males were obtained. From the larval, nymphal, and especially from adult characters the ticks were found to constitute a new species, *Ornithodoros aquilae* Cooley. This form is closely related to *O. talaje* (Guerin-Méneville, 1849) and *O. kelleyi* Cooley and Kohls 1941, and can easily be confused with them.

The adult stages of this tick have not been found in nature. Other ectoparasites collected in this study were of little or no significance; they were not found so frequently nor so consistently on all species of raptorial birds as were the *Ornithodoros aquilae*. Of these the Mallophagon *Degeeriella fusca* (Nitz.) was the second most consistent form collected.

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LONGEVITY OF THE AMERICAN HERRING GULL

BY HUBERT MARSHALL

THE longevity of birds has long been a subject of popular interest as well as a problem of biological importance. Prior to the last decade most longevity records were, of necessity, based on birds in captivity since returns from banding operations have only recently made possible an accurate estimate of the longevity of birds in their natural habitats. Gurney (1899), Mitchell (1911), and Flower (1926, 1938) have compiled records of the ages attained by birds in captivity and have attempted to evaluate the reliability of the many claims to extreme age set forth in the literature of the last several centuries. From their compilations it is apparent that individual passerine birds occasionally live for 20 years and that larger birds live on rare occasions to 50 or even 80 years of age. All three writers agree that the oldest bird, the record of which is beyond dispute, is a European Eagle-Owl (*Bubo bubo*) which lived in captivity not less than 68 years. Extreme as this age may seem, Flower (1938) is prepared to accept the record of a Griffon Vulture (*Gyps fulvus*) which lived for 117 years, although he notes that this record is not beyond question. These records give some estimate of the extremes of avian longevity, but the mass of the data make it clear that, even in captivity, individuals of most species have not been known to live greatly in excess of 10 to 20 years.

In the past 25 years many North American species have been banded in sufficient numbers to provide adequate data on the maximum as well as average ages reached by birds in the wild. The present paper presents a review of the literature on the maximum age reached by the Herring Gull (*Larus argentatus*), both in captivity and in the wild, and presents a study of the average natural longevity of the American Herring Gull (*Larus a. smithsonianus*).—The author is indebted to Chandler S. Robbins for many helpful suggestions and to Frederick C. Lincoln who has read the manuscript.

POTENTIAL LONGEVITY

Potential longevity is the maximum age reached by any individual of a species, irrespective of the environmental conditions under which it lived. Among birds the greatest recorded ages are almost invariably found among individuals kept in captivity where adequate food and protection from extremes of weather, as well as from predators, usually assure a far more optimum environment than is obtained by birds in the wild. Hence, it is no accident that the oldest Herring Gulls were reared as pets or in zoos.

Pearson (1935) has recorded the oldest Herring Gulls so far reported—a pair which lived for 49 and 45 years respectively and were survived by three descendants, all more than 30 years of age. The younger bird of the pair, the female, accomplished the further unexpected feat of laying eggs every season for 42 consecutive years (Gross, 1940). Other gulls have lived almost as long. Gurney (1899) reports one which lived not less than 44 years. Richie (1935) reports another which had been in captivity for 35 years in 1935 and which, according to Flower (1938), finally died at an age of at least 41 years. Many references to Herring Gulls less than 25 years old are found in the literature.

Flower (1938) has calculated that the 20 oldest Herring Gulls he could find had lived an average of 21 years, 11 months, and of the 20 birds, three were still alive at the time his calculations were made.

In an earlier paper, and using all reliable sources of information, Flower (1926) recorded individuals of 909 species which had lived six years or longer. Of these, 609 lived over ten years, 137 over twenty years, and 41 over thirty years. Since a number of Herring Gulls between 40 and 50 years of age have been reported, it is apparent that few species have a longer potential longevity.

POTENTIAL NATURAL LONGEVITY

Under the rigors of a natural environment, it is to be expected that potential longevity would be greatly reduced. Schüz (1936), in a summary of European banding records, reports the recovery of banded Herring Gulls of 21, 22, 23, and almost 25 and 26 years of age. Even more remarkable is the record of "Gull Dick," who for 24 years visited the neighborhood of Brenton's Reef lightship in Narragansett Bay where he was easily recognized by markings, voice, and disposition. He appeared annually and remained in the vicinity of the lightship from October 12 to April 7, during which time he regularly ate boiled pork and fish fed him by the crew. Although he never was banded, his presence was repeatedly confirmed and reported on many occasions by MacKay (1892, 1893, 1894, 1895, 1896, 1898).

