

## SOME ANIMAL LIFE TABLES

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[The data available for the construction of animal life tables are usually much less complete than is the case with human lives. Generally speaking they consist of samples of dead animals with their approximate ages at death, or possibly samples of live animals with their approximate ages; but there is rarely any possibility of linking the number of deaths with a corresponding number of living exposed to risk, and the samples themselves are probably biased. Consequently, very different methods have to be employed from those customarily adopted for human life tables, but it is thought that actuaries will be interested and stimulated by the ingenious way in which the problems have been tackled and by the results.—Eds. *J.I.A.*]

ANY branch of knowledge is improved by a background. We understand English history better if we can compare it with that of other countries. We understand human anatomy better if we can compare man's structure with that of other animals. So it may be hoped that actuarial science will benefit by a study of animal populations. No attempt will be made in this note to summarize the large amount of work which has been done on this subject. Deevey (1947) and Allee *et al.* (1949) may be consulted for a fairly comprehensive bibliography.

Ideally, we should like to count a population of animals from their origin at fertilization to their death. This is extremely difficult, and has probably been done only by Varley (1947). More usually we are content to begin with the laying of an egg, or at birth, as we do with man, where our knowledge of pre-natal mortality is very scanty.

Animal life tables fall into two groups. It is quite possible to count a captive population of potentially mobile animals, such as flies or mice, daily, and to deduce their laws of mortality under these conditions, when they are certainly protected from predators and may be so from disease. Alternatively we may try to make a life table under natural conditions. This is most easily done for animals which stay put for most of their lives. Thus Hatton (1938) cleared some areas of rock, so that the swimming larvae of barnacles could settle on them in July, and then made monthly counts of the population of barnacles which had fixed itself on these areas. Varley (1947) followed up several species of insects living in galls which could be collected in any month of the year. Since they mostly passed a year in the gall, but only lived for a week or so in the winged state, his life table, based on population counts in over 50,000 galls, is fairly complete and more accurate than most human tables.

Life tables for more mobile wild animals, including birds, can be obtained only indirectly. Thus Murie (1944) picked up skulls of 608 wild sheep (*Ovis dalli*) on an American mountain, estimating their age from annual rings on their horns. But the greatest contribution in this field has been made by Lack (1950) and his colleagues on British birds. The reference given is to a recent summary, which contains a full bibliography and a discussion of several population problems. The most satisfactory of several methods used is the following. The mortality of eggs and unfledged young was estimated by repeated visits to a number of nests. Young birds were ringed shortly before

they left their nests and a fraction of the numbered rings was recovered. This varied from under 1% in the robin to 14% in the lapwing. Methods used by other workers included observation of live colour-ringed birds, trapping, the ratio of adults to juveniles, and so on.

Lack's results are described first because of their great simplicity. British birds are mostly hatched from April to July. Mortality both in the nest and in the first few months of independent life is heavy; just how heavy is not known exactly, for the figures have an obvious bias. Birds, whether resident or migrant, usually scatter in their first year, but stay near the nest till they have learned to fly fairly efficiently. So each bird-ringer is likely, during the dangerous period before flight is fully efficient, to pick up his or her own ringed fledglings, whereas a little later they have spread out over a wide area. Lack, therefore, bases his tables on mortality (or, more exactly, rings recovered from dead birds) during each calendar year. That is to say, birds whose corpses are discovered between the first and second New Year's Day of their lives are said to have died at the age of one year, and so on.

Now suppose a total of  $N$  dead ringed birds have been collected, the oldest being, say, 14 years old. If we are making our life table in 1952 we reject all data on birds ringed since 1938 (though a simple correction would allow us to use them). Suppose that of our  $N$  birds  $d_x$  have died at the age of  $x$  years, it is at once obvious on examining the data that the observed values of  $d_x$  approximate to a geometrical series. Assuming that the expected values form a geometric series, we can then find an estimate of its common ratio with its standard error, and apply the  $\chi^2$  test to see if our observed and calculated results are in agreement. Lack and others have calculated a number of such ratios, but have not calculated their standard errors nor tested the goodness of fit.

