and they could not be included in the survival data. These nests, however, did provide some collateral information, and are included in Table 1. This table contains routine breeding-success data, and can be used to relate this study to similar material derived from other nest-study investigations, such as those listed by Lack (1954: 75).

In order to compare mortality of eggs and nestlings, it was necessary to determine the length of the period they were contained in the nest (Table 2). It will be noted that for both species the eggs and young are exposed to environmental hazards for about the same period. Other things being equal, it could be prophesied, therefore, that their losses would be similar. Information on this point can be gathered by examination of survival curves.

SURVIVAL

Survival curves are presented for the Red-wing (Figure 1) and for the Yellow-head (Figure 2). All curves in this paper are expressed on a semi-logarithmic scale; with this scale a uniform rate of mortality results in a straight line extending from zero days to fledging. Deviations to the left of such a line are termed positive skewing, those to the right represent

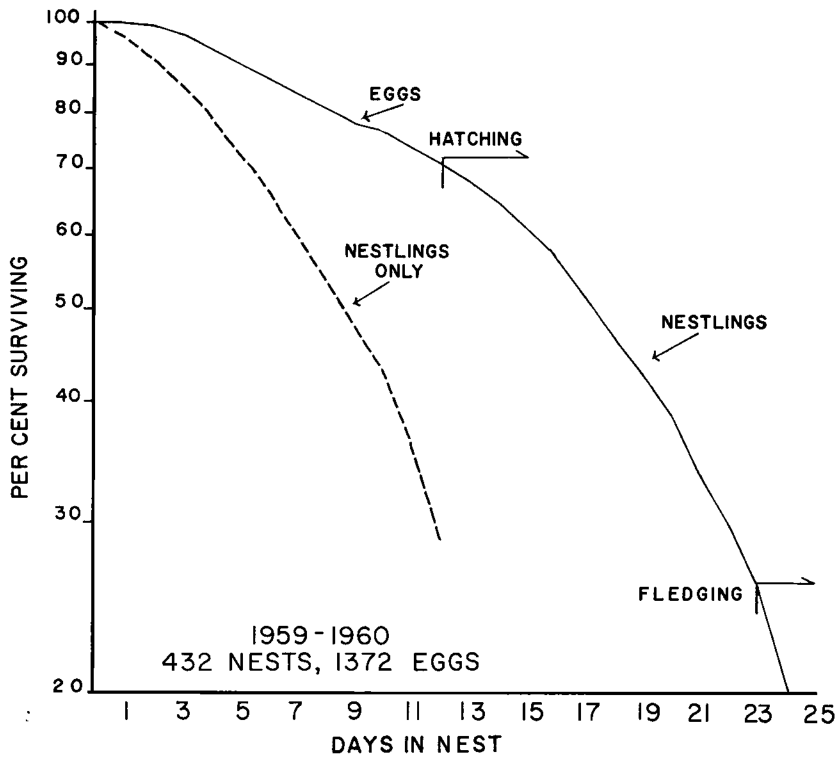

Figure 1. Red-winged Blackbird; survival of eggs and nestlings (all nests).

negative skewing. Species with their heaviest mortality in the early days would show positive skewing, those with the greatest losses during later periods would show negative skewing.

In the case of the Red-wing the mortality rate is definitely greater among the nestlings; about 21 per cent of the eggs produced fledglings, and the entire curve shows strong negative skewing.

The mortality curve for the Yellow-head also shows negative skewing, though not as marked as that in the Red-wing. About 28 per cent of the eggs produced fledglings. After an initial "flat" period during oviposition, mortality was essentially uniform until the twenty-second day. The sharp decline here in the curve doubtless reflects early fledging as well as loss, since the two could not always be distinguished in the field.

