

## AGE GROUPS AND LONGEVITY IN THE AMERICAN ROBIN: COMMENTS, FURTHER DISCUSSION, AND CERTAIN REVISIONS

DONALD S. FARNER

SINCE the publication of an analysis of the recoveries and returns of American Robins (*Turdus migratorius*), banded as young, in terms of age groups, mortality rates, survival rates, and longevity (Farner, 1945), publications of other investigators and the results of the author's own further studies make it desirable to present certain comments, additions, and observations.

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### THE INITIAL DATE FOR THE ESTIMATION OF LONGEVITY, LIFE EXPECTANCY, AND AGE GROUPS

In the estimation of longevity, life expectancy, and age groups from the records of recovered birds which were banded as young it is necessary to fix an arbitrary initial date. To avoid bias in the sample of recovered birds this date must be placed sufficiently beyond the time of departure from the nest to allow the banded young to disperse. There is not sufficient information for the evaluation of the high rate of mortality before this dispersal and there is also the possibility that a dead banded bird of the year may have a better chance of being recovered through the activity of the bander before the dispersal than after. The initial calculations for the American Robin were based on the first of August as had been done by Lack (1943a, b, c, d) in his studies on several European species. On this basis, a higher mortality rate was obtained for the American Robin for the first year than when a later date, such as the first of November, was used. Because it could not be demonstrated satisfactorily whether this rate was actually higher or only apparently so because of bias of the sample, the earliest date by which it appeared that the migratory habits of the species would insure the necessary dispersal of the banded young was selected. The date thus chosen was November 1. Kraak, Rinkel, and Hoogerheide (1940) in their analysis of the records of recovered Lapwings used January 1 as the initial date; Marshall (1947) has used September 1 in his study of

Herring Gulls; whereas Plattner and Sutter (1947) used November 1 in their studies on Tits and Nuthatches. The question was raised (Farner, 1945: 58) whether the higher first-year mortality rates found by Lack, using August 1 as the initial date, were real or the result of bias of the sample in the manner described above. In consequence of this suggestion Lack (1946a, b) has reanalyzed the data on the European Blackbird, the Song Thrush, the Starling, and the Lapwing. The results indicate that the higher rates calculated from August 1 are genuine and not the result of biased samples, and that this higher mortality rate persists approximately through December. Lack, however, (1946a: 263) suggests that in the future, annual mortality rates based on records of banded birds be calculated as of January 1. This procedure should eliminate the possibility of biased samples as well as the period of increased and unstable juvenile mortality rate following the departure from the nest. Of minor consideration is the increased ease of calculation with January 1 as the initial date. The author agrees with Lack's recommendation that such future studies involving records of banded birds be based on the first January 1 as the initial date, at least for passerine species. It seems desirable, therefore, to present a recalculation of the more pertinent data of the earlier analysis of recovered Robins despite the fact that the results show no significant differences if one considers the size of the samples. (See Table 1, lines 1, 2, and 3; and Table 2, lines 1 through 4.)

Studies of the type presented in this paper are based on two fundamental assumptions. First, the sample used is sufficiently random and unbiased to allow the calculation of a mortality rate and the construction of an average pattern of death about which the annual mortality rates and the patterns of death in the total population each year should fall in approximately normal frequency curves. Secondly, the population of the species involved is relatively stable, *i. e.*, its number is approximately the same on the same date each year, for example, on the successive January firsts of this study. The second assumption is particularly involved in calculations of longevity from annual mortality rate.