Let  $s$  be the fraction of birds (assumed constant) which survive for one year after any date. Then of the  $N$  ringed birds reported, we expect  $(1-s)N$  to have died at the age of 1 year,  $s(1-s)N$  at the age of 2 years, and so on. That is to say

$$d_x = s^{x-1}(1-s)N.$$

Given the observed values we apply the method of maximum likelihood by differentiating

$$L = \sum_{x=1}^{\infty} d_x \log[s^{x-1}(1-s)N],$$

$$\frac{dL}{ds} = \frac{\sum_{x=1}^{\infty} (x-1)d_x}{s} - \frac{\sum_{x=1}^{\infty} d_x}{1-s}.$$

On equating to zero we have an unbiased and efficient estimate

$$\hat{s} = \frac{\sum (x-1)d_x}{\sum x d_x} = 1 - \frac{N}{\sum x d_x}.$$

Differentiating again we find

$$(\sigma_{\hat{s}})^{-2} = -\frac{d^2 L}{ds^2} = \frac{\sum (x-1)d_x}{s^2} + \frac{\sum d_x}{(1-s)^2},$$

whence

$$\sigma_{\hat{s}} = (1-\hat{s})\sqrt{(\hat{s}/N)}.$$

The appended table gives data for lapwings (*Vanellus vanellus*) ringed in Britain. Dr Lack has kindly given some details not included in his paper.  $N=593$ ,  $\Sigma xd_x = 1733$ , so

$$\hat{s} = .65782 \pm .01139,$$

From this value the expectations of column 3 were calculated. It will be seen that the deviations from expectation have no systematic trend, and that  $\chi^2$  has the remarkably low value of 5.5 for 8 degrees of freedom. A slightly lower value could, of course, be obtained by choosing  $s$  so as to minimize  $\chi^2$ ; but this is a biased estimate, and much harder to calculate.

### Data on *Vanellus vanellus*

$$s = .65782$$

| $x$<br>(1) | $d_x$<br>(2) | $(1-s)s^{x-1}N$<br>(3) | $d_x - (1-s)s^{x-1}N$<br>(4) | $\chi^2$<br>(5) |
|------------|--------------|------------------------|------------------------------|-----------------|
| 1          | 198          | 202.91                 | -4.91                        | 0.119           |
| 2          | 134          | 133.48                 | +0.52                        | 0.002           |
| 3          | 90           | 87.81                  | +2.19                        | 0.055           |
| 4          | 51           | 57.76                  | -6.76                        | 0.791           |
| 5          | 48           | 38.00                  | +10.00                       | 2.632           |
| 6          | 23           | 24.99                  | -1.99                        | 0.158           |
| 7          | 21           | 16.44                  | +4.56                        | 1.265           |
| 8          | 9            | 10.816                 | -1.816                       | 0.305           |
| 9          | 6            | 7.115                  | -1.115                       | 0.175           |
| 10         | 5            | 13.679                 | -0.679                       | 0.034           |
| 11         | 6            |                        |                              |                 |
| 12         | 1            |                        |                              |                 |
| 13         | 0            |                        |                              |                 |
| 14         | 1            |                        |                              |                 |
| 14+        | 0            |                        |                              |                 |
| Total      | 593          | 593.000                | 0.000                        | 5.536           |

These data do not stand alone. Several other birds give about equally good fits to a law of constant mortality, though there are exceptions. Certainly Lack's law of constant mortality is quite as well supported by the data as the Gompertz-Makeham hypothesis for man. The values of  $s$  for British birds range from 35% for the mallard and 38% for the robin, up to 69% for the heron. The figures for such sea-birds as the gannet and fulmar petrel will certainly be much higher, probably over 90%, but just because of their long lives data are not yet available. Swedish data give the remarkably high value of 80% for the swift as compared with only 37% for the English swallows.

The most striking exception to the law of constant mortality occurs among birds of which a substantial fraction is shot. Their mortality from gunfire is highly concentrated in the first two years of life, and those which escape for two seasons have mostly learned to avoid this cause of death. The mortality figures, however, are to a certain extent suspect in the case of birds killed for sport or food. Thus ringed ducks shot in the lawful season are doubtless often reported. Those shot in the close season are less likely to be reported; and if they are, will rarely be reported as shot. The reporting of birds actually shot as 'found dead' must increase the apparent mortality from 'natural' causes. There may be a similar reluctance to report such birds as robins caught in traps.

We see, then, that for the lapwing and most other birds studied, the force

of mortality and the expectation of life are independent of age after the first 6–8 months. They are not, of course, independent of season. In fact, British birds which do not migrate have a high mortality in winter, and migrants are in danger while migrating. The expectation of life of a resident on 1 March is considerably longer than on 1 December. It is clear that if  $s$  were constant throughout the year the force of mortality would be  $-\log_e s$ , and the expectation of life  $-(\log_e s)^{-1}$ . Thus the force of mortality is  $\cdot 419$  and the expectation  $2\cdot 39$  years for lapwings. The business of an office insuring the lives of birds would be peculiar. The premium for an egg would be extremely high, that for a nestling only slightly lower. The age of clients would be irrelevant provided it exceeded 8 months; but the time of year would be of considerable importance.