The greatest recorded age for a banded Herring Gull on the North American continent is that of No. 207898, banded in July, 1922, by W. S. McCrea on Hat Island, Michigan, and found dead by D. McDonough on Beaver Island, Michigan, in June, 1939, after an elapsed time of almost 17 years. Since few Herring Gulls were banded in this country before 1921, it is to be expected that older birds will be recovered in the future. Whether North American Herring Gulls will eventually be found as old as those already recovered in Europe is a question depending upon differences, if any, between subspecies, and upon differences in environment. The evidence now at hand is insufficient to warrant speculation on this question.

AVERAGE NATURAL LONGEVITY

Average natural longevity may be defined as the mean age attained by a species in the wild. Few studies of average natural longevity have been attempted because it requires large numbers of recoveries of birds banded as young and subsequently recovered. The American Herring Gull admirably fulfills this requirement since thousands of young gulls banded at the nesting site have been recovered and reported to the Fish and Wildlife Service in Washington, D. C.

The assumptions on which such a study is based have been discussed by Farner (1945). Briefly, it must be assumed that individuals of a species which were banded as young and subsequently found dead constitute a normal sample of that element of the population dying each year. Since only a small percentage of the young birds are banded each year, and since only a few of these are recovered, the banding returns actually show only the average age of those birds banded and recovered dead by humans. There is no reason to suppose, however, that these birds do not represent an average sample of the birds dying every year; hence, the calculated longevity is undoubtedly close to that for the population as a whole.

Several important considerations, however, must be taken into account. While it is true that adult birds recovered dead represent a fair sample of the entire population, this does not apply to young birds found dead in the first several months after leaving the nest. The number of recoveries during this period depends largely upon whether or not the banders revisit the nesting island. If the banders return, many dead chicks are recovered, giving a disproportionate weight in the sample to those young birds which die before leaving the island. If the banders fail to return, few recoveries are reported during the first several months of the bird's life and the sample is disproportionately weighted with older birds. To avoid this difficulity, longevity expectancy is ordinarily calculated from an arbitrary date (September 1 in this study) when most or all fledglings have left the nesting area. After this date it is probable that dead individuals of all age groups have an equal chance of being recovered.

Secondly, since the number of birds banded varies from year to year, the mortality conditions prevailing in years of heavy banding will be unduly weighted in the population sample. This cannot be denied, but the data were collected over a 25-year period and hence it seems likely that years of severe or of moderate mortality are distributed evenly between years of heavy and light banding.

And lastly, a difficulty arises from the fact that birds dying of certain causes are more likely to be recovered than other birds, and that these causes may operate disproportionately on different age groups. Lack (1943c), for example, has shown that shooting is differential according to age for both the Black-headed Gull (*Larus r. ridibundus*) and the Lesser Black-backed Gull (*Larus fuscus graellsii*), since the young birds are more easily shot. So few banded Herring Gulls are shot in North America that no provision or correction was made for this factor. No doubt other causes of death are disproportionately represented in the present data, but whether these are differential according to age or form a sizable proportion of the data is difficult to determine. The cause of death is recorded for only a minority of the recoveries, but from an inspection of the banding returns it seems likely that no serious error arises from the data being heavily weighted with any particular cause of death.

The banding returns used in this study are from the files of the Division of Wildlife Research, United States Fish and Wildlife Service. Returns were used only from birds banded as young (June, July, and August) in the years prior to 1940 and subsequently recovered dead. September 1 was selected as the arbitrary date from which all longevity estimates were calculated. After this date there were almost no recoveries at the banding sites, indicating that young birds had left the vicinity and were as likely to be recovered as any other age-group in the population. Since the data on life expectancy subsequently presented apply not to a natural population, but only to that portion of the population surviving to the first September 1, it would be desirable if some estimate of the mortality between hatching and September 1 could be made. This would enable the calculation of the true average natural longevity. Certain technical difficulties, however, prevent its being attempted in the present paper.

The calculated estimates of life expectancy as well as the age-group composition of a stable population of Herring Gulls are shown in Table 1. A total of 3,806 recoveries were found which met the requirements of the study, a sample more than adequate in size. Columns 2 and 3 of Table 1 indicate the rate at which a population of young gulls is decimated under conditions of a natural environment. It is seen that of every 100 birds surviving to the first September 1, only 40 are alive a year later, 25 two years later, 17 three years later, and so on until in ten years the population has dwindled to almost nothing. That only 40 per cent of the birds alive on the first September 1 survive for another year is indicative of the rigors of the natural environment.

Viewed in another light, columns 2 and 3 of Table 1 show the age-group composition of a Herring-Gull population on September 1, provided the population is stable. Thus, for every 100 young there are 40 second-year birds, 25 third-year birds, and so on. Unless the population is assumed to be stable, the indicated age-group composition will vary with time. Since the data were collected over a 25-year period, they would represent the average composition of the population for that period if an equal number of birds had been banded each year. However, the heaviest banding of Herring Gulls was done between 1936 and 1939, and hence the population considered in this paper is somewhat less representative of the period between 1921 and 1935.