The annual mortality rate ( $M$ ), as of a selected initial date, which in this study is the first January 1 in the life of the bird, may be obtained by dividing the number of birds which were alive on the initial date and which died during the ensuing year by the total alive on the initial date. In this study the mean  $M$  is obtained by dividing the number of birds recovered between the first and second January firsts (291) by the total number of dead birds recovered ( $M = 291/597 = 49\%$ ). Likewise, since the annual survival rate ( $S$ ) may be obtained by dividing the number of those which were alive at the initial date and which survived the ensuing year by the total number in the sample, in this study ( $S = 306/597 = 51\%$ ). In these calculations the mortality rate is actually based on the year following the first January 1 and it is assumed that

the mortality rate is approximately the same in all age groups, which is substantially true. However, to avoid inaccuracies which may occur because of different mortality rates in different age groups, the method used by Lack (1948: 266) and in my earlier paper (Farner, 1945: 62) is used in line 3 of Table 2. In this method the mortality rate is calculated by dividing the total deaths (597) by the total of birds alive on all January firsts (1148). This process may be expressed as:

$$M = \frac{D_1 + D_2 + D_3 \cdots}{D_1 + 2D_2 + 3D_3 \cdots}$$

where  $D_1, D_2, D_3$ , etc., are the numbers of birds recovered each year, after the first January first.  $M$  thus computed is actually a weighted average of  $M$  values for each age group; the weighting factor, in each case, is the number of individuals on which each  $M$  is based.

Thus, in this study,

$$M = \frac{597}{1148} = 52\%$$

$$S = 100 - 52 = 48\%$$

In comparing my calculations with those of Lack an important difference in method should be mentioned. Lack (1948: 264–266) assumes, in calculating expectancy, that there is a uniform monthly distribution of deaths and that the mean period lived after the beginning of the year in which death occurs is 0.5 years. This period is herein designated as  $p$ . According to Lack the purpose of this arbitrary value is to avoid the effect of seasonal bias in the recovery of dead birds. The assumption of a uniform monthly distribution only crudely approximates the effect of the action of a uniform mortality rate. For example, an annual survival rate of 50%, is the result of a monthly survival rate of 94.8%. (Monthly survival rate =  $\sqrt[12]{\text{annual survival rate}}$ ; see Tinbergen, 1946: 30.) Thus the mean period ( $p$ ) after the first of the year lived by the birds which die during the year would be about 0.45 years which is scarcely significantly different from Lack's assumption of 0.5 years.

In the calculation of  $p$  by the use of the monthly survival rate ( $\sqrt[12]{S}$ ), it is assumed that the mean period lived by birds in the month in which their deaths occur is 0.5 months. This involves, in principle, an error analogous to Lack's assumption in the use of annual mortality rates, that is, the mean period ( $p$ ) lived during the year of death is 0.5 years. However, the error is scarcely significant in consideration of the accuracy of the data to which these calculations are compared. In the calculation of  $p$  from  $S$ , accuracy depends on the interval selected; for example, the application of a weekly survival rate ( $\sqrt[52]{S}$ ) gives greater refinement than the use of the monthly rate. The general equation for the calculation of the population size ( $N_t$ ) at a given time  $t$  is

$$N_t = N_0 (\sqrt[12]{S})^t \quad (1)$$

where  $N_o$  is the size of the population (number of live birds) at the beginning of the year (January 1);  $N_t$  is the number of birds alive at time  $t$ ;  $t$  is time from the first of the year expressed in terms of selected time intervals;  $i$  is the number of time intervals in the year; and  $S$  is the annual survival rate. If  $i$  is 12 equal time intervals, *i.e.* months, where  $t = 6$ ; or, if  $i$  is 365 equal time intervals, *i.e.* days, and  $t = 211$ , reference is made to a period extending from 1 January to the end of the sixth month, June.

From equation (1) an equation for the calculation of  $p$ , the mean period lived during the year of death, can be erected:

$$p = \frac{(N_o - N_1) \frac{1}{2i} + (N_1 - N_2) \frac{3}{2i} + (N_2 - N_3) \frac{5}{2i} + \dots + (N_{i-1} - N_i) \left( \frac{2i-1}{2i} \right)}{N_o - N_o S} \quad (2)$$