The method employed involves several assumptions, but its validity has been verified in many ways. For example, the mortality of lapwings can be estimated from the ratio of juveniles to adults in flocks. Starlings have been ringed both as nestlings and as adults of unknown age. The whole population in a small area has been caught and ringed with different colours in different years, and so on. Finally, for starlings, there is a satisfactory concordance between mortality and fertility.

If we assume that fertility, like mortality, is independent of age after 8 months, many problems in bird demography become very simple. In particular, it can be shown that the rate of increase or decrease of a population is the sum of a number of geometric series (some of which may have complex common ratios) equal to the age at which the birds become mature. In small birds which breed at a year old, if we assume that almost all adults breed, and if  $k$  be the fraction of eggs yielding birds which live for at least a year, the total population is  $k + ks + ks^2 + \dots = \frac{k}{1-s}$  of the number of eggs laid per year. Thus,

in a species with an average clutch-size of 5 per pair, and  $s = \text{about } \frac{1}{2}$ ,  $k = \text{about } \frac{1}{5}$  if the population is to remain approximately constant.

We may ask whether the force of mortality would finally increase through senility if we had much larger numbers. Lack (1943) reports a ringed Irish robin which lived for at least 11 years. The annual survival of robins is 38% in England, so only 2·3 out of 100,000 robins should survive so long. Many fewer than 50,000 robins have been given coloured leg rings. This and similar isolated data suggest that so far from the force of mortality increasing, it may actually fall off, a few exceptionally tough birds living to a relatively very great age.

Birds show an initially high force of mortality declining to a constant level. Fish which lay numerous eggs show the same fall far more strikingly. According to Sette (1943) the American mackerel lays about a million eggs per year. During the ten or so weeks of larval life the daily mortality increases from 12% to a maximum of 40%, and then falls off. About 4 per million reach the age of 70 days, with a length of two inches. After this mortality falls off greatly, and an adult fish has an expectation of life of about a year. Thus the force of mortality is some hundred times greater for larvae than for adults, and there is no evidence of a senile rise. All marine animals, such as oysters and sea urchins, which lay very numerous small eggs, must have life tables of this type.

A few wild animal populations give life tables of the human type, with a fairly heavy infantile mortality, a period of vigour, and a high senile death rate. This is perhaps not surprising in wild sheep. It is more remarkable that

Edmondson (1945) found it in microscopic rotifers. It must however, be remembered that these were observed under very favourable conditions.

Animals with an annual life cycle naturally give very irregular  $l_x$  curves. Thus barnacles in northern France have a heavy winter mortality, probably due to frost, unless they settle near low water mark. Varley's (1947) gall flies also had a heavy winter mortality, owing to mice eating the galls.

The only nearly complete classification of causes of mortality, which can be compared with that of the Registrar General, is that of Varley on gall insects. About 1% of the eggs laid gave rise to adults in the next generation. Apart from mice, the main cause of death was parasitic insects which lay their eggs in or on the grubs. This parasitism is the main influence regulating the size of the population, since a large number of hosts in any given year leads to a large number of parasites in the next year, and perhaps even in the next two years.

Animal populations, as Elton (1927) pointed out, are rarely regulated in the Malthusian manner by food shortage. Varley's gall midges never infested even half the available flowers. In a case where food might well be expected to be the limiting factor, Crombie (1946) found that grain-eating beetles limited their population size by cannibalism, that is to say the eating of eggs and larvae by adults, provided that the food was renewed at regular intervals. Perhaps this behaviour comes under Malthus's category of 'vice'.

If we turn to animal populations kept in laboratories under conditions where there are no deaths from hunger, predation or overcrowding, and disease is kept down so far as possible, we get a wholly different picture, which has been summarized by Teissier (1934). Teissier was able to fit a number of life tables by assuming that

$$\mu_x = e^{a(x-b)} - 1, \quad \text{when } x > b,$$

that is to say, that the force of mortality is negligible up to a certain age, and then increases rapidly, though not so rapidly as on the Gompertz-Makeham hypothesis. Often, as in mice, the fit was only obtained by neglecting infantile mortality. Similarly, in the case of insects, life was generally taken to begin with the emergence of the imago from the pupa, a process which has its casualties apparently as inevitable as those of human birth. For many animals under optimum conditions  $b$  is positive, that is to say there are no deaths in the first days or even months of life. This is so even for such a doomed creature as the male silkworm moth, which cannot eat. Other animals have a negative  $b$ , and begin dying off at once. Thus *Drosophila melanogaster* may be said to be slightly senile before it leaves its puparium.