Column 5 of Table 1 shows the proportion of the various age classes which die every year. It is seen that 60 per cent of the first-year birds and a much lower percentage of the older birds—36 per cent on the average—die each year. This trend is reflected in the calculation of life expectancy shown in column 6. Expectation of further life on the first September 1 is 1.5 years. Those birds which survive to their second September 1, however, have a further expectation of life of 2.3 years. The calculated expectancy for additional years ranges between 1.9 and 2.4 years. That mortality during the first year is far heavier than in succeeding years indicates, undoubtedly, the relative inexperience of first-year birds as compared with the ability of older birds to avoid danger and secure an adequate food supply. Farner (1945), in his study of the American Robin (*Turdus migratorius*), found no differences in life expectancy in the first and succeeding years. Lack (1943a, b, c, d.) likewise found no important differences for the European Blackbird (*Turdus m. merula*), Starling (*Sturnus vulgaris*), Song-Thrush (*Turdus e. ericetorum*), English Robin (*Erithacus rubecula melophilus*), and Lapwing (*Vanellus vanellus*). Several other species, however, showed important increases in life expectancy from the first to second year. The European Woodcock (*Scolopax rusticola*), for example, rose from 1.7 to 2.2 years; the Black-headed Gull (excluding birds reported shot), from 1.8 to 2.4 years; the Lesser Black-backed Gull (excluding birds reported shot), from 1.8 to 2.5 years; and the European Cormorant (*Phalacrocorax c. carbo*) from 1.6 to 3.0 years. All these, it will be noted, are birds of the marsh or open water.

Column 6 of Table 1 shows that 1.5 years is the expectation of further life for that portion of the Herring Gull population surviving to the first September 1. Hence, to determine the longevity expectancy of this portion of the population it is necessary to add to 1.5 years an estimated period equal to the time elapsed from the date of hatching to September 1. A brief perusal of the literature (Deusing, 1939) indicates that June 1 may not be too early as an average date for the hatching of Herring Gulls. This would add 0.25 year to the life expectancy as calculated from September 1, and would indicate a total longevity expectancy of 1.75 years for those Herring Gulls surviving to the first September 1.

CALCULATION OF LONGEVITY FROM MORTALITY RATE

The average natural longevity may be calculated by either of two methods: (a) by calculation from the mean age of birds recovered dead, as is done (in modified form) above, and (b) by calculation from the ratio of young birds to adults, which in a stable population indicates the annual mortality rate.

The mortality rate may be defined as the percentage of the population which dies annually. In a stable population, the birds which die each year are replaced annually by an equal number of young. Hence, the mortality rate is the average ratio of first-year birds to the total population, since the number of young alive on a given date is equal to the number of birds in the total population which will die during the forthcoming year. In the present study, column 2 of Table 1 provides the necessary data for calculating the mortality rate. The ratio of young to the total population is 3,806 to 8,081, or 47 per cent per year. Hence, on the average, 47 per cent of the Herring Gulls alive on September 1 die during the year and are annually replaced by an equal number of young which survive from the nesting season to September 1.

Burkitt (1926) provided a formula whereby the longevity expectancy might be calculated from the mortality rate when he showed that $Y = 1/M$, where Y represents longevity expectancy and M the mortality rate. Substituting in Burkitt's formula, it is found that the longevity expectancy of juvenile Herring Gulls living on September 1 is 2.1 years. Burkitt's formula, however, is predicated upon the assumption that mortality is spread evenly throughout the September 1–August 31 year; i.e., that the average date of death is six months from September 1. Calculation of the mortality data by months, however, shows that most deaths take place in the early part of the year since the population is greater at that time and because weather conditions are more severe. The data show that the average date of death is slightly less than four months from September 1, or somewhat more than two months sooner than assumed in Burkitt's formula. Applying this correction to the answer derived by formula, a corrected longevity expectancy of 1.9 years is determined. This is 0.15 year greater than the longevity expectancy of 1.75 years calculated from the mean age of birds recovered dead.

COMPARISON OF RESULTS OF DIFFERENT STUDIES

In the several studies dealing with life expectancy and average natural longevity of birds, different arbitrary dates have been selected from which to calculate the age of birds recovered dead. Lack (1943a, b, c, d), for example, used August 1; the present study uses September 1, and Farner (1945) used November 1. The selection of different dates does not necessarily invalidate comparison of results between studies, but several implications arising from this situation have not been discussed elsewhere and can profitably be mentioned here.

As a general rule, the greater the period between hatching and the date from which life expectancy estimates are made, the greater will be the calculated longevity expectancy and with some species the same is true for the expectation of further life. This variation in longevity expectancy, with change in the date from which longevity estimates are calculated, is due to the fact that on different dates one is dealing with different populations; i.e., the population of a species on September 1 is different from what it was on August 1.