Substituting  $N_o (\sqrt[i]{S})^t$  for  $N_1, N_2, N_3, \dots, N_{i-1}$ , where  $t = 1, 2, 3, \dots, i-1$ ,

$$p = \frac{(N_o - N_o S^{1/i}) + 3(N_o S^{1/i} - N_o S^{2/i}) + 5(N_o S^{2/i} - N_o S^{3/i}) + \dots + (2i-1)(N_o S^{(i-1)/i} - N_o S)}{2i(N_o - N_o S)} \quad (3a)$$

$$= \frac{(1 - S^{1/i}) + 3(S^{1/i} - S^{2/i}) + 5(S^{2/i} - S^{3/i}) + \dots + (2i-1)(S^{(i-1)/i} - S)}{2i(1 - S)} \quad (3b)$$

$$= \frac{(1 - S^{1/i}) [1 + 3S^{1/i} + 5S^{2/i} + \dots + (2i-1)S^{(i-1)/i}]}{2i(1 - S)} \quad (3c)$$

From (3c) can be developed the general equation for the calculation of  $p$ .

$$p = \frac{1 + S^{1/i}}{2i(1 - S^{1/i})} - \frac{S}{1 - S} \quad (4)$$

As previously indicated, the calculation of  $p$  becomes increasingly refined as  $i$  increases. Moreover,  $p$  computed as the limiting value as  $i$  approaches infinity, can be expressed in the equation

$$p = \frac{-0.4343}{\log_{10} S} - \frac{S}{M} \quad (5)$$

(N.B.  $1 - S = M$ )

This constitutes a continuous solution for  $p$  taking into account the constant effect of  $M$  on the population.

As the annual mortality rate decreases,  $p$  approaches 0.5 years; however, as the annual mortality rate increases  $p$  decreases significantly to less than 0.4 years at an annual mortality rate of 80%. On analysis of the distribution of the recoveries of Robins in the sample used in this study (see Table 4) birds recovered dead may fail to display a uniform monthly distribution. However, until indicative studies are forthcoming, it seems necessary to remain uncertain as to whether such a sample is the result of biased seasonal recovery as suggested by Lack, or the result of a true seasonal variation in mortality rate, which is highly probable, and which is constant from year to year, or both.

## THE RELATION BETWEEN MEAN LONGEVITY AND ANNUAL MORTALITY RATE

The reciprocal relation between annual mortality rate ( $M$ ) and mean longevity ( $Y$ ) *beyond the selected initial date* in a stable population has been used for calculating each of these from the other. The formula of Burkitt (1926: 97), which is impractical in its original form, and the simplified forms employed by Nice (1937: 191), Farner (1945: 65), Marshall (1947: 194), and Hann (1948: 10), when used to calculate longevity, in reality assume that all birds which die during a given year actually live to the end of that year, or that there is a period which may approximate 0.5 years between the date of hatching and the initial date in which case a *mean total longevity* is calculated for *those alive on the initial date*. The former is readily apparent if an annual mortality rate of 100% were assumed. Then in accordance with the unmodified reciprocal relation,

$$Y = \frac{1}{1.00} = 1 \text{ yr.}$$

Thus, all of the birds would attain the age of 1 year. Therefore, all must die on the last day of the year! The same reasoning, although less obvious, is involved in using this relationship with other mortality rates. Because of the particular dates involved, the calculations presented in the previous paper (Farner, 1945: 66, Table 7) give approximations for the total mean longevity, from the date of hatching, for birds surviving the first November 1, since at that date the birds are approaching 0.4–0.5 years in age. The artificial nature of this application and the restricted conditions thereof make its further usage inappropriate.

Mean longevity ( $Y$ ), as of the selected initial date (first January 1 in this study), can be calculated from the formula,

$$Y = \frac{1}{M} - (1 - p), \quad (6)$$

where  $p$  is the mean period of survival after the first of the year for birds which die during the year. If Lack's assumption of a uniform monthly distribution of deaths is accepted,  $p$  is 0.5 years. If a uniform mortality rate is operative throughout the year and if the annual mortality rate is not greater than 50%,  $p$  is probably not significantly less than 0.5 years. If  $p$  is calculated, maximum accuracy is actually obtained by use of the continuous solution for  $p$  equation (5) which substituted in equation (6) gives a simple calculation for  $Y$ ,

$$Y = -\frac{0.4343}{\log_{10} S} \quad (7)$$

However, if the mortality pattern is known definitely to deviate from that of a uniform rate,  $p$  should be calculated directly. For example, if the monthly