Table 1 shows nestling and egg survival approximately equal in the Red-wing, and nestling survival superior to egg survival in the Yellow-head. This apparent discrepancy with Figures 1 and 2 results from inclusions of nests where mortality could not be dated in Table 1. These were mainly

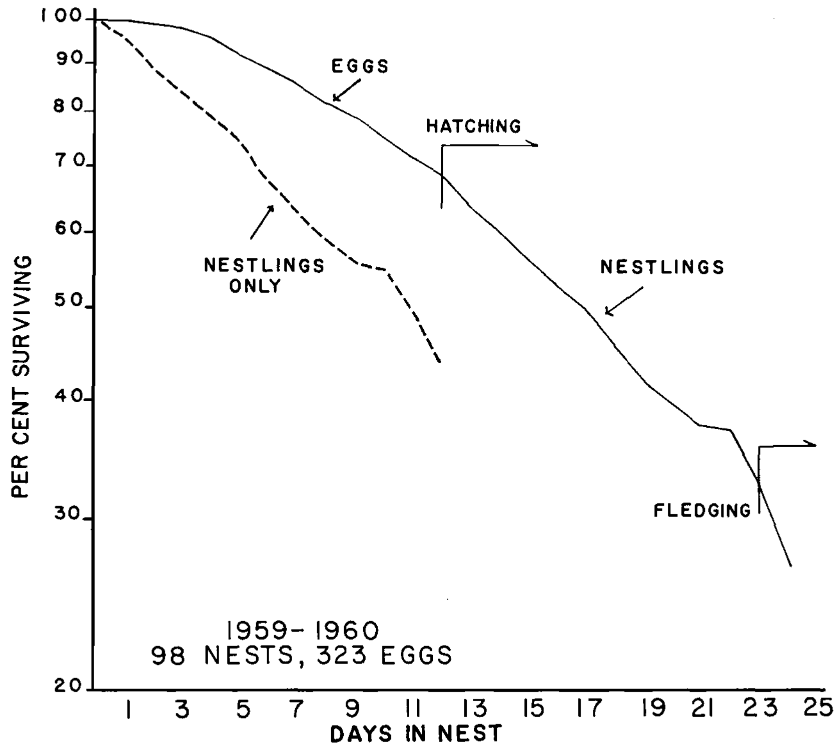

Figure 2. Yellow-headed Blackbird; survival of eggs and nestlings (all nests).

nests where the entire clutch was lost. However, had it been possible to include these nests in the curves, their shapes would not have been changed significantly. In this respect note that the percentage of eggs producing fledglings is very similar in Table 1 and Figures 1 and 2.

The adults were not marked in this study, so original attempts could not be safely distinguished from renestings. Sample size precludes breaking the data down into early and late nests; in general the success improved as the season advanced.

Obviously, over-all nesting success was very poor among the birds sampled in this study. However, reference to summaries of nesting success in altricial species (Lack, 1954: 75; Nice, 1957) shows great variation in nesting success, and since heavy losses in blackbird colonies are frequently noted (Fautin, 1941), the data here presented probably do not represent abnormal seasons.

Both species proved to be persistent renesters after failure, which is typical in cases where there is a low percentage of success (Nice, 1957). Since much of the mortality depicted in Figures 1 and 2 is therefore com-