This difference in longevity expectancy and expectation of further life arising from different dates from which longevity estimates are made results from one or both of two reasons:

(a) The expectation of further life for some species such as the American Herring Gull, Black-headed Gull, and European Cormorant is greater at the beginning of the second and subsequent years of life than at the beginning of the first year of life. This is to say that as the bird progresses through the first year of life, its expectation of further life progressively increases. Hence, in studies of such species, the later the arbitrary date from which longevity estimates are calculated, the greater will be the calculated expectation of further life. Consequently, it is desirable to select as early a date as possible and thus include in the study as large a portion of the total population as possible.

(b) Longevity expectancy of juveniles alive on a given date is the sum of the expectation of further life on that date and the period elapsed between that date and the date of hatching. Since the expectation of further life does not ordinarily decrease with time, the longevity expectancy increases the later the date selected, due to the increase in the time elapsed between this date and the date of hatching. Hence, the later the date selected, the greater will be the calculated longevity expectancy.

It is seen that (a) applies only to those species in which the expectation of further life increases with time and affects both the expectation of further life and the longevity expectancy. On the other hand, (b) affects only the longevity expectancy and applies to all species. It is suggested that these considerations may be of assistance in reconciling differences between studies of longevity expectancy of a species when different dates are selected from which estimates of life expectancy are made.

LONGEVITY OF NATURAL AND PROTECTED POPULATIONS

Lack (1943a) makes an interesting comparison between the life expectancy of protected populations (human or laboratory-animal) and avian populations. It is known, for example, that human life expectancy in the United States is approximately 65 years as compared with a potential longevity of slightly more than 100 years. Those Herring Gulls which survive to their first September 1 have a further life expectancy of 1.5 years as compared with a potential longevity of 49 years (and possibly much greater considering the inadequacy of present knowledge). Hence, Herring Gulls live about 3 per cent and human beings about 65 per cent of their potential life spans. The difference between average natural longevity and

TABLE I

SURVIVAL OF HERRING GULLS BANDED AS YOUNG AND SUBSEQUENTLY RECOVERED DEAD

1. *Year (starting Sept. 1)*	2. *No. alive at start of year*	3. *% alive at start of year*	4. *No. dying during year*	5. *% of those alive at start of year dying during year*	6. *Expectation of further life on Sept. 1 (years)*[1]
1st	3806	100	2298	60	1.5
2nd	1508	40	569	38	2.3
3rd	939	25	274	29	2.4
4th	665	17	191	29	2.3
5th	474	12	185	39	2.0
6th	289	8	138	48	1.9
7th	151	4	59	39	2.1
8th	92	2	26	28	2.2
9th	66	2	25		
10th	41	1	22		
11th	19		6		
12th	13		5		
13th	8		4		
14th	4		0		
15th	4		3		
16th	1		0		
17th	1		1		

[1] Calculated by averaging, for the birds alive on each September 1, the number of months between the selected September 1 and the date of death for each bird. It is assumed that all birds dying within a given month died on the 15th day of the month.

potential longevity is a rough measure of the severity of the natural conditions under which a species lives and gives some hint of the difference in the age-group composition of the two populations.

An additional comparison is of some interest. Column 6 of Table 1 shows that there is little or no decrease in the expectation of further life as the Herring Gull advances in age; i.e., a bird eight years old has as much expectation of further life as at any previous time after the first year. Hence, expectation of further life for the Herring Gull, after the first year, is not increased by additional experience or greater physical maturity and seems almost wholly independent of the decline in vigor attendant with old age and senescence. In a human population, on the other hand, expectation of further life decreases steadily with advancing age, after the first three years, because the conditions of modern life assure that relatively few individuals die before death takes its great toll in the years of old age and natural decline.

SUMMARY

A review of the literature on the life expectancy of the Herring Gull revealed that the oldest known gull lived in captivity and died at the age of 49 years. A number of gulls which lived more than 25 years are mentioned. The greatest known age for the European Herring Gull in the wild was found to be almost 26 years; on this continent the greatest recorded age is almost 17 years.

The assumptions on which a study of average natural longevity are based are discussed and data are presented which lead to the following conclusions:

(a) The longevity expectancy of that portion of the American Herring Gull population which survives to the first September 1 is 1.75 years.

(b) The expectation of further life on the first September 1 is 1.5 years and in succeeding years varies between 1.9 and 2.4 years.

(c) The age-group composition of the Herring Gull population is such that only 40 per cent of the birds survive one year, 25 per cent for two years, and only 1 per cent for ten years.

The longevity expectancy of juveniles alive on September 1 is calculated from the mortality rate and differs by only 0.15 year from that calculated from the mean age of birds recovered dead.

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