pattern of deaths shown by Table 4 is actually unbiased,  $p$  would be 0.34 years. However, until differentiation can be made between true and biased monthly mortality patterns within the year, it seems advisable to follow Lack's assumption of a uniform monthly distribution of deaths or the assumption of the action of a uniform mortality rate throughout the year providing that the annual mortality rate is not in excess of 50%. Then, in either case the equation becomes

$$Y = \frac{1}{M} - 0.5. \quad (6a)$$

The applicability of this equation is illustrated by using the mortality rate, 52%, from lines 3 and 4 in Table 2, indicating a mean longevity ( $Y$ ) of 1.4 years compared with the actual mean longevity of 1.3 years and the calculated value of 1.4 years obtained by following Lack's assumption of a uniform monthly distribution of deaths. Assuming the operation of a uniform mortality rate ( $p = 0.44$ ) the calculated  $Y$  would be 1.3 years.

The mean longevity, as of the initial date, for Robins is compared with that of some other passerine species in Table 3. Although the calculations in Table 3 are based on a variety of initial dates they are actually quite comparable since all initial dates (except Bourlière, 1947) are well beyond the period of unstable mortality rates between departure from the nest and the first winter, and further since it now appears to be generally true in passerine species that the annual mortality rate and life expectancy beyond this unstable period do not vary appreciably with time. Erickson's calculation (1938: 309) of longevity in a small population of Wren-tits using the original Burkitt formula indicate a total mean longevity of 4.4 years for birds which survive to the first breeding season. By deducting the age at the first breeding season and correcting the Burkitt formula one would obtain a mean longevity of about 3 years as of the first March. On the other hand, the statement (p. 310) that 36% of the adults die each year would indicate a mean longevity of 2.3 years as of the first March. Both calculations ascribe an unusual longevity for such small birds. Further investigations on the population dynamics of this species would be of considerable interest.

The formula,  $Y = \frac{1}{M} - (1 - p)$ , is particularly useful in instances where mortality statistics are available but in which the ages of the birds at death are unknown.

#### MONTHLY DISTRIBUTION OF DEATHS

The monthly distribution of deaths, as indicated by recovered birds, is recorded in Table 4. There is a preponderance during the first part of the year over the expected distribution based on the operation of a uniform mortality

rate or the expected distribution based on Lack's assumption of a uniform monthly occurrence. Whether this reflects a true distortion in the mortality curve or, as Lack suggests, a bias in favor of finding dead birds during these months, is not apparent. A comparison of the distribution of deaths among birds between their first and second January firsts to deaths among older birds (lines 1 and 2, Table 4) does not yield a tangible clue. The bearing of this on the value of  $\hat{p}$ , as shown by Table 4, is obvious. This problem of the monthly distribution of deaths through the course of the year deserves careful investigation.

#### THE USE OF BIRDS RECOVERED BY TRAPPING IN THE CALCULATION OF ANNUAL MORTALITY RATE

Plattner and Sutter (1947: 20) have questioned the reliability of samples which combine records of birds recovered dead and birds recovered by trapping. Combining these 2 types of records assumes that death and trapping function at approximately equal rates for all age groups. Their data (p. 21) indicate that the mortality rate calculated from a trapped sample (number of birds in first year after initial date divided by total number in sample) is higher than that calculated from the samples of birds recovered dead. The basic assumption in the calculation of  $M$  from a trapped sample is that, were the trapped sample a truly random sample, then in a stable population the birds in their first year after the initial date must be numerically equivalent to the number of deaths, during the preceding year, of birds which had passed the initial date. Hence, dividing the number trapped in their first year after the initial date by all trapped after the initial date should give an annual mortality rate. The results, however, indicate that in trapping there is bias in favor of young birds. An examination of the data on the Robin confirms this suggestion. (Compare rates in Table 2.) Similar data for the Cardinal (*Richmondia cardinalis*) to be published subsequently indicate a similar bias in trapping in this species. Further investigation is needed to determine to what extent bias in trapping may affect the calculation of mortality rate from birds of unknown age, trapped and banded, and subsequently recovered dead.