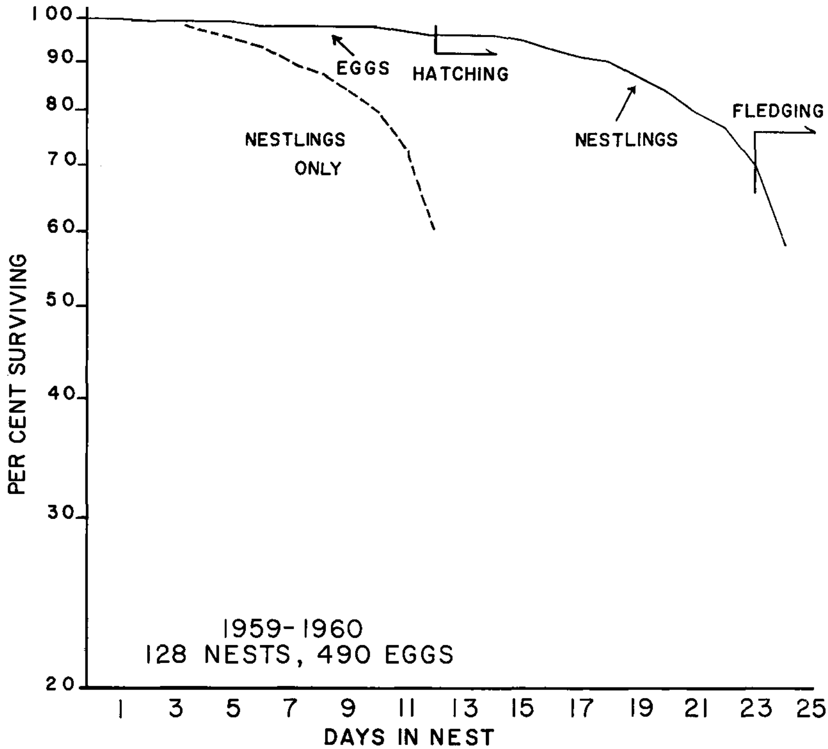

Figure 3. Red-winged Blackbird; survival of eggs and nestlings (successful nests only).

pensated for, it is of interest to examine survival in those nests which did proceed to a successful fledgling. When this is done, quite different curves appear.

Figure 3 presents such material for the Red-wing. Here about 58 per cent of the eggs produced fledglings. Egg mortality is negligible, and occurs at a uniform rate; losses are considerably increased during the nestling period, and this part of the curve is strongly skewed.

The pattern in the Yellow-head (Figure 4) is much the same, with the negative skewing during the nestling period less pronounced.

All the curves were subjected to statistical analysis by the grouped Chi-square method. Interpretation of the results is not simple. In the Red-wing, the entire curve is significantly skewed in both Figures 1 and 3; egg mortality is of the straight-line type, but the curve of nestling mortality is strongly skewed. In the Yellow-head, while the entire curve again has significant negative skewing in both Figures 2 and 4, neither egg nor nest-

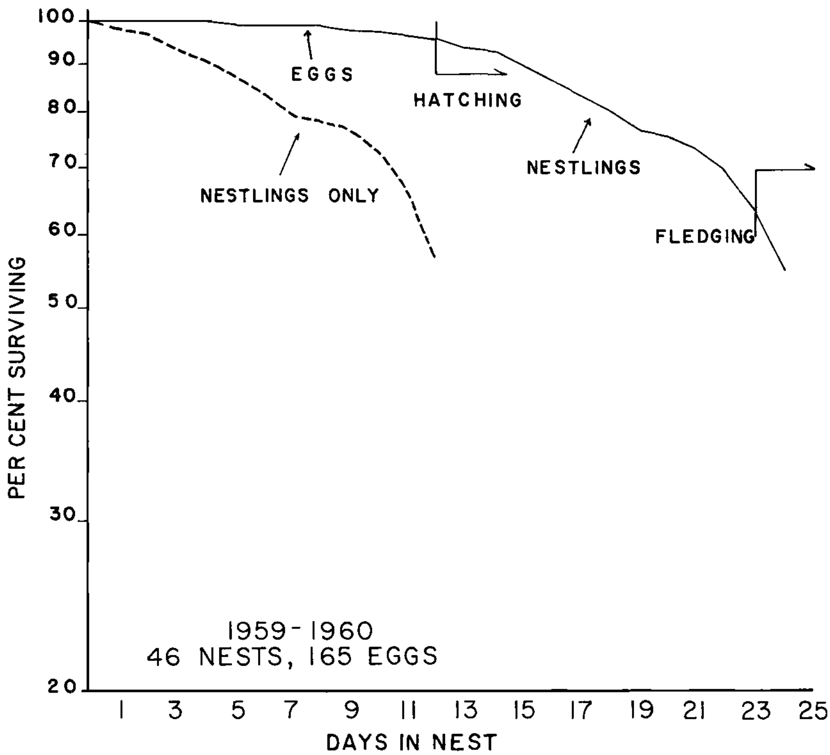

Figure 4. Yellow-headed Blackbird; survival of eggs and nestlings (successful nests only).

ling mortality alone varies significantly from the straight-line type in either figure.