Mice kept under normal laboratory conditions have a life table not unlike those of Western European human populations about the year 1900. The graph of  $l_x$  inflects at the age of 5 or 6 months, when about 25% of the mice are dead. 65% survive to one year, and only 17% to two years, so that a mouse year corresponds to about 30 human years. Under the best laboratory conditions yet achieved there is an infantile mortality of 5% or so, and then hardly any deaths till the age of 18 months is reached. Teissier's equation fits human mortality curves after the age of 60 pretty well, and suggests that under sufficiently hygienic and peaceful conditions almost all of us would reach 50 years; but if so less than half would reach 75, and the present frequency of centenarians would not be doubled. Meanwhile, however, the mice, after infancy, seem to be rather better protected from disease than any human community.

However that may be, we have here a background for human vital statistics of which the most remarkable feature is, perhaps, the constant mortality of small birds. From the point of view of a robin redbreast in a cage, almost all deaths are accidental. If, on the other hand, free robins could think, they might console themselves with the thought that senility was not one of the fates which they need fear.

If the fertility of small birds is independent of age, which seems to be nearly true, the theory of population growth and fluctuation becomes extremely simple. For the number of future progeny expected from every adult member of the population is the same.

There may be animals in which the expectation of life increases continuously with age. This may be so for many fish under natural conditions. It certainly goes on increasing, as we saw, for a considerable time. Thus in a species where the expectation of life was equal to the age, or better to the age plus one week, no members would live for ever, but a small fraction would live for a very long time. A centenarian aware of the facts would pity a child with an expectation of only a few years, but would envy a bicentenarian.

A few authors, notably Small (1949) and Simpson (1944), have attempted the much more ambitious task of constructing life tables for species and genera. A species or genus may, of course, come to an end in two very different ways. All its members may perish, or they may evolve into something so different as to deserve a different name. A palaeontologist who finds a particular species only in certain strata cannot always distinguish between these two possibilities. Small, who works with diatoms (microscopic plants with very characteristic siliceous skeletons) believes that he can distinguish sharply between 'evanescent' species, which only last a million years or so, and 'permanent' ones, which have sometimes endured for fifty million years without showing any sign of senility. Simpson prefers to work with genera, since vertebrate palaeontologists have difficulties in distinguishing species. He finds that the life table for a genus varies very much in different groups. Thus in the Carnivores, a rapidly evolving group, the mean life of a genus is about  $6\frac{1}{2}$  million years, in the Lamellibranchs (bivalved molluscs) about 80 million. These figures are based on genera now extinct. The distribution is very skew positively. Out of 423 living lamellibranch genera, 10 are over 250 million years old, and show no sign of senility. Some of them have given rise to other genera without themselves dying out. The life table for genera looks rather like a life table for the people of Luggnagg, as reported by Gulliver. These included a few struldbrugs, who lived for an indefinite time; so, while it would have been quite possible to calculate a median life expectation, the mean duration of life was large, indeed infinite. The carnivores also have a positively skew distribution of generic lives, but there is no suggestion of struldbrug genera, and their generic  $l_x$  graph is remarkably like that for small flies with a mean life of 14 days. However, the incompleteness of the geological record implies that the life of a genus is often underestimated.

The time has hardly come when an actuary could be of much value to palaeontologists. I believe, however, that the work done by the British Trust for Ornithology and the Sir Edward Grey Institute of Ornithology at Oxford has already reached the stage where actuaries might take an active interest in it. There are marked differences between different populations. For example, the Swiss starlings are significantly more fertile and shorter lived than the English ones. I have deliberately avoided some of the more difficult problems

which arise in such work, partly because I hope to solve some of them. One arises from a gradual increase or decrease of interest in bird-ringing which leads to an increase or decrease in the fraction of ringed birds picked up. Such an increase will lead to an increase in the birds' apparent mean lives. This bias does not appreciably affect the data of the table. Another problem is the specification of 'good' and 'bad' years for birds. This is fairly simple for non-migratory species. Here birds killed by hard frosts will probably be picked up, but few migrants killed in foreign countries or at sea will be recorded, and an excessive number of such deaths will show by a diminution of the deaths in all later years. Given the rather small numbers available, special tests of significance are required. There are still more serious problems to be tackled at a later date. Thus it is obvious that bird-ringing schemes can only be carried out with fairly common birds. This means that each species will tend to be studied in the area to which it is best adapted; but birds are highly mobile, and there may be a considerable loss by emigration to areas where the death rate exceeds the birth rate. We have very little idea of its extent.

It will be seen that the problems of the actuary in this sphere are peculiar. Thus the following is a strictly mathematical one. A random sample of a population is marked, the ages being unknown. The times between marking and death of a number of animals are recorded. From these it is required to construct a life table. It is, however, possible that such problems may suggest cognate problems in human vital statistics. If so, their study will be justified.

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