#### LOSS OF BANDS

Analyses of the type presented here, as well as those by, among others, Lack (1943*a, b, c, d*), Lack and Schifferli (1948), Marshall (1947), Hann (1948), Bourlière (1947), and Nice (1937), assume that the sample of birds banded as young and recovered dead is typical of the population. This obviously assumes that there is no appreciable loss of bands or if there is, it operates randomly and independently of age. Thus, the chance of loss by an individual is the same regardless of age attained at death. Kortlandt (1942: 178, 201, 205), in a detailed investigation of a colony of European Cormorants in Holland, observed the loss of bands and calculated indirectly that the loss of bands, although conjectural, together with loss account-

able to "accidents" incidental to banding and the wearing of bands, could be as high as 10%. Lockley (1942) has reported the loss of bands, because of wearing, among Manx Shearwaters and Stuart (1948: 198) is of the opinion that this must occur among British Cormorants. Among passerine species, Lovell (1948) has reported the removal of bands by Cardinals and summarizes other published records of such removal. Linsdale's (1949) investigations at the Hastings Reservation indicate that there may be some loss of bands, as a result of wearing, among Brown Towhees and Spotted Towhees. The replacement of worn bands is not an uncommon procedure in the operation of a banding station. Bands which become sufficiently worn to warrant replacement have been carried 3 years or more. Obviously any loss of bands at a uniform annual rate, or at a rate that increases with age, would result in the calculation of an exaggerated mortality rate and too low a life expectancy. Because of limited sizes of samples, the calculations on passerine birds possible at this time usually have little significance beyond the second or third year. It seems unlikely that errors which may be introduced by the loss of bands should be of a magnitude greater than that of other errors inherent in the method. This assumption, however, should be tested by studies directed towards ascertaining the extent to which bands are lost. At least 2 approaches to the problem are apparent. First, some important information could come from large banding operations in the form of data on the length of time between banding and the time when replacement of the worn band is necessary. Second, an index of some significance could be established by banding with 2 bands (1 on each leg or 2 on 1 leg); the index would be the ratio of the number of double-banded birds recovered with a single remaining band to the total double-banded birds recovered with either 1 or 2 bands. This is based on the probability that the 2 bands would be unlikely to wear at the same rate. Data thus obtained should be correlated with the size, and manufacturer's lot, of band. The data would be of increasing importance as studies, of the kind presented here, become more refined with the accumulation of greater numbers of records. Calculations beyond the third year, when errors due to the loss of worn bands might become important, will then be based on significant numbers of records. The necessity, then, of reasonably precise information on band loss is obvious.

#### SUMMARY

1. At least in studies involving passerine species, it is suggested that calculations involving longevity, mortality rates, etc., using data from banded birds, be based on the first January 1 in the life of the bird as the initial date in accordance with the suggestion of Lack. The data on the American Robin, presented in an earlier paper have accordingly been recalculated and tabulated.

2. In the calculation of mean longevity ( $Y$ ) from mean annual mortality rate ( $M$ ) by the use of the reciprocal relation of  $M$  and  $Y$  in a stable population,  $Y$  must be based on the same initial date as used in the original calculation of  $M$ .  $Y$  is therefore to be defined as the mean longevity *as of the prescribed initial date*. If it is desirable to calculate a *total mean longevity* from birth, for those alive on the initial date, the mean period from hatching to the prescribed initial date must be added to  $Y$ . A *true total longevity* from birth for all birds hatched is difficult to estimate because of the high and unstable mortality during the first few months after hatching.

3. In the calculation of  $Y$  (as of the prescribed initial date) from  $M$  it is neces-

sary to correct the simple reciprocal to allow for the continuous action of  $M$  throughout the year. This is accomplished in the equation,

$$Y = \frac{1}{M} - (1 - p) \quad (6)$$

where  $p$  is the mean period lived during the year in which death occurs.