Discussion

The uniform rate of egg loss in all of the curves is not surprising, since the eggs are essentially identical in appearance during their entire existence, and do not display varying behavior patterns. An egg of any given age therefore is no more or less vulnerable to loss than an egg of any other given age.

Nestlings, in contrast, increase in size over a period of time, and exhibit behavioral changes. These result in variable mortality and in general appear to increase vulnerability to environmental hazards, as compared with eggs. Increased losses among the young Red-wings possibly are associated with such things as more frequent trips to and from the nest by the adults, jostling of each other by the young, and predation brought about by begging calls. The larger size of the parents, the deeper and more robust

TABLE 3
CAUSES OF EGG AND NESTLING MORTALITY

Factor	*Red-winged Blackbird*				*Yellow-headed Blackbird*			
	Eggs		*Young*		*Eggs*		*Young*	
	Number	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
Broken	0	0	–	–	3	1.5	–	–
Disappeared[1]	92	10.7	107	24.1	42	21.6	22	39.3
Predation	583	67.9	284	63.7	102	52.6	21	37.5
Nest tipped	20	2.3	5	1.1	2	1.0	0	0
Infertile	38	4.4	–	–	7	3.6	–	–
Died in nest	–	–	23	5.2	–	–	13	23.2
Embryo died	11	1.3	–	–	3	1.5	–	–
Removed by cowbird[2]	5	0.6	0	0	1	0.5	0	0
Storm or flood	50	5.8	21	4.7	18	9.3	0	0
Deserted	59	6.9	4	0.9	16	8.2	0	0
Totals	858	100	444	100	194	100	56	100

[1] No obvious sign of predation, and nest not completely emptied.
[2] Disappearance, followed by deposition of cowbird egg.

nest, and the generally deeper water at the nest site conceivably could be factors influencing the lesser incidence of mortality in the Yellow-head.

Successful breeding attempts in these species are characterized by a small loss of eggs (Figures 3 and 4). Where egg-loss is more extensive, the nesting attempt frequently failed (Table 1, and Figures 1 and 2). It is well known that birds are most prone to desert their nests during the early stages of a breeding effort, and this doubtless was an important factor in the unsuccessful cases.

Table 3 shows the various causes of mortality in those cases where it could be determined. Obviously, predation is by far the most important single cause, but it is also clear that the various factors affect eggs and nestlings with varying intensities. For example, eggs were deserted much more readily than young, as just mentioned, but single nestlings disappeared from a brood distinctly more often than did single eggs from a clutch. This possibly reflects activity of the young, which may occasionally fall from the nest. Premature fledging of disturbed young may also account for some losses. One factor not shown in Table 3 is adult mortality, since, in the absence of marked birds, it could not be measured.

The most striking differences between the Red-wing and the Yellow-head are in loss of young due to predation, and in death of young in the nest. Factors possibly affecting the first case have already been described. For death of young in the nest, the figure for the Yellow-head seems unusually high; in the Common Grackle, *Quiscalus quiscula,* Petersen and Young (1950) found only 3 per cent mortality from this cause, and Young

(1949) found only 2 per cent of the nestlings dying in a study of six species. Since the sample of Yellow-head young was small, this may represent chance variation.