4. Providing the  $M$  is not in excess of 50%, placing  $p$  at 0.5 years, as suggested by Lack, approximates a uniform mortality rate. If  $M$  exceeds 50%, and a uniform mortality rate is assumed,  $p$  should be calculated by applying a monthly (or weekly, for additional refinement) mortality rate as described on page 70. Maximum refinement may be obtained by a continuous solution for  $p$ , in which  $p$  is computed as the limiting value as  $i$  approaches infinity.

$$p = \frac{-0.4343}{\log_{10} S} - \frac{S}{M} \quad (5)$$

If  $p$  is thus calculated, rather than obtained by direct observation, a substitution may be made into the equation (6) for the calculation of  $Y$ , giving the simple expression,

$$Y = \frac{-0.4343}{\log_{10} S} \quad (7)$$

Actually because of the probability of non-uniform mortality rates within the year,  $p$  should, if possible, be obtained from the observed annual mortality pattern and  $Y$ , if to be calculated, should be obtained by use of equation (6).

5. Whereas it is true that the simple reciprocal of the mortality rate gives an approximately total mean longevity from birth for those birds alive on the initial date *providing* that the period between hatching and the initial date is a fraction of a year, this is a coincidence operating within restricted conditions in which  $1-p$  approximates the mean period from birth to initial date. Since it does not have general application it is suggested that its use be discontinued.

6. As suggested by Plattner and Sutter for Tits and Nuthatches, there is apparently bias in retrapping Robins; this bias exaggerates the number of young birds with the result that  $M$ , when calculated on the basis of the ratio of birds in the first year after the initial date to older birds, is too high.

TABLE 1  
*Life Expectancy (e) in the American Robin on Successive January Firsts<sup>1</sup>*

DESCRIPTION OF SAMPLE		e IN YEARS <sup>2</sup>				
Cause of death	Number dead	1st Jan. 1	2nd Jan. 1	3rd Jan. 1	4th Jan. 1	5th Jan. 1
All causes.....	597	1.3	1.2	1.0	1.0	1.3
Killed by cat.....	48	1.3	1.1	—	—	—
Shot.....	51	1.4	1.2	—	—	—
All causes <sup>3</sup> .....	597	1.4	1.3	1.1	1.1	1.4

<sup>1</sup> Compare with Farner (1945: 69, Table 9). The records used here are the same as in the previous analysis except for birds which were recovered between the first November 1 and the first January 1; also a few records, unusable in the previous analysis, have now been adequately verified and have been included.

<sup>2</sup> In the calculation of *e* in lines 1, 2, and 3, for each Robin recovered dead the time elapsed between the selected January 1 and the date of death (actual date of recovery) was calculated to the nearest month from its card in the files of the United States Fish and Wildlife Service. The expectancy (*e*) for a particular January 1 was then obtained by calculating the mean period from the selected January 1 to the date of death for all birds alive on that January 1. For convenience in comparison with other authors the means were then expressed in years.

<sup>3</sup> Calculated according to the procedure of Lack (1948: 265-266) in which it is assumed that each bird which dies during the year lived for half of the year in which it died; Lack makes this assumption because of the possibility of "seasonal bias in the chances of recovery." Deevey (1947: 284, 295) has also pointed out that *e* may be calculated by use of the formula,  $e_x = \frac{T_x}{l_x}$ , where  $T_x$  is the total individual-years (individuals  $\times$  years to be lived) as obtained from his "life table" for *x* years, and  $l_x$  is the number of individuals alive at the beginning of the year *x*. Both Lack and Deevey assume an approximately uniform distribution of deaths through the year; this will be discussed further in this paper.

TABLE 2  
*Age-Group Composition of American Robins Based on January 1<sup>1</sup>*

DESCRIPTION OF SAMPLE	TOTAL ALL AGES	YEAR OF LIFE						RATIO <sup>2</sup> ADULT YOUNG	S %	M %
		1st	2nd	3rd	4th	5th	6th +			
All recoveries . . . . .	824	438	204	109	50	13	10	88:100	47 <sup>3</sup>	53 <sup>3</sup>
Same, in <i>per cent.</i> . . . . .	100	53	25	13	6	2	1			
Recovered dead . . . . .	597	291	154	94	40	9	9	See footnote 4	48 <sup>4</sup>	52 <sup>4</sup>
Same, in <i>per cent.</i> . . . . .	100	49	26	16	7	1	1			
Recovered alive <sup>5</sup> . . . . .	217	143	48	15	7	3	1	52:100	34	66
Same, in <i>per cent.</i> . . . . .	100	66	22	7	3	1	1			

<sup>1</sup> Compare with Farner (1945: 59, 62; Tables 1a, 1b, 4, 5). The records used here are the same as in the previous analysis except for birds which were recovered between the first November 1 and the first January 1; also a few records, unusable in the previous analysis, have now been adequately verified and have been included.

<sup>2</sup> Used in this study as the ratio of birds which on January 1 have attained at least their second January 1 to those which have attained their first January 1. Here, 386:438 = 88:100.

<sup>3</sup> Per cent *per annum* after first January 1, assuming a stable population. Survival rate = 1 - mortality rate. In a stable population the annual mortality rate equals the ratio of surviving first-year birds to the total population, since the number of young surviving from each year (taken in this study as those alive on their first January 1) is equal to the number of second-year and older birds which have died during the year, provided that the mortality rate is the same for each age group.

<sup>4</sup> From mortality rate (1 - survival rate) computed by dividing the total number of deaths (597) by the combined total of birds alive on all January firsts (1148). This is the more accurate method since it takes into account any differential mortality rates that may exist. It is the same method as employed by Lack (1948:266) as expressed by the formula,

$$M = \frac{D_1 + D_2 + D_3 \dots}{D_1 + 2D_2 + 3D_3 \dots}$$

where  $D_1, D_2, D_3$ , etc., are the numbers of deaths during the first, second, third, etc. years of life respectively. The survival rate would be 51% (mortality rate 49%) if calculated on the same basis as the line above. Compare with Farner (1945: Table 5, p. 62.)

<sup>5</sup> Mostly by trapping.

TABLE 3  
*Mean Natural Longevity (Y) of Some Passerine Species<sup>1</sup>*

SPECIES	NUMBER OF RECORDS	Y IN YEARS	HOW OBTAINED	INITIAL DATE	REFERENCE
American Robin . . . . .	597	1.3	R	1st Jan. 1	This paper
American Robin . . . . .	597	1.4	C	1st Jan. 1	This paper
European Blackbird . . . . .	258	1.9	R	1st Jan. 1	Lack (1946a)
Song Thrush . . . . .	262	1.55	R	1st Jan. 1	Lack (1946a)
British Robin . . . . .	130	1.1	C	1st Aug. 1	Lack (1943d)
European Redstart . . . . .	383	1.1	C <sup>2</sup>	Breeding season	Ruiter (1941)
Song Sparrow . . . . .	54	2.0	C <sup>3</sup>	April	Nice (1937)
Song Sparrow . . . . .	54	1.9	R <sup>4</sup>	April	Nice (1937)
Starling (England) . . . . .	154	1.6	R	1st Jan. 1	Lack (1946a)
Starling (Netherlands) . . . . .	205	1.5	C <sup>5</sup>		Kluijver (1935)
Starling (Switzerland) . . . . .	306	1.1	R	1st Jan. 1	Lack and Schifferli (1948)
Oven-bird . . . . .	38	1.7	C <sup>6</sup>	Breeding season	Hann (1948)
Great Tit . . . . .	252	1.4	C <sup>7</sup>	1st Nov. 1	Plattner & Sutter (1947)
Great Tit . . . . .	225	1.1	C <sup>8</sup>	1st Nov. 1	Plattner & Sutter (1947)
Blue Tit . . . . .	69	1.4	C <sup>9</sup>	1st Nov. 1	Plattner & Sutter (1947)
Marsh Tit . . . . .	89	1.6	C <sup>9</sup>	1st Nov. 1	Plattner & Sutter (1947)
Rook . . . . .	121	1.4	R	Departure from nest	Bourlière (1947)

R = mean longevity ( $Y$ ) obtained by averaging the ages (from initial date) at death of birds banded as young and subsequently recovered dead. C = mean longevity as of initial date calculated from mortality rate ( $M$ ),  $Y = 1/M - 0.5$ .

<sup>1</sup> Compare with Farner (1945: 67, Table 8) in which  $Y$  is the approximate *total longevity* for individuals alive on the initial date.

<sup>2</sup> From Ruiter's data (1941: 204, Table VIII) indicating an annual mortality rate (breeding season to breeding season) of 62%. This agrees with Lack's (1946a: 262) interpretation. Ruiter's statement (p. 210), that the mean age attained by young which return to the breeding area is 27 months, excludes birds which die before their first breeding season.

<sup>3</sup> Recalculated from the annual mortality rate (April to April) of 40% "in a well-situated population."

<sup>4</sup> Nice gives her data as of the date of birth for those alive at the beginning of the first breeding season. Here these data have been adjusted, by deduction of 0.8 years (the period between birth and the first breeding season), to give  $Y$  (observed) as of the initial date, *i.e.*, the beginning of the first breeding season. Actually Nice's sample contains many birds which were certainly more than a year old at the beginning of the breeding season. Since  $e$  does not change appreciably, the value of  $Y$  obtained by including these individuals is not

modified appreciably. If the 18 known first-year birds in this sample are used alone, the observed  $Y$  as of the beginning of the first breeding season is 1.7 years. This lower value coincides with Nice's statement that these birds were subjected to an unfavorable removal of cover.

<sup>5</sup> Recalculated from the annual mortality rate of 50%. Kluijver's calculation of 3.0 years is total longevity for birds which reach breeding age (1-2 years) and excludes birds which die before this time.

<sup>6</sup> Recalculated from the annual mortality rate (breeding season to breeding season) of 46%. The "mean minimum life span" of 2.2 as calculated by Hann (1948: 6) is not comparable since it is a minimum mean span from birthdate for birds which have survived at least to the first breeding season.

<sup>7</sup> Calculated from the annual mortality rate in a sample of birds banded at unknown ages.

<sup>8</sup> Calculated similarly from a sample of birds banded as young.

<sup>9</sup> Calculated similarly from a mixed sample, *i.e.*, birds banded as young and birds banded at unknown ages.

TABLE 4

*Monthly Distribution of Deaths as Indicated by Robins Recovered Dead with Comparisons to Theoretical Distributions Based on Uniform Monthly Distribution of Deaths and on Uniform Monthly Mortality Rate*

PERIOD	DESCRIPTION	NUMBER	PER CENT PER MONTH												$p^1$
			Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	
1st Jan. 1- 2nd Jan. 1	Actual recoveries	286	15.0	15.7	9.1	15.0	18.5	11.5	4.2	3.5	2.5	1.7	2.1	1.0	
After 2nd Jan. 1	Actual recoveries	311	10.6	14.5	11.3	16.7	12.2	9.3	8.7	2.6	5.1	2.6	1.3	5.1	
Total after 1st Jan. 1	Actual recoveries	597	12.7	15.1	10.4	15.9	15.2	10.4	6.5	3.0	3.8	2.2	1.6	3.2	0.34
Total after 1st Jan. 1	Theoretical, uniform monthly distribution <sup>2</sup>		8.3	8.3	8.3	8.3	8.3	8.3	8.3	8.3	8.3	8.3	8.3	8.3	0.50
Total after 1st Jan. 1	Theoretical, uniform monthly mortality rate <sup>3</sup>		11.4	10.8	10.0	9.5	8.9	8.5	7.9	7.3	7.0	6.7	6.2	5.8	0.44

<sup>1</sup>  $p$  = mean period lived after January 1 of year in which death occurred.

<sup>2</sup> See Lack (1948: 265-266).

<sup>3</sup> Based on annual mortality rate of 52% (or annual survival rate of 48%), calculated using the formula,  $p = \frac{-0.4343}{\log_{10} S} - \frac{S}{M}$ .

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DEPARTMENT OF ZOOLOGY, STATE COLLEGE OF WASHINGTON, PULLMAN, WASHINGTON