In other species an entirely different situation may prevail. Thus McClure (1942) found that nestling survival was superior to egg survival in the Mourning Dove, *Zenaidura macroura*. The flimsy construction of the nest could be involved here, and McClure felt that the ability of the young to cling to the twigs of the nest, and the greater stability produced by their weight, were factors in their better survival. The Brown-headed Cowbird, *Molothrus ater*, provides another example of nestling survival superior to egg survival, as shown by data on the fate of 879 eggs (Young, *in press*). Rejection of the cowbird egg by the host species is probably a major factor in this case. Marchant (*in* Lloyd, 1960) points out that a species with conspicuous eggs but quiescent young might have a particularly heavy egg-loss, while the reverse could be true in species with cryptically colored eggs and active, noisy young. On this point Beer and Tibbits (1950) note that vocalization by Red-wing nestlings becomes particularly evident on the seventh and eighth days. Allowing 12 days for incubation, this would place them at about day 19 in Figures 1 and 3. No change in the mortality pattern at this point of development can be detected from the present data.

Figures 1 and 2 give the best over-all picture of mortality during the entire reproductive attempt. Despite the abundance of papers on breeding-success studies, the magnitude of the loss commonly occurring during the nesting of small altricial birds is often not fully realized. Although this can be shown in tabular form, it is more readily apparent from a curve, and of course the rate of loss at various ages (age-specific mortality) can be most simply shown by a curve.

There seems to be no reason why the shape of the nest-period survival curve should be associated with the degree of nesting success, and there is no suggestion of any such relationship in the curves here presented.

In Deevey's (1947: 286) excellent paper the statement is made that the life curves of most vertebrates are negatively skewed. This is true of the segments of the life curves shown in this paper, but it should be clear that the entire life curve for either species would show strong positive skewing, reflecting the high mortality in the early stages. Composite life curves, using both nesting data and banding records, have been published for the Herring Gull, *Larus argentatus* (Paynter, 1949), for the salt-marsh Song Sparrow, *Melospiza melodia samuelis* (Johnston, 1956), and for the Robin, *Turdus migratorius* (Young, 1955). All show distinct positive skewing.

Survival curves for other vertebrates previously published have mainly been segments of the life curve, usually with the anterior end missing (Deevey, 1947). Since the first days of life represent one of the periods of greatest mortality, accumulation of data concerning this period is essential to a fuller understanding of population dynamics. Information of this sort is slowly accumulating, so eventually survival curves and life tables may be available for a good variety of native forms. In all cases this will give us better information on population dynamics, and in those species important as reservoirs of disease, or as crop pests, or as game, it may be of basic importance in control or management. For example, Fichter (1959) has suggested that windbreak plantings might be effective in reducing the particularly severe egg loss in the Mourning Dove. Another case where population data are of direct interest is in the current study of blackbirds, and their crop depredations (Meanley, 1961).

Considerable additional study still must be made before any more detailed discussion would be appropriate. If data on age-specific mortality, particularly at early ages, are gathered for more species, perhaps group patterns will appear. Egg and nestling losses, and the ratio between them, possibly vary from one taxonomic group to another, and doubtless are influenced by geographic location, nesting habitat, season, and other factors. Much of the material currently being presented in reports on studies of breeding success could profitably include information on age-specific mortality.

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SUMMARY

Information presented on age-specific mortality in the eggs and nestlings of the Red-winged Blackbird and the Yellow-headed Blackbird suggests that nestling mortality exceeds egg mortality in both species. The survival curve for the egg-nestling period is negatively skewed, and the skewing is accentuated when only eggs and nestlings from successful nests are considered.

The rate of egg-loss was uniform in both species. In the Red-wing the curve of nestling mortality is negatively skewed, but it is of the straight line type in the Yellow-head.

Predation was the most important cause of mortality. Egg-loss from desertion was in excess of nestling loss from that cause.

Other species, such as the Mourning Dove and the Brown-headed Cowbird, show egg mortality greater than nestling mortality.

Due to the great mortality in the early life stages, positively skewed life curves appear to be typical for small passerine birds